# STATUS OF MOOSE POPULATIONS AND CHALLENGES TO MOOSE MANAGEMENT IN FENNOSCANDIA

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ABSTRACT: In the Fennoscandian countries, Norway, Sweden, and Finland, moose (Alces alces) populations began to increase rapidly in the 1960s and have since then been among the most productive and heavily harvested moose populations in the world. At the start of the 20th century, the total annual harvest was < 10,000 moose, whereas in 2000, the annual kill reached about 200,000. The winter population was estimated to be about 500,000. In Sweden and Finland, the highest harvest numbers (and presumably population density) were recorded in the first half of the 1980s and in Finland again in the late 1990s and during the beginning of the 2000s. In Norway, the 1990s was the decade of the highest harvest numbers. The current regional moose density during winter varies from < 0.2 to about 2 moose/km<sup>2</sup> within Fennoscandia. Locally, the density may far exceed this level in typical wintering areas (e.g., 5-6 moose/km<sup>2</sup>). In general, the current densities are lower in the north than in the south and higher in Norway and Sweden than in Finland. The strong increase in harvest and the present high densities are explained by several factors. First, modern forestry clear-cutting practices have provided Fennoscandian moose with prime habitats in the form of early succession stages. Accordingly, the current carrying capacity is likely to be relatively high compared to the situation 50-100 years ago. The current trend, however, is towards less activity in the forest and a decreasing proportion of forests found at an early successional stage. This may increase the food limitation already seen in several populations; i.e., in all three countries, body mass and recruitment rates have been found to decrease with increasing density. Second, the introduction of sex and age-specific harvesting in the early 1970s has increased the general productivity of the populations. By focusing the harvest on calves, yearlings, and adult males, the proportion of productive females, the mean age of females, and the annual recruitment rate have increased. Simultaneously, the proportion and mean age of males have decreased, and in some populations, this has been associated with delayed parturition dates and lower fecundity; i.e., due to inadequate number of males for timely reproduction. Third, mortality other than hunting is low, and only near the eastern border of Finland with Russia has predation by wolves and bears had a notable effect on productivity figures. This situation is about to change with increasing populations of large carnivores in all of Fennoscandia during the 1990s. The management principles have been quite similar within Fennoscandia, although differences in legislation have resulted in national and regional differences in management performance. In general, moose managers take advantage of data collected by hunters during the hunting season (e.g., hunting statistics, number, sex, and age of moose observed) to monitor population development and determine hunting quotas. Moreover, in all three countries, the issues of traffic accidents and damage to forestry and agriculture play a central role in moose management and discussions concerning optimum population sizes.

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During the last 100 years, the status of moose has changed from being a relatively rare species to becoming a widely distributed and dominating species all over the forested part of Fennoscandia: Norway, Sweden, and Finland (Fig.1). Less than 10,000 individuals were harvested annually at the start of the 20th century. In contrast, more than 200,000 (0.3 moose/km<sup>2</sup>) were harvested annually during the most recent years. This strong increase in harvest, and presumably population size, appears to have several causes, with changing practice in forestry (increas-



Fig. 1. The Fennoscandian area: Norway, Sweden, and Finland. Counties in Norway: 1=Rogaland, 2=V-Agder, 3=A-Agder, 4=Telemark, 5=Vestfold, 6=Østfold, 7=Akershus, 8=Buskerud, 9=Hordaland, 10=Sogn and Fjordane, 11=Oppland, 12=Hedmark, 13=Møre and Romsdal, 14=S-Trøndelag, 15=N-Trøndelag, 16=Nordland, 17=Troms, 18=Finnmark. Regions in Sweden: Southern Götaland, Eastern Götaland, Western Götaland, Eastern Svealand, Western Svealand, Southern Norrland, Northern Norrland. Regions in Finland: Coastal Finland, Inland Finland, Oulu district, Lapland. ing frequency of clear cuts) and introduction of sex and age-specific harvesting probably being the most important. The absence of bears (*Ursus arctos*) and wolves (*Canis lupus*) was another factor that facilitated the increase in the populations (e.g., Cederlund and Markgren 1987, Østgård 1987).

The increasing density of moose has been appreciated by hunters, but has also caused frustration among landowners and the authorities because of the negative impact on commercial forests and highway traffic safety (e.g., Solbraa 1998, Hakkila and Kärkkäinen 1999, Edenius et al. 2002). In addition, there has been growing concern about the impact of high densities and the intensive harvesting on the moose population itself. High densities are commonly associated with decreasing body condition, fecundity, and survival (e.g., Sæther 1997, Gaillard et al. 1998), and intensive harvesting may have consequences for the population dynamics beyond the direct effect on the population growth rate. The proportion of adult males has, for instance, seriously decreased in many populations following the introduction of a sex- and age-specific harvesting regime in the early 1970s, with possible demographic and genetic effects (e.g., Nygrén 1986, 1990; Ericsson 1999; Sæther et al. 2003). There were several attempts to halt the population growth and stabilise the population size in Fennoscandia during the 1980s and 1990s, but these attempts often resulted in large population fluctuations. Legislative, administrative, and social factors were involved in the failures (Nygrén 1998a). In addition, there was a lack of experience with the high density and productivity of the strongly female-biased populations, as well as limited data on population performance. Thus, to be able to perform sustainable moose management, there is an evident need for consecutive information on moose population dynamics



and demography at each of the local, regional, and national scales.

Part of the process towards a better understanding and management of the moose population is to recall and analyse past population development and experience with various methods of moose management. In the present paper, therefore, we summarise the development and current status of the Fennoscandian moose populations with respect to harvest, population density, and population structure. Previously, papers on the status of moose in Fennoscandia were presented as a part of the proceedings from the 2nd International Moose Symposium in Uppsala, Sweden in 1984 (Cederlund and Markgren 1987, Nygrén 1987, Østgård 1987), and accordingly, we will mainly focus on developments during the last 20 years in the present paper. We also provide a brief overview of present day moose management systems in Fennoscandia, and finally, present some future challenges for moose management in the three countries.

#### **METHODS**

The status of Fennoscandian moose populations is described mainly by the use of hunting statistics and systematic moose observations performed by moose hunters ("moose observation monitoring"). Traditionally, harvest statistics have been assumed to provide a reasonably proxy to the variation in moose density in Norway and Sweden (Cederlund and Markgren 1987, Østgård 1987), recognizing time lags due to delays in the decision-making process (e.g., to settle the right quota size; Cederlund and Markgren 1987, Solberg et al. 1999). The relationship between the variation in harvest and moose density has since been confirmed in several independent studies (e.g., Solberg et al. 1997, 1999).

