

Biased adult sex ratio can affect fecundity in primiparous moose *Alces alces*

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Recruitment rate has declined in many Norwegian moose *Alces alces* populations during the last two decades and at the same time the population size has increased and the proportion of males to females has decreased. Although density-dependent food limitation may explain part of the decrease in productivity, we evaluated to what extent the decline could also be a result of an insufficient number of males in the populations to fertilise all females. To test this hypothesis, we compared, based on ovary analyses, the age-specific variation in fecundity rates in eight Norwegian moose populations with annual variation in the adult sex ratio. Differences in female age and body mass explained a significant proportion of the variance in the probability of pregnancy. In addition, there was a significant relationship between the population sex ratio and the probability of pregnancy among 2-year-old females, but not the probability of pregnancy of older females. Because biased sex ratio only affects first-time breeders, the effect on the population recruitment rate may be limited. However, we also call attention to other possible effects of biased sex ratio, e.g. delayed parturition date, which in the long term may decrease population productivity through effects on survival and fecundity.

Key words: Alces alces, biased sex ratio, fecundity, fertilisation, male age, moose, recruitment rate

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Human harvesting may differ widely from natural mortality in shaping population structure and composition (e.g. Solberg, Sæther, Strand & Loison 1999, Solberg, Loison, Sæther & Strand 2000). In animals with large antler size and body mass, harvesting for meat or other products is often directed at larger individuals or at one or the other sex (e.g. Ginsberg & Milner-Gulland 1994, Fitzsimmon, Buskirk & Smith 1995, Solberg et al. 2000). Similarly, in populations managed to maximise the yield, exploitation may actively involve manipulation of the sex and age structure to increase the productivity of the populations (Caughley 1977). The knowledge about the effects that such selective harvesting has on the normal population processes is, however, often lacking. For instance, in polygynous species only a small number of males may be needed to fertilise a large number of females, suggesting that the productivity of the population may be improved by a reduction in the proportion of males (Caughley 1977). However, although this strategy should ideally rely on data on the number of females a male can fertilise under natural conditions, empirical studies on the capacity of males to fertilise several females are limited and difficult to accomplish (Ginsberg & Milner-Gulland 1994). Variation in fecundity can also result from other factors than a shortage of males. In several ungulates, age at maturity, and to some extent fecundity, are condition-dependent (Sæther 1997), and large variation in body condition can therefore swamp possible effects of a biased sex ratio. A few experimental studies dealing with these problems have been performed in highly polygynous species like elk *Cervus elaphus* (Noyes, Johnsen, Bryant, Findholt & Thomas 1996) and fallow deer *Dama dama* (Komers, Birgersson & Ekvall 1999). They showed that the age of males may be as important as their relative number for the reproductive performance of females. However, these results are difficult to extrapolate to species with different mating systems. Indeed, larger consequences of a bias in the sex ratio may be expected for less polygynous species (Ginsberg & Milner-Gulland 1994), like the moose *Alces alces* and roe deer *Capreolus capreolus*.

In Norway, the moose is among the most important wildlife resources (DN 1995). During the past 30 years it has been intensively managed to maintain a high productivity that allows high annual harvest rates (Østgård 1987, Sæther, Solbraa, Sødal & Hjeljord 1992, DN 1995). This management goal has been achieved by use of sex and age-specific harvest quotas, focusing mainly on calves and adult males to maintain a high proportion of adult reproductive females in the population (Østgård 1987, Haagenrud, Morow, Nygren & Stålfelt

1987). Following the change in harvest system, and despite relatively high harvest rates (e.g. Solberg et al. 1999), most populations have increased in density during the last 30 years (e.g. Østgård 1987, Haagenrud et al. 1987, Solberg, Heim, Sæther & Holmstrøm 1997, Solberg et al. 1999). At the same time, the proportion and mean age of adult males in many populations have become very low (Solberg et al. 1999; Fig. 1) following the tendency to issue more hunting permits for males than females and the hunters' preferences for

