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Hunter observations of moose *Alces alces* as a management tool

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Pre- and post-harvest population size and the structural composition of the moose *Alces alces* population in the Vefsn valley in northern Norway estimated by the use of cohort analysis were compared to population density indices derived from hunter moose observations during 1968-1993. The moose observation index (moose seen per hunter day) was able to predict the same trend in the post-harvest population size in 84% of the cases, and was significantly linearly related both to pre- and post-harvest population size. The moose observation index was more closely related to the post- than to the pre-harvest population size, probably because the main part of the harvest took place during the first week of the hunting season, whereas the observation index was based on aggregated values collected over two weeks. Moreover, the observation index tended to overestimate population size when hunting success was high, indicating that factors influencing hunting success may also affect the probability of detecting moose. The recruitment rate (calves per female) recorded by the hunters was also closely related to the recruitment rate estimated by the cohort analysis, suggesting that the observed recruitment rate may provide a useful index of the recruitment to the population. We suggest that further improvements of moose recordings as a management tool can be obtained if the data are analysed separately for shorter periods (e.g. week, day) of the hunting season because this will probably reduce the impact of annual variation in harvesting rates on the estimates.

Key words: cohort analysis, hunter observations, hunting statistics, moose, population trends

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Assessing the size of game populations is an important task in both wildlife management and wildlife research. For large herbivores, census methods are often based on aerial surveys, e.g. for moose *Alces alces* (Tärnhuvud 1988). The advantage of these methods is that the precision of the population estimates can be calculated by the choice of an appropriate sampling design. However, large financial costs often restrict the use of aerial surveys in moose management.

Another approach in assessing the population size of harvested species has been to use information gathered during the harvest period. For instance, catch-per-unit-effort methods have long traditions in population ecology (Seber 1982, Krebs 1989). One problem associated with the use of such indirect methods, however, is to relate the variation in the derived indices to fluctuations in population size. In this paper, we examine how indices based on obser-

vations by hunters during the hunting season can be used to predict fluctuations in a moose population in northern Norway. Such data are routinely collected from several populations all over Fennoscandia (Østgård 1987, Ericsson 1993, Ericsson & Wallin 1993), but the reliability of the several indices derived from this material has not yet been quantitatively examined. Using long-term records (i.e. 26 years) of a moose population, we investigate whether moose observations by hunters reflect the variation of the population size and recruitment rate, estimated independently by the use of cohort analysis (Solberg, Sæther, Strand & Loison 1999). In addition, we examine whether variables related to hunting conditions or population composition influence the ability to predict population size and recruitment rate from the moose observations. Finally, we suggest possible improvements of indices for future population trend monitoring.

Methods

Study area and climate

The data used in the study were collected in the municipalities of Vefsn, Grane and Hattfjelldal in the Vefsn valley in the southern part of the county of Nordland in northern Norway (65°20'-66°00'N latitude) during 1967-1995. The area lies within the boreal vegetation zone and is mostly covered with spruce *Picea abies* and pine *Pinus sylvestris* forests, and farmland along the valley floors. Birch *Betula pubescens* forests and alpine pastures dominate the higher slopes. Forests (and bogs) constitute about 1,709 km^2 of the total area, and are relatively evenly distributed over the three municipalities. All of the forested area was utilised for moose hunting.

The climate of the area is relatively mild due to its proximity to the sea, with a mean monthly temperature of 1.3°C and annual precipitation of 1,200 mm. Large annual variation in monthly temperature, precipitation and snow depth was recorded (Solberg & Sæther 1994). Measurements of annual mean monthly temperature, snow depth and precipitation during 1968-1995 were obtained from the Norwegian Meteorological Institute in Oslo. The variables were measured at the Majavatn meteorological station in Grane.

