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Ovibos moschatus.

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Ovibos Blainville, 1816

Ovibos Blainville, 1816:76. Type species *Bos moschatus* Zimmermann.

Bosovis Kowarzik, 1911:107. Type species *Bos moschatus* Zimmermann.

CONTEXT AND CONTENT. Order Artiodactyla, Suborder Ruminantia, Infraorder Pecora, Family Bovidae, Subfamily Caprinae, Genus *Ovibos*. *Ovibos* was placed with the takin (*Budorcas taxicolor*) in the tribe Ovibovini by Simpson (1945).

Ovibos moschatus (Zimmermann, 1780)

Muskox

Bos moschatus Zimmermann, 1780:86. Type locality between Seal and Churchill rivers, Manitoba, Canada.

CONTEXT AND CONTENT. Context given in generic account above. Allen (1913) recognized the following subspecies:

O. m. moschatus (Zimmermann, 1780:86), see above.

O. m. niphoecus Elliot, 1905:135. Type locality head of Wager Inlet, Keewatin.

O. m. wardi Lydekker 1900:157. Type locality Clavering Island, Greenland. Tener (1965) rejected *O. m. wardi*, and, with some equivocation because of the small sample of specimens available to him, also rejected *O. m. niphoecus* and concluded that *O. moschatus* is a monotypic species.

DIAGNOSIS. The muskox superficially resembles the American bison (*Bison bison*) but is considerably smaller. Weights are about two-thirds those of adult bison of the same sex and the legs are relatively shorter. Long, dark brown guard hairs extend nearly to the ground and cover an extremely fine, cashmere-like underhair. Creamy white to yellowish stockings and saddle contrast with this dark coloration. The skull is massive with protruding orbits (Fig. 1). The horncores in young are lateral and deflected slightly upward. In adults the horncores are deflected downward and slightly forward then turn upward again. In adult males the horns come together in a massive boss. The tail is vestigial and the muffle narrow and lunate. Four mammae are present.

GENERAL CHARACTERS. This moderate sized ruminant attains 1.2 to 1.5 m height at the shoulder with a large head, short neck and tail, and short, stocky legs (Fig. 2). Adult males from the Canadian mainland reach 380 kg (Tener, 1965). Those from the introduced Nunivak Island population (*O. m. wardi*) are somewhat smaller. Although only a few have been weighed, females are estimated to be approximately 60% of the weight of males (Lent, 1978; Tener, 1965). In captivity adult males have reached approximately 650 kg, females about 300 kg (Lent, 1978).

According to Allen (1913) mean basal length of skull in old males was 466 mm and 442 mm in *O. m. moschatus* and *O. m. wardi*, respectively. Tener (1965) recalculated these values from Allen's published raw data and concluded that mean basal length in the *O. m. moschatus* sample was 443 mm, thus the samples were not significantly different. In Tener's (1965) own samples, greatest zygomatic width for skulls of adult males from eight geographic areas ranged from 162 mm to 177 mm. No significant differences were found among these mean values, however, nor among several other measurements and skull length-width relationships.

A preorbital gland is well developed in both sexes, even in calves. The lenticular shaped structure lies in a shallow groove on the lachrymal bone. It consists of a hair-lined pocket surrounded by glandular material (Lönnberg, 1900; Sack and Ballantyne, 1965).

Calves at birth weighed 8 to 15 kg (Blix et al., 1984; Frisby et al., 1984; Lent, 1978). Uspenski (1984) noted great variability in weights from individuals captured on Nunivak Island. One-year-old females weight ranged from 45.3 to 101.9 kg (n = 17, $\bar{X}$ = 72.2); 1-year-old males from 45.3 to 96.6 kg (n = 11, $\bar{X}$ = 79.7). Among 2-year-olds, females ranged from 93.3 to 143.6 kg (n = 7, $\bar{X}$ = 120.0) and males from 126.0 to 149.5 (n = 2, $\bar{X}$ = 137.8). These mean values were higher than those reported by Lent (1978).

Lönnberg (1900) described numerous aspects of the soft anatomy of muskox, comparing each with those of sheep (*Ovis aries*), bovids, or caribou (*Rangifer tarandus*) but was unable to establish a clear picture of phylogenetic relationships based upon these anatomical features. He was first to note that the squared-off shape and warty laminae of the lips were well suited for browsing on Arctic willows (*Salix* sp.) and similar prostrate woody growth forms. McDonald and Freeman (1984) measured 44 body and organ dimensions in a single adult female. They concluded that body conformation is more like that of oxen than that of caprine species.

DISTRIBUTION. The present natural distribution of muskoxen (Fig. 3) represents some expansion of this range over the past few decades in conjunction with protection, increasing numbers, and possibly more favorable climatic conditions. Islands such as Prince Patrick and Mackenzie King in the Canadian Arctic have been recolonized (Miller et al., 1977). Similarly, range expansion is reported from the Queen Maud Gulf area (Gunn et al., 1984). It is not certain to what extent animals may cease using and later recolonize such islands without human interference, but wandering between islands is well documented (Urquhart, 1982).

Fluctuations in distribution in Greenland have been well documented over the years (Thing et al., 1984; Vibe, 1958, 1967), particularly in relation to climatic fluctuations. Based on the frequency of occurrence of certain dental anomalies, Henrichsen (1981, 1982) concluded that muskoxen of northeastern Greenland (from Scoresby Sund north and west around the coast to Nyeboe Land) are divided into three relatively isolated populations. By these criteria, the northernmost population is related more closely to muskoxen of Ellesmere Island, Canada. Thing et al. (1984) considered the current distribution in northeast Greenland to be approaching that of the previous extended period of favorable conditions (1920–1940).

