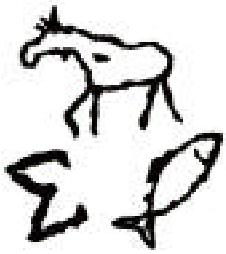
— MANAGEMENT OF A HEAVILY HARVESTED POPULATION

Anne Luoma



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Moose hunting in Finland — management of a heavily harvested population

Anne Luoma

This thesis is based on the following articles which are referred to in the text by their Roman numerals:

I Lehtonen, A. 1998. Managing moose, ***Alces alces***, population in Finland: hunting virtual animals. — ***Annales Zoologici Fennici*** 35: 173-179.

II Luoma, A., Nygrén, T., Ruusila, V., Ranta, E. & Kaitala, V. 2002. Dynamics of a heavily harvested moose population in Finland. — Manuscript.

III Kaitala, V., Ranta, E., Luoma, A., Nygrén, T. & Ruusila, V. 2002. Bulls, cows and calves, elements of moose harvesting. — Manuscript.

IV Ranta, E., Luoma, A. & Kaitala, V. 2002. Spatial-temporal synchrony in harvested moose population in Finland. — Manuscript.

V Ranta, E., Luoma, A., Kaitala, V. & Nygrén, T. 2002. Moose harvesting in Finland. — Manuscript.

VI Luoma, A., Ranta, E. & Kaitala, V. 2001. Moose ***Alces alces*** hunting in Finland – an ecological risk analysis. — ***Wildlife Biology*** 7: 181-187.

VII Luoma, A., Ranta, E. & Kaitala, V. 2002. Significance of landscape structure on moose population management. — Manuscript.

CONTRIBUTIONS

	I	II	III	IV	V	VI	VII
Original idea	IKP	IKP	IKP	IKP	IKP	IKP	IKP
Study design and methods	AL	AL,ER TN,VR VK	VK,AL ER,TN VR	ER,AL VK	ER,AL VK,TN	AL,ER VK	AL,ER VK
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MOOSE HUNTING IN FINLAND
- MANAGEMENT OF A HEAVILY HARVESTED POPULATION

Moose in Finland – now and before

In 2001 the winter population size of moose (***Alces alces*** L.) was approximately 120 000 animals in Finland (Ruusila et al. 2002). At the same year 66 951 individuals were killed in the harvest (hunting statistics of Hunters' Central Organization) and the meat value of those animals was 40 million euros. These are convincing evidences that moose is the most important game animal in Finland and that harvest plays major role in moose population dynamics. Due to the importance of moose, its population size has been monitored for decades. There are some estimations of moose population size even from the beginning of the 1900's (Nygrén 1984, 1987, I). The organised collection of moose data was initiated in 1970's (Nygrén 1984, Nygrén & Pesonen 1993). However, regardless of a long data series on moose population size and other population parameters, many features of the dynamics of the Finnish moose population have remained unknown.

The moose population size in Finland (as well as the annual harvest rate) has varied greatly during the last few decades (Fig. 1). Moose was protected in almost everywhere in Finland in 1969 - 1971, a spell of time when systematic moose management begun (Nygrén 1984). Population size increased extremely rapidly ten years, showing exponential type of population increase. In the beginning of 1980's, however, the winter population size was levelled down (with intensive harvesting) to circa 80 000 individuals (Nygrén 1996). In 1990's, the population size decreased for a few years, and thus, the harvest rates were obliged to be limited. In the past few years, the population size has once again increased and harvest rates have been increased to limit the population growth (Nygrén et al. 2000). A comparable process has also occurred in moose populations in Sweden and Norway (Cederlund & Markgren 1987, Østgård 1987, Haagenrud et al. 1987, Ericsson 1999) probably for same reasons; not to undervalue the effect of similar environmental conditions, the harvest policies and other management actions have been more or less alike in these countries.

