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Evaluation of four methods used to estimate population density of moose *Alces alces*

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Various survey methods are used to monitor and manage ungulate populations. The choice of optimal method depends on estimation accuracy, management objective and financial constraints. Here we compare estimates produced by four different methods for estimating population size, i.e. aerial counts, hunter observations, pellet group counts and cohort analysis. A Swedish moose *Alces alces* population was studied during 1973-2005 in the Grimsö Wildlife Research Area (135 km^2). The highest correlation was found between cohort analysis and aerial counts ($r = 0.69$, $P < 0.05$), and the hunter observations and the aerial counts ($r = 0.76$, $P < 0.10$). The different methods produced relatively consistent trends in population estimates over years. Pellet group counts prior to 1997 were not significantly correlated with the other methods, probably due to unrepresentative spatial sampling. A comparison of the aerial and pellet group counts in 2002 and 2006, showed that the average defecation rate was estimated at approximately 14 pellet groups per day per moose. Our results show the importance of having representative spatial sampling in pellet group surveys and indicate that hunter observations can be a useful tool for estimating long-term population trends even in moderately sized areas.

Key words: aerial count, cohort analysis, deer, hunter observations, management, monitoring, pellet group counts

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An effective system for monitoring wildlife populations enables management and decision-making by providing reliable data on the number of animals, distribution, individual growth rate, reproduction and sex/age composition. Over the years several different survey methods have been used to monitor ungulate populations, including aerial surveys, pellet group counts, direct observations (e.g. hunter observations and drive counts), hunter harvest statistics and snow-track counts (Timmerman 1974, Mayle et al. 1999, Solberg & Sæther 1999). Three of these methods are commonly used within Fennoscandian moose *Alces alces* management, i.e. aerial surveys, pellet group counts and hunter observations (Haagenrud et al. 1987, Lavsund et al. 2003, Wennberg DiGasper 2006).

However, the methods vary in terms of reliability (accuracy and precision), costs, information obtained and time period surveyed (Fuller 1991, Mayle et al. 1999, Barnes 2001, Campbell et al. 2004, Smart et al. 2004, Månsson et al. 2007; Table 1). Such differences (see Table 1) make it difficult to select the most suitable method for management, indicating that further evaluation of the different methods is needed. For moose, aerial surveys have probably been the most accepted and frequently used method for monitoring population densities and trends (Timmerman 1974, Jachmann 2002, Wennberg DiGasper 2006, Pople et al. 2007). Two other methods commonly used to estimate ungulate populations are pellet group counts (Neff 1968, Barnes 2001, Wennberg DiGasper 2006) and direct observations such as hunter observations (Haagenrud et al. 1987, Ericsson & Wallin 1999, Solberg & Sæther 1999, Wennberg DiGasper 2006). These two methods differ from aerial surveys in that they result in an indirect measure, i.e. an index of the number of animals (Neff 1968, Ericsson & Wallin 1999, Solberg & Sæther 1999, Andersen et al. 1992). Hunter observations are provided by moose hunters and include the number of moose observed, the number of active hunters, and the time (hours) spent hunting per day during the first week of the hunting season.

The objective of our study was to combine information from several survey methods in a long-term study to: 1) improve our understanding of the accuracy, concordance and usefulness of these methods, and 2) improve our understanding of the population development within a moose management area in terms of animal numbers, age-sex structure and migration.

We did this by comparing estimates of moose density provided by the four census methods (cohort analysis, aerial counts, pellet group counts and number of moose observations per hunter day) used within the Grimsö Wildlife Research Area. Data from a 30-year period was used to reconstruct the population size using cohort analysis (Fryxell et al. 1988, Ferguson 1993, Solberg et al. 1999). Age-specific natural mortality rates were estimated using radio-collared moose in the area in order to provide input parameters for the reconstruction of the moose population. By comparing methods we also estimated a conversion factor for transforming indices obtained from pellet group counts into aerial counts, and evaluated the importance of migration as a contributory factor to population development.

Table 1. Comparison of different methods used to survey moose.

	Aerial counts	Pellet group counts	Hunter observations
Sex structure	Yes	No	Yes
Reproduction (calf/cow)	Yes	No	Yes
Remote areas	Good	Harder[a]	Good[b]
Large areas $>1{,}000$ km^2	Good	Harder[c]	Good
Costs	Costly	Intermediate	Cheap
Absolute numbers	Yes	No	No
Surveyed time window	Snapshot	Entire winter period	Snapshot
Weather sensibility	High	Low	Low

[a] Accessibility - need of forest roads for transportation.
[b] Surveys are conducted in areas where hunting takes place.
[c] Short time period with good conditions i.e. many field workers needed during a short period when surveying large areas.

Material and methods

Study area

The 135 km^2 Grimsö Wildlife Research Area, located in south-central Sweden (59°5'N, 15°5'E), is a rugged plateau with elevations ranging within 100-150 m a.s.l., and is composed of low flat ridges with till and boulders interspersed with bogs and swamps. The area comprises 72% forest, 18% bogs, 7% lakes and rivers, and 3% meadows and farmlands. Mature forest stands are dominated by Scots pine *Pinus silvestris*, Norway spruce *Picea abies*, and birch *Betula pubescens* and *B. pendula*. Rowan *Sorbus aucuparia*, aspen *Populus tremula*, and willows *Salix* spp. are preferred moose browsing species but occur rarely within the mature stands. Forest management is intensive, with clear-cutting of 3-10 ha patches and old forest replaced by planting. The period of rotation in the forest stands is 80-100 years. Early succession after logging consists of birch, aspen and willow with an understorey of common hair grass *Deschampsia flexuosa*, bilberry *Vaccinium myrtillus*, cowberry *V. vitis-idea* and heather *Calluna vulgaris*. Climate is typical for inland, central Sweden, with winter temperatures down to -20°C and summer temperatures up to 25°C. Mean daily temperature is 16.3°C and -4.4°C in July and January, respectively. Snow cover is normally present from December to March with a mean snow depth of 25-30 cm in February. Annual precipitation averages 670 mm with a maximum in July (average = 86 mm; Swedish Meteorological and Hydrological Institute). Other ungulates within the research area include roe deer *Capreolus capreolus*, whose population densities ranged between approximately 1-5/km^2 during the study period (Å. Pehrson, unpubl. data). Potential moose-predators, such as wolf *Canis lupus* and brown bear *Ursus arctos*, were not present within the study area during the study period (Wabakken et al. 2001, Swenson et al. 1998).

