

FACTORS AFFECTING DETECTABILITY OF MOOSE *ALCES ALCES* DURING THE HUNTING SEASON IN NORTHERN NORWAY

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ABSTRACT: The use of hunter observations of moose (*Alces alces*) to index variation in population size and structure is based on the assumption that there is a monotonic relationship between moose seen per hunter-day and population size of moose. For this relationship to also be proportional, the probability of detecting a given moose should increase proportionally with the number of hunters and days hunting; i.e., a doubling of the number of hunter-days should double the probability of detecting a moose. Moreover, to obtain a precise index, the index should be independent of moose reproductive status, date of hunting season, weather conditions, and hunting area. We examined the influence of these factors on the probability of detecting individually radio-collared moose in a population in northern Norway. Our results support a proportional relationship between the number of moose seen and the number of hunters observing them. Moreover, we found no difference in observation rate among female moose in relation to the number of calves following them. However, large variation existed in the proportion of possible moose observed by different hunting teams. This can result in varying observation rates between years in situations where large annual variation exists in the number of days hunted by each hunting team. We therefore recommend that the pooling of observation data should be performed over a more carefully selected period of the hunting season (e.g., the first hunting week) rather than over the whole hunting season.

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Sustainable moose (*Alces alces*) management depends on regular information about population size and structure to determine the annual number of hunting permits. In Norway, the two most frequently used methods are aerial censuses and observational data obtained by hunters during the hunting season (Solberg and Sæther 1999). Aerial census of the population may be a relatively precise method given the choice of an appropriate sampling design (Caughley 1974, Tärnhuvud 1988), but the method is expensive, and therefore of restricted local use. Moreover, because of the long sea-

sonal migrations that occur in many Fennoscandian moose populations (Cederlund et al. 1987, Sweanor and Sandegren 1988, Sæther et al. 1992, Andersen and Sæther 1996), the size and distribution of the population during winter, when censuses normally occur, may differ extensively from the population during the autumn hunting season. In practice, the winter estimates may therefore be of limited use for local moose managers.

A much less costly method than aerial censuses is to estimate the change in moose density and structure based on moose ob-

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servations obtained and reported by hunters during the hunting season (Crichton 1993, Andersen and Sæther 1996, Ericsson and Wallin 1999, Solberg and Sæther 1999). This method has been in regular use as a management tool in Norway since the mid-1980s and in one area since the late-1960s (Solberg and Sæther 1999). The data obtained from these reports includes total number of observed (corrected for known duplications) and shot moose by sex and age, as well as the hunting effort (Andersen and Sæther 1996, Solberg and Sæther 1999). Such data are frequently used to estimate the change in population density (moose seen per hunter-day), sex structure (male per female), and recruitment rate (calves per female).

Studies that have examined the relationship between moose observations by hunters and independent estimates of population size obtained through other methods all found support for a general monotonic relationship between the equivalent measurements (Fryxell et al. 1988, Ericsson and Wallin 1999, Solberg and Sæther 1999). However, the observational indices did not always show the same direction of population change as other independent estimates of population size or structure (Ericsson and Wallin 1999, Solberg and Sæther 1999), and did not increase proportional with the population size. For instance, based on the relationship between hunter observations and independent measures of population size among different populations, Ericsson and Wallin (1999) found a diminishing increase in the moose seen per hunter-day with increasing moose densities. Similarly, Solberg and Sæther (1999) found that the moose seen per hunter-day tended to overestimate population size in years with high hunting success, indicating that the probability of detecting a given moose co-varies with conditions that lead to high hunting success (e.g., weather conditions). In turn,

this variation in the probability of detecting a moose among years reduces the precision of observation indices as a predictive management tool.

One suggested factor that may affect the probability to observe a moose is the number of hunters participating in the hunt (Ericsson and Wallin 1994). Although more hunters are likely to observe more moose, the number of moose observed may not necessarily increase in proportion to hunting effort; i.e., because observation efficiency may decrease with the number of hunters. Alternatively, if more hunters lead to more intense hunting, and subsequently greater movement of moose, moose may expose themselves more often to the hunters. Different sex or age groups may also expose themselves with different probability, or groups of animals may be more easily detected than singletons. As a consequence the moose seen per hunter effort and recruitment indices (e.g., calves per female) may vary in relation to variation in population structure. These effects may be of minor importance for estimating the general trend over years for a population; i.e., the relationship may still be monotonic (sensu Williams et al. 2002), but may be a major impediment for developing moose observation indices into a more precise management tool.