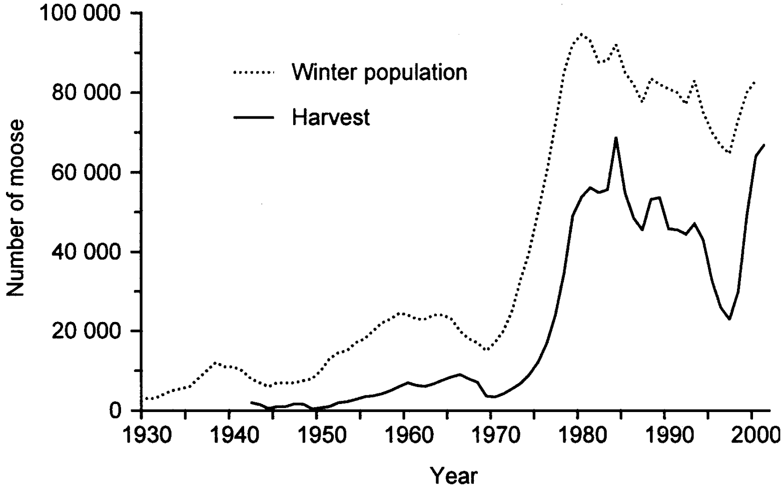

Fig. 1. ***Changes in moose winter population size and harvest in Finland during 1930 - 2000 (for more of the subject, see, e.g., Nygrén 1984, 1987, 1996).***

The aims of moose population management has varied from very low hunting rates, or even protection, to let the population size to increase (like in the beginning of 1970's and in 1990's), to very intensive harvesting to limit the population growth and to minimize damages caused by moose (like in mid 1980's and in last few years). A general goal of the management actions has been stable moose population size with relatively high reproduction rate, which would ensure high harvest rates. The population densities are supposed to be approximately 2 - 5 moose/10km^2 (Nygrén et al. 1999). These densities are attained in most parts of Finland, but locally there are large differences (e.g., Ruusila et al. 2002).

To reach the management goals, the main commission is to understand the basic population dynamics of moose, and the factors influencing them. If the main features of population growth are discovered we would be able to predict the moose population size in the coming years. A most important challenge is that harvesting has a major impact on the moose population size and its sex and age structures. Selective hunting changes the ratio of bulls and cows (Nygrén & Pesonen 1993). Because the trend has been towards harvesting low reproductive animals and saving older, and thus more reproductive cows (Nygrén 1983, Nygrén 1997, Ericsson et al. 2001), the implemented harvest changes the age-structure of population (Nygrén 1987). A similar management strategy to increase the reproduction rate is used also in Sweden (Cederlund & Markgren 1987, Ericsson 1999). Due to harvest affecting not only the population size but also its structure, it is not an easy task to find suitable harvest strategies maintaining population sizes and sex and age structures stable.

The data

Finnish Game and Fisheries Research Institute (FGFRI) has collected data about moose population in 1974 - 2000 throughout Finland. The data used here is from twelve game management districts (covering circa 2/3 of the area of Finland). The data of 27 years consist of harvest (harvest statistics) and some population parameters, such as sex ratio, reproduction rate, and estimation of autumn population size (based on moose observation data collected annually during the hunting season). Most of the original data are presented in chapter II.

The FGFRI mastered data collection and assessment on the winter herd size is from 1974 - 1996 (Fig. 2). They have used the census results, hunters' observation data, as well as harvest statistics to get the best possible estimation about winter herd size (this was done by T. Nygrén and M. Pesonen). During this time period the Finnish moose population have been harvested by using the harvest rates based on the accurate estimations about demand of harvest and restriction moose population size. Beginning with 1997 the census method of winter population size has somewhat changed and Hunters' Central Organization took over the responsibility of collecting the data and keeping the records of winter population size. Also, there are some changes how the data are treated to calculate sex ratio and the number of calves produced by cows (Fig. 2). The data previous to 1985 is modified afterwards to correspond to later data (done by T. Nygrén and M. Pesonen), i.e., to represent the population before annual harvest, but due to some lacking information the data periods are not identical. No changes have taken place in collection of harvest data, cows, bulls and calves killed annually in the autumn harvest. In the chapters (II - V) the moose data are treated assuming that changes in data amassing (Fig. 2) would not have any major influence on the conclusions drawn. As this is not so self-evident, I'll next repeat the relevant analyses splitting the data into different parts (Fig. 2). The results for the period 1974 - 2000 will be taken as the reference point.

