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Change-in-sex ratio as an estimator of population size for Norwegian moose *Alces alces*

Erling J. Solberg, Vidar Grøtan, Christer M. Rolandsen, Henrik Brøseth & Scott Brainerd

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Effective management of ungulates requires regular estimates of population abundance, but these are often expensive and hard to obtain. We therefore examined if change-in-ratio (CIR) estimation methods, in combination with age- and sex-specific data on moose *Alces alces* observed and killed, could be a cheap alternative for estimating moose abundance in Norway. We used the large number of moose observations reported by moose hunters and estimated pre-harvest adult population size based on annual changes in adult sex ratio. Similarly, we estimated 1) annual recruitment rate based on the proportion of calves observed during the hunting season, 2) the harvest rate, and 3) the natural mortality rate based on variation in recruitment rate and harvest rate. During 1991-2000, annual variation in abundance was correlated with two of three independent indices of moose density, indicating that the CIR methods provide relatively precise estimates of abundance. Similarly, the estimated average natural mortality rate was similar to natural mortality rates of radio-collared moose in Scandinavia, and the estimated abundance was close to what we expected based on the annual harvest. However, large annual variation in estimated rates of natural mortality indicated that over- and underestimation of population abundance occurred for some years. This was likely due to the fact that harvesting occurred during periods of moose observations. Because we had no independent estimates of abundance, we were unable to estimate the bias. Hence, we concluded that variation in CIR abundance is a sensitive index of moose density, but that more studies are needed to determine the accuracy of CIR estimates as measurements of abundance. Future studies should focus on smaller populations with independent estimates on abundance, and base CIR estimation on changes in sex ratio within the hunting season to reduce the number of possible confounding effects.

Key words: Alces alces, change-in-ratio, moose, Norway, population size estimation

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Obtaining inexpensive, precise and unbiased estimates of population densities is a continuous challenge in moose *Alces alces* population management. Moose densities in Fennoscandia usually are estimated by aerial and ground censuses (e.g. moose pellet-group counts; Härkönen & Heikkilä 1999), but these are often expensive (e.g. aerial censuses) and encumbered with error sources that are not easily quantified (e.g. Timmerman & Buss 1998). Use of mark-recapture (or resight) methods (William et al. 2002) is likely to provide more unbiased and precise estimates of abundance, but these too are expensive. A related alternative that potentially is less expensive is the change-in-ratio (CIR) method (Kelker 1940, Krebs 1999). This method estimates population size from the observed change in ratio of two groups (e.g. males and females) following a known removal (e.g. by hunters) from the same groups (Paulik & Robson 1969, Krebs 1999). Critical conditions are that the two groups are easily distinguishable, that removals from (or gains to) both groups are known, and that the proportions of the two groups in the harvest are different from the proportions in the pre-harvest population (Krebs 1999).

These conditions are met in the Norwegian moose population. Adult (≥ 1 year old) males are antlered during the hunting season and therefore are easily distinguishable from calves and females, whereas females are easy to distinguish from calves based on size. Moreover, since more male than female permits are normally issued, harvest is male biased, and likely leading to changes in adult sex ratios from pre-hunt to post-hunt. Finally, a large number of moose observations are recorded annually as part of the national moose observation monitoring programme (Jaren 1992, Solberg et al. 1997). This programme collects number, sex and age (calf or adult) of moose observed by moose hunters during the hunting season, from which several indices on population structure and density can be calculated and used in local management (Jaren 1992, Solberg & Sæther 1999). Most important are 'moose seen per hunter day' as an index of population density, and 'calves per female' and 'males per female' as indices of recruitment rate and adult sex ratio, respectively. These indices provide relatively precise information on the temporal development in population density and structure within a given area (Ericsson & Wallin 1999, Solberg & Sæther 1999, Sylvén 2000, Solberg et al. 2002), but the observation data have not been used to estimate population abundance.

The aim of our study was to explore the possible use of CIR methods for estimating moose population trends and abundance in Norway. During the study period 1990-2000, we collected observations from nearly the complete distributional range of moose (183,000-268,000 moose observations annually). From annual changes in sex ratio we estimated variation in population abundance during the study period and tested the accuracy by comparing the estimates with other indices of population density and structure. We then discussed the possibilities of further improvement of CIR-estimation techniques for estimating moose population abundance, and evaluated to what extent this method may also become a useful tool for local management in the future.

Methods

Study sites

Our study spans most of the distributional range of moose in Norway (Fig. 1). Exceptions include some municipalities from which data are missing (see below),