In this study, we used hunter observations of individually radio-collared moose to examine how the detection probabilities of moose vary within and among hunting areas. More specifically, we tested to what extent variation in hunting effort, moose movement, and weather conditions were associated with the probability of detecting a moose.

STUDY AREA

The study was carried out in the municipality of Bardu (69°N) in the County of Troms, northern Norway. The area is situ-

ated within the medium boreal and the northern boreal vegetation zones (Moen 1998). Dominating tree species on the mountain sides are birch (*Betula pubescens*) and Scots pine (*Pinus sylvestris*), interspersed with rowan (*Sorbus aucuparia*), aspen (*Populus tremula*), grey alder (*Alnus incana*), bird cherry (*Prunus padus*), and willow species (*Salix* spp.) along the rivers (Sæther and Heim 1993, Solberg et al. 1999). During the summer there is a high production of herbaceous plants, including many important browse species like *Cicerbita alpina*, *Equisetum fluviatile*, *Athyrium filix-femina*, *Matteuccia struthiopteris*, and *Dryopteris expansa* (Sæther and Heim 1993). The area has cold winters (mean January temperature -10.4°C), cool summers (mean July temperature 13.0°C), and a mean yearly precipitation of 652 mm.

The municipality of Bardu is currently divided into 29 hunting zones ($\bar{x}=25.27\text{ km}^2$, $\text{SD}=24.31$). Eleven of them were included in the present study ($\bar{x}=19.45\text{ km}^2$, $\text{SD}=4.31$). Each hunting zone had 1 team of hunters, with an average of 6.4 ($\text{SD}=2.1$) hunters per team during the study period.

METHODS

Data Collection and Measurements

Adult moose were captured by darting from a helicopter during February/March in 1996 and 1997. The animals were subsequently ear-tagged and fitted with 5 cm wide radio-collars.

Before the 1997 hunting season the radio-collared females were approached on foot and the number of calves with the females was recorded. During the period September 25 - October 18, radio-collared moose within the selected hunting zones were triangulated with a precision level of ± 100 m once per day, at approximately the same time (i.e., ± 2 hours) each day. The interval between September 25 and October 18 included 2 periods with hunting (Sep-

tember 25 - October 1 and October 10 - October 18). No hunting occurred between October 2 - 9.

Each team of hunters in the study area recorded the number of radio-collared moose observed daily and the number of calves present with the radio-collared females. They also recorded the locality of the observation, and whether any radio-collared individuals or calves following them were shot. By triangulating radio-collared moose each day we also knew how many of the radio-collared moose were present in areas with hunters. The probability of detecting a moose was defined as the proportion of still living radio-collared moose within hunting zones with active hunting that were observed each day. If a radio-collared moose was with certainty observed twice or more by the same team, these observations were not recorded. This is in accordance with the standard procedure for recording moose observed by hunters on the observation form (see below). On one occasion the same individual moose was observed in 2 different hunting zones on the same day, and was counted as 2 observations in the data analysis.

From the moose observation forms completed each year by all hunting teams (Andersen and Sæther 1996, Solberg and Sæther 1999), we calculated the daily mean number of hunters in a team and the daily number of teams that were hunting.

The daily distance moved by individual moose was calculated as the linear distance in meters between the positions on consecutive days (m/day). Because the radio-collared moose were not followed continuously, the estimates of movement underestimated the actual distance moved by the moose.

The proportion of radio-collared moose that crossed borders between hunting zones each day was used as an index of interzonal movement. This variable was calculated as

the number of radio-collared moose found in a different hunting zone than the preceding day divided by the total number of radio-collared moose present in the study area the same day.

The proportion of radio-collared females with calf/calves in hunting zones with active hunters was used to reflect the structural composition of the moose population. All climatic variables were measured at Bardufoss Meteorological Station and provided by the Norwegian Meteorological Institute in Oslo. Both temperature and the amount of precipitation decreased during the study period.