The reconstructed population

During 1967-1993, the population size was estimated using cohort analysis (Fry 1949, Lowe 1969, McCullough 1979, Fryxell, Mercer & Gellately 1988, Fryxell, Hussel, Lambert & Smith 1991, McCullough, Pine, Whitmore, Mansfield & Decker 1990, Ferguson 1993, Solberg et al. 1999). The rationale of cohort analysis is that the minimum population in previous years can be reconstructed using age-specific data of individuals collected at specific times, for instance based on individuals harvested or killed by other man-related activities (Fryxell et al. 1988, 1991, Solberg et al. 1999). In the present case, population fluctuations were reconstructed based on 6,996 moose harvested during 1967-1995; of these 6,752 (96.5%) were aged in the laboratory (Haagenrud 1978). Non-aged animals of each sex were distributed among the age groups according to the ratio of aged animals to the total number of animals harvested in a particular year. For instance, in 1975 only 45 of 49 adult females harvested were aged. The number of females within each adult (>1 year-old) female age group that year was therefore multiplied by 49/45 = 1.09 to correct for the missing individuals (Solberg et al. 1999). An estimated 25% of the pre-harvest population was harvested each year (Solberg et al. 1999).

To control for individuals that die from natural causes or traffic accidents, independent estimates on annual age-specific mortality of moose were used to adjust the annual number of individuals in the population in a specific year (Fryxell et al. 1988, 1991, Solberg et al. 1999). Due to lack of appropriate data from Norway, we used age-specific survival data from radio-collared moose from the Kenai Peninsula in Alaska (Bangs, Bailey & Portner 1989). In this particular population, predation by bears and wolves was low, leading to high age-specific annual survival (range: 0.90-0.97; Bangs et al. 1989). Indeed, the main cause of mortality was accidents with motor vehicles, which is also assumed to be the main cause of death apart from hunting in the Vefsn area. Unfortunately, we lack a complete record on the number, sex and age of moose killed by motor vehicles each year in this area. The low mortality due to causes other than hunting suggests that annual variation in this mortality rate have little influence on the population size estimated by cohort analysis.

During the study period, 99% of all individuals from a cohort had been harvested after seven years for males and 14 years for females (Solberg et al. 1999). Accordingly, completed cohorts only existed until 1981 for females and 1988 for males. For the

remaining years, cohorts (and population size) were estimated using age-specific hunting vulnerability from completed cohorts in combination with the age-specific number of moose already harvested from incomplete cohorts. This method depends on the assumption that hunting effort and age-specific hunting vulnerability are relatively stable from year to year (e.g. Fryxell et al. 1988, Solberg et al. 1999). However, even for the latest cohort in the study (born in 1993), an estimated 60% of the cohort had already been harvested by 1995, suggesting that variation in hunting effort may have only limited effects on population estimates. Nevertheless, for some of the most recent years, variation in hunting effort or age-specific hunting vulnerability may have influenced the population estimates (Solberg et al. 1999). We refer to Solberg et al. (1999) for further information about the cohort analysis and independent estimates of the population size.

Four different variables were estimated by cohort analysis (see data in Appendix 1):

1) Pre-harvest population size: Population size immediately before harvesting;
2) Post-harvest population size: Pre-harvest population size minus the annual harvest;
3) Pre-harvest recruitment rate: Number of calves per female ≥1 year old immediately before harvesting;
4) Post-harvest recruitment rate: Number of calves per female ≥1 year old immediately after harvesting.

Regulation of the harvest

Two different systems of partitioning the quota to different categories of animals were practised in the area during the period of study. From 1967 to 1972 hunting permits were divided into males, females, and 'free' animals (male or female). Since 1973, the quotas have been specified as calves, yearlings and adult (>1.5 year) males and females, respectively. Calves, juveniles and adult males comprise the largest proportion of the quota in order to restrict the harvest on productive females, creating a lower mean age of males than of females in the study area (Solberg et al. 1999).

The timing of the hunting season has changed little during the study period. From 1968 to 1979, the hunting season lasted two weeks from 27 September until 10 October. During 1980-1993 the hunting season was prolonged and lasted until 31 October. Since 1983, the season has opened on 25 September. An exception existed for the municipality of Hattfjelldal where the hunting season started on 10 September during 1985-1991. Since 1983, there has been a one-week break in the middle of the hunting season, first from 9 to 15 October during 1983-1991 and then from 2 to 9 October during 1992-1993. Most of the moose harvested within the hunting season were shot during the first week of the hunting season (mean = 59%, sd = 10%).

From the harvest records we calculated the following two variables (see data in Appendix 1):

1) Harvest rate: Annual harvest divided by the pre-harvest population size;
2) Hunting success: Percentage of the annual hunting quota harvested each year.