Since the introduction of moose observation monitoring in the early 1970s in Finland and in the mid-1980s in Norway and

Sweden, variation in moose density and population structure have been estimated from the numbers of moose observed during the hunting season. The observation monitoring is a systematic recording and collecting of sex and age (calf or adult) of moose observed by moose hunters during the hunting season. Several indices of population structure are calculated from the observation monitoring data (e.g., Nygrén and Nygrén 1976, Solberg and Heim 2002). The most important indices are "calves/ adult", "calves/cow", and "cows/bull" as indices of recruitment rate and adult sex ratio, respectively. In addition, indices of population density are calculated in Norway and Sweden as "moose seen per hunter day" and in Finland as "moose seen per team-hunting day". In Finland, hunters also provide estimates of the number of moose left on their hunting grounds after the hunting season. Despite the crude sampling procedure and a high number of likely confounding variables (variation in weather, hunting skills, number of hunters, hunting methods, etc.), the observation indices are found to provide precise information on the temporal development in population size and structure within a given area (Ericsson and Wallin 1994, 1999; Solberg and Sæther 1999; Solberg et al. in press), provided that the number of observations is relatively high (Ericsson and Wallin 1994, Sylvén 2000).

In Finland, more than 5,000 hunting clubs annually record 200,000 – 300,000 moose observations and, in Norway, approximately 200,000 observations are added annually to the database (Rolandsen et al. 2004). In Sweden, these data were not yet available in 2002 for analysis on a national level (J. Kindberg, Svenska Jägareförbundets viltövervakning, personal communication) despite having been collected on a local level since the early 1980s. The only reliable and systematic statistics available in Sweden are therefore from the harvest



statistics (Svenska Jägareförbundets **20** viltövervakning 2002).

To get a rough estimate of the moose density within and between countries, we used data from moose observation monitoring and harvest data, and to some extent data from aerial and other types of surveys during winter. In Finland, retrospective analysis of previous years' population estimates was also used for the period 1983 – 1996 (Nygrén 1984, Nygrén and Pesonen 1993).

# **RESULTS AND DISCUSSION** Harvest, Traffic Accidents, and Population Development

Since the early 1970s, Fennoscandian moose populations, as indexed by the annual harvest, have varied widely both temporally and regionally. In Sweden and Finland, the highest harvests were recorded in the first half of the 1980s, and in Finland again in the late 1990s and early 2000s (Figs. 2, 3, and 4). In Norway, the harvest increased during the 1970s and 1980s until it more or less stabilized during the 1990s (Figs. 2 and 5). The all-time annual record of moose kills was 174,709 in Sweden (in 1982), 84,524 in Finland (in 2002), and 39,309 in Norway (in 1999) (Fig. 2). In 2003, the total harvest



Fig. 2. Number of moose harvested in Fennoscandia, 1971–2003.



Fig. 3. Annual variation in the accumulated harvest of moose in different regions of Sweden during the period 1972-2001. The regions are from bottom-up (see Fig. 1): Southern Götaland, Eastern Götaland, Western Götaland, Eastern Svealand, Western Svealand, Southern Norrland, and Northern Norrland.



Fig. 4. Annual variation in the accumulated harvest of moose in 4 regions of Finland, 1964-2003. The regions are from bottom-up (see Fig. 1): Coastal Finland, Inland Finland, Oulu district, and Lapland.

was about 225,000 moose in Fennoscandia: Norway 38,600, Sweden 103,185, and Finland 84,466.

The number of moose traffic accidents covaries to a large extent with the annual harvest during the period with available





Fig. 5. Annual variation in the accumulated harvest of moose in different counties of Norway during the period 1971-2003. The counties are from bottom-up: Østfold, Akershus, Hedmark, Vestfold, Buskerud, Oppland, Telemark, A-Agder, V-Agder, S-Trøndelag, N-Trøndelag, Nordland, Troms, Finnmark, Rogland, Hordaland, Sogn og Fjordane, Møre og Romsdal (in counties 14-18 the annual harvest is still very modest). Concerning counties cf. Fig. 1.

data in Fennoscandia (Figs. 6-8). Although this index varies with several factors (e.g., the severity of the winter; Andersen et al. 1991), it is commonly assumed to be closely associated with moose density (e.g., Lavsund and Sandegren 1991; Solberg et al. 1997, in press; Haikonen and Summala 2000). In Norway, the number of moose killed in traffic accidents peaked in 1993 (Fig. 6). A similar relationship is present in Sweden from the period 1972-1999 (Seiler 2003; Fig. 7). The number of accidents peaked in 1980, 2 years prior to the peak in the moose harvest, whereas another peak appeared in the late 1980s, 2 years prior to the second peak in the number of harvested moose. This time difference is consistent with the assumption that harvesting is the main driver of population fluctuations and that the number of road-kills is a fair index of population density (Solberg et al. in press).

In Finland, 1,100 - 3,000 moose accidents were reported annually during the period 1976-2003 (Fig. 8). The number of

accidents does not correlate as well as in Sweden and Norway (Figs. 6-7) with the large annual fluctuations in harvest, but seems to be a rather good index of popula-



Fig. 6. Annual variation in the number of moose harvested and reported dead in accidents on roads and railways in Norway, 1 April 1987 to 31 March 2002. Data are reported for the hunting year from 1 April to 31 March in year t+1.





Fig. 7. Annual variation in the number of moosevehicle collisions and harvested moose in Sweden, 1972-1999. Trends in Swedish moose harvest correlate significantly with the number of police-reported vehicle collisions with moose ( $r^2=0.77$ , n=30, P<0.0001) (after Seiler 2003).

tion density in Finland (Fig. 8).

The winter moose population in Finland was estimated to be between 66,700 (1996) and 113,000–125,000 animals (2002) in the period 1981-2002 (Nygrén 1996a, unpublished data; Ruusila et al. 2002), whereas in Norway, Solberg et al. (in press) estimated the total Norwegian moose population during winter to be between 90,000 (1995) and 117,000 (2000) in the period 1991-2000.



Fig. 8. Annual variation in the number of moosetraffic accidents and harvested moose in Finland, 1976-2003. Data on moose accidents are from the Finnish Road Administration/Road traffic accident data bank.

The Swedish moose population in the winter of 2000/2001 was estimated to be around 250,000. Thus, almost 500,000 moose may have roamed the forests of Fennoscandia during winter at the start of the new millennium.

#### **Regional Population Density**

The winter density of moose in 2000/ 2001 for all countries combined (forested areas in Fennoscandia cover approximately 650,000 km<sup>2</sup>; Global Resource Assessment 2000 FAO, www.fao.org) was 0.7-0.8 moose/km<sup>2</sup> or slightly less than 1.0 moose/ km<sup>2</sup> in Norway and Sweden and approximately 0.5 moose/km<sup>2</sup> in Finland.