Calf and adult survival

A cohort analysis is mainly based on age and sex information from harvested animals, but natural mortality has to be accounted for in order to obtain reliable estimates of population size. Consequently, we estimated mortality rates attributable to causes other than hunting for radio-collared moose (both adults and calves). During 1980-2000, 63 adult females and 44 adult males were captured and equipped with radio-collars. The age of moose captured and collared was estimated by tooth wear of the incisors (Skuncke 1949). Radio-tracking was normally performed once a week (Cederlund & Lemnell 1979). For further details on adult moose tagging, see Cederlund et al. (1989).

Over the entire study period, radio-collared males and females were followed for an average of 2.4 (SD = 1.8) and 5.6 (SD = 3.6) years, respectively. Mean age of all radio-collared males and females was 4.8 (SD = 2.9) and 9.9 (SD = 5.3) years, respectively, whereas the maximum age for males and females was 12 and 21 years, respectively. In the spring of 2005, none of the males and only nine females were still alive. In total, 68% of the males were shot during the hunting season, 18% died of natural causes, whereas contact was lost with 14% of the collared moose due to malfunctioning radio-collars. Among females, 48% were shot during the hunting season, 30% died of natural causes, 8% were lost from the study for unknown reasons (possibly due to malfunctioning radio-collars) and 14% were still alive in the spring of 2006.

Survival rates for calves through their first winter were estimated by observing radio-collared moose cows and counting their calves on different occasions during the year, and also by using radio-collared calves. Newborn calves (1-10 days old) were captured within Grimsö Wildlife Research Area during 1993-2001. See Ericsson et al. (2001) for further details on moose calf tagging.

Harvest data

Since 1973, the number of moose shot each year within the Grimsö Wildlife Research Area has been recorded. The data used in the present study included 2,065 observations of shot animals of known sex and age. Another 53 moose (2.5%) were shot in the research area but were excluded from further analyses due to missing information on age or sex. For all adult moose shot, mandibles were collected and used for age determination in the laboratory by counting the number of layers in the cementum annuli of the first molar (Markgren 1969).

Aerial counts

During 1977-2006, the size of the moose population in the Grimsö Wildlife Research Area was estimated by aerial counts from helicopter on 12 occasions. The method used during 1977-2002 was total counts of moose (N = 11) based on line-transect surveys, with 300 m between transect lines (LeResche & Rausch 1974, Tärnhuvud 1988). The surveys were performed in winter after the moose hunt, 1-2 days after snowfall and only when at least 20-40 cm of snow covered the ground and temperatures were below 0°C. In our comparison between methods, we used aerial counts not corrected for sightability, whereas the aerial counts were corrected for sightability in the defecation rate estimation (with a sightability factor estimated from the aerial survey in 2006).

In 2006, an aerial count was performed as a sample of the research area, comprising 15 plots of 2 × 2 km (equal to 44% of the research area). A correction factor for sightability in 2006 was achieved by applying a mark-recapture procedure (Krebs 1999) of plots that were surveyed twice by using two different helicopters and observers. The first helicopter to survey a plot worked along north-south transects and positioned all moose observations by GPS. These observations were treated as marked moose. The second helicopter repeated the survey along east-west transects as soon as the first helicopter left the plot (recapture). Hence, the two helicopters flew on transects perpendicular to each other to ensure that both previously observed and non-observed moose could be observed from the second helicopter. The estimated sightability factor should therefore be close to unbiased. Furthermore, the sightability factor was estimated from an expanded survey covering more than the Grimsö Wildlife Research Area (42 surveyed plots and 244 moose observations) to increase the estimation accuracy.

Moose observations

During 1984-2005, hunters recorded the number of moose observed during the first week of the regular hunting season within the research area. This method has been widely used in both Sweden and Norway since the mid-1980s as an index of moose population size (Jaren 1992, Ericsson & Wallin 1999, Solberg & Sæther 1999) and is based on the assumption that a change in observation rate per time unit reflects a true change in the population. Each observation of an individual moose is recorded either as adult male, adult female without calves, adult female with one calf, adult female with two calves, lone calf or moose of unknown status. In this study the data is presented as the number of moose observations per day per hunter (Table 2).

Pellet group survey

Moose pellet group surveys have been carried out annually in the research area since 1977. During 1977-1998 only the southeastern part of the research area (approximately 20% of the total research area) was surveyed. Permanent squared sample plots (5 × 10 m) were distributed 100 m apart along transects 200 or 400 m apart. The number of sample plots included in the survey was approximately 400, except for the first two years when only 175 and 209 squares were surveyed (see Table 2).

Starting in 1997, a different sampling method was used ('new pellet group survey'), based on 32 permanent 1 × 1 km squares systematically distributed over the total research area. Each square had 20 (five along each side) permanent circular sample plots of 100 m^2 (Fig. 1), resulting in a total of 640 sample plots. The old and the new pellet group surveys were both performed in 1997 and 1998 to allow validation that the two methods gave comparable results.

In both surveys, all sample plots were checked annually and cleaned for moose pellet groups in autumn (early October), while the number of new pellet groups was counted in spring (late April to early May). Consequently, we collected data on the number of pellet groups produced by moose during a specific time period (i.e. number of days) during the winter season.

