

PREDATION AND MULTIPLE KILLS OF MUSKOXEN BY GRIZZLY BEARS

PATRICIA E. REYNOLDS, U.S. Fish and Wildlife Service, Arctic National Wildlife Refuge, 101 12th Avenue, Room 236, Fairbanks, AK 99701, USA, email: patricia_reynolds@fws.gov

HARRY V. REYNOLDS, Alaska Department of Fish and Game, 1300 College Road, Fairbanks, AK 99708, USA, email: harry_reynolds@fishgame.state.ak.us

RICHARD T. SHIDELER, Alaska Department of Fish and Game, 1300 College Road, Fairbanks, AK 99708, USA, email: dick_shideler@fishgame.state.ak.us

Abstract: A population of muskoxen (*Ovibos moschatus*), successfully restored to northeastern Alaska in the 1970's, has become a source of food for grizzly bears (*Ursus arctos*). We tested whether grizzly bear predation on this population of muskoxen increased over time and described multiple kills of muskoxen by grizzly bears. We identified bear-muskox events from data collected between April 1982 and June 2001 during bear and muskox surveys and radiorelocation flights and from field notes, mortality records of radiocollared muskoxen, and other observations made by biologists, pilots, and local residents. Ninety-two bear-muskox events observed in 1982–2001 included 46 known kills, 37 possible kills or scavenging events, and 9 chases. Ten of 61 radiocollared muskoxen that died between 1982 and 2001 were killed by bears and 14 others were possibly killed or scavenged. The number of known kills and possible kills or scavenging increased significantly over time. Multiple kills, where 2 or more muskoxen were killed from a group, contributed to the number of known kills. Twenty-eight of 46 muskoxen (61%) killed by bears died during multiple kills. Twenty-two of these deaths occurred in 1998–2001. Ten marked grizzly bears were implicated in single or multiple kills, suggesting that several bears in northeastern Alaska became proficient predators of muskoxen in spite of the group-defensive behavior and formidable horns of muskoxen. The low numbers of muskox calves observed in 2000 and 2001 (<5 calves/100 females >2 years of age) may be due in part to predation of neonatal calves by grizzly bears. The successful return of muskoxen to northeastern Alaska has created a predictable source of large mammal protein for some grizzly bears.

Ursus 13:79–84 (2002)

Key words: Alaska, grizzly bears, multiple kills, muskoxen, *Ovibos moschatus*, predation, scavenging, surplus kills, *Ursus arctos*

Grizzly bears and muskoxen overlap in their distribution on the mainland of northern Canada, as well as in Alaska where muskoxen have been reestablished in recent decades (Klein 1988). Tener (1965) stated that predation by grizzly bears on muskoxen is rare, but more recent evidence (Gunn and Miller 1982, Case and Stevenson 1991, Clarkson and Liepins 1993, Shideler and Hechtel 2000) indicates that grizzly bears can be effective predators of muskoxen.

Muskoxen were extirpated from Alaska in the late 1800s but were successfully restored in 1969 and 1970 when animals from Greenland stock were translocated to areas near the Arctic National Wildlife Refuge (Arctic NWR) in northeastern Alaska (Reynolds 1998a). Muskoxen live in the Arctic NWR and adjacent regions throughout the year. Grizzly bears are seasonally active from late March to late October and occupy winter dens for the remainder of the year (Shideler and Hechtel 2000). Objectives for this paper were: (1) to test the hypothesis that predation of muskoxen by grizzly bears in northeastern Alaska increased over time; and (2) to describe incidents in which grizzly bears killed more than one muskox.

STUDY AREA

The study area was on the eastern arctic slope of Alaska, USA, between the Colville River and the Clarence River (Fig. 1). Approximately 24,700 km², this area included coastal plain and foothills in the Arctic NWR to the east and coastal plain adjacent to oilfields at Prudhoe Bay to the west. The study area was underlain by continuous

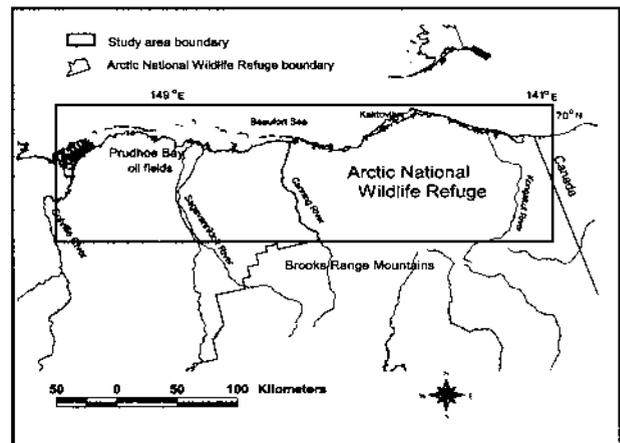


Fig. 1. Map of the grizzly bear-muskox study area in northeastern Alaska, USA.