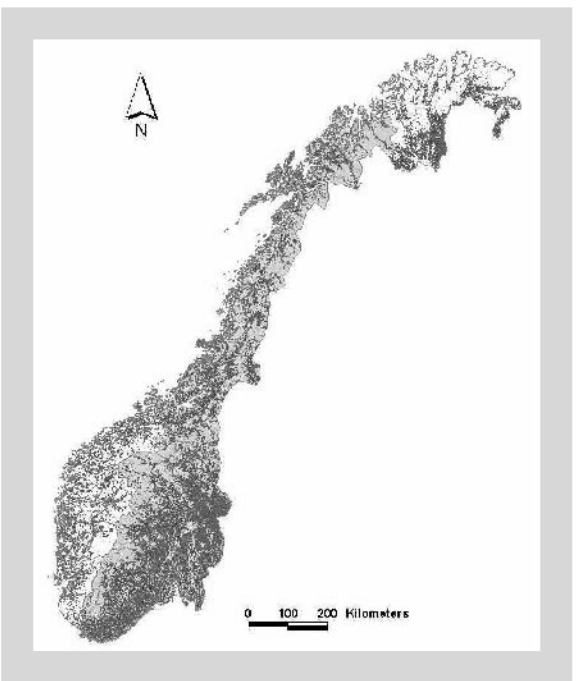


Figure 1. Counties from which data were provided (shown in light grey) and forested areas (dark grey). Moose data from the west coast counties and the northernmost county of Finnmark (white areas) were not included.

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and some newly established moose populations in western and northern Norway (see Fig. 1) where moose densities are low and harvest is irregular.

The study area is within the boreal vegetation zone, except for the very southern part that falls within the nemoral vegetation zone. Norwegian moose range is diverse and heterogeneous with respect to both vegetation and climate. Sæther & Heim (1993), Solberg & Sæther (1994), Sæther et al. (1996), Solberg et al. (1997), Hjeljord & Histøl (1999) provide detailed descriptions of the Norwegian moose range.

Hunting statistics and moose killed by other causes

Moose hunting in Norway is regulated by sex- and age-specific quotas decided by municipal wildlife management boards. These authorities are also responsible for reporting local moose harvest statistics (i.e. sex, age, number), as well as other incidental mortalities (e.g. induced by traffic accidents, disease, poaching, predation) to the national statistical bureau (Statistics Norway: http://www.ssb.no) at the end of each regulatory year (1 April-31 March).

Distribution of moose

The distributional range of moose, as provided by the annual hunting statistics (Statistics Norway), includes all forests and bogs within each municipality with moose hunting, but not open farmland (agricultural fields), lakes, urban areas and land above the tree line. In total, 101,201 km^2 were defined as moose habitat within our total study area. For comparison, the complete forested area in Norway is estimated to be about 120,000 km^2 (Anon. 1998).

Moose observations

Our population data were based on moose observations recorded by hunters during the moose hunting season each year. The leader of each team of moose hunters reported daily observations and the number of observers on a specific form. All observations of moose, during all phases of the day's hunt were included. Observations were divided into six categories: 1) calves, 2) yearling and adult males, 3) yearling and adult females without calf, 4) females with one calf, 5) females with twins, and 6) individuals of unknown sex and/or age. Verified cases of duplicate observations of the same moose are not reported (e.g. to avoid multiple reports of a moose seen simultaneously by two or more hunters). Observations from each team are then summarised by local wildlife management boards and reported to county wildlife authorities.

Formal reporting of moose observed during the hunting season has been compulsory for each hunting team throughout Norway since 1986. However, early records from several municipalities were poor, due to unfamiliarity with the system, as well as poor reporting and recording routines. Reporting improved by the end of the 1980s, and since 1990 > 90% of all municipalities with moose harvests have reported these observations each year.

For our analyses, we used observation and harvest data from 14 counties within the main moose distribution area (see Fig. 1) during 1990-2000. Observational and harvest records were complete for 240 municipalities, or 84% of all municipalities with moose hunting in Norway. Harvest within these municipalities constituted 87-90% ($\bar{x}$ = 89%) of all moose harvested in Norway.

Sample size and basic relationships

During 1990-2000, on average 216,778 moose (range: 177,750-236,489) were observed annually, of which 89% (range: 89-90%) were recorded by sex and age. Similarly, an average of 31,611 moose (range: 25,944-35,003) were killed on an average of 426,697 hunter days (range: 363,904-458,815) each hunting season. The annual harvests were typically male biased, both for calves ($\bar{x}$ = 52% male, range: 51-54%) and adults ($\bar{x}$= 59% male, range: 56-64%). The practice of sex- and age-specific harvesting was introduced in Norway in the early 1970s to increase the annual productivity in moose populations (Solberg et al. 2002). However, recently harvesting of males has decreased in many counties due to a desire to increase the proportion of males, and stabilise or decrease moose density. Accordingly, after two decades of increase, the national moose harvest has not shown subsequent increase during the 1990s, indicating that the moose population abundance has been relatively stable.

Calculating the population abundance based on change-in-ratio of moose observations

To calculate population abundance, we used the generalised change-in-ratio estimator (Paulik & Robson 1969):

$$N_1 = (Q_x - p_2Q) / (p_2 - p_1) \qquad (1),$$

where N_1 is the population abundance at time 1, p_1 the proportion of x-animals in the population at time 1, p_2 the proportion of x-animals in the population at time 2, Q_x the net change of x-animals between time 1 and 2, and Q is the net removal (x + y animals) from the total population between times 1 and 2 (Paulik & Robson 1969).