Cohort analysis

The number of adult moose, and population structure prior to the hunting season, was reconstructed for the period 1973-2005 using data collected from animals shot within the research area during that period. The maximum age recorded for shot females and males was 21 and 13 years, respectively. Therefore, all males born before 1990 and all females born before 1984 were assumed to have died before the end of the study period. These are the 'complete cohorts', whereas male cohorts born after 1990 and female cohorts born after 1984 are referred to below as 'incomplete cohorts'. For animals shot between 1973 and 1990, 99% of the females were shot before the age of 15 and 99% of the males were shot before the age of seven.

Complete cohorts

Following the method developed by Fryxell et al. (1988), and extended by Solberg et al. (1999), we reconstructed the complete cohorts for each sex separately from the following equation (Equation 2 in Fryxell et al. (1988)):

$$N_{i,t} = (N_{i+1,t+1}/p_i + K_{i,t}) \qquad (1)$$

where $N_{i,t}$ = number of animals of age i year t, p_i = age specific survival, and $K_{i,t}$ = number of animals shot aged i year t.

The number of animals in each sex-age class was calculated using Equation 1 recursively with $N_{i,t} = K_{i,t}$ for males in age class i = 13 and for females in age class i = 21. The adequacy of this method assumes that there is a maximum age beyond which no animals survive, that age-specific survival is known and is constant over years, and that the population is closed with no migration (Fryxell et al. 1988). We also performed a cohort analysis with a lower maximum female age of 15 years (following Solberg et al. 1999), which had little effect on the population development (correlation between the two time series was 0.987) but resulted in a 20% population size decrease. We therefore used 21 years as maximum female age in our final analyses.

Incomplete cohorts

The expected number of animals born before 2005, and expected to be shot after 2005, was calculated following Solberg et al. (1999), where the expected number of animals to be shot in the future is predicted from sex-specific curves of cumulative proportions shot in relation to age in the past (Fig. 2). The number of animals in each cohort born after

Table 2. Descriptive statistics for data used in estimating moose population size by: aerial counts, pellet group counts, hunter observations and cohort analysis. The data were collected within the Grimsö Wildlife Research Area, Sweden, during 1973-2006. Numbers of observed moose per 1,000 ha from the aerial counts are given without correction for sightability. The ratios of marked moose observed during the aerial surveys are given as Number of marked moose observed:Total number of marked moose in the area.

	Aerial counts				Pellet group surveys[e]		Hunter observations		Cohort analysis
					Pellet groups per 100 m^2				
Year	Area surveyed (1000 ha)	Observations per 1000 ha	Ratio of marked moose observed	Proportion < 1 km from the border	Old survey	New survey	Number of adult moose observed	Observations per hunter per day	Number of adult moose per 1000 ha
1973									5.49
1974									6.32
1975									6.91
1976									8.76
1977	11.5	18.2[a]	-	37%	0.312[d]				11.66
1978	13.5	14.7[a]	-	49%	0.105[d]				12.57
1979	13.5	13.3[a]	-	47%	0.746				14.03
1980					0.534				18.43
1981	10.5	19.2[b]	-	48%	0.554				19.09
1982	13.5	21.0[a]	-	45%	1.139				18.01
1983					0.690				17.06
1984	13.5	14.2[a]	3:9	35%	0.715		127	0.900	15.21
1985	13.5	17.7[a]	4:5	52%	0.515		190	1.021	15.56
1986					0.417		159	0.815	13.69
1987	13.5	14.0[a]	21:24	44%	0.469		85	0.574	13.51
1988	13.5	12.7[a]	5:13	37%	0.357		106	0.675	13.02
1989					0.656		75	0.568	13.53
1990					0.385		103	0.715	13.51
1991					0.444		89	0.689	13.43
1992					0.609		70	0.404	13.82
1993					0.504		63	0.443	12.86
1994	13.5	13.9[b]	12:17	53%	0.571		59	0.404	12.92
1995					0.770		50	0.364	11.46
1996					0.386		26	0.273	10.31
1997					0.360	0.328	35	0.472	0.884
1998					0.520	0.322	28	0.358	0.781
1999						0.317	39	0.469	0.682
2000						0.343	52	0.520	0.723
2001						0.331	53	0.563	0.686
2002	13.0	12.2[c]	10:14	32%		0.471	40	0.388	0.641
2003						0.453	39	0.475	0.754
2004						0.573	54	0.587	0.645
2005						0.347	45	0.417	0.562
2006	13.5	8.3[c]	-	-		0.326			

[a] 95% observed according to guidelines by Tärnhuvud (1988).

[b] 84% observed according to guidelines by Tärnhuvud (1988).

[c] Estimated percentage of moose observed from sampling-resampling equal to 73%.

[d] Only 200 sample plots (50 m^2) surveyed. 400 sample plots were surveyed in 1979 to 1998.

[e] The annual ratio between the variance and the mean of pellet groups per plot was between 1.1 and 6.1 for the 'old pellet group survey' and between 1.8 and 3.3 for the 'new pellet group survey'.

1990 was calculated from the observed numbers shot within the cohort and the number expected to be shot in the future using Equation 1.

