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Moose *Alces alces* hunting in Finland - an ecological risk analysis

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The moose *Alces alces* population in Finland has been managed for sustained harvest since 1970 by regulating annual hunting quotas. However, against all expectations the population size declined in the 1990s. An ecological risk analysis approach was used to build a growth model with annual harvest for the moose population. In the model there is stochasticity in the parameters representing population dynamics. We shall address: 1) whether the population decline could be due to a mismatch between harvest and anticipated population growth rate, and 2) to what extent hunting the moose population down to a much lower target size succeeds. A central element in this is the assumption that the estimate of the pre-hunting population size errs. First, the probability of a population decline due to hunting increases from values close to 0% up to 100% in a very narrow range (15-25%) of harvest rates. Even with high birth rates the risk of a population decline was substantial when the hunting rate exceeded 25% for cows and 37.5% for calves and bulls. The 1974-1994 moose harvest rate was, on average, ca 45% of the population size in autumn. The high rate suggests that the harvest might have been too intense in that period to keep the population stable. Second, we set the target to reduce the moose population drastically (to say 50% of the existing population size). Assuming that the estimates of the population size may err, our analysis shows that the achieved population size after the severe harvest is far below the size we aimed at.

Key words: Alces alces, Finland, harvesting, management, moose, risk analysis

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One way to find out how the size and structure of a population will change in future falls into the domain of ecological risk analysis (Burgman, Ferson & Akcakaya 1993). Within this frame the relevant population parameters (e.g. birth rate and death rate) can be assumed to be probabilities of those events and simulation techniques can be used to anticipate how the target population may change in time under various scenarios (Klejnen & van Groenendaal 1992). Predictions of ecological risk analysis models are not exact, but they give us the means to estimate the future state of the population when managed according to various strategies (Pooch & Wall 1993). Thus, ecological risk analysis is a useful tool when managing game animal populations. It helps to define the consequences of various hunting scenarios on changes in population size and in its future dynamics (Burgman et al. 1993).

Here we shall apply the toolbox of ecological risk analysis to assess how the Finnish moose *Alces alces* population should be harvested. This is a broad topic and we shall narrow our scope down to evaluate how intensive annual harvest rates can be for the moose population to remain stable without population declines. Using the same tools we shall also evaluate to what extent managers will succeed if they set a target in one season to reduce the moose population to 50% of its present size. The risk analysis ingredient here is that we assume that the estimates of the present population size may err in an unknown way. Thus, our contribution adds to the literature in which ecological risk analysis is used to address harvesting strategies in Scandinavian game management (Kokko, Lindström & Ranta 1997, Kokko, Pöysä, Lindström & Ranta 1998, Kokko, Helle, Lindström, Ranta, Sipilä & Courchamp 1999).

Size, age structure and sex ratio in the moose population has been managed in Finland since the beginning of the 1970s by selective hunting (Markgren 1974, Nygrén & Pesonen 1993). During 1970-1980 the winter population as well as the harvest increased almost exponentially, but in the 1990s the population size declined unexpectedly (Lehtonen 1998). At that time moose hunting was intensive all over Finland. Moose is an economically very important game species in Finland, and the hunting policy is based on regional licences issued by the Finnish Ministry of Agriculture and Forestry. The number of local licences is based on estimates of previous population sizes and the productivity of populations in the particular region. The population estimates are provided by hunters, who make their assessments based on observations of moose during the hunting season and just after the annual harvest (e.g. Nygrén 1984, Nygrén & Pesonen 1993).

We first estimate the risk of population decline in the Finnish moose population due to hunting. For this purpose we developed a population model for moose with an annual harvest rate. By altering the harvest rate we score the probability that the moose population will decline due to hunting during a 10-year period. Thus, with the help of virtual hunting, we seek a sustainable harvest rate policy for moose in Finland.

Two aspects need to be taken into account when deciding on the proper size for the moose population. Moose is not only an economically important game animal, which should be maintained as numerously as possible, but it also causes damage to young forest stands of pine *Pinus sylvestris* and birch *Betula pubescens* (e.g. Sweanor & Sandegren 1989, Andrén & Angelstam 1993, Heikkilä & Härkönen 1993), and is a traffic hazard. In the last decade, the compensation to forest owners for the damage caused by moose amounts to ca 1.7 million EUR per year. If the moose population increases sharply, the damage and thus the compensation will also increase. The number of moose/car crashes is also likely to increase as the moose population increases.