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For removal studies, different times are typically before and after a hunting season, but in principle may be any period of time between two censuses of population classes (Krebs 1999). We only had one estimate of population sex ratio per year, and thus our CIR estimator was based on change in males per females between years following sex-differential harvesting. In practice, this may not differ widely from before and after the hunting season in a given year, because the observed population structure more closely resembles post-harvest than pre-harvest populations (Solberg & Sæther 1999). Thus, the proportion of female calves and adults observed in the population in year t-1 will approximate the proportion of adult females in the population before harvesting in year t, provided that there are no sex differences in the natural mortality during the period between hunting seasons. The latter assumption, however, may not be critical as long as the natural mortality rate is low (Paulik & Robson 1969).

Calves were not specified by sex on the observation forms because calf sex is difficult to determine in the field. To provide the necessary information on calf sex ratio, one might assume equal (i.e. 50:50) recruitment rates for male and female calves to the autumn population. Alternatively, the distribution of male and female calves in the harvest can be used to estimate calf sex ratio if calves are harvested independent of sex, and there are large numbers of calves harvested each year (7,958-11,775 annually during our study period). We used the latter method since male and female calves are assumed to be equally vulnerable to hunting (e.g. Sæther et al. 2004), and since there was significant annual variation in harvest sex ratio of calves (range: 51-54% male calves; $F = 29.28$, $df = 1, 9$, $P < 0.001$), indicating that the actual calf sex ratio in the population varied during the study period.

The above method for CIR estimation is based on the assumption that males and females have equal chance of being observed in both the first and second sample (Krebs 1999). Although not thoroughly tested with respect to hunter moose observations, males are sometimes assumed to be observed proportionally more frequently than females because they are more active during the rut (e.g. Lorentsen et al. 1991, Ericsson & Wallin 1996). However, by comparing the variation in observed sex ratio in one population during 25 years with two other indices of population sex ratio (from train kills and by back-calculating sex structure using cohort analysis), Solberg et al. (2003) did not find the observed rate to be systematically overestimated, and concluded that the observed sex ratio reflects the population sex ratio. Preferably similar examinations should be performed also in other populations, but for the present study we assume equal sightabilities.

Calculating confidence intervals

Confidence intervals for CIR estimates can be calculated in two ways, depending on sample size (Paulik & Robson 1969, Krebs 1999). Since we had a large sample of observations, we used the normal approximation:

$$\text{Variance}(N_1) = N_1^2\,(\text{variance}(p_1)) + N_2^2\,(\text{variance}(p_2)) / (p_1 - p_2)^2 \quad (2),$$

where

$$N_2 = N_1 - Q \quad (3)$$

$$\text{Variance}(p_1) = p_1\,(1 - p_1) / n_1 \quad (4)$$

$$\text{Variance}(p_2) = p_2\,(1 - p_2) / n_2 \quad (5)$$

and where n_1 and n_2 are the total sample size of observations used to estimate the ratio p_1 at time 1 and p_2 at time 2, respectively. This variance formula assumes binomial sampling with replacement, which is in accordance with the sampling procedure and reporting of moose observations.

Calculating rates of recruitment, harvest, and finite annual population growth from data on moose observations and harvest

The CIR method provides an estimate of adult population abundance prior to the hunting season. To estimate harvest rate (H), we divided the annual harvest of adult moose with the corresponding population abundance. Similarly, we estimated the annual recruitment rate (Rec) as the proportion of calves observed in the population during the hunting season. The latter is actually an estimate of recruitment rate in the total population, but assuming that calves and adults die with the same rates during the forthcoming year, Rec in year t-1 can be used as an estimate of the proportion of yearlings that are recruited into the adult population in year t. Accordingly, the population abundance is expected to neither increase nor decrease from year t-1 to year t when H_{t-1} equals Rec_{t-1}, assuming no natural mortality. When natural mortality (M_{nat}) from year t-1 to t is included, the total mortality rate (M_{tot}) can be calculated using the formula:

$$M_{tot} = 1-((1-H_{t-1}) * (1-M_{nat})) = M_{nat} + H_{t-1} - H_{t-1} * M_{nat} \quad (6),$$

assuming that natural mortality generally occurs outside

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the hunting season. Correspondingly, the population will be stable when:

$$Rec_{t-1} = M_{nat} + H_{t-1} - H_{t-1} * M_{nat} \quad (7),$$

or may grow with a finite annual rate, R, of:

$$R_t = Rec_{t-1} - (M_{nat} + H_{t-1} - H_{t-1} * M_{nat}) \quad (8).$$

Similarly, by rearranging the equation to solve for M_{nat}:

$$M_{nat} = (Rec_{t-1} - H_{t-1} - R_t) / (1 - H_{t-1}) \quad (9),$$

we can calculate the natural mortality rate, given that we have independent estimates on the annual finite population growth rate, $R_t = (N_t - N_{t-1}) / N_{t-1}$.

The different elements of Equation 9 are not estimated independently as both R_t and H_{t-1} are based on the estimated adult population abundance prior to the hunting season (the CIR estimate). If the basic variables are accurately estimated, we would expect M_{nat} to reflect rates observed in independent studies of natural mortality in Scandinavia. However, it should be noted that when several variable quantities (e.g. Rec_{t-1}, H_{t-1}, R_t) are combined in a mathematical formula, as is done here, the end result may indeed be very uncertain (Paulik & Robson 1969, Skalski & Millspaugh 2002), and the result should therefore be interpreted with caution.