The estimates of the expected number of animals to be shot in the future assume constant hunting effort each year and also that there has been no change in hunting strategy. During the years from 1984 to 1998 (when complete data on total number of hunter days was available) the number of hunter days was proportional to the reconstructed population size (ln(hunter days) = 0.97ln(population size), SE = 0.008). It was therefore concluded that hunting was constant. The hunting strategy, however, changed around 1982 from a male-biased hunting strategy to a strategy for an even sex ratio. Consequently, the sex-specific curves of the cumulative proportion shot differed before and after 1982. However, in additional cohort analyses (results not

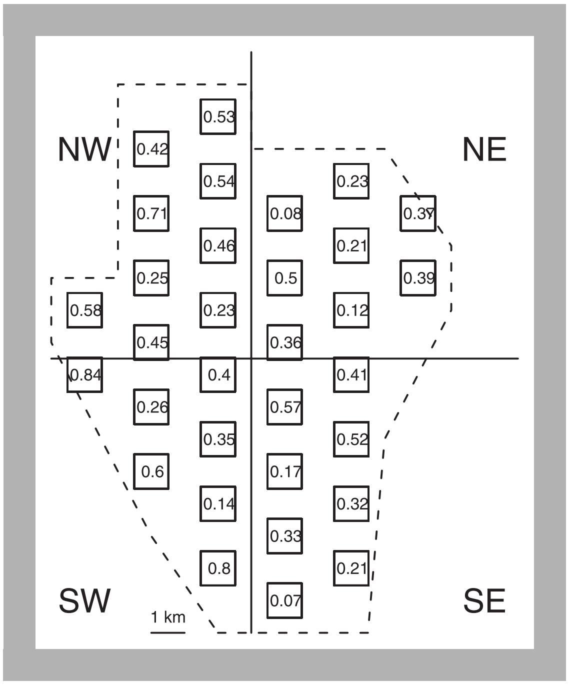

Figure 1. Description of the data from the new pellet group survey. Average number of pellet groups per 100 m^2 within the 32 subareas of the Grimsö Wildlife Research Area. The four subregions (NE, SE, SW, NW), used in the subsequent statistical analysis are also shown.

shown), these differences did not generate any considerable changes in the reconstructed population. The sex-specific curves of cumulative proportion of moose shot were therefore based on all years from 1973 to 1990.

Sensitivity analysis of the reconstructed population

The applied cohort analysis is a deterministic method based on several estimated parameters and uncertain assumptions, and it is therefore important to perform sensitivity analyses (e.g. Eberhardt 2002) to check how uncertainty in these parameters affects the output. We calculated the effect of small changes in natural mortality, cumulative proportion shot and number of moose shot on estimated population size. We also checked the assumption of no migration by comparing estimated adult sex ratio obtained from the cohort analysis and aerial surveys.

Statistical analyses

To estimate the natural mortality needed for the cohort analysis, we estimated both survival of calves through their first winter and adult survival. The probability of calf survival was modelled with logistic regression (Proc GENMOD in SAS). Calves

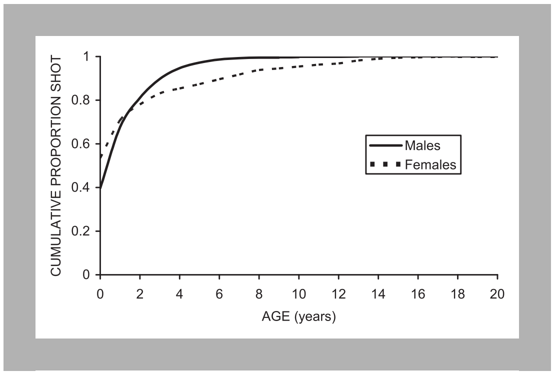

Figure 2. Cumulative proportion of shot moose within the Grimsö Wildlife Research Area estimated from data covering 1973-1990.

from the same mother were treated as repeated measurements. The explanatory variables included were: age = the age of the mother in years; age^2 = age × age; year = the birth year of the calf; $year^2$ = year × year; twin = binary dummy variable equal to 1 if the calf was born as a twin and 0 otherwise. Sex was not included as a possible explanatory variable because this characteristic was not always determined on capture.

Adult survival was analysed with Cox regression and possible differences between sexes and cohorts were tested. The survival library in the statistical package R (R Development Core Team 2004) was used for these analyses.

The new pellet group counts of moose were analysed in order to gain an understanding of the geographical distribution of moose density within the research area. The number of pellet groups per sample plot was analysed as a dependent variable in a generalised linear model with log link function (i.e. a log-linear model). The explanatory variables were year (class effect), four subregions (class effect) and the interaction of year and subregion (class effect). In a preliminary analysis the distance from the midpoint of the research area was also included as a covariate. The four subregions correspond to the four large quadrates (NE, SE, SW, NW) in Figure 1. The GLM library in the statistical package R (R Development Core Team 2004) was used for these analyses and P-values were based on likelihood ratio tests.

The daily defecation rate per moose in the study area was estimated based on the population size obtained from the aerial counts in 2002 and 2006 and the number of pellet groups counted in these two years. These were the only two years with available estimates based on both aerial counts and pellet group surveys from the entire research area. The estimates were obtained as x/(yz) where x is the estimated number of pellet groups in the area, y is the estimated number of moose, and z is the number of days over which the pellets have accumulated between early October and late April. The variances (V_x, V_y and V_z) of the three estimates (x, y and z, respectively) used in the formula were combined using the delta method (e.g. Casella & Berger 2001) to obtain a standard error of the daily defecation rate:

$$SE = \sqrt{\left(\frac{1}{yz}\right)^2 V_x + \left(\frac{x}{y^2 z}\right)^2 V_y + \left(\frac{x}{yz^2}\right)^2 V_z} \quad (2)$$

The aerial count is a snapshot of the population size during one day in late winter, whereas the pellet group counts give accumulation of pellets over the whole winter. V_y was approximated by the number of animals observed inside the research area during aerial counts < 1 km from the border.

Time series analysis

A correlation analysis was performed to compare the similarities between the estimates of moose density. The pairwise comparisons were based on a variable number of years because the different methods started at different times during the total study period.

