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Göran Ericsson & Kjell Wallin

The accuracy of hunter observations (moose seen per hunter day) as a source for various population parameters in moose *Alces alces* L was evaluated. We found an overall positive correlation between density and observation index. The strength of the relationship was similar in all of the three counties studied. The observation index levelled off with increasing density (>1.0 moose/km²). Sightability of moose differed significantly among two of the three counties studied which makes comparisons between the regions difficult. However, adjusting the regional observation index by independent estimates of population size enables comparisons over larger areas. We found a probability of 0.81 that a change in observation index also reflects the direction of a change in population size. The reproductive rate calculated from hunter observations (Σcalves)/(Σfemales) was correlated with the observed mean recorded reproductive rate among radio-collared moose in a county. Furthermore, moose reproduction as estimated from hunter observations was positively correlated among counties in northern Sweden indicating large-scale synchrony. Our findings indicate that hunter observations of moose reflect moose population size and reproductive rate reasonably well, and can be used to monitor population fluctuations. If calibrated, one may use observation indices for estimates of population size in local moose management as an alternative or supplement to more costly monitoring methods. If not calibrated, observational data may be misleading if they are used as a density indicator.

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Several different census methods have been used to monitor wild populations of mammals (Caughley & Sinclair 1994). Aerial surveys are probably the most accepted and widely used method to census large mammals. Numerous studies have tested, improved and debated the accuracy of aerial surveys (Caughley

1974, Gasaway & Dubois 1987, Steinhorst & Samuel 1989). Although aerial surveys normally provide a density estimate as well as demographic information, high costs often limit their general use in wildlife management. Among others, Neff (1968) and White (1992) proposed pellet counts as one alternative census method for large ungulates. However, the pellet count method does not normally give any demographic information although it is sometimes possible to distinguish between pellets from females and males and pellets from various age groups (MacCracken & van Ballenberghe 1987, Khan & Goyal 1993, Alvarez 1994). Furthermore, the use of ungulate pellet counts to estimate density is normally restricted to the winter period, but sometimes density information from other seasons, for instance from before the hunting season, is required.

A majority of North American wildlife agencies use hunter observations to monitor trends of moose populations in combination with other information (Crichton 1993). In the Nordic countries, hunter observations of moose have been used for more than 15 years to monitor moose populations in larger areas. In most areas, they are the only source of information regarding population changes (Hagenrud, Morow, Nygren & Stålfelt 1987, Jaren 1992, Nygren & Pesonen 1993). In Scandinavia, there is a growing interest in using this method to monitor other species than moose, e.g. the brown bear *Ursus arctos* (Elgmork 1991, Swenson, Sandegren & Söderberg 1996).

The moose hunt in Sweden, and thus the observational effort, is immense. As many as 250,000 people participate in the moose hunt each year (Ekman 1992). We have found that an average hunting day lasts for 6.8 hours (G. Ericsson & K. Wallin, unpubl. data). Assuming that an average moose hunter goes hunting for at least 6 days a year (J. Kindberg, Swedish Association for Hunting and Wildlife Management, Research Unit, Uppsala, pers. comm. 1997), would mean that Swedish moose hunters in total spend 1,500,000 days, or 10,200,000 hours looking for moose each year.

Despite common use in moose management in both North American and the Nordic countries, there is a substantial lack of basic knowledge on the relationship between moose observations and population density (Crichton 1993, Ericsson & Wallin 1994). There is a need for theoretical development and controlled tests to ascertain quantity and quality in data collection and analysis. The use of hunter observations rests on the basic assumption that a change in observation rate per time unit reflects a change in the population density; this has been shown to be true for some species, e.g. wolf *Canis lupus* (Creté & Messier 1987). For moose, however, this relationship is not well established (but see Fryxell, Mercer & Gellately 1988, Solberg & Sæther 1999).

In this paper, we ask two questions: 1) is there a general relationship across regions between moose density and hunter observation rate, and 2) does variation in hunter observation rates correspond to changes in population density? To answer these questions, we compare moose observations per hunter day with density estimates obtained from aerial surveys and hunting statistics. Furthermore, we analyse the relationship between the reproductive rate derived from hunter observations of moose and those estimated from a study population of radio-collared moose.