Population density estimated from 'moose observations'

The observation indices were estimated from moose observation forms completed by the leader of each team of moose hunters from 1968 to 1993. The number of moose observed and the number of hunters in the teams were reported for each day during the first two weeks of the hunting season. All observations of moose were recorded, except for moose that definitely had been observed by the same hunter or other hunters in the team the same day. Observed moose were classified into six different categories; calves, yearling and adult males, yearling and adult females without calves, females with one calf, females with twins, and individuals unidentifiable to sex or age.

Reporting moose observations was compulsory for the leader of each team hunting in state forests (about half of the total area) during 1968-1984. Since 1985, the reporting has been compulsory for all hunting teams, although some reports may have been missing in the first years after the reporting of observations was initiated (M. Håker, pers. comm.). During the study period, an average of 1,887 (range: 682-3,926) moose were observed annually during the two first weeks of the hunting season, distributed over, on average, 4,227 hunter days (range: 2,072-6,785).

From the annual moose observation records we calculated the following three population indices (see data in Appendix 1):

1) Observation index: Total number of moose observed per hunter day;
2) Observed sex-ratio: Total number of yearling and adult males divided by the total number of yearling and adult females;
3) Observed recruitment rate: Total number of

calves divided by the total number of yearling and adult females.

Data analyses

We first compared the observation index with the variation in the pre- and post-harvest population size using linear regression analyses, and then tested for a non-linear relationship by applying a polynomial regression analysis to the data (Sokal & Rohlf 1981: 671-690). Next, we examined the effect of variation in harvest rate, hunting success, adult sex ratio and variation in recruitment rate on the residual variation in the relationship between the observation index and the pre- and post-harvest population size. We examined the effect of harvest rate because large variation in the proportion of moose removed during the observation period presumably would influence the number of moose left to observe. Similarly, hunting success can be assumed to index the prevailing hunting conditions, and, accordingly, the observation conditions. For instance, poor hunting weather could lead to low hunting success as well as few moose observations per hunter day. Finally, we examined whether variation in adult sex ratio or recruitment rate could explain differences in the predictive power of the moose observation index. Such a relationship may appear if the probability of detecting a moose differs among different categories (e.g. sex, calfing status) of animals. Accordingly, we expected the observation index to overestimate population size during years of high male/female ratios because males are more active than females during the rutting period (Andersen & Sæther 1996), and therefore are more likely to be observed than females. Similarly, we examined whether the observation index overestimated population size during years of high recruitment rates because groups (female with one or two calves) may be more easily discovered than single females.

The effects of these additional independent variables were first examined using partial correlation analyses while simultaneously controlling for the pre- or post-harvest population size. Then, in order to evaluate the importance of the different variables in explaining the variation in the observation index, we conducted multiple regression analyses with all possible combinations of independent variables entered into the model. Based on the model selection criteria 'Cp of Mallows' (Draper & Smith 1981: 299), we present and discuss the two 'best' models. The 'Cp of Mallows' follows the principle of parsimony, measuring a trade-off between models with a low residual sum of squares, but a large number of parameters, and simple models with a larger residual sum of square and a low number of parameters. The best models minimise the Cp.

Because of the time series properties of the data, two major adjustments were made in the analyses. First, because we expected our time series to covary beyond only displaying similar trends (e.g. they are correlated because both change with time), we presented the relationship between detrended variables. Detrending was accomplished using residuals from the regression of the variable on time (Chatfield 1996). All variables used in the analyses (see Appendix 1) were significantly related to time ($P \leq 0.06$) and were therefore detrended.

Second, several of the time series revealed significant autocorrelation, which, if not accounted for, may lead to spurious tests of significance (e.g. Myers, Mertz & Barrowman 1995). To account for the autocorrelation in dependent and independent variables, we therefore corrected the degrees of freedom of the correlation analyses by a method proposed by Bartlett (1946), which has been used in several recent studies (Myers et al. 1995, Post, Stenseth, Langvatn & Fromentin 1997, Post & Stenseth 1998, Solberg et al. 1999). This method modifies the tests of significance by adjusting the degrees of freedom (df): $N' = N (1-a_1a_2) / (1+a_1a_2)$, in which N' is the adjusted df, N the number of paired observations, and a_1 and a_2 are the first order autocorrelation coefficients for the two series.