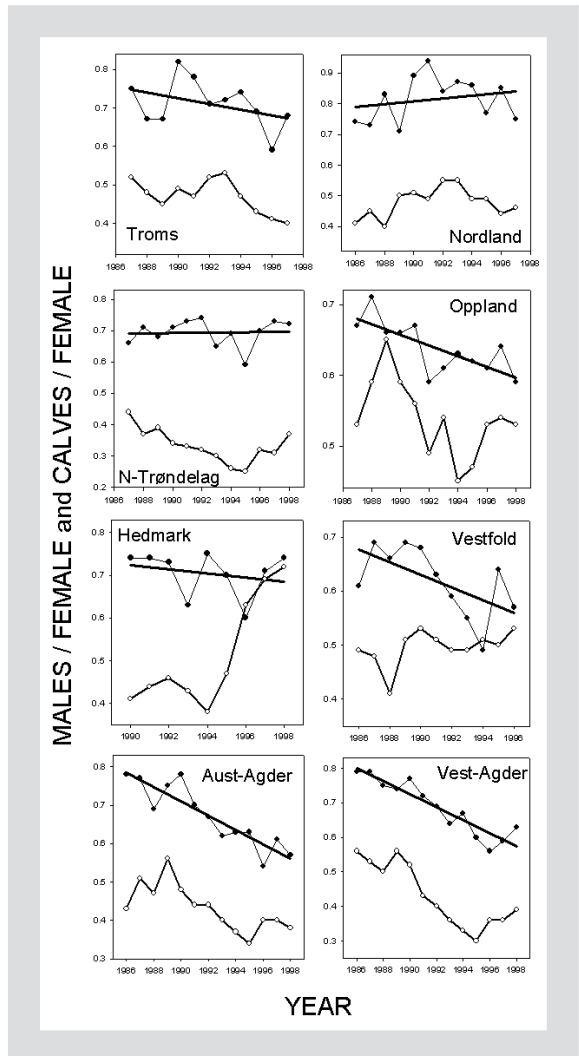


Figure 1. Recruitment rate expressed as calves per female (●) and sex ratio expressed as males per female (○) based on observations by hunters during the hunting season in the eight study populations during the periods for which observation data were available. Trend lines indicate least square regression. Troms: $r = -0.40$, $N = 11$, $P = 0.228$; Nordland: $r = 0.24$, $N = 12$, $P = 0.46$; Nord-Trøndelag: $r = 0.08$, $N = 12$, $P = 0.796$; Oppland: $r = -0.73$, $N = 12$, $P = 0.007$; Hedmark: $r = -0.23$, $N = 9$, $P = 0.548$; Vestfold: $r = -0.62$, $N = 11$, $P = 0.042$; Aust-Agder: $r = -0.91$, $N = 13$, $P < 0.001$; Vest-Agder: $r = 0.93$, $N = 13$, $P < 0.001$.

males (Solberg et al. 1997). As a decrease in recruitment rate (calves per female) has taken place in many Norwegian moose populations (Solberg et al. 1997, 1999; see Fig. 1) during the same period, many local moose managers have expressed concern about the potential association between the biased sex ratio and the productivity of their populations. The observed reduction in recruitment rates could, however, also be due to density-dependent food limitation (e.g. Sand 1996, Solberg et al. 1999), as fecundity in moose depends on body condition (Sæther & Haagenrud 1983, 1985, Sand 1996). Accordingly, the apparent high harvest rates may be maintained merely by decreasing the sex ratio (increasing the proportion of females) rather than by high recruitment rates. To determine the causes of the decrease in reproductive performance, it is therefore necessary to disentangle the respective roles of both density-dependence and other effects on body condition, and the role of varying adult sex ratios. In this paper, we explore how the age specific probabilities of pregnancy vary with varying adult male:female sex ratio in eight Norwegian moose population, while we simultaneously control for variation in several possibly confounding variables in the statistical models.

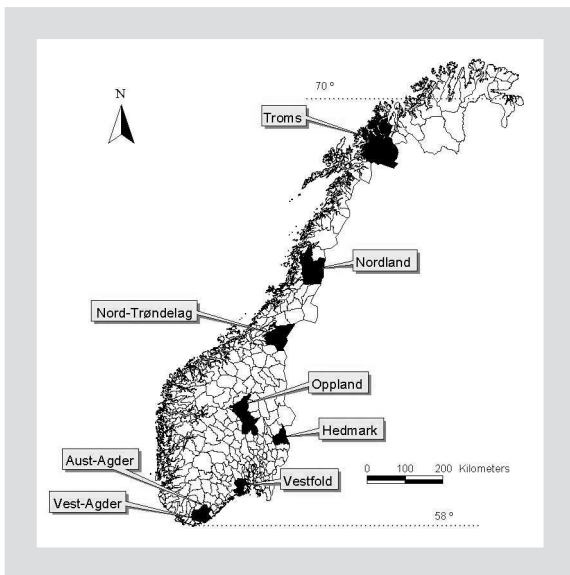


Figure 2. Location and names of the eight Norwegian study areas from which data are used in the analyses. Sampling in Aust-Agder (A-A) and Vest Agder (V-A) occurred in spatially connected populations, but was temporarily separated in time (1991-1995 and 1997-1998 in A-A and V-A, respectively). In the other areas, harvest data from 1991-1998 were used, except in Nordland and Troms for which data from 1991-1997 were used.

Material and methods

Study areas

The material was sampled in eight different populations along a north-south gradient (Fig. 2) covering the most important regions where moose are harvested in Norway. As part of the National Moose-Monitoring Program these moose populations have been monitored annually since 1991 (Solberg et al. 1997). All study areas are situated within the boreal vegetation zones, except for the two southernmost populations which also embrace part of the nemoral vegetation zones (Archibold 1995). The Nordland, Nord-Trøndelag and Hedmark study areas (see Fig. 2) are located in mainly coniferous forests of Scots pine *Pinus sylvestris* and Norway spruce *Picea abies*, whereas in Troms and Oppland, large part of the study areas are covered by birch *Betula pubescens* in addition to Scots pine. In the three southernmost study areas (Vestfold, Aust- and Vest-Agder) the forests consist mainly of Scots pine, Norway spruce and birch in the interior, and coniferous forests mixed with birch, oak *Quercus robur* and to some extent beech *Fagus sylvatica* along the coast (Solberg et al. 1997). The four northern areas (Troms, Nordland, Nord-Trøndelag and Oppland) are characterised by large valleys covered with forest to the timberline at approximately 500 (Troms) - 1,000 (Oppland) m a.s.l., whereas in the south, all areas are below the timberline and characterised by undulating hills (Hedmark) or a broken topography (Vestfold, Aust- and Vest-Agder). For further information on the study areas, see Sæther & Heim (1993), Solberg & Sæther (1994), Sæther, Andersen, Hjeljord & Heim (1996), Solberg et al. (1997) and Hjeljord & Histøl (1999).

Material

The data collected were carcass mass (approximately 55% of total live body mass; Markgren 1982), lower jaws and ovaries from moose harvested during the autumn hunting season (Solberg et al. 1997). Based on the jaws collected, the age of each individual was determined in the laboratory using tooth replacement patterns in calves and yearlings (Peterson 1955) and the number of layers in the secondary dentine of the incisors in adults (Haagenrud 1978).

