Management and Regulated Harvest of Moose (*Alces alces*) in Sweden

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Abstract

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Moose management has contributed to the large changes in the Swedish moose population during the last decades. Simulation experiments and monitoring of population parameters are two tools in the management system studied in this thesis. They can be used to increase the understanding of effects of different harvest strategies on game animals.

A simulation model has been used to show how moose populations in south-central Sweden are affected by different hunting strategies and how factors like sex-ratio, age structure, and reproductive traits regulate population development. The population in the model can be effectively regulated by altering the hunting pressure between the productive (females) and non-productive (males and calves) categories. Use of models shows that some harvest strategies may have long lasting effects on the population. Different goals and populations require different harvest strategies. A goal does not have to be a single product (number of moose shot, kg of meat, or number of trophy males). It could be based on several sub-goals, where economic weights reflect preferences for the relevant products.

Observation rates of moose reported by Swedish hunters are used to monitor moose populations. The accuracy of population parameter estimates can be improved by using observation rates obtained from large sampling areas. The quality required of the monitored parameters, together with the regional or local variation, should decide the size of the sampling areas. Hunter moose observation rates were affected by hunting efforts (individual hunting team, team size), length of observation period and by the various moose categories. Observation rates of male moose and different categories of females were modelled very differently. Identification, standardisation and calibration of relevant parameters and monitoring methods can improve the estimates of population size and its changes.

Future moose management needs an integration of biological, technical, economic and human dimensions. Decision-makers should answer a number of questions before deciding on regulation strength of the population and number of moose to harvest. Finally, in order to obtain a complete management system consisting of planning, acting (regulation), monitoring and feed back, I particularly suggest an examination of how individual hunters view the hunt and its management.

Keywords: decision-making, hunter, meat yield, monitor, observation, sampling, simulation, survey, trophy

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Contents

Appendix

Papers, I-IV

The present thesis is based on the following papers, which will be referred to by their Roman numerals:

I. Sylvén, S., Cederlund, G. & Haagenrud, H. 1987. Theoretical considerations on regulated harvest of a moose population – a simulation study. *Swedish Wildlife Research*, Supplement 1, Part 2, 643-656.

II. Sylvén, S. 1995. Moose harvest strategy to maximize yield-value for multiple goal management – a simulation study. *Agricultural Systems 49*, 277-298.

III. Sylvén, S. 2000. Effects of scale on hunter moose (*Alces alces*) observation rate. *Wildlife Biology 6*, 157-165.

IV. Sylvén, S. & Yuen, J. Hunting team impact on hunter moose (*Alces alces*) observation rate. (Manuscript).

Introduction

Background

Proper management of moose requires consideration of the animal in its ecological context, of the people who value this species and of particular social aspects. In Sweden, the moose has become a national symbol. One reason for this is the large impact the moose and its harvest has in the Swedish society. In recent years about 250 000 hunters (Ekman, 1992) have harvested around 100 000 moose annually (Official harvest statistics, Figure 1). Assuming an average carcass weight of 130 kg (Hansson & Malmfors, 1978) the moose harvest in 2001 (105 000 moose) contributed with 13,65 million kg of moose meat. This was close to 10% of the Swedish production of cattle meat 2001 or more than the Swedish consumption of sheep and horse meat (Swedish Meats statistics 2001). Moose meat is nutritious with its low fat content (Hansson & Malmfors, 1978; Hawley, Sylvén & Wilhelmson, 1983; Crichton, 1998). The moose and its harvest are natural and cultural resources which have great economic value (Hawley, Sylvén & Wilhelmson, 1983; Johansson, Kriström & Mattsson, 1988; Mattsson, 1990; Cederlund & Sand, 1991; Ekman, 1992; Pettersson, 1992; Boman, Kriström & Mattsson, 2000; Boman, Bostedt & Hörnsten, 2002). However, at high population densities, moose in Sweden can have adverse socio-economic effects, such as damage to commercial forests (Lavsund, 1987) and a high incidence of moose-related traffic accidents (Lavsund & Sandegren, 1991; A. Seiler, pers. comm.).

Since the late 1960s, the moose population has multiplied as indexed by the annual Swedish harvest. With a modest reduction of moose numbers due to poaching, predators (Haglund, 1974) and disease, the increase has mainly been attributed to increased forage supply and changes in moose harvest strategies. A shift away from forest grazing of domestic animals (Ahlén, 1975) coincided with a change in forest management from small-scale to large-scale logging (Strandgaard, 1982). This created large areas of tree and shrub species suitable for browsing and an excellent habitat for moose (Cederlund & Bergström, 1996). The maturation age of females, the proportion of females conceiving (fertility) and the average number of calves per female giving birth (fecundity) relates to the carcass weights and age of the animal (Sæther & Haagenrud, 1983; Sand, 1996a), reflecting environmental conditions (Sand, 1996b, Sand *et al.*, 1996; Sand & Cederlund, 1996). Delayed age at maturity has been found in a population with the relatively largest females (northern populations compared with southern), suggesting that the relationship between age at maturity and body mass differs regionally (Sæther *et al.*, 1996).

Moose management has contributed to the large changes in the Swedish moose population during the last decades (Cederlund & Marklund, 1987; Cederlund & Bergström, 1996; Ericsson, 1999). Compared with most other game species, the moose harvest is strongly regulated with regard to number, age and sex of the moose to be shot each year. After a population peak in the late 1970s and early 1980s the population size has been considerably reduced. At present the winter population is assumed to be 200 000 - 250 000 moose (A. Wetterin, Swedish

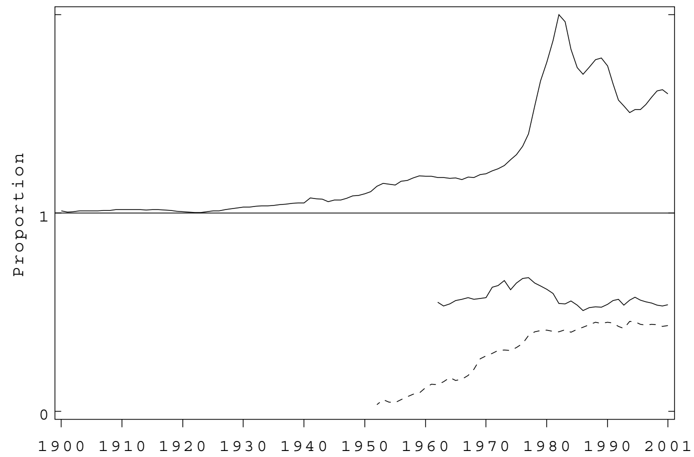

Figure 1. Official moose harvest in Sweden during the 20th century. The upper half shows the relative total moose number harvested (relative to the maximum which was 174 709 in 1982). The lower half presents proportion males of adult moose in the harvest (—) and proportion calves of total moose in harvest (- - - -).

Environmental Protection Agency, pers. comm.). By restrictions in adult male and female harvest, and in number of calves harvested, the regulation of the moose populations is to a large extent assigned to the hunters through their hunting teams/clubs. Calves and males have the lowest survival during the hunt, whereas female moose have the highest probability of survival (Cederlund & Sand, 1991; Ericsson, 1999; Ericsson & Wallin, 2001). The hunters use calves as an indicator of the reproductive value for female moose (Sand, 1996a; Ericsson *et al*., 2001). Females with no calves indicates pre- or post-reproductive ages. Protection of females with calves and a high proportion of calves in the harvest (the latter often making up 30 - 50 % of the harvest) results in a relatively high mean age among females in the surviving population. In addition, harvest pressure on males reduce the mean age among males in the surviving population (Sylvén *et al*, 1979; Solberg *et al*., 1999). In a population in northern Sweden, Ericsson & Wallin (2001) found that adult males faced a 3.4 times higher mortality rate during the hunt than the females, and the selective harvest of females resulted in a 2.5 higher potential population growth rate compared to a random harvest of females (Ericsson, 1999).

Although the change in harvest strategy has been a success in terms of hunting opportunities, it has became apparent that populations can get out of control. People responsible for the management systems have to set appropriate goals and use proper management tools for regulated harvesting of moose populations. Prerequisites for regulated harvesting, such as goals, harvest strategies, monitoring methods and in some cases population modelling have to be decided through surveys of knowledge about local moose populations and impinging factors. Apart from expected public interests (*i.e.* individuals, group, municipality, society), land-owner representatives, harvest administrators and the hunter organisations are important in this process. Without their knowledge about effects of various harvest strategies and of monitoring methods or systems the Swedish moose management may result in labile moose populations unable to fit any goals and management plans.