In each pairwise comparison, the time series $y_1(t)$ and $y_2(t)$ were analysed as two random walks around the means μ_1 and μ_2. The modelled random walks $u_1(t)$ and $u_2(t)$ included an auto-correlation with a one year time lag such that:

$$\begin{aligned} u_1(t) &= r_1 u_1(t-1) + \varepsilon_1(t) \\ u_2(t) &= r_2 u_2(t-1) + \varepsilon_2(t) \end{aligned} \quad (3a)$$

and

$$\begin{aligned} y_1(t) &= \mu_1 + u_1(t) \\ y_2(t) &= \mu_2 + u_2(t) \end{aligned} \quad (3b),$$

where r_1 and r_2 are the two auto-correlation coefficients, and the residuals ε_1 and ε_2 are normally distributed with variances σ_1^2 and σ_2^2, respectively. A time lag of one year was chosen because the changes in the moose population size were rather slow and not erratic. The residuals are independent between years and within time series, but correlated between time series for common t:

$$Cov(\varepsilon_1(k), \varepsilon_2(l)) = \begin{cases} \rho\sigma_1\sigma_2 & \text{for } k = l \\ 0 & \text{for } k \neq l \end{cases} \quad (4)$$

where ρ is the cross-correlation which measures the dependency between the two time series and k and l are indexes for years. Note that if there is no auto-correlation then ρ is simply the correlation between $y_1(t)$ and $y_2(t)$.

The maximum likelihood estimates of μ_1, μ_2, σ_1^2, σ_2^2, r_1, r_2 and ρ were obtained with Fisher scoring (e.g. Pawitan 2001). The main parameter of interest is ρ, and so we tested the null hypothesis $\rho = 0$ with a likelihood ratio test. This analysis was not performed on the aerial counts since there were several years between each count and the effect of auto-correlation could therefore be ignored. Furthermore, the number of years in which both the old and the new pellet group surveys were performed were too few for a time series analysis.

Results

Moose harvest in the research area increased during the 1970s and peaked in 1982 with harvest rates > 4 times larger than in 1973 (Fig. 3). In the late 1970s, a local hunting strategy within the research area was applied with the objective of reducing the number of adult males per female in the living population. Consequently, harvest of adult males was 5-6 times larger than the harvest of adult females during 1976-1983. Since 1984, the sex ratio of harvested adult moose has been relatively stable, averaging 51.5% males and 48.5% females over the years, while the proportion of calves of all harvested moose has been around 54%.

Estimates of natural mortality used in the cohort analysis

Calf survival

During 1993-2001, 85 marked calves (27 females, 37 males and 21 calves of unknown sex) from 32 different females were checked for survival from August to April. Of the 85 calves, 19 (22.3%) were born as twins, and nine (10.6%) died of natural causes during their first winter, resulting in an average survival rate of 0.89 for all calves. Survival was not significantly related to birth year, birth year squared, twin or single, age of mother, or age of mother squared ($P > 0.2$).

Adult survival

Survival analyses, excluding harvest-related mortality of adult moose, showed no significant effects of

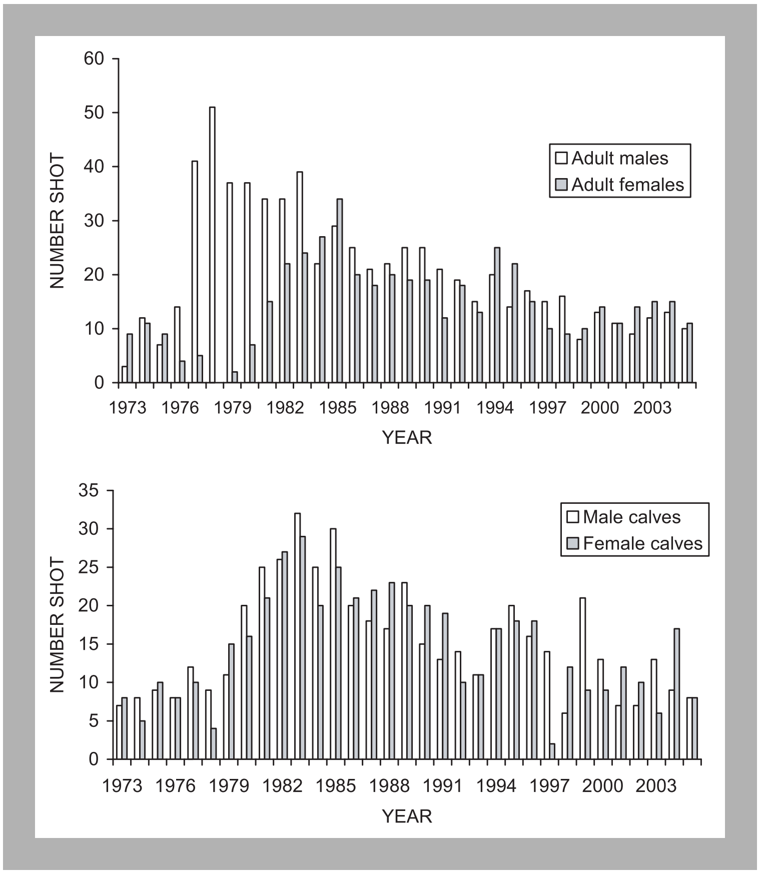

Figure 3. Number of calves and adults shot per year within the Grimsö Wildlife Research Area.

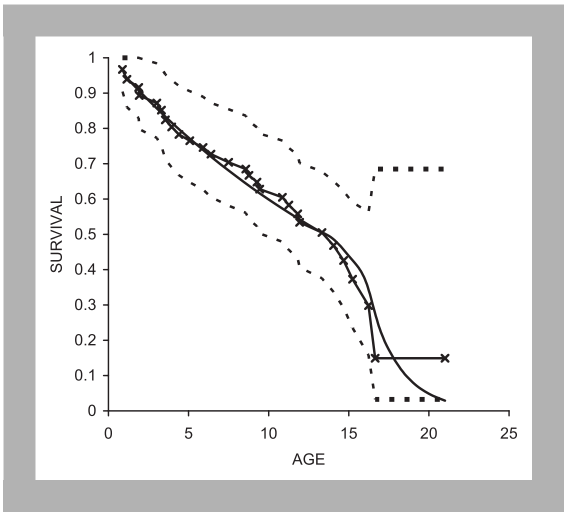

Figure 4. Estimated survival curve of adult moose. Dashed curves show 95% confidence limits and smoothed curve corresponds to the approximation used for the reconstruction.

birth year (P = 0.25), and no significant differences between sexes (P = 0.22). Consequently, survival was analysed for males and females combined (Fig. 4). The survival rate for both sexes combined corresponds approximately to an age-specific survival of 0.95 for 1-13 year-olds, 0.9 for 14-year-olds, 0.85 for 15-year-olds and 0.6 for older animals (see Fig. 4). These were the natural survival rates used in the cohort analysis.