Analyses and predictions

We tested the hypothesis that CIR methods can be used to provide accurate estimates of adult moose population abundance 1) by comparing the annual variation in population abundance with variation in three independent indices of moose density (precision), and 2) by comparing estimated natural mortality rates to similar rates estimated from independent studies (bias). The three indices of population density were: 1) the number of adult moose seen per hunter day across all observations within the study area (see Solberg & Sæther 1999, Ericsson & Wallin 1999), 2) the number of moose-car collisions and 3) the number of moose-train collisions in Norway. The number of moose-vehicle collisions has previously been found to provide a reasonable index of moose density (Solberg et al. 1997, Timmerman & Buss 1998), although this index may also vary with winter snow depth and temperature (Andersen et al. 1991, Gundersen & Andreassen 1998). Because fewer railroads than roads exist within moose habitats in Norway, we expected a closer annual covariation between moose population abundance and number of moose-car collisions.

We expected natural mortality rates as estimated by Equation 9 to be low and to have low variance because densities of large carnivores, such as wolves *Canis lupus* and bears *Ursus arctos*, are very low in Norway (approximate number of wolves: < 35, and bears: < 40 in 2002; Solberg et al. 2003), and accordingly, all Scandinavian studies outside carnivore core areas (e.g. wolf territories) report low natural mortality of adults, and slightly higher and more variable mortality rates of calves (Lorentsen et al. 1991, Sæther et al. 1996, Stubsjøen et al. 2000, Ericsson & Wallin 2001, Ericsson et al. 2001; Table 1). There is also a slight tendency for mortality of calves to be higher in the north than in the

Table 1. Reported natural mortality rates (NMR in %; unrelated to hunting) of radio-collared adult moose and their calves in different study populations in Scandinavia. N refers to the number of individual calves and the number of adult*years in the studies. Adult mortality rates from Stubsjøen et al. (2000) are annual averages across the study period, whereas mortality rates from Sweden are the pooled result of age-specific data reported in the two studies cited. Because abundances in our study are estimated just prior to the hunting season and therefore do not include calves that may have died during their first summer, reported calf mortality rates are for the winter season only.

Study site	Study period	Season	Age and sex group	N	NMR	References
N-Trøndelag	1987-1990	Nov-Apr	Calves	76	1	Lorentsen et al. 1991
C. Norway						
Troms,	1984-1990	Oct-May	Calves	68	3	Sæther et al. 1996
N. Norway						
Oppland,	1984-1987	Oct-May	Calves	15	6	Sæther et al. 1996
S. Norway						
Hedmark,	1985-1990	Oct-May	Calves	46	<1	Sæther et al. 1996
S. Norway						
Østfold	1985-1987	Oct-May	Calves	22	<1	Sæther et al. 1996
S. Norway						
Tromsø	1996-1999	Nov-May	Calves	100	3	Stubsjøen et al. 2000
N. Norway		Annually	Adult females	167	2	
Beiarn	1995-1999	Nov-May	Calves	65	17	Stubsjøen et al. 2000
N. Norway		Annually	Adult females	93	3	
Vega,	1992-1999	Nov-May	Calves	151	2	Stubsjøen et al. 2000
N. Norway		Annually	Adult females	127	5	
Robertsfors,	1991-1998	Jan-May	Calves	351	11	Ericsson et al. 2001
N. Sweden		Annually	Adult females	532	3	Ericsson & Wallin 2001
		Annually	Adult males	288	3	

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south (see Table 1), but as moose density is much higher in the south than in the north (e.g. Solberg et al. 1997), and as the majority of moose are adults (≥ 1 year old), we expected the average mortality from causes other than hunting to be < 5% for the entire Norwegian population.

Obviously a better test of the accuracy of abundance estimates would be to compare these with independent estimates of moose abundance or density, i.e. as provided by aerial surveys. Such surveys are conducted on an irregular basis in several moose areas in Norway, but given the scale of the study area (101,201 km^2) and large geographical variation in moose density (Solberg et al. 2003), independent abundance estimates for the complete study area would have to be estimated with very large confidence intervals. In addition, such estimates would probably be seriously overestimated as aerial surveys are mainly conducted in areas where moose aggregate during winter.

All analyses were run in SPSS (SPSS 2002), and all significance levels were two-tailed. The net population growth rate, $\lambda = n_t/n_{t-1}$, when averaged over years, was calculated as geometric mean and not arithmetic mean as population growth is inherently a geometric process (Case 2000).