Predictions and Data Analysis

We tested several assumptions regarding the use of 'moose seen per hunter-day' as an index of variation in population density. This involved (1) the variation in the number and spatial distribution of the observers, the hunters; (2) the climatic conditions that may influence the visibility in the forest; and (3) the structural composition of the moose population. First, the number of moose observed may vary with the number of hunters. The basic assumption behind the use of moose seen per hunter-day as an index of density is that the number of moose observed increases proportionally (that is, with a coefficient not different from 1) with the number of hunters observing. Thus, given a fixed population density within a given area, the moose seen per hunter-day will be independent of the number of hunters in the area. This is not trivial as the moose seen per hunter-day has been suggested to decrease with increasing number of hunters because of decreasing observation efficiency (Ericsson and Wallin 1999). However, increasing number of hunters may also observe more moose per hunter-day because more hunters lead to higher disturbance and movement of moose, thus increasing chances for moose to be observed

(Ericsson and Wallin 1996). Accordingly, the use of moose seen per hunter-day may be a poor index of population density if the number of hunters varies.

Another possibility is that the observation rates vary with the area used for hunting independent of the number of hunters, as hunting over large areas may be expected to decrease the number of 'sanctuaries' where moose may hide. In the study area, each hunting team hunted exclusively within fixed hunting areas, suggesting that the disturbance and movement may be expected to increase with the number of hunting teams hunting at a given time.

The observation rate may also vary with the variation in climate and the progress of the season (i.e., date within hunting season) as this may affect the visibility in the forest, hence the chance to observe a moose. Here, we test whether the observation rate varies with the level of precipitation and with the progress of the hunting season. High level of precipitation is usually associated with low visibility. Similarly, the transparency of the forest is assumed to increase with the progress of the hunting season because of proceeding leaf fall. Because a high proportion (> 50%) of the study area is covered with deciduous forest (birch, willow, rowan, and alder), progression of leaf fall is likely to have a significant effect on the observation rate.

Finally, we examined whether the observation rate varied with the structural composition of the population. For instance, females with calf/calves may be easier to detect because of the larger group size, or alternatively less easy to detect if they are more elusive to protect their calf/calves. Thus, the proportion of moose observed may either decrease or increase with the proportion of females with calves in the area. Here, we examined to what extent the observation rate varied among radio-collared females with different reproduc-

tive status and tested to what extent the observation rate changed as the proportion of radio-collared females with calf/calves decreased during the hunting season.

The factors affecting the number of moose observed each day were examined using Poisson regression with a log link function (Proc GENMOD, SAS Institute 1996), as the observed number of radio-collared moose was expected to have a Poisson probability distribution. In general we modelled the expectation in the Poisson distribution λ as a curve linear function of covariates of interest such that;

$$I = aM\bar{x}^{b_1} n^{b_2} i^{b_3} s^{b_4} t^{b_5} p^{b_6} d^{b_7} z^{b_8} \quad (1)$$

On log scale this model takes the form;

$$\begin{aligned} \log(I) = & \ln(a) + \ln(M) + b_1 \ln(\bar{x}) + b_2 \ln(n) \\ & + \ln(i) + \ln(s) + \ln(t) + \ln(p) + \\ & + \ln(d) + \ln(z) \end{aligned} \quad (2)$$

To adjust for the daily variation in the number of radio-collared moose within hunting areas, we used the logarithm of all radio-collared moose within hunting areas as an offset variable; i.e., the exponent of the parameter (M) equal to 1 (see equation 1). In addition, we included the total number of hunters (mean number of hunters in a team (\ln), number of hunting teams ($\ln n$)) as offset, as we assumed the observed number of radio-collared moose to increase in direct proportion to the number of hunters (the null hypothesis).