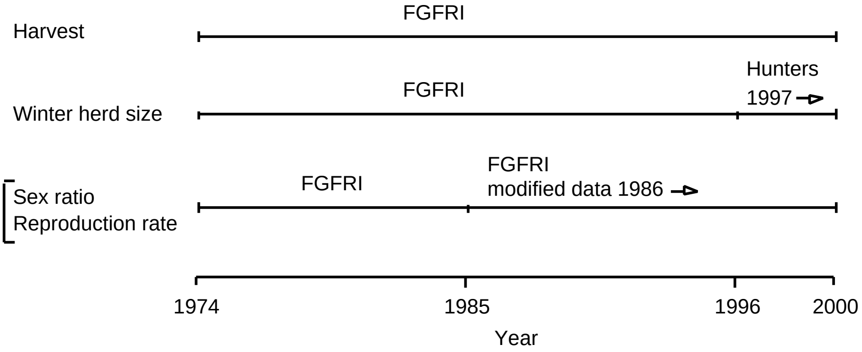

Fig. 2. ***The Finnish moose data, 1974 - 2000. Annual harvest data are collected with a matching way during the whole study period. Collection and reporting of the winter population data were done by the FGFRI for the period 1974 - 1996. Since 1997 response of the census was handed to the Hunter's Central Organization in Finland. This shift may have introduced some changes in data collecting and pre-processing procedure. For sex ratio and reproductive rate the data for 1974 - 1985 are pre-processed slightly differently as for 1986 - 2000 before reporting them. (This data is from Nygrén et al. 1999, 2000). Sketch drawn after discussion with T. Nygrén.***

Hunters' Central Organization in Finland has been responsible of collecting and reporting the winter numbers of moose during the past few years, 1997 - 2000 (Fig. 2). An obvious question then becomes: Is this shift in responsibilities visible in any way in the data? I'll address the question in two steps. First, in II first order autoregressive time series process, AR(1), is fitted to the entire data. When the autoregressive coefficients, $\boldsymbol{a}_1$, for cows, bulls and calves in different management districts (table 1 in II), based on 1974 - 2000 data, are compared against those calculated excluding the years 1997 - 2000, the outcome is almost identical (Fig. 3A). This lends support for the conclusion that the final years do not have any substantial influence of the conclusions drawn form the data on fluctuations in numbers of cows, bulls and calves in the 12 management districts.

Harvest data have been collected with a similar manner throughout the entire study period. However due to the 1997 shift, I calculated the harvest function parameters for the entire period (fig. 7 in II) and for the truncated period. The outcome is rather clear-cut, the intercepts (Fig. 3B) and slopes (Fig. 3C) are almost indistinguishable for the two time periods. Unfortunate

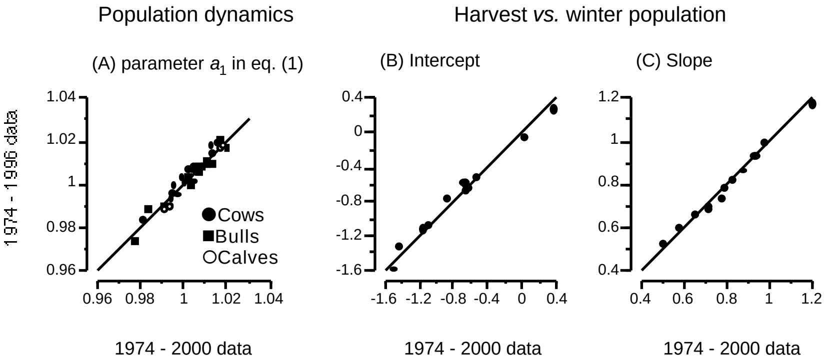

Fig. 3. ***(A) Comparison the autoregressive parameter, a_1, in eq. (1), in II, when calculated over the whole study period and for the FGFRI -period (1974 - 1996). (B and C) Similar comparison for the parameters of the harvest function.***