When testing for the significance of coefficients of single and multiple regression analyses with autocorrelated variables, we used Pearson and partial correlation analyses, respectively, with adjusted df. The corresponding df and P-values are denoted df_{adj} and P_{adj}, respectively. The first order autocorrelation (Royama 1992) of the variables in Appendix 1 ranged from small and not-significant (e.g. 0.25, 'males per female') to substantial (e.g. 0.84, 'pre-harvest population size'). All first order autocorrelations were positive.

Wildlife managers may be particularly interested in how to predict population density (size) from the observation index. Because the observation index is the dependent value in the regression model, we followed the procedure of inverse prediction (Sokal & Rohlf 1981: 496-498) to estimate the 95% confidence interval for the relationship between the observation index and the pre- and post-harvest population

size, respectively. Using sign test (Sokal & Rohlf 1981), we also analysed whether the observation index was able to predict a change in population size in the same direction as found by cohort analysis.

To examine the ability of the observed recruitment rate to reflect the 'true' recruitment rate, we correlated the observed recruitment rate with both the pre-harvest and post-harvest recruitment rates based on the reconstructed population. Moreover, because the observed recruitment rate is based on the aggregated values from the first two weeks of the hunting season, variation in the number of harvested calves per harvested female may have some influence on how precisely this index can predict the recruitment rate in the population. Accordingly, by use of a multiple regression analysis, we tested to what extent the number of harvested calves per harvested female could explain an additional proportion of the variation in the observed recruitment rate.

All statistical analyses were performed using SPSS for Windows (Spss Inc., 1996). All P-values were two-tailed.

Results

What explains variation in the observation index?

The observation index was positively related to both the pre-harvest and post-harvest population sizes estimated by the cohort analysis (Figs. 1 and 2). A linear regression analysis showed that 45% of the variation in the observation index was explained by the pre-harvest population size, whereas 62% of the variation in the observation index was explained by the post-harvest population size (Table 1). Comparing the original values (not detrended) revealed an even closer relationship (R^2 = 0.58 and R^2 = 0.71 using the pre- and post-harvest population size, respectively). However, accounting for autocorrelation in the time series, only the relationship between the observation index and the post-harvest population size was significant (see Table 1). No polynomial term (square or cubic) could explain an additional part of the variation in the observation index (P > 0.10), indicating that, within the present range of population sizes, the relationship between the observation index and population size was approximately linear. Moreover, no qualitatively different final results were obtained when using ln-transformed compared to non-transformed data. Hence, in the subsequent analysis, we employed linear regression of non-transformed values (although detrended) to describe the relationship between the observation index and the population size.

The auxiliary independent variables could all explain a proportion of the variation in the observation index when simultaneously controlling for pre- or post-harvest population size (Table 2). First, the

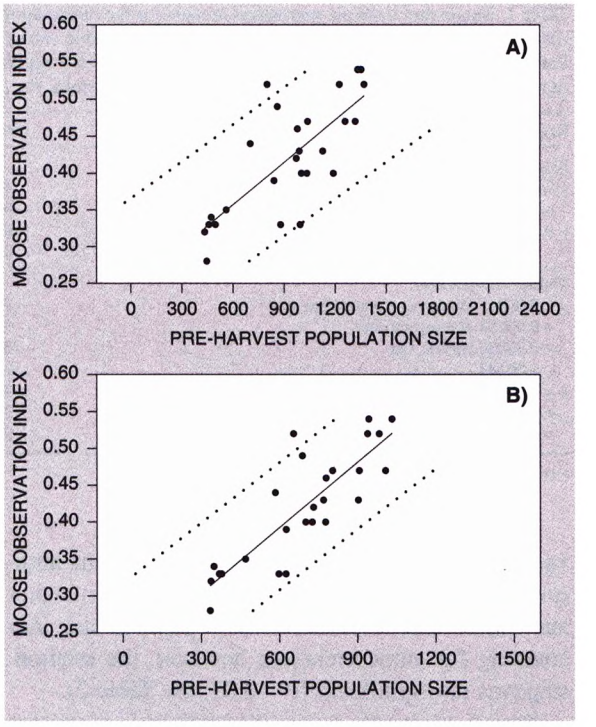

Figure 2. Moose observation index in relation to the pre-harvest population size (A) and the post-harvest population size (B), with regression slope (solid line) and 95% confidence limits (broken lines) given for the inverse prediction of population size from the observation index.

