

EFFECTS OF COMBINED PREDATION BY BROWN BEARS AND GRAY WOLVES ON MOOSE POPULATION DYNAMICS; WHAT MORE DO WE NEED TO KNOW?

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The Swedish Environmental Protection Agency has asked the Scandinavian Brown Bear Research Project to give a summary of the present knowledge of the effect that large carnivores have on the moose population, now that wolves are becoming established within the brown bear's distribution area in Sweden. We were also asked to identify areas where our present knowledge should be improved.

The new Swedish moose management system requires information about predation, both from wolves and bears, but also their combined effect. This is a complicated area of research, because it is important to understand the effects of predation by each predator separately, any synergistic effects of predation, and interactions, such as one predator causing the other to kill more or fewer prey. In addition, we should know how often we should expect that these species actually overlap enough to effect a given moose population. This overlap can occur at two scales; habitat overlap and range overlap. The Scandinavian Brown Bear Research Project (SBP) and the Scandinavian Wolf Project (Skandulv) have conducted studies of several of these questions already and also have ongoing studies. We will discuss these subjects separately first and focus on identifying areas where our present knowledge should be improved.

Effects of wolf predation on moose

Skandulv has prioritized studies of wolf predation on moose and has published several scientific papers based on the results of these studies (e.g., Sand et al. 2005, 2006, 2008, Eriksen et al. 2008). These studies have documented a lower per capita demographic impact of wolf predation on moose populations in Scandinavia than in North America, perhaps due to lower wolf density relative to moose density, smaller pack size, lower proportion of adult moose in the wolves' diet, and differences in hunting behavior in Scandinavia (Gervasi et al. 2012).

Effects of brown bear predation on moose

Studies in Dalarna showed similar individual predation rates by adult bears on moose calves during periods of high and low ratios of bear density to moose densities and studies in Norrbotten showed similar rates. These rates were similar to that reported from North America (Swenson et al. 2007, Kindberg et al. 2012, Rauset et al. 2012,). Individual bear predation rates on adult moose were very low in Dalarna and somewhat higher in Norrbotten, but still lower than has generally been reported from North America (Berger et al. 2001, Kindberg et al. 2012, Dahle et al. 2013).

Habitat overlap between wolves and bears

A study in Hedmark, southeastern Norway, showed that, although bears and wolves both selected forested habitats, with >80% distributional overlap, bears preferred less rugged and higher elevation terrain and their kill sites were in more forested habitats closer to forest edges compared with wolves (May et al. 2008). Both species occurred at low densities in this study area.

Implications for management

Several studies from North America have implicated large carnivore predation as an important factor in the demography of moose populations (Gasaway et al. 1992, Boertje et al. 1996, Testa 2004), although there is disagreement about this conclusion (Boutin 1992, National Research Council 1997). However, it is evident from the short summaries given above, that Scandinavian moose managers should not base their management on results of predation studies from North America alone. Modeling results from Scandinavia have shown that wolves, and especially bears, exert a smaller demographic effect on moose populations than hunters, because hunters take a higher percentage of adult moose with a high reproductive value (Gervasi et al. 2012). Nevertheless, both wolf and bear predation is largely additive to human harvest and other mortality causes (Swenson et al. 1999, Nilsen and Solberg 2006, Swenson et al. 2007). This means that changes in moose hunting management are necessary in order to accommodate wolf mortality when wolves colonize an area that previously did not have wolves. Nilsen et al. (2005) have reported on the options available to managers of moose populations to deal with the presence of wolf mortality. Jonzén et al. (2013) extended this work, by modeling the effects of wolf and bear predation on the harvest of moose. These results have been popularized and published in Swedish to be more accessible to Swedish managers (Sand et al 2011a, b). Information is also available on a website, including an interactive model that managers can use to make informed decisions regarding moose harvest with varying densities of wolves and/or bears (<http://www.slu.se/algforvaltning>). The software “Älgfrode”, widely used in Swedish moose management to calculate harvest, also includes effects of predation by bears and/or wolves.

Areas requiring improved knowledge and proposals

As is evident from the short summary above, there is already a considerable amount of knowledge about the effects that wolf and bear predation has on moose population dynamics, and the ability of moose populations to sustain hunter harvest with and without this predation. However, our knowledge is best for single-predator species systems and our understanding of multiple predator systems in Scandinavia is based on modeling exercises. These modeling studies confirmed the complex nature of predator-prey interactions in large terrestrial mammals and showed that different carnivores preying on the same prey species can exert a dramatically different demographic impact, even in the same ecological context, as a direct consequence of their predation patterns. Therefore, the most important lack of knowledge today is; how do wolves and bears really interact and prey on a moose population in an area of sympatry?

Here are several questions that we consider relevant to answer in this regard and we feel that the most reasonable approach to answering this question is to study it in two phases; 1) a less

intensive phase, documenting patterns of distribution and moose densities and calf production and behavioral relations between bears and wolves in the area of sympatry, and 2), if the studies in the first phase suggest important synergistic effects due to predation by both bears and wolves, an intensive study of bear and wolf predation on moose population dynamics, using GPS telemetry, in the area of sympatry.

Phase 1

1) How much will the distribution of bears and wolves overlap? Both the wolf and the bear populations have been increasing and expanding towards each other, and now there is an area of overlap. However, policy goals will result in a stable wolf population in the future and perhaps a lower bear population. Given this new and more static situation, will wolves continue to establish new territories within the distribution area for bears, or will they prefer to establish territories in areas without bears? This is an important question to answer, because the answer will allow us to predict how much of the moose's distribution area will be impacted by two large predators in the future.

2) When wolves and bears occur sympatricly, how much do they influence each other's predation rates? When two sympatric species of large carnivores, a specialist and a generalist, share the same prey, their combined effects on the prey population may be different than expected (Andrén et al. 2011, Mattisson et al. 2001a, b). Thus, we must be cautious when transferring expectations from modeling or theory to a new system. It is important to document whether cleptoparasitism by wolves and/or bears can influence the overall predation rates of the other species. If so, it is important to estimate the extent of the changed predation rates. Such a study would involve visiting sites where wolves or bears have killed moose (from GPS clusters) and use cameras to determine if the other species utilizes the kill, forcing one species to make more kills.

3) Does the regional variation in bear density, wolf density, and combined bear and wolf density correlate with moose density or calf-cow ratios in the autumn? Although this is just a proposed correlational study, and many other potentially relevant explanatory factors would have to be included, a Sweden-wide analysis of known wolf density, Björnobs (Kindberg et al. 2009, and Älgobs data could indicate if the combined predation of these two predators was having a synergistic effect on moose densities and/or calf recruitment.

Phase 2

4) If the results of studies 1-3 suggest that the combined predation by wolves and bears is a significant problem for moose harvest management, a field study should be conducted. Such a study would be based on radiocollared moose, bears and wolves in their area of sympatry and should focus on a) kill rates of calves and adult moose by following different categories of GPS-marked bears and wolves using clusters of positions (Sand et al. 2005, Rauset et al. 2012) and b) the effect of predation on moose population size by combining censuses of moose (pellet counts in co-operation with Svenska Jägareförbundet with the recent estimate of the bear population in Dalarna and Gävleborg (Kindberg & Swenson 2013). The results should be compared with previous results from single-predator systems to estimate the added effect of having both predator species.

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