The annual probability of pregnancy in the different regions and years was determined by the presence and appearance of luteal structures in ovaries of moose harvested in the study areas (see Simkin 1965, Sæther & Haagenrud 1985, Sand 1998 for use in moose, and Langvatn 1992, Langvatn, Bakke & Engen 1994 for use in red deer). The ovaries were removed from the uterus and stored in formalin, and subsequently cut in slices

for ocular examination of different luteal structures (Langvatn 1992). Only females from which both ovaries were collected were used in the analysis. Pregnancy was determined by the presence of *corpora rubra* (1-3 depending on the number of calves). *Corpora rubra* (new pigmented scar) develop in the ovaries shortly after parturition as a regressing stage of the *corpora lutea verum*, which originate from ovulated Graafian follicles after conception (Langvatn 1992, Langvatn et al. 1994). Accordingly, the presence of *corpora rubra* in the ovaries of females harvested in the autumn is related to pregnancy during the immediate preceding gestation (Langvatn 1992, Langvatn et al. 1994). The number of *corpora rubra* may also be used to estimate the number of calves produced (Sæther & Haagenrud 1985, Sand 1998), but for this study we only recorded the presence or absence of *corpora rubra* as our main interest concerned the probability of pregnancy and not the number of offspring.

Female body masses were aggregated to age-specific annual means. Because of the low number of older individuals harvested, data were only used up to the age of 10 and pooled for individuals 4-10 years of age. To reduce the variance due to low sample sizes, all means based on five individuals or less were excluded from the analyses. Moreover, because the probability of pregnancy is age dependent and increases up to about four years of age (Solberg et al. 1997), we split the material into three categories: 2-year-old (first-time breeders), 3-year-old and 4-10 year-old (prime-age) females, respectively. Older females were excluded from the analyses as the probability of pregnancy tends to decrease in old-aged females (Sæther & Haagenrud 1985, Ericsson 1999, Solberg et al. 2000) and because the sample size of females older than 10 years was small.

Adult (≥ 1 year old) male mean age in the population was indexed by the male mean age of the harvest age distribution. In addition, we calculated the proportion of inexperienced males (proportion of yearling and 2-year-old males in the male harvest sample), and the proportion of prime-aged males (proportion of ≥ 5 -year-old males in the male harvest sample). Even if yearling males are found to be able to fertilise females (Schwartz, Regelin & Franzmann 1982; B-E. Sæther, unpubl. data) they may be considered as socially immature because they are generally smaller (e.g. Solberg & Sæther 1994) and display a less developed rutting behaviour than older males (Miquelle 1990, Bubenik 1998). It should, however, be noted that both the mean age and the proportion of inexperienced and prime-aged males are only indexes of variation in male age structure as hunter preferences (e.g. for old and large males) may bias the sam-

ple in direction of older males (Solberg et al. 2000). Age-specific samples of males were available for the complete period in Nordland, Oppland and Hedmark, for two years in Troms, Nord-Trøndelag, Vestfold and Aust-Agder, and for one year in Vest-Agder.

The adult sex ratio and population density were estimated based on the number, sex and age of moose observed by moose hunters during the hunting season each year. In addition to the number of hunter days, this information is compulsory and must be reported by the leader of each hunting team after the hunting season each year (Solberg & Sæther 1999). Data on moose observations averaged 5,466 (range: 2,735-8,689) observations per year and region, distributed over, on average, 10,074 hunter days (range: 4,113-16,792).

Based on the observation data for the complete hunting period, we estimated the population sex ratio as the observed number of adult (≥ 1 -year old) males per adult female (see Fig. 1). Variation in population density was indexed by the number of moose seen per hunter day in year t-1. This index has been found to reflect the variation in population structure and density within populations (Solberg & Sæther 1999, Ericsson & Wallin 1999). For instance, Solberg & Sæther (1999) found that annual variation in the post-harvest population size in the Vefsn region over 25 years (as estimated by the use of cohort analysis) explained 62% of the variation in moose seen per hunter day. Almost similar results were found by Ericsson & Wallin (1999) who compared moose observation rates with results of aer-

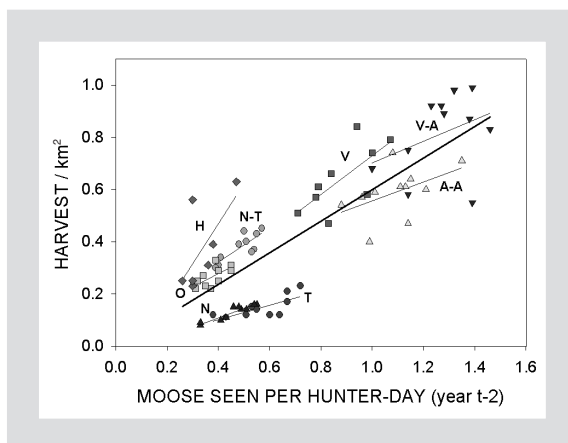


Figure 3. Relationship between the annual variation in harvest per km² and the annual variation in the number of moose seen per hunter day in year t-2 within the eight study areas (T = Troms (●), N = Nordland (▲), N-T = Nord-Trøndelag (○), O = Oppland (■), H = Hedmark (◆), V = Vestfold (■), A-A = Aust-Agder (△), V-A = Vest-Agder (▼)) expressed by the thin regression slopes, and for all data included in the analyses by the thick slope. The regression equation based on all data is: $y = 0.60x - 0.006$, $R^2 = 0.69$. Data are from all or part of the period 1987-1998.

ial winter counts of moose. In contrast, the number of moose seen per hunter day may only give a rough indication of the differences in densities among populations because observation conditions and hunting methods may differ from population to population (Ericsson & Wallin 1999). In the present material, however, the moose harvest per km² (another index of density) was quite closely correlated to the number of moose seen per hunter day in year t-2 (Fig. 3), suggesting that moose seen per hunter day may indeed be used as a rough index of density. As expected, the observation rate in year t-2 gave the closest relationship to the harvest per km², because harvesting tends to be delayed in relation to the fluctuations in population size (Solberg et al. 1999).