This highlights the need of access to management tools, such as models which illustrate what can happen, how a certain harvest strategy affects the population and the yield, and which strategies fit the local population and the goal set. In addition, gaps in information and demographic data may be identified and sensitivity analysis of identified factors can be conducted. Emphasis could be directed towards use of relevant monitoring methods with regard to identified key factors and data deficiencies. Swedish hunters frequently use observation rates of moose for monitoring their moose populations, a cost-effective ground based survey method performed during the first part of the hunt. This method is also in use in the other Nordic countries and in North America (Crichton, 1993). However, there is a lack of understanding of the relations between hunters' moose observations and 'true' moose density (Crichton, 1993; Solberg & Sæther 1999).

Attention should be given to local application of regulation actions that have to be adapted to different management areas or to an entire region. (Stålfelt, 1974; Sylvén *et al.*, 1979; Cederlund & Sand, 1992; Cederlund & Bergström, 1996; Luoma, 2002). Regional authorities and local hunting teams/clubs are involved in the regulation decisions. Today, one common regulation variant is that county administrators determines the number of animals that are to be shot in a particular area. Consensus with land-owners according to the acceptance of forest or agriculture damages and moose-vehicle accidents is promoted (H. von Essen, Swedish Association for Hunting and Wildlife Management, pers. comm.). Another variant is when the county administrators have accepted moose-management plans developed by the hunting teams/clubs, where the number of animals shot is adjusted over several years by the hunters themselves to meet the goal defined in the plan. The latter management code was introduced in the mid-1990s, and the area managed with this code compared with the total registered moose harvest area has increased from 9% in 1993/94, to 17% in 1997/98 and to 26% in 2001/02. In addition, environmental conditions differ strongly in Sweden (Ahti, Hämet-Ahti, & Jalas, 1968; Pershagen, 1969; Nilsson, 1990). Environmentally related body mass variation (Sand, Cederlund & Danell, 1995; Ericsson, Ball & Danell, 2002), and associated reproductive variation have been found (Sand, 1996b, Sand *et al.*, 1996; Sand & Cederlund, 1996). This variation and the use of local harvest strategies cause various moose populations to develop differently and thus require different management plans.

Figure 2 demonstrates the variation in relative annual numbers of moose harvested and in applied harvest strategies for four counties. The latter is visualised as proportion males of adult moose in the harvest and proportion calves of total moose in harvest. It is obvious that harvest strategies and yield differ between counties. Nevertheless, age- and sex selective harvest recommendations and applications are usually astonishingly uniform all over the country. The expanding proportion of locally based hunter regulated moose management units may increase the variation in future choice of goal, harvest strategy, moose categories harvested and management tools. Another important management factor is the time-delay

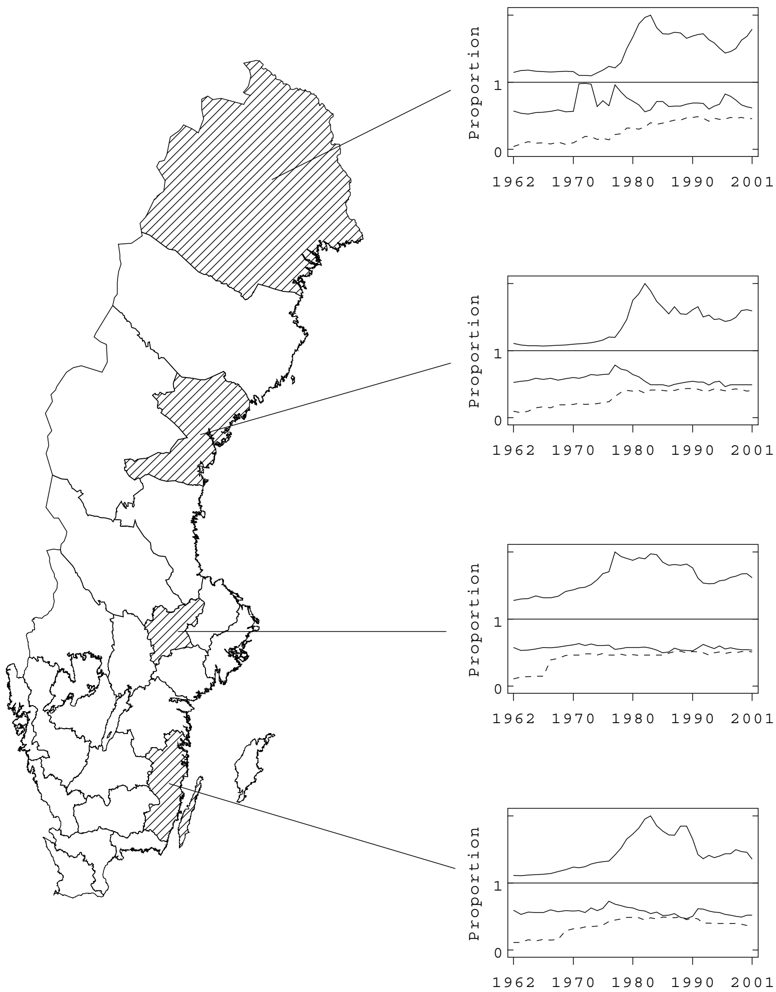

Figure 2. Official moose harvest in Sweden 1962-2001 in four counties (BD, Y, U and H from north to south). The upper half of each small figure shows the relative total moose number harvested (relative to the maximum in each county which was 11 378, 15 653, 3712, and 7191 in counties BD, Y, U, and H in 1983, 1982, 1977, and 1983, respectively). The lower half presents proportion of males of adult moose in the harvest (—) and proportion of calves of total moose in the harvest (----).

between an 'extreme' harvest, monitoring of the harvest effect, and the harvest strategy correction (Jaren, 1992; Sand *et al*., 1996; Solberg *et al*. 2000). Factors involved are the natural time-delay such as the fact that females starts to reproduce after 2-4 years (Ericsson *et al*., 2001), and that the hunters responsible have a tendency to change harvest strategies slowly (Jaren, 1992; Luoma, 2002).

Aims of the thesis

The general aim of this thesis is to examine if present knowledge about moose demography and dynamics, and present survey methods, are appropriate for developing proper management tools for regulated harvest of moose populations in Sweden. Regulation of moose populations needs a well-anchored management system, where relationships between goals, harvest strategies, population development and yield are well understood. Simulation experiments and reliable monitoring of relevant population parameters are a good way to increase this understanding.

I have evaluated four aspects of the management system of moose in Sweden. The specific management aspects of papers I to IV are as follows:

1. Harvest strategy effects – to show how a moose population is theoretically affected by different hunting parameters and how some important parameters, such as age structure and sex ratio among adults and calves at given female age-specific productivity, determine the population development (I).
2. Goal of the regulation – to simulate sex- and age-selective combinations in order to identify the maximum harvest strategy for single and multiple production goal, *i.e.* total number of moose harvested, number of trophy males harvested, or amount of meat from the harvested moose. Furthermore, the sensitivity of each maximum harvest strategy to different economic weights of each product was examined (II).
3. Size of observation or sampling area for hunter observation rates of moose – to determine the minimum size of a observation or sampling area that can be used to obtain reliable population estimates (III).
4. Hunting effort effects on hunter observation rates of moose – to examine whether variables related to the hunting effort, *i.e.* the observation period, the individual hunting team and the team size, influence the observation rates of different moose categories (IV).

Simulations of harvest strategies and population development, an educational tool

Computer simulations may be basically theoretical or they may apply to real harvest situations. In the first alternative, relevant to papers I and II, the model is used educationally in order to inform hunters and managers about the basic processes in moose population dynamics. New understanding of a system is a significant benefit of the very simulation process (Grant, 1985). Another advantage is that a large number of trials can be made with immediate results which enhance the understanding of the system and consequently the ability of a proper management (Pojar, 1981*)*. However, difficulties can arise regarding the choice of model. The model to use depends on the aim of the simulation study and if required data, in this case demographic data, are accessible. A simple and valid model based on few assumptions is often more serviceable than one with a more complex structure (Seber, 1982). There is an optimum of complexity to maximise reality and understanding (Costanzo & Sklar, 1985).

