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DOES WOLF PREDATION ALONE LIMIT THE MOOSE POPULATION IN PUKASKWA PARK?: A COMMENT

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Abstract: We re-evaluated information presented in Bergerud et al. (1983) and suggest that no firm conclusions can be drawn with respect to factors limiting moose populations at Pukaskwa National Park (PNP), Ontario, and that predation by wolves alone does not limit moose at Isle Royale, Michigan. We comment on 3 aspects of their paper: methods, other limiting factors, and their model. Three alternative hypotheses are presented based on our discussion of effects of weather, food, cohort vulnerability, and other sources of mortality.

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Bergerud et al. (1983) reported that predation by wolves (*Canis lupus*) limited the moose (*Alces alces*) population in PNP, Ontario. Hypotheses they considered as explanations for moose population regulation were reproduction, starvation, egress, and predation. In extending their views to wolves and moose on Isle Royale, Michigan, Bergerud et al. (1983) excluded the possibility that the moose's forage base or other factors influenced wolf predation effects. We argue that the available data for PNP are inadequate to reveal moose population characteristics and present alternate hypotheses explaining the difference in moose density between PNP and Isle Royale.

ADEQUACY OF THE PUKASKWA DATA

We believe the methods used did not generate data of sufficient quality or quantity to support the conclusions. Our review of the original unpublished reports, prepared for Parks Canada by A. T. Bergerud and W. Wyett (Superintendent, PNP, Bag Serv. 5, Heron Bay, Ont., Can.), suggested several shortcomings in the data collection procedures. Aerial census of moose can best be used as an indicator of trends over time (Gasaway et al. 1983) and therefore every effort should be made to eliminate biases among years. Bergerud et al. (1983) used several different survey methods (different plot sizes, no stratification in 1976, 1.5% of the area surveyed in 1975, ≥ 2 methods of determining aggregate size, and different no. plots), thereby reducing comparability among years. Although methods were

fairly constant over the latter 3 surveys, only 4-5% of the park was censused and no plots were flown in the low stratum. Their survey method does not permit estimation of variance but Bergerud et al. (1983) assumed homogeneity of variance in extrapolating moose density from the high stratum to the low stratum, using a ratio of track abundance in each stratum from transects. We suggest that it is not possible to infer a statistically valid trend from these data.

Most of the significance of their regression line (Bergerud et al. 1983:980) comes from the low value (387 animals) obtained in the 1979 census. This value is probably an underestimate that should have been expected because there was about 150 cm of snow on the ground during the survey. Snow depths > 75 cm restrict moose movement (Kelsall and Prescott 1971), making the animals difficult to find in heavy cover, thereby lowering aerial estimates.

Bergerud et al. (1983) reported only 14 wolves in PNP in 1979, but this is misleading as another 11 were near the area. Given that several pack sizes were estimated from tracks, there was either little or no change from previous years.

REVIEW OF HYPOTHESES

We believe Bergerud et al. (1983) prematurely rejected alternate hypotheses explaining population regulation of moose in PNP and the higher moose density at Isle Royale. We agree that reproduction is not a likely explanation in view of extensive data on moose reproduction elsewhere. Low recruitment among moose generally results from poor survival, although large variations in yearling reproduction and twinning rates have been linked to nutritional plane (Markgren 1969). Data on twinning rates of

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moose were gathered by Bergerud et al. (1983) from a nearby hunted population and not from the Pukaskwa herd.

Starvation does not adequately address the influence of moose nutrition on demography. Bergerud et al. (1983) dismissed moose forage effects with the simple statement that moose were not dying of starvation. Clearly, more subtle influences of the availability of moose forage on reproduction, growth, and survival are possible, including several inferred from studies at Isle Royale (Peterson 1977, Peterson et al. 1982). We argue that forage availability may help explain different moose densities at PNP and Isle Royale. Moose in both areas do not exist in "similar boreal forest habitats" (Bergerud et al. 1983:985). In fact, the southwestern section of Isle Royale is of the Great Lakes-Saint Lawrence forest type (Rowe 1972), characterized by sugar maple (*Acer saccharum*) and yellow birch (*Betula alleghaniensis*) communities developed on deep glacial tills. This area supports more moose than the northeastern section of the Island, which is boreal-type habitat more similar to PNP. Mature and semi-mature stands of jack pine (*Pinus banksiana*) and jack pine-black spruce (*Picea mariana*), characteristic of poor soils with low nutrient availability, occupy 15–20% of PNP and $\leq 1\%$ of Isle Royale. Other differences such as shallower soils with greater bedrock exposure at PNP should also be pointed out. A poorer forage base at PNP could result in a lower rate of increase for moose by affecting growth and reproduction.