There are clear benefits to gain from moose hunting. This prompts managers to keep moose populations as large as possible without allowing the moose to overexploit their food resources. On the other hand, moose-caused forest damage and traffic accidents prompt managers to reduce populations to a level where moose numbers are low enough for the damages they cause to be negligible. These contrasting considerations prompt managers to keep the moose population size at the level where the benefits gained from moose hunting exceed the costs. If the moose population grows too large in some years, the pressure to increase harvest will certainly be intense enough to limit possible harmful damage by moose to a minimum.

Against this background our second aim was to create a scenario, in which the population has grown so large that in the next hunting season harvesting will be very intensive in order to reduce moose numbers to, say, an agreed level of 50% of the existing population size. Because hunting quotas are based on population size estimates, we studied what happens if the intensive hunting is based on inaccurate estimates of moose population size as well as on erring estimates of population growth.

Material and methods

Sustainable moose hunting?

The Finnish Game and Fisheries Research Institute has kept moose hunting statistics for the past 25 years. For this period data are available on regional moose population sizes from 15 game management districts in Finland; and data from 12 game management districts covering the years 1974-1995 are presented in Figure 1. The population size estimates are based on hunter observations of moose during the hunting period in autumn and on snow track censuses in winter. The game management district-specific numbers of killed animals are taken from the annual hunting statistics. An analysis of covariance indicates that there are no differences in hunting rates among the different game management districts (ANCOVA: $F_{10,216} = 1.36$, $P = 0.20$). The data thus show that the average harvest rate, represented by the slope of the regression line (see Fig. 1), over the past 20 years has been approximately 45% of the moose population size in autumn before the opening of the hunting season. This rate represents an extremely high hunting pressure.

In what follows, we shall develop a population model for moose and use it to assess the harvest rate that a moose population can tolerate without declining in size. We constructed an age-structured population model to trace the development of a closed moose

Figure 1. Number of animals killed and the population size in autumn (just before the opening of the hunting season) during 1974-1995. The mean annual hunting rate is 45% of the population size in autumn. The 12 different symbols each represent a game management district in Finland. The common regression line describing the relationship between the population size and the number of animals killed is inserted, and its slope gives the long-term average probability for a moose to be killed during the hunting season.

population. The model was built with demographic stochasticity: calving rate, mortality, and hunting mortality were taken as probabilities for every individual in the corresponding age (calves, yearlings or adults) or sex group. Because of these stochastic elements, the simulations were replicated 100 times and the outcome indicates the quasi probability that the population size declined due to hunting pressure.

Our model sets the population density at 45 animals/100 km^2. The recommendation by the Finnish Ministry of Agriculture and Forestry for the population density is 20-50 individuals/100 km^2. The sequence of events in the simulation model is: In the beginning of the year we check each individual from each age and sex group to see if they have survived the winter. In spring each adult female has a probability of giving birth to a calf of 0.7-1, which is approximately the real calving rate of the Finnish moose population. We assumed that equal numbers of female and male calves were born. In Scandinavia, this ratio is very near to 1:1 (Hirvonen, Danell, Lehtilä, Niemelä & Wallin 1994). We kept track of the numbers of calves, cows and bulls. The maturation of calves into adult individuals took two years (Sæther & Heim 1993, Sæther & Haagenrud 1985, Sand & Cederlund 1996). In autumn, during the hunting season, each individual (even the calves) has a stage-specific probability of dying as a result of hunting. Surviving individuals continue to the next year. The time-window of each simulation run was 10 years, after which the initial and final population sizes were compared.

In the harvest we had two different hunting strategies: (i) both sexes and all age-classes were hunted equally or (ii) bulls and calves were harvested 1.5 times harder than cows. The latter is more realistic, because during the last 20 years Finnish hunting policy has favoured the harvesting of calves (Nygrén & Pesonen 1993, Nygrén, Pesonen, Tykkyläinen & Wallén 1999). The hunting mortality of cows in the model ranged within 0.1-0.35 of the population size in autumn just before the opening of the hunting season. Similarly, in the unequal harvest scheme the hunting mortality of bulls and calves varied within 0.15-0.525. The non-hunting mortality (numbers of moose killed by predators or poachers, winter starvation or in traffic accidents) in Finland is considered very low compared to the hunting mortality. Usually, with low predation pressure the non-hunting mortality of adult moose is low (e.g. Albright & Keith 1987, Fryxell, Mercer & Gellately 1988, Bangs, Bailey & Portner 1989). Thus the non-hunting mortality (equal for all individuals) in the model was set as either 0.01 or 0.05 of the population size just after the hunting season.