We then examined alternative models by including one or a combination of the different explanatory variables (mean distance moved by radio-collared moose (d), interzonal movement of moose (i), temperature (t), precipitation (p), date within the hunting season (z), and the structural composition of the moose population (s) as covariates (equation 2), and finally by test-

ing models where \ln and/or $\ln n$ were included as covariates rather than offset variables. In this case we tested to what extent the variation in the observed number of radio-collared moose changed with the number of hunters with a coefficient different from 1, and/or to what extent variation in number of hunting teams influenced the number of observations. Because of the generally small data set (low power), we only tested models with 1 or 2 covariates included at a time.

The statistical significance of the different models was tested using the likelihood ratio test based on the change in deviance (SAS Institute 1996). The change in deviance between 2 nested models, e.g. $D(H_0) - D(H)$, is approximately chi-square distributed, with $p - p_0$ degrees of freedom where p and p_0 are the number of parameters under the models H and H_0 , respectively. If an independent variable significantly ($P < 0.05$) reduced the error deviance (D), we rejected H_0 (no effect, a proportional relationship between moose observed and number of hunters) in favor of the more general model H .

RESULTS

During the study period, 23 radio-collared moose were located within the selected hunting zones. Of these, 6 were females without calves, 8 single-calf females, 8 females with twins, and 1 male. The timing of the harvest of radio-collared moose or calves following radio-collared females indicated that most moose were shot during the first week of hunting (Table 1).

The proportion of radio-collared moose observed varied among days (0.16 ± 0.11), and generally decreased during the hunting season ($r = -0.63$, $n = 16$, $P = 0.009$). During the same period of time, the mean number of hunters, the number of hunting teams, temperature, precipitation, and interzonal

Table 1. The number of radio-collared moose or calves following radio-collared females shot during the hunting season in Bardu in 1997. The number in parentheses gives the % shot each week.

Hunting week	Period	Number of shot animals		
		Adults	Calves	Total
1	September 25 - October 1	5	9	14(60.9)
2	October 10 - October 16	2	2	4(17.4)
3	October 17 - October 23		1	1(4.3)
4 ¹	October 24 - October 31	2	2	4(17.4)

¹ The fourth hunting week includes one extra day (i.e., 8 days).

movement of moose decreased (Table 2). The proportion of radio-collared females with calf/calves in hunting zones with active hunters increased (Table 2), while the distance moved by radio-collared individuals was unrelated to time (Table 2).

Comparing the different models indicated that no combination of covariates better explained the variation in number of moose observed than the null hypothesis (Table 3, Fig. 1). An alternative model with interzonal movement of moose as a covariate was the best alternative model, but not significantly different from H_0 (Table 3). The model including the mean number of hunters hunting and the number of hunting teams as covariates also indicated a lower

deviance, but not significantly different from H_0 (Table 3, Fig. 1). Indeed, regressing the number of observed moose (with moose present as offset) on the total number of hunters (mean number of hunters, number of hunting teams), revealed that the slope did not significantly deviate from 1 (Fig. 1). Other combinations of covariates such as date within season, temperature, precipitation, proportion of females with calves, and distance moved by moose (m/day), did not significantly contribute when the number of hunters simultaneously was kept as an offset variable. Thus, given the present power, we cannot reject the null hypothesis that moose observed is a direct proportional function of the moose present in the area

Table 2. Matrix of Pearson correlation coefficients for independent variables, where z = date within the hunting season, \bar{x} = mean number of hunters in a hunting team, n = number of hunting teams, t = temperature, p = precipitation, s = proportion of radio-collared females with calves, d = mean daily distance moved by radio-collared moose, and i = interzonal movement of moose.

Independent Variables	z	\bar{x}	n	t	p	s	i
\bar{x}	-0.76***						
n	-0.82***	0.84***					
t	-0.85***	0.87***	0.82***				
p	-0.67**	0.44	0.50*	0.65**			
s	0.87***	-0.72**	-0.87***	-0.70**	-0.52*		
i	-0.69**	0.52*	0.67**	0.69**	0.41		
d	-0.41	0.33	0.33	0.18	0.11	-0.64**	0.49

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

Table 3. The best models explaining daily variation in the number of radio-collared moose observed (dependent variable) during the hunting season. Model 1 is the null hypothesis (H_0) and models 2 and 3 are the 2 best alternative models. $D(H_0) - D(H)$ is the change in deviance between H_0 and the alternative models. M = the number of radio-collared moose present in hunting zones with active hunters, \bar{x} = mean number of hunters in a hunting team, n = number of hunting teams, and i = interzonal movement of moose.