The computer simulation model used for the studies (I & II) is a modified version of a model designed for cervid populations (CERPOP) by Rusten & Digernes (1977) (Eriksson, Sylvén & Wilhelmsson, 1979; Eriksson, 1984). This deterministic model simulates an age- and sex-structured matrix with a yearly cycle consisting of four main seasons/events: winter (non-hunting mortality), spring (calving), summer (calf mortality) and autumn (rutting and hunting season). Density-dependent relationships were not included in the model. Age- and sex-selective harvesting can be simulated. Several ways to specify a hunting strategy are offered, including possibilities to control the sex-ratio between mature animals, and the population size among the surviving animals. The model also offers possibilities to constrain the harvest in chosen age/sex classes (*e.g.* skew hunting pressure between male/female yearlings, proportional protection of adult females due to number of calves, proportional protection of adult males due to age). In addition, meat yield and number of moose shot can be optimised in some of the harvest strategies offered. Several management-oriented cases have been simulated with this model. The main principle was to keep most harvest parameters in the model fixed, except the one of interest, and compare the simulated results in relative terms. As a result, information about differences in population development and yields resulting from different harvest strategies or optimisation alternatives is provided. In addition, data gaps were identified and the significance of using relevant and reliable demographic data in the simulations was illuminated.

Modelling of moose harvest dynamics for management planning

Population dynamics reflect the incidence of birth and death. In addition, populations can sometimes be affected by migration, and birth, death and migration can be related to the density of the population (Begon, Harper & Townsend, 1990; Royama, 1992; Stearns, 1992). Caughley (1976, 1977) and Caughley & Sinclair (1994) described, in an applied approach, the optimal harvest theory of sustained yield and the maximum sustained yield. Sutherland (2001) reviewed the literature on sustainable exploitation, including moose harvest publications, and organised the main issues by identifying essential principles and by describing the benefits, problems and uses when determining levels of exploitation. Sutherland argued that adaptive management (Walters, 1986) is an underused tool, and that monitoring populations and adjusting harvest regulations according to long-term population changes, is often the best method.

Population modelling of harvest dynamics was introduced to ungulate management in the late 1960s and early 1970s (Gross, 1969; Walters & Gross, 1972). Since that time, a variety of modelled effects due to moose harvest dynamics in Fennoscandia have been published (Sylvén *et al.,* 1979; Ryman *et al*., 1981; (I), (II); Lehtonen, 1998; Solberg, 1998; Solberg *et al.*, 1999; Ericsson, Boman & Mattson, 2000; Luoma, Ranta & Kaitala, 2001; Sæther, Engen & Solberg, 2001). Timmerman & Buss (1998) have reviewed corresponding North American publications. Ratio estimates, life tables, cohort analysis, harvest and population data analysis provide inputs to a number of models. The aim is usually to understand how the population and the yield is affected by different harvest strategies, in either a short-term or a long-term perspective. Management decisions can in some cases be based on the results.

Population modelling of harvest dynamics in moose populations varies due to a large range of modellers and users. The simplest consist of single persons and moose managers calculating population responses on spreadsheets or in other programs (Timmerman & Buss, 1998; C. Nilsson, Knivsta local moose hunting association, pers. comm.). The most complex consist of scientific teams with a combined diversity of skills aiming to create full models based on individual moose (Walters, 1992). Thus, the use of the results should fit to the aim of each study and the quality of the demographic data. If used for decision making, the extent of the decision should thus be related to the aim and data quality and, particularly, to the fit of the model to the real population.

Monitoring of moose population parameters

Effective management of a game population requires ongoing assessment of parameters that indicate or enumerate its size and growth rate. These can b*e* total counts, sample counts, mark-recapture or various indirect methods (Caughley, 1977; Cochran, 1977; Seber, 1982; Krebs, 1989; Caughley & Sinclair, 1994). Interpretation of such information is improved when monitoring several parameters and when time series are available (Timmerman & Buss, 1998). The effort and cost of collecting data need to be consistent with the intensity and objectives of the management (Walters & Green, 1997).

Aerial surveys, from fix-wing aeroplanes and helicopters, are considered to be the most accurate survey method for moose although dependent on a number of more or less well-controlled factors (Caughley, 1974; LeResche & Rausch, 1974; Gasaway & Dubois, 1987; Anderson & Lindzey, 1996; Timmerman & Buss, 1998). Densities and distributions are estimated for all individuals independent of age or sex, for adults and calves, or adult males, adult females and calves. Population data can be estimated in a reliable way and reduce statistical and visibility biases if sampling designs fit the population, the management objectives and the landscape context (Burnham, Anderson & Laake, 1985; Pollock & Kendall, 1987; Skalski, 1994; Timmerman & Buss, 1998). Double sampling or use of sightability adjustment are some proposed alternatives to improve estimates of aerial surveys (Crête *et al.*, 1986; Tärnhuvud, 1988; Steinhorst & Samuel, 1989; Rivest *et al*., 1990; Samuel *et al*., 1992), and population indices surveys (Eberhardt & Simmons, 1987). Aerial surveys are expensive, and have severe requirements on survey conditions, *e.g.* weather, snow cover and observer experience. Erratic snow conditions constrain the use of the method in southern Sweden. Aerial photographs and thermal infrared imagery have, so far, constraints when applied in moose surveys (Timmerman & Buss 1998). Adjustments have be made for vegetation barriers, other ungulates and sun-heated rocks. Expensive but successful applications in North America have been presented (Adams *et al*., 1997; Bontaites, Gustafson & Makin, 2000).

Pellet group surveys estimate actual or relative population densities in an area during a given time period (Neff, 1968). Densities are estimated based on the number of pellet groups counted, and an assumption of how many pellet groups a moose produces per day. The counting of droppings is work intensive and the method has constraints. Regional and habitat differences such as rainfall, temperature and insect abundance affect the decomposition rate of the pellet groups. In addition, the decomposition rate differs between adults and calves due to differences in forage intake, forage passage and digestibility (Andersen *et al*., 1992; Timmerman & Buss 1998).

Forest damage surveys, and to some extent surveys of browsing pressure, estimate the influence on forest trees and food resources by wild ungulates. Neither of the methods give any numeric estimate of the moose population densities, but are used as indicators of desired or undesired levels of the moose density in an area. Another ground based survey method is counting of moose tracks, though this is sparsely used in Sweden. Counting of animal tracks in fresh snow is used systematically in the Finnish wildlife triangle surveys (Lindén *et al*., 1996).

Information collected from dead animals are also important when monitoring population changes. Disease status can provide additional information about the population, though in the future moose diseases will probably be less visible due to increasing predation (Stéen, Olsson & Broman, 2002). Highly significant is the determination of age-related reproductive performance, and age-distributions among harvested animals. Markgren (1969) described the female moose reproductive organs and how to count number of eggs shed from the ovaries. Age can be determined by examining tooth eruption and wear (Stålfelt, 1992), or by counting the number of annual cementum layers of either the first molar (Markgren 1969; Wolfe, 1969) or the incisors (Sergeant & Pimplott, 1959; Haagenrud, 1978). Wallin, Cederlund & Pehrson (1996) describe prediction of body mass from chest circumference. All these methods need continuous improvement, calibration control and training of the observers (Dalton & Francis, 1988).

Finally, we have the most common ground survey alternative in Sweden, hunters' moose observation rates, reported by thousands of hunters that harvest and observe moose, usually in the same areas each year. In addition, hunter harvest statistics are reported to the regional hunting authorities. These data are used as relative measures of population density and trends in reproductive rates. Since 1985, hunter observations have been collected on a national basis in Sweden. Observations and hunter-days were recorded for each active hunting day during the first week of the moose hunt. Hunting teams (with observational effort documented by the number of hunters in the team) were asked to record number of male moose, female moose with one or two calves, females without calves, solitary calves and unclassified moose. The observation period included all activities associated with the hunt during the day. From these data, the observation rate was calculated. Corrections were not made for double observations or moose shot. In 1997 some changes that are still in practise were introduced. Instead of recording the observation effort as hunter-days, number of hunter-hours are used. The observation period was extended from the active hunting days during the first week to the first seven active hunting days within the first 30 days of the season. The observation questionnaires from the hunting teams are returned free to the local sections of the Swedish Association for Hunting and Wildlife Management, where they are computerised. All local data are gathered at the central level. The Swedish Association for Hunting and Wildlife Management informs that at least 5000 hunter-hours are needed (http://vww.jagareforbundet.se/viltvetande/alg/algforvaltning.asp, 20/12/02). The observation time required for reliable estimates has been analysed by Ericsson & Wallin (1994).