Egress remains a viable hypothesis because a dispersal sink (Tamarin 1980) exists outside the Park, in the forms of early successional habitat (logging), hunting mortality, and accidents. Bergerud et al. (1983) acknowledged that yearling moose tend to disperse, and we suggest that it is significant that all 3 moose killed by trains and 2 of 3 moose dying of unknown causes (Bergerud et al. 1983:table 3) adjacent to the Park were yearlings. There would be net egress even if moose were as apt to enter PNP as leave it. Although there is little evidence that dispersal regulates moose populations, lack of egress has been considered the primary reason for the high moose density on Isle Royale (Peterson 1977, Allen 1979, Owen-Smith 1983).

Predation is a viable hypothesis explaining low recruitment and population regulation in moose populations preyed upon by wolves. Peterson and Page (1983) pointed out such effects

on Isle Royale. Bergerud et al. (1983) reported wolf:moose ratios for Isle Royale as 1:30–80. However, using more recent data, the mean ratio between 1969 and 1984 was 1:29 (Peterson 1977) and is similar to that reported for PNP. Therefore, we suggest that numerical abundance of predator and prey is not an adequate explanation of prey equilibrium levels.

The remaining difference between PNP and Isle Royale raised by Bergerud et al. (1983) was the alleged greater "space requirement" of moose in PNP, but they provided no definition. For example, "space requirement" could refer to escape terrain or escape opportunity. Water provides a major defense against wolves in summer (Stephens and Peterson 1984). If escape opportunity is a primary determinant of moose density, we might expect that the higher number of lakes, islands, and amount of shoreline on the northeast half of Isle Royale would lead to higher moose densities there compared to the southwest half. However, the opposite is true.

ALTERNATE CONSIDERATIONS

We argue that the Bergerud et al. (1983) predation hypothesis is simple yet inaccurate because of several critical weaknesses that should be considered. First, they dismissed black bear (*Ursus americanus*) predation completely. Bears are important predators of moose calves (Franzmann et al. 1980, Messier and Crête 1985). Black bears are common in PNP and were a nuisance problem during the first year of operation (R. Hamilton, PNP, pers. commun.). Second, they ignored possible synergism between food and predation. Differences in the moose's forage base are thought to underlie the contrasting trajectories of the Isle Royale moose population in the early 1970's and the early 1980's, when wolf:moose ratios were virtually identical (Peterson et al. 1984). Third, Bergerud et al. (1983) suggested that moose decreased during their study, yet they provided no explanation. From their overall conclusions, one would infer that wolf numbers, or at least wolf predation rate, must have increased. However, predation rates were not measured and wolf numbers showed no consistent trend during their study. Fourth, it was suggested that the rather small mean pack size of wolves in PNP may reflect "... the secondary dispersion of wolves to increase searching effectiveness" (Bergerud et al. 1983:986). An alternative explanation, not considered by these authors, is that the small pack size reflected pri-

mary dispersal of wolves resulting from lack of food (food for wolves means vulnerable moose, not just any moose). The latter explanation is consistent with general theories of pack-size regulation in wolves (Zimen 1976, Packard and Mech 1980).

Fifth, the proposed Bergerud et al. (1983) model ignores the effects of weather on moose populations. In support of their hypothesis, Bergerud et al. (1983) reanalyzed calf frequency among wolf kills at Isle Royale and attempted to correlate these with a snow index. Because no correlation was found for calves in the wolf kill from the same winter or previous winter, they seemed to imply that there is no evidence for snow depth affecting calf vulnerability to wolves or cohort viability through an in utero effect. However, absence of evidence in a selected data set is not absence of a more general relationship. Peterson and Allen (1974) demonstrated an increased calf kill by wolves when snow depth exceeded 76 cm at the time of the kill. The snow index used by Bergerud et al. (1983) was a monthly maximum from November through April and wolf-kill data were collected during only 33% of that period. Also, their snow index did not consider crusted snow conditions, which could have a great influence on predation rates in some years.