permafrost and was snow-covered from September through mid-May. Major landscape features included braided north-flowing rivers and flood plains, coastal plain and foothills, small areas of thaw-lakes, and rugged mountains on the southern border (Walker et al. 1983). Vegetation was arctic tundra with shrubs (willow, *Salix* spp.; arctic dryad, *Dryas integrifolia*) and forbs (variegated horsetail, *Equisetum variegatum*) on partially vegetated gravel bars of rivers, tussock-shrub (sheathed cottongrass, *Eriophorum vaginatum*) and low-shrub (planeleaf willow, *Salix plantifolia*; dwarf arctic birch, *Betula nana*) communities on the slopes of rolling hills, and wet-graminoid communities (water sedge, *Carex aquatilis*; narrowleaf

cottonsedge, *Eriophorum angustifolium*) in poorly drained flat areas (Bliss 1981).

METHODS

During the past 2 decades, we studied grizzly bears and muskoxen in northern Alaska using radiotelemetry (Reynolds and Garner 1987, Reynolds 1993, Reynolds 1998a, Reynolds 1998b, Shideler and Hechtel 2000, Reynolds 2001). To document the relationship between grizzly bears and muskoxen, we reviewed information collected between April 1982 and June 2001, including survey and radiorelocation data from muskox and bear surveys, field notes, and observations reported by biologists, pilots working in the study area, and local residents. We reviewed mortality records of 60 radiocollared muskoxen that died between 1982 and 2001 and summarized factors associated with these deaths.

We defined a bear–muskox event as an interaction between the 2 species categorized as: (1) chases (bears stalking or chasing muskoxen); (2) possible kills or scavenging (bears feeding on muskox carcasses or carcasses eaten by bears, bears attacking muskoxen, or incidents of known scavenging); or (3) known kills (observed kills or other evidence, including tracks or physical trauma to a carcass, indicating that a muskox was killed rather than scavenged by a bear). We listed each chase or mortality (known kill or possible kill) as a different event. The total number of known or possible kills did not include deaths of neonatal calves or late-term fetuses with females (5 killed and 1 killed or scavenged). We calculated the number of known kills and possible kills that occurred in each month and each year. Both single kills and multiple kills were observed. We defined multiple kills as incidents where ≥ 2 muskoxen were killed from the same group, either during a single attack or several attacks over a few days while the group remained at the same location. Because many winter-related mortalities in arctic areas occur in May and June, we defined a year as 1 July–30 June. We used linear regression analysis (Zar 1984) to determine if the number of known or possible kills/scavenging of muskoxen by grizzly bears increased over time.

RESULTS

We documented 92 grizzly bear–muskox events from April 1982 through June 2001. Of these, 46 (50%) were known kills, 37 (40%) were possible kills or scavenging, and 9 (10%) were chases. Deaths of 61 radiocollared muskoxen documented during this period included 10 (16%) killed by bears and 14 (23%) eaten and possibly killed by bears (Fig. 2). This suggests 16–39% of adult muskox mortalities were caused by grizzly bear preda-

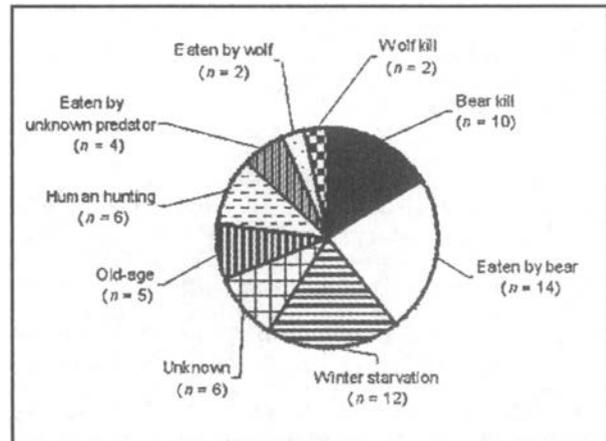


Fig. 2. Factors associated with mortalities of 61 radiocollared muskoxen that died between April 1982 and June 2001 in northeastern Alaska, USA.

tion. In northeastern Alaska, grizzly bears were associated with 24 muskox carcasses; by contrast, wolves (*Canis lupus*) and unknown predators were associated with 8 muskox carcasses (Fig. 2).