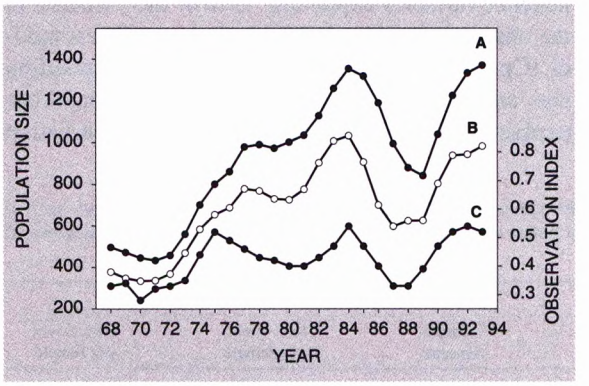

Figure 1. Annual variation in the estimated population size (left axis) before (A) and after (B) the hunting season, and annual variation in the observation index (C, right axis).

Table 1. Single and multiple regression models for the observation index of moose in the Vefsn Valley, Norway, (y) in relation to population size, annual harvest (total number of moose harvested each year), hunting success, and observed number of adult males per female. Partial correlation coefficients (Partial r) given in italics are significant ($P < 0.05$) after correcting the degrees of freedom for autocorrelation (see text for further explanation). For single regressions, the partial r is the Pearson correlation coefficient.

Regression equation	Partial T	R^2	F	Partial r
Single regressions:				
y = 0.00025 Pre-harvest population size	4.40***	0.45	19.36***	0.67
+ 0.00035	0.04			
y = 0.00035 Post-harvest population size	6.21***	0.62	38.60***	*0.78*
- 0.00038	-0.05			
Multiple regressions:				
y = 0.00015 Pre-harvest population size	3.18**	0.79	28.22***	0.56
+ 0.00584 hunting success	3.47**			0.59
- 0.38800 harvest rate	-2.98**			-0.53
- 0.00104	-0.17			
y = 0.00020 Post-harvest population size	3.35**	0.76	36.84***	0.57
+ 0.00649 hunting success	3.75***			*0.62*
- 0.00022	-0.03			

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

variation in the annual harvest rate reduced the ability of the observation index to predict variation in pre-harvest, but not in post-harvest population size. Accounting for autocorrelation, however, the relationship was not significant ($P = 0.07$, see Table 2).

Second, there was a positive relationship between hunting success and the observation index when simultaneously controlling for variation in population size (see Table 2), indicating that the observation index may overestimate population size in years with high hunting success. However, no significant correlation was found between the hunting success and the variation in the mean monthly precipitation, temperature or snow-cover in September or October ($P > 0.10$), and no climatic variable could explain a significant additional part of the variation in the observation index ($P > 0.10$). Moreover, the hunting success was significantly related neither to the annual number of hunter days ($r = 0.12$, $P > 0.10$), nor to the number of hunter days in relation to the harvest quota ($r = -0.23$, $P > 0.10$). Hence, no evidence was found that weather conditions or hunting effort affected the hunting success.

Third, the observed proportion of males in the population explained a significant proportion of the variation in the observation index, when controlling for either pre-harvest or post-harvest population size (see Table 2). Accordingly, in years with a relatively large proportion of males in the population, the observation index tended to overestimate the population size. However, a non-significant relationship appeared when accounting for the autocorrelation in the time series (see Table 2; pre-harvest: $P = 0.07$, post-harvest: $P = 0.10$). Finally, the observation index overestimated population size during years of high recruitment rates, suggesting that the relative detectability of females may increase with the proportion of calves in the population.

By comparing the possible combination of independent variables in various models by their 'Cp of Mallows', we selected two models (see Table 1). The best model ($Cp = 5.03$) combined pre-harvest population size, harvest rate and hunting success as independent variables explaining 79% of the variation in the observation index, whereas the second best model ($Cp = 6.225$) combined post-harvest population size and hunting success as independent variables, explaining 76% of the variation in the observation

Table 2. Partial correlation between the observation index and four independent variables when simultaneously controlling for pre-harvest or post-harvest population size. Partial correlation coefficients given in italics were significant ($P < 0.05$) after correcting the degrees of freedom for autocorrelation (see text for further explanation).

