THE DECLINE OF MOOSE IN ONTARIO - A DIFFERENT VIEW

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Abstract

The argument is made that the decline in the moose population in some sections of Ontario has resulted from the additive effects of wolf predation and hunting. It is further argued that moose populations coexisting with wolves cannot be increased by habitat management that aims solely at improving food and shelter resources. The carrying capacity for moose when wolves are present is limited by the lack of space to successfully interact with wolves. We need to manage space to provide moose with increased advantages in avoiding predators.

The moose (Alces alces) population in Northwestern and Northeastern Ontario has declined since the 1960's by percentages ranging from 20 - 75 percent; populations in southern Ontario have not declined (Anonymous 1979). The annual harvest has varied around a mean of 13,000 animals since 1960 whereas the total hunters have increased from 34,107 in 1960 to 90,714 in 1974. Hunter success has declined from 33 percent in 1960 to 15 percent in 1974 and was still 15 percent in 1979 (Ministry records, Wildlife Branch, Toronto). Not only is the yield extremely low but expectations for the future are minimal. The strategic land use plan for the Northwest Region has set a moose target of 70,126 moose in 265,229 km^2 (92,744 mi^2) by the year 2000 and a harvest rate of 11 percent for 7,500 animals per year (Anonymous 1980). The Ministry states: ..."evidence strongly suggests that in most of Northern Ontario, excessive hunting is the major factor reducing the moose herd and keeping the population below that which the range can support." (Anonymous 1979). I present a different view in this paper.

I counted the moose and wolves (Canis lupus) in Pukaskwa National Park (1,878 km^2), Ontario in 1975 and 1976 (Bergerud 1975, 1976) and my associate in these counts, B. Wyett, continued the annual counts in 1977, 1978 and 1979 (Wyett and Keesey 1977, 1978, 1979). The final paper on these results is in press (Bergerud et al. 1981). The dynamics of this population should be a test of the hunting decline hypothesis since the annual harvest in Pukaskwa Park was probably less than 25 animals per annum averaged over the five years.

The results of these censuses showed a moose population that either remained stable or more likely declined (Fig. 1). If we consider that the intrinsic rate-of-increase (r_m) should be at least 0.35 the population could have increased to over 2,000 animals by 1979. In cause and effect argument, the supposed cause of decline, hunting, was mostly absent, while the supposed effect, a stable or declining population, was present. Thus the supposed cause is not necessary. Clearly this population was limited even though hunting was extremely low.

The reproductive rate of moose in this area of Ontario was high. An examination of 36 pregnant females showed 20 with twin embryos (Bergerud et al. 1981). This is the highest twinning percentage in the literature (cf. Rolley and Keith 1980).

During the five years we had no evidence of winter starvation. Again, the percentage fat in bone marrow from 10 animals dying in late winter during the worst winter (1978-79) averaged 83 percent; an exceptionally high figure (cf. Franzman and Arneson 1976, Peterson 1977).

The lack of herd growth was due to low recruitment. The percentage of calves in January and February (C/C+Y+A) was 11 percent (n = 304). In all years