Ten marked bears killed muskoxen in northeastern Alaska. Nine other marked bears possibly killed, scavenged, or chased muskoxen. Five of these 19 marked bears were associated with muskoxen on 2 or 3 occasions. Bears chasing, eating, or killing muskoxen often were alone (16 events), but also were seen with 1 or 2 other adult bears (3 events) or cubs or yearlings (3 events).

The number of known kills and possible kills or scavenging increased significantly (slope (b) = 0.505, 18 df, P = 0.0001) between 1982 and 2001 (Fig 3). The number of known kills of muskoxen by grizzly bears ranged from 0–2 deaths/year before 1993, 1–4 deaths per year in 1994–97 and 5–10 deaths/year in 1998–2001.

The increase in known kills was due primarily to an increase in deaths resulting from multiple kills of muskoxen by grizzly bears (Fig. 3). Of 46 deaths from known grizzly bear predation, 28 muskoxen (61%) died during 10 multiple kills (Table 1). Twenty-two (79%) of these 28 mortalities occurred between May 1998 and June 2001 (Table 1). By contrast, 18 muskoxen died of bear predation during single kills: 9 single kills took place between 1987 and 1997 and 9 single kills occurred in 1998–2001.

Bears made multiple kills of muskoxen only from April through early June (Table 1). Eight of 10 multiple kill incidents (24 of 28 deaths) occurred in April and May when muskoxen were calving, bears were emerging from winter dens, and the ground was still snow-covered. Grizzly bears made single kills of muskoxen in July–September (9 deaths) as well as in April–June (9 deaths).

Six different marked bears were involved in 4 multiple

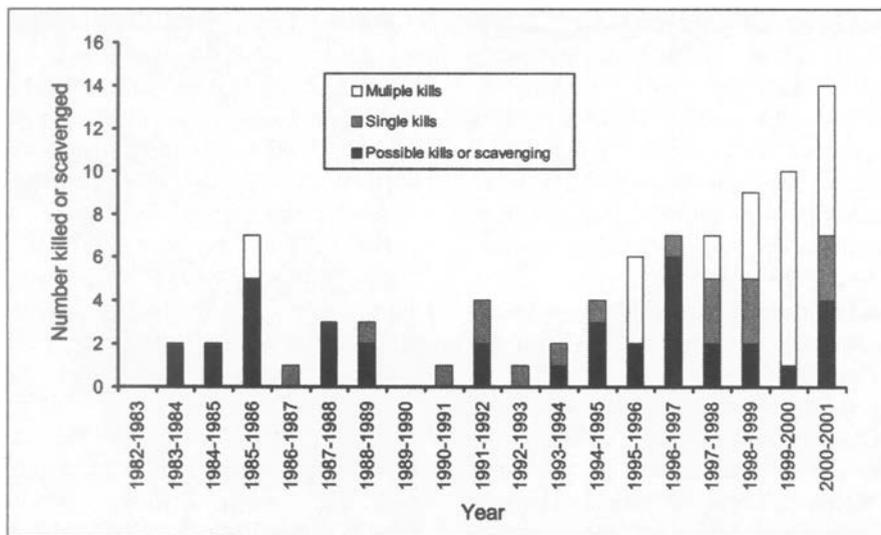


Fig. 3. Number of muskoxen killed or scavenged by grizzly bears, April 1982–June 2001, northeastern Alaska, USA.

kill incidents (Table 1). In addition, a bear or bears killing 3 muskoxen on the Okerokovik River in 2000 were likely different animals than those implicated in kills on the Canning River because of the distance between the multiple kill sites. One 12-year-old male bear (No. 054) killed a single muskox in 1998 and made multiple kills in 2000 and again in 2001 (Table 1).

One multiple kill involved a female grizzly bear (No. 019, age 18) and 2 of her adult female offspring (No. 018, age 5 and No. 037, age 7; Table 1). These bears killed an adult female and an adult male muskox from a group of about 24 in late May 1998 on the Itkillik River. Both carcasses were located in areas of deeply drifted snow (S. Hamilton, Alaska Department of Fish and Game pilot, Fairbanks, Alaska, USA, personal communication, 1998).