FOSSIL RECORD. The subfamily Ovibovinae originated in Asia and gradually differentiated during the Tertiary. The genus *Boopsis* in the Pliocene and lower Pleistocene and the genus *Megalovis* of the Villafranchian are thought by many to be similar to the ancestral form of *Ovibos*, if not directly ancestral (Crégut-Bonnoure, 1984).

The primitive muskox *Soergelia* was widespread in Eurasia and also is reported from a few Pleistocene (Kansan time) sites in North America (Kurtén and Anderson, 1980). Harington (1977) considered it a lowland-adapted muskox that probably was replaced by more specialized forms (*Symbos*, *Praeovibos*). He also considered *Budorcas* to be a direct descendent of the small-horned, upland "stem muskox." In North America, the genus *Symbos*, the woodland muskox, occurred in plains and savannahs from central Alaska to southern new Jersey and persisted until about 11,000 years B.P. *Symbos* was related closely to *Ovibos*, derived from the same Asian ancestral stock but perhaps better adapted to temperate climates. *Bootherium* is considered congeneric with *Symbos* by Kurtén and Anderson (1980) but not by Harington (1977).

Praeovibos and *Ovibos* coexisted in the middle Pleistocene. Although their ranges fluctuated considerably, neither was tied as closely to cold-dominated climates as was once thought. *Praeovibos* was especially ubiquitous and even *Ovibos* seemingly did well in steppe and even temperate forests (Crégut-Bonnoure, 1984). *Ovibos* was first present in Alaska in Illinoian time; specimens from the northern Yukon have been dated at over 54,000 years old, and the genus extended widely to the south in the Wisconsinan glaciation (Harington, 1970, 1977). *Ovibos*, including both *O. moschatus* and

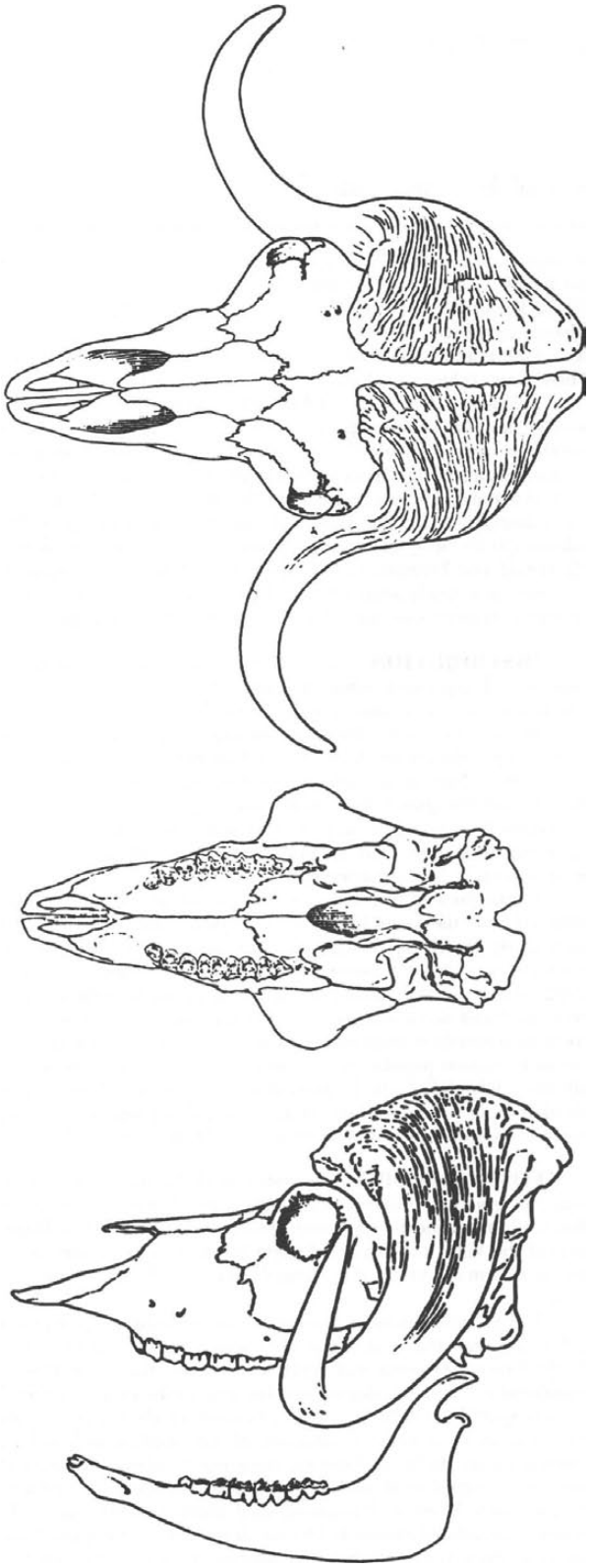

FIG. 1. Dorsal, ventral, and lateral views of the skull and lateral view of mandible of male muskox said to be approximately 7 years old, Wager Inlet, Canada. Adapted from Bee and Hall (1956).

the now extinct *O. pallantis* (questionably a separate species), reached a maximum extent in the Würm glaciation then diminished in range rapidly, leaving *O. moschatus* surviving in Siberia until 3,000 to 4,000 years ago (Harington, 1970; Uspenski, 1984).

FIG. 2. Muskox group. From left to right, adult male, yearling, calf, and adult female. Photo by T. Smith.

FORM AND FUNCTION. Blix et al. (1984) reported that newborn muskox calves have deep body temperatures ranging between 37.7 and 41.3°C and can tolerate ambient temperatures as low as −30°C, but when such a temperature is combined with a wind of 10 m/s neither the excellent insulative qualities of their coat nor high metabolic heat productions prevented hypothermia. Brown adipose tissue is present in large amounts at birth, providing a great capacity for thermogenesis. Insulative value of fur was drastically reduced by wind, from 3.2 W m^{-2} $°C^{-1}$ to 10 W m^{-2} $°C^{-1}$, suggesting the importance of the mother in providing a wind shelter for calves and of calves selecting a favorable microclimate (Jingfors, 1984).