Can observed sex ratio be used as an index of population sex ratio?

To examine if the observed sex ratio could be used as an index of the variation in the population sex ratio, we reconstructed the number of adult males and females in the Vefsn moose population (the Nordland population in Figure 2) and compared the proportion of adult males with the similar proportion based on hunter observations for the same period and area (Solberg & Sæther 1999). The cohorts were reconstructed using cohort analysis (virtual population analysis) and catch-at-age data on 8,780 individuals (96% of all harvested moose in the area). Analysis of catch-at-age data using cohort analysis is one of the most important methods of assessing temperate fish stocks (Fry 1949, Hilborn & Walters 1992), and is also increasingly used in ungulate research (e.g. red deer: Lowe (1969); white tailed deer *Odocoileus virginianus*: McCullough (1979), Fryxell, Husel, Lambert & Smith (1991); moose: Fryxell, Mercer & Gellately (1988), Ferguson (1993), Ferguson & Messier (1996), Solberg et al. (1999, 2000); and caribou *Rangifer tarandus*: Eberhardt & Pitcher (1992)). Provided that data have been collected over a long enough time period to allow several of the cohorts to pass completely through the population, and that mortality due to other causes than hunting/harvesting is small, the minimum number of individuals alive in a specific year can be reconstructed (Fryxell et al. 1988). In the present case, completed cohorts (99%) existed until 1987 for females and until 1994 for males. For the remaining years, cohorts were estimated using age-specific hunting vulnerability from completed cohorts in combination with the age-specific number of moose already harvested from incomplete cohorts. To control for the individuals that died from natural causes or traffic accidents, we used (in the lack of appropriate data

from Norway) independent age-specific survival estimates from radio-collared moose in the Kenai Peninsula in Alaska (Bangs et al. 1989). Previously, the Vefsn moose population has been reconstructed a number of times using the same procedure (Solberg et al. 1999, 2000, Solberg & Sæther 1999), and was last reconstructed from 1967 to 1995 (Solberg et al. 2000). We added data from two more years and reconstructed the population until 1997.

We also compared the variation in the hunter observed sex ratio with the sex ratio of moose killed in train collisions in the Vefsn area during winter (provided by Martin Håker, Statskog-Nordland, Norway). The sex ratio of moose killed by train is not necessarily an unbiased estimate of the population sex ratio, but may be a useful corrective of the sex structure obtained from other sources. We used data on 194 adult moose killed by train and subsequently sex-determined in the Vefsn area during 1974-1997.

Statistical analyses

We modelled the combined effects of female age, cohort-specific mean female body mass and the population sex ratio on the probability of pregnancy by fitting generalised linear models to the data by maximum likelihood technique (SAS Institute inc. 1996). The probability of pregnancy was estimated as the number of pregnant females over the total number of females examined (events/trial model syntax, SAS Institute Inc. 1996). The explanatory variables included the categorical factor age and two covariates: the cohort-specific female body mass and population sex ratio, as well as the 2-way interactions between age and each of the two covariates. Because body mass and sex ratio were expected to affect the probability of pregnancy through the effect on the probability of ovulation and impregnation in the previous autumn, we used the cohort-specific mean body mass and sex ratio recorded in year t-1 as covariates to explain the probability of pregnancy.

Because male age may be important for the capacity to impregnate females, we also included the effect of the mean adult male age as reflected by the harvest age structure in the model. This was performed in a separate model because of the significantly lower sample available with male age compared to population sex ratio and cohort-specific female body mass.

To control for the potentially confounding effects of site-specific variation in climate, density and habitat quality on the effects of sex ratio, we added study area, the cohort-specific body mass and the interaction between study area and sex ratio in the age-specific models. In

this context, cohort-specific body mass was used as an index of the effect of climate and density. Previous studies, reviewed in Fowler (1987) and Sæther (1997), show that site-specific differences in habitat quality (both climate and density related) affect variation in probability of pregnancy mainly through the effect on body mass. Accordingly, as long as the effect of the cohort-specific body mass was controlled for in the models, we expected no additional effect of study area on the probability of pregnancy. Because of the many populations and few years available for analyses (in particular in Vest-Agder with only two years of data) we reduced the number of populations by pooling the data from Vest-Agder with the data from Aust-Agder. This can be justified as the samples from Aust-Agder and Vest-Agder were from spatially connected populations, but temporarily separated in time. Moreover, to reduce the complexity of many parameters in the models (e.g. age and the possible 2- and 3-way interaction terms), we performed this analysis as separate models on each age group.

We also analysed the effect of the cohort-specific body mass and adult sex ratio on the probability of pregnancy with density added as a categorical factor. The factor 'density' was included to examine the potential different effect of adult sex ratio at low compared to high population density. Because the average distance between males and females may be expected to be higher at low population density, we predicted a stronger effect of population sex ratio on the probability of pregnancy at low than at high density. Based on the number of moose seen per hunter day (see Fig. 3), we calculated a density factor with two values: < -0.5 standard deviations (low density), and > 0.5 standard deviations (high density) of the distribution, while the intermediate values ($-0.5 < SD = 0.5$) were excluded from the analyses. Although this reduced the sample size available for analysis, it was done to increase the probability that we tested the interaction based on a significant difference in density (due to the relatively rough estimation of the density variable based on moose seen per hunter day). As above, and for the same reasons, we performed these analyses as separate models on each age group.

