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Wolf Predation on Moose: Do Wolves Control Moose Population Densities?

by Christie A. McCloud

The structure of ecological communities is based, in part, on the relationship between predators and prey. Many believe wolves may be highly effective in controlling overpopulated ungulate populations. Several studies have documented ungulate population control by wolves. They suggest that as a concentrated food source increases, wolf populations will have decreased mortality and increased natality (Messier, 1985), and as wolves increase in number, more prey will be taken. This will, in turn, decrease the size of prey populations (Smith, 1980). Some authors disagree with this idea of regulatory predation. They suggest that wolf predation does not regulate ungulate populations, but that predator-induced mortality of ungulates is compensatory, that is based on removal of individuals that would have died of other causes anyway. Research on interactions between wolves and moose indicates that there is still controversy over the possible role of wolf predation as a regulatory factor. Do wolves control their ungulate prey populations or is the mortality they induce only compensatory?

Most of the field data obtained on regulatory versus compensatory mortality has been inconclusive. This is often due to poor techniques in data collecting and to the difficulty in controlling other influential factors such as predation by species other than wolves, food availability for ungulates, and the effects of weather. In the present paper, I review the evidence for and against the regulatory hypothesis.

SUPPORT FOR THE REGULATORY PREDATION HYPOTHESIS

In 1983, Bergurud et al. estimated that wolves killed more moose than the number of calves born in Ontario, Canada. They reported a 1:25 wolf-moose ratio, which is a lower ratio than that reported in most comparable studies (Bergurud et al., 1983). Bergurud et al. also claimed that black bears were uncommon in the area, and the mortality rate in moose could not be influenced by these other predators. Bergurud et al.s data supports regulatory mortality for moose population control. Other researchers became critical of Bergurud et al.s work because small numbers of kills observed annually, small areas were observed, observations were made only after snowfall, and survey techniques were varied from year to year.

Additional support for the regulatory hypothesis comes from Gasaway et al.(1983) Their data showed increases in moose populations in interior Alaska after reductions were made in the wolf populations during the 1950s. This moose population peaked in the 1960s, and began a dramatic decrease from 1965 to 1976 when wolf predation accounted for 13-34% of calf mortality. Again, in 1976, the wolf population was reduced by wildlife management and the rate of moose mortality decreased. Population increases in caribou as wolf populations decreased were also important because caribou make up a significant percentage of the wolf diet (Ballard et al., 1987). Wolf-moose ratios were estimated at <1:30, a ratio similar to that observed by Bergurud et al. (1983).

Although these studies seem to support the hypothesis that wolves are the main limiting factor in moose populations, it is important to consider alternative hypotheses. Much of the research supporting wolf regulation introduces confounds that, in many studies, were not explored thoroughly. For example, in 1984, Gasaway et al. continued to support the wolf regulatory hypothesis but pointed out other possible limiting factors that should be taken into account, including moose food supply, hunting, and winter severity .

SUPPORT FOR THE COMPENSATORY MORTALITY HYPOTHESIS

Thompson and Peterson (1988) pointed out a number of problems with studies proposing that wolf predation on moose is regulatory. Thompson and Peterson (1988) published research on two areas of wolf populations: Pukaskwa National Park in Ontario,Canada and Isle Royale in Michigan. In Pukaskwa National Park, research was inconclusive due to the small amount of data collected. On Isle Royale, however, important factors influencing the moose populations were documented. Different techniques from Bergurud et al. (1983) and other previous wolf-moose population studies were used in an attempt to improve reliability. Aerial surveys were found to be the best way of observing trends over a period of years. The aerial surveys used in the Thompson and Peterson research were controlled with more consistency than surveys in previous studies. Thompson and Peterson also suggested other problems with previous research, particularly the lack of consideration of confounds in Bergurud et al. (1983). Thompson and Peterson introduced new influential factors such as starvation rates of moose, general health of moose, availability of food sources for moose, black bear predation on moose, and the effects of severe weather. Thompson and Peterson also criticize the small amount of area observed by Bergurud et al. (1983).

Speculation on Pukaskwa National Park populations dealt with black bear abundance as one major impact on moose populations (Thompson and Peterson, 1988). Severe winter conditions with deep snow are also suggested as increasing predation and decreasing the size of moose calves. This idea was also based on previous research showing that winter severity caused greater predation, more starvation in moose, and decreased survival of moose calves in Isle Royale (Mech, 1987).