enough, the data accessible to us for fluctuations in numbers of cows, bulls and calves (III) and corresponding harvest data is too short (1991 - 2000) to be used in any meaningful statistical comparison between 1991 - 1996 vs. 1997 - 2000.

The temporal divider for the sex ratio and reproduction data is 1984 – 1985, when a change took place in pre-processing of the data published in annual reports by the FGFRI. Sequential data (i.e., autocorrelated data), like these, hamper effectively any simple comparisons in statistical terms, or render the analysis too complex for this short time series (12 and 15 consecutive years). For the number of calves produced per cow the 95% confidence limits around the grand average are 0.81 - 0.87 for the first period and 0.84 - 0.92 for the second period. This suggests modest changes in calving rate, but also considerable overlap between the two periods. For sex ratio the corresponding 95% confidence limits are 0.59 - 0.63 and 0.60 - 0.63, indicating substantial overlap (for management district specific data in calf production and sex ratio, see fig. 4 and fig. 5 in II). Synchrony levels in sex ratio average 0.69 and 0.62 for the two time periods, and the correlations with distance are –0.34 and –0.22. The corresponding figures for calf production are 0.35, 0.49, –0.31 and –0.50.

Aims of this thesis

The main aim of this thesis was to investigate and characterise the major population parameters and features affecting the moose population dynamics and harvest in Finland. This was mainly carried out by modelling the moose population dynamics and using the data as a source of parameter values and as a reference against which theoretical findings are contrasted. In this case, population modelling gives us a tool to understand the dynamics and changes in the population from which we have data or estimates of parameter values.

The problem was pursued from several aspects. First, the dynamics of the heavily harvested moose population were described and characterized. By using time series analysis (e.g., Box and Jenkins 1976, Royama 1992) for the existing moose data, the changes in moose population sizes and the effects of harvest on the population can be assessed (II).

Second, the population data were fitted into simple population growth models including harvest. With these models the near future of population sizes were to be predicted (I, V). Estimating the population sizes of forthcoming years is an important component in the management of game animals in general. In these studies, as well in later simulations, the population growth was based on the reproduction rates of cows.

Third, dividing the population into sex and age-classes (adult cows, adult bulls, calves (i.e., individuals in their first and second year) it was possible to create more specific harvest systems. The aim of the study was to analyse whether the harvest strategies are different among the game management districts, and whether the strategies to harvest cows, bulls and calves vary (III).

Fourth, spatial aspects were addressed by including dispersal into population models. How independent the game management districts are from each other? The dispersal of individuals may affect the similarity and the synchrony of the population dynamics in different districts. When modelling several different age and sex specific harvest scenarios and dispersal rates, one is seeking for scenarios where the data best support the model (IV). This is not to say that the scenario matching best with the data is the only explanation for the emerging synchronicity pattern. Since very little is known about the dispersal of moose in Finland, this study may give some general insight into dispersal patterns.

Fifth, an ecological risk analysis was carried out. Most commonly, a risk analysis is used in studies of endangered species (e.g., Ranta et al. 1996, Akçakaya & Raphael 1998), but also the risk of quasi-extinction can be calculated for harvested species (Kokko et al. 1997). For Finnish moose population assessing risk of population decline due to harvesting is relevant as the results suggest what kind of harvesting scenario can be the most feasible in maintaining current population (VI). When connecting the dispersal into the risk analysis and comparing the risks of population decline in different landscapes the effect of dispersal barriers can be illustrated (VII).