Simulation experiments and exploring a monitoring method

General relationships between regulation goals, harvest strategies, population development and yield: Simulation experiments (I, II)

In spite of an increasing access to theoretical knowledge of general harvest strategy effects on game animals, there is an educational need for examples of general relationships for decision makers, managers and hunters. Thus, relationships calculated in computerised simulations of harvest strategy effects can be used as a management tool. Five cases which have management implications are presented in (I). These are the effects of varying sex- and age ratio in harvest, effects of population reduction from overkill, effects of an unstable age structure among females in the population, and optimisation of meat harvest with varying sex-ratios in the population. Maximal yield-value of single or multiple goals, where economic weights reflect preferences of the moose products (number of moose shot, kg of meat and trophy males) are compared in (II).

Regulation of productive and unproductive animals

A population can be effectively regulated by altering the hunting pressure between the productive (adult females) and the non-productive (calves and adult males) animals. This is in accordance to population dynamic theory, which suggests that a calf has relatively low impact on future population growth compared with an average female that has given birth for the first time (Stearns, 1992). The productivity and hence population numbers are highly sensitive to changes in the sex-ratio among productive adults and to the age structure among adult females. An increase in the proportion of young animals in the harvest will increase the proportion of adults and productive animals in the winter population, assuming a constant size after harvest. As a general result, the average age in the productive segment will increase. Thus, the change in age-structure affects the population growth. Density-dependence and male shortage effects, *e.g.* socio-biological and reproductive trade-offs, are not controlled for in the simulations. It is important to monitor the variation in reproductive traits between populations, regions and years. Age-selective harvesting in populations with large reproductive variation between age groups may cause large changes in population development. In practice it is difficult, during the harvest, to identify females from a specific age-group. Early in the hunting season, it may be possible to distinguish young and old females (those without calves) from middle-aged particularly productive animals (those with twin calves).

One influential age-selective factor is the annual recruitment of first breeders. Recruitment is the replacement in the winter population of a full-grown animal by a first-breeder, *i.e.* replacing an old-female when their reproductive value starts to decrease. This decline starts generally at 12 – 15 years of age (earlier in northern than southern Sweden) (Ericsson *et al*., 2001; http://jagareforbundet.se/viltvetande./alg/algreproduction.asp, 20/12/02). To achieve optimum recruitment one has to consider the age-structure of the surviving females, the fertility, fecundity, and numbers of breeder animals. Effects due to recruitment deficiencies (over- or underestimations) will be discovered when the first breeders give birth or when missing first breeders are expected to do so. This will occur with a time-delay as female moose start to reproduce between the age of 2 and 4 years (Ericsson *et al*., 2001).

Harvest strategies optimising hunting opportunities, meat or trophy male

Of the harvest strategies examined, those retaining the highest proportion of highly productive females in the remaining population resulted in the highest population increase and hence the best yield in terms of moose shot (*cf.* 'Regulation of productive and unproductive animals'; Figure 3a). There are primarily two harvest strategy factors required to reach the optimal number of moose shot (II): (a) sex-selective harvesting increasing females among the adults, assuming no negative trade off due to the resulting sex-ratio bias among adults; (b) age-selective harvesting such as a high proportion of calves in the harvest, and an annual recruitment of first breeders adapted to compensate for all types of female losses, *i.e.* natural mortality and harvest.

In many areas the management authorities question how to optimise yield of meat and still maintain a fairly large number of hunting opportunities. Both optimisation of meat yield and hunting opportunities are primarily increased by sex- and age-selective harvesting in favour of highly productive females (Figure 3b). However, the meat yield is a function of the age- and sex-specific growth rates of the population and the weight of harvested individual moose carcasses. Thus, carcass weights of shot animals will affect the result. Simulations, based on population data from south-central Sweden (I, II) show that sex-selective harvesting that increases females among the adults was favourable for the meat yield. The simulations also show that optimal meat yield was combined with a high proportion of calves in the harvest when produced by females of high-reproductive

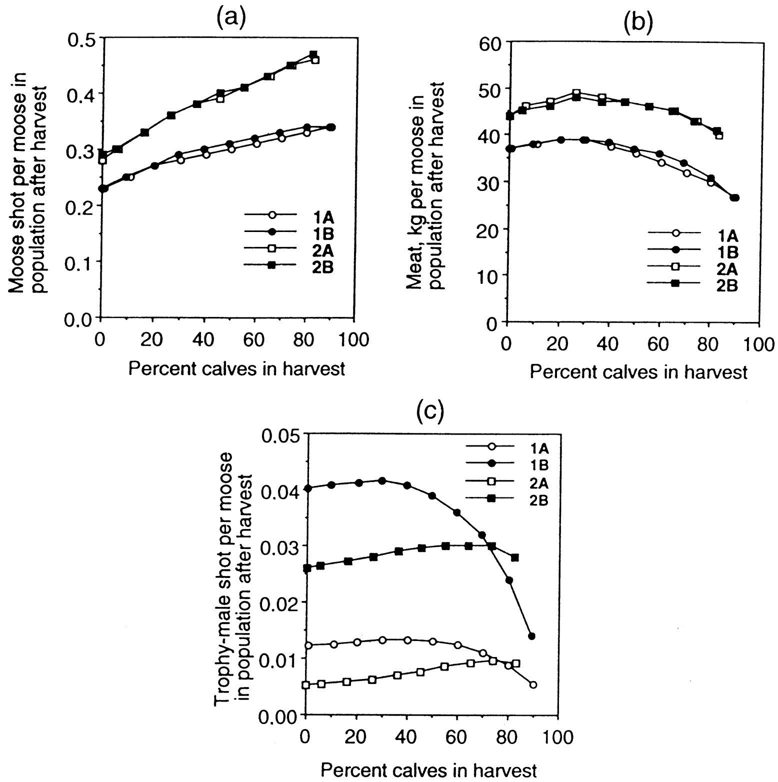

Figure 3. Yield per moose in population after harvest in terms of: (a) number of moose shot, (b) meat (kg carcass), and (c) number of trophy males shot from simulations with various adult sex-ratios after harvest (one or two females per male, 1 or 2, respectively), age-selective hunting pressure on males (reduced harvest of 6-9 year-old-males or 2-5 year-old-males, A or B, respectively), and proportion of calves in harvest (0-90%). (From figure 2 in paper II).

values. Consistent with earlier simulations (Sylvén *et al*, 1979), proportions of calves in the harvest for optimal meat yield (19-20%) were lower in populations with equal adult sex-ratio than in populations with two adult females per male (26%-40%). Among the latter simulations (sex-ratio, 2:1), the population with the lower-reproductive values and lower carcass weights produced most with a lower proportion of calves in the harvest (*cf.* 26% (II), and 40% (I)).

Many hunters argue that yearlings should be shot instead of calves, thus providing a higher meat yield. The assumption is that meat production is favoured in a population with many fast-growing animals, so the moose calves should be kept alive until they reach yearling stage. Case 1 (I) shows that an increased percentage of calves in the harvest increases the number of moose to be harvested (at constant winter-size), but lowers the average carcass weight. As described earlier, harvest strategies devised to optimise meat yield will be affected by individual annual body growth and population increase, *i.e.* number and carcass weights of calves and adults harvested. Consequently, in populations with low-reproductive values, a lower proportion of calves in the harvest (keeping a proportion of calves for another year until harvested as yearlings) results in optimal meat yield. However, an increased winter mortality of calves and practical difficulties in identifying yearlings in the next year hunt will favour harvest strategies of shooting young animals as calves. This strategy will increase the number of hunting opportunities and reduce the total meat yield.

The simulations of sex- and age-selective effects on trophy male yield were based on an assumption of a correlation between age and antler points (II). The hunters are expected to count the antler points before shooting. Two alternatives of moose male regulation were compared. These were a reduced harvest of 6-9 year-old-males (strategy A) or 2-5 year-old-males (strategy B). The number of trophy males was most affected by age-selective hunting pressure on males and second most by sex-selective harvesting (Figure 3c). The highest trophy male yields were obtained by concentrating hunting pressure on yearling males and trophy males (strategy B). The harvest of yearlings was followed by a period of reduced harvest intensity that lasted until the animals had reached trophy male age, *i.e.* 6 years-old (Gasaway *et al.*, 1987). However, a reduced harvest of 2- to 5-year-old-males may involve problems owing to large variations in the number of antler points of similarly aged males.

Single goals or multiple goals?