Model		Deviance	$D(H_0) - D(H)$	df	P
1	$\lambda = -5.89 \pm 0.13M\bar{x}n$	12,14			
2	$\lambda = -6.38 \pm 0.55M\bar{x}ni^{1.88 \pm 2.00}$	11,06	1.08	1	> 0.1
3	$\lambda = -7.96 \pm 2.82M\bar{x}^{0.173 \pm 0.797}n^{2.916 \pm 1.640}$	10,44	1.70	2	> 0.1

and the number of hunters observing.

In order to examine whether group size affects the probability of observing a moose, we compared the probability of observing female moose in relation to the number of calves following them. No significant difference was found among the categories ($\bar{x} \pm SE$; 0.16 ± 0.04 , 0.20 ± 0.07 , 0.10 ± 0.04 for females without calves, single calf females, and females with twins, respectively;

$\chi^2 = 2.62$, $df = 2$, $P = 0.27$). Similarly, no significant relationship was found between the rate of movement and whether the females were without calves, single calf females, or females with twins ($\bar{x} \pm SE$; 1728 ± 549 m/day, 1076 ± 154 m/day, 1645 ± 471 m/day, for females without calves, single calf females, and females with twins, respectively; $F = 0.75$, $df = 2$, $P = 0.49$) or precipitation ($r = 0.12$, $n = 15$, $P = 0.67$).

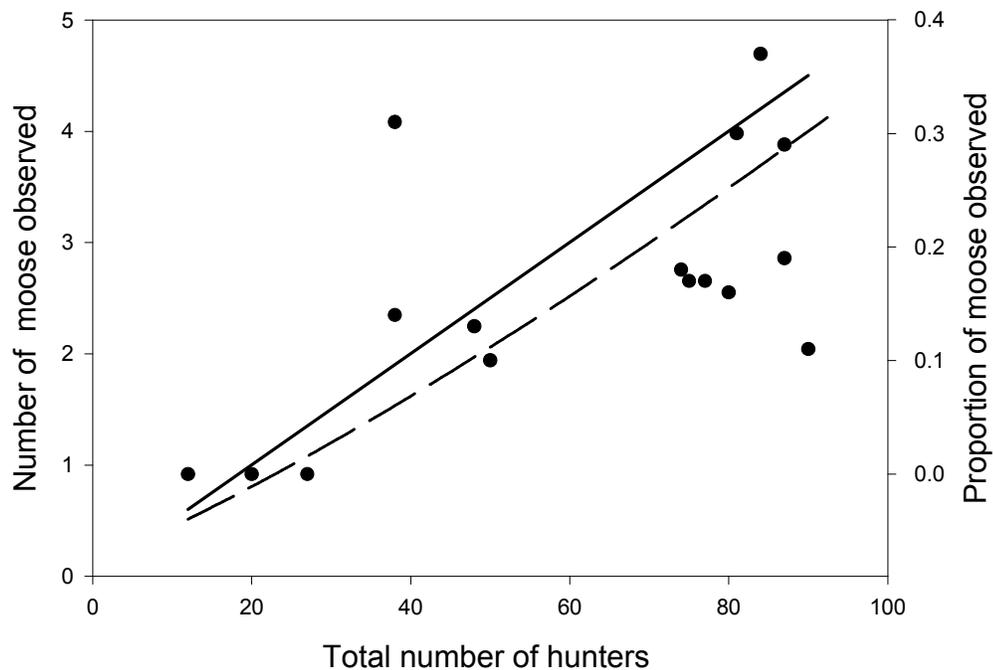


Fig. 1. The number of radio-collared moose observed given a fixed number (16) of radio-collared moose present (left axis, stippled line) and the proportion radio-collared moose observed (right axis, filled circles) in relation to total number of hunters. The solid line represents a proportional relationship between number of moose observed and number of hunters.