There is a significant inverse relationship between calf size and winter severity prior to birth (Peterson et al. 1982). The link between calf vulnerability to wolves and calf size has not been established, but we believe it is significant that when calf size is small there is a high occurrence of calves in winter kills by wolves and the converse when calves are large (Peterson and Page 1983).

Much of the fluctuation in numbers of moose may be explained by winter severity. Mech et al. (1987) showed that cumulative winter effect was a major determinant of changes in moose numbers at Isle Royale. Thompson (1980) was able to demonstrate a direct relationship between number of calves and winter severity (snow depth and crust conditions) and number of yearlings and winter severity in Ontario. The effects of winter severity could be mediated by several factors, including starvation, predation, or poor neo-natal survivorship.

Our understanding of wolf-prey interaction will not advance if we deny the possibility of multifactorial hypotheses. These need not be so complex as to be untestable. For example, Mes-

sier and Crête (1985) suggested a model including predation and food effects on moose numbers. A specific, short-term test of a hypothesis explaining fluctuations of Isle Royale wolves and moose was proposed by Peterson et al. (1984). Bergerud et al. (1983) suggested that in the absence of wolves, food availability has no impact on altering vulnerability to predation. But given no limitations by food or weather, will not the influence of predation be greatly different? We urge Bergerud et al. (1983) to more adequately consider the evidence in support of this assertion.

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PREDATION IN THE DYNAMICS OF MOOSE POPULATIONS: A REPLY

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Abstract: The moose (*Alces alces*) population in Pukaskwa National Park, Ontario varied from 0.4 to 0.2 moose/km² from 1975 to 1984 and was limited by wolf (*Canis lupus*) predation. Other noninsular moose populations coexisting with wolves, both hunted and unhunted, are also limited at densities of $\leq 0.4/\text{km}^2$ when recruitment (R) equals natural mortality (M_n) at a ratio of about 30 moose/wolf. When moose inhabit ranges without wolves, densities commonly reached 2-3 moose/km² and food supplies become the limiting factor.

J. WILDL. MANAGE. 52(3):559-564

Bergerud et al. (1983) censused moose and wolves in Pukaskwa National Park from 1975 to 1979 and tested 4 hypotheses relating to factors potentially limiting the increase of the herd. There were <25 moose/wolf and the wolves killed sufficient moose to prevent an increase. We concluded that wolf predation was limiting the increase of the herd rather than food supplies, weather, or egress.

Since our study (Bergerud et al. 1983), both Gasaway et al. (1983) and Messier and Crête (1985) reported moose/wolf ratios of <30 moose/wolf in areas where wolf predation had stabilized moose numbers at lower densities than those dictated by food supplies. Fuller and Keith (1980) also reported that predation was limiting moose in an ecosystem with 28 moose/wolf. Gasaway et al. (1983) proposed that wolves would limit numbers when prey/predator ratios were <30 moose/wolf. Keith (1983) showed that wolves killed a mean of 8.5 moose/wolf/year and that this kill rate would stabilize moose numbers in unhunted populations with about 30 moose/wolf and a potential finite rate of increase about 1.28.

Thompson and Peterson (1988) rebutted our

paper (Bergerud et al. 1983) and have argued that we should consider multifactorial hypotheses. Note that it is their terminology that stresses wolf predation alone. We used the term "limiting factor" as defined by Leopold (1933:39): "one [factor] often far outweighs all the others in the extent to which it pulls down the unimpeded increase rate." A limiting factor so defined does not deny that other factors (e.g., bear predation or hunting) can contribute to the lack of increase. Although Thompson and Peterson (1988) argue that we should adopt a multifactorial approach, they stress the role of a single factor, weather, in the dynamics of moose populations they have studied (Thompson 1980, Mech et al. 1987).

CENSUS METHODS

Thompson and Peterson (1988) have questioned the reliability of our aerial census methods. They used different aerial methods to measure population growth but their procedures are less reliable than ours. They have generally relied on fixed-wing aircraft (Peterson 1977, Thompson 1979); we used helicopters in all 5 years. Also, they did not incorporate into their