The study (II) shows that simulation models together with a simple economic calculation can facilitate the decision-making process in moose management. My aim was to illustrate how one can consider maximal yield value of single goals or multiple sub-goals. Single goals involved the products *number moose shot*, *kg of meat yield*, or *number of trophy males*. Multiple goals were formed by assigning a high or low economic weight to each of the single goals, and then calculating the total value of all three products. The product *kg* of *meat* were based on Swedish market prices. The products *one moose shot* and *one trophy male shot* were based partly on findings of willingness-to-pay (Mattson, 1990), and a list of European trophy fees for red deer (Furniss, 1991). The low economic weight alternative of *one moose shot* placed a lower hunting value on calves than on adults. This study concentrated on finding the rank of yield responses to different harvest strategies with no effects from other factors. Long time-sequences were purposely simulated in order to reach a theoretic 'steady state' and then the harvest strategy effects were compared. The results indicate general differences between harvest strategies. Final yield values are influenced by simulated harvest yields and the economic weights used. It was evident that the maximal yield value for multiple goal management was higher than single goal management, except for the trophy male goal (Figure 4). The harvest strategy used promoted the highest proportion of adult females (two per adult male after harvest) and a reduced harvest of 2-5-year-old-males. The proportion of calves in the harvest was of less importance when applying this harvest strategy (strategy 2B in figure 3). Recommendations of a strategy that maximises a single product, such as number of trophy males shot, may only be appropriate if the economic weight for the maximised product is high enough to compensate for the reduced yield of the other products (moose shot and meat).

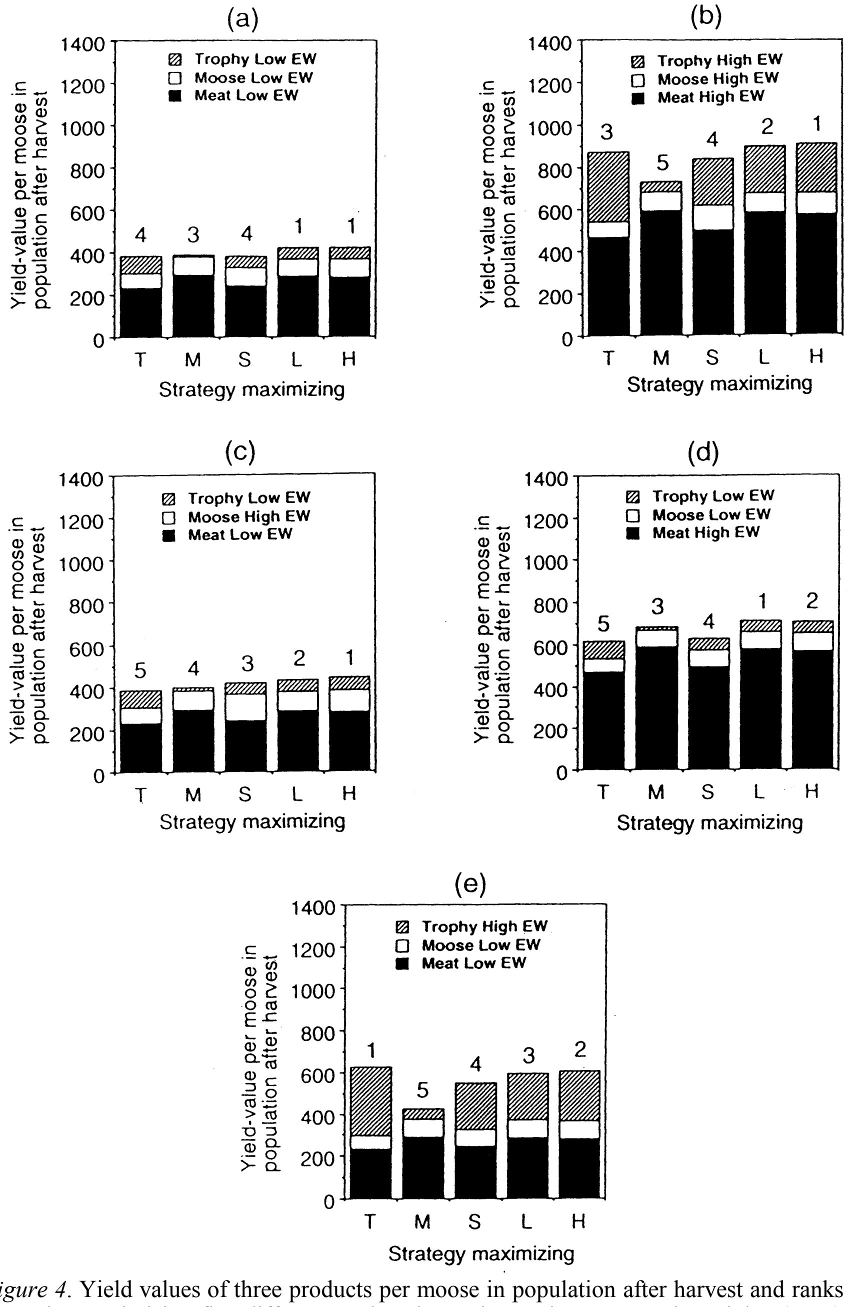

Figure 4. Yield values of three products per moose in population after harvest and ranks of strategies maximising five different goals, when using various economic weights (EWs) of the products. Goals maximised were as follows: number of trophy males shot (T), meat yield (M), number of moose shot (S), total yield value based on low EWs (L), and total yield value based on high EWs (H). Combinations of low or high EWs of the maximised products are presented in the figure from (a) to (e). (From figure 4 in paper II).

Assessment of population parameters by hunters' observation rate (III, IV)

To effectively manage a game species its population dynamics must be thoroughly understood. Lack of surveys and sporadic or biased surveys may result in local or regional populations getting out of control. Monitoring methods to estimate animal numbers with acceptable precision are needed. Several survey methods may be used. However, data collection of large animals such as moose is usually very expensive. Effort was therefore focused on a cost-effective monitoring method, where data is collected close to the moose, *i.e.* collected by the hunters. The method, hunter observation rates of moose during hunt, is based on the assumption that a change in observation rate per time unit reflects a change in the population density (Ericsson & Wallin, 1999; Solberg, & Sæther, 1999). This method has been frequently used in Fennoscandia during the last few decades (Jaren, 1992; Nygren & Pesonen, 1993; Ericsson & Wallin, 1996). Thousands of hunters observe and harvest moose, usually in the same areas each year.

Attention to scale when deciding the management unit

The study presented in paper III focused on determining how large a sampling area and consequently a management area should be to provide useful population estimates. When deciding a proper management unit, attention to context and scale is needed. Hunters tend to use small areas, and one hunting team may cover 20 - 40 km^2 or less. Many hunting teams co-operate in larger units, and the unit sizes differ largely within Sweden. For example, registered average areas for management units 2001 varied according to the system of how to allocate hunting permissions. Where this was determined by the county administrators, the average sizes were 92 km^2 (N=667), 15 km^2 (N=756), 12 km^2 (N=138), and 6,6 km^2 (N=678), for counties BD, Y, U and H, respectively. Where this was determined by responsible hunting teams, the average sizes were: 645 km^2 (N=24), 297 km^2 (N=31), 106 km^2 (N=38), and 129 km^2 (N=40), for the same counties. Neither of these average management sizes can be recommended as the ideal size. Recommended sizes for sampling areas depend on the variation in the data, adjustments or standardisations performed and the accuracy and precision demand on the estimates. Empirical experience in central Sweden indicates that hunters' observation rates of moose could be satisfactorily used in areas of 300-3000 km^2 and that areas between 1200-2000 km^2 were the best (G. Ledström, County Administrative Board of Västernorrland, pers. comm.). Sizes of 1000-3000 km^2 are consistent with studies in North-America (Kale, 1982; Fryxell, Mercer & Gellately, 1988). Migration movements and aerial surveys may require larger sampling areas, but the areas should not be too large. Local moose populations within a large area may develop differently, which could be monitored incorrectly when pooling data for the total area (G. Ledström, pers. comm.). Consequently, a sampling area should not be too small, and to be functional as management unit of local populations it should not be too large.