Mean values for composition of five milk samples collected in August from captive animals were total solids, 21.1%; fat, 10.9%; total protein, 11.9%; lactose 2.1% and ash, 1.2% (Baker et al., 1970). Tener (1965) reported total protein in two milk samples taken from muskox collected approximately 1 and 4 days after parturition as only half of that in the samples examined by Baker et al. (1970) but lactose values were much higher (3.6%) and 4.2%). Baker et al. (1970) attributed low lactose levels in their samples to fermentation before analysis. Excluding lactose values their findings were similar to those for caribou and reindeer (*Rangifer tarandus*; Hatcher et al., 1967) but Baker et al. (1970) stated that fatty acids of high molecular weight are less prevalent in muskox milk than in milk from other Arctic species. No information is available on volume of milk production or on composition changes with stage of lactation.

Frisby et al. (1984) used a commercial lamb-milk replacer for raising muskox calves. When diluted to a 25% formula it provided good weight gain and little scouring, even though proportion of lactose was higher and proportion of protein lower than in muskox milk.

Hand-reared calves gained an average of 0.6 kg daily during their first 30 days (Blix et al., 1984). A difference between growth rates of males and female calves was reported by Hubert (1974) but not by Frisby et al. (1984). Energy intake of hand reared calves was similar to domestic lambs (1.2 to 1.7 kj $kg^{-0.75}$ day^{-1}), so weight maintenance and growth requirements are similar to domestic sheep, but maintenance energy requirements appear to be higher (Frisby et al., 1984). Functional rumination seems to begin extremely early in the muskox, in captivity as early as 3 weeks (Chaplin, 1984) and in the wild perhaps even in the first week (Flood et al., 1984).

In experimental feeding trials, muskoxen showed a marked decline in voluntary food intake in winter from 102 g $kg^{-0.75}$ day^{-1} to 38 g $kg^{-0.75}$ day^{-1} (White et al., 1984). This is in conformity with results from other northern ungulates, notably caribou and reindeer.

REPRODUCTION AND ONTOGENY. Calves usually are born from midApril through June. Extremes reported from Nunivak Island are 5 April and 19 June (Lent, 1978). Most births on Banks Island, Canada, occur before 1 May (Tessaro et al., 1984). Alendal (1971*a*) reported rare births in late summer in Norway. Thus, regional variation seems to occur, but no populations show the extreme breeding synchrony of caribou (Lent, 1966). I found no significant tendency for birth times of 109 calves born in captivity at Fairbanks, Alaska, to occur at a particular time of day.

Earlier workers generally believed that twins occurred in muskoxen. However, Lent (1978) and Gunn (1982) reported no documented instance of viable twins in free-living populations. One observation made in Norway (Alendal, 1979) and another made on

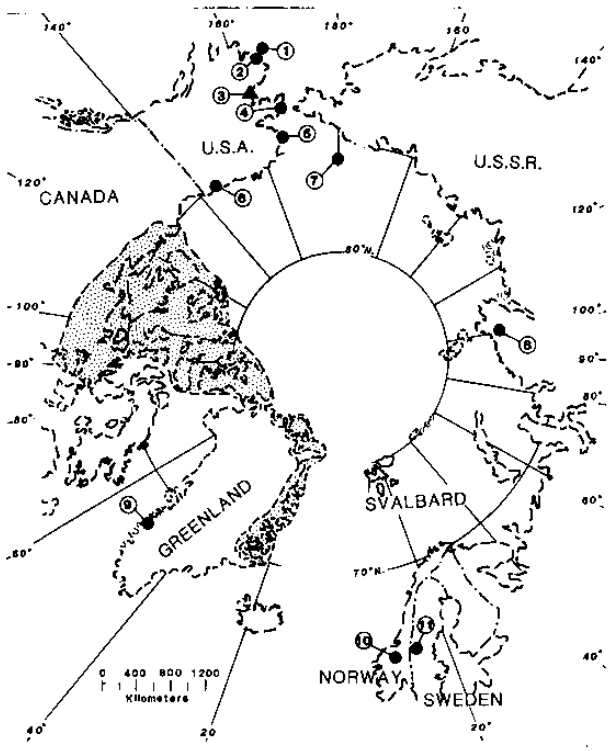

FIG. 3. Current distribution of muskoxen including transplant locations (closed circles) and domestication project site (closed triangle): 1, Nunivak Island; 2, Nelson Island; 3, Unalakleet; 4, Seward Peninsula; 5, Kukpuk River; 6, Arctic National Wildlife Refuge; 7, Wrangel Island; 8, Taimyr Peninsula; 9, Søndre Strømfjord; 10, Dovre Mountains; 11, Härjedalen area. Stippled area indicates approximate location of present natural distribution.

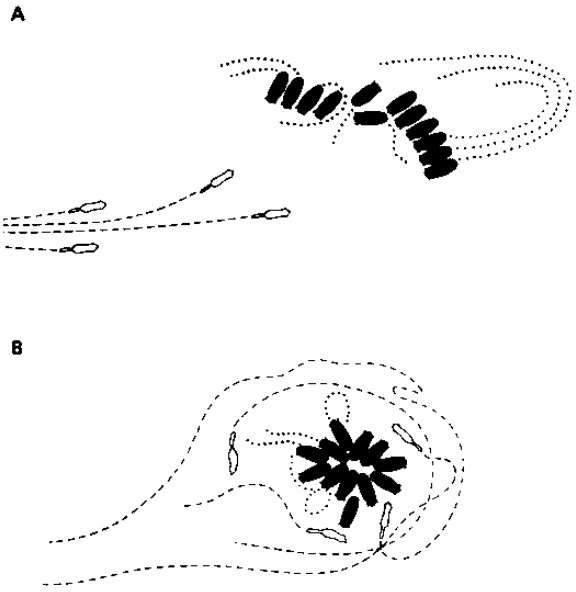

FIG. 4. Typical dynamics of defense formation (A) and response to circling wolves (B). From Gray and Peers (no date), with permission of National Museums of Canada.

