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Source: Wildlife Biology, 6(1) : 41-52

Published By: Nordic Board for Wildlife Research

URL: <https://doi.org/10.2981/wlb.2000.036>

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Age-specific harvest mortality in a Norwegian moose *Alces alces* population

Erling Johan Solberg, Anne Loison, Bernt-Erik Sæther & Olav Strand

Solberg, E.J., Loison, A., Sæther, B-E. & Strand, O. 2000: Age-specific harvest mortality in a Norwegian moose *Alces alces* population. - Wildl. Biol. 6: 41-52.

The annual age- and sex-specific patterns of harvest mortality in a Norwegian moose *Alces alces* population during a period of 17 years for females and 24 years for males were estimated using cohort analysis. In males the harvest mortality increased with age, whereas in females the pattern was U-shaped with higher harvest mortality of less fecund young (1-3 year) and old (≥ 10 years) age classes, and lower harvest mortality of prime age (4-9 years old) females. In both sexes, the calf harvest mortality was low, although it increased with increasing calf quotas following a change from an indiscriminate to a sex- and age-specific hunting system during the study period. In adult males, the mortality pattern was opposite of what was expected based on the previously reported higher susceptibility to hunting of young than old males, indicating that hunter selectivity for large (old) males affected the pattern. Moreover, the selectivity of the hunters decreased as the hunting pressure increased, suggesting that the hunters became less selective when the mean time available per moose in the quota decreased. Among adult female age groups, the variation in harvest mortality increased with the proportion of calves per female in the population prior to hunting. This was mainly because of relatively higher mortality of post-prime females, supporting our expectation that hunters avoid shooting females with calves and thus increase the harvest of less fecund age groups during high recruitment years. The observed selectivity led to harvest mortality that differed significantly from patterns of natural mortality, even where the mortality is mainly due to wolves *Canis lupus* and bears *Ursus arctos*. This may have consequences for the life history evolution of both male and female moose. The potential ecological, evolutionary and management implications of the results are discussed.

Key words: *Alces alces*, cohort analysis, harvesting, Norway, moose, mortality

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Received 7 July 1999, accepted 22 February 2000

Associate Editor: Jean-Michel Gaillard

Many mammal populations exhibit large age-specific variation in mortality due to differential vulnerability to predation, accidents and diseases (Caughley 1966, 1976). Typically, young and very old individuals suffer higher mortality than prime age individuals (Caughley 1966, Linnell, Aanes & Andersen 1995, Gaillard, Festa-Bianchet & Yoccoz 1998, Loison, Festa-Bianchet, Gaillard, Jorgenson & Jullien 1999), as young and old individuals are more vulnerable to environmental stress, or more likely to be killed by predators (e.g. moose *Alces alces* predated by wolves *Canis lupus*; see Peterson 1977, Peterson, Woolington & Bailey 1984). In a large part of the world, however, large carnivores are either seriously reduced or have been exterminated, leaving human harvesting as the main source of mortality in ungulates. For instance, in Norway and large parts of Sweden where densities of large carnivores are low, human harvesting may be the cause of more than 85% of the mortality in moose populations (Sæther, Solbraa, Sødal & Hjeljord 1992, Ericsson 1999). In such populations, the age- and sex-specific mortality caused by human harvesting may be very different from the mortality pattern caused by carnivores (e.g. McCullough 1979, Crête, Taylor & Jordan 1981, Crête 1987), thereby imposing different selection pressure on current populations. Despite often being the most important cause of mortality, little empirical data exist on the magnitude and age-specific pattern of harvest mortality in ungulate species (but see Fryxell, Mercer & Gellately 1988, Boer 1988, Cederlund & Sand 1991, Langvatn & Loison 1999, Ericsson 1999). To understand the population dynamics of harvested ungulate populations, we need information on age- and sex-specific harvest mortality. We therefore examine the temporal variation in harvest mortality of different age and sex classes in a Norwegian moose population and try to disentangle the factors that may produce the observed pattern. More specifically, we would like to determine if hunter selectivity affects age-specific harvest mortality in moose.

Material and methods

Study area and material

To examine the pattern of harvest mortality, we used data from the moose population in the Vefsn valley, northern Norway (65°20' - 66°10'N latitude) during 1967-1997. The study area, which is dominated by the Vefsn valley with smaller valleys forking off (Fig. 1), is situated within the boreal vegetation zone; it is