In Norway, the highest densities of moose are found in the southeastern and central parts (Fig. 9), with an average winter density between 1 and 2 moose/km<sup>2</sup>, and



Fig. 9. Mean annual moose harvest in Norway per km<sup>2</sup> of forest and bogs below the timberline in different municipalities within counties (demarcated by black lines; see Fig. 1), 1999-2001. White: no hunting; light gray: 0.01 – 0.10; gray: 0.11-0.40; dark gray: 0.41-0.70; and black: 0.71 – 1.20 moose/km<sup>2</sup>, respectively. Note that the coastline is demarcated in black.



for a few municipalities slightly above 2 moose/km<sup>2</sup> (Solberg et al. 2003). In the more continental parts of southern Norway and inner parts of northern Norway, the average moose density is lower, but may in effect be much higher during winter due to concentrations in restricted wintering areas. In particular, in areas with deep snow, moose tend to congregate on the valley floor or in low elevation areas with less snow during winter (Sæther et al. 1992, Hjeljord 2001). In these areas, densities may far exceed 2 moose/km<sup>2</sup> over large areas (e.g., Sæther et al. 1998). For instance, in the central parts of Troms (area 17, Fig. 1), moose from the mainland part of the county tend to concentrate in 2 valleys during winter where the average density may reach as high as 5-6 moose/km<sup>2</sup> in the core distribution areas (20-50 km<sup>2</sup>) (B.-E. Sæther, J. Solberg, and M. Heim, unpublished data). The lowest moose density is found along the west coast, particularly in



Fig. 10. Moose post-hunting population density (moose/km<sup>2</sup>) in relation to forest land in Sweden, 1972 – 2001. The figures must be regarded only as a rough index of the population density. Regions as given in Fig. 1.

the more central coastal regions, where moose are still a rare sight and hunting is prohibited (Fig. 9, Solberg et al. 2003). To some extent these low densities may be a temporary phenomenon as moose quite recently have colonized these areas.

In Sweden, the highest winter densities of moose (calculated using harvest data) during recent years (2001) are found in central Sweden (Svealand, Figs. 1 and 10) with densities of 1.1 - 1.2 moose/km<sup>2</sup>. Slightly lower densities are found in southern Sweden (Götaland, Figs. 1 and 10, 0.6 - 0.9/km<sup>2</sup>) and northern Sweden (Norrland, Figs. 1 and 10,  $0.4 - 0.9 \mod km^2$ ). The lowest moose densities are found in the southernmost part of Sweden, an area dominated by farmland, and in the northernmost part of the country, which has very low forest productivity. In these northern regions, winters are usually 1-2 months longer than in the south and snow is deeper, (between 0.5 and 1 m; Sveriges Nationalatlas Skogen 1996, Sveriges Nationalatlas Klimat, sjöar och vattendrag 1997). As in northern Norway, seasonal migrations to wintering areas are common in these regions, and may locally exceed the average density by as much as 5 times (Sweanor 1987, Ball et al. 2001).

In Finland, the most preferred habitats for moose are in Coastal Finland (Fig. 1), especially in the southwestern archipelago and the west coast where the snow depth does not restrict moose mobility and the growing season is longer than in other parts of Finland (Fig. 11). Historically, these areas have had the greatest moose densities in spite of efforts to reduce population density in areas where the human population and traffic densities are the highest. The highest densities reached to date were in southern Finland during the winter 1977-78 (Fig. 12), with average densities of some game management districts exceeding 1.1 moose/km<sup>2</sup>. Subsequently, densities in both



Coastal and Inland Finland were reduced to 0.4 - 0.5 moose/km<sup>2</sup> (Fig. 12). In the Oulu district, where the population increase during the 1970s was much slower (Fig. 12), the densities increased to the same level as in Coastal and Inland Finland. In Lapland, the average densities of moose were lower, but even there, the highest densities before 1996-97 were achieved in the mid-1980s.

The stable period ended after a change in legislation during the second half of the 1990s. At first the densities decreased, especially in Inland and Eastern Finland where the density decreased below 0.25 moose/km<sup>2</sup> in some game management associations. Some associations in the easternmost areas of Finland, where large carnivore populations exist and have a significant effect on moose productivity (Nygrén 1980), protected the moose for 1- 3 years (Nygrén 1998b).

Data comparable to density figures for

1974-96 in Finland are not available for the late 1990s. However, according to moose density indices (Fig. 13), there were about 0.6 moose/km<sup>2</sup> in Coastal Finland, 0.5 moose/ km<sup>2</sup> in Inland Finland and 0.3 moose/km<sup>2</sup> in the Oulu district (Nygrén et al. 2000). Since then, densities first increased and then decreased to an average level of 0.35 moose/ km<sup>2</sup> in the winter of 2003/2004 (Ruusila et al. 2002, 2004).

# **Changing Population Structure and Population Condition**

There has been a significant change in moose population structure in Fennoscandia during the last 30 years. Prior to 1970, moose were mainly harvested as yearlings or older, with both sexes almost equally represented. However, as part of the strategy to increase population density in the early 1970s, age- and sex-specific harvesting was introduced in Norway (Østgård



Fig. 11. Density gradients of the Finnish moose population, 1977-1996 (moose/km<sup>2</sup> of dry land area). Modified from Nygrén 1996b. Moose densities as calculated in Fig. 12







1987) and Sweden (Cederlund and Markgren 1987), and similarly, new hunting principles were adopted in Finland after the protection of moose from 1969-1971 (Nygrén 1987). The focus of the harvest was put on bulls and juveniles (calves and yearlings), leaving an increasing proportion of productive adult cows in the population. The result was an immediate strong increase in the harvesting of adult males (Fig. 14), whereas the calf harvest was initially low due to a reluctance to shoot calves (Fig. 15). Since then, however, there has been a gradual change of attitude and at present calves are harvested at a rate approximately proportional to their presence in the population in Norway, and at even higher proportions in Sweden and Finland (Fig. 15).

In contrast to the proportion of calves, the proportion of males in the adult harvest



Fig. 13. Moose density indices (estimation of hunters of moose/km<sup>2</sup> of dry land area and moose seen/team hunting day) in 3 regions of Finland, 1975-1999 (data from Finnish Game and Fisheries Research Institute). Moose densities as calculated in Fig. 12. Regions as given in Fig. 1.

has decreased compared to the 1970s (Fig. 14). This is likely a reaction to the previously intensive harvesting of males, leaving a decreasing proportion of adult males in the population. For instance in Norway, adult males comprised 40-50% of the yearling





Fig. 14. Bulls per cow in the moose harvest in Sweden, Finland, and Norway, 1972–2001.



Fig. 15. The proportions of calves in the moose harvest in Sweden, Finland, and Norway, 1972 –2001.

and adult population in the early 1970s (Sæther et al. 2001), whereas the proportion of males is currently less than 30% in many populations and in some populations closer to 20% (Fig. 16). Similarly, the proportion of males decreased quickly in southern Finland during the 1970s and early 1980s (e.g., Nygrén 1986), but later that trend was slowed as a result of changes in harvest recommendations (Fig. 17). No comparable figures are available for Swedish populations. However, since on average there are a similar proportion of adult males in the harvest in Sweden as in Finland (Fig. 14), we believe the proportion of adult males in the Swedish population to be higher than in Norway and comparable to the situation in Finland.