Devon Island (Pattie, 1986) apparently represent authentic occurrences of twinning. In the Devon Island case, the cow and twins were observed in summer then were found dead in emaciated condition in winter. Dinneford and Anderson (1984) reported 3.9% of 125 pregnant females in two Alaskan populations were carrying twin fetuses. Even in captive herds, such as the one at the University of Alaska, known to be on a high plane of nutrition, no viable twins and only one case of still-born twins have been reported (Wilkinson, 1970). In any event, twinning must be insignificant in terms of population dynamics.

Dinneford and Anderson (1984) stated that there was no significant deviation from equality in the fetal sex ratio, although male fetuses predominated in two populations, and Spencer and Lensink (1970) also showed a statistically significant preponderance of male calves in one of these same populations (Nunivak). Alendal (1971*b*) reported the gestation period to range from 244 to 252 days, based on four well-documented records.

Henrichsen and Grue (1980) reported that cementum annuli are laid down regularly in incisors every year between September and January, starting at age 16 months. Savelle and Beattie (1983) compared techniques for counting annuli and reported that only standard thin-sectioning without decalcification gave satisfactory results. Lent (1974) found close agreement (within 1 year) among observers ageing muskoxen by use of annuli. However, Gronquist and Dinneford (1984) reported a general tendency to underestimate age of 18 known-age specimens and such low agreement among observers that they considered the technique unreliable. Half of their specimens were from animals raised in captivity.

Development of horns proceeds rapidly during the first 4 to 5 years and shows marked sexual dimorphism. Thus, horn characteristics are useful for determining sex and age of individuals in the field. Age of bulls over 5 years cannot be determined reliably but condition of the horn tips and boss provides clues to relative age (Smith, 1976). Pohle (1981) provided a useful series of photographs showing these changes in a captive male over successive years. The horncores in both sexes are weakly rooted during the first year or so, making care essential in capturing wild calves or handling captive ones (Lent, 1978).

Although he rejected *O. m. wardi* as a valid subspecies, Tener (1965) noted that individuals from the eastern Arctic and Greenland tend to have more white on the frontal area of the head, paler saddles, and stockings. The function of the whitish saddle is debatable but it accentuates the size of the fore shoulders. Such accentuation is even more pronounced in mature bulls in summer, when old hair accumulates loosely on the fore shoulders. This is suggestive of a role in dominance or threat displays.

Because of interest in the sale of products made from qiviut, the soft, extremely fine underwool, much attention has been paid to its production and properties (Wilkinson, 1974, 1975). The mean diameters of qiviut fiber samples taken from individual fleeces ranged from 13.0 to 17.3 μm, comparable to cashmere and vicuna (*Lama vicugna*) fibers. The long (up to 58 cm) guard hairs sampled from individuals typically had mean diameters in excess of 80 μm. Moulting begins about the first of April and seems to be controlled by a combination of photoperiod and temperature. The directional sequence of moulting generally is anterior to posterior and ventral to dorsal as in sheep and goats, but in contrast to cattle. Adults in good health may yield 2 kg or more of quiviut. It is collected by combing captive animals and also is gathered from vegetation in habitats used by free-ranging muskoxen.

ECOLOGY. The natural range of muskoxen generally occurs in regions of low precipitation where winter snow cover is either shallow or is disporportionately distributed so that there are areas of accessible winter forage (Lent, 1978; Lent and Knutson, 1971; Spencer and Lensink, 1970; Vibe, 1967). In his study of past climatic fluctuations in Greenland, Vibe (1967) concluded that muskox abundance and distribution have fluctuated in response to long-term shifts in climate. During periods of cold, stable winter weather, muskox abundance was high. Periods of unstable, maritime weather patterns, particularly those resulting in winter rains and ice layers in the snow or on the ground surface, caused major declines in muskox numbers.

Thomas et al. (1981) believed there are refugia, centers of abundance and long-term favorable conditions, in the Canadian Arctic on Melville, Banks, Axel Heiberg, Devon, and Ellesmere islands. They concluded that these areas act as centers for natural dispersal and restocking after severe environmental conditions lead to extirpation of other populations.

Muskoxen from a Beringian refugium (Harington 1970, 1977) persisted along the arctic coastal and foothills zones in Alaska until the 1850's or possibly the 1870's (Allen, 1912). Abundance possibly

was declining in this area because of the general warming trend and the introduction of firearms to the coastal Eskimos may have tipped the balance toward extirpation (Bee and Hall, 1956; Hone, 1934). However, based on the historical study by Burch (1977) of events in the Canadian subarctic, extirpation might have occurred without the impetus of firearms.

Considering their remoteness from centers of human population and their relative lack of economic importance, the extent to which muskoxen have been transplanted in circumpolar regions is surprising. Perhaps this is to some extent because of the paucity of large mammal species. At some sites, introduction of muskoxen has doubled species diversity of local ungulates. Attempts to capture, transplant, or domesticate muskoxen commenced in the 1870's (Inman, 1899).