The models were first run with all explanatory variables included. We then tested for the most parsimonious model by manually stepwise excluding and including the different independent variables. We considered the model with the lowest Akaike information criterion (AIC) score to be most parsimonious (Sakamoto, Ishiguro & Kitagawa 1986). We used the AIC for model selection because this criterion is well adapted for analysis of data from observational studies, and because AIC as a model selection criteria, contrary to vari-

ous hypothesis testing approaches, is based on a well-developed theoretical foundation (Burnham & Anderson 1998). Differences in AIC (absolute value) between models of one or less ($\Delta AIC \leq 1$) were considered insignificant (for a general discussion of AIC see Sakamoto et al. 1986, Lebreton, Burnham, Clobert & Andersen 1992, Burnham & Andersson 1998). Since the response variable followed a binomial distribution we applied generalised linear models with logit link function (PROC GENMOD; SAS Institute Inc. 1996) to the data. All other statistics were performed using SPSS (Spss 1999). All tests were two-tailed.

Results

Observed sex ratio as an index of population sex ratio

There was a positive and significant correlation between the proportion of adult males in the reconstructed

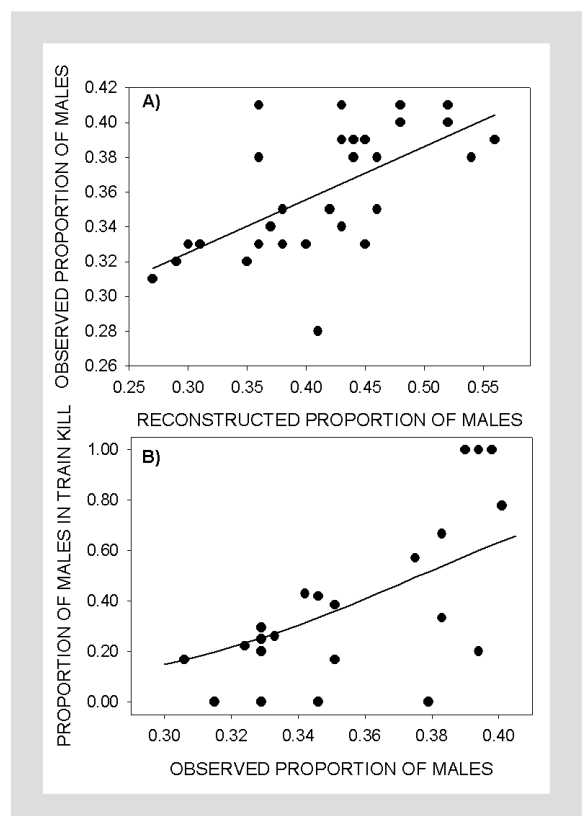


Figure 4. Proportion of adult males observed during the hunting season in Nordland in relation to the proportion of adult males in the reconstructed population after the hunting season during 1968-1997 (A), and the proportion of males in train kills ($N = 194$) during 1974-1998 in relation to the hunter observed proportion of adult males during the preceding hunting season (B). Slopes are estimated by least square (A) or logistic regression (B).

Vefsn population and the proportion of males observed during 1968-1997 (Fig. 4A). The variation in the observed proportion of males correlated slightly better with the post-harvest (Spearman rank correlation: $r_{sp} = 0.69$, $N = 30$ $P < 0.001$) than with the pre-harvest proportion of males in the population ($r_{sp} = 0.68$, $N = 30$ $P < 0.001$). Also the proportion of males in train kills was positively related to the variation in the observed proportion of males (logistic regression: $y = e^{(-8.59 + 22.84x)} / (1 + e^{(-8.59 + 22.84x)})$; see Fig. 4B). For the period with comparable time series (1974-1997), the average proportion of males observed (mean = 0.35, SE = 0.01) was similar to the proportion of males in train kills (mean = 0.35, SE = 0.03), but on average lower than the pre-harvest (mean = 0.48, SE = 0.01) and post-harvest proportion of males (mean = 0.40, SE = 0.01). The smaller difference between the post-harvest sex ratio and the observed sex ratio probably arose because the observed indices are influenced by variation in harvesting (Solberg & Sæther 1999), whereas the general higher sex ratio in the reconstructed population may be due to higher rates of female than male natural mortality (see Discussion). All in all however, we conclude that the annual variation in the observed sex ratio gives a fair reflection of the population sex ratio.

Variation in sex ratio and male age

According to the hunter observations, the observed sex ratio varied between 0.25 and 0.69 adult males per female among regions and years during the study period (see Fig. 1), with an average of 0.46 males per female. For the years with available pregnancy data, the highest proportion of males was found in Hedmark in 1997 (0.69 males per female) and the lowest in Nord-Trøndelag in 1995 (0.25 males per female). Similarly, the mean male age varied among regions and years, ranging from 1.63 in Hedmark in 1991 to 2.54 in Oppland in 1991. The observed sex ratio increased with the mean age of adult males in the populations ($r_{sp} = 0.24$, $N = 32$, $P = 0.181$), but not significantly. In fact, the relationship was closer between the sex ratio in year t-1 and the mean male

age ($r = 0.51$, $N = 32$, $P = 0.002$), possibly because the mean age is a product of the population age structure before harvesting, whereas the observed sex ratio more resembles the population sex ratio after hunting.

In general, the mean male age was very low in all populations (mean = 2.05, SD = 0.25) with the consequence that a high proportion of the male population consisted of inexperienced males (mean = 74.2%, SD = 7.6). Thus, considering the fact that male moose usually grow to the age of five or older before they reach maximum body size (e.g. Sæther & Haagenrud 1985, Solberg & Sæther 1994), only 6.1% (SD = 3.2) of the adult male population in the study sample belonged to this age class (≥ 5 years old).