Six incidents of multiple kills took place on the Canning River (Table 1). In late April 1999, a hunter from the village of Kaktovik reported a grizzly bear feeding on

a large muskox carcass with 3 other carcasses of smaller muskoxen buried by a bear nearby (Mike Agiak, Inupiat hunter, Kaktovik, Alaska, USA, personal communication, 1999).

During 14–18 April, 2000, 2 bears killed 7 muskoxen from a group of ~29 animals on the Canning River (D. Sowards, Arctic NWR pilot, Fairbanks, Alaska, USA, personal communication, 2000). The kill site was about 5 km west of where 4 muskoxen had been killed the previous year. On-site observations of tracks and examination of the carcasses on 22 April suggested that a bear (observed on a carcass of an adult male muskox) killed 2 muskoxen and that a different, larger bear killed 5 muskoxen (C. Bedingfield, Alaska Department of Public Safety, Coldfoot, Alaska, USA, personal communication, 2000). Tracks indicated that the large bear, coming from the carcass of an adult muskox, inflicted lethal wounds on 2 adult females and a yearling before killing and feed-

Table 1. Multiple kills of muskoxen where 2 or more were killed from a group by grizzly bears in northeastern Alaska, USA, 1986–2001.

Date	Location	Marked bears	Marked muskoxen		Number, sex, and age of muskoxen killed by bears
			in group		
May 1986	Niguanak River	unknown	unknown		2 yearlings ^a
May 1996	Ivishak River	unknown	unknown		4 calves ^a
May 1998	Itkillik River	018, 019+037	unknown		1 adult F, 1 adult M
May 1999	Canning River	unknown	unknown		4 adults ^b
Apr 2000	Canning River	030	4971		1 adult M, 1 adult ^b
Apr 2000	Canning River	054	4971		2 adult F, 2 adults ^b , 1 yearling
May 2000	Okerokovik River	unknown	0100 ^c		1 adult F, 1 2-year M, 1 calf ^d
Apr 2001	Canning River	033	0117		2 adults ^b
Apr 2001	Canning River	054	0117		1 adult M, 1 adult F, 1 yearling
Apr 2001	West of Canning River	unknown	0117 ^c		2 adult F, 1 calf ^d

^a Sighting not verified

^b Sex of adults not determined

^c Radicollared muskox killed

^d Calves not counted in total killed

ing on a fifth animal. All carcasses examined appeared to be in good physical condition, and at least one female was pregnant. After being attacked by the larger bear, the muskox group ran down the Canning River and likely split into smaller groups. We located the radiocollared female muskoxen associated with the group >60 km north in early June with only 10 other animals. Movements of this magnitude are unusual for muskoxen in late May and early June (Reynolds 1998b).

In June 2000, we found shed radiocollars from 2 bears near the multiple kill sites on the Canning River. A radiocollar from a young male (No. 030, age 7) was located between 2 muskox carcasses. The radiocollar from a large male (No. 054, age 14) was near the carcass of an adult female muskox. Muskoxen involved in these bear attacks likely defended themselves; a horn hooked beneath these collars could have ripped them off. Another incident of a bear losing a collar while killing a muskox occurred in 1995, when we found the shed radiocollar of a large male grizzly bear (No. 020, age 22) near the carcass of a large adult male muskox.

Another multiple kill occurred in the eastern part of the study area in April or May 2000 (Table 1). A radiocollared female muskox, observed in a group of 30 on 5 April 2000, was found dead and consumed by 8 June 2000. We found additional remains of a 2-year-old male muskox and a calf near the dead female. The close proximity of all 3 carcasses and the presence of numerous bear scats indicated that they were killed and eaten by one or more bears.

In 2001, 3 incidents of multiple kills of muskoxen by grizzly bears occurred on the Canning River (Table 1). Between 18 April and 20 April, a marked grizzly bear (No. 033, age 10) killed 2 muskoxen from a group of ~60 on the Canning River, 9 km south of the site where 7 muskoxen were killed in April 2000. Bear No. 054 (age 15), which had killed 5 muskoxen on the Canning River in 2000, made another kill from this group before 26 April. By 30 April, carcasses of 2 more muskoxen were seen near the first carcasses, and a different bear was feeding on one of these carcasses (D. Sowards, personal communication, 2001). Unlike the previous year, some of the muskoxen remained in the vicinity of the first kills and subsequently sustained additional predation. We found remains from an adult male, an adult female, and a yearling muskox as well as the eartag from bear No. 054 when we visited the location in late June 2001.