Cohort analysis

The cohort analysis showed that the population size grew from an all-time low in 1973 with 5-6 moose per 1,000 ha to a peak in 1981 with 19 moose per 1,000 ha (Fig. 5). After 1981 the moose population decreased continuously during the 1980s and 1990s, reaching a level of approximately 7-8 moose per 1,000 ha in the late 1990s and early 2000s. The pattern of a sharp increase during the 1970s and a somewhat slower decline in the late 1980s follows the general pattern of the Swedish moose population (Cederlund & Markgren 1987, Lavsund & Sandegren 1989).

Comparison of population density estimates produced by the different methods

Population density

Aerial counts did not show the same major increase during the 1970s as compared to the reconstructed population. However, aerial counts did not start until 1977 and the first year produced a relatively high estimate compared to aerial counts in the two following years. Despite the lack of a consistent pattern in the late 1970s, a significant correlation between the aerial counts and the reconstructed population size was found for the period 1977-2002 (r = 0.69, N = 11, P = 0.02; Table 3). The estimated correlation between hunter observations and the aerial counts was also high (r = 0.76), but not significant (N = 6, P < 0.10). However, estimates from these two methods were comparable for only six years. All other correlations between time-series estimates were low and non-significant.

The time-series estimated by cohort analysis showed high auto-correlation (see Table 3), which

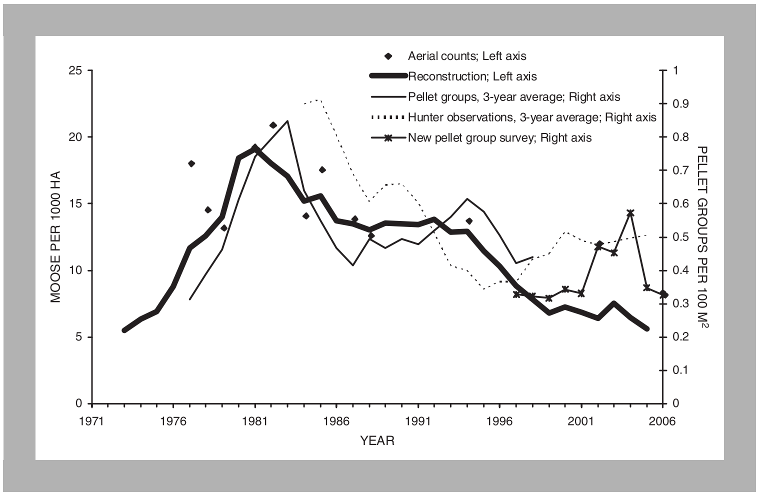

Figure 5. Population density (per 1,000 ha) estimated from the reconstruction. The population density was estimated as the total number of adults prior to the hunting season divided by the size of the research area (135 km^2). The reconstruction results are compared to aerial counts (moose per 1,000 ha), pellet groups (per 100 m^2) and hunter observations (observed moose per hunter per day). In the figure, the aerial counts have not been corrected for sightability.

was expected since the calculation of year-specific population size in the cohort analysis depends on the previous year's population size. The hunter observation data also showed high auto-correlation (see Table 3), which indicates that hunter observation can be used to follow population trends.

Correction factors for sightability

The estimated proportion of animals observed during the aerial count in 2006 was 0.73 (SD = 0.03). This corresponds relatively well to the average proportion of animals with radio-collars observed in previous aerial counts (0.67, SD = 0.22; see Table 2). It is therefore likely that the aerial counts prior to 2006 underestimated the true population size, and that the sightability of 84-95% suggested by Tärnhuvud (1988) generally produces underestimates of the true population size.

Table 3. Auto-correlations within time-series (lower diagonal[a]) and the correlation between the time-series (upper diagonal[b]). Number of years in each analysis is shown in parentheses.

	Reconstruction	Hunter observations	Old pellet survey	New pellet survey	Aerial counts[c]
Reconstruction	-	0.20 (22)	-0.06 (22)	-0.03 (9)	0.69* (9)
Hunter observations	0.94\1.00	-	-0.37 (15)	0.31 (9)	0.76† (6)
Old pellet survey	0.18\0.96	0.03\1.00	-	d	0.40 (10)
New pellet survey	0.49\1.00	0.44\-0.10	d	-	d

† $P < 0.10$ for the null hypothesis that the correlation is 0.

* $P < 0.05$.

[a] The lower diagonal values show the auto-correlations with a one year time-lag. The two auto-correlations are given as $r_1\backslash r_2$ where time series 1 is given by the row name and time series 2 is given by the column name.

[b] Correlation between the elements in the auto-correlated time series.

[c] The Aerial counts were analysed as independent between years.

[d] < 3 observations.

Estimated defecation rate

The daily defecation rate was estimated from the aerial survey and pellet group counts in 2002 and 2006. The number of moose within the research area, estimated from aerial counts, was 225 (in 2002) and 163 (in 2006). The estimated total number of pellet groups within the research area was 638,500 (SD = 1,441) and 440,100 (SD = 1,218), and the number of days over which the pellet groups had accumulated was 197 (SD = 5.0) and 202 (SD = 7.1) in 2002 and 2006, respectively. The estimates of daily defecation rates were 14.41 (SE = 0.71) in 2002 and 13.36 (SE = 0.83) in 2006.