Material and methods

Observational data

During the first week of the moose hunt, each hunting team recorded the number of bulls, females with one or two calves, females without calves, solitary calves and unclassified moose. They also recorded the number of hunters each day. The observation period includes all activities associated with the hunt during the day. From these data, the observation rate, O, (moose seen per hunter day) was calculated as

$$O = \Sigma N_{obs} / \Sigma(N_{hunters} \cdot N_{days}),$$

where N_{obs} is the number of moose observed, $N_{hunters}$ is the number of hunters and N_{days} is the length of the observation period. Corrections for multiple observations of the same individual moose were not made. As a measure of reproductive rate the number of observed calves divided by the number of observed females $(\Sigma calves)/(\Sigma females)$ was used. Data were compiled and processed at local management unit level.

Population estimates

The Swedish Hunters' Association conducted the aerial surveys from fixed wing aircraft or helicopter during January-March, i.e. after the hunting season which lasted from September to December. Normally, the aerial surveys are initiated 24-72 hours after a snowfall. We used the actual numbers of moose
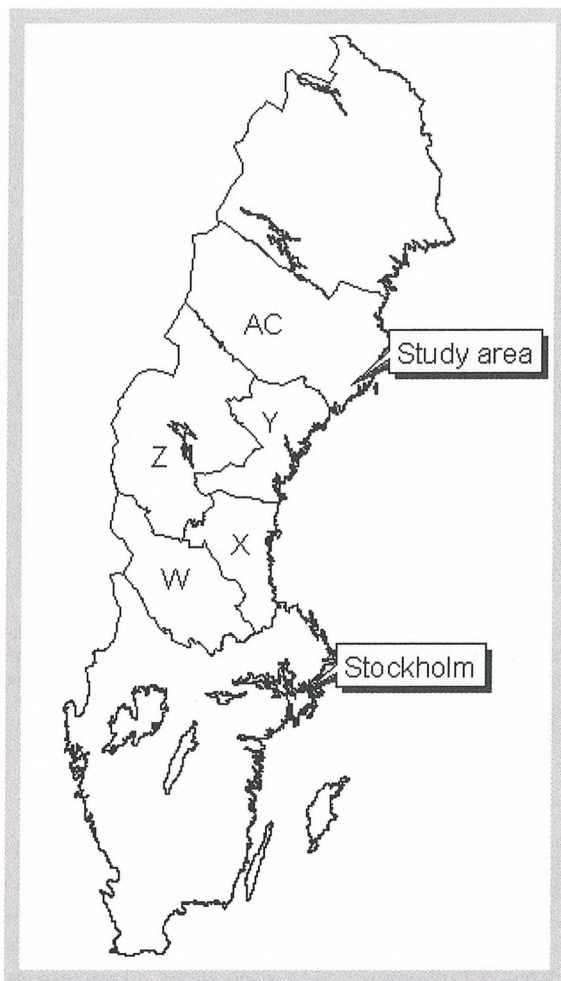
Figure 1. Location of the counties in which the study was performed: Västerbotten (AC; 59,148 km²), Jämtland (Z; 55,461 km²), Västernorrland (Y; 22,605 km²), Gävleborg (X; 19,657 km²), and Dalarna (W; 29,890 km²). In the Robertsfors (64°12'N, 20°45'E) study area situated ca 600 km north of Stockholm in AC, we used radio-collared moose for independent estimates of reproduction.

from three counties (Fig. 1): Västerbotten (AC; 59,148 km², N = 31), Dalarna (W; 29,890 km², N = 15), and Jämtland (Z; 55,461 km², N = 9). To test if changes in the number of moose seen per hunter day reflected changes in the 'true' population among years we used data from 16 different management units (mean = 1,400 km², range: 137-3,000 km²). No accurate estimates of observational effort exist at county level, but the number of members in the largest association for hunters on May 30, 1997, can be used as an indicator of relative effort (AC: 11,787 hunters, W: 11,686, X (Gävleborg; 19,657 km²): 8,948, Z: 9,141, Swedish Association for Hunting and Wildlife Management 1997, pers. comm.).