Inaccurate population estimates

Our task now is to study the impact of inaccurate population size estimates on management of moose in Finland. We used the model developed above to calculate the change in population size between winter and autumn. The change is due to birth of calves in spring. The scenario is as follows: There is an estimate of the population size after the hunting season as well as an estimate of the number of new-born calves. Using these data the managers can derive an estimate of what the moose population size would be just before the next hunting season. The annual number of hunting licenses sold by the authorities is based on these estimates for each game management district. We wanted to explore what would happen if the estimates of population size and female fecundity rate both were incorrect, and managers still allowed the moose population to be intensively harvested using, without bias, the inaccurate estimates as if they were precise.

Considering the wrong estimate of population size: In this study we took a moose population of 10,000 individuals as the actual, but too dense winter population. In our scenario the population structure, i.e. the number of females, males and calves, was taken to match the Finnish moose population data. However, we created frequency distributions of the winter population size estimates. These biased population estimates were taken to fluctuate between 8,000 and 12,000 individuals. As nothing is known of the error term in the esti-

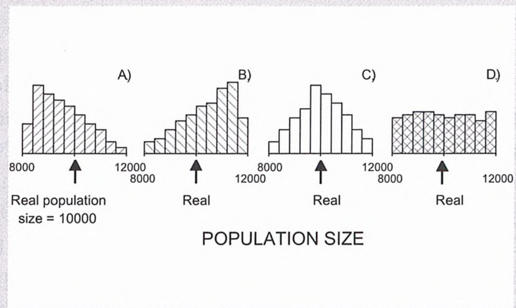

Figure 2. Four types of estimation distributions. In all cases the real moose population size is taken to be 10,000 animals and the estimates of this population range within 8,000-12,000 individuals. In A) the population size is underestimated in most of the cases whereas in B) it is overestimated in most of the cases. In C) the estimates are normally distributed so that the population size estimations near the real population size (10,000) are the most probable ones, and in D) the estimates are evenly distributed so that each population size estimate between 8,000 and 12,000 is just as probable as the others.

mates of the moose population size in Finland we decided to use four (skewed to the right, skewed to the left, symmetrically peaked and uniform) differing frequency distributions (Fig. 2). The hunting policy, i.e. the number of licences sold, is based on these biased estimates.

Considering the biased estimate of female fecundity: During summer new calves are born but the biased population growth rate is assumed to be 1.5 times the estimated winter population size. This value of annual population growth has been used during the last few years in moose management in Finland (Nygrén et al. 1999).

In our scenario the managers decide, prior to the hunting season, that the prevailing population is too dense causing too much damage to young forest stands and too many traffic accidents. It is agreed to reduce the moose population to 5,000 individuals during the hunting season. Now, if the moose managers had unknowingly estimated the population size wrongly in winter and had also made errors in assessing the population growth over spring and summer, the outcome of the harvest might be somewhat different from what the managers were aiming at. We are specially interested in the extent to which errors in the population size estimate and errors in the assessment of the growth rate of the population will lead to population sizes below those aimed at (in this case 5,000 individuals). Loyal to the tradition in ecological risk analysis we also repeated our simulations 1,000 times, each time drawing the initial population estimate from the four frequency distributions (see Fig. 2).

Results

The probability of a decline in the population size increases very steeply once the hunting rate has increased above a certain level (Fig. 3). There is no major difference between the two hunting strategies, i.e. whether the harvest is equal for calves, bulls and cows (see Fig. 3A,B) or whether the cows are hunted somewhat less than calves and bulls (see Fig. 3 C,D). When the harvest rate of cows exceeds 0.3 of the population size in autumn (0.45 in bulls and calves), the population size declines regardless of how high the birth rate is. If the birth rate is lower, the decline already begins with lower hunting rates. This is the case when non-hunting mortality is at the lowest, i.e. 0.01 of the winter population size (see Fig. 3B,D). If non-hunting mortality is higher (0.05 of the population size), all populations decline when the harvest rate is 0.25 for cows and 0.375 for bulls and calves (see Fig. 3A,C). We also used a longer time-window (50 years) in our simulations. The major results, as reported above, did not change. The only difference detected when using a longer time-window was that the probability of population decline increased from values close to zero up to 100% even in a much narrower range of hunting rates (0.17-0.22). However, due to the fact that moose hunting quotas are decided