As for data collected on Isle Royale in 1988, analysis suggested that the availability of food sources for moose were a main determinant of the moose densities (Thompson and Peterson, 1988). It seems that there may be some correlation with food availability and winter severity that needs further exploration.

Other data collected in South Central Alaska provides additional insight (Ballard et al., 1987). The data supported some control of moose populations by wolves. Wolf diets consisted of approximately 70% moose over the period of the study. However, during most of the year, wolves preyed upon moose calves in proportion to their percentage in the population. During the 1970s, the wolf-moose ratios suggested wolves as important limiting factors while during the early 1980s, it seemed that wolves were not preventing the moose population from growing. For the most part, Ballard et al. could not obtain conclusive data for evaluating the wolf-moose ratios. A more important aspect of the study, perhaps, is the idea of wolf pack size as a factor for moose population numbers. Ballard et al. found that as wolf pack size increased, the number of moose killed per wolf decreased. This is an interesting limiting factor on moose populations. In essence, it asserts that where wolves are located in large packs, the consumption of moose would be less per wolf than in an area with small wolf packs. It is certainly a possibility that could benefit from further research.

DISCUSSION

No definitive conclusions can be made concerning regulatory or compensatory predation on moose populations based on the research done to date. However, there is a strong suggestion that wolf predation may cause primarily compensatory mortality in moose and other ungulate populations. Several environmental factors need further exploration in order to piece together the complex relationship between wolf and moose populations. The factors introduced by Thompson and Peterson (1988), such as starvation rates in moose, bear predation, and effects of severe weather, seem to provide a promising area for continuing research.

Studies with other prey populations show that declines in prey populations are often due to malnutrition and starvation even in the presence of natural predators. In 1984, Keith et al. found decreases in bone marrow fat of snowshoe hares. They suggested that this malnutrition in prey could eventually lead to the higher predation rates on snowshoe hares. Also, in Minnesota, studies with white-tailed deer populations showed a 62% mortality rate in fawns due mostly to starvation and disease (Fuller, 1989). Wolf predation in this study accounted for only 4% of total fawn mortality.

Many studies have also asserted that bears are a major cause of moose and other ungulate mortalities. Thompson and Peterson found an abundance of black bears in Pukaskwa National

Park (1988), and grizzly bears are relatively abundant predators in Alaska as well (Ballard et al., 1983). In 1991, Ballard et al. found that 73% of the mortality in moose was caused by brown bears. Other more recent studies have also suggested that bears are a major limiting factor in moose populations (Schwartz and Fransmann, 1991; Gasaway et al., 1992).

Winter severity can be an important factor in regulating moose populations. Many studies documented snow depth and winter conditions; these records show a correlation between increased winter severity and increased mortality (Mech et al., 1987; Thompson and Peterson, 1988; Fuller, 1989). This correlation makes sense if one follows a sequence of events from a severe winter to decreased food availability to smaller moose calves born to higher predation rates on these weakened calves. Overall, severe winters cause decreases in nutritional status of moose and other ungulates that could cause them to be more susceptible to predation. Effects of winter severity also directs attention to differences in densities at different times of the year. Seasonal change may play a role in natural fluctuations in moose population densities. It could be beneficial to document these fluctuations by season to observe if trends exist and if they are consistent.

The inconsistency in the research leads me to conclude that wolves are not the primary cause of moose population fluctuations. There are too many environmental components that contribute to greater predation on moose and other ungulates. There also seems to be a need for research that collects data on comparable variables with comparable techniques so that the observations represent specific, reliable effects of wolf predation.

Because wolves and moose have coexisted for some time, it is unlikely that wolf predation alone causes moose populations to diminish. Further research in this area may benefit from a greater emphasis on factors such as effects of winter severity, general health of moose populations, and influences of pack size on moose densities, rather than actual predation rates. Ratios give only a general trend in population densities rather than the causes for these ratios. Research on moose populations existing without wolf predation may also clarify the effects of other environmental factors controlling moose populations. In conclusion, there is much work to be done in the future to determine the extent to which wolf predation on moose is regulatory or compensatory.

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