The populations in AC and Z are partly migratory (G. Ericsson & K. Wallin, unpubl. data) so we cannot rule out that immigration or emigration at the scale of the management units may have contributed some error to our population estimates. Unfortunately, the data needed to evaluate the size of this possible error are not available as this would require a marked population in each management unit to test for net losses or gains of animals due to migration between the hunting period and the aerial censuses. However, the size of the management units is larger in areas (mean size of AC = 2,200 km² vs a mean size of Z = 4,600 km²) where migration is thought to be important (e.g. in more mountainous areas). In addition, we have no reason to believe that aerial censuses are biased towards summer or winter ranges. Thus, as no date on this are available, we assumed that movements in and out of a particular management unit are approximately equal during the time from the hunting period to the aerial censuses.

Reproductive rate
We used reproductive data from a study population of radio-collared females in Robertsfors (64°12'N, 20°45'E) in AC (see Fig. 1). The number of >1-year-old females studied were 40, 40, 65, 59, 64 and 62 for the years 1991-1996, respectively. We determined the number of calves born by checking twice weekly during May-June. The week before the hunting season started, we counted the number of calves that had survived the summer. Because moose reproduction shows a large age-dependency and because our sample of radio-collared females does not reflect the age distribution of the population, we determined the yearly reproductive rate as follows:

1) the yearly, age-specific reproduction was deter-

observed from the aerial censuses in the absence of reliable sightability correction factors. Thus, our figures are therefore conservative estimates of moose numbers. We calculated the population densities at the start of the hunting season by adding the total harvest to the figures given by the aerial survey. In the analyses, we assumed that mortality from non-hunting causes during this short time period is negligible (G. Ericsson & K. Wallin, unpubl. data). We included all management units where at least one aerial survey had been carried out since 1985.

To evaluate the correlation between moose observation index and population density, we used data

mined separately for 2-, 3-, 4- and ≥5-year-old females;

2) the proportion of each age class was determined from females killed during the hunt (N = 377);

3) for each age class the estimated number of calves per cow was multiplied with the proportion of females belonging to the respective age class in the population and then summed for all age classes.

We then compared our estimates with the numbers observed by the hunters during the first week of the hunt. We assume that this reflects the age-distribution of the population as less than 6% of the entire moose population is killed during the first week of the hunting season (Ericsson & Wallin 1994), and as adult females were harvested randomly with respect to age during the study (G. Ericsson & K. Wallin, unpubl. data). We did this comparison for the local management unit of 3,130 km^2 covering our study population, and for the counties of AC, Y (Västernorrland; 22,605 km^2), and Z (see Fig. 1).

We determined the age of females by tooth wear and eruption during the marking event (Skuncke 1949). In our study population, age determination by tooth wear is an accurate method to an age of five years (G. Ericsson & K. Wallin, unpubl. data). From our sample of killed moose, the lower part of the jaws were retrieved and age determined by tooth cementum analysis (e.g. Fancy 1980). We performed all statistical analyses using SAS/STAT® (SAS Institute 1989).

Results

Density and observation index

The overall correlation between moose density and hunter observation rate was significant (Fig. 2, r = 0.51, N = 55, P < 0.0001). The correlation coefficient was of a similar order (see Fig. 2, AC: r = 0.69, N = 31, P < 0.0001, W: r = 0.59, N = 15, P = 0.020, Z: r = 0.58, N = 9, P = 0.10). A linear regression model with hunter observation as dependent variable was significant for AC and W (AC: intercept = 0.213, P = 0.036, β = 0.438, P < 0.0001, W: intercept = 0.219, P = 0.004, β = 0.145, P = 0.020), whereas for Z it was not significant (Z: intercept = 0.221, P = 0.002, β = 0.088, P = 0.100).

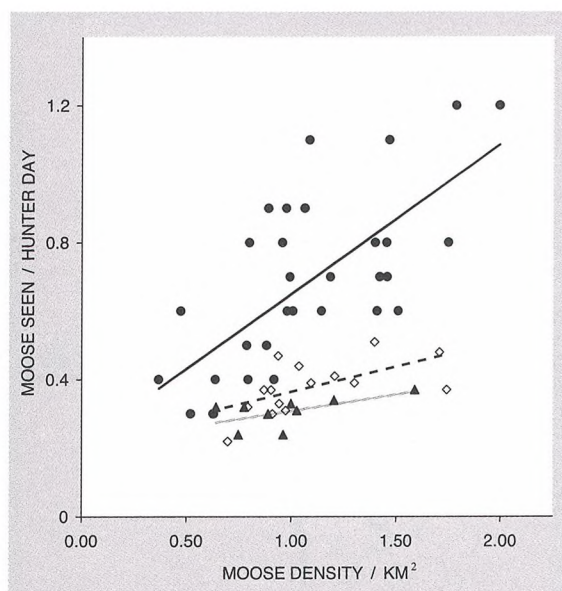The slopes (β), but not the intercepts, differed between AC-W and AC-Z, whereas W and Z did not