Old and new pellet group counts

Data from the older pellet group surveys were obtained from the southeastern quadrate of the research area whereas the new pellet group survey includes sample plots throughout the research area (see Fig. 1). Therefore it was possible to test whether the southeastern subregion was a representative part of the research area. This proved not to be the case. The moose density varied significantly ($P < 0.001$) between different sub-regions (see Fig. 1), which is a probable explanation of the poor correspondence between the old pellet group survey and the other three measures of moose density (see Fig. 5), and also the poor correspondence between the old and the new pellet group survey in 1997 and 1998 (see Fig. 5). In the same analysis, we found no evidence ($P = 0.2$) that the moose density increases (or decreases) in the peripheries of the research area, which means that the border effect is not greater (nor less) than could be expected from the size of the research area. The deviance divided by the degrees of freedom in the log-linear model was close to one (1.3), indicating that the number of pellet groups was

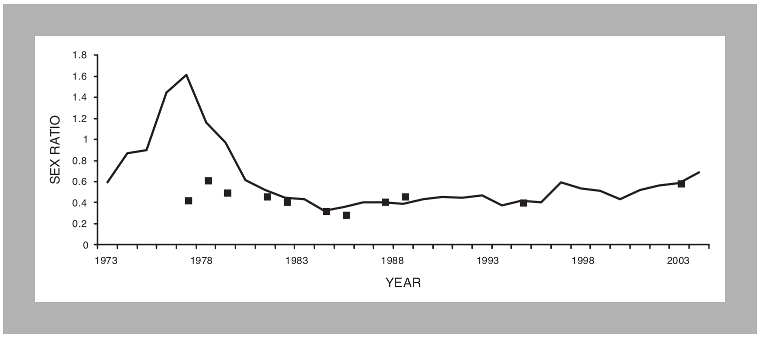

Figure 6. Sex ratio of adults (males : female). Estimates from the reconstruction and aerial counts given as line and squares, respectively.

randomly distributed throughout the research area (after adjusting for the class effects of year, subregion and the interaction of year and subregion).

Sensitivity analysis of the reconstructed population

Assumption of no migration

During1976-1983, an excess of male adults were shot (see Fig. 3). Contrary to what we expected, however, the proportion of adult males was unrealistically high during 1973-1980 in the reconstructed population (Fig. 6). This suggests net immigration of males during these years.

Estimated survival

The reconstructed population was sensitive to the estimated age-specific survival of females > 15 years old, previously estimated to be 0.6. This parameter was estimated from the survival analysis of radio-collared moose and had relatively large standard errors (see Fig. 4). A decrease in the age-specific survival of old females from 0.6 to 0.5 resulted in a change in the maximum density in 1981 from 19.0 to 22.8 moose per 1,000 ha, whereas an increase in old female survival from 0.6 to 0.7 resulted in a lowered density in 1981 of 17.6 moose per 1,000 ha.

The main cause of the sensitivity in 1981 was that one female was born in 1979 and shot at the age of 21 in 2000. In the cohort analysis, this single female corresponds to 54 calves born in 1979 given that the age-specific survival of old females is 0.6, and to 163 calves born in 1979 if the same age-specific survival is 0.5. Calibrating this parameter by the population size estimated from the aerial counts indicates that the age-specific survival of old females would be 0.52.

Estimates for incomplete cohorts

After 1990, the reconstructed moose population was based on incomplete cohorts and so the precision of the estimated moose density declines towards the end of the study. For the complete cohorts an additional female calf shot increases the total number of females by one, whereas if an additional female calf was shot in the cohorts born after 2002 the total number of females increases by 1.5. Consequently, the estimates were rather insensitive to the number of calves shot.

We also studied how a small change in the cumulative proportion shot (see Fig. 2) affected the reconstructed population. If the cumulative proportion shot was reduced by one percentage unit for all ages up to the age of 10, then the estimated number of females increased by 1% in 1997, 4% in 2002 and 5% in 2005. Consequently, the density estimates for 2002 and later were especially sensitive to the cumulative proportion shot, and the reconstructed population therefore may have been less accurate after 2002.

Discussion

We have compared and evaluated the results from four different methods of estimating moose density in a long-term study: aerial counts, cohort analysis, pellet group surveys and hunter observations. All methods gave similar general results in terms of the size and development of the moose population during the 30-year period. However, different methods gave somewhat different absolute estimates of the population size and of the population development during the last 10 years of the study.

Aerial counts

Aerial counts provide absolute estimates of population size at a certain point in time during the annual population cycle. This method may yield estimates of high accuracy given that relevant correction factors for the proportion of non-observed moose are available. A number of studies in North America have provided a wide range of estimates of sightability (mean: 0.71, range: 0.38-0.97; Timmermann 1993), or a sightability correction factor (SCF; 1.03-2.60) between studies, where the estimates depend on a number of factors such as type of aircraft (helicopter or fixed wing), type of forest, moose density, experience of crew, and snow and weather conditions (Timmermann & Buss 1998).

Using a number of aerial counts from different areas with radio-collared moose in Sweden during the 1980s, Tärnhuvud (1988) suggested correction factors that mainly were based on the type of weather conditions during aerial counts. However, the average proportion of radio-collared moose observed (67%) of the total number present (N_{total} = 82) within our study area during aerial counts was clearly lower than the estimates presented by Tärnhuvud (1988) for good (95%) and intermediate (84%) snow conditions using a helicopter with experienced personnel. This is also corroborated by the fact that the sampling-resampling technique used at the end of the study period (2006) provided estimates of sightability (73%) that corresponded well with the average proportion of radio-collared moose observed over the whole period. We conclude that general application of sightability estimates should be avoided and that area and survey specific estimates should be developed.

Pellet group counts

A pellet group survey may constitute a good method for analysing population trends but merely gives an index of population density if not combined with an estimate of animal defecation rate.