	Independent variable			
Observation index	Harvest rate	Hunting success	Obs. males per female	Obs. calves per female
Pre-harvest population size	-0.65***	*0.69***	0.46*	*0.58***
Post-harvest population size	-0.33	*0.62***	0.42*	0.39*

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

index. However, in both models there was a high level of multicolinearity, as hunting success was related to both the pre-harvest population size ($r = 057$, $N = 26$, $P < 0.01$), the post-harvest population size ($r = 0.65$, $N = 26$, $P < 0.001$), and the harvest rate ($r = -0.40$, $N = 26$, $P < 0.05$). Moreover, accounting for autocorrelation in the time series revealed that no variable, except hunting success, explained a significant proportion of the observation index.

Estimating population size and fluctuations from the observation index

Providing 95% confidence interval for the relationship between the observation index and the pre-harvest (see Fig. 2a) and post-harvest population size (see Fig. 2b) revealed large uncertainty in predicting population size by use of the observation index. The asymmetric position of the confidence interval in relation to the regression line arises as a consequence of the inverse prediction of the population size. Similarly, the observation index was not able to significantly predict the trend in the pre-harvest population size (sign test, $P > 0.1$) as the two variables changed in similar direction in only 15 of 23 cases (two cases excluded as the observation index showed no change). In contrast, the observation index significantly predicted the trend in the post-harvest population size in 19 of 23 cases (sign test, $P < 0.01$), or, more specific, with a probability of 0.83.

The observed recruitment rate as an index of population recruitment rate

The observed recruitment rate was highly correlated both with the estimated pre-harvest recruitment rate ($r = 0.75$, $N = 26$, $P < 0.001$, $df_{adj} = 17$, $P_{adj} < 0.001$), and the estimated number of calves per female in the population after the hunting season ($r = 0.72$, $N = 26$, $P < 0.001$, $df_{adj} = 17$, $P_{adj} < 0.001$). The recruitment rate from the pre-harvest population (mean = 0.85, SD = 0.21) was on average higher than the observed recruitment rate (mean = 0.74, SD = 0.10) (paired t-test, $t = -4.16$, $df = 25$, $P < 0.001$). In a multiple regression analysis, the number of harvested calves per harvested female could not explain an additional significant ($P > 0.1$) proportion of the variance in the observed recruitment rate.

Discussion

Our study demonstrates that the number of moose observed per hunter day can be used to predict the directional and quantitative change in population size in moose. This is in agreement with Fryxell et al. (1988) who found a significant positive relationship between the moose observation index and the population size based on cohort analysis, but the relationship they found was weaker than the one we found in our study. However, when repeating the comparison with a cohort analysis model (CAGEAN, Deriso, Quinn & Neal 1985), Ferguson (1993) found correlations comparable to our results, and where the two indices deviated, this seemed to be due to errors in the cohort analysis rather than in the number of moose seen per hunter day (Ferguson 1993). On the other hand, as observed by the large confidence limits of the inverse prediction of the population size, the observation index alone is not an appropriate index to predict the absolute population size. For instance, given an observation index of 0.48, the estimated post-harvest population size with 95% confidence will range between 597 and 1,228 moose (see Fig. 2b). If we want to predict the pre-harvest population size, the predictive power of the observation index is even lower due to the larger residual variation around the regression line, and in turn, wider confidence interval (see Fig. 2a).

Our analyses gave no indications of a non-linear relationship between the observation index and the reconstructed population size. However, G. Ericsson & K. Wallin (unpubl. data) concluded, based on the relationship between hunter observations and population size among different populations, that a 'saturation' effect exists at population densities above one moose per km^2, e.g. at high density the observation index levels off with increasing density. In the Vefsn area, population density never exceeded one moose per km^2 (max = 0.8 moose/km^2) during our study period. However, the potential non-linearity in the relationship between the observation index and population size should be considered when making predictions for high-density populations.

The observation index was a better predictor of population size after than before the hunting season, probably because of the effects of hunting on the relative number of moose present during the observation period. Because the observation index is based on aggregated numbers of moose observed during the first two weeks of the hunting season, the proportion of moose removed may strongly influence the accuracy of the observation index. For instance, during the study period, 59% of the annual harvest

was on average harvested during the first week of hunting (range: 10-20% of the population), indicating that for most of the observation period, the moose population was more similar to the post-harvest than to the pre-harvest population size. This was also indicated by the larger contribution of harvest rate in explaining variation in the observation index when combined with the pre-harvest population size than with the post-harvest population size. Local managers should therefore mainly employ the observation index to estimate post-harvest population trends.