Figure 2. A positive correlation between the estimated moose density and the number of moose seen per hunter day existed for the counties described in Figure 1 (r = 0.51, P < 0.0001). Different areas are indicated by different slopes (AC: solid line, ●, β = 0.44; W: broken line, ◇, β = 0.15; Z: dotted line, ▲, β = 0.09). A linear regression model was significant for AC and W, but not for Z (AC: P = 0.0001, W: P = 0.020, Z: P = 0.10).

differ (P = 0.05, Dummy variable regression; Kleinbaum, Kupper & Muller 1987). The slope (β) differences between AC-W indicate that moose observations per hunter day from different areas are not directly comparable with each other. Comparisons among areas from different regions are useful in many situations, but are not necessary for local use of the method. However, to make such a comparison possible we apply the regression model used above between observation index and the independent estimate of true population densities for the counties. As O = α + βN, a standardised observation index could be estimated as (O-α)/β. Standardising each observation made different areas in the counties comparable. The overall correlation between the standardised observation index and population density was highly significant (r = 0.659, N = 55, P = 0.0001; Fig. 3).

Moose categories

Density estimates and observational data from W and Z distinguished between adults and calves, which made it possible to look for differences in observation rate between these categories. For both adults and calves, there was an overall significant correla-
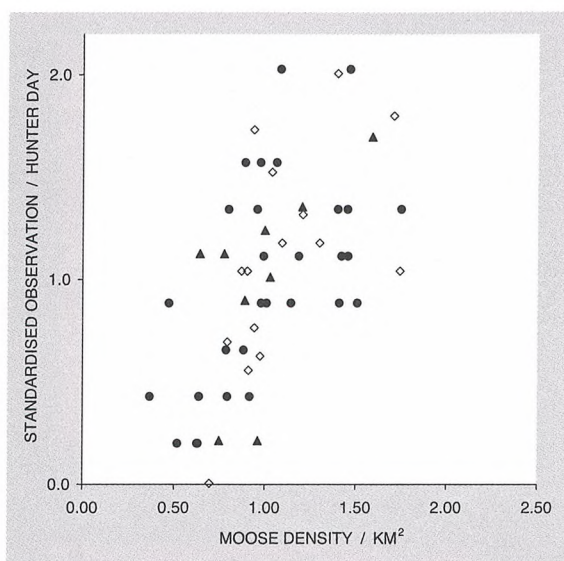
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Figure 3. Overall correlation between estimated moose density and standardised observations per hunter day $(O - \alpha)/\beta$ was highly significant (AC: ●, W: ◇, Z: ▲, r = 0.659, N = 55, P = 0.0001).

tion ($r_{adults} = 0.67$, P = 0.0003; $r_{calves} = 0.61$, N = 24, P = 0.0013). In Z, observations of adults showed the weakest correlation with density; otherwise the correlations were significant or close to significant (W: $r_{adults} = 0.63$, P = 0.012; $r_{calves} = 0.50$, N = 15, P = 0.055, Z: $r_{adults} = 0.42$, N = 9, P = 0.266; $r_{calves} = 0.75$, P = 0.020). When a linear regression model was applied for each county and category, we observed a relationship between observation rate and density in W (W_{adults}: intercept = 0.34, P = 0.83, β = 2.64, P = 0.012, W_{calves}: intercept = 0.14, P = 0.20, β = 1.83, P = 0.055). For Z we only observed a relationship between observation rate and density for calves, not for adults (Z_{adults}: intercept = 0.08, P = 0.85, β = 2.19, P = 0.27; Z_{calves}: intercept = - 0.19, P = 0.25, β = 4.71, P = 0.020). Thus, what caused the general non-significant relationship between density and moose observation in Z was the lack of relationship for adults.