Main results

Fluctuations in population size and harvesting

Both the population size (winter herd size) and harvest (number of killed animals) has fluctuated dramatically during the study period, but there is no clear periodicity in moose population fluctuations. The cause of the changes in population size is management policy, its goals and tools: annual harvest rate. Annually, a considerable part (60 - 80%) of the winter population is killed by hunters (II, V, VII). There are no doubts that moose population in Finland is regulated by harvesting. Still, some uncertainties in population parameters (i.e., dispersal rates and possible under or over estimations of population size) make the management difficult and impose problems for a proper management. The current understanding is that local moose populations are held by harvesting in constant state of exponential growth (see also below).

The moose harvest in all management districts appears to be an autocorrelated process of order one, AR(1). The fluctuations in harvest appear to be red in colour (II), i.e., harvest rate of any year is correlated with harvest rates of a previous year (Kaitala et al. 1997). This says that if the harvest rate is low (high) in one year, it is likely to be low high) in the next year, too. Thus, if there has been major changes in management acts, their influence has been smoothened by inertia implicit in the population renewal process.

Exponential growth and AR(1)

We found that the moose population data provide extremely good fit with simple exponential population growth model (II, III, V). There is a strong growth potential in the Finnish moose population and now it is purposefully maintained to get annually a large bag. Annual harvest rates exceed 60% of winter population and selective harvesting increases the productivity of the population. A most interesting observation is that evidence for density dependence in influencing moose population renewal is hard to detect unambiguously at the current moose densities (II, V). High harvest rates, which follow the increases of moose population, seem to neutralise the effect of density dependence.

The winter population size is an autoregressive process of order one (AR(1)) in all districts (II, V). This means that the winter herd size of a particular year is dependent only on the population size of the previous year. This is an unexpected result since moose is a long living animal (e.g., Peterson 1977, Wolfe 1977, Ballard et al. 1991, Solberg et al. 2000, Ericsson & Wallin 2001). Thus, longer delays in the feedback process would have been expected. The intensive harvest dominates changes in moose population size, and it may also bring out the AR(1) process. Also, annual harvest rates (V) and reproduction rates in most of the districts (II) are AR(1) processes, and thus, the population renewal process has a memory of only one year.

Predicting the population size

Predicting future is an important skill in the practice of management of any game animal population. For this goal there is a need to know the effect of the harvest of the current year on the population sizes of forthcoming years. Accurate predictions up to several years are very difficult to generate (Lindström & Kokko 1996). A simple model (I) did not give very encouraging results. Not only predictions few years ahead proved to be unreliable, but also predictions to only one year ahead were erroneous in some cases (I).

When attempting to transfer the parameters that give very good fit in one game management district to the other districts, and thus trying to create a portable model, which could predict the population sizes in all districts, the match between data and the model disappears (V). This indicates that moose harvesting is a spatial process and both the population size predictions and the estimations of annual harvest quotas should be done in every game management districts. Thus, the effect of spatiality should also be taken into account in the population dynamics of moose.

Harvesting strategies

Although there are different harvesting policies among the management districts, the district-wise harvest rates tend to increase when winter herd size is increasing (II, III).

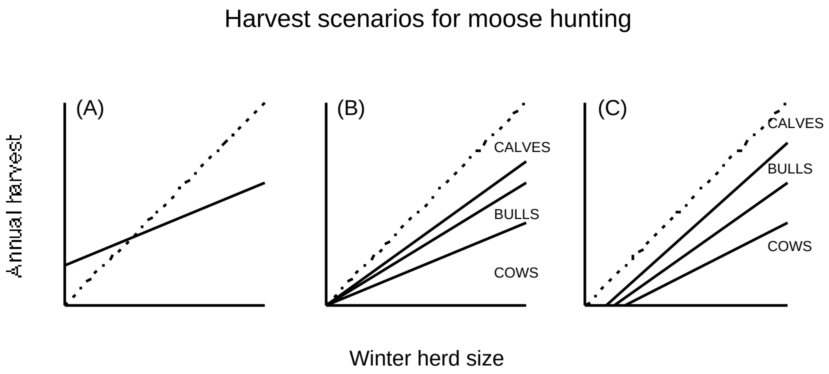

Fig. 4. ***Different harvest scenarios for moose hunting. Annual harvest is graphed against winter herd size (the 1:1 line is indicated with the dotted line). Moose harvesting in Finland most likely follows the scenario in (C).***