The observation index also tended to overestimate the pre- and post-harvest population size in years with high hunting success. Hunting success could be assumed to reflect several factors that may also influence observation conditions, such as the prevailing weather conditions during the hunting season, but no significant relationship existed between the hunting success, or observation index, and the climatic variables. It is, however, doubtful that our crude climatic variables were able to intercept the importance of good and bad hunting weather. Other weather variables such as the frequency of days with strong wind or fog during the annual hunting seasons may be expected to have a stronger influence on the hunting and observation conditions. Unfortunately, we have currently no such data available.

The number of hunters participating in the hunt may constitute another factor that is affecting both the hunting success and the observation index. If more hunters lead to more intense hunting with more disturbance and movement of the moose, as indicated by Ericsson (1993), the moose may expose themselves more often to the hunters, which in turn may lead to higher hunting success and relatively higher numbers of moose observed per hunter day. In our study, hunting success was not significantly related to the number of hunter days or to the number of hunter days relative to the number of hunting permits ($P > 0.1$). However, this could be due to the fact that the number of hunter days is more closely related to the number of days hunting than to the number of hunters present, and, accordingly, there is no effect of increased disturbance due to more hunters. Unfortunately, only incomplete data exist on the annual number of hunters participating in moose hunts during our study period, but results from Sweden indicate that the number of hunters have a strong positive influence on the relative number of moose observed per hunting effort (Ericsson & Wallin 1993). Based on our results, no strong conclusions can therefore be drawn on the importance of the hunting success to increase the predictive power of the observation index. It should also be noted that hunting success consists of two variables rather than one, indicating that changes in hunting success may reflect changes in annual harvest, hunting quota or both. However, a very high correlation between annual harvest and hunting quota ($r = 0.96$), as well as high autocorrelation ($r > 0.68$), seriously restricts the interpretation and power of models analysing the individual contribution of these two variables.

The close association between the observed and the reconstructed recruitment rates also suggests that the observed number of calves per female in the population may provide a useful index of annual variation in recruitment rate. However, the lower estimates of the recruitment rate based on observations compared to the rate obtained from the reconstructed population indicate that the observed rate underestimates the true recruitment rate in the population. This may be due to a tendency of the moose hunters to underestimate the real reproductive status of the females observed as females with twins may be more difficult to observe than single-calf females and/or females without calves. However, the observation index rather tended to overestimate population size in years of high recruitment rate, indicating that the detectability increased with the number of calves. Alternatively, the reconstructed population overestimates the true recruitment rate. This could happen if the cohort analysis overestimates the male segment in relation to the female segment in the population (Solberg et al. 1999). Indeed, in their comparison of reproductive estimates based on hunter observations and radio-collared animals, G. Ericsson & K. Wallin (unpubl. data) found recruitment estimates based on hunter observations to be higher than estimates based on radio-collared individuals, indicating that the discrepancy between the observed and reconstructed recruitment rates in our studies may have been due to the cohort analysis overestimating the recruitment rates.

Several studies on ungulate species have recorded close associations between fecundity rates, population density, and quality and quantity of food resources (see review in Sæther 1997). Observed recruitment indices could be utilised to assess the prevailing population condition (Hanks 1981, Franzmann & Schwartz 1985), preferably in combination with other inexpensive indices of population conditions such as body mass and age at maturity (Hanks

1981). On the other hand, the observed recruitment rate in the present population may be exceptional as local hunters are reluctant to shoot calves and calf-rearing females (M. Håker, pers. comm.). As a consequence, hunting had only a small impact on the calves/female ratio in the population during the observation period. In other populations with a higher annual variance in the proportion of calves harvested, greater sampling variance in the observed recruitment rate may occur.

For the future, we suggest a few changes in the sampling procedures, which may improve the use of the observation index. Rather than only using the aggregated values collected over two weeks as at present, we suggest collection of daily observations, harvest size and number of hunters because this may provide more detailed information that can be used to improve the index. For instance, if data covering a shorter period are analysed, this may reduce the impact on the observation index of variation in harvest rate. More detailed information may also be a useful foundation for developing more advanced 'catch-per-unit-effort' techniques or 'change in ratio' methods (Seber 1982, 1986, Krebs 1989, Laake 1992, Udevitz & Pollock 1992). Indeed, such techniques may provide estimates on the actual population size and not only an index on population fluctuations (Laake 1992, Udevitz & Pollock 1992). The relatively large fraction of the population removed during the hunting season (mean = 25%, Solberg et al. 1999), as well as the differential hunting of males and females and high harvest of calves in many moose populations, may facilitate the use of both methods (Krebs 1989). Alternatively, techniques that combine the catch-per-unit-effort and the observation data may be constructed to increase the precision of the population estimates (Routledge 1989).