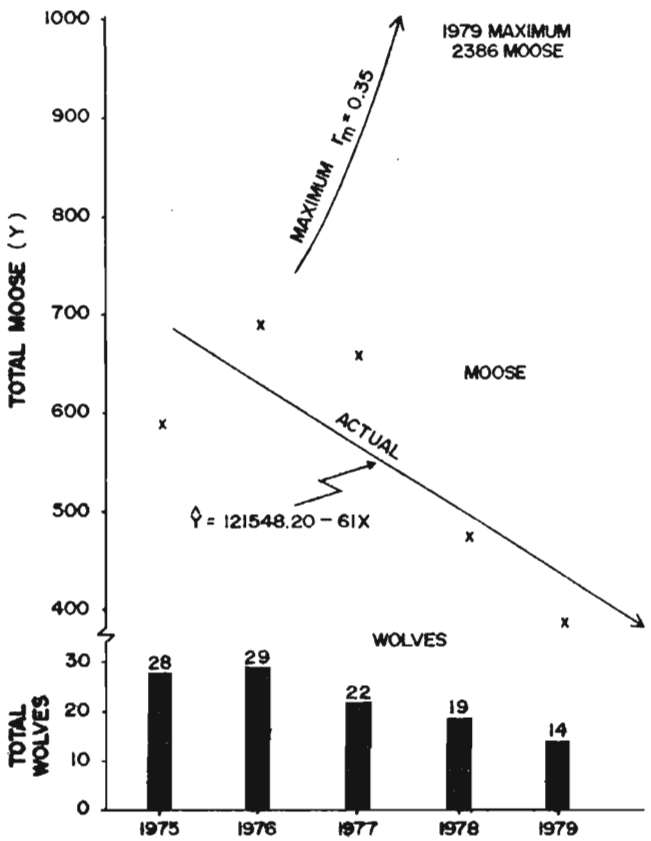

Figure 1. The census results of moose and wolves from 1975 to 1979. The wolf population did not decline as drastically as indicated - more wolves were seen outside the Park in later years.

combined the percentage was only 6 percent in 1978 (n = 115). Since calves are highly vulnerable to wolf predation in their first winter of life (Peterson 1977) it is likely that the final yearling recruitment was possibly as low as 8 percent or less. If adult mortality is 13 percent (Peterson 1977) and hunting mortality was 2-3 percent the population may have declined at an annual rate of about 8 percent.

In both Minnesota and British Columbia low percentages of moose calves were related to wolf numbers. Karns (1972) found 9-15 percent moose calves in northeastern Minnesota where wolves were common and 30-35 in northwestern Minnesota where wolves were rare. In British Columbia I found a significant difference ($P < 0.001$) in calf percentages between high and low wolf densities (Bergerud 1977):

High Wolf Density (1 wolf/80-150 km^2)	7% moose calves (n = 401)
Low Wolf Density (1 wolf/150+ km^2)	20% moose calves (n = 188)

The density of wolves at Pukaskwa (1/65 km^2) was much greater than British Columbia yet the prey base in the Park is much less diversified than in British Columbia. It would be expected that a population of 29 wolves would take 122 short yearlings and adults during the winter season (0.6 moose/wolf/month, Mech 1966) of which over 30 percent could be calves (Peterson 1977). The low recruitment at Pukaskwa was due to selective predation by wolves.

I think the Isle Royale study exemplifies a general principle that can be applied to the Ontario decline. Over an 18-year period the mean recruitment added to the Isle Royale herd was 13 percent and the mean annual natural mortality of adults was 13 percent (Peterson 1977). In this simple moose-wolf-beaver (Castor canadensis) system there was no surplus for hunting - if

the herd had been hunted it would have declined. I hypothesize that in systems where wolves are undisturbed and common they frequently crop the potential annual surplus, hence populations should frequently decline at rates approaching the additive removal taken by hunters.

Note that the populations in Ontario that declined are in the north and west whereas the populations in the south have not declined. It is in the south where the urban centers are located. But wolf populations in the south have declined because of deer (Odocoileus virginianus) declines (Kolenosky 1978). The harvest of moose in Sweden clearly indicates populations do not necessarily decline with extreme harvests in the absence of predation. Hunting alone as the Ministry argues, has probably not caused the decline in Ontario.

Also the Ministry argues that predation is not involved in the decline: ..."It is doubtful that predation has resulted in the decline in moose populations, but wolves and man certainly compete for a finite number of moose." (Anonymous 1979). This seems like a nonsequitur. If we compete, then it follows that if man has contributed to the decline, so has the wolf - in areas where wolves are common. The wolf's contribution is to reduce the recruitment (percentage of calves) to a point where there is hardly any surplus left for man's harvest. Then man comes along and his harvest results in a decline. The two harvests are additive and together too much.

Another argument sometimes voiced by biologists is that man can outcompete the wolves and thus "get away" with our harvest. Wolf students now argue that wolf numbers are adjusted to the prey biomass (Haber et al. 1976, VanBallenberghe 1975, Collins and Mech 1978). Thus the sequence as I see it is that with undisturbed wolves this predation results in a moose life equation of $m_x = q_x$. It we harvest the moose we reduce the prey biomass.

The wolves must then readjust their numbers through proximate controls (Collins and Mech 1978); yet when their numbers again stabilize they will still limit the moose population by balancing $m_x = q_x$. The harvests of man are like a staircase down in numbers. Of course, overhunting can ultimately result in so few prey that wolves must switch prey, move, or decline.