When searching more complicated combinations (different strategies for bulls, cows, calves) of district-wise harvesting, the data shows some common terms (III). First, bulls and calves are harvested more intensively than cows (the target has been to get higher reproduction rates (Nygrén & Pesonen 1993). Second, there is a minimum population size for harvesting. If local population size is too low, there is no harvesting (negative intercept). This indicates a linear harvesting with a threshold. However, in some cases intercept is very close to zero, in which case the harvesting strategy can also be directly proportional to the extant population size.

When modelling these two strategies (Fig. 4), the population dynamics stabilise much more easily with threshold proportionalstrategy. Also, a linear harvest with threshold gives higher yield than a strategy without the threshold. Similar kind of results has been found by Sæther et al. (2001). In addition, it is possible to have higher harvest rates for calves than for adults and still maintain a stable population size (III).

Risk of population decline due to harvesting

Different harvest strategies have also been used in the search for sustainable harvest rates. Concentrating on the risk of population decline, there is little difference between two main hunting strategies (VI): harvesting fewer females than males and calves (as the harvest strategy has been in Finland last three

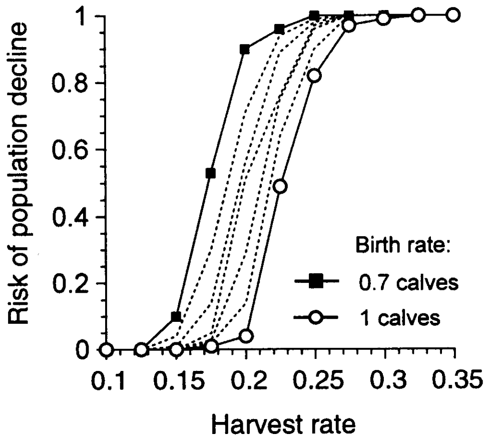

Fig. 5. ***Relationship between harvest rate and the risk of population decline for different birth rates (ranging from 0.7 to 1.0 calves per cow).***

decades) or harvesting all three groups equally. The risk of the decline in population size is more dependable on the productivity of the population than the difference in the strategies. Interestingly enough, in every scenario used (VI) the risk of decline in population size increases very rapidly in a very narrow range of harvest rates, i.e., the population seems to be very sensitive to too intensive harvesting (VI); (Fig. 5).

An interesting finding was derived in the scenario where the extant population size was "assumed" to be 10 000 individuals with the management aim being to reduce it down to 5 000 in one hunting season. In this system uncertainties in assessing population size, however, introduce bias in the estimates (e.g., skewness). To a surprise, the heavy harvesting in these scenarios quite frequently (VI) resulted to final population size much smaller than the targeted one (Fig. 6). This underlines the significance of estimating correctly enough the extant population size. Otherwise unwanted endcomes are likely emerge.

Landscape structure and risk of population decline

In general, there are notable differences between moose populations in the different game management districts (I, II, V). Harvest rates use are often different between the local populations (II). It also appears that, when using a simple population renewal process with harvesting, the model parameters are not unambiguously portable between