Following the change of harvest systems there was an increase in the production of calves all over Fennoscandia (e.g., Koivisto 1963; Nygrén 1984, 1987; Solberg et al. 1999; Nygrén et al. 2000). A part of this was probably due to an increase in the proportion of adult females in the populations. However, by relaxing the harvest of adult moose females from an intensive harvest pressure and by intensifying the calf harvest, the average age of females in the populations also increased, which positively influences fecundity (Nygrén 1990, Solberg et al. 1999). Selective harvesting of adult females may have further enhanced this development (Cederlund and Markgren 1987, Wallin 1992, Solberg et al. 2000). Many hunters select females based on the numbers of calves accompanying the females during the hunt and try to select those without calves in preference to those with 1 or 2 calves. Highly reproductive females may consequently experience higher survival. Accordingly, Ericsson (1999) showed that the cost of reproduction in Sweden was reversed for the high-reproductive female segment aged 5-10 years. Entering the hunt with 2 calves was more beneficial for survival than entering with 1 calf or no calves. Females 5-10 years old not giving birth had a 3.2 times higher risk of being killed during the hunt. This selective harvest resulted in a 2.5 times higher potential growth rate for the population versus a random harvest of adult females.

Probably as a result of selective harvesting, the present productivity of the Finnish moose population is the highest ever recorded. In autumn 1999, the average number of calves/female was 1.01 in Coastal



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Fig. 16. Norway. Annual variation in (A) moose seen per hunter-day, (B) adult (≥ 1-year-old) males per female, (C) calves per female, and (D) calves per calf-rearing female (twinning rate) in different counties of Norway during the period 1986-1998. Data from "moose observation monitoring". Counties as given in Fig. 1.



Fig. 17. Annual variation in the number of males per female in 4 regions of Finland, 1975-1999.Data from moose observation monitoring; Finnish Game and Fisheries Research Institute. Regions as given in Fig. 1.

Finland, 1.02 in Inland Finland, 0.91 in Oulu district, and 0.78 in Lapland (Figs. 1 and 18; Nygrén et al. 2000). Until 2002, there was no significant change (Ruusila et al. 2001, 2002). In Norway, the numbers of observed calves/female also increased during the initial phase through to a peak in the early 1990s and have since been decreasing over large areas. The decrease has been associated with increasing population density and decreasing body masses of calves and yearlings and is generally assumed to be caused by density-dependent food limitation (Solberg et al. 1997, 2002).

In spite of high moose densities in Fennoscandia, no clear density effect has been found that could explain the large





Fig. 18. Annual variation in the number of calves per female in 4 regions of Finland, 1975-1999.Data from moose observation monitoring; Finnish Game and Fisheries Research Institute. Regions as given in Fig. 1.

scale fluctuations in the population density. In all three countries, however, some density-related factors have been studied and do seem to locally have an effect on population dynamics. In Norway, moose body mass has been decreasing since the 1970s, following increasing densities (Solberg et al. 1997, Hjeljord and Histøl 1999) and, as mentioned above, calves/female ratios have decreased in many populations during the last 30 years (e.g., Solberg et al. 1997, 2000). In Sweden, body mass and fecundity decreased in several populations following the high moose densities in the early 1980s (Sand et al. 1996). Similarly, in Finland, the average productivity and body mass decreased at the beginning of 1980s after the peak density years, but increased again during lower density periods of the 1990s (Nygrén 1997). In other high density populations in southern Sweden and southern Norway, body mass and recruitment rates decreased following increasing density, but currently show no sign of increase again despite significant reduction (>50%)in population density (e.g., Solberg et al. 2002, Broman 2003). This indicates that long time lags in the effect of high density (through maternal effects or vegetation), or alternatively, that the range quality (carrying capacity) may be significantly reduced (e.g., Solberg et al. 2002, Broman 2003).

### Factors behind Population Development

Recognizing that harvesting is among the most important factors behind the variation in moose density in Fennoscandia, it is of interest to describe some of the underlying processes leading to the observed population development during the last 30 years. In general, the increasing moose densities are assumed to be a reaction to the introduction of age and sex-specific harvesting in the early 1970s and relatively light harvesting due to a general desire to increase moose hunting opportunities (Nygrén 1984, Cederlund and Markgren 1987, Østgård 1987). As the population density increased, however, the number of moose killed on the roads and railroads by cars and trains (Figs. 6, 7, 8) and damage to forestry also increased (Lavsund 1987, Lavsund and Sandegren 1991, Seiler 2003). In Sweden and Finland, these problems resulted in public opinions that the moose population had to be reduced, which led to the peak harvest in the early 1980s. Similarly, in Sweden, the second peak in the late 1980s is regarded to be a reaction to a still ongoing discussion concerning moose-forest interactions. In 1988, a special report, "Älgen och skogen" (Moose and Forestry) was published (Rülcker 1988), and in 1990 proposals concerning population goals for moose were presented by the government (Fransson 1990).

Forestry concerns in the late 1990s were again reflected in increased harvest (Svenska Jägareförbundets Viltövervakning 2002) driven at least to some extent by forestry stake-holders (Carlestål 2000). Special survey methods were introduced to measure the level of damage to commer-



cially valuable trees, as well as to species important to biological diversity (Skogsstyrelsen 2002) and by the late 1990s forest agencies had presented goals concerning acceptable levels of different kinds of forestry damage. One goal was that yearly levels of certain types of damage to pine saplings must not exceed 2 %, and that willows (*Salix* spp.), aspen (*Populus tremula*), and rowan (*Sorbus aucuparia*) must be able to regenerate.

Following similar problems in Norway, there were several attempts to stabilize the population size during the 1980s, especially in the southeastern part of the country where the growth rate was exceptionally high during the 1970s and early 1980s. In the more western and northern counties, where the density increased more slowly due to a slower introduction of the new hunting regime (Østgård 1987), a similar response was observed in the early and mid-1990s. During the initial stabilizing phase the effort to halt the population increase often resulted in over- and under-harvesting due to local inexperience with the dense and highly productive female-biased populations. This was exacerbated by a lack of appropriate census data on moose density, as data from moose observation monitoring was of little use in moose management until the late 1980s. Since then, population indices derived from moose observation monitoring are increasingly used as a tool in local moose management in Norway, and the frequency of apparently uncontrolled fluctuations in the annual harvest have decreased.

Management of moose in Finland has been very target-oriented. The public discussion about management goals began in the mid-1970s and the first density goals were set in 1976 (Nygrén 1987). In Coastal Finland, the maximum tolerable density was thought to be 0.7 moose/km<sup>2</sup> of dry land (lakes excluded) compared to 1.0 moose/ km<sup>2</sup> of forestry land. In short order this was considered to be too many moose and the density goals were adjusted down in 1980 and revised again in 1984, 1988, 1994, and 1995. Among the principal early reasons for lower density goals was the negative effect of high densities on moose calf production. Later, the goals for maximum densities were based on the tolerable number of traffic accidents (Fig. 8) and damage to forestry and agriculture. Unlike in Sweden and Norway, moose damage on private land in Finland is compensated for with money from license fees.

Up to 1993, management decisions were made at a centralized level. The Finnish Game and Fisheries Research Institute (FGFRI) played an important role and provided annual recommendations for license numbers and selective hunting after the density goals were set (Nygrén and Pesonen 1993). Moose observations and retrospective population analyses had an important position in population monitoring. Later, the hunting legislation was reformed and a system of locally operated moose management areas was adopted in 1993. The game management districts and associations became more independent, and the management of the moose population less coordinated. A couple of years later, the first problems with decreasing densities were experienced (Nygrén 1996a). The number of licenses was cut drastically (Nygrén et al. 1999), and, after the second rapid population increase, the amount of forest damage and the number of traffic accidents (Fig. 8) increased to intolerable levels. In 2002 and 2003, a larger number of moose were harvested than ever before in Finland (Fig. 4).

