IMPLICATIONS OF PREDATOR-PREY RELATIONSHIPS TO MOOSE MANAGEMENT

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Predator–prey relationship studies conducted in North America within the past decade suggest that moose (*Alces alces*) mortality due to wolf (*Canis lupus*) predation is additive rather than compensatory. After a moose population has declined from factors such as severe winters, overharvest, declining range carrying capacity, and/or predation, limits on moose population growth due to wolf predation can occur. In simple wolf–moose systems, predators can maintain moose at low levels for decades.

Prior to the mid-1970s both brown (*Ursus arctos*) and black (*Ursus americanus*) bears were thought to be scavengers rather than predators of moose. Studies of neonatal moose mortality indicate that both species of bear can be successful ungulate predators. Bear predation is the primary cause of mortality in some moose populations and, similar to wolf predation, is an additive source of mortality. Experimental bear reduction programs have demonstrated that calf moose survival can be improved by temporarily reducing bear numbers.

Most moose populations produce adequate numbers of calves to enable population growth. When growth fails to occur, it usually is the result of high neonatal mortality. The relationship between habitat carrying capacity and ungulate density is confounded by predation. Managers attempting to provide sustained yields of moose for human use will find predator management a necessity in systems containing naturally regulated predator populations.

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Introduction

The interactions of moose (*Alces alces*) with other species was reviewed by Wolfe (1974). At that time wolves (*Canis lupus*) were considered the only effective predator of moose in North America. Other predators such as bear (*Ursus sp.*), cougar (*Felis concolor*), and coyote (*Canis latrans*) were considered to be of "limited" importance to moose. It was generally conceded that wolves could exert a significant regulatory effect on moose if such predation focused on calves. Otherwise, wolf predation was believed to be of a "sanitation" nature whereby wolves helped to maintain stable populations and cull out inferior individuals (Wolfe 1974, Mech 1970).

The controversy of whether predation was an important limiting factor on ungulate populations continued during the 1970s. Connelly (1978) stated that a selective review of the literature could reinforce any desired view on the subject of predation. Although this still remains somewhat true, recent research has altered most biologists' opinions of the potential importance of predation to ungulate populations.

The purpose of this paper is to review North American moose-predator studies which have been conducted within the past decade and to interpret their implications to moose management.

Wolf Predation

The effects of wolf predation on moose populations have been examined in Alaska by Haber (1968, 1977), Peterson (1982), Peterson et al. (1982), Gasaway et al. (1977, 1983), and Ballard et al. (1981 a, b, 1987 b), in Alberta by Fuller and Keith (1980), Mytton and Keith (1981), and Hauge and Keith (1981), and at Isle Royale, Michigan by Peterson (1977), and Peterson and Page (1983). A brief review of these studies follows.

Tanana Flats, Alaska

Moose populations on the Tanana Flats, Alaska, increased in the 1940s and 50s in response to mild winters, favorable range conditions, and predator control by the federal government (Bishop and Rausch 1974). Following a peak in moose numbers in 1960, the population declined to a low in 1975 (Gasaway et al. 1983). In 1975 moose calf numbers declined from an estimated 94 calves/100 cows at birth to about 15 calves/100 cows by autumn. Wolf predation was estimated to have removed a large proportion of calves, primarily during summer, and 13 to 34 % of the winter moose (calves and adults) population from 1973 through 1975. Gasaway et al. (1983) concluded that severe winters, human harvest and wolf predation combined caused a rapid decline in moose numbers.

Wolf reduction was initiated in 1976 and wolf numbers were reduced by 61 % (Gasaway et al. 1983). Calf and yearling moose survival were estimated to have increased 2 to 4-fold, adult mortality was reduced from 20 % to 6 % annually, and the moose population increased as a result of wolf control. Autumn calf/cow ratios increased from 15/100 prior to wolf control in 1975 to 51 calves/100 cows in 1976 following wolf control. Initial calf production in 1977 and 1978 was 111 and 116 calves/100 cows for moose greater than 24 and 36 months of age, respectively.

Prior to wolf control, early winter moose and wolf densities in 1975 averaged about 183 and 16/1 000 km^2, respectively: a moose/wolf ratio of about 12/1. By 1978 moose densities had risen to about 229/1 000 km^2 while wolf densities had been reduced to about 5/1 000 km^2: a ratio of about 44 moose/wolf.

Although quantitative estimates of black bear (*Ursus americanus*) density were not available, black bears were considered common while brown bear (*Ursus arctos*) densities were estimated at 15/1 000 km^2 (Gasaway et al. 1983). Neither bear species were considered an important cause of moose mortality. Both caribou (*Rangifer tarandus*) and sheep (*Ovis dalli*) occurred in sufficient numbers to be alternate sources of prey for bears and wolves. Gasaway et al. (1983) concluded that starvation, hunting, and wolf predation were additive, rather than compensatory mortality factors. When predator populations are naturally regulated, wolf predation can keep moose populations at relatively low levels over long periods of time. In such cases moose managers would be forced to restrict human harvest and wait for a natural recovery of the moose populations. This action could span decades or even longer if predator populations were not reduced.

Nelchina Basin, Alaska

Moose populations in the Nelchina Basin experienced historical fluctuations similar to those in interior Alaska (Bishop and Rausch 1974). Moose populations increased through the 1940s and 50s, peaked in 1960, and then declined. Moose mortality was high during the decline due to starvation and wolf predation. The moose population was expected to rebound following years of mild winters but recruitment continued to decline. Wolf numbers had increased from a low of about 12–35 (0.3–0.8 wolves/1 000 km^2) in 1953 to an estimated maximum range of 350–450 (8–11 wolves/1 000 km^2) by 1965 (Rausch 1967, 1969). Moose numbers declined from 1960, reaching a low of about 476 moose/1 000 km^2 by 1975. There appeared to be an inverse relationship between wolf and moose numbers.

Because of the moose population decline, a wolf reduction program was initiated in a 7 250 km^2 portion of the Basin in 1976. From 1976 to 1978 wolf densities were reduced annually by 42 to 52 % or from about 7/1 000 km^2 in fall 1975 to 2/1 000 km^2 in spring 1978 (Ballard et al. 1981 b, 1987b). Prior to wolf removal the moose/wolf ratio was about 64/1, while afterward there were about 224 moose/wolf. However, calf recruitment, as reflected by autumn calf/cow ratios, did not increase significantly in comparison to areas where wolf reduction programs were not conducted (Ballard et al. 1981 b). Part of the reason was that wolf densities also declined in the nonreduction areas due to public hunting and trapping, but also because brown bear predation was identified as the most significant source of calf mortality throughout the Basin (Ballard et al. 1981 a). Brown bears (24/1 000 km^2, Miller and Ballard 1982 b) caused most of the calf mortality prior to and during the wolf reduction. Black bear density was low and they were not an important source of mortality in the study area. Caribou were present in sufficient numbers to constitute alternative prey for both predator species.