A panacea frequently offered to increase moose in Ontario is to improve the habitat: ..."improved habitat, in combination with close regulation of the harvest can ensure that moose populations increase to numbers approaching the carrying capacity" (Anonymous 1979). But this view overlooks the mechanics of how such a population could actually increase. The stable density of any moose population represents the equilibrium point where recruitment equals adult deaths (Fig. 2). For a stable herd to increase either the reproductive rate must be increased and/or the death rate reduced (Fig. 2).

Now how will more food and shelter increase either of these parameters? For the moose near Pukaskwa I doubt if it is possible to improve the twinning rate (54%). No one has provided evidence of a lack of productivity for moose in Ontario. Even if productivity was improved wolves might simply take more calves. On Isle Royale when the twinning rates were high (1958-64) the percentage of calves in winter was 14.4 (n = 5) and when twinning rates were low (1966-73) the calf percentage averaged 13.4 percent (Peterson 1977). More food and shelter will not reduce the death rate, since there are no moose reported starving in Ontario (Cumming 1974). More food and shelter will not permit moose populations in areas with high densities of wolves to increase.

Further, biologists that want to increase moose populations coexisting with wolves, should consider the "paradox of enrichment" principle (Rosenzweig 1971). May (1976:53) explains the paradox: ..."If the environmental carrying capacity for the prey, K, is much larger than the equilibrium prey density

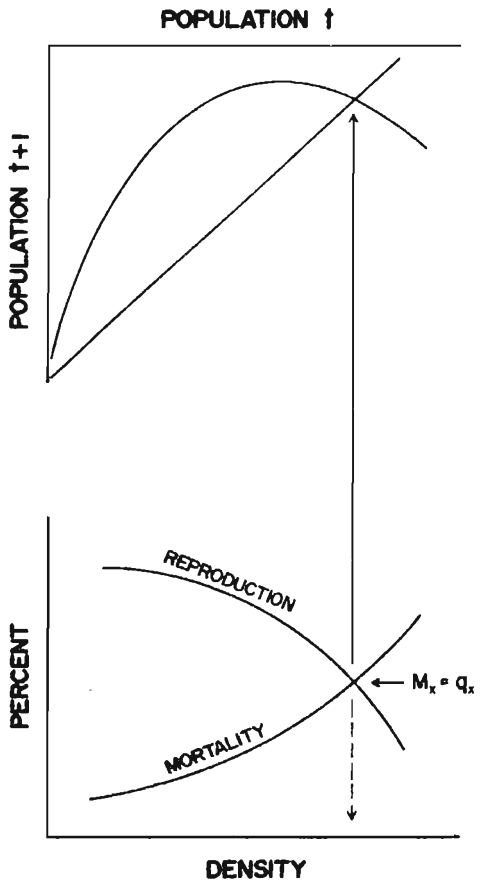

Figure 2. A stable population is one in which recruitment (m_x) and mortality (q_m) are in equilibrium (mostly from Holling 1973).

in the presence of predators, the stabilizing elements contributed to the dynamics by the prey density dependence will be relatively weak. This underlies the "paradox of enrichment" whereby increasing K makes for lowered stability and eventually for stable limit cycle behaviour." The Isle Royale studies show that the food dependent K is much higher than that equilibrium resultant from predation (Keith 1974, Caughley 1977, Bergerud et al. 1981); one can also think of the Kenai where high moose densities existed before the reinvasion of wolves (Bailey 1978). However, even in the presence of wolves the moose on Isle Royale are affected partially by density-dependent effects resultant from their interaction with food and weather (Peterson 1977). Thus the preconditions for the paradox do exist for moose. Moose biologists could possibly unstabilize moose populations and cause declines by enriching food resources, in their attempt to increase the density-dependent K value for moose.

The recent decline of deer (Odocoileus heminonus) on Vancouver Island (Hebert et al. 1980) provides another challenge to the traditional view that we should manage winter habitats for food and shelter requirements. Biologists on Vancouver Island in the 1960's and 1970's were successful in having suitable winter cover left by timber companies along streams and other locales where it was deemed critical that cover be left for winter yards. Hebert (pers. comm.) predicts the deer will concentrate in the areas in hard winters.