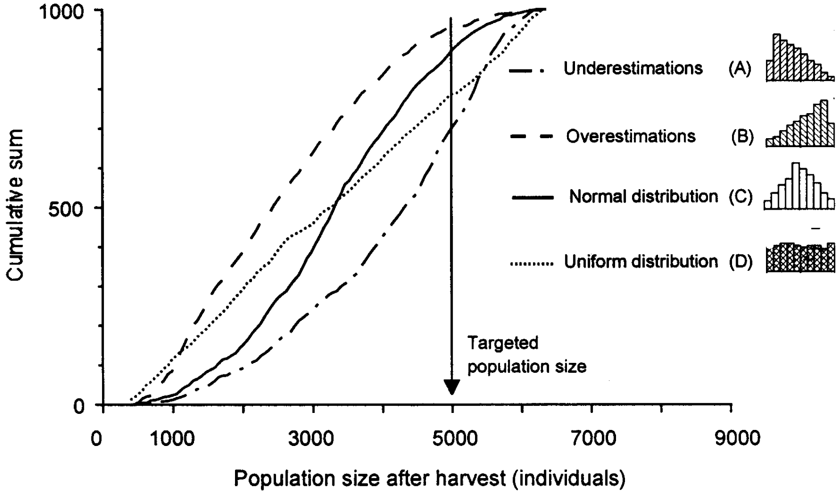

Fig. 6. ***The cumulative sum of population size after hunting. The lines represent the four types of estimation distributions in histograms A - D. The targeted population size is 5 000 individuals. Most of the cases end up with a population size that is much lower than the targeted size.***

management districts (V). One explanation is the local management policy, which may vary among the districts. The strategy may also be the same for all management districts but locally moose populations are in different state. Evidence hits that also moose populations are spatially structured with redistribution of individuals being of importance for population processes.

Very little is known about the dispersal patterns of moose in Finland. It certainly occurs in moose populations, and data from other countries indicate that dispersal is common mostly among the young animals (calves and yearlings) (Gasaway, Dubois & Brink 1980, Waser & Jones 1983, Ballard, Withman & Reed 1991). However, in Sweden dispersal does not occur at all in some populations (Cederlund & Sand 1992). It is unknown if similar non-dispersing behaviour is possible also in Finnish moose population.

Moose dispersal seems to affect the population vulnerability to harvest. If the dispersal is limited by a reason or another, the risk of decline in population size substantially larger with lower

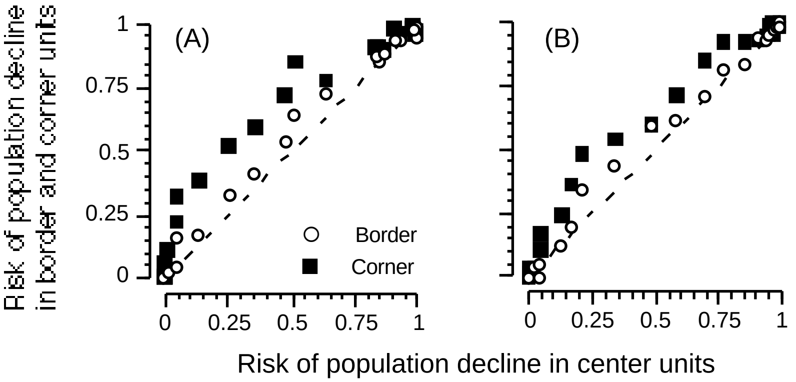

Fig. 7. ***The risk of population decline in bordering*** (○) ***and corner*** (●) ***units in the "landscape" (VII). The dashed line indicates equal risk of population decline in all units. When the dispersal is limited (like in border and corner units) the risk of population decline is higher than in area where dispersal is more unlimited (central units). This happens roughly in a similar manner when (A) all individuals and (B) when only young moose (< 2.5 years old) disperse.***

harvest rates than in areas with free dispersal (VII; Fig. 7). However, this is highly dependent on the proportion of dispersers in the population and also on the length of dispersal distances. For these parameters the data from Finnish moose population are scarce.

The district-specific moose data show patterns of synchrony so that all the population parameters (the winter population size of bulls, cows, and calves separately, as well as the reproduction rate, sex ratio, and harvest (Fig. 8)) are in close synchrony between the nearest districts and the synchrony is diminishing with increasing distance (IV). The dispersal of young individuals (calves and yearlings) can explain these patterns of synchrony, as seen in the data. We can conclude that moose population dynamics are a spatial process where the nearest sub-populations affect most strongly to each other.