Simulation modeling was an important tool for evaluating the effects of predator reductions on moose (Ballard unpubl. data). Simulation models suggested that reductions in wolf numbers and mild winters during the study had allowed the moose population to increase at a rate of about 3–5 % annually even though wolf predation was determined not to be the primary mortality factor. These data suggested that wolf and brown bear predation were additive sources of mortality.

Kenai Peninsula, Alaska

Historical moose population fluctuations on the Kenai Peninsula were similar to those of interior Alaskan populations (Spencer and Hakala 1964, Bishop and Rausch 1974); however, a major difference was that wolves were absent from about 1915 to about 1960 (Bishop and Rausch 1974, Peterson and Woolington 1982). In addition, Bishop and Rausch (1974) believed that the Kenai moose population either stabilized or continued to grow until 1970–71 as a result of browse provided by a 1947 fire. During winters 1971–72 and 1972–73, almost entire calf crops were lost due to deep snows and decreased browse availability. High winter calf mortality continued throughout the 1970s. The wolf population became reestablished and moose were the primary ungulate prey. By 1976 wolf densities had increased to about 17/1 000 km^2 and resulted in a moose/wolf ratio of about 45/1 (Peterson 1982). Moose twinning rates ranged from 22 to 70 %.

Moose calf mortality studies conducted in 1977 and 1978 suggested that predators killed 49 % (23) of 47 collared calves between birth and mid-summer (Franzman et al. 1980). However, wolves were responsible for only 11 % (3) of the total mortalities (27), while black bears were responsible for 59 % (16) and brown bears for 11 % (3). During winter wolves preyed upon older, relatively healthy, adult moose which had a high incidence of debilitating factors and on malnourished calves (Peterson 1982). In spite of predation from both bears and wolves, moose numbers increased in the late 1970s and early 1980s, apparently as a result of mild winters and increased forage production resulting from a 1969 fire which increased moose productivity. Based on other Alaskan studies (Gasaway et al. 1983, Ballard et al. 1981 a, b), bear and wolf predation were considered additive mortality factors (Franzmann, pers. comm.).

Mt. McKinley National Park, Alaska

The dynamics and food habits of 2 wolf packs were studied in Mt. McKinley National Park from 1966 to 1974 (Haber 1977). During winter calves and older moose were killed by wolves. Haber (1977) suggested that wolf predation in both winter and summer was of a compensatory nature. Based upon his observations of 2 wolf packs, a model describing wolf–moose relationships was formulated (Haber 1977, Walters et al. 1981). The model suggests that moose populations stabilize at various equilibria in response to natural and/or man-caused perturbations. Haber (1977) maintained that wolf predation had little impact on moose under natural conditions but that it would lead to drastic declines when prey populations were overharvested by man. Other catastrophes could act in a similar manner but he maintained that winter severity by itself was not of sufficient magnitude to cause moose population declines.

Van Ballenberghe (1980) criticized Haber's (1977) and Walters' et al. (1981) theories of multiple equilibria as unappropriate for moose because their models were based on poorly understood relationships and contained several qualitative "flaws".

Northern Alberta

The population dynamics of moose and wolves were studied in northern Alberta from 1975 to 1978 (Fuller and Keith 1980, Hauge and Keith 1981). Moose and wolf densities averaged 180 and 6 (range 4–14)/1 000 km^2, respectively, resulting in about 30 moose/wolf. Differences in wolf density within this area were attributed to food availability. During winter 1 wolf pack killed an average of 1 moose every 4.7 days (Fuller and Keith 1980). Annual calf moose mortality was 73 %, of which 29 % was due to wolf predation (Hauge and Keith 1981). Calf mortality was highest (39 %) in the first month of life. Calf/100 cow (>12 mos. of age) ratios ranged between 50–122 ($\bar{x}$=72/100 during May and June) immediately after parturition. By late winter (February–March) those ratios had dropped to between 39–43 calves/100 cows. Annual yearling and adult moose mortality was estimated at 24 % due to hunting and wolf predation (Hauge and Keith 1981). Fuller and Keith's (1980) data suggested that because 15 % of the adult and yearling moose were dying from wolf predation and this approximated the annual recruitment (19 %) of yearlings, wolf predation was the major limiting factor on this moose population. They also concluded that wolf prey selection and hunting success patterns in northern Alberta were similar to those reported elsewhere in North America in that wolves killed a disproportionate number of young, old and probably debilitated moose. Black bears were numerous in the study area and were suspected to have caused appreciable calf mortality (Hauge and Keith 1981). No estimates of black or brown bear density were available. The only alternate ungulate prey was a small population of caribou.

One of the highest reproduction and calf survival rates for moose in North America was recorded by Rolley and Keith (1980) and Mytton and Keith (1981) in a second study where wolves and brown bears were absent and black bears were scarce. Over a 13-year period (1965–1978) there was a winter average of 106 calves/100 cows (range 78 to 146) and a mean twinning rate of 41 % (Rolley and Keith 1980). Initial production of calves in spring of 1976 was estimated at 167 calves/100 cows (Mytton and Keith 1981). Annual adult and calf mortality rates were 16 % and 33 %, respectively (Rolley and Keith 1980). They concluded that the high reproductive rates were a result of abundant browse and the low mortality rates of calves due to the lack of predators.

Isle Royale, Michigan

For 26 years the Isle Royale study has continued to provide valuable insights into predator–prey relationships (Mech 1966, 1970, Shelton 1966, Wolfe 1977). Mech (1966) concluded that in the late 1950s and early 60s wolf and moose populations reached a state of dynamic equilibria whereby wolves eliminated heavily parasitized, diseased, old, or otherwise inferior individuals from the population. In this case wolves were maintaining the moose population at a level below that which the habitat could support. Peterson (1977) re-examined the data and concluded that there were indications of an increase in moose numbers during the 1960s and wolves did not control the moose population. Wolf numbers remained relatively stable through this period. In the 1970s calves and young adult moose became vulnerable to wolf predation due to severe winters. Moose numbers declined from 1 200 to 600 and wolf numbers increased from 20–22 to 41 (Peterson 1979). Wolf numbers continued to increase and peaked in 1980 even though moose numbers had already declined (Peterson et al. 1982, Peterson and Page 1983). By 1982 the wolf population had declined dramatically, after which the moose population began to increase, apparently in response to the wolf population decline (Peterson and Page 1983).