In early June, a pilot saw a bear kill 3 muskoxen (2 females and a calf) west of the Canning River about 50 km north of the April kill site (W. Audi, air taxi pilot, Kaktovik, Alaska, USA, personal communication, 2001). One dead animal was a radiocollared female associated with the same group of ~60 muskoxen involved in the April 2001 multiple kill (Table 1).

Because bears killed adult muskoxen, predation on muskox calves also likely occurred. The deaths of young muskoxen were difficult to detect because of the remoteness of the study area and the rapidity with which small carcasses can be consumed. In mid-May 1996, 1 or more bears reportedly killed 4 of 5 newborn calves in a group of about 25 muskoxen wintering near the Ivishak River–Echooka River confluence (D. Neel, air taxi operator, Happy Valley, Alaska, USA, personal communication, 1996; Table 1). Although we were not able to confirm this event, reports of similar events exist (Clarkson and Liepins 1993, Gunn and Fournier 2000). In addition to direct mortalities, grizzly bears also caused indirect mortalities to young calves. In May 1988, a male grizzly killed an adult female from a group of 22 muskoxen. The group ran in panic and 2 or 3 young calves likely died after being abandoned. In April 1998, 3 calves were left behind by a group fleeing from bears that killed 2 muskoxen, and in May 2000, 3 calves died after being separated from a group running from humans, or animal predators near Kaktovik, Alaska.

DISCUSSION

We made our first observation of a kill of an adult muskox by a grizzly bear in the Arctic NWR in June 1987, 5 years after we began our studies and 18 years after muskoxen were released in northeastern Alaska. The founding population of about 35 muskoxen reached a peak of 386 animals in 1986 within regions first occupied in the Arctic NWR (Reynolds 1998a). In 1987–2000, the number of muskoxen in these same regions ranged from 189–310. Muskoxen also were expanding their range into regions west of the Arctic NWR by 1986 (Reynolds 1998a). We documented the first kill of a muskox by a grizzly bear in these western regions 8 years later, in 1994. By 1995, numbers of muskoxen west of the Arctic NWR peaked at >300. The lag between the first appearance of muskoxen in a geographic region and incidents of known kills suggests that predation by grizzly bears did not occur until the density of muskoxen reached levels that increased the likelihood of encounters between bears and muskoxen.

Multiple kills of adult muskoxen by grizzly bears in northeastern Alaska are relatively recent events. Until 1997, documented predation by grizzly bears on muskoxen older than yearlings involved solitary adults or only one animal from a group. Ten radiocollared bears made single or multiple kills, and 5 bears were associated with more than one bear–muskox event. This suggests that, over time, several grizzly bears became proficient predators of muskoxen. Predation on muskoxen poses risks for grizzly bears because muskoxen defend themselves against

predators by running together and wheeling to face an approaching bear or wolf (*Canis lupus*) with a wall of horns. Adult muskoxen also dart out of a defensive group to attack an approaching predator. Horns can be lethal weapons against bears. One radiocollared male grizzly bear (No. 031, age 11) had serious puncture wounds from a muskox when it was captured in June 1995, but it survived the injuries. Another marked male bear (No. 056, age 5) died several weeks after receiving wounds from an adult male muskox during an attack in June 2000. Status of the muskoxen in these encounters was not determined. The recovery of radiocollars from 3 bears near muskox carcasses also suggests that muskoxen defend themselves against bears.

Some multiple kills of muskoxen by grizzly bears in northeastern Alaska appeared to be incidents of surplus killing in which predators kill more than can be eaten immediately. Surplus kills of ungulates by large predators are relatively rare events (DelGiudice 1998). Most reported incidents have involved wolves (Kruuk 1972, Bjärvall and Nilsson 1976, Eide and Ballard 1982). Unique environmental conditions such as deep snow that impedes movements of prey likely contributed to incidents of surplus killing (Mech et al. 1971, Miller et al. 1985, Patterson 1994).