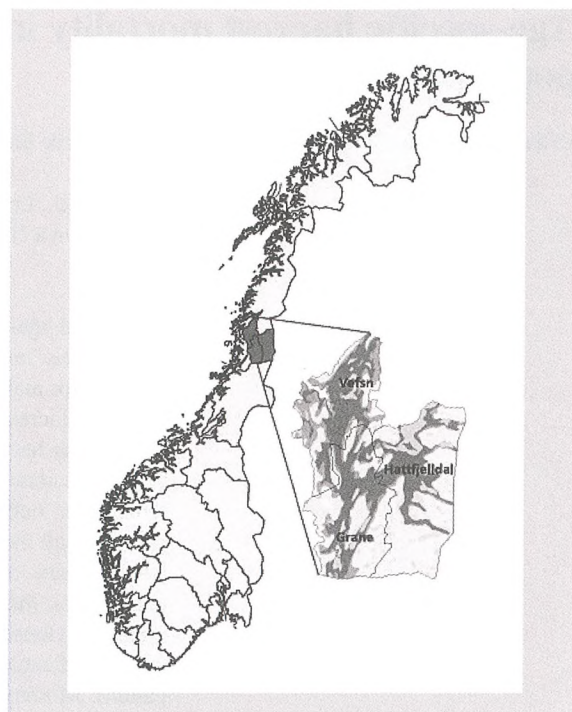


Figure 1. Location of the Vefsn study area in Norway. The dark-shaded areas in the enlarged map indicate forested areas.

mostly covered with spruce *Picea abies* and Scots pine *Pinus sylvestris* forests, with farmland along the valley floors. Birch *Betula pubescens* forests and alpine pastures dominate higher on the slopes. Forests (and bogs) constitute about 1,709 km² of the total area of 6,381 km² (including lakes), and are relatively evenly distributed over three municipalities. The total forested area is utilised for moose hunting (Hunting statistics, Statistics Norway). The moose population in the area is confined to the forested valleys and is partly isolated from other nearby populations. However, moose may disperse through forested mountain passes in the south and east as well as along the fjord in the west. During the study period, the population has mainly increased, from approximately 450 individuals in the early 1970s to 1,350 in the mid-1980s and early 1990s (0.07-0.21 moose/km²) with a distinctive decline in the early and late 1980s (Table 1; Solberg, Sæther, Strand & Loison 1999).

During the study period, 7,812 moose were harvested from the population; of these the ages of 7,615 (97%) individuals were determined either from ontogenetic development (calves and yearlings; Peterson 1955) or by counting the number of layers in the secondary dentine of the incisors (Haagenrud 1978). These techniques

Table 1. Population characteristics and hunting statistics in the Vefsn moose population during 1967-1990. Hunting pressure = quota size/population size.

Year	Population size	Hunting pressure	Proportion of quota attributed to calves	Calves per female (≥ 1 year old)	Calves per female in the harvest
1967	520	0.40	0.00	0.65	0.06
1968	497	0.36	0.00	0.76	0.11
1969	472	0.36	0.00	0.55	0.06
1970	445	0.39	0.00	0.64	0.17
1971	433	0.35	0.00	0.68	0.06
1972	458	0.28	0.00	0.80	0.14
1973	560	0.24	0.00	1.14	0.00
1974	702	0.22	0.00	1.10	0.05
1975	801	0.24	0.00	0.84	0.13
1976	861	0.27	0.00	0.71	0.10
1977	978	0.29	0.10	0.99	0.24
1978	990	0.30	0.19	0.67	0.16
1979	972	0.34	0.13	0.61	0.21
1980	1002	0.35	0.04	0.82	0.30
1981	1034	0.34	0.15	0.93	0.30
1982	1127	0.27	0.11	1.03	0.38
1983	1259	0.26	0.21	0.88	0.31
1984	1353	0.29	0.18		
1985	1318	0.45	0.29		
1986	1189	0.56	0.25		
1987	994	0.61	0.27		
1988	879	0.45	0.10		
1989	841	0.35	0.06		
1990	1039	0.32	0.06		

are widely used to age moose (e.g. Sæther & Haagenrud 1983, 1985, Fryxell et al. 1988, Sæther et al. 1992, Sand 1996, 1998, Ericsson 1999) and other cervids (e.g. Langvatn & Loison 1999), and the methods seem very precise when tested on moose of known age (e.g. moose radio-collared as calves or yearlings; B-E. Sæther, E.J. Solberg & M. Heim, unpubl. data). All over Norway, hunters are obliged to record the sex and age (calf, yearling, adult) of each moose killed; therefore it may be readily assumed that all legally harvested moose have been reported by hunters.

Estimating harvest mortality

Based on the catch-at-age, we reconstructed the annual age structure using cohort analysis (e.g. Fryxell et al. 1988, Fryxell, Hussel, Lambert & Smith 1991, Solberg et al. 1999). Female age groups were reconstructed for 1967-1983 and male age groups were reconstructed for 1967-1990 (Fig. 2). The longer time series of males than of females was because females generally live longer than males (see below) which makes it necessary to consider a longer time period before it is safe to assume that a whole female cohort has died. However, to restrict the number of years a cohort stays in the population (the oldest moose was 21 year old), we terminated the cohorts at the age at which an average of 99% of all individuals within a cohort had been harvested. This gave a terminal age of 14 years in fe-

males and seven years in males (Solberg et al. 1999). As we have no reasons to believe that hunters avoid old-age animals (Fryxell et al. 1988), this suggests that almost all individuals not succumbing to other causes of death than hunting were included in the sample.