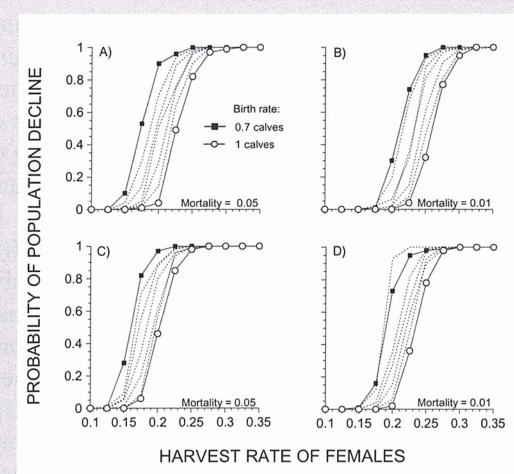

Figure 3. Relationship between female harvest rate and the probability of population decline for birth rates of 0.7-1 calf/female and non-hunting mortalities of 0.05 and 0.01, respectively. Higher female harvest rates increase the probability of a rapid decline in population size. In A) and C) all age-classes and sexes are hunted equally, and in B) and D) calves and bulls are hunted 1.5 times harder than cows. The dotted lines represent birth rates of 0.75-0.95 calves/cow, with intervals of 0.05. The results are based on 100 replications for each parameter value combination

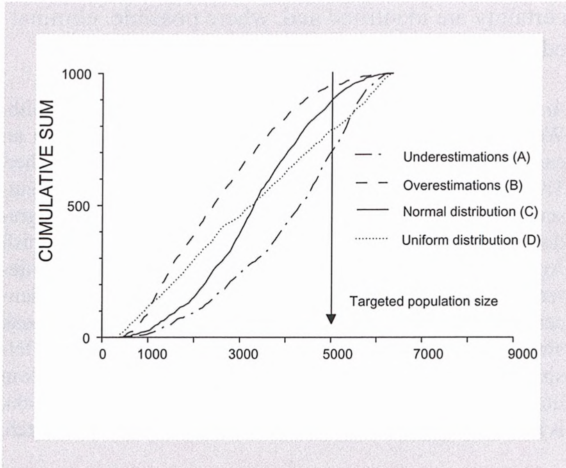

Figure 4. Cumulative sum of the population size after hunting for what is considered a 'realistic' population structure for Finnish moose, based on 1,000 simulations for each of the estimation distributions given in Figure 2 (A-D, indicated in parentheses after the symbols of the curves) and with a targeted population size of 5,000 individuals. In most of the cases the end result was a population size much lower than the targeted size (see text for further details).

annually, we prefer to report our risk analysis results using only a 10-year time-window.

The results of the second part of our study show that biased population estimates may lead to overharvesting but also to underharvesting, depending on the type of estimation error. The targeted and real population sizes after harvesting are shown in Figure 4. In most cases we ended up with much lower population sizes than intended and this happened with all kinds of error types. This means that the fecundity of the population was overestimated because not all of the winter population sizes were overestimated. To overcome the overestimate of fecundity and to concentrate on the inaccurate population size estimates, we changed the real population into a slightly more productive one by increasing the proportion of mature females and thus the number of calves born into the population. As a result of this change we obtained a too low population size after harvesting in half of the cases (Fig. 5). When the tendency is to overestimate the population size (overestimation curve in Figure 5, and Figure 2B) overharvesting follows. This is the case even if female fecundities were much higher. On the other hand, if there is a tendency to underestimate the population size (underestimation curve in Figure 5 and Figure 2A), there is more flexibility in setting the harvest rate.