Early introductions of animals taken from East Greenland, included persistent efforts in the 1940's and 1950's to establish them in the Dovre Mountains of Norway (Fig. 3), unsuccessful attempts in Iceland, and a transplant to Spitzbergen (Lønø, 1960). An initial breeding effort at Fairbanks, Alaska, in the early 1930's was followed in 1935 and 1936 by release of all stock on Nunivak Island, Alaska.

In the 1950's, the first domestication effort was initiated in Vermont with stock brought from the Canadian mainland Arctic (Lønø, 1960). This domestication center was largely abandoned and replaced by a larger scale effort at the University of Alaska, Fairbanks, with stock from the Nunivak Island population that, in the meantime, had grown to several hundred head (Wilkinson, 1971).

Also in the 1960's, muskoxen from East Greenland were released at Søndre Strømfjord in West Greenland, outside of their natural range (Fig. 3). This population apparently increased more rapidly than any other known, from 27 in the mid 1960's to about 600 in 1982 (Thing et al., 1984).

Numerous transplants from the Nunivak Island population have led to establishment of five wild populations on mainland Alaska (Fig. 3). Two of these are within the range occupied by muskoxen in Alaska before their 19th Century extirpation (Lent, 1971, 1978). The successful transplants to the Arctic National Wildlife Refuge are of particular significance because they resulted in a population that is well established and showing significant growth within the historic range of the species (Jingfors and Klein, 1982; Reynolds and Ross, 1984).

Smith (1984) estimated 1,178 animals in these wild populations (including Nunivak Island) and an additional 139 in three captive herds. The largest of these captive groups, the domestication-project herd of 125 head, was moved from Fairbanks to Unalakleet by 1977.

Forty muskoxen from Nunivak were taken to the USSR in 1975. These, along with 10 animals obtained from Banks Island, Canada, in 1974, have been successfully reproducing. As of 1983 there were 82 muskoxen in the eastern Taimyr Peninsula and 21 on Wrangel Island (Uspenski, 1984). Uspenski (1984) cited references to evidence that muskoxen survived in the eastern Siberian Arctic until relatively recent times.

Recent estimates of muskox numbers are far higher than those available to Lent (1978) who concluded that world-wide numbers were about 25,000. Urquhart (1982) estimated numbers in Canada to be 45,000 ± 11,000 and Thing et al. (1984) gave a new estimate for Greenland of 20,700 muskoxen. These higher numbers in part reflect expanding populations in the last decade.

Graminoids, especially sedges (*Carex* sp.) play a major role in summer diets of muskoxen (Bos, 1967; Parker, 1978; Rapota, 1984; Tener, 1965; Thing, 1984; Wilkinson et al., 1976). Such heavy use of graminoids usually occurs in bogs and wet meadows. Selection of succulent, green growing parts also is reported (Alendal, 1976; Tener, 1965). In spring or early summer, *Eriophorum* sp. may be especially preferred (Robus, 1984) when nitrogen content is high (Chapin et al., 1980).

In other cases or in the same populations, summer use of browse, especially willows (*Salix* sp.) may be equally frequent or even more so than graminoids (Parker, 1978; Robus, 1984; Tener, 1965).

Almost all authorities also report opportunistic selection of forbs that in a few cases (Parker, 1978, for example) are significant portions of total dietary intake and in many instances may be significant nutritionally.

At a domestication project at Unalakleet, Alaska, in an area of tundra and shrub-tundra, confined muskoxen made heavy use of both sedges and shrubs in summer (McKendrick, 1981). In addition, alder (*Alnus crispa*) twigs were taken to such a degree that numerous plants were killed. Overgrazing and trampling disturbance in tussock tundra, and in mat and cushion tundra, led to an increase in sedges and a decline in standing crop of shrubs.

Woody species were heavily used at all seasons on the Canadian mainland where muskox populations occur within the limits of the boreal forest (Tener, 1965). *Salix* species, especially *S. alaxensis*, were favored in summer. The winter diets include large proportions of Labrador tea (*Ledum decumbens*), crowberry (*Empetrum nigrum*), ground birch (*Betula glandulosa*) and species of *Vaccinium*. Heavy dependence upon a similar array of woody species on upland sites is reported for Nunivak Island (Bos, 1967; Lent, 1978), but those animals wintering on coastal dunes used primarily beach rye grass (*Elymus aerenarius mollis*) and beach pea (*Lathyrus maritimus*).

In contrast, graminoids, especially *Carex*, *Eriophorum*, and *Poa*, were principal constituents of winter forage in Jameson Land, Greenland (Thing, 1984). Similarly, Parker (1978) found sedges to be the most frequent plant group in rumen samples of muskoxen collected in winter from Devon and southern Ellesmere Islands. In fecal samples from other high Arctic sites, representing late winter and spring feeding, roughly 50% of identifiable fragments were woody fibers and over one-third were sedges. Specimens from Axel Heiberg Island showed a significant frequency (29.5%) of grass fragments. On Bathurst Island, during a period when starvation and population decline was evident, muskox seemed to be more dependent on xeric communities. Percent marrow fat, as an indicator of body condition, was positively correlated with abundance of woody fragments and inversely correlated with abundance of moss fragments (Parker, 1978; Parker et al., 1975). The introduced muskoxen in the Taimyr of the U.S.S.R. depend upon both graminoids (*Carex bigelowii* and *Eriophorum polystachon*) and willows in winter, but also make heavy use of *Dryas octopetala* in mid and late winter (Rapota, 1984).

Lent and Knutson (1971) confirmed the feeding behavior patterns of muskoxen on Nunivak Island, that result in selection of winter feeding areas where wind reduced or eliminated snow cover. Such areas were prevalent along cliff edges and on tops of coastal dunes representing less than 3% of the land surface of the island. Other winter feeding sites occurred where vegetation, particularly bent-over stalks of *Elymus*, supported the snow cover, leaving an airspace and allowing animals to break away pieces of slab snow. In general, they found muskoxen to be more selective than reindeer. On Bathurst Island animals also fed frequently where vegetation provided air space under the snow cover (Gray, 1973). Apparently, muskoxen are not as well adapted morphologically to digging through deep snow as are reindeer and caribou (Klein and Staaland, 1984; Thing, 1977).