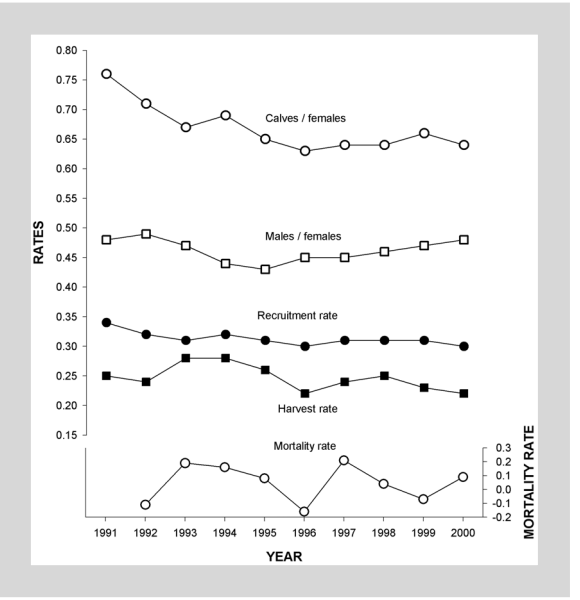


Figure 2. Annual variation in the observed number of calves per adult female, adult males per adult female (adult sex ratio), recruitment rate (based on observation data) and harvest rate (adult moose harvest/adult population abundance). The lower graph (right axis) indicates the natural mortality rate as estimated from the harvest rate, recruitment rate and finite annual population growth rate (see Methods for more details).

Results

Annual variation in sex-biased harvesting

During our study, there was significant variation in harvest sex ratio of both calves and adults and, accordingly, the observed adult sex ratio varied among years (Fig. 2). Most extreme was the population sex ratio in the mid-1990s when the observed proportion of adult males was as low as 30% (0.42 males per female; see Fig. 2). Since then there has been a gradual increase in adult male:female ratio following an increasing proportion of adult females in the harvest. As a consequence of biased harvesting, the sex ratio changed from one year to the next for all years. However, the Δp, or difference between p_1 and p_2 (Equation 1), never exceeded 0.08 (range: 0.05-0.08). This is considered low and may lead to large confidence intervals for CIR estimates if sample sizes are small (Paulik & Robson 1969). However, given the large sample size in our study (n_1: $\bar{x}$ = 192,606, range: 157,541-209,906 and n_2: $\bar{x}$ = 132,333, range: 104,319-144,585), the 95% confidence intervals were rather small ($\bar{x}$ = 7,428; Fig. 3).

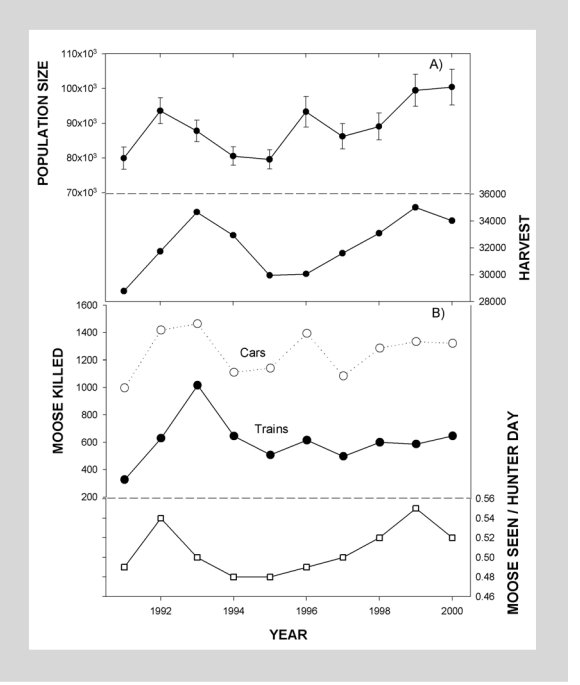


Figure 3. Annual variation in A): the estimated adult population size (95% CI) and annual harvest, and B): number of moose-vehicle collisions and the annual variation in the moose observed per hunter day (an index of density) based on moose observations from the entire study area.

Moose population abundance and correlation with other population indices

According to the CIR estimates, the population abun-

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dance of adult moose prior to the hunting season varied between 79,600 (1995) and 104,000 (2000) during our study. Similar figures for all of Norway would be about 89,500 (1995) and 117,000 (2000), given that the proportion of moose killed within the study area (89%) is representative for the distribution of moose in the country. Moreover, assuming that the observed recruitment rate is a precise average for Norway, the total population size during our study ranged between 129,710 (1995) and 167,000 (2000) moose immediately before the hunting season.

Population abundance peaked in 1992, 1996 and in 1999-2000 (see Fig. 3). Three other independent population density indices had a similar pattern (see Fig. 3), although moose-vehicle collisions peaked in 1993 rather than in 1992 (as the CIR estimate). Accordingly, the variation in adult population abundance correlated significantly both with the adult moose seen per hunter day ($r = 0.79$, $N = 10$, $P = 0.006$) and the number of moose killed in car-collisions ($r = 0.70$, $N = 10$, $P = 0.024$), but not with the number of moose killed in train-collisions ($r = 0.28$, $N = 10$, $P = 0.44$).

The estimated number of adult moose in the population constituted 60-72% of the number of adult moose observed and recorded by sex. Thus, each adult moose in the estimated population was on average seen 1.5 times during the hunting season.

Annual variation in recruitment rate, harvest rate and natural mortality rate

The annual population growth rate ($\lambda = n_t/n_{t-1}$) varied between 1.17 (1992, 1996) and 0.92 (1994, 1997), but was mostly positive (geometric mean $\lambda = 1.018$). Because the recruitment rate decreased during the study (see Fig. 2), a larger adult population was necessary to produce a given number of calves at the end than at the start of the study period. The decrease in recruitment rate was mainly due to a decreasing number of observed calves per female, and to a lesser extent an increasing number of adult males per female at the end of the study period (see Fig. 2).