Peterson (1977) stated that there were "no adequately documented cases of wolf predation imposing a long-term limit on ungulate populations independent of environmental influences". He concluded that predation which increased because of prey vulnerability was not of a compensatory nature and could be considered additive. More recently, Peterson and Page (1983) concluded that recent responses in calf moose recruitment suggest a more "substantial role for wolf predation during and following the moose decline". These authors now believe that relationships between wolves and moose are "unstable cyclic interactions".

Bear Predation

Despite brown bears being recognized as serious predators in Scandinavia (Haglund 1974) and in the USSR (Danilov 1983) in North America both brown and black bears have been considered scavengers of moose. However, Cowan (1944 cited by Hosley) believed grizzly bears were more significant than wolves as summer predators of moose in western Canada. Chatelain (1950) reported that both brown and black bear scats indicated that both species fed on calf and adult moose on the Kenai Peninsula although it was unclear whether these moose had been killed by bears or were scavenged. Le-Resche (1968) observed 2 instances of brown bears killing moose calves near Palmer, Alaska. He believed, and Ballard et al. (1980) later confirmed, that moose calves more than 6 weeks of age could, in many instances, successfully evade bears. Other than these few references, most of the literature portrayed both species of bears as scavengers of moose and other ungulates (Jonkel 1978).

Black Bear

Idaho. The first evidence that black bears were significant predators on ungulates was provided by Schlegel (1976) working on elk (*Cervus elaphus*) calves in Idaho. Although this study did not involve moose, it is relevant because his techniques were later used on moose and with similar results. Elk calf/cow ratios had declined to 13–28 calves/100 cows in the mid-1970s. Between 1973 and 1975 newborn calves were fitted with radio collars equipped with mortality sensors to determine causes of neonatal mortality. Total mortality of 53 bonded calves was 68 % (36) with predation by black bear accounting for 69 % (25) of the mortality between parturition and early July.

About 65 % of the black bear population was transplanted away from a study area in 1976 in an attempt to evaluate the effects of reduced bear density on calf survival (Schlegel unpubl. data). In 1977 and 1979 38 elk calves were collared to determine the effcet of the transplant on elk calf survival. Fifty percent (15) of the 30 bonded calves died, all from predation. Black bear predation accounted for 60 % (9) of the total mortalities. Thus, the bear transplant reduced bear predation on collared calves by about 36 %. Winter calf survival increased from 20 calves/100 cows in 1976 to 61 calves/100 cows in 1977 (op. cit.). Although some bears probably returned to the capture site fairly rapidly after being transplanted (for example see Beeman and Pelton 1976), it was clear that a temporary two-thirds reduction in the black bear population resulted in about a 200 % increase in calf survival as reflected by calf/cow ratios. Calf/cow ratios were also high during the second year (51/100) (Schlegel unpubl. data).

Predation between predator species may be at least partially compensatory. In the Idaho elk study other predator species were not manipulated and mountain lion predation on collared calves increased from 9 % to 17 %. However, the increase in lion predation did not prevent a significant increase in overall calf survival. Both wolves and brown bear were rare in this study area but mountain lions were relatively abundant. No attempt was made to maintain the bear population at the lower density.

Immigration and a high return of transplanted bears and resumption of heavy rates of predation were presumed to be the cause of the low calf/cow (27/100) ratios 3 years after initiation of the transplant. Return of the low ratios suggests that the bear population had recovered from the experimental removal. Schlegel (unpubl. data) demonstrated that at least in the short term, a temporary reduction in black bear numbers resulted in increased elk calf survival. Further, the first and second year's cohorts experienced relatively good survival throughout the remainder of each year and both became productive members of the adult population.

Kenai Peninsula, Alaska. The first indication that black bears were a significant predator of moose was provided by Franzmann and Peterson (1978). On the Kenai Peninsula where 3 potential predator species (black bear, brown bear, and wolves) exist, the overall mortality on 47 collared calves in 1977 and 1978 was 57 % with black bears accounting for 16 (59 %) of the total mortalities (27). Brown bears and wolves each killed 6 % of the collared calves and each were responsible for 11 % of the total mortalities. Black bear, brown bear and wolf densities were estimated at 189 ($\bar{x}$ computed from Schwartz et al. 1983), 12 (Schwartz unpubl. data), and 17 (Peterson 1982)/1 000 km^2, respectively. Moose densities were 750/1 000 km^2 resulting in 45 moose/wolf and 2.9 to 5.6 moose/black bear. Wolf, black bear and brown bear predation were considered additive sources of mortality (Franzmann pers. comm.).

Cumberland Delta, Saskatchewan. Black bears were implicated as a significant source of moose calf mortality in Saskatchewan when fall calf/cow ratios in a 90 km^2 study area increased from between 20 to 30 to 77 calves/100 cows following black bear removal in 1983 (E. Kowal pers. comm.). Calf/cow ratios outside of the bear removal area were significantly lower (38 calves/100 cows) than those in the removal area. Moose productivity at parturition was estimated at 120 calves/100 cows in 1981 (Kowal and Runge 1981). Although black bear densities were not documented prior to or following the experiment, it was believed that most bears were removed before the onset of calving. Wolves occurred in low numbers and brown bears were nonexistent in the study area. Thus similar to Schlegel's (unpubl. data) findings on elk, when black bears constitute a significant source of neonate mortality, large reductions in bear numbers can substantially increase moose calf survival rates.

Summary. Wilton (1983) recently summarized observations of black bears preying on ungulates in North America. He concluded that black bears should be considered an effective predator of ungulates throughout their range. We concur with this suggestion and suspect that future studies will illustrate that where black bears are the most numerous predator, they will also be the most significant neonate mortality factor.

Several investigators have mentioned,

based primarily on scat analyses, that black bears occasionally feed on adult moose. Consequently, it has been presumed that the bears were scavenging. However, it has been documented in several cases that black bears can and do prey on adult moose (Ballard and Miller unpubl. data). However, they are not considered significant predators on adult moose in North America.