# Moose Hunters, Hunting Rights, and Hunting Methods in Fennoscandia

Hunting is a very popular activity in Fennoscandia, and depending on the number



of moose licenses issued, a large number of hunters are hunting moose. For instance in Finland, about 100,000 hunters hunted moose in 1999, whereas 2 years earlier, when the moose quota was significantly lower, there were only 69,000 hunters (Koskela and Nygrén 2002). In Norway, about 200,000 persons hunt annually, of which 56,000 are currently hunting moose (Statistics Norway 2002; http://www.ssb.no). The similar figure in Sweden is about 300,000 hunters, of which 80% take part in moose hunting (Ekman 1992).

The moose itself has no owner in Fennoscandia (e.g., Nygrén 2000), but the landowner holds the hunting rights. The landowner can in turn lease the hunting rights to hunters.

The start and the duration of the hunting season vary within and between countries. In Finland, the season begins on the last weekend of September and continues until December 15th. In Norway, the season is currently from 25 September to 30 October, but with local variation at both ends of the season. The longest seasons are found in Sweden, where moose can be hunted for a minimum of 70 days and, in some areas, for as long as 3.5 months. Moose hunting begins in the first week of September in northern Sweden and in the second week of October in southern Sweden. In addition to this system, there is a system of short (5 days or less) open seasons for small areas in which usually only one moose may be harvested.

Moose hunting is a social activity that often involves one or several dogs and a large group of people, of which several may not carry a gun (beaters). In Finland, for instance, an average hunting team has 18 members and a hunting area of 5,600 hectares (Koskela and Nygrén 2002). Hunting with dogs is most popular (73 % of hunting days), but also flushing with beaters is common (19 % of moose hunters do not carry a weapon) (Koskela and Nygrén 2002). Although less detailed information is available from Norway and Sweden, similar hunting methods are common in both countries.

## Current Moose Management, Harvest Regulations, and Management Goals

The general mechanism for regulating the number of moose to be harvested is a licence system, with licences issued by local or regional authorities. In Norway, the number of moose hunting licences is set by the municipality wildlife management authority in accordance with an established "minimum area" for each licence (Danielsen 2001). Until 2001, the County Governor settled the "minimum area" (Jaren 1992), but this responsibility is now delegated to the municipality. The size of the "minimum area" may vary among municipalities, and even within municipalities, depending on the local moose density and the planned development of the moose population in the municipality.

Moose hunting can only occur within the legal hunting season set by the national hunting authorities (Directorate for Nature Management) and on land defined as a moose hunting area by the municipal wildlife management authorities. The number of licences is issued in accordance with the size of the hunting area and the local "minimum area". The minimum hunting area for one licence (one moose) is the same size as the "minimum area" in that municipality or part of municipality. Licenses may be specified as to sex and age categories (calf, adult female, adult male) or, alternatively, as a number of un-specified animals in cases where the hunting area has an approved population management plan of 3-5 years duration. The population management plans have to describe in detail the desired number and proportion of each sex and age-category of moose to be harvested during the planning period. To be approved, the man-



agement plan must also be compatible with municipal moose management goals; i.e., to what extent the local authorities want the moose density to increase or decrease.

Changes in population density and structure in Norway are, in most municipalities, determined by the use of data from moose observation monitoring and to some extent by irregular winter aerial surveys (Solberg and Saether 1999). Since the introduction of new hunting regulations in 2002, hunting areas with an approved population management plan are given the complete hunting quota for the planning period at the outset. The approval may be withdrawn or amended by the municipality if the harvest deviates significantly from the approved plan and/or if the status of the moose population radically changes.

The new practice of locally based moose population management plans is part of a gradual decentralization of wildlife management in Norway. The intention is to provide more precise moose management in accordance with local management goals (Danielsen 2001). Jaren (1992) and Danielsen (2001) provide more detailed information about moose management in Norway.

In Sweden, moose hunting licences are issued by the county authorities and specify the number of adults and calves that may be harvested. However, in specific "Moose management areas", which due to their large size and shape are assumed to hold their 'own' moose population, the number of moose to be harvested is decided by the landowners and hunters themselves. These "Moose management areas" have been introduced to decrease the administrative work of the county authorities, and to inspire hunters to be more responsible in managing their local moose population. However, a shortcoming of this management system is that the information concerning the density and other traits of the populations often are inadequate to set regulations to achieve specific density goals (e.g., Broman 2003). The main methods used to follow changes in population density and structure are by the use of data from moose observation monitoring and in some areas by winter aerial surveys.

In Finland, the 15 game management districts each determine the number of hunting permits issued. Since 1993, a single licence has granted the right to shoot either 1 adult moose or 2 moose calves. The minimum area needed for a permit is 10 km<sup>2</sup>. In most cases, only one hunting club can hunt in a hunting area, except in large state-owned areas in Northern Finland where local inhabitants have hunting-rights in their own municipality and several hunting clubs can hunt moose simultaneously in the same area. Earlier, the number of licences issued for hunting clubs was based on information from local hunters, hunting authorities (game management associations and districts), and FGFRI moose researchers, as well as annual negotiations between hunting authorities and stakeholders. At present, the game management districts and associations produce the information needed for management, as well as deciding management goals and numbers of permits more independently, on the understanding that the density margins from 1995 are to be maintained.

The main management goal in Norway, Sweden, and Finland has been to maintain a highly productive moose population that tolerates large annual harvest quotas. Also, stability of the population has been a common goal for all countries; in Norway as stability of harvest and in Finland as stability of the post-harvest population. Finland is the only country that has official density goals set by the Ministry of Agriculture and Forestry. Since 1995, the goal has been to have 0.2 - 0.5 moose/km<sup>2</sup> of dry land (compared to 0.26 - 0.65 moose/km<sup>2</sup> of forestry



land) in most of the country (Nygrén 1997). In the northernmost areas the goal has been lower, 0.05 - 0.3 moose/km<sup>2</sup> of dry land (i.e., about the same as per forestry land in Northern Finland where more than 90 % of areas consist of forestry land). In Norway and Sweden, the goals are more local and less uniform, and higher moose densities are more readily tolerated than in Finland.

### **Future Challenges**

Future challenges for moose management in Fennoscandia are numerous. An important challenge concerns the recent change from a centralized to a decentralized system of moose management. In all Fennoscandian countries, local decisionmaking has been accepted as the future system of moose management. To what extent this will improve or worsen the management is not yet known, but the critical comments are many (e.g., Nygrén and Nygrén 1994, Nygrén 1998a, Broman 2003). A commonly asked question is what are the capabilities of local hunters to apply their knowledge of moose population dynamics? In Finland, for instance, local hunters (=game management associations) now are responsible for collecting information, for analyzing and determining the population status, for deciding population goals and license numbers, and for determining the composition of the harvest. In small hunting areas, this is an impossible task for the local hunters because moose summer and winter areas are usually larger than the area of the association. In addition, the goals can differ extensively between neighboring associations.