Effects of the size of the sampling or observation area on correlations between hunter's moose observation rates and moose density estimates have been evaluated (III). The results confirm that hunter observation rates were affected by sampling

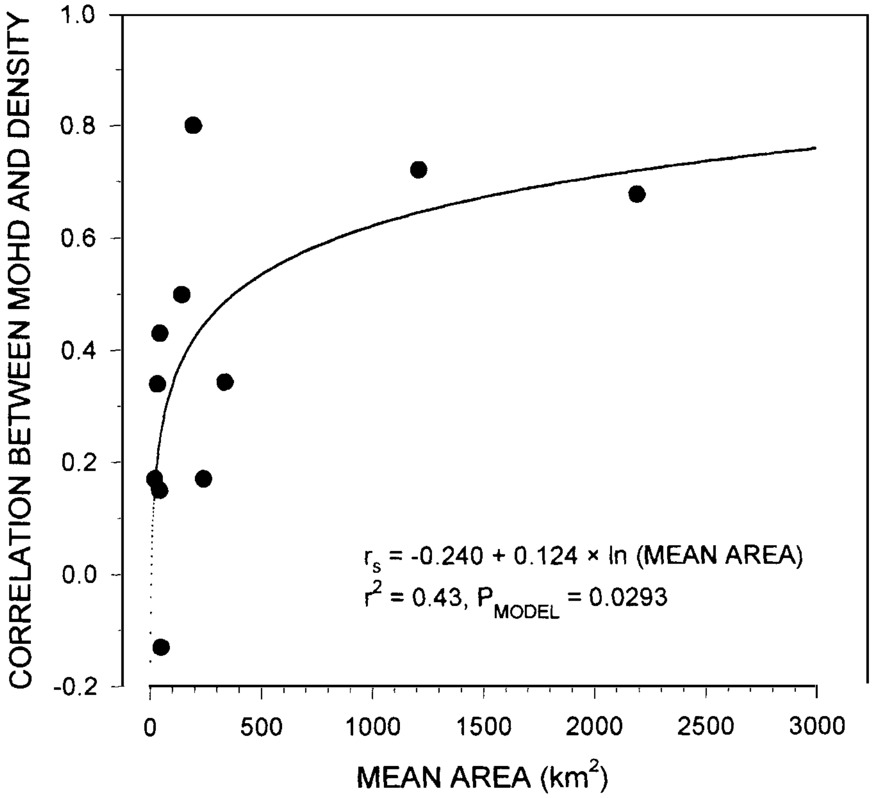

Figure 5. Asymptotic relationship found between the mean area size of the analysed county/area size groups and the Spearman rank correlation (r_s) between estimates of hunters' moose observations per hunting day and standard moose density estimates. The correlation for the largest areas is based on data from the county of Västerbotten in northern Sweden (see Ericsson & Wallin, 1999) (after figure 3 in paper III).

area size. Correlations between observation rates and moose densities indicate that there is a positive asymptotic relationship between the accuracy of the observation rate and sampling area. As the sampling area increases, so does the accuracy of the hunter observation rate (Figure 5). It was concluded that the accuracy of density estimates could be improved by using hunter observation rates obtained in sampling areas larger than 500 km^2. Size-differences of the management units in northern and southern Sweden (larger units in north) limit the general use of this conclusion. Other north-south differences connected to hunting suggest that observation rates and consequently the sampling area are affected by latitude. Estimates of smaller management units may be improved when using year-to-year surveys within homogeneous management units. One consequence will be that similar management solutions ought to be developed for blocks of similar conditions.

Effects of hunting effort on observation rate

Identification, standardisation and calibration of factors that affect the hunter's moose observation rates is a way to improve the estimates of population size and its changes. The hunting effort is a complex factor which integrates sub-factors covered by the individual hunting team characteristics (hunter age, motives for hunting, hunting methods, experience, traditions etc.). Ericsson & Wallin (1994) proposed that half the variation among the number of observed moose was explained by the hunting teams, and that differences in hunting method affects the observation rate, *e.g.* hunting by driving dogs or stalking. Factors related to moose behaviour may also affect the observation rates of moose. These include group size, home range, movements and speed of hunted moose (Gustafsson & Cederlund, 1994; Ericsson & Wallin, 1996;.C.M. Rolandsen *et al.*, unpublished data), and different escape behaviour of males and females (Baskin, Ball & Danell, 2002). An important factor is the variability in the ability to separate moose of different age and sex (Ball, Ericsson & Wallin, 1999; Ericsson & Wallin, 1999; Solberg & Sæther, 1999). Differences due to the population composition could affect total population estimates. The observed ratio between calves and females has been found to reflect the true reproduction rate (Ericsson & Wallin 1999, Solberg & Sæther 1999). No evidence indicating that the ratios between males and females can be used in a similar manner has been found in the literature.

In paper IV, we examine whether variables related to the hunting effort in terms of the observation period, the individual hunting team and the team size influence the observation rates of different moose categories. The observed variation was affected by hunting efforts (individual hunting team and team size), and length of observation period, and apparently varied between the various moose categories. The hunting effort declined with the season, which may explain certain problems of fitting adequate models. Observation rates of population categories such as male moose and different categories of females (with different numbers of calves) were modelled very differently. The complex hunting effort factor covered by the individual hunting team had the largest impact on the observation rates. In addition, the team size had effects on the observation rates of male moose, females with two calves and total moose. In these cases larger teams resulted in higher observation rates, probably due to a larger number of alert eyes and more movements, both by man and moose. This may be a result of local differences in hunting recommendations, hunting effort and, consequently, the hunting pressure. Thus, prerequisites for use of observation indices ought to be regionally or locally standardised and adjusted, including factors such as adequate sampling areas, selected observation period, training of observers, differences between moose categories and calibration with independent measurements.

Towards adaptive moose management and an improved monitoring system

Components of a regulated moose management system

A wildlife population may be managed in one of four ways: (1) make it increase, (2) make it decrease, (3) harvest it for a sustained yield, or (4) leave it to itself but keep an eye on it. In order to pursue proper management three questions should be asked: (i) what is the desired goal?; (ii) which management option is therefore appropriate?; and (iii) by what action is the management option best achieved? The first answer requires a judgement of value, the others technical judgements (Caughley and Sinclair, 1994). The answers are associated to the following components of regulated moose management; *to plan* (A), *to act* (B) and *to monitor* (C). All components should include immediate corrective actions.

A. Planning, which involves:
(a) Defining the management unit based on available information (biological, geographical, administrative, technical, economical, hunting traditions etc.).
(b) A collaborative decision-making approach involving all stakeholders. Communication of available scientific and empirical information associated with the local or regional moose population and impinging factors.
(c) Defining clear goals, *e.g.* a multiple goal of products and factors weighted according to preferences (values), and how strong the regulation should be.
(d) Making the system adaptable and accountable, in accordance with stakeholder commitments of accuracy and precision. Models for educational purpose would be useful in the process of understanding. Forecasting models can be applied if model and data give reliable predictions (high quality data and validated models). Monitoring methods and necessary parameters need to be identified and chosen.

B. Acting and regulating step. Strong regulatory actions need to be closely examined, possibly by high precision monitoring and experiments.

C. Monitoring, analysis and feed back step: Results based on accumulated data, experience, and evaluations of observed effects (*e.g.* experimental results) should be used to modify the earlier steps.

The management chain, A-C, needs to be applied for each specified management unit. Figure 6 shows a flow diagram of two moose management paths, associated with either intermediate or strong regulation of the moose population. The diagram describes a simplified part of a large multidisciplinary management system. Parallel use of modelling for analysis (A, d) and monitoring for verification of various parameters (C) is an important way to determine the effectiveness of a given management process. There are numerous approaches in the literature describing all kinds of management systems, by mathematical models, simulations, expert systems, decision-making systems etc. The stakeholders have to decide the strength of the regulation. Decisive for the choice of either an intermediate or strong moose regulation would be knowledge regarding the moose populations and