Brown Bear

Nelchina Basin, Alaska. Brown bears were also not considered significant predators of moose in North America until newborn moose calves were radio-collared and intensively monitored. In the Nelchina Basin of southcentral Alaska, 55 % of 120 radio-collared calves died before 1 November with brown bears accounting for 79 % of the mortalities (Ballard et al. 1981). Ninety-four percent of all mortalities occurred prior to 19 July. Adult bears preyed upon both calf and adult moose an average of 1/11.7 and 1/43.7 bear-days, respectively (Ballard et al. 1987 a). Brown bears preyed heavily on calf moose until mid-July and then continued preying on adult moose and caribou but at reduced rates. Brown bear numbers were reduced in a 3 436 km^2 portion of the Nelchina study area in 1979. In spring and early summer 1979 a total of 47 brown bears were captured and transplanted 145 to 286 km from the original capture site. The 47 transplanted bears represented about 60 % of the bear population (Miller and Ballard 1982 a). Although 60 % of the radio-collared bears eventually returned (Miller and Ballard 1982 b), they were not present during the 6-week period following calf parturition when most mortality previously occurred; bears returned within an average of 58 days, (range 19–133 d). Calf survival from parturition to 6 months increased from 32 calves/100 cows (>12 months of age) in 1978 prior to the transplant to a record high of 52 calves/100 cows in 1979 (Ballard et al. 1980, 1981, 1982, Ballard and Miller 1987). A model of the moose population suggests that survival was even higher than that indicated by autumn calf/cow ratios which include an unknown proportion of sexually immature moose.

Historically there had been an inverse relationship between winter severity and subsequent spring calf moose productivity and/or survival in the moose population within the bear transplant area (Ballard et al. 1982, unpubl. data). The winter prior to the bear transplant had been relatively severe and calf/cow ratios were expected to be lower than normal. Although this same area had been part of a wolf reduction experiment earlier, wolf densities in the area ranged from 2.5 to 6/1 000 km^2 prior to removal. Brown bear densities prior to removal were estimated at 24/1 000 km^2 and black bears were uncommon (Miller and Ballard 1982 a). At the reported wolf densities, which were relatively low in comparison to other areas in North America, wolves did not kill significantly more moose calves in the absence of brown bear predation, i.e. decreased calf mortality from brown bears was not compensated by increased mortality from wolf predation. After 1979 both bear and wolf densities increased. Wolf densities increased from about 6/1 000 km^2 in autumn 1979 to 7.5/1 000 km^2 in autumn 1980 (Ballard et al. 1981 b, 1987 b). As expected, calf survival declined in subsequent years after the bear transplant. In the year following the transplant, calf survival was similar (31 calves/100 cows) to precontrol, but much lower than the previous year. By autumn 1981, however, calf survival and presumably bear populations had returned to precontrol levels: 30 calves/100 cows in both autumn 1981 and 1982.

Southern Yukon Territory. Brown bears have also been found to constitute a significant source of moose calf mortality in the southern Yukon Territory (Larsen and Gauthier 1987). In 1983, 87 % of 60 radio-collared calves and 15 calves of radio-collared adults died prior to 6 months of age; 91 % died by the end of the year. Brown bears accounted for 63 % of the calf deaths and wolves and black bears accounted for 26 % and 2 %, respectively. Similar to Alaska studies (Ballard et al. 1981 a), 93 % of all calf moose mortalities occurred prior to the end of July.

Moose were the most abundant (333/1 000 km^2) prey species in the Yukon study area. Sheep and caribou densities were estimated at 270 and 20/1 000 km^2, respectively (Larsen unpubl. data). Initial calf production was estimated at 115 calves/100 cows ($\geqslant$24 months of age), however, by early winter calf ratios had dropped to approximately 30/100 cows (Larsen and Gauthier 1987). Estimates of brown bear densities were not available but they were suspected to be similar to those of southcentral Alaska (Miller and Ballard 1982 b). Black bears were considered common but less abundant than brown bears. Wolf densities were estimated at about 13/1 000 km^2 (Hayes, unpubl. data). Predation was also an important adult moose mortality factor; 4 (12 %) of 33 adult radio-collared cows were killed by predators between May and 1 November.

Summary. In both the Alaskan and Yukon studies where brown bears have been found to be the most important predator of moose, other predators such as wolves and/or black bears have also been present. This suggests that brown bears are capable of competing with other predators for calf moose for at least 1–2 months following parturition and perhaps longer in some areas. Therefore, for at least 1/4 of the nondenning period bears can be considered efficient predators of moose.

Although brown bears have only been identified as significant predators of moose in 2 adjacent areas of North America, they are suspected to be major predators in several other areas of Alaska and Canada (unpubl. data). Densities of bears in these areas may be greater than those in areas where brown bears are not known to be significant predators, suggesting that predation on moose calves could be partially density dependent on densities of both bears and moose. However, even at relatively low moose densities it may be efficient for bears to prey on moose calves particularly if traditional calving areas are utilized. In such cases bear predation could still be a significant cause of neonate mortality. At moderate to high moose density, bears may actively hunt moose and could be a major factor contributing to a moose population decline by greatly reducing recruitment. An example of the latter is on the Alaska Peninsula where portions of the moose population have declined by 60 % since 1970 (Sellers and McNay unpubl. data). The decline is due to low recruitment as a result of suspected brown bear predation (Sellers and McNay unpubl. data). Moose densities in this area were estimated at 348/1 000 km^2, while bear densities were thought to range from 77 to 116 bears/1 000 km^2, a moose/bear ratio of between 3/1 and 5/1 (op. cit.).

Recent identification of bears as significant predators of moose in North America leads to speculation on whether such predation was occurring during earlier moose–bear studies, or if it is a recent phenomenon. We suggest that black and brown bears have always been effective predators on moose based upon the following: (1) The majority of bear food habit studies have been on analyses of opportunistically collected scats, which probably underrepresented food habits during spring and early summer seasons when bears are a primary predator of moose. (2) Since black bears frequently skin and evert hides of young cervids (Schlegel 1976, Franzmann et al. 1980), little if any identifiable material would be present in the scats of black bears feeding heavily on young cervids. Although brown bears do sometimes evert hides, about half of the carcasses observed in both the Nelchina Basin (Ballard et al. 1981 a) and the Yukon (Larsen 1987) possessed hide and hooves, suggesting that these are not preferred food items and thus bear scats may contain a low frequency of identifiable remains. An additional factor which also complicates identification of brown bears as predators is that they sometimes surplus kill (Kruuk 1972) calf moose, eating only the brains and viscera (Ballard unpubl. data). Scats comprised predominantly of flesh are diarrhetic and would decompose quickly. Also, many of these scats are deposited close to the consumption site and thus collection would have to be made in close proximity to the carcass. Therefore, it would not be surprising that ungulate food material would not appear frequently in scats. (3) When ungulate remains have been identified in bear scats, their importance has been underestimated due largely to speculation that the material represents carrion and also because animal remains based on volume data are greatly underestimated due to digestive reduction (Smith 1984). (4) Lastly, the significance of bear predation on calves would be underestimated from both telemetry studies and scat analyses if the programs were not conducted during the short (6–8 weeks) time period that calves are most vulnerable to predation.