Professional managers and researchers in Sweden and Norway have expressed similar concerns. The general view is that moose hunters may have direct interest in the resource itself, but not necessarily have deep insight into moose population dynamics or interest in moose management. This may change in the future if local communities, or larger aggregations of local communities, are willing to invest the necessary resources in developing local expertise. Alternatively, moose management may be delegated to traditional management agencies, while local involvement is restricted to formulation of goals (Broman 2003).

Another challenge to future moose management concerns the negative effects of selective harvesting and high population density. In all three countries, but especially in Norway, the proportion of adult males in the population has decreased significantly during the last 30 years. In populations with extreme sex-bias, Sæther et al. (2003) and Solberg et al. (2002) reported delayed parturition and lower fecundity, most likely due to an inadequate number of experienced males for timely reproduction. The same type of decrease in adult male proportions and calf production was experienced in Finland after the peak harvest years in the early 1980s before the number of adult males/females was adjusted over a couple of years by femaledominated harvesting (Nygrén 1986, Nygrén and Pesonen 1993). The mechanism needed to get more males back in the populations is simple in theory -a better balance in the adult kill. However, in practice this appears to be a difficult task as the hunters' will to protect productive cows is strong, and may even be opposed by judicial impediments. For instance in Finland, it is forbidden by law to kill a cow with a calf.

Another factor that is going to complicate moose management in the future is the increasing densities of both wolves and brown bears in all three countries. In Scandinavia, wolves were "functionally extinct" from the early 1960s until late 1970s – the first breeding (since 1964) was recorded in northern Sweden in 1978, and again in 1983 at the border between Norway and Sweden further south (Wabakken et al. 2001). In



Finland, stray wolves live all around the country, but the strongest populations have in the course of the 20th century existed along the south-eastern border zone (Nyholm 1996). The present population in Scandinavia probably descend from a few dispersing individuals from this border population between Finland and Russia (Flagstad et al. 2003). Although current numbers in Fennoscandia are still low (around 100-120 wolves in Norway and Sweden (Wabakken et al. 2004) and at least 150-165 in Finland (Kojola 2004)), the overall trend is for an increase. Similarly, brown bears are slowly increasing in numbers in Finland (at least 800-830 in 2003; Kojola 2004) and Sweden (around 1,000 in the mid-1990s; Sandegren and Swenson 1997) and significantly more in 2004 (Kindberg et al. 2004), and are slowly recolonizing Norway along the Swedish border (< 50 individuals in 2003; Solberg et al. 2003). In core bear areas, predation by bears on moose calves can be significant (Swenson et al. 2001), and although it is unlikely that there will be social acceptance for high wolf densities in Fennoscandia in the near future (e.g., Palviainen 2000), their presence will have to be taken into account locally when setting moose harvest quotas (Kojola and Nygrén 1998, Solberg et al. 2003).

Probably the largest challenge in the future, at least in Norway and Sweden, is how to deal with the impact of high moose densities on the forest ecosystem. The effects of dense moose populations on forest biodiversity are a focus for research and discussion in both Sweden (Persson et al. 2000, Edenius et al. 2002) and Norway (e.g., Solbraa 1998). Similarly, reports of decreasing body condition and reproduction in high-density areas receive increasing attention. Particularly in parts of southern Scandinavia, where calf production and body masses have not increased despite significant reductions in moose densities, there is

growing concern that chronic high moose densities have created permanent or longterm changes in the forest that may take a long time to recover (e.g., Punsvik 2004). Alternatively, the frequency of forestry activity may be a primary stimulus of mooseforest management imbalances. During the last 30-40 years, modern forestry practices have provided Fennoscandian moose with prime habitats in the form of early succession stages created by clear-cutting. Accordingly, the current carrying capacity is assumed to be high compared to the situation 50-100 years ago (Sæther et al. 1992). The current trend, however, is towards a change in the activity in forestry - more cleaning and less clear-cutting which means that a decreasing proportion of forests are found at an early successional stage (Rolstad et al. 2002, Skogsstyrelsen 2004). In Finland the situation is different, as the densities of moose are much lower and forest statistics do not indicate any decrease in the area of forest clear-cutting. Still, the increasing numbers of traffic accidents and forest damage have generated a wish to also decrease the moose density in Finland.

#### REFERENCES

- ANDERSEN, R., B. WISETH, P. H. PEDERSEN, and V. JAREN. 1991. Moose-train collisions: effects of environmental conditions. Alces 27: 79-84.
- BALL, J. P., C. NORDENGREN, and K. WALLIN. 2001. Partial migration by large ungulates: characteristics of seasonal moose ranges in northern Sweden. Wildlife Biology 7:39-47.
- BROMAN, E. 2003. Environment and moose population dynamics. Doctoral thesis, Department of Environmental Sciences and Conservation, Göteborg University, Göteborg, Sweden.
- CARLESTÅL, B., editor. 2000. År älgen ett hinder för att nå de skogspolitiska målen? (Is moose an obstacle to reach



the goals of the forestry policy?). Kungliga Skogs och Lantbruksakademiens Tidskrift 139:2:1-97.

- CEDERLUND, G., and G. MARKGREN. 1987. The development of the Swedish moose population, 1970-1983. Swedish Wildlife Research Supplement 1:55-62.
- DANIELSEN, J. 2001. Local community based moose management plans in Norway. Alces 37:55-60.
- EDENIUS, L., M. BERGMAN, G. ERICSSON, and K. DANELL. 2002. The role of moose as a disturbance factor in managed boreal forest. Silva Fennica 36:57-67.
- Екман, H. 1992. Social and economic roles of game and hunting. Pages 64-71 in R. Bergström, H. Huldt, and U. Nilsson, editors. Swedish Game – Biology and Management. Svenska Jägareförbundet, Stockholm, Sweden.
- ERICSSON, G. 1999. Demographic and life history consequences of harvest in a Swedish moose population. Ph.D. Thesis, Swedish University of Agricultural Sciences, Umeå, Sweden.
- , and K. WALLIN. 1994. Antal älgar som ses - bara en fråga om hur många som finns? Att observera älg – en fråga om täthet, rörelser och synbarhet. Mimeo, 31 pp. Swedish University of Agricultural Sciences, Department of Animal Ecology, Umeå, Sweden. (In Swedish).
- \_\_\_\_\_, and \_\_\_\_\_. 1999. Hunter observations as an index of moose *Alces alces* population parameters. Wildlife Biology 5:177-185.
- FLAGSTAD, Ø., C. W. WALKER, C. VILÀ, A. K. SUNDQVIST, B. FERNHOLM, A. K. HUFTHAMMER, Ø. WIG, I. KOYOLA, and H. ELLEGREN. 2003. Two centuries of the Scandinavian wolf population: patterns of genetic variability and migration during an era of dramatic decline. Molecular Ecology 12:869-880.