Effects of population sex ratio, mean body mass and male and female age on the probability of pregnancy

The variation in the probability of pregnancy was best explained (i.e. lowest AIC value) by the full model including female age, population sex ratio in year t-1, cohort-specific female body mass in year t-1 and the 2-way interactions sex ratio*female age, and body mass*female age (Table 1A). The significant interaction effect of sex ratio*female age was caused by a positive effect of sex ratio on the probability of pregnancy among 2-year-old females, but not among older females ($P = 0.41$; Fig. 5). Similarly, the interaction between body mass and female age was caused by a stronger effect of body mass on the probability of pregnancy among 2-year-old than among older females (Fig. 6). There was no significant correlation between the variation in sex ratio and body mass of 2-year-old ($r = 0.15$, $N = 41$, $P = 0.334$) or older females (3-year olds: $r = 0.18$, $N = 36$, $P = 0.281$; 4-10 year olds: $r = -0.06$, $N = 50$, $P = 0.671$).

Testing separate models on different age classes indicated that the probability of pregnancy among 2-year-old females increased significantly with sex ratio ($df = 1$, 38, $\chi^2 = 7.65$, $P = 0.006$) and the cohort-specific body mass ($df = 1$, 38, $\chi^2 = 14.87$, $P < 0.001$), whereas only the cohort-specific body mass significantly af-

Table 1. Probability of pregnancy in relation to female age, cohort-specific female body mass, population sex ratio (males per female), and the interaction effects including female age. The Δ AIC shows the difference in AIC between the 'best' (A) and second 'best' (B) model.

Model	Dependent variable	Independent variables	df	χ^2	P	Δ AIC
A	Probability of pregnancy	Female age	2, 118	30.88	0.000	0
		Cohort-specific body mass in year t-1	1, 118	17.92	0.000	
		Population sex ratio in year t-1	1, 118	2.86	0.076	
		Cohort-specific body mass in year t-1*female age	2, 118	11.57	0.003	
		Sex ratio in year t-1*female age	2, 118	6.92	0.031	
B	Probability of pregnancy	Female age	2, 121	27.77	0.000	3.92
		Cohort-specific body mass in year t-1	1, 121	19.64	0.000	
		Cohort-specific. body mass in year t-1*female age	2, 121	13.35	0.001	

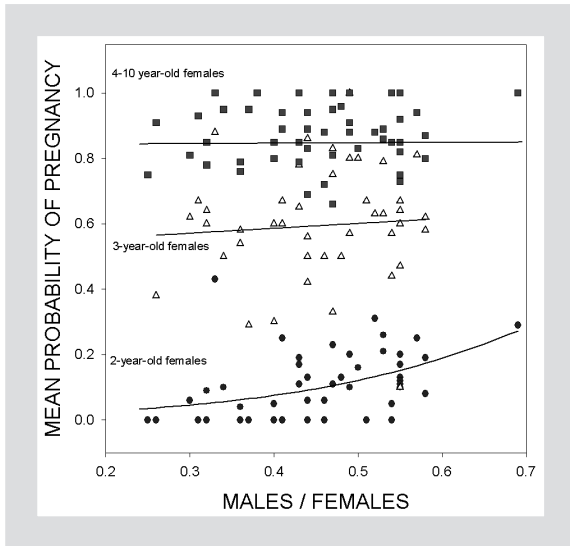


Figure 5. Mean probability of pregnancy for 2-, 3- and 4-10 year-old female moose within population and year in relation to observed population sex ratio (males per female) in year $t-1$. The curves were fitted to the logistic equation; $y = e^{(a+bx)} / (1 + e^{(a+bx)})$, where y is the individual probability of pregnancy (1 or 0), a and b are constants, and x is the independent variable.

affected the probability of pregnancy of 3-year-old females ($df = 1, 34, \chi^2 = 4.44, P = 0.035$). No significant effects of body mass or sex ratio were found on the probability of pregnancy among 4-10 year-old females ($P > 0.755$).

When analysing the above age-specific models on the

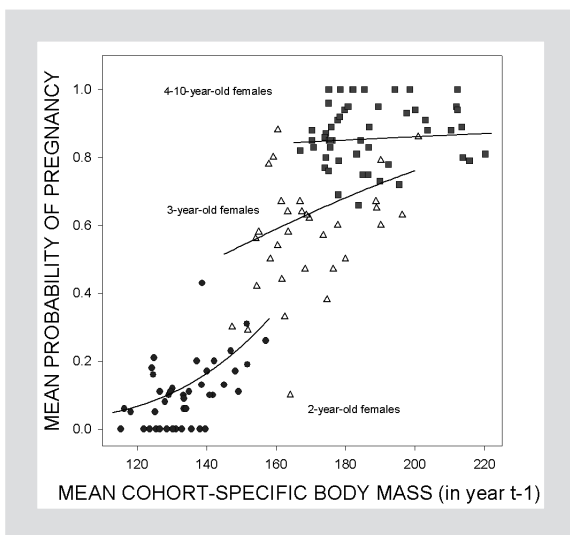


Figure 6. Mean probability of pregnancy for 2-, 3- and 4-10 year-old female moose within population and year in relation to mean cohort-specific female body mass in year $t-1$. The curves were fitted to the logistic equation; $y = e^{(a+bx)} / (1 + e^{(a+bx)})$, where y is the individual probability of pregnancy (1 or 0), a and b are constants, and x is the independent variable.

restricted sample with available data on mean male age, we found no significant contribution of mean male age to the probability of pregnancy when it was included alone in the models ($P > 0.463$) or in combination with sex ratio and/or the cohort-specific body mass ($P > 0.360$). However, neither did sex ratio explain a significant proportion of the probability of pregnancy in any age group ($P > 0.111$). Indeed, only the cohort-specific body mass in 2-year-old females explained a significant proportion of the probability of pregnancy in this restricted sample ($df = 1, 19, \chi^2 = 5.46, P = 0.019$).