Discussion

Studies conducted over the past decade indicate that predation by wolves, brown bear, and black bear, either singularly or in combination, can be a major source of mortality to moose. Gasaway et al. (1983) Ballard et al. (1987 b, unpubl. data), Schlegel (unpubl. data), and Kowal (unpubl. data) have demonstrated through predator removal programs that under certain conditions predation can exert substantial control and even limit population size. The significance of predation will depend on the combined effects of other factors (food, weather, hunting, disease, etc.) acting on a moose population and the abundance of alternate prey. Contrary to earlier views, it is now concluded that predation mortality is additive rather than com- predation constitutes a large source of Keith (1974) that in pristine ecosystems, predations constitutes a large source of noncompensatory mortality which at a minimum reduces prey density or may be regulatory.

Although most predation mortality may be additive, there is little evidence that predation by itself causes moose populations to permanently decline. All relatively long-term (>10 years) studies list combinations of severe winters, deteriorating range conditions, predation, or over hunting as the factors precipitating declines. Predation, however, is often identified as one of, if not *the* main factor which prevents a population from recovering from a decline. The inverse relationship of wolf numbers to deer, moose, and caribou numbers in Alaska and Canada (Skoog 1968, Bishop and Rausch 1974, Olson 1979, Bergerud 1978, Gasaway et al. 1983, and Ballard et al. 1987 b) is evidence of the impact wolves can exert on their prey. Such a relationship may exist between bears and moose, although extensive evidence is lacking.

The impact of predation may increase as prey numbers decrease, i.e. "anti-regulatory" control (Lidicker 1978). Predation can sustain a decline or maintain prey populations at low numbers for long periods, even though the initial cause of the decline may no longer be a major limiting factor. Gasaway et al. (1983) suggested that some predator-prey systems lack sensitive, fast acting feedback mechanisms which regulate predators relative to declining prey. Thus "the balance of nature" concept where fluctuations in predator and prey closely mimic one another does not necessarily apply to all predator–prey systems. Loose regulatory feedback systems have been demonstrated in recent studies on wolves and deer (Mech and Karns 1977) and on wolves and moose (Peterson and Page 1983). In those predator–prey systems, predator numbers did not decrease until approximately a decade after prey declines. Gasaway et al. (1983) documented a similar loose feedback response in a single predator-multiple prey system in Alaska. They speculated that the escape of prey from control by predators may be infrequent and short-lived and may be cyclic in nature. Whether these fluctuations are cyclic or not probably depends in part on the predator and prey densities, availability of alternate prey, and the type (obligate vs. facultative) and number of predators involved.

The dependency of an obligate carnivore such as the wolf on one or more ungulate species in winter and continued high dependency in summer has been well documented (Mech 1970, Peterson 1977, Fuller and Keith 1980, Ballard et al. 1987 b). In comparison, facultative carnivores like brown and black bears with a broader food base may prey on moose for relatively short periods in the spring, however, they probably do not rely on them year-round. Regulatory feedback systems involving those predators would likely be less well defined compared to systems involving wolves. Feedback mechanisms in multi-predator–multi-prey systems would likely be very complicated. Anti-regulatory control in these types of systems could extend beyond decades.

To maintain high sustainable moose harvests while allowing a wolf and/or a bear population to fluctuate in a natural fashion is impossible. Even in the simplest wolf–moose system whether wolves "regulate" or "control" (Keith 1974) moose numbers, there would be greatly reduced harvests of moose by humans in a naturally regulated predator–moose system, except during the short time period when the moose population was able to escape the restraints of wolf predation. For example, hunting could have been allowed to occur on Isle Royale in the late 1960s and more recently in the early 1980s (Peterson 1977, Peterson and Page 1983) when the moose population escaped from predation. In these cases where a moose population could be subjected to harvests, a moose manager would have to react quickly and harvest the additional increment. Conversely, when the moose population began to decline, the manager would have to react promptly by eliminating or reducing harvest to avert aggravating the decline through an overharvest. The other options that a manager has (Gasaway et al. 1983) are to accept dramatic natural fluctuations in prey numbers and wait for a more or less natural change in events, or to hasten the increase of prey by reducing predators. These authors concluded that reducing or eliminating human harvests will have little effect once predation levels are sufficient to cause a prey decline or to maintain prey at low densities. They recommend that harvest control is best used in conjunction with other remedial actions. We agree that predator reduction in conjunction with reduced harvest levels is the appropriate short-term management action if the objective is to increase the moose population. Long term solutions may include increased predator harvest by hunters and trappers supplemented with more intensive periodic reductions by management agencies. At low moose population levels, any human harvest would be additive mortality, contributing to a population decline. Even at relatively high moose population levels it is important that hunter kill be properly apportioned to each sex-age class in those moose populations subjected to heavy levels of bear and wolf predation; otherwise a manager could initiate a population decline (Van Ballenberghe and Dart 1982, Van Ballenberghe 1983).

The impact of wolf and/or bear predation on a moose population can only be accurately assessed if the magnitude and causes of mortalities to all cohorts in the moose population are determined over at least one annual cycle. In moose populations calves represent the largest single cohort at parturition and thus a large proportion of the overall population. If neonatal calf survival is low, the potential overall impact on the population is high, therefore, the predator(s) responsible for low survival of calves will likely represent the largest source of mortality on the entire population. Managers should concentrate their efforts on identifying the largest source of mortality and take appropriate action to reduce its effect on the population by the most efficient means available. For some moose populations it is conceivable that severe losses to adult moose, particularly in simple wolf–moose systems, could be the most important source of mortality.