There is little or no competition between caribou (reindeer) and muskoxen or at least relatively little overlap in habitats and feeding sites selected (Lent and Knutson, 1971; Parker and Ross, 1976; Wilkinson et al., 1976). However, competition with the Svalbard (Spitzbergen) reindeer (*Rangifer tarandus platyrhynchus*) may have played a significant, if not dominant, role in the extirpation of the introduced muskox population on that island (Alendal, 1976; Klein and Staaland, 1984). The latter authors suggested that the Svalbard reindeer is specialized both morphologically and behaviorally to exploit a niche more similar to that of the muskox, including greater dependence on a high fiber content in the diet than in most other *Rangifer* populations. Except for an extremely prostrate growth form of *Salix polaris*, Svalbard lacks the willows present in almost all other winter ranges of muskoxen.

Muskoxen show a predilection for grazing on cliff-edge habitats. In summer these are associated with cliff-nesting birds and highly fertilized vegetation. In winter, such steep and exposed slopes are relatively snow-free. Mortality from falls in such feeding areas has been reported frequently (Alendal, 1976; Klein and Staaland, 1984; Lent, 1978; Spencer and Lensink, 1970).

The high variability of reported muskox diets reflects the variability of habitats ranging from high polar desert to subarctic continental vegetation. Clearly the species is an adaptive forager but generally showing large intake of fibrous, larger plants when such are available.

Muskoxen are relatively sedentary, particularly in comparison to caribou or reindeer. Daily movements usually are less than 10 km/day (Gunn, 1982; Parker and Ross, 1976; Reynolds, 1984).

Movements of greater distances occur over sea ice between islands in the Canadian Arctic Archipelago for example (Freeman, 1971; Miller et al., 1977). Such movements obviously are necessary for the documented natural recolonization of islands where populations were extirpated, but little is known about frequency or stimuli for these movements. Muskoxen tend to move onto shorefast ice around Nunivak Island where stable pack ice is absent, and become stranded on small ice floes or tiny offshore islets (Smith, 1984; Spencer and Lensink, 1970).

Until the 1970's, muskox populations were assumed to have inherently low intrinsic rates of increase. Tener (1965) and Hubert (1977) accepted the opinion of early writers that calving in successive years was a rare occurrence. Pedersen (1958) believed calves might be produced in successive years if a cow's nutritional condition was good. This contention has now been well substantiated for wild populations (Alendal, 1971*c*; Gunn, 1982; Lent, 1978; Spencer and Lensink, 1970).

Similarly, Tener (1965) and most early researchers thought that females generally did not calve until their fourth year and that males generally were 6 years old before they could hold a harem and participate in breeding. Early observations of cows in captivity giving birth at 3 or even 2 years (Oeming, 1965; Tener, 1965) are now supplemented with records of such events in wild populations, although largely limited to introduced groups (Alendal, 1971*c*; Jingfors and Klein, 1982; Lassen, 1984; Lent, 1978). Maximum productivity for an individual free-ranging female seems to be approached by a muskox cow born in 1965 in the Dovre Mountains of Norway and part of a small group that wandered 200 km to Sweden in 1971. She produced either 10 or 11 calves between 1968 and 1980 (Alendal, 1974, Lundh, 1984).

In contrast, there are numerous reports of populations in which no calves were produced in certain years (Gray, 1973; Pedersen, 1936; Tener, 1965; Vibe, 1958). These authors implicated severe winter conditions, either ice or exceptionally deep snow, as the cause of such reproductive failures. Pedersen (1958) suggested that these conditions sometimes produce a delayed effect in that females are in such poor condition in spring that they cannot recover in summer, do not attain estrus, thus do not produce a calf the following year even if that winter was not so severe. There is no strong evidence from other sources to support this concept. Gray (1973) reported an almost total absence of rutting behavior on Bathurst Island during 1968–1970, suggesting that females were not entering estrus.

The widely varying estimates of mortality of calves are based on changes in proportions of calves and yearlings to total populations. Lent (1978) reported low mortality (15%) from Nunivak Island based on cow/calf ratios and estimates of adult winter mortality and even lower rates are suggested by the data of Lassen (1984). In contrast, Tener (1965) reported mortality in excess of 50%. Similar high mortality is reported by Hubert (1977) for Devon Island.

Gunn (1982) suggested that winter mortality may be higher for yearlings than for calves, but there is little evidence to support this view. Both Parker et al. (1975) and Lent (1978) reported a preponderance of adult age classes in carcasses. Relative observability of carcasses could have biased these samples, however, and, in the instance of the Parry Islands material of Parker et al. (1975), there was low recruitment in preceding years, thus few if any younger animals were present. They found over half of the winter kills to be over 10 years old. In contrast, Lent (1978) found that only three of 28 dead adults were over 9 years old at time of death. Both authors reported a preponderance of males in winter kills, as did Smith (1984). Maximum age at death was reported to be 24 years (Buckley et al., 1954).

The Nunivak herd increased at an average rate of 16% until 1968 (Spencer and Lensink, 1970). Even higher annual rates of increase of 17, 23, and 24% were reported for more recent introductions in Alaska (Jingfors and Klein, 1982). These rates occurred after an initial short "adjustment" period of slow or no growth.