Snow conditions may have contributed to the ability of bears to catch muskoxen in northeastern Alaska. Although we had no snow measurements, photographs of kill sites and late melt of winter snow in June 2001 suggested that snow was deep in the area where multiple kills occurred in April. Grizzly bears in northern Alaska emerge from dens in April and May. Muskoxen also give birth in late April and May and are less mobile during the calving season (Reynolds 1998b). The occurrence of multiple kills from April to early June, but not in summer when bears made single kills, suggests that muskoxen are more vulnerable to predation in late winter–spring.

The number of radiocollared bears and muskoxen and the frequency of surveys varied throughout the 2 decades of this study. However, the greatest number of radiocollared animals and wildlife surveys in the Arctic NWR occurred in 1982–86 and biological studies continued with less intensity from 1987–93. In 1995–2001, the muskox population was monitored less frequently with a relatively stable number of radiocollared animals. Grizzly bear research in the Arctic NWR ceased after 1993, although studies of grizzly bears in the Prudhoe Bay area began in 1991. Although variability in effort could have contributed to variability in the data, including events in 1986, the increase in predation from 1994 to 2001 was likely not due to increasing study intensity.

Increasing predation by grizzly bears may be affecting the dynamics of this reestablished muskox population. The

number of calves lost due to direct or indirect mortalities from grizzly bears is unknown. In 2000 and 2001, calf:female ratios in the Arctic NWR were <5 calves/100 females >2 years old in late June, compared to an average of 29 calves/100 females in 1995–99 and 48 calves/100 females >2 years in 1990–94 (P. Reynolds, unpublished data). Predation by grizzly bears or harassment related to predation events may affect neonatal calf survival. Bears have been implicated in population declines in moose (*Alces alces*) numbers through predation of young calves (Bergerud and Page 1987, Boertje et al. 1988, Gasaway et al. 1992).

The availability of muskoxen as a food resource for bears in northeastern Alaska has implications for the dynamics of grizzly bear populations. Grizzly bears in northern Alaska have limited food resources that are only seasonally available. Bears that have access to caribou (*Rangifer tarandus*) or fish have higher productivity and survival (Reynolds and Garner 1987, Hilderbrand et al. 1999). Caribou are present in large numbers between late May and mid July when females of the Porcupine caribou herd give birth to calves on the coastal plain of the Arctic NWR. Caribou from the Central Arctic herd are available in coastal areas between June and August from the Canning to the Colville rivers. Moose and Dall's sheep (*Ovis dalli*) live year-round in the mountains and foothills in low densities. But in April through early May when grizzly bears emerge from dens, winter conditions still prevail and few food resources are available. The return of muskoxen to northeastern Alaska provides a predictable source of large mammal protein for grizzly bears. We speculate that bears that consume muskox, particularly those that make multiple kills, may be more productive than those without access to this resource.

ACKNOWLEDGMENTS

We thank M. Agiak, L. Akootchook, W. Audi, C. Bedingfield, B. Boyle, K. Butters, R. Cameron, D. Dufour, F. Rexford, S. Hamilton, M. Herndorf, J. Hechtel, B. Lenart, D. Neel, R. O'Brian, L. Quakenbush, D. Sowards, S. Lyons, and J. Vandenberg for providing observations of bears and muskoxen. The U.S. Fish and Wildlife Service, Arctic National Wildlife Refuge, the Alaska Department of Fish and Game, B.P. Exploration (Alaska), and Phillips Alaska Inc. provided funding for this study.

LITERATURE CITED

- BERGERUD, A.T., AND R.E. PAGE. 1987. Displacement and dispersion of parturient caribou as antipredator tactics. *Canadian Journal of Zoology* 65:1597–1606.
- BJÄRVALL, A., AND E. NILSSON. 1976. Surplus killing of reindeer by wolves. *Journal of Mammalogy* 57:585.