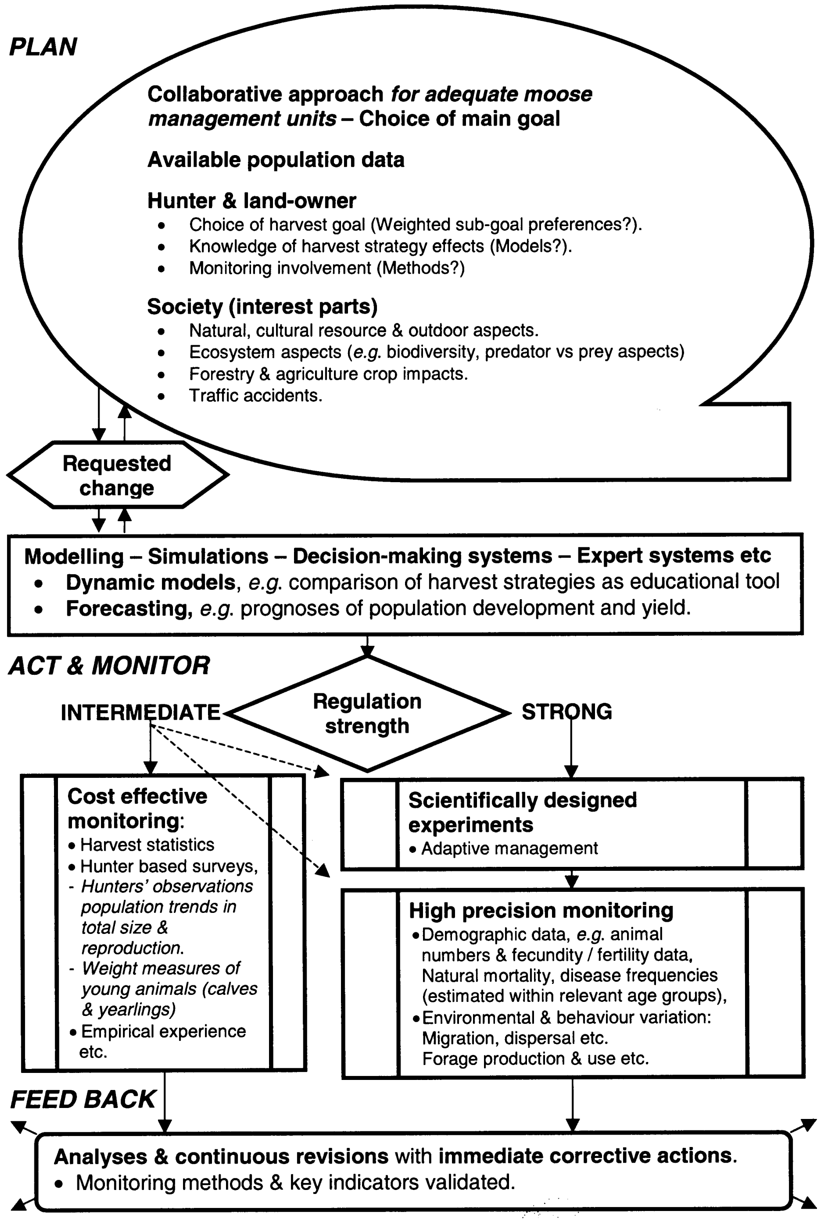

Figure 6. Flow diagram of steps from concepts to practise in applying two moose management paths, associated with either intermediate or strong regulation of the moose population. Steps in this process are to plan, to act, and to monitor, including an immediate corrective feed back. The path chosen will determine the type and significance of management tools to use, *e.g.* type of monitoring methods and potential experiments. High precision monitoring and/or experiments may be used, or sometimes are needed, for intermediate regulation, but cost-effective monitoring (with low precision) should not be used for strong regulation applications (------).

the hunters. The stakeholders will affect the strength of the regulation. This includes their hazard willingness, and their interest in potential experimental activities. Other factors that may affect the strength of the regulation include the quantity and quality of monitored estimates, and how experience is fed back to earlier steps in the management chain. An intermediate regulatory approach may fit conventional moose management, based on population data estimates of acceptable accuracy and relatively low precision. I suggest that strong regulation only should be applied in populations managed in accordance with adaptive management theory (Walters, 1986). Bormann *et al.* (1999) defined adaptive management as an approach to manage complex natural systems that builds on learning, based on common sense, experience, experimenting, and monitoring, and on adjusting practises based on what has been learned.

The regulation strength chosen will determine the type and significance of management tools to use. Models for educational purposes, the first management tool discussed in this thesis, fit both intermediate and strong regulation. I suggest forecasting models as a prerequisite when applying strong regulation, together with a parallel control of the population development and yield in the field. Simple deterministic models used in the papers (I) and (II) compare relative effects due to changes in one or several specified factors. A complex, stochastic model may be the way to visualise long-term development of a specific population, *e.g.* due to non-linear density-dependence (Solberg *et al*, 1999, Sæther, Engen & Solberg, 2001). Monitoring methodology, the other management tool discussed in this thesis, has a main position in the choice of intermediate or strong regulation management. Large deficiencies in estimations of population associated data may result in a population out of control. Regulated moose management is a continuous and dynamic process, which requires constant improvements and supervision. A final stage can never be reached because of interaction factors that are very dynamic.

Swedish moose management

Today, most moose hunters in Sweden are aware of the importance of high numbers of female moose in the reproducing population. One reason for this knowledge is that mandatory theoretical and proficiency tests are required for new hunters since 1985 (Nordström, 1992). General harvest recommendations in Sweden are to have a high proportion of young animals in the harvest, and to regulate the rate of population increase by changing the relation between adult males and adult females in the harvest (H. von Essen, Swedish Association for Hunting and Wildlife Management, pers. comm.). However, the effects of the chosen harvest strategies on the population development, and thus the yield is less well known. Although an expanded calf harvest in a growing population has been easy to accept, it seem to be more difficult for the hunters to accept a reduction of the adult harvest in a shrinking population (H. von Essen, pers. comm.). Hunter think it should be meaningful to harvest. This means that they require both hunting opportunities and meat (H. von Essen, pers. comm.). Trophy males are mostly seen as a bonus. General goals and harvest strategies might be difficult to implement all over Sweden. Environmental, regional, economic, technical and human values differ. Hunters need information and recommendations associated directly with their region and their management unit.

Harvest strategies imposed during the last decades

Practical experience shows that it has been difficult for local managers to predict and measure the effects of different hunting strategies. That was the reason why the management-oriented cases in paper (I), and partly in paper (II), were simulated and discussed.

There has been a considerable overkill of males for decades. A dominance of males among the calves in the harvest data of the 1970s together with growing populations meant that a high male harvest could be accomplished without a distorted sex ratio in the winter population (Haagenrud & Lørdahl, 1979). However, a male harvest higher than the sex-ratio at birth in a stable (or shrinking) population will distort the sex-ratio (case 2, in paper I). Today the sex-ratio at birth is lower than in the 1970s. The male proportion among officially harvested calves in Sweden decreased from 59% in 1968 to 52% in 2001, a rate corresponding to about 2 promille per year (t=10.76, 34 d.f.). In extremely female-biased populations, where low mean ages among adult males are common, one might find trade-offs. Solberg, Sæther & Heim (2002) found a positive association between the mean age of adult males and the proportion of male calves produced. Ginsberg & Milner-Gulland (1994) suggest that sex-biased harvesting in ungulates may not be optimal, or viable, in the long-term.

Trophy male optimisation implies age-selective harvesting of males. The hunters select adult males by counting antler points based on the assumption of a high correlation between age and antler points. Thus, calculating age by observing the antlers could lead to animals in undesired age-classes being harvested (E. Broman, pers. comm.). Decision-makers, having a strong preference for trophy males, would conduct age-selective harvest of young males (calves, yearlings), full-grown capital males and 'retrogression' males (if there are any left) (II). If applying a strong regulation effort, I suggest long-term monitoring and modelling for analysis of population effects (Figure 6). The proportion of calves in the harvest was of less importance when applying this harvest strategy, assuming that many of the surviving calves were shot as yearlings. In practise, it is difficult to separate yearlings from older moose with few antler points. Therefore many of the young animals have to be harvested as calves, and an intermediate calf harvest quota would probably be the most realistic alternative. Another hunt-connected problem in age-selective male harvesting is that it can be difficult to reach harvest quotas for specific age groups, which have experience from previous hunting. The vulnerability and movement of a moose is believed to be related to previous experience with hunters (Fryxell, Mercer & Gellately, 1988). Geographical variation in the antlers of Norwegian moose in relation to age and size has been found (Sæther & Haagenrud, 1985). When deciding antler point limits in a region, this variation needs to be taken into account. Male moose carry capital antlers earlier in southern than in northern Sweden (Wallin, Ericsson & Cederlund, 1996). Depending on the selection rate, optimisation of trophy male may need to be managed as 'strong regulation' (Figure 6). Accordingly, life-history and demographic traits of the population have to be thoroughly monitored.

Reduction of the winter population has frequently been necessary during the last decades. Case 3 (I) shows simulations of either a general overkill of adult females or a general overkill of the whole population. This case implies that relative stability in sex and age structure is important for optimal harvest regimes. In practice, general overkill might be difficult to achieve. Hunters may not be co-operative and accurate population data needed for precise management may be difficult to obtain. Reduction of a moose population should be accomplished by a careful combination of overkill of adult females and the whole population. Case 4 (I) illustrates the immediate effect of different female age structures on calf production. The calf production might vary considerably from year to year until the age structure is stabilised. If harvest policy under such circumstances is based on inaccurate population data this might be fatal for the population development.