Many populations are found to show spatial synchrony (Ranta et al. 1995a,b, Bascompte & Sole 1997, Bjørnstad et al. 1999, Lindström et al. 2001). Here the novel finding was that synchronism in various population parameters can also arise in a heavily harvested population.

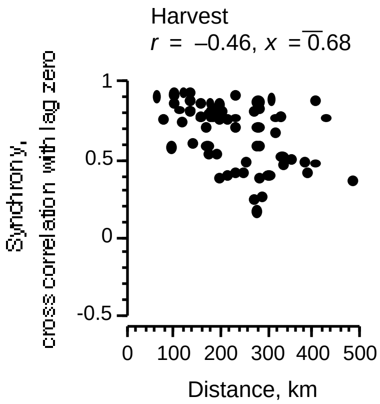

Fig. 8. ***Synchronous fluctuations in harvest rate, when compared among all management districts in pairs, show a decrease in temporal match against increasing distance correlation coefficient between synchrony level and distance is inserted together with the overall average synchrony in the data).***

Conclusions

The aim of this thesis was to investigate long-term patterns in Finnish moose population dynamics and possibly make some suggestions for the population management. There are no straightforward answers to many challenges set for the moose management. However, based on my research (I - VII) some conclusions can be made. These I will briefly mention below.

Moose is not only a valuable game animal, but it causes considerable forest damages (e.g., Heikkilä & Härkönen 1993) and traffic accidents (Rajamäki & Mänttäri 2001) in Finland. So the pressure in managing moose population size is two-sided: to minimise the damage and still maintain harvestable population densities. Nowadays the goal is to delimit the population size rather than to minimise the risk of local population decline, this being a new angle to harvesting theory. But in both directions the main problem with sustainable harvest rates remains open.

Harvest rates define the moose population size in Finland and also the population structure is affected by active harvest actions. The moose harvest has a temporal structure, which may exist on its own or be a reflection of the temporal structure of annual moose numbers. However, on the background the management policies are the driving force of the changes in the moose population, and the management actions create the population sizes and structures we see in the practice. In general, the population size is dependent on harvest rate, which in its turn effects on the population size. Both are created and maintained by each other.

Moose harvesting is a spatial process (IV, V). The non-portability of the population parameters between the management districts indicates that there are significant local differences between the districts. Also, the neighbouring sub-populations have a strongest effect to each other. This finding may have important consequences on moose harvest policies. More studies have to be carried out to find out, which sub-population sizes should be used as basis for harvesting strategies. For example, should it be the winter herd size in the management district, or a weighed average of a focal management district and those of neighbouring it. And also, how large an area should be counted as reasonable sub-population size for management decisions to be operational.

The analysis considering the harvest strategies support threshold-proportional harvesting over proportional strategies. Still, strict recommendations for all the management districts to use a certain management policy or to unify the harvest policies among the management districts are not wise. These analyses show a general approach to the problem of sex- and age class-specific harvesting. Thus, judging from the data, the harvest policies in various management districts do not seem to follow any clearly articulated principle. One major problem is that in addition to selective hunting and sex or age specific harvest guidelines, hunters harvest what is available. It is not possible to order exactly what individuals can be harvested. More detailed age-specific data would be needed for more specific studies of moose population structures. To mention one, the fact that fecundity in moose is strongly age-specific (Nygrén 1983, Solberg et al. 1999, Ericsson et al. 2001) is not taken account in these analyses.

This thesis provides a view to Finnish moose population dynamics. It also reminds us that many uncertainties in the population parameters jeopardise the management of moose populations. The uncertainties also make it hard to predict long-term consequences of various management actions. It has also to be remembered, that any population data series, as extensive in time and space as here, is always based on estimations. Over the time sampling and data pre-processing methods may be subject of modifications. Also, a different systematic error in the phase of population increase and decrease is possible (Solberg & Sæther

1999). These are all likely to influence the available data. However, the current analyses are carried out using the best published data on moose populations in Finland. The results of the research should be interpreted keeping in mind the quality of the data.

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