On average, 31% of observed moose were calves, and presumably the adult population consisted of the same average proportion of yearlings (see Methods). Similarly, hunting removed on average 25% of the adult population each year (see Fig. 2), whereas the estimated natural mortality averaged 4.8% during the study period, as predicted. However, there was large annual variation in the natural mortality rate (see Fig. 2), particularly during 1992, 1996 and 1999 when the estimated natural mortality rate had to be negative to fit the variation in adult population abundance and recruitment rate. Similarly, in 1993, 1997 and 2000 mortality rates were unexpectedly high (see Fig. 2), indicating that some of the assumptions involved in estimating recruitment rate or population abundance were violated.

Discussion

Our results indicate that the change-in-ratio technique as employed here may provide reasonably precise estimates of moose population abundance. The population abundance was estimated with narrow confidence intervals, and the variation in abundance was closely correlated with two of three independent population indices. The weaker relationship was with the moose-train collisions, as predicted. Thus, variation in abundance provided by the CIR method appeared to be a sensitive index of moose density. Similarly, the estimated average natural mortality rate was low and in accordance with the mortality rate predicted by independent studies of mortality of moose in Scandinavia (see Table 1). This suggests that the estimates may also be unbiased with respect to the actual moose abundance. However, as indicated by the large annual variation in estimated natural mortality rate, it is likely that one or several assumptions involved in the estimating procedure have been violated.

One possible reason for the variable mortality rates may be the long period (one full year) between samples. A closed population is a critical assumption for estimating abundance (Krebs 1999), and unknown gains or losses between sampling periods potentially could lead to biased estimates (Paulik & Robson 1969, Krebs 1999). For instance, if large variation existed in natural mortality of calves, observed calves per female in the population in year t-1 would be a poor estimate of the proportion of yearlings in the adult population in year t (recruitment rate). Previous analyses indicated that the natural mortality rate of calves is slightly higher and more variable than the mortality rate of adults (Stubsjøen et al. 2000; see Table 1). If mortality rates covary over large areas, e.g. due to spatially correlated winter severity (e.g. Aanes et al. 2003), this could lead to varying calf mortality even at the large scale as in our study. Unfortunately, we do not have the necessary data to further investigate this hypothesis. However, if the average natural mortality of calves is higher than for adults, the recruitment rate may be slightly lower than indicated in Figure 2, and the estimated natural mortality rate will be smaller.

The population abundance estimate may also be vulnerable to gains or losses between sampling periods. If the population experiences an unknown natural mortality

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or net dispersal in or out of the population between the first sampling period and the period of removals (as in our study), the estimator N_1 in Equation 1 can not be used to estimate population abundance at the time of the first sampling period (Williams et al. 2002). N_1 may, however, still be used to estimate abundance just before the removals and after the period of natural mortality (as in this study) if the two groups experience the same mortality (or emigration) rates, but not if they differ (Williams et al. 2002). Although few data exist on natural mortality rates in male and female moose in Scandinavia, the available data indicate that they are small and rather similar (see Table 1; E.J. Solberg, unpubl. data) and therefore are unlikely to influence the CIR estimates to any great extent.

When applying CIR methods to the moose observation data, we believe the most likely major source of error is that moose are harvested during the sampling period. An important prerequisite for estimating population abundance based on CIR methods is that the second population survey is conducted after the removal of animals from the population. In our study, this was not the case as the observed sex ratio was a composite of all males and females observed during the hunting season. In a previous study, Solberg & Sæther (1999) found that an observed moose population more closely resembled the population near the end rather than at the start of the season, but not necessarily at the very end. This may have only minor effects on estimates as long as observational conditions and hunting performance are similar from year to year. However, if the proportion of observed moose harvested each day during the hunting season varies between years (Rolandsen et al. in print), the sex ratio estimate based on all observations may resemble more the sex ratio in the middle of the season in some years and at the end of the season in other years. This will, in turn, cause biased abundance estimates because sex-specific removal is based on all moose killed during the complete season. Hence, in years when the observed sex ratio (p_2 in Equation 1) reflects the population sex ratio in the middle of the hunting season (Δp becomes smaller than expected because p_2 is overestimated), the population abundance will be overestimated (Equation 1). In the subsequent year, however, abundance will be underestimated because p_2 in the estimate from year t becomes p_1 in the estimate for year t+1, e.g. the abundance estimates are serially dependent.

Such deviations in observed sex ratio probably also caused the high natural mortality rates estimated during our study. For instance, in 1992, 1996 and 1999, when the estimated natural mortality rates were negative, the estimated population growth rates were large (λ = 1.17, 1.17 and 1.12, respectively) for a harvested moose population of this size (e.g. Solberg et al. 1999), and probably an overestimate. Overestimated population growth rates (R, in Equation 9) will lead to underestimation of the natural mortality rates. Similarly, the large positive mortality rates estimated for 1993, 1997 and 2000 appeared immediately after years with overestimated population growth rates. This would be expected if population growth rate was overestimated because abundance in year t was overestimated (rather than underestimated in year t-1). Small deviations in the observed sex ratio may therefore generate alternating over- and underestimated abundance estimates (or vice verse), which may explain why the estimated average natural mortality rate was in accordance with expectations, whereas the annual rates were not. The data presented in Figure 3, however, indicate that the estimated variations in population abundance were not all due to over- and underestimation as similar fluctuations were also apparent in the population indices (e.g. the peaks in 1992, 1996 and 1999), although less extreme.