Pellet group counting is a widely used method in the management of deer populations (Neff 1968, Timmermann 1974, Mayle et al. 1999). The accuracy of this method has been questioned (Fuller 1991, 1992, White 1992), but several studies have also shown realistic estimates and consistency in population trends and size between different independent methods (Neff 1968, Mandujano & Gallina 1995, McIntosh et al. 1995, Barnes 2001). Pellet group counts provide indices that can be calculated into absolute numbers of animals (Neff 1968, Timmerman 1974, Mayle et al. 1999). However, reliable interpretation of absolute numbers requires estimates of the rate of defecation (i.e. number of pellet groups produced per individual per day) and knowledge about the length of the period of pellet accumulation. However, the defecation rate of moose varies between studies and seems to depend on the type of habitat, forage quality and forage composition (Neff 1968, Andersen et al. 1992). A variation in defecation rate has a large impact on the calculated absolute number of individuals in an area.

Our results show that the defecation rate derived by comparing aerial counts and pellet group counts in the field for specific years (14 pellet groups per moose per day) is similar to, or in the lower range of, those reported for moose in captivity (Franzmann et al. 1976a,b, Oldemeyer & Franzmann 1981) and for some free-ranging populations (Jordan & Wolfe 1980, Joyal & Ricard 1986, Andersen et al. 1992, Jordan et al. 1993). Several authors (Andersen et al. 1992, Neff 1968, Person 2003) have shown that the defecation rate may depend on the herbivore population structure and the amount and quality of available forage. Therefore, pellet group surveys should be used with caution in areas where the population structure or the availability of different browsing species changes considerably between years or over time. In this study, moose population size did not change dramatically between the two aerial estimates (2002 and 2006) when the defecation rate was estimated. Neither did forestry practices nor age distribution nor composition of forest stands change dramatically during this 5-year period. This fact may be an important cause of the high correspondence between the two estimates.

Moreover, estimation from the old pellet group survey showed low correlation to other estimates of population size but the overall trend, estimated as 3-year averages, was similar to the trend in estimates from other methods. Our analysis of the data based on the new pellet group survey indicates the importance of distributing sampling units over the entire study area.

Hunter observations as a management tool

Solberg & Sæther (1999) and Sylvén (2000) have shown that hunter observations can be a useful tool for moose population management, since several important population measures can be derived from these: population size index, sex ratio and recruitment rate. Sylvén (2000) found that an area of 500 km^2 is needed if the hunter observations are to be used as an accurate population index. However, our results indicate that hunter observations can also be a useful tool for estimating long-term population trends even in smaller areas (130 km^2). However, Mysterud et al. (2007) found that hunter observations of red deer *Cervus elaphus* was also influenced by the harvest techniques. Thus, changes in harvest techniques within a hunting district as well as differences in harvest techniques among hunting districts have to be taken into account when evaluating hunter observations.

Sylvén (2000) did not include spatial autocorrelation between hunter observations in smaller areas. However, because hunting districts close to each other are more likely to have similar observation statistics, combining data from several neighbouring small districts may improve the precision of moose observation indexes for management purposes. Hunting districts close to each other are more likely to have similar observation statistics even though the area of each district is small. Our results indicate that hunter observations can be useful over a long time period in moderately sized areas, and if support was available from surrounding hunting districts, then this should be improved even further.

Cohort analysis

Reconstruction of historical population size can be a good complement for analysing trends in population development. However, this method depends on a number of assumptions and requires independent estimates of natural mortality in the study population. Unlike most other moose populations, natural mortality could be estimated from radio-collared animals for our study population, but was biased towards young and middle-aged individuals. Unfortunately, reconstructed population size proved very sensitive to survival estimates among old females (>15 years), resulting in relatively large confidence intervals for this age class, thereby contributing to uncertain estimates of population size.

Our cohort analysis rests on the assumption of no net immigration or emigration, an assumption that was shown to have been violated in the current study during the initial phase of the study period due to seasonal immigration of males during the mating and harvest season. However, this was probably a result of an extreme harvest strategy aimed at drastically reducing the male segment of the adult moose population. From the cohort analysis it was estimated that >80 adult males must have immigrated during the second half of the 1970s in order to have a proportion of males equal to 0.5 in the population, as estimated from aerial counts. However, in the years after 1980, we found no evidence for changes in net migration since the proportion of males was constant (see Fig. 6). Nevertheless, if no aerial counts had been performed during this period, erroneous conclusions about population size (see Fig. 5) and the adult sex ratio (see Fig. 6) may have been drawn. Furthermore, a cohort analysis is difficult to use as a management tool since the estimates of population size in the most recent years are the ones most uncertain.

Estimates of the reconstructed population size yielded consistently lower estimates than aerial counts. A number of factors may be invoked to explain these differences. For example, seasonal migration into the study area during the winter season may have resulted in higher winter estimates compared to the reconstructed population. However, earlier studies of radio-collared moose do not support this explanation (Cederlund & Sand 1991, 1994). The only logical explanation that we could find for the discrepancy between aerial counts and reconstructed population size is that the natural mortality of radio-collared moose has been overestimated and that reconstruction estimates were sensitive to the existence of a few old shot females in the data set. Calibrating the reconstruction with the aerial counts corrected for 70% sightability gives a natural mortality for old females of slightly less than 50%, which is lower than the average estimate for this age class, but well within the confidence interval of the survival analysis (see Fig. 4).

Conclusions

Our results emphasise the importance of developing area-specific estimates of sightability correction factors for aerial counts of moose. This could be done either by using radio-collared moose or by using the sampling-resampling technique of sample plots during field counts.

If pellet group counts are to be used as a measure of population size and trends, this method should in some years be combined with aerial counts to estimate site-specific rate of defecation.

Our results also indicate that hunter observations can be used to follow long-term population size development, even in relatively small management areas.

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