Such concentrations of the deer in the residual stands would make them excessively vulnerable to predation - the wolves would know where to hunt. Small isolated timber patches then should act as traps (Hebert pers. comm.).

D. Euler (1981) has argued at this conference that a great deal is known on the winter habitat needs of moose and that the Ministry's habitat guidelines

to local biologists and foresters are an adequate place to start. These guidelines (Anonymous 1981) seem to repeat the Vancouver Island experience. They emphasize winter habitats, and stress food, shelter, and edge. But moose in Ontario do not commonly starve; nor is it likely that low quality winter food is a major factor in reproduction (cf. Klein 1970). The animals don't starve but they are killed throughout the winter by wolves. The emphasis in the management of winter habitats must be on reducing predation risk and not on food and shelter per se. To follow those guidelines in my view will likely result in a further decline of moose in Ontario.

The habitat management of the future should not be directed at providing more food and shelter but in mitigating the wolf-moose interaction in favor of moose. One can think of many avenues of approach. One is to increase the area of search for wolves. At present logging results in the converse, it concentrates moose in the remaining forest stands (Fig. 3). Logging also provides avenues of access (logging roads) that increase the speed and effectiveness of search for wolves. Another specific is to provide suitable habitat where snow cover is more likely to be favorable to moose in interactions with its predators. Residual stands should be left in areas far removed from traditional wolf travel routes. Yet another approach is to manage habitats so that cover and food are left in escape habitats, islands in rivers, etc. When we concentrate moose, this effectively increases their access to predation. When we improve the mobility and effectiveness of the predator, we intrude into the zero sum game of life for moose. Not only do we favor the predator in its adaptive race with its prey, but we crop the prey as well, and fail to redress the balance by effectively harvesting the predator. No wonder moose populations decline when man enters the natural equation.

We have to change our concept of carrying capacity. In an ecosystem with effective predators the moose population is not limited by the food

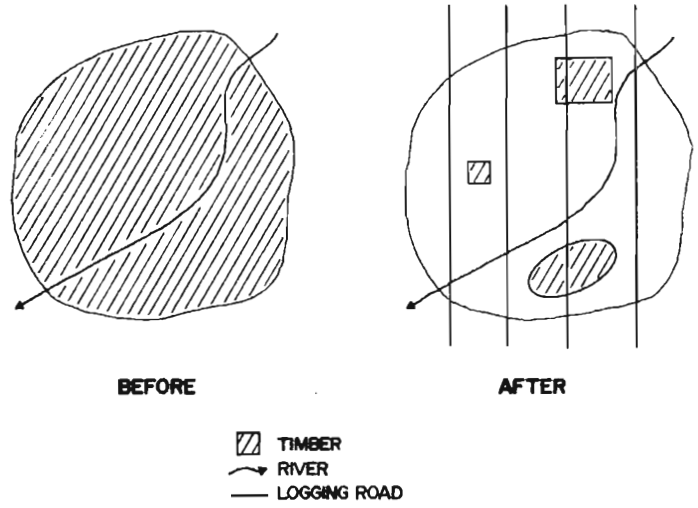

Figure 3. Before logging (left) wolves travel the river in the winter. The vulnerability of moose may vary between winters depending on snow cover and their concentration at low elevations. After logging (right) the moose are concentrated in the remaining tree cover - the wolves know where to search. Also, wolves can travel logging roads in the non-snow seasons, which will increase their rate and effectiveness of search. Also, they will travel the roads in winter if plowed or compacted by snow machines. Logging increases the heterogeneity of the environment improving the opportunity for wolves to locate moose.

and shelter requisites. It is limited by space (cf. Hilborn 1975). It requires more space for moose to effectively interact with their predators, so that $m_x = q_x$ and the prey persists, than the space required to find sufficient life requirements for satisfactory reproduction and longevity. In the future we must manage habitats to minimize the space necessary for successful moose interactions with their natural predators. Future research will have to be directed at learning how wolves use the habitat to find moose before and after logging, and how moose use different kinds of habitats to avoid predation. Only when we know a lot more about hunting and escape strategies of predator and prey can we begin to manage the habitat.

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