It is obvious that the selective hunt applied during the last decades in Sweden, with increased calf harvest and protection of adult females, has resulted in increasing mean ages among the survivors. An observed trend of decreasing calf carcass weights indicates that more factors are involved, such as forage shortage and density-dependence effects (Broman *et al*., 2002). In order to support management activities within any management unit, such trends need to be monitored, and the reasons behind these changes should be examined.

How to improve monitoring by hunters' observation rates

The use of hunters' observation rate of moose have been found to be cost-effective and well-anchored among hunters. In papers (III) and (IV), I suggest awareness of sampling unit size, observation period, hunting effort effects (hunting team and team size) and effects related to different moose categories. Variation in observation rates can be large. The minimum observation effort required to achieve a sufficient level of accuracy for a given management unit has to be identified. The sampling variation can probably be reduced by carrying out year-to-year surveys within homogeneous management units, *e.g*. by standardising factors such as hunting activity, observation activity and vegetation cover (Ferguson, Oosenburg & Mercer, 1988; Fryxell, Mercer & Gellately, 1988; Anderson & Lindzey, 1996). Blocks with similar conditions should give rise to similar sampling and management units.

Training is another way to improve the estimates. The required precision of the estimates may also decide if training of specially pre-selected observation teams will suffice, or if all hunting teams should be trained. I also suggest identification of certain moose categories for monitoring. They should be demographically important, *e.g*. total moose or females without calves. The latter is to a large extent sub-adult females, *i.e*. the recruitment segment. However, increasing predation on moose calves may change the observation rate value of females without calves. The significance of the observation rates of a moose category may interact with the observation period according factors such as differences between male and female categories. The observation period ought to be carefully selected (IV; C.M.

Rolandsen *et al.,* unpublished data). Other important factors are choice of observation unit to use, *e.g.* hunting-day (III, IV) or, hunting-hour (Ericsson & Wallin 1999), and crucial factors as hunting method (Gustafsson & Cederlund 1994, Ericsson & Wallin 1996; Ball, Ericsson & Wallin, 1999). In northern Sweden, hunters observed more females when hunting with dogs, and a strong relationship between the observation rate of moose females and good weather (also for hunters with dogs) was found (Ball, Ericsson & Wallin, 1999). However, no weather (precipitation) effects on the observation rates was found in Norway (C.M. Rolandsen *et al.,* unpublished data), which suggests that this factor is complex.

It would be desirable to be able to forecast moose population sizes and changes with reliable and cost-effective monitoring methods. Paper (IV) suggests that there are possibilities to construct a forecasting model that adjusts for hunting effort. However, further studies are needed. Forecasting models need to be adapted to adequate management units by experiments and continuous monitoring, and they have to be verified by other survey methods.

Management steps

First, in the planning step (Figure 6), an 'adequate' management unit has to be selected. Main requirements are (i) that the unit covers similar conditions (*i.e.* biological, geographical, administrative, technical, economical, hunting traditions etc), and (ii) that the measurements taken within the unit will satisfy the demand on accuracy and precision of the requested parameters (III, IV). The variation and requests on the parameters, together with the regional or local variation, decide the size of the sampling areas. Different parameters may need differently sized sampling areas. It is important to identify limiting sampling size factors (both the minimum and maximum size), which will affect the size of an adequate management unit in a region. Management units of small sizes need to co-operate over larger areas, otherwise the result of the monitoring system will go astray. Trends in northern Sweden, *e.g.* larger properties, more area per hunter and higher proportion of loose dogs searching for moose, suggest that the size of the management units for hunters' observation rates could be larger in northern than southern Sweden (G. Ledström, pers. comm.; III). Dispersal and migration movements are other important factors to adjust for when the time comes to decide on management units. Sub-adult moose were found to be highly philopatric (no dispersal) in south-central Sweden (Cederlund & Sand, 1992). According to these authors, managers may carefully consider conditions conducive to dispersal, such as local density in relation to food resources, and sex-age distribution. Occurrence of long, seasonal migrations in moose populations in northern Sweden (Cederlund, Sandegren & Larsson, 1987; Sweanor, 1987; Sweanor & Sandegren, 1988; Ball, Nordengren & Wallin, 2001) also strongly affects the size and spatial co-ordinates of proper management units.

Second, collaborative work by hunters, land-owners and other parts of society is necessary. Often different parties have different or competing interests with regards to moose. For example, for hunters and many landowners the interest in moose is as the producer of desired products, recreation, and the social and interpersonal relationships resulting from hunting (I, II), but for forestry, agriculture and other landowners it can be a pest animal. The society in general has interest in the moose as a meat resource, an outdoor-recreation resource (Boman, Bostedt & Hörnsten, 2002; Ericsson & Heberlein, 2002), and as a component in the arts. The moose is also seen as a party in vehicle-moose accidents (Lavsund & Sandegren, 1991), as a browsing animal affecting the biological diversity (Bergström, 2000), and as prey to the increasing predator populations (Swenson *et al*., 1994; Wabakken *et al*., 2001). Ericsson, Boman & Mattson (2000) believe that comparisons between the bioeconomic effects of outcomes of different harvest strategies are necessary when evaluating the pros and cons in resource management. Such comparisons could provide wildlife managers with information which combines biology and economics (Clark, 1976; Getz & Haight, 1989; Tietenberg, 1996). The use of weighted economic values in order to identify the maximum harvest strategy for single and multiple production goals may be seen as a simplified alternative (II).

Third, is the action and regulating step. Nation-wide general regulation recommendations have been applied. For example, to increase the proportion and mean age of moose adults, the Swedish Association for Hunting and Wildlife Management recommends a harvest of 1 adult per 30 – 50 km^2, a large proportion of calves and a harvest period of at least 2-3 weeks (H. von Essen, pers. comm.). This recommendation skips the first step in the management chain and lands directly in the decision-making stage labelled *regulation strength* (Figure 6). It is a task in the planning step to identify the answers to a number of questions before the choice of the regulation strength and number of moose to harvest is decided. The strength depends on a number of factors, *e.g.* the goal and population parameters (sex-age-structure), which may differ between management units. I suggest more attention should be paid to the variation of relevant parameters affecting the management and regulation of moose in Sweden (Figure 6). The example presented probably ends up as an intermediate regulation in many management units. However, if the recommendation turns out to be strong regulation, high precision monitoring and adaptive management are needed. It is important to follow the management chain as far as possible. In addition, there is limited information concerning how the individual hunter views the management and regulation of moose. If the hunters lack understanding (and therefore motivation), there is a risk that the management and selective choices will go astray.

Fourth, one of the most important management tools would be proper monitoring. The quality and cost differs between methods available. In order to improve the total value of the population parameter estimates, various methods may complement each other (Sylvén, Jernelid & Bergström, 1994). Long-term monitoring programmes for moose management may be cost-effective methods that monitor population parameters. Examples are hunters' observation rates of moose (Ericsson & Wallin, 1999; Solberg & Sæther; 1999; III, IV) and prediction of body mass from chest circumference (Wallin, Cederlund & Pehrson, 1984). Programmes could include forecasting of total population trends, and of population condition and structure with regard to demographically important moose categories. It would be advantageous to have examples of 'experimental' management units in different regions, and to develop and implement a set of performance indicators. An advisory service could be a complementary way to support managers, so they would know what to monitor and when they are successful.

Conclusions

In spite of an increasing availability of theoretical knowledge about the effects of general harvest strategies on game animals, there is a need to transfer this species-specific information to decision makers, managers and hunters. Thus, the relationships calculated regarding moose in computerised simulations of harvest strategy effects should be provided as management tools.

Simulations can visualise general relationships between regulation goals, harvest strategies, and the development and yields of defined moose populations. A goal does not have to be a single product, *e.g.* hunting opportunities or meat yield. It could be based on several sub-goals, where economic weights reflect preferences for the relevant products.

Demographic and environmental variation affect the management system and the regulated moose harvest. Thus, one of the most important management tools will be proper monitoring and forecasting programmes. Standardisation should be a prerequisite for the use of observation rates since the estimated composition of the real moose population will be biased without calibration or adjustment of the observation rates of different moose categories. Regionally adequate sampling areas (management units), relevant observation periods, and differences among observed moose categories due to differences in hunting effort need to be further examined. Certain key indices may be identified. I suggest further application and evaluation of complementary survey methods.

Future moose management needs an integration of biological, technical, economic and human dimensions. It would be advantageous to have 'experimental' management units in different regions, to develop and to implement a set of performance indicators. An advisory service could be a complementary way to support managers. Finally, in order to obtain a complete management chain consisting of planning, acting (regulation), monitoring and immediate corrective feed back, I particularly suggest an examination of how individual hunters view the hunt and its management.

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