The slopes for each category did not differ between the counties (Dummy variable regression, Kleinbaum, Kupper & Muller 1987, P > 0.47). This suggests that the strength of the relationship between observation rate and density may be of the same magnitude within the same area for calves and adults, but not always comparable between different areas (see above).

Detecting population changes

We examined if the method is capable of detecting changes in population size. We compared the between-year changes in observation index with changes in population density estimates. We used data from the 16 management areas for which density estimates for more than one year existed. Hunter observations tended to give estimates of growth rate (O_t/O_{t-1}) that were larger than those based on aerial surveys and hunting statistics (N_t/N_{t-1}, Wilcoxon Matched-Paired Sign-Ranks Test: Z = 1.57, N = 22, P = 0.12, Fig. 4). Two outliers in the data set highly influenced the outcome of the analyses. In both cases, moose observations per hunter day showed no population change while the independent measure showed a change of 1.28 and 1.93. We excluded the latter observation that deviated 4.05 standard deviations from the mean (Cooks distance = 6.81, Cook & Weisberg 1982) due to a suspected measurement error, and because such a growth rate is unrealistic. The correlation between the yearly rate of change (N_t/N_{t-1}) measured by observation index and the density estimate was close to significant (r = 0.41, N = 21, P = 0.068, Fig. 5). (Excluding the first outlier (1.28, Cooks distance = 2.52) produced a significant correlation (r = 0.60, N = 20, P = 0.005)). A linear regression analysis revealed [Population Change (Observations)] = 0.716 + 0.298*[Population
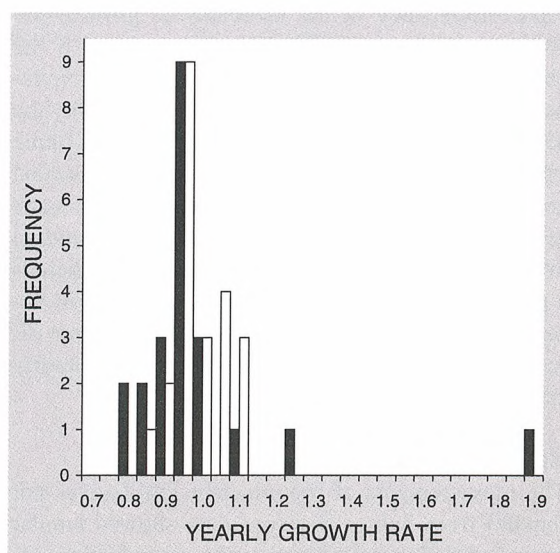

Figure 4. Growth rates calculated from moose hunter observations (open bars) tended to be higher than those obtained from the independent density estimates (aerial surveys + hunting statistics, solid bars, Wilcoxon Paired Sign-Ranks Test, Z = 1.57, N = 22, P = 0.12).
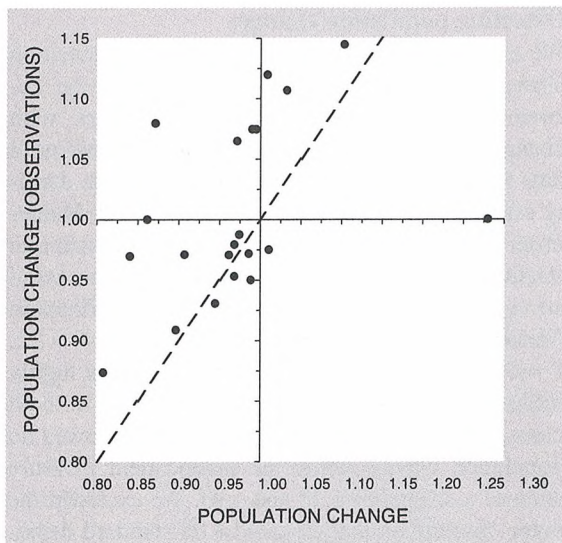
Figure 5. The correlation between the population change calculated from aerial survey plus hunting statistics and the observation index was close to being significant ($r = 0.41$, $N = 21$, $P = 0.068$). A linear regression between the two measurements of population change was significant ($t = 4.79$, $N = 21$, $P = 0.0001$), and the slope was close to being significantly different from unity ($t = 1.94$, $N = 21$, $P = 0.068$).