High rates of increase are not limited to introduced populations. The Banks Island population was nearly or totally extirpated before 1900 by Eskimo hunting. During the 1950's to 1970's, this population entered into an eruptive phase with an estimated overall annual growth rate of 13% and for certain years a rate of up to 25% (Urquhart, 1982; Vincent and Gunn, 1981). Immigration to Banks from other islands may have contributed to the increases.

As Lent (1978) noted, these growth rates equal or exceed what Leslie (1965) thought to be the theoretical maximum rate of increase for the species of 23%. Leslie (1965) discounted the likelihood of breeding in successive years, did not recognize the possibilities for breeding before 3 years of age and underestimated the survival rate of calves under favorable conditions.

Although a few instances of predation by grizzly bears (*Ursus arctos*) or polar bears (*Thalarctos maritimus*) have been reported (Gunn and Miller, 1982; Thing et al., 1984), the wolf (*Canis lupus*) is the only significant predator of muskoxen. Information in the earlier literature, summarized in Tener (1965), is largely anecdotal. Only Freeman (1971) attempted a quantitative analysis. Based on a small sample he suggested that nearly half the losses in his study population were related to wolf predation.

Muskox populations have been highly vulnerable to predation by man (Hone, 1934). Interest in the species by Neolithic man was intense. Gessain (1981) provided a map of 76 prehistoric sites in Europe with representations of *Ovibos* and illustrations of many examples of these diverse art forms. In historic times, Eskimo and Chipewyan Indian hunters were able to extirpate populations even with little or no dependence upon firearms (Burch, 1977; Stefansson, 1921).

Parasites from fecal samples taken from captive muskoxen include protozoa (*Eimeria* sp.), infecting 75% of 101 specimens; cestodes (*Moniezia* sp.) in 4%, and nematodes of several genera (Samuel and Gray, 1974). Lung worms frequently have been a health problem in captive animals, as has contagious ecthyma (Dieterich et al., 1981). In samples from wild muskoxen 82% of 216 showed evidence of parasite infection. *Capillaria* sp. and *Trichuris* sp. found in captive animals were not detected in wild populations but eggs of *Moniezia* sp. were more prevalent.

Webster and Rowell (1980) found helminths (*Marshallagia marshalli* and *Nematodirus helvetianus*) in intestines of two free-ranging muskoxen collected on Devon Island. These same two species plus *Monieza expansa* and *Taenia hydatigena* were found in muskoxen collected on Ellesmere Island.

Infections of the central nervous system, principally by *Corynebacterium pyogenes*, were reported in a number of captive muskoxen (Beckley and Dieterich, 1970). Rangiferine brucellosis (*Brucella suis* biotype 4) was isolated from a male muskox killed in the district of Keewatin, Northwest Territories, Canada (Gates, 1984).

Censuses of muskoxen generally are conducted in spring when hours of daylight are increasing but the dark animals are still conspicuous against a snow-covered terrain. On Nunivak Island and a few other areas where animals concentrate, snowmachines were used successfully (Lent, 1971; Spencer and Lensink, 1970). Aerial surveys at 200 and 600 m altitude were used elsewhere (Gunn, 1982; Lassen, 1984).

Jonkel et al. (1975) used succinylcholine chloride to successfully immobilize muskoxen but found that effective dosages were highly variable and weights difficult to estimate. Sernylan was used successfully on Nunivak Island (Gunn, 1982). The use of large nets and snowmachines to capture younger age classes of muskoxen has also been most effective on Nunivak (Gunn, 1982; Lent, 1978).

BEHAVIOR. Muskoxen are social, gregarious animals almost always encountered in groups, except for lone, mature males that in summer may comprise 4% to 9% of observed muskoxen (Tener, 1965). Groups composed only of males also occur in summer and fall. Tener (1965) reported mean group sizes, excluding lone males, of 15 to 20 in winter and 10 to 15 in summer. Similarly, average group size on Melville Island declined from 17.2 in March–April to 10.0 in July–August (Miller et al., 1977).

Group composition is relatively stable in summer (Gray, 1973; Smith, 1976). Because females are almost always in groups, males do not gather females to form harems as much as they take possession of existing groups by driving away young adult males and detering egress of females, beginning as early as June. Such groups are appropriately considered harems because they are defended and stability is promoted by the harem male. Nevertheless, splitting and fusion of groups occasionally occurs even much later in summer (Gray, 1973, 1979; Smith, 1976). Lone males do not necessarily clump around harems or even in areas where harems are abundant (Smith, 1976).

Male-male encounters or dominance fights consist of various behavioral components, including roaring, horning, and pawing of ground; the head-tilt, a lateral display; and head-swinging displays, head-pushing and butting, charging and clashing (Gray, 1973, 1984; Smith, 1976). Gland-rubbing, a behavior in which the preorbital gland is rubbed against the inside surface of the foreleg, is common

in other stress situations, as when men or predators approach a male, and during rutting challenges and dominance contests.

Wilkinson and Shank (1976) described carcasses of six bulls injured during combat; they suggested rutting injuries might have accounted for 5 to 10% of male mortality on Banks Island. Other observers have not confirmed such a high incidence of rut-related injuries (Gray, 1973; Smith, 1976).

Courtship behavior and testing of the sexual readiness of females begins sporadically in early summer and becomes an almost full-time activity for harem bulls in August and September as cows approach estrus. Smith (1976) suspected that intragroup synchrony of estrus may occur as in domestic cows (Fraser, 1968). Gray (1973) and Smith (1976) both describe the sexual behavior of muskoxen in the wild. Gray (1973) did not observe copulations, apparently because females in his study herd on Bathurst Island did not enter estrus that year. Smith (1976) observed 16 copulatory sequences, each lasting 15 to 30 min. Actual coitus was brief, as is typical for ungulates, lasting 5 to 6 s.