FRANSSON, J. 1990. Skada av vilt. SOU

1990:60. (In Swedish).

- GAILLARD, J-M, M. FESTA-BIANCHET, and N.
  G. YOCCOZ. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology and Evolution 13:58-63.
- HAIKONEN, H., and H. SUMMALA. 2000. Hirvikanta, liikenne ja hirvikolarit. Liikenneministeriön julkaisuja/Publications of the Ministry of Transport and Communications 20: 1-105. Edita Ltd., Edita, Finland. (In Finnish with English summary).
- HAKKILA, P., and M. KÄRKKÄINEN. 1999. Hirvestäjä metsänomistajan kukkarolla. Metsätieteen aikakauskirja 1:139-146. (In Finnish).
- HJELJORD, O. 2001. Dispersal and migration of northern forest deer – are there unifying concepts? Alces 37:353-370.
- , and T. HISTØL. 1999. Range-body mass interactions of a northern ungulate – a test of hypothesis. Oecologia 119:326-339.
- JAREN, V. 1992. Monitoring Norwegian moose populations for management purposes. Alces Supplement 1:105-111.
- KINDBERG, J., J. SWENSON, S. BRUNBERG, and G. ERICSSON. 2004. Prelimiär rapport om populationsutveckling och-storlek av brunbjörn i Sverige, 2004. En rapport till Naturvårdsverket från Skandinaviska Björnprojektet 31 maj 2004.12.14. (In Swedish).
- KOIVISTO, I. 1963. Hirvikantamme rakenteesta, lisääntymisestä ja verotuksesta/ Composition, productivity and kill of the Finnish moose (*Alces alces*) population. Suomen Riista 16:7-22. (In Finnish with English summary).
- KOJOLA, I. 2004. Suurpetojen lukumäärä ja lisääntyminen vuonna 2003. Riistantutkimuksen tiedote 194:1-7. (In Finnish).



, and K. NYGRÉN. 1998. Karhun ja suden vaikutus hirvikantaan. Jahti 1:8-9. (In Finnish).

- Koskela, T., and T. Nygrén. 2002. Hirvenmetsästysseurueet Suomessa vuonna 1999./Moose hunting clubs in Finland 1999. Suomen Riista 48:65-79. (In Finnish with English summary).
- LAVSUND, S. 1987. Moose relationships to forestry in Finland, Norway and Sweden. Swedish Wildlife Research Supplement 1:229-244.

\_\_\_\_\_, and F. SANDEGREN. 1991. Moosevehicle relations in Sweden: a review. Alces 27:118-126.

NYGRÉN, K. 1980. Susien vaikutuksesta hirvikantaan / Effect of the wolf on the moose population. Suomen Riista 28:71-78. (In Finnish with English summary).
2000. Kenelle riista kuuluu. Jahti/

. and T. NYGRÉN. 1976. Hirvi Ja Hirvenmetsästys Suomessa. Riistantutkimusosaston Tiedonantoja 2: 1-33. (In Finnish).

NYGRÉN, T. 1984. Hirvikannan inventointi ja verotuksen suunnittelu Suomessa / Moose population census and planning of cropping in Finland. Suomen Riista 31:74-82. (In Finnish with English summary).

. 1986. Hirvitiheydet pienentyneet, kannan rakenne edelleen vääristynyt. Riistantutkimusosaston monistettu tiedote 47:1-4. (In Finnish).

\_\_\_\_\_. 1987. The history of moose in Finland. Swedish Wildlife Research Supplement 1:49-54.

\_\_\_\_\_. 1990. The relationship between reproduction rate and age structure, sex ratio and density in the Finnish moose population. Proceedings of the XVI Congress of the International Union of Game Biologists, Vysoké Tatry, Štrebské Pleso, ÈSSR.

\_\_\_\_. 1996a. Hirvikanta pienimmillään

19 vuoteen, rakenne entistäkin naarasvaltaisempi. Riistantutkimuksen tiedote 145:1-28. (In Finnish).

- . 1996b. Hirvi. Pages 103-108 in H. Lindén, M. Hario, and. M. Wikman, editors. Riistan jäljille. Riista- ja kalatalouden tutkimuslaitos, Edita, Helsinki, Finland. (In Finnish with English summary).
- . 1997. Hirvikanta ja sen säätely. Pages 39-52 *in* J. Kairikko, J. Aatolainen, P. Louhisola, T. Nygrén, and S. Takamaa, editors. Hirvieläinten metsästyksen käsikirja. Gummerys Kirjapaino Oy, Jyväskylä, Finland. (In Finnish).
- . 1998a. Voimistunut hirvikanta tuottavampi kuin koskaan – taustalla muutokset lainsäädännössä, menettelytavoissa ja tavoitteissa. Riistantutkimuksen tiedote 154:1-17. (In Finnish).

. 1998b. Metsä kasvattaa hirvet, ihmiset ja pedot korjaavat sadon. Pages 64-65 *in* Sellua sivistystä sahanpurua. Metsäklusteri Pohjois-Karjalassa. Pohjois-Karjalan Metsäkeskus & Pohjois-Karjalan Liitto. (In Finnish).

, and K. NYGRÉN. 1994. 20 vuotta hirvihavaintoja. Riistantutkimuksen tiedote 129:3-15. (In Finnish).

\_\_\_\_\_, and M. PESONEN. 1993. The moose population (*Alces alces* L.) and methods of moose management in Finland, 1975-89. Finnish Game Research 48:46-53.

, \_\_\_\_, R. TYKKYLÄINEN, and M. WALLÉN. 1999. Hirvijahdin kohteena rakenteeltaan kuntoutunut ja erittäin hyvätuottoinen kanta. Riistantutkimuksen tiedote 160:1-13. (In Finnish).

, R. TYKKYLÄINEN, and M. WALLÉN. 2000. Syksyn suurjahdin kohteena erittäin tuottava, nopeasti kuntoutunut hirvikanta. Riistantutkimuksen tiedote



Jakt 4: 6-9. (In Finnish).

168: 1-16. (In Finnish).

- NYHOLM, E. 1996. Susi (*Canis lupus*). Pages 38-41 *in* H. Lindén, M. Hario, and M.Wikman, editors. Riistan jäljille. Riista- ja kalatalouden tutkimuslaitos, Edita. Helsinki, Finland. (In Finnish with English summary).
- Østgård, J. 1987. Status of moose in Norway in the 1970's and early 1980's. Swedish Wildlife Research Supplement 1:63-68.
- PALVIAINEN, S. 2000. Suurpedot Pohjois-Karjalassa – pohjoiskarjalaisten luonnonkäyttäjien kokemuksia suurpedoista/Large terrestrial carnivores in North Karelia – experiences of North-Karelian nature-users concerning large terrestrial carnivores. Pohjois-Karjalan Liiton julkaisu 51:38-154. (In Finnish with English summary).
- PERSSON, I.-L., K. DANELL, and R. BERGSTRÖM. 2000. Disturbance by large herbivores in boreal forests with special reference to moose. Annales Zoologici Fennici 37:251-263.
- PUNSVIK, T. 2004. Fylkesmannens plass i framtidas hjorteviltforvaltning? Hjorteviltet 14:41-43. (In Norwegian).
- ROLANDSEN, C. R., E. J. SOLBERG, and V. GRØTAN. 2004. 'Sett elg'-materialet i Norge 1984-2002. Hjorteviltet:6-13.
- ROLSTAD, J., E. FRAMSTAD, V. GUNDERSEN, and K. STORAUNET. 2002. Naturskog i Norge. Definisjoner, økologi og bruk i norsk skog- og miljøforvaltning. Aktuelt fra skogforskningen 1-2002:1-53.
- RUUSILA, V., M. PESONEN, S. HEIKKINEN, A. KARHAPÄÄ, R. TYKKYLÄINEN, and M. WALLÉN. 2004. Hirvikannan koko ja vasatuotto pienenivät vuonna 2003. Riistantutkimuksen tiedote 196:1-9. (In Finnish).