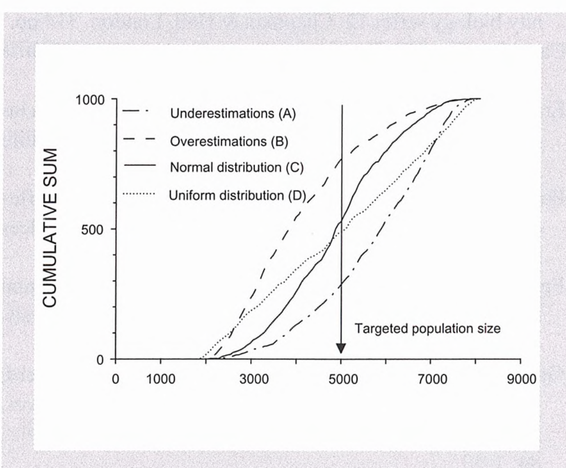

Figure 5. Cumulative sum of the population size after hunting for what is considered a 'productive' population structure (increased proportion of mature females; Fig. 4) for moose, based on 1,000 simulations for each of the estimations given in Figure 2 (A-D, indicated in parentheses after the symbols of the curves) and with a targeted population size of 5,000 individuals. Mostly the targeted population size was reached, but the results differed much for the four types of estimation distributions (errors; see text for further details).

Discussion

Our results are in line with the earlier studies by Fryxell et al. (1988) and Solberg, Sæther, Strand & Loison (1999) who showed that harvesting does have a strong effect on the population dynamics of moose. Our results also suggest that hunting rates for the Finnish moose population have been too high, at least in some years, compared with sustainable harvest rates. If 45% of the population in autumn is killed annually, the population size will certainly decline.

During the past 30 years, there is no evidence that the Finnish moose population has been near its carrying capacity so that population density would have limited reproduction. Not even when the population was at its highest in the 1970s and 1980s were there any signs of increasing non-hunting mortality or decreasing reproduction. This is in contrast with results available from some North American moose populations, for which increased population densities and competition for food have had important effects on population dynamics (e.g. Peterson, Page & Dodge 1984, Messier 1991, Ferguson, Bisset & Messier 2000). In Norway, however, where moose populations probably are more similar to those in Finland, moose populations have been found to be weakly regulated by density-dependent processes (Sæther, Andersen, Hjeljord & Heim 1996, Solberg & Sæther 1999).

Predation rate on moose is considered to be currently low in Finland. The effects of increasing numbers of wolves *Canis lupus* and brown bears *Ursus arc-*

tos, as recently observed in eastern Finland (Kojola & Laitala 2000), are not yet known. Elsewhere, predation is a strong mortality factor for moose populations (Gasaway, Stephenson, Davis, Shepherd & Burris 1983, Messier & Crête 1985, Ballard & Larsen 1987, Messier 1991). Thus, in future, the increasing numbers of predators might locally increase the non-hunting mortality of moose. Such local differences must be considered when planning hunting strategies for different game management districts.

The population size estimates that are used in the calculations for the number of hunting licenses to be issued are based on hunter observations (e.g. Nygrén 1984, Nygrén & Pesonen 1993). These estimates are considered to be reliable, although the method has been criticised (Ericsson & Wallin 1999, Solberg & Sæther 1999). Solberg & Sæther (1999) claim that hunter observations provide a good basis for estimating directional and quantitative changes in population size, but they do not give the absolute population size. They also state that hunter observations tend to overestimate the population size in years of high recruitment rates. This may have been the situation in Finland for some years in the 1980s and 1990s. Overestimation of the population size together with too intense hunting rates are probable causes of the population decline. As a conclusion, the hunting rate should be lowered from the level applied during the last 20 years.

Uncertainty is a major difficulty in sustainable use of game populations (Milner-Gulland & Mace 1998). Two sources of uncertainty are especially difficult to handle, viz. demographic stochasticity and environmental stochasticity (May 1974). Births and deaths are the central elements in population dynamics and these are subject to demographic stochasticity especially in small populations. Population size in Finnish moose is high across most of the country. Thus, we can rule out demographic stochasticity as a factor of major significance for management of moose. Environmental stochasticity, even in the case of a big animal like moose, can temporarily affect female fecundity and calf survival. However, there is not much that can be done to avoid environmental stochasticity.

We do not know how uncertainties connected with various sampling methods affect estimates of present moose population sizes in different parts of Finland. Yet, as we have shown (see also Caughley 1974), these biases in population estimates can cause a substantial mismatch between the targeted population size and the size achieved after heavy management-related culling. As stressed by Milner-Gulland & Mace (1998) no proper management can be done unless the sources of uncertainty are identified and, where possible, eliminated.

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