Wolves will likely be the highest profile source of mortality of the 3 predator species since wolf kills are more visible, particularly during winter months when snow cover facilitates spotting kills. Because of the time of year and the relatively short time interval in which bears are effective predators on calves, their significance may not be recognized unless intensive studies are carried out. Recent advances in neonatal ungulate radio collar designs and telemetry systems have been crucial in enabling biologists to discover that bears were significant causes of mortality, rather than merely scavengers. If we assume from recent data that bears have always been an important source of neonatal ungulate mortality, it may explain the apparent failure of wolf, coyote, cougar and other control programs which were aimed at increasing the survival of not only moose but other ungulate neonates. In such cases biologists observing large calf or fawn losses occurring shortly after parturition in conjunction with frequent sightings of known predator species would have assumed a cause and effect relationship. Predator control aimed at the most common predator species would have been initiated and an effort made to measure pre and post control young/adult ratios. Lack of response in the ratios would have been observed and the biologist would have concluded that some other limiting factor had replaced predation. In reality the wrong predator species may have been controlled or it may have simply been a secondary source of mortality on the neonates or perhaps only a significant source of adult mortality. In either case measurement of young/adult ratios would prove misleading and changes in adult mortality would probably be too small for a manager to measure with the techniques available for short-term studies.

Most moose managers will rarely have to deal with only one species of predator. Most moose ranges in North America will contain at least 2 of the 3 predator species. Where wolves and bears are significant sources of mortality, both must be reduced if benefits to the moose population in the shortest time period are desired. However, that decision would depend on the time period defined by management objectives. Further investigation into the possibility of compensation among and within predator species is needed. For example, if both bears and wolves were important predators the reduction of bear numbers may temporarily increase calf survival. However, high predation losses to wolves either in summer and/or winter could negate any increases. Also, if not all bears are removed from an area, the remaining bears may compensate by killing more moose calves/bear as was partially the case in southcentral Alaska (Ballard et al. 1980 b, Ballard and Miller 1987) or by having bears which had not previously killed moose take advantage of the available prey. The following should be considered before embarking on a removal program.

Results of experimental bear transplants discussed earlier (Schlegel unpubl. data, Kowal unpubl. data, Ballard et al. 1982, Ballard and Miller 1987) suggest that managers could anticipate a large increase in calf moose survival if bear numbers could be drastically (60 %) reduced. Whether such increases would occur beyond the short term is not yet known, but increases of the magnitude reported probably could not be sustained indefinitely as the habitat carrying capacity would eventually be exceeded. Permanent reduction of a bear population by 60 % could have serious consequences on the viability of the bear population. Whether smaller reductions in bear numbers would increase calf survival proportionately is unknown. Transplanting bears could be an effective temporary tool for improving moose calf survival in small areas, but it is expensive and probably impractical for large areas. Also, if the transplanted bears are preying on moose, movement of these bears into other areas, unless widely dispersed, could impact moose survival in the receiving areas. This would only be a consideration if maintenance of the receiving moose population was also a management objective.

If certain sex-age classes of bears preyed disproportionately on moose, then perhaps managers could manipulate hunting regulations to favor harvest of these particular groups. For brown bears, however, the limited data suggest that all adult brown bears and family groups with the exception of sows with first-year cubs prey on moose (Ballard et al. 1981 a, 1987 a). If small decreases in bear numbers result in increased moose numbers, the manager usually only has a vague idea of bear densities and only a vague idea of the effect of his harvest program on them; therefore, he would have a poor understanding of when and how long to initiate such a program or whether it was successful.

Some evidence suggest that harvesting certain sex-age classes of bears, particularly large boars, may actually stimulate the reproductive and/or survival rate of the bear population (Young and Ruff 1982). Therefore, a manager could conceivably aggravate the problem further by increasing the numbers of bears through trophy sport hunting programs. The harvest of nontrophy bears and/or sows with cubs through sport hunting will prove difficult and perhaps impractical due to socio-political factors. Further investigation is needed into the effects of gradually lowering bear numbers and its subsequent effects on moose and bears. Beginning in 1984 the Yukon Department of Renewable Resources embarked on a sport hunting program directed at reducing brown bear numbers in selected management units to improve moose calf survival. Results from that study may provide guidelines to managers coping with bear predation problems.

Bear populations may be slow to recover from intentional reduction programs due to their relatively low fecundity rates (Murie 1944, Craighead et al. 1969, Pearson 1975). Wolves on the other hand have relatively high reproductive rates, can withstand heavy harvest, and can rebound from reduction programs within 1 or 2 breeding seasons (Ballard et al. 1981 b, 1987 b and Keith 1983). The slow reproductive potential of bears might be considered advantageous because short-term reduction programs would have long-term benefits to moose. However, caution should be exercised given the potential for overharvest and long-term consequences for bear populations. In comparison, wolf reduction programs may have short-term (1–3 years) benefits to moose and usually require annual removal which is expensive (Ballard and Stephenson 1982).

International concern for the status of these predators must also be considered. Brown bear have been eradicated from a large portion of their former range in North America, are now on the International Union for the Conservation of Nature endangered species list, and are protected in many North American jurisdictions. Programs designed to reduce bear populations to enhance moose populations will cause alarm, but it must be remembered that the loss of brown bears in North America resulted from the loss of large tracts of habitat coupled with uncontrolled harvest. Bears like any other wildlife species, can be properly managed so long as adequate habitat remains. Well designed bear reduction programs should not result in permanently reduced bear populations. Fortunately, most northern ecosystems are not attractive for agriculture or forestry and consequently do not face the same development threats as southern areas. Wolves, like brown bear, have been reduced substantially from their former range and are considered endangered in half of North America. However, so long as suitable habitat and prey remains available, with protection, wolves can recover quickly from overharvest due to their high reproductive rates. Black bear have adapted well to agricultural practices and occur in much of their historical range in North America.

The decision whether to remove predators, which species to remove, and at what level, will depend on management objectives of individual programs. Presumably, management programs stem from broader management policies which are developed through public participation. If the management objective is to stimulate moose population growth to ensure an annual harvest, then predator control is inevitable in most areas where predators are naturally regulated. It follows that the choice of predators and the level of removal would depend on the desired moose population level and the time period within which that level is to be achieved. Based on differences in vulnerability and reproductive capability, wolf control programs should have a wider acceptance by both professionals and the public because of less likelihood of long-term consequences.