Moreover, comparing the rate of movement before and after females lost their calf/calves by hunting, 4 females decreased their rate, whereas 3 females increased their rate of movement (\bar{x} difference = 171 m/day; paired t-test, $t = 0.38$, $n = 7$, $P = 0.72$), indicating no general difference in movement before or after the calves were killed. Thus, no difference in observation frequency or behavior was found in relation to whether females had calves or not.

DISCUSSION

The use of observational data to monitor changes in population size and structure is based on several assumptions (Ericsson and Wallin 1999, Solberg and Sæther 1999, Hochachka et al. 2000), among which is the assumption that the number of moose observed increases proportionally with the number of hunters. Previous analyses, however, have indicated that the moose seen per hunter-day increases with population size, but with a slope less than 1 (Ericsson and Wallin 1999; Solberg and Sæther 1999). As the number of hunters also tends to increase with population size, we therefore expected the lack of proportional increase to be due to an increasing saturation of the number of observations as the number of hunters increases (Ericsson and Wallin 1999). Also the practice in Norway of not reporting moose that with certainty were observed by other hunting team members the same day is likely to generate a disproportional relationship between the number of moose observed and number of hunters. Although we observed a tendency of a disproportional slope (Fig. 1), we could not reject the hypothesis of a proportional relationship between the number of moose observed by hunters and the number of moose present. Thus, other compensatory mechanisms may also influence the number of moose observed; e.g., the movement pattern of moose as the number of hunters

increase. In the present study, interzonal movement (i.e., the proportion of moose that cross borders between hunting zones) of moose decreased with decreasing number of active hunting teams (Table 2), with a possible response being that relatively fewer moose are seen, and registered, by more than 1 team of hunters on the same day. Also, due to the low sample size, we cannot completely exclude the possibility that the lack of significant deviance from a proportional relationship could be due to low statistical power.

Another factor that may affect the moose observed per hunter-day and the recruitment indices is different detectability of moose depending on sex, age, or number of calves in company with female moose. In two recent contrasting studies, Solberg and Sæther (1999) and Ericsson and Wallin (1999) suggested that managers could either underestimate or overestimate recruitment rate based on hunter observations because of different observation rates of females with calves and females without calves. In the present study, however, the probability of detecting a female moose did not differ significantly in relation to her reproductive status. Gustafsson and Cederlund (1994) indicated similar results in a study with 16 radio-collared female moose during the hunting season. Hence, we now have similar results from 2 independent studies indicating that reproductive status does not affect observation rate. Accordingly, the number of moose seen per hunter day and the observed calves per female should not be affected by annual variation in the proportion of calf-rearing females in the population.

A third factor that may affect the observation rate is the distribution of observations among hunting teams and to what extent hunting teams vary in the time spent hunting among years. For instance, Ericsson and Wallin (1999) found that the slope be-

tween the moose seen per hunter-day and moose density differed among hunting areas, indicating that hunting teams differed in their efficiency in finding and recording moose; i.e., because observation skills or observation conditions varied among the different teams and hunting areas. Variation among years in the number of days the different teams are hunting may therefore introduce variation in the observation index that is not caused by variation in moose density. Indeed, in the present study, the 3 hunting teams that finished the hunt earliest had the highest proportion of observations (58%) compared to other teams (17%). Because the practice in Norway is to pool moose observation data over the whole hunting season (Solberg et al. 1997), variation in the time spent hunting among teams and years may generate variation in the moose seen per hunter day even if the population density is stable. This may also explain why Solberg and Sæther (1999) found that moose seen per hunter-day tended to underestimate population size in years with low hunting success. During such years, teams with relatively low observation frequency may spend more time hunting to fulfill their quota, hence contribute many hunter-days and few observations to the index. Because most moose in Norway are harvested during the first week (Solberg et al. 1997), prolonged hunting effort may lead to an index that more resembles the post-harvest population density than during years when the effective hunting season is shorter (Solberg and Sæther 1999). We therefore suggest that pooling data over more carefully selected periods of the hunting season (e.g., the first hunting week) may provide better indices of variation in population size and structure. By so doing, we would expect less variation among years in the period observations are collected in different zones, and therefore more similar conditions for observing moose among hunt-

ing teams. In turn, these indices may give more precise estimates of changes in population density and structure.

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