This shows how even small errors in the observed sex ratio may affect the population estimates. Unfortunately, the effects of such deviations increase as the magnitude of the change in sex ratio (Δp) becomes smaller (Paulik & Robson 1969). Accordingly, Paulik & Robson (1969) found that it is practically useless to try to determine the population abundance in situations in which $\Delta p < 0.05$. They also questioned the use of the method when $\Delta p < 0.10$, although Conner et al. (1986) seemed to obtain reasonable estimates of abundance for deer *Odocoileus* spp. with a Δp of 0.07. In our study, Δp varied between 0.05 and 0.08, which therefore may be marginal for obtaining reasonable estimates. The trend of harvesting fewer adult males during more recent years (see Fig. 2) may restrict the use of this method even further in many areas in the future.

In areas where biased harvesting does occur, however, CIR methods can supplement other population estimation methods. We suggest that the change in sex ratio then should be calculated within seasons to reduce the possible influence of external factors. This will reduce the length of time between sampling periods and so reduce the obscuring effect of sex-specific variation in natural mortality and dispersal, and will remove the necessity of estimating p_1 based on the sex ratio among both calves and adults. Short-term estimation of change in sex ratio will also alleviate the serial dependence of population estimates between years. To be able to do this, moose observations would have to be recorded for each date during the season, and not aggregated across seasons (Rolandsen et al. in print). By recording sex-

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specific numbers of daily observations in the start (e.g. first day, p_1) and end of the season (e.g. the last five days, p_2), the effect of hunting while observing will also have less influence on the estimates. Obtaining an appropriate sample size is a concern, but with the present high number of moose observations recorded, we believe an adequate sample exists which may provide quite accurate estimates, at least at a regional scale.

We conclude that CIR abundance estimates (see Fig. 3) based on moose observation provide another index to determine variation in moose density. Compared to moose seen per hunter day, which is regularly used as a population density index in moose management in Norway, CIR estimates may have several advantages. For instance, moose seen per hunter day can be sensitive to unequal conditions for observing moose between years (Solberg & Sæther 1999, Ericsson & Wallin 1999), and catch (observations) per effort indices do not necessarily scale linearly to density as they may be sensitive to variation in effort (e.g. Williams et al. 2002, Van Deelen & Etter 2003). Variation in sex ratio is less likely to be influenced by variation in observation conditions, and does not to the same extent depend on variation in hunting effort. Hence, CIR abundance may provide a valuable independent index, and possibly an even more precise index of density than the moose seen per hunter day.

Whether CIR estimates, as calculated here, can also be used as unbiased estimates of moose abundance is less certain as we have no independent estimates on moose abundance on this scale to compare with. Accordingly, we had to evaluate the accuracy of the estimates based on the relationship between CIR abundance, harvest and the observed recruitment rate (estimated natural mortality; Equation 9) in relation to independent estimates of natural mortality in moose (see Table 1). On average, the estimated mortality rate compared satisfactorily with the independent estimates, but given the acknowledged annual bias due to observing during the hunting season, and the fact that the different elements in Equation 9 were not estimated independently (see Methods), we call for cautious interpretation of the abundance estimates. Future studies should try to avoid these constraints by estimating moose abundance in smaller populations with independent estimates of population abundance, and based on changes in sex ratio within the same hunting season.

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References

Aanes, R., Sæther, B-E., Solberg, E.J., Aanes, S., Strand, O. & Øritsland, N.A. 2003: Synchrony in Svalbard reindeer population dynamics. - Canadian Journal of Zoology 81: 103-110.

Andersen, R., Wiseth, B., Pedersen, P.H. & Jaren, V. 1991: Moose-train collisions: Effects of environmental conditions. - Alces 27: 79-84

Anonymous 1998: STORTINGSMELDING NR 17. 1998. Verdiskaping og miljø - muligheter i skogsektoren (Skogmeldingen). - Landbruksdepartementet, Governmental white paper on forestry in Norway, available at: www.odin.no/lmd. (In Norwegian).

Case, T.J. 2000: An illustrated guide to theoretical ecology. - Oxford University Press, Oxford, 449 pp.

Conner, M.C., Lancia, R.A. & Pollock, K.H. 1986: Precision of the change-in-ratio technique for deer population management. - Journal of Wildlife Management 50: 125-129.

Ericsson, G. & Wallin, K. 1996: The impact of hunting on moose movements. - Alces 32: 31-40.

Ericsson, G. & Wallin, K. 1999: Hunter observations as an index of moose Alces alces population parameters. - Wildlife Biology 5: 177-185.

Ericsson, G. & Wallin, K. 2001: Age-specific moose (Alces alces) mortality in a predator-free environment: Evidence for senescence in females. - Ecoscience 8: 157-163.