In southcentral Alaska where brown bears are the main cause of calf mortality and wolves are an important source of adult mortality, a 50 % annual reduction in wolf numbers reduced adult and calf winter mortality sufficiently to allow the moose population to slowly increase (Ballard et al. 1980 b, 1981 b, 1982). Simulation population modeling has been an important tool in understanding the potential impacts of predator–prey relationships on moose management. Moose population modeling suggested that the population in southcentral Alaska would have continued to decline had wolf numbers not been reduced. Conversely, after several years of reduced wolf numbers, modeling suggested that the wolf population could be allowed to increase to precontrol levels without causing a moose population decline (Ballard et al. unpubl. data). This was in spite of wolf predation only being a secondary mortality factor.

Managers attempting to manipulate moose populations to provide sustainable human harvests could do so simply by eliminating all predators and replacing predation mortality with human harvests. Such a scenario could produce large numbers of moose for harvest, particularly if combined at the same time with a habitat manipulation program to increase range carrying capacity. However, such a system would not eliminate natural catastrophes or alleviate all problems. We have assumed that in no case would a wildlife manager prefer to maximize moose harvests by permanently eradicating predators, however, with increasing human populations' managers will be forced to set populations goals for both predators and their prey. Under such pressure he undoubtedly will need an entire array of information to ensure perpetuation of all species in other than park settings.

Despite the biological justification for predator control, the directions of a management program will, in most cases, be based on socio-political factors. The manager should be fully aware that scientific facts and/or proper experimental design may have little bearing on whether he will be allowed to initiate remedial actions.

Recent predator control programs have forced management agencies to reevaluate and defend policies to the general public which outline the use of wildlife and define priority species. These are philosophical as opposed to biological issues and are often the basis of controversy surrounding predator control programs. Most biologists now accept the fact that predation can limit at least some moose populations. Slight shifts in adult and calf survival rates can drastically change rates of growth in moose populations and significantly alter predator–prey relationships (Keith 1974, Van Ballenberghe 1983, Peek and Eastman 1983, Gasaway et al. 1983, Ballard et al. 1987 b).

Leopold (1933) initially proposed the concept of ungulate–predator ratios as a useful tool for evaluating the importance of predation. Both Mech (1966) and Pimlott (1967) established ungulate/wolf ratios at which wolf predation would regulate or not regulate ungulate populations. More recently, Gasaway et al. (1983) summarized current thought concerning simple moose/wolf ratios as follows: (1) at less than 20 moose/wolf, predation is great enough to regulate the moose population, (2) at 20–30 moose/wolf, predation may regulate a moose population but this depends on the combined effects of other mortality factors, and (3) at greater than 30 moose/wolf, predation can be significant but may not necessarily limit population growth. They suggested that such ratios would be useful in assessing simple moose–wolf relationships and that these relationships would be the clearest to interpret at or near their extremes. Ratios, however, only allow the manager to assess the potential level of predation as they do not reflect vulnerability, prey age structure, or actual predation rates. When additional predators and other ungulate species are present, the utility of such ratios becomes questionable without additional data, which is both costly and time consuming for a manager to collect. For example, in southcentral Alaska the initial moose/wolf ratio exceeded 50/1 and, therefore, wolf predation would not have been considered an important source of mortality based upon a simple ratio assessment (Ballard et al. 1987 b). However, as discussed earlier, a reduction in wolf densities allowed the moose population to slowly increase.

Ultimately, habitat (food) dictates at least the potential for an area to support moose. Traditionally, biologists explained ungulate population dynamics through direct habitat relationships. Ungulate population declines and low calf/cow ratios were often attributed to declining range conditions. Bergerud (1974, 1978) and Gasaway et al. (1983) have challenged this interpretation, suggesting that vegetation–ungulate relationships are confounded by predation. Misjudging the predation–ungulate relationship in some areas has resulted in inappropriate management of ungulates and predators. In these cases biologists have patiently sat back and waited for the range to recover, only to become frustrated when a moose population failed to respond. Most likely, high neonatal mortality, rather than declines in productivity, were probably the real cause for the depressed population.

In terms of calf production low rates of natality in moose are rare. The lowest pregnancy and twinning rates for moose in North America were 60 % (Franzmann 1981) and 2 % (Pimlott 1959), respectively, while the highest rates were 93 % (Rausch and Bratlie 1965) and 70 % (Franzmann and Schwartz 1985), respectively. Most moose populations tend to be on the higher end of this scale. Even with the lower rates, biologists observing fall calf/cow ratios of 10 to 20/100 have reason to suspect high neonatal mortality. This does not, however, diminish the importance of higher natality rates, nearly all of which have been attributed to better nutrition (Pimlott 1959, Markgren 1969, Franzmann and Schwartz 1985). The response of a moose population to high levels of mortality is quite different at 160 calves/100 cows versus 75 calves/100cows at parturition. Therefore, managers should continually strive to maintain optimum moose forage if maximum or high yields are to be obtained with or without high levels of bear and/or wolf predation.

Although the vegetation–moose relationship primarily influences the predator–prey relationship through productivity and high overwinter survival of prey, it may also influence the magnitude of predator losses by altering habitat use by predators. Schwartz and Franzmann (1980) initially suggested that black bear killed proportionally more newborn moose calves in spruce forests versus more open habitat types. In the spruce forest, which was preferred black bear habitat on the Kenai Peninsula, Alaska, black bears killed 42 % of 24 radio-collared moose calves while in earlier successional stages, which were not preferred bear habitat, black bears killed 0 % of 8 marked calves. These preliminary findings suggested that managers would not only increase moose productivity but may reduce early neonatal losses by manipulating habitat to favor early vegetation successional stages where black bears were the primary predator. Since that time additional moose calf mortality studies in spruce and more open habitats have not completely supported this hypothesis (Franzmann et al. 1984). However, remains of moose appeared more often in black bear scats collected in spring and early summer in spruce forests (53 %) versus more open habitats (38 %) (Smith 1984). The problem warrants further investigation.