Adding study area to the age-specific models, along with sex ratio and cohort-specific body mass, revealed no significant site-specific effect on the variation in probability of pregnancy in any age group ($P > 0.09$). When excluding the effect of the cohort-specific body mass, however, study area significantly explained part of the variation in the probability of pregnancy in both 2-year-old ($df = 6, 33, \chi^2 = 13.00, P = 0.043$) and 3-year-old females ($df = 6, 28, \chi^2 = 15.65, P = 0.016$), but not among 4-10 year-old females ($df = 6, 42, \chi^2 = 10.39, P = 0.109$). Accordingly, a large proportion of the variation in the annual mean body mass was due to variation among populations (Analysis of variance: 2-year olds: $R^2 = 0.78, N = 41, P < 0.001$; 3-year olds: $R^2 = 0.77, N = 36, P < 0.001$; 4-10 year olds: $R^2 = 0.83, N = 49, P < 0.001$) suggesting that population differences in habitat quality were translated into variation in fecundity through the effect on body mass. Moreover, sex ratio appeared to have the same effect on the probability of pregnancy of 2-year-old females in all study areas as there was no significant sex ratio*study area interaction ($df = 6, 26, \chi^2 = 6.80, P = 0.340$).

The interacting effect of population density

To examine the potential for differential effects of population sex ratio at high and low density, we successively included the factor 'density' (see Methods) as well as its interaction effect with population sex ratio into age-specific models with probability of pregnancy as dependent variable. No significant interaction existed between population sex ratio and density ($P > 0.240$) in any age group, and models including the interaction effect were less parsimonious than more simple nested models ($\Delta AIC > 2.04$) in all age groups. The best nested models included a positive effect of population sex ratio in 2-year-old females ($df = 1, 21, \chi^2 = 7.79, P = 0.005$), and density in 3-year-old ($df = 1, 18, \chi^2 = 8.59, P = 0.003$) and 4-10 year-old females ($df = 1, 30, \chi^2 = 3.13, P = 0.077$), respectively. In general, the probability of pregnancy was higher in low than in high-density populations.

Discussion

Our results suggest that the low proportion of males found in some populations and years significantly affected the conception rate in young primiparous females, whereas the reproductive performance of older females was unaffected by variation in adult sex ratio (see Fig. 5). The effect on pregnancy rate became apparent even at a relatively moderately biased sex ratio, which supports previous studies suggesting that the mean fertilisation capacity in male moose may be relatively low (Bubenik 1987, Aitken & Child 1993). Compared to species such as red deer, reindeer and fallow deer, male moose have small testicles relative to their size (Clutton-Brock, Guinness & Albon 1982). They may therefore have small semen reserves and consequently cannot breed successfully with a large number of receptive females within a short time period (Møller 1988). Moreover, as testicle size in moose increases with age (Bubenik & Timmermann 1982), the decreasing pregnancy rate with increasing bias in sex ratio may also be associated with the low mean age in populations with low proportion of males (Bubenik 1998). Compared to non-hunted populations (e.g. Peterson 1977), the proportion of prime-aged individuals in Norwegian moose populations is in general very low (this study, Solberg et al. 1997). Thus, although we did not find a significant contribution of male age to the probability of pregnancy in the present study, the generally low male age in all populations and years may have facilitated a negative effect of biased sex ratio on the pregnancy rate.

Several factors may affect the minimum proportion of adult males necessary to avoid problems in the reproductive performance of moose. In North America, the tundra moose *Alces alces gigas*, which is typically a harem breeder (Bubenik 1987), may tolerate more biased sex ratios than the less polygamous taiga moose *Alces alces americana* and *Alces alces andersoni* (Bubenik 1987), without any apparent effects on reproduction (see Schwartz 1998). Working with tundra moose in Alaska, Schwartz, Hundertmark & Spraker (1992) did not detect any change in the number of calves per female or pregnancy rate *in utero* as the sex ratio increased from 0.16 to 0.29 males per female. In contrast, Aitken & Child (1993) found significant effects on both conception date and rate when the proportion of adult males of a taiga moose population in British Columbia increased. The latter study involved a range of sex ratios (0.38-0.66) within the range of sex ratios found in our study. In an extensive telemetry study of two populations of moose in Quebec, Canada, Laurian, Quillet, Courtois, Breton & St-Onge (2000) were able

to test several hypotheses concerning behavioural and demographic changes due to changing adult sex ratio, but did not detect any significant differences among populations regarding the reproductive outcome. Compared to our study, however, the range of sex ratios in Laurian et al.'s (2000) study populations was higher (0.38-0.93 males per female), possibly explaining the lack of significant effects. Indeed, as they did not include yearlings in their sex ratio estimates, and because the sex ratio in yearlings tend to be less biased than in older age groups, it is likely that the bias of sex ratios including yearlings would have been even smaller.