The mother-infant relationship in muskoxen is the "follower" type (Lent, 1974); the two maintain close and frequent contact. No attempt is made by the prepartum or postpartum mother to isolate herself from others. The calf is immediately a member of the group, and social contacts of all types including social play are an immediate and important element of such life (Gunn, 1982; Jingfors, 1980, 1984; Lent, 1974).

Nursing is relatively frequent at first (six to eight times a day) but frequency declines markedly after 2 months of age (Lent, 1974). A comparison of an introduced population in Alaska, with a Bathurst Island population, indicates more time was spent suckling and weaning was later in the latter population, probably because of poorer nutritional condition (Jingfors, 1980).

Delayed weaning was suggested to be the factor influencing whether or not a female has a calf in successive years (Tener, 1965; Wilkinson, 1971). However, evidence for this belief is weak and, conversely, the Bathurst Island females studied by Gray (1973) that showed no behavioral evidence of estrus, also had no accompanying calves.

Activity periods, alternately one of feeding and one of rest, are about 2.5 h duration (Gray, 1973). He and Sittler and Kempf (1984) found that muskoxen in summer spent nearly twice as much time feeding as resting. Jingfors (1980), however, reported slightly more time resting than feeding.

Gray (1973) described the digging of feeding craters through the snow. Alternate pawing with right and left forefoot was observed when hard snow was involved. Under certain conditions, as when slab snow must be broken and removed, the head (either the rostrum or chin) may be used (Gray, 1973). Agonistic behavior and displacement of one individual by another at snow craters occurs frequently, suggesting dominance classes, if not a strict dominance hierarchy (Gray, 1973).

Although the defense formation of muskoxen is a feature of great popular interest, illustrated and described in a variety of publications (Fig. 4), there is little systematic, quantitative information on this behavior. Typically, in response to disturbance, cows, calves, and juvenile animals run to a mature bull that becomes a focal point. A line or gentle arc of animals forms, more or less tightly pressed together, depending upon the immediacy of the perceived threat. There is much jostling, some conspecific agonistic behavior, and rubbing of preorbital glands. If threatening stimuli are from more than one direction or if there is circling of the muskoxen, as by wolves, a circle or a star will be formed. Buttocks may be pressed together; and lone animals or small groups may back up to rocks or other large objects (Gray, 1973).

Gray (1970, 1973) and Tener (1965) reported that the defense formation generally is effective against wolves and that most animals taken by wolves are lone animals or ones cut off from a group when defense formations are formed or as animals regroup. Such groups sometimes break formation and stampede providing wolves an opportunity to isolate and kill an individual (Gray 1970, 1973).

Miller and Gunn (1980, 1984) studied the defense formation and flight responses to overflights by helicopters to assess the potential impacts of human-induced disturbance and stress. Approximately 75% of individuals participated in defense formations and 44% galloped or cantered. Some short-term habituation occurred.

GENETICS. Tietz and Teal (1967) and Heck et al. (1968) both reported the chromosome number as 2N = 48. Heck et al. (1968) pointed out that the *nombre fondamental* is 60, consistent with all known bovid species. The acrocentric X chromosome is similar to that of several caprine species and different from bovine genera *Bos* and *Syncerus*. Heck et al. (1968) also noted some similarities between autosomes of the muskox and the Himalayan tahr (*Hemitragus jemlahicus*). Nevertheless, they concluded that the karyotype of the muskox ". . . is very dissimilar from all other Bovidae so far considered" (Heck et al., 1968:178).

The chromosome number for the takin was reported to be 52 (Bogart and Benirschke, 1975). These authors did not find this to be inconsistent with the hypothesized close relationship between the takin and muskox, presuming that two metacentric pairs in the muskox resulted from fusion of four pairs of small acrocentric chromosomes found in the takin. Giemsa banding of the X chromosome in the takin showed it is also like that of most other Caprinae.

Cream-colored individuals and similar mutant color variations have been reported (Gunn, 1985). Polled individuals also have been sighted occasionally and Wilkinson (1971) believed hornlessness to be controlled by a dominant allele.

REMARKS. The generic name, *Ovibos*, was adopted by Blainville (1816) when removing the muskox from the genus *Bos*. His efforts to show a composite genus combining features of both *Ovis* and *Bos* were in part based on the mistaken belief that the muskox had only two teats, thus making it different from all bovines (Allen, 1913).

Serological work by Moody (1958) helped to establish the caprine affinities of *Ovibos*. However, many modern authors (Kowalski, 1976; Simpson, 1984; Walther, 1984) have dropped the idea of a particularly close relationship between the muskox and the takin. Others (Gunn, 1982; Schaller, 1977) continued to place the two genera in the tribe Ovibovini.

The origin of the common name is obscure. It has been suggested (Wilkinson, 1971) that it has nothing to do with "musk" or musk glands, but rather originates from the French rendering of an Ojibwa Indian word for wet tundra and bogs, thus of the same origin as the English word "muskeg." Gotch (1979) erroneously stated that a musky odor originates from the preorbital glands. The famous Arctic explorer Stefansson (1921, 1924) objected to the common name "muskox" because of the absence of musk glands and musky odor. He proposed adoption of *Ovibos* as a common name but, perhaps more realistically, at other points used "polar cattle"; a name suggested to promote the domestication and economic value of the species. Despite the generally well attested high palatability of muskox flesh, two of the earliest references to the species, in 1720 and 1747, clearly made reference to a strong musky flavor to the meat (Allen, 1913).

Some writers have promoted use of the Greenland Eskimo (Inupiat) name (variously spelled Omingmak, Oomingmak or Umingmak), meaning "bearded one" (Bee and Hall, 1956; Gray and Peers, no date; Wilkinson, 1971, 1977). The Inupiat word for the underhair "qiviut" has been more widely adopted.

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