Where moose habitat is deteriorating, predators can greatly alter the level of human harvest which a slowly declining moose population can withstand. A conceptual model of this process is depicted in Fig. 1, which we believe illustrates the situation in southcentral Alaska and southern Yukon where natural fires have been suppressed for the past 30–40 years. Under these circumstances moose populations begin declining in response to a combination of factors such as severe winters, overhunting, and decreased carrying capacity. What had been nonregulating levels of predation now becomes more important and may cause a decline or prevent population growth. Predation at a point becomes the primary limiting factor even though the carrying capacity of the habitat has declined at the same time. The moose population's ability to sustain human harvest also declines even though ultimately habitat carrying capacity would have caused a reduction in harvest, but not to as low a level nor at such a fast rate as with heavy levels of predation. Although a number of limiting factors, including food, can initiate a decline in

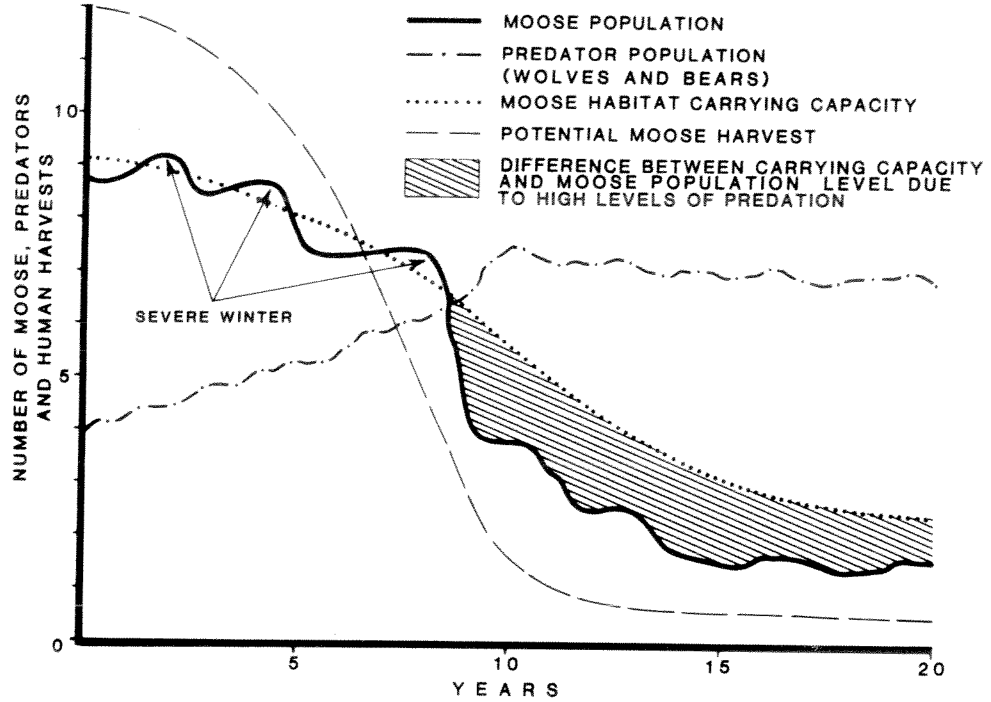

Fig. 1. Conceptual model of relationships between moose population levels (in thousands), habitat carrying capacity, and human harvest levels (in hundreds) in relation to naturally regulated predator populations in North America.

moose numbers, no recent studies have documented a sufficient increase in productivity and survival as a result of increased forage after the decline to compensate for predation (Gasaway et al. 1983).

Wildlife managers attempting to manage moose for high production and harvest levels in the long term should have an active habitat manipulation program. Unfortunately, in North America most wildlife managers do not have land management authority and are usually relegated to setting seasons, methods and means of harvest, and bag limits. In such cases managers must convince the public and land managers of the importance of maintaining optimum habitat for moose if high productivity and resulting large harvests are to be sustained.

Summary and Conclusions

Predation by one or more of the three major predators (wolves, brown bears, black bears) in North America may constitute a major source of mortality to a moose population. The magnitude of which may be great enough to regulate, or even limit the size of the moose population. Predation becomes increasingly important when it occurs in concert with other sources of mortality such as hunting, severe winter, and deteriorating habitat. Once a moose population has been reduced, predation may then represent the major factor limiting its growth. If left alone moose population growth may be limited by predation for decades or longer in most natural situations. Eventually the result could be low numbers of moose, which may or may not be followed by low numbers of predators (bears have alternate food sources and consequently may not decline like wolf populations) for long periods of time.

The primary objective of wildlife management has been to manipulate wildlife populations to achieve specified goals. Today, the primary goal of most management agencies is to maintain wildlife populations at, or near, the carrying capacity of the range to ensure maximum return to consumptive and nonconsumptive users. In light of the growing desire by nonconsumptive users that natural fluctuations be allowed to occur, and the growing competition between predators and man for the same resource, some objectives may need to be redefined. If wildlife management's primary objective is to be limited to monitoring natural fluctuations and allowing hunting only during periods of positive growth, we would predict long periods with low moose numbers. As well, the need for studies to determine interrelationships between wildlife species would not exist.

We believe that management objectives in most jurisdictions will continue to focus on maximizing biological potential, however, we are now faced with the challenge of manipulating more than one component of the system. Wildlife managers will find that it is difficult, if not impossible, to maintain both predator and prey species at optimum levels in the same system. Many jurisdictions do not possess either the funds or manpower to accurately determine the status of the wildlife populations they are attempting to manage. In the past, prey populations have sometimes been overharvested and predator populations underharvested. It is clear that a more holistic approach is required. This is not to suggest that whole scale predator reduction programs be implemented, but we should continue to learn how predators, prey, and man interact by designing and implementing well-thought-out management programs, and then carefully documenting the results. One approach is to manipulate predators and simply monitor the prey response. This has the advantage of being able to demonstrate whether or not a prey population would increase in the absence of predators. Another approach is to identify the cause and magnitude of mortality as a justification for predator removal. Ultimately, however, predators would have to be removed to demonstrate that the prey population could increase in their absence. The latter approach is generally more acceptable to the public.

Obviously, managers attempting to manipulate moose populations to provide maximum sustainable harvests could do so simply by eliminating all predators and replacing predation mortality with human harvest. Such a scenario would produce large numbers of moose harvest, particularly if combined with habitat manipulation to maintain a high carrying capacity. In some situations predator control programs could be so successful at stimulating moose population growth that managers might be faced with a different sort of problem, i.e. too many moose and not enough hunters to control their numbers. This is currently the problem in Sweden where few natural predators remain.

We believe that permanent eradication of predators is not a justified management objective, but that significant reduction of predators in areas where moose are considered priority is a reasonable objective. To ensure viable predator populations in the future, areas should be identified where predators are given priority.

Managers, with increasing human demands, will be forced to set population goals for both predators and their prey. Before such programs can be successfully implemented, managers will need a better understanding of the relationships among and between predator and prey species. The full spectrum of implications of predator–prey relationships to moose managers remains undefined, owing to the dynamic and diverse nature of predator–prey systems. The need for more long-term studies, with a holistic approach, in a variety of systems is clearly required before all of the ramifications are known.

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