Future improvements may also include a better understanding of factors affecting the probability of recording individuals of different sex, age and status (calves or no calves). Our results indicate (despite partly non-significant due to high autocorrelation, see Table 2) that the observation index overestimate population size in years with higher proportions of males or females with calves in the population. As several Scandinavian studies seem to conclude that males are more active than females in the autumn (Lorentsen, Wiseth, Einvik & Pedersen 1991, Ericsson 1993, Gustafsson & Cederlund 1993), males may be assumed to expose themselves more often to the hunters than females. Similarly, females with calves may be more easily detected than females without calves due to their 'group structure', or perhaps because they tend to seek particular habitats. However, only detailed studies of the segregation and activity patterns of radio-collared individuals during the hunt may help determine the effect of variation in population structure on the preciseness of the observation index.

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Appendix I. Estimated population characteristics, harvest records and moose observation indices for the moose population in the Vefsn Valley, Norway. The harvest rate is the annual harvest divided by the pre-harvest population size. Hunting success is the annual harvest in relation to the annual number of hunting permits.

Year	Pre-harvest population size	Post-harvest population size	Total harvest	Harvest rate	Hunting quota	Hunting success	Observation index	Pre-harvest calves per female	Observed calves per female	Observed males per female
1968	497	378	119	0.24	177	67.23	0.33	0.76	0.58	0.70
1969	472	348	124	0.26	168	73.81	0.34	0.55	0.59	0.64
1970	446	334	112	0.25	176	63.64	0.28	0.64	0.59	0.68
1971	434	337	97	0.22	153	63.40	0.32	0.68	0.69	0.68
1972	458	368	90	0.20	130	69.23	0.33	0.80	0.74	0.69
1973	561	470	91	0.16	133	68.42	0.35	1.14	0.77	0.65
1974	702	584	118	0.17	152	77.63	0.44	1.10	0.76	0.65
1975	801	654	147	0.18	190	77.37	0.52	0.84	0.77	0.64
1976	861	688	173	0.20	229	75.55	0.49	0.71	0.76	0.62
1977	979	779	200	0.20	280	71.43	0.46	0.99	0.82	0.66
1978	990	769	221	0.22	295	74.92	0.43	0.67	0.71	0.61
1979	973	731	242	0.25	331	73.11	0.42	0.61	0.72	0.67
1980	1002	726	276	0.28	353	78.19	0.40	0.82	0.70	0.62
1981	1035	777	258	0.25	348	74.14	0.40	0.93	0.68	0.52
1982	1128	903	225	0.20	299	75.25	0.43	1.03	0.84	0.54
1983	1259	1007	252	0.20	333	75.68	0.47	0.88	0.67	0.54
1984	1353	1032	321	0.24	388	82.73	0.54	0.79	0.69	0.60
1985	1319	907	412	0.31	597	69.01	0.47	0.60	0.66	0.49
1986	1190	701	489	0.41	670	72.99	0.40	0.64	0.62	0.50
1987	995	598	397	0.40	610	65.08	0.33	0.80	0.71	0.47
1988	880	625	255	0.29	392	65.05	0.33	0.93	0.83	0.40
1989	842	626	216	0.26	296	72.97	0.39	0.78	0.71	0.51
1990	1039	804	235	0.23	330	71.21	0.47	1.44	0.91	0.48
1991	1226	939	287	0.23	366	78.42	0.52	1.22	0.94	0.49
1992	1334	944	390	0.29	469	83.16	0.54	0.99	0.84	0.53
1993	1370	983	387	0.28	494	78.34	0.52	0.99	0.90	0.53
Mean	929	693	236	0.25	321	73.00	0.42	0.85	0.74	0.58
(SD)	(310)	(219)	(112)	(0.06)	(151)	(5.45)	(0.08)	(0.21)	(0.10)	(0.08)