Ericsson, G., Wallin, K., Ball, J.P. & Broberg, M. 2001: Age-related reproductive effort and senescence in free-ranging moose, Alces alces. - Ecology 82: 1613-1620.

Gundersen, H. & Andreassen, H.P. 1998: The risk of moose Alces alces collision: A predictive logistic model for moose-train accidents. - Wildlife Biology 4: 103-110.

Härkönen, S. & Heikkilä, R. 1999: Use of pellet group counts in determining density and habitat use of moose Alces alces in Finland. - Wildlife Biology 5: 233-239.

Hjeljord, O. & Histøl, T. 1999: Range-body mass interactions of a northern ungulate - a test of hypothesis. - Oecologia 119: 326-339.

Jaren, V. 1992: Monitoring Norwegian moose populations for management purposes. - Alces Supplement 1: 105-111.

Kelker, G.H. 1940: Estimating deer populations by a differential hunting loss in the sexes. - Utah Academy of Science and Art Letters 17: 6-69.

Krebs, C.J. 1999: Ecological methodology. - Benjamin/Cummings, Menlo Park, California, 620 pp.

Lorentsen, Ø., Wiseth, B., Einvik, K. & Pedersen, P.H. 1991: Elg i Nord Trøndelag, Resultater fra elgundersøkelsene 1987-1990 om vandringsmønster, brunst, kalvinger og døde-

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lighet. - Fylkesmannen i Nord Trøndelag, Miljøvernavdelingen rapport nr. 1, 208 pp. (In Norwegian).
Paulik, G.J. & Robson, D.S. 1969: Statistical calculations for change-in-ratio estimators of population parameters. - Journal of Wildlife Management 33: 1-27.
Rolandsen, C.R., Solberg, E.J., Tufto, J., Sæther, B-E. & Heim, M. in print: Factors affecting detectability of moose Alces alces during the hunting season in northern Norway. - Alces 39.
Sæther, B-E., Andersen, R., Hjeljord, O. & Heim, M. 1996: Ecological correlates of regional variation in life history of the moose Alces alces. - Ecology 77: 1493-1500.
Sæther, B-E. & Heim, M. 1993: Ecological correlates of individual variation in age at maturity in female moose (Alces alces): the effects of environmental variability. - Journal of Animal Ecology 62: 482-489.
Sæther, B-E. Solberg, E.J., Heim, M., Stacy, J., Jacobsen, K.S. & Olstad, R. 2004: Offspring sex ratio in moose Alces alces in relation to paternal age: an experiment. - Wildlife Biology 10: 51-57.
Skalski, J.R. & Millspaugh, J.J. 2002: Generic variance expression, precision, and sampling optimization for the sex-age-kill model of population reconstruction. - Journal of Wildlife Management 66: 1308-1316.
Solberg, E.J., Heim, M., Sæther, B-E. & Holmstrøm, F. 1997: Oppsummeringsrapport, Overvåkningsprogram for hjortevilt. - NINA Fagrapport, 30, 68 pp. (In Norwegian).
Solberg, E.J., Ringsby, T.H., Sæther, B-E. & Heim, M. 2002: Biased adult sex ratio can affect fecundity in primipareous moose. - Wildlife Biology 8: 109-120.
Solberg, E.J., Sand, H., Linnell, J.D.C., Brainerd, S., Andersen, R., Odden, J., Brøseth, H., Swenson, J., Strand, O. & Wabakken, P. 2003: Store rovdyrs innvirkning på hjorteviltet i Norge: Økologiske prosesser og konsekvenser for jaktuttak og jaktutøvelse. - NINA Fagrapport 63, 75 pp. (In Norwegian).
Solberg, E.J. & Sæther, B-E. 1994: Male traits as life history variables: annual variation in body mass and antler size in moose (Alces alces). - Journal of Mammalogy 75: 1069-1079.
Solberg, E.J. & Sæther, B-E. 1999: Hunter observations of moose Alces alces as a management tool. - Wildlife Biology 5: 43-53.
Solberg, E.J. Sæther, B-E., Strand, O. & Loison, A. 1999: Dynamics of a harvested moose population in a variable environment. - Journal of Animal Ecology 68: 186-204.
SPSS 2002: SPSS for Windows, release 11.5.1. - SPSS, Inc.
Stubsjøen, T., Sæther, B-E., Solberg, E.J., Heim, H. & Rolandsen, C. 2000: Moose (Alces alces) survival in three populations in northern Norway. - Canadian Journal of Zoology 78: 1822-1830.
Sylvén, S. 2000: Effect of scale on hunter moose (Alces alces) observation rate. - Wildlife Biology 6: 157-165.
Timmerman, H.R. & Buss, M.E. 1998: Population and harvest management. - In: Franzmann, A.W. & Schwartz, C.C. (Eds.); Ecology and Management of the North American Moose. Smithsonian Institutional Press, London, pp. 141-171.
Van Deelen, T.R. & Etter, D.R. 2003: Effort and the functional response of deer hunters. - Human Dimensions of Wildlife 8: 97-108.
Williams, B.K., Nichols, J.D. & Conroy, M.J. 2002: Analyses and management of animal populations, modelling, estimation and decision making. - Academic Press, London, 817 pp.

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