Despite the fact that the observed sex ratios appear to be a reasonably good index of variation in the population sex ratio (e.g. see Fig. 4), we have less knowledge about the ability of the observed sex ratio to reflect the right magnitude of the population sex ratio. Because males are usually found to be more active than females during autumn (e.g. Hauge & Keith 1981, Lorentsen, Wiseth, Einvik & Pedersen 1991, Cederlund & Sand 1994, Ericsson & Wallin 1996), and so possibly are more easily detectable than females, a common assumption has been that hunter observations overestimate the proportion of males. According to the reconstructed sex ratio (see Fig. 4), rather the opposite seems to be the case. However, this may as well be due to underestimation of the number of females in the reconstructed population, as the sex ratio calculated by the cohort analysis is sensitive to differences in survival rates between males and females. For instance, allowing slightly lower survival rates for females than for males (2%) in the cohort analysis leads to on average similar sex ratios between the observed and reconstructed population (E.J. Solberg, unpubl. data). Whether this is a real sex-specific difference in survival rates must await further independent investigations (preferably on radio-collared individuals). Given the similar sex ratio in both the observed population and the winter train kills, however, we assume that the magnitude of the observed sex ratio is a more likely reflection of the population sex ratio than the reconstructed values based on the cohort analysis.

The outcome of a given sex ratio on the fecundity may vary depending on population density and distribution, e.g. males may encounter, and fertilise, more females per time unit in high than in low density populations (Schwartz 1998). Therefore, we had expected a more severe effect of biased sex ratio in northern Norway, where, according to the harvest record, the population density was less than one fifth of the density in southern Norway (see Fig. 3). The lack of any significant effects of density, however, indicates that this effect is not

very strong. This could happen if moose, independent of population density, aggregate in certain areas during the rutting season to facilitate breeding, which is often observed for the North American tundra moose (Bubenik 1998) and in some areas with restricted hunting pressure in northern Norway (Andersen & Sæther 1996). However, based on radio tracking of moose in intensively hunted Norwegian moose populations, we have found no evidence of aggregations of moose during the rut that can support this assumption (B-E. Sæther, E.J. Solberg & M. Heim, unpubl. data). Alternatively, the overall density may be less important than male age. Although little is known about the breeding behaviour of moose in Scandinavia, large variation in breeding capacity with age may be expected in moose, as this species have highly age-structured populations with large age-specific variation in male size (Sæther & Haagenrud 1985, Solberg & Sæther 1994, Sand, Cederlund & Danell 1995), and potentially also in semen production and courtship behaviour (Bubenik 1998). According to Bubenik (1998), the courting behaviour of North American moose does not develop completely until they are at least three years old, which suggests that close to 75% of the adult males in our study populations displayed immature courtship behaviour. Indeed, this may even be an underestimate, as old-aged males may be overrepresented in the hunting material because of hunting selectivity (Solberg et al. 2000). Younger males are also found to be less active and use smaller home ranges during autumn than older males (Cederlund & Sand 1994), indicating that the probability of females to encounter males during the rut may decrease as the mean age of males decreases.

Some studies of ungulate species also suggest that females tend to avoid breeding with young males (Clutton-Brock, Price & MacColl 1992, Komers et al. 1999). As a consequence, females may delay oestrus or conception until preferred males are available. In a study of fallow deer Komers et al. (1999) showed that females exposed to young males tended to delay oestrus compared to females exposed to prime-aged males. Similarly, after experimentally manipulating the male age structure, Noyes et al. (1996) found significantly later conception dates in red deer populations containing yearling males than in populations containing prime-aged (5-year-old) males. If inexperienced females need stronger stimuli from males to accept mating, such a mechanism may explain why first-time breeders are more affected by biased sex ratios than more experienced females. Alternatively, if inexperienced females do not seek out males during the rut to the same extent as older females, the chances to get pregnant may be lower.

We conclude that the long-term biased harvesting of males may have some effects on the reproductive output in Norwegian moose populations. Because the effect was mainly working through reduced fecundity among first-time breeding females, the relative impact on the population recruitment rate may be low. Based on their presence in the harvest, the 2-year-old females constituted on average 19% (SD = 2) of the adult (≥ 1 year old) female population, and showed only a modest pregnancy rate (mean = 9%, SD = 4; see Fig. 6), and twinning rate (based on ovary analyses; mean = 15%, SD = 10). In comparison, ≥ 3 -year-old females constituted approximately half of the adult females in the harvest (mean = 45%, SD = 8) with both high pregnancy- (mean = 60%, SD = 9; see Fig. 6) and twinning rate (mean = 52%, SD = 10). It is therefore unlikely that the effect of biased sex ratio on the impregnation rate alone is responsible for the declining recruitment rate observed in Norwegian moose populations. Indeed, we believe that density-dependent food limitation following the large increase in moose density in Norway may account for most of the decline in recruitment rate (Solberg et al. 1997, 1999). Density-dependent food limitation was also suggested to affect fecundity in Swedish moose (Sand 1996) and was indicated by the negative effect of density on the probability of pregnancy found in this study, although the latter may also be due to other factors correlated to the variation in density (e.g. variation in food quality and climatic conditions; Sand et al. 1995, Solberg et al. 1997). However, the effect of biased sex ratio on fecundity of first-time breeders should not be ignored by wildlife managers, as the variation in population sex ratio may also affect recruitment rate through an effect on the date of parturition (e.g. Schwartz & Hundertmark 1993, Taquet, Ouellet, Courtois & Laurian 1999; B-E. Sæther, E.J. Solberg & M. Heim, unpubl. data). As pointed out above, increasing evidence indicates that female fallow deer and red deer may postpone oestrus and/or conception if exposed to young and inexperienced males. If similar mechanisms operate in moose populations with biased sex ratio, the result may be increasing variation in birth date, and subsequently autumn body condition (Schwartz, Hundertmark & Becker 1994, but see Laurian et al. 2000). In such a case the effect of biased sex ratio on the recruitment rate may be two-fold; direct by reduced probability of pregnancy, and indirect by reduced autumn body condition and possibly reduced over-winter survival of the calf (Schwartz et al. 1994). In addition, age at first reproduction may increase and fecundity decrease, following a poor start in life (Sæther & Haagenrud 1983, 1985).

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