change] where the intercept differed from zero ($t = 4.79$, $N = 21$, $P = 0.0001$), and the slope was close to being significantly different from unity ($t = 1.94$, $N = 21$, $P = 0.068$). This further suggests that there is some discrepancy in the estimates of growth rate between the two methods. We also analysed if the observation index was capable of detecting a population change in the same direction as that found by the independent density estimate. In 13 of 16 cases (three observations excluded as one of the method revealed no change, i.e. ties) the two methods gave the same result which was significantly different from random drawing (Sign-test, $P = 0.011$). Consequently, there is a probability of about $^4/_5$ (0.81) that a change in observation index will reflect a change in the same direction as that observed via the independent density estimate.

Reproductive rate

The measurements of reproductive rate (calves per female) from hunter observed data showed similar annual variation as the per capita reproduction observed among radio-collared moose (Fig. 6). The between-year variation in reproductive rate seems to be correlated over larger areas in northern Sweden. Only one of these observed patterns was significant-
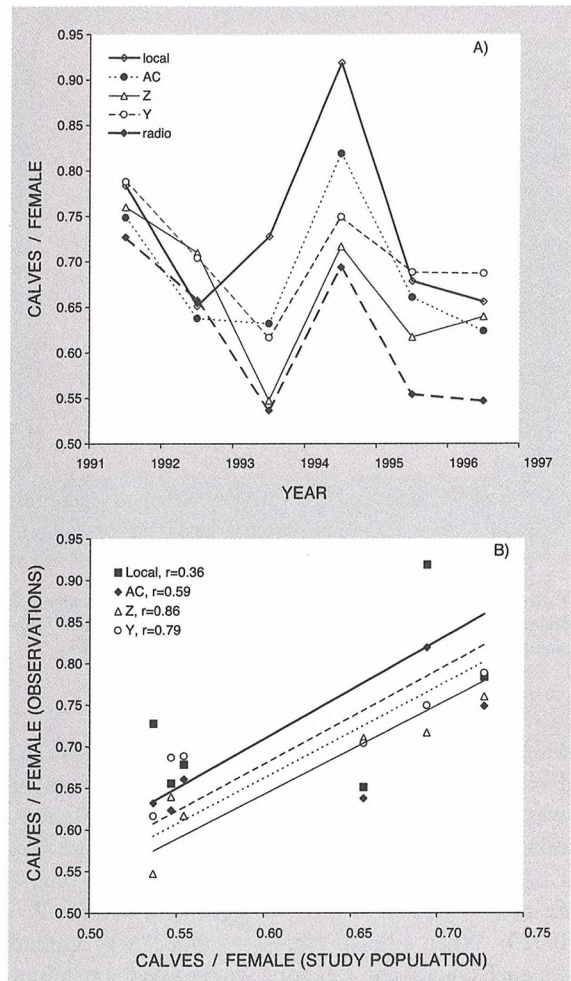

Figure 6. Between-year variation in moose reproductive rates (A) shows a temporal correlation among the counties of AC, Z and Y in northern Sweden, and with the radio-collared local moose population in AC ($r^2 > 0.60$, $P < 0.21$). The strengths of the relationships (B) are shown by the coefficients of determination (r^2).

ly correlated, but the number of years is only six ($r_{AC-Y} = 0.75$, $P = 0.09$; $r_{AC-Z} = 0.64$, $P = 0.17$; $r_{Z-Y} = 0.95$, $P = 0.004$). The correlation between the local management unit of the study area and the study population was not significant ($r_{local} = 0.60$, $N = 6$, $P = 0.21$). For AC, which holds the marked population, the correlation was smaller than for the counties farther away ($r_{AC} = 0.77$, $P = 0.07$). For those, we found a significant correlation between the reproductive rate of the local radio-collared females and that observed in the counties 200 and 400 km away ($r_Y = 0.89$, $P = 0.02$ and $r_Z = 0.93$, $P = 0.006$, respectively).