- BLISS, L.C. 1981. North American and Scandinavian tundras and polar deserts. Pages 1–17 in L.C. Bliss, O.W. Heal, and J.J. Moore, editors. *Tundra ecosystems: a comparative analysis*. Cambridge University Press, Cambridge, England.
- BOERTJE, R.D., W.C. GASAWAY, D.V. GRANGAARD, AND D.G. KELLEYHOUSE. 1988. Predation on moose and caribou by radio-collared grizzly bears in east central Alaska. *Canadian Journal of Zoology* 66:2492–2499.
- CASE, R., AND J. STEVENSON. 1991. Observations of barren-ground grizzly bear (*Ursus arctos*) predation on muskoxen (*Ovibos moschatus*) in the Northwest Territories. *Canadian Field Naturalist* 105:105–106.
- CLARKSON, P.L., AND I.S. LIEPINS. 1993. Grizzly bear, *Ursus arctos*, predation on muskox, *Ovibos moschatus*, calves near the Horton River, Northwest Territories. *Canadian Field Naturalist* 107:100–102.
- DELGIUDICE, G.D. 1998. Surplus killing of white-tailed deer by wolves in northcentral Minnesota. *Journal of Mammalogy* 79:227–235.
- EIDE, S.H., AND W.B. BALLARD. 1982. Apparent case of surplus killing of caribou by gray wolves. *Canadian Field-Naturalist* 96:87–88.
- GASAWAY, W.C., R.D. BOERTJE, D.V. GRANGAARD, D.G. KELLEYHOUSE, R.O. STEPHENSON, AND D.G. LAURSEN. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. *Wildlife Monographs* 120.
- GUNN, A., AND B. FOURNIER. 2000. Calf survival and seasonal migrations of a mainland muskox population. Northwest Territories Department of Resources, Wildlife and Economic Development, File report 124. Inuvik, Northwest Territories, Canada.
- , AND F.L. MILLER. 1982. Muskox bull killed by barren-ground grizzly bear, Thelon game Sanctuary, N.W.T. *Arctic* 35:545–546.
- HILDEBRAND, G.V., C.C. SCHWARTZ, C.T. ROBBINS, M.E. JACOBY, T.A. HANLEY, S.M. ARTHUR, AND C. SERVHEEN. 1999. The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. *Canadian Journal of Zoology* 77:132–138.
- KLEIN, D.L. 1988. The establishment of muskox populations by translocation. Pages 298–317 in L. Nielsen and R.D. Brown, editors. *Translocation of wild animals*. Wisconsin Humane Society, Milwaukee, Wisconsin, USA.
- KRUK, H. 1972. Surplus killing by carnivores. *Journal of Zoology* (London), 166:233–244.
- MECH, L.D., L.D. FRENZEL, JR., AND P.D. KARNS. 1971. The effect of snow conditions on the vulnerability of white-tailed deer to wolf predation. Pages 51–59 in L.D. Mech and L.D. Frenzel, Jr., editors. *Ecological studies of the timber wolf in northeastern Minnesota*. U.S. Forest Service Research Paper No. NC-52.
- MILLER, F.L., A. GUNN, AND E. BROUGHTON. 1985. Surplus killing as exemplified by wolf predation on newborn caribou. *Canadian Journal of Zoology* 63:295–300.
- PATTERSON, B.R. 1994. Surplus killing of white-tailed deer, *Odocoileus virginianus*, by coyotes, *Canis latrans*, in Nova Scotia. *Canadian Field-Naturalist* 108:484–487.
- REYNOLDS, H.V., AND G.W. GARNER. 1987. Patterns of grizzly bear predation on caribou in northern Alaska. *International Conference on Bear Research and Management* 7:59–68.
- REYNOLDS, P.E. 1993. Dynamics of muskox groups in northeastern Alaska. *Rangifer* 13(2):83–89.
- . 1998a. Dynamics and range expansion of a reestablished muskox population. *Journal of Wildlife Management* 62:734–744.
- . 1998b. Ecology of a reestablished population of muskoxen in northeastern Alaska. Ph.D. Dissertation, University of Alaska, Fairbanks, Alaska, USA.
- . 2001. Reproductive patterns of muskoxen in Alaska. *Alces* 37:403–410.
- SHIDELER, R.T., AND J.L. HECHTEL. 2000. Grizzly bears. Pages 105–132 in J.C. Truett and S.R. Johnson, editors. *The natural history of an arctic oil field*. Academic Press, New York, New York, USA.
- TENER, J.S. 1965. Muskox in Canada: a biological and taxonomic review. *Canadian Wildlife Service Monograph* No. 2.
- WALKER, D.A., P.J. WEBBER, AND K.R. EVERETT. 1983. 1:63,360 scale geobotanical mapping studies in the Arctic National Wildlife Refuge, Alaska. Institute of Arctic and Alpine Research Plant Ecology Laboratory, University of Colorado, Boulder, Colorado.
- ZAR, J.H. 1984. *Biostatistical analysis*. Prentice-Hall, Inc., Englewood Cliffs, New Jersey, USA.

Received: 28 May 2001.

Accepted: 27 February 2002.

Associate Editor: Derocher.