, \_\_\_\_, R. TYKKYLÄINEN, and M. WALLÉN. 2001. Hirvikannan kasvu pysähtyi, mutta naaraita säästävä verotus pitänyt vasatuoton korkeana. Riistantutkimuksen tiedote 173:1-11. (In Finnish).

- \_\_\_\_\_, \_\_\_\_, \_\_\_\_, and \_\_\_\_\_. 2002. Hirvikanta lähes ennallaan suurista kaatomääristä huolimatta. Riistantutkimuksen tiedote 180:1-12. (In Finnish).
- RÜLCKER, J. 1988. Älgen och skogen. Problemställningar och förslag till lösningar. Slutrapport från älg/ skoggruppen. (In Swedish).
- SÆTHER, B.-E. 1997. Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. Trends in Ecology and Evolution 12:143-149.
  - , R. ANDERSEN, O. HJELJORD, and M. HEIM. 1998. Ecological correlates of regional variation in life history of the moose *Alces alces*: reply. Ecology 79:1938-1939.
- , M. HEIM, E. J. SOLBERG, K. S. JACOBSEN, R. OLSTAD, J. STACY, and M. SVILAND. 2001. Effekter av rettet avskytning på elgbestanden på Vega. Norwegian Institute for Nature Research, Fagrapport 049. (In Norwegian).
- E. J. SOLBERG, and M. HEIM. 2003. Effects of altering adult sex ratio and male age structure on the demography of an isolated moose population. Journal of Wildlife Management 67:455-466.
- , K. SOLBRAA, D. P. SØDAL, and O. HJELJORD. 1992. Sluttrapport Elg-Skog-Samfunn. Norwegian Institute for Nature Research, Forskningsrapport 28. (In Norwegian).
- SAND, H., R. BERGSTRÖM, G. CEDERLUND, M. ÖSTERGREN, and F. STÅLFELT. 1996. Density-dependent variation in reproduction and body mass in female moose *Alces alces*. Wildlife Biology 2:233-245.

SANDEGREN, F., and J. SWENSON. 1997.



Björnen – viltet, ekologin och människan. Svenska Jägareförbundet, Stockholm, Sweden.

- SEILER, A. 2003. The toll of the automobile: wildlife and roads in Sweden. Doctoral thesis, Swedish University of Agricultural Sciences, Umeå, Sweden. Silvestria 295.
- SKOGSSTYRELSEN. 2002. Enkel älgbetningsinventering ÄBIN. Skogsstyrelsen http://www.svo.se. (In Swedish).
  - . 2004. Skoglig statistikinformation. http://www.svo.se/fakta/stat/ default.htm.
- Solberg, E., V. GRØTAN, C. M. ROLANDSEN, H. BRØSETH, and S. BRAINERD. In Press. Change in sex ratio as an estimator of population size for Norwegian moose. Wildlife Biology.
- , and M. HEIM. 2002. Monitoring moose in Norway: see them, shoot them, measure them and eat them. Pages 16-19 *in* Moose and Deer, a special issue of "Hjorteviltet" periodical for moose and deer in Norway.
- , \_\_\_\_, B-E. SÆTHER, and F. HOLMSTRÖM. 1997. Oppsummeringsrapport, Overvåkningsprogram for hjortevilt. Norwegian Institute for Nature Research Fagrapport 30. (In Norwegian).
- , A. LOISON, B-E. SÆTHER, and O. STRAND. 2000. Age-specific harvest mortality in a Norwegian moose *Alces alces* population. Wildlife Biology 6:41-52.
- , T. H. RINGSBY, B-E. SÆTHER, and M. HEIM. 2002. Biased adult sex ratio can affect fecundity in primipareous moose. Wildlife Biology 8:109-120.
- , and B-E. SÆTHER. 1999. Hunter observations of moose *Alces alces* as a management tool. Wildlife Biology 5:43-53.
- , O. STRAND, and A. LOISON. 1999. Dynamics of a harvested moose

population in a variable environment. Journal of Animal Ecology 68:186-204.

- H. SAND, J. LINNELL, S. BRAINERD,
   R. ANDERSEN, J. ODDEN, H. BRØSETH, J.
   SWENSON, O. STRAND, and P. WABAKKEN.
   2003. Store rovdyrs innvirkning på
   hjorteviltet i Norge: Økologiske
   prosesser og konsekvenser for jaktuttak
   og jaktutøvelse. Norwegian Institute
   for Nature Research Fagrapport 63.
   (In Norwegian).
- SOLBRAA, K. 1998. Elg og skogsbruk, biologi, økonomi, beite, taksering, forvaltning. Skogsbrukets Kursinstitutt, Biri, Norway.
- STATISTICS NORWAY. 2002. http://www.ssb.no.
- Svenska Jägareförbundets Viltövervakning. 2002. Avskjutningsstatistik 1960-2001. (In Swedish).
- SVERIGES NATIONAL ATLAS. 1996. Skogen. (In Swedish).
- \_\_\_\_\_. 1997. Klimat, sjöar, och vattendrag. (In Swedish).
- SWEANOR, P. Y. 1987. Winter ecology of a Swedish moose population: social behavior, migration and dispersal. Swedish University of Agricultural Sciences, Department of Wildlife Ecology, Report 13.
- Swenson, J. E., B. DAHLE, and F. SANDEGREN. 2001. Bjørnens predasjon på elg. NINA Fagrapport 048: 1-22.
- SYLVÉN, S. 2000. Effects of scale on hunter moose *Alces alces* observation rate. Wildlife Biology 6:157-165.
- WABAKKEN, P., Å. ARONSON, H. SAND, T. H. STRØMSETH, and I. KOJOLA. 2004. Ulv i Skandinavia. Statusrapport for vinteren 2003-2004. Høgskolen i Hedmark. Oppdragsrapport nr. 5.
- , H. SAND, O. LIBERG, and A. BJÄRVALL. 2001. The recovery, distribution, and population dynamics of wolves on the Scandinavian peninsula, 1978-1998. Canadian Journal of Zool-



ogy 79:710-725. WALLIN, K. 1992. How to model moose population ecology? Alces Supplement 1:121-126.