Discussion

Our data show a general relationship between hunter observations of moose and moose density. Only two comparable studies exist, and both use cohort analysis to backcalculate moose abundance and composition, so the basis of comparison with our data is somewhat limited. Fryxell et al. (1988) concluded that observed moose per hunter day was a valid index of moose abundance. Similarly, according to Solberg & Sæther (1999) moose observations by hunters accurately reflected fluctuations in moose density and annual reproduction in a moose population in northern Norway. Although we show a general relationship, the non-significant relationship between density and observations for Z ($P = 0.10$, $N = 9$) indicates that hunter observations may not be useful in all regions. However, this may be a statistical problem as the number of units was only nine and as the independent density estimate may be biased. The bias may arise from seasonal migration, but we believe that this is not the case as the management units in Z are large (mean = 4,600 km^2). Thus, the net effect of seasonal migration should be close to zero for each unit. Instead, we believe that one potential source of bias is the use of both helicopter and fixed wing aircraft.

The overall relationship between observation index and density is rather weak ($r^2 = 0.26$, see Fig. 2). To some extent, this was caused by differences among areas. The coefficient of determination increased as the area from which the population data were collected decreased ($r^2 \geq 0.35$, see Figs. 2 and 3). This suggests that the method is useful for monitoring local moose populations for management purposes if the relatively low precision of a single measurement is taken into account. Thus, it cannot be directly used as an index of population density. There are also large, unique effects tied to the local population, which may make comparisons among areas difficult. However, for correlative studies among areas the method might still be useful.

Potentially, there might also be other problems with a local use of hunter observations. The differences in observation rate for a given moose density (see Fig. 2), suggest large geographical differences in the possibility of observing moose. Several factors may influence the possibility of observing moose, e.g. vegetation structure, temporal changes in the vegetation, moose behaviour, hunting methods, and the composition of the moose population (Crichton 1993, Ericsson & Wallin 1994). These factors might also change locally during long-term monitoring. For instance, if the observed spatial variation is due to differences in forest age structure we might experience considerable local variation if we observe the population for an extended period of time. Thus, there will always be a need for local calibration of the index with other independent methods. If such methods provide a density estimate, it will also be possible to calibrate and convert the observation index to moose density. A successive reduction in study area, in order to reduce spatial variance, will eventually lead to a statistical problem. The number of observations becomes too small to yield a precise estimate of the observation rate. We have shown elsewhere that 8,000-10,000 hours of observations are needed to detect a local population change of 10% with 95% confidence (Ericsson & Wallin 1994). Thus, there will probably be some optimal area where the observation rate measurement most efficiently can be applied.

In addition to density estimates, measurement of reproductive rate is a central parameter in the management of moose populations and can be accurately derived from observational data. The determination of the ratios of different categories of animals (e.g. sex ratio, calves per females) is not as much influenced by unequal sightabilities as density estimates. Thus, the method has a good potential for observational data made during the same year, and the consequence is that the method can be used as a rough index for regional variation in population density. Furthermore, our results suggest that hunter observations have potential as a tool for monitoring reproductive rates in moose (see Figs. 5 and 6). The reason for the lack of perfect correlation could be unequal sightability of females with calves and females without calves. Groups of animals are more often easily discovered than single animals (e.g. Dehn 1990, Uetz & Hieber 1994). This is in accordance with our results on the measurements of reproductive rates from observational data, which are higher than measurements of reproductive rates based on radio-collared animals. However, there may be other reasons why the estimate is high relative to the control population. For instance, differences in behaviour during the hunting season exist between females with and females without calves (Ericsson & Wallin 1996).

The annual population change measured by the two methods was correlated, although the relationship was not strong (see Fig. 4). We found no signifi-

cant differences in the results obtained with the two methods, but the independent density estimate (aerial surveys + hunter kill) tended to give lower estimates than the observational index data. Both methods predicted the same directional change of the population in four of five cases.

Clearly, observational index can provide managers with some information about moose density, population development and annual reproductive rate, although the precision is not too high. Without regular calibration of the observation rate with independent measurements of moose density, it may be misleading as a density indicator. On the other hand, with calibration, the use of hunter observations can serve in the local moose management together with more costly methods such as aerial surveys. As a measurement of reproductive rate the usefulness of observational data (Σcalves)/(Σfemales) seems to be reliable. If hunter observation data are collected, processed and analysed during each year's hunt (e.g. after the first week), the harvest during the later part of the hunting season could be adjusted. This would be especially useful in situations where calves are harvested later than adults, as it opens up the possibility of adjusting calf harvest to the reproduction of the respective year.

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