A minimum number of moose alive at a given age and of a given sex and in a given year was obtained by simply adding the sex-specific number of moose harvested of each cohort in the current year and in the subsequent year up to the terminal age of the sex

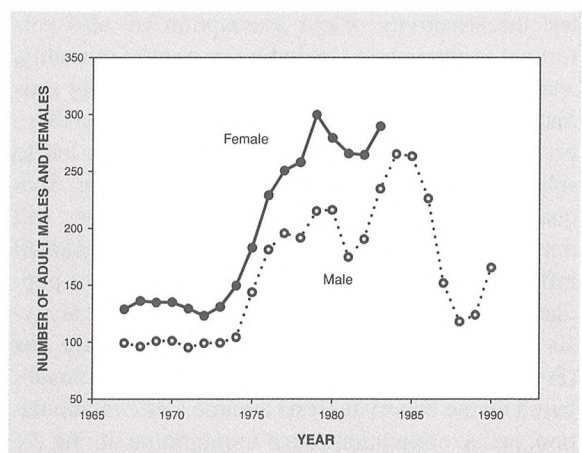


Figure 2. Annual number of adult (≥ 2 years old) female and male moose in the Vefsn valley during 1967-1983 for females and 1967-1990 for males according to the cohort analysis.

(Solberg et al. 1999). However, to make the age structure more realistic, we also controlled for individuals that died from natural causes, poaching and in traffic accidents. We used independent age-specific survival estimates from radio-collared moose in the Kenai Peninsula in Alaska (Bangs, Bailey & Portner 1989). In this particular population, predation by bears *Ursus arctos* and wolves was low, leading to high age-specific annual survival, although slightly decelerating with age (0.97, 0.91, and 0.90 in 1-5, 6-10 and 11-15 year old moose of both sexes; Bangs et al. 1989). Age-specific mortality data at such a detailed level are presently not available from Norway, although a recent study of radio-collared moose in a nearby population suggests that the annual survival of adult (>1 year old) females are within the range of mortality values used in our study (Stubsjøen 1999). In a study of the age-specific natural mortality of radio-collared male and female moose, Ericsson (1999) found similar results in northern Sweden. Thus, we believe that our mortality estimates fit to the Vefsn population reasonably well. The local management authorities considered poaching to be only a minor cause of mortality during the study period (<1% of the population annually; M. Håker, pers. comm.).

Calculation of age-structure by use of cohort analysis depends on two additional assumptions. First, the method assumes no annual variation in the cohort specific natural mortality, for instance due to fluctuations in weather and population density (Fryxell et al. 1988). This effect may be of minor importance in large mammals after their first year of life, because of their generally high and stable survival (Fowler 1987, Sæther 1997, Gaillard et al. 1998). However, to test the sensitivity of our assumption we also performed analyses by 1) including no natural mortality, and 2) using the inverse age-specific mortality estimates (i.e. lower prime age survival compared to post-prime survival). Neither of the changes led to substantially different harvest mortality (see Fig. 6) or qualitatively different results, and therefore they will not be presented. The test results suggest only a small influence of variation in natural mortality on the population size and structure estimated by cohort analysis as long as the values of natural mortality are low (Fryxell et al. 1988). Second, the abundance estimates based on the cohort analysis assume a closed population, i.e. no emigration or net immigration during the study period (Hilborn & Walters 1992). As we possess no quantitative data on dispersal in the Vefsn population, this assumption cannot be evaluated, but we

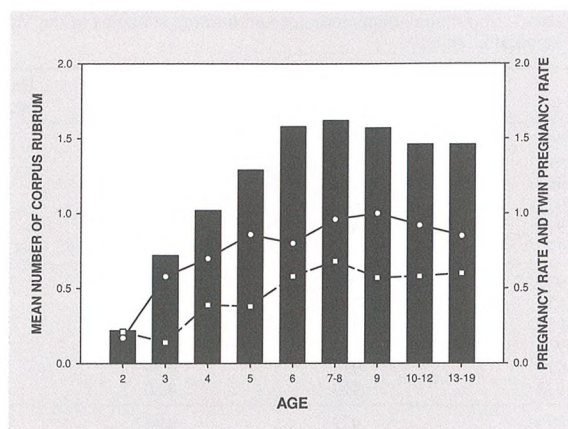


Figure 3. Mean number of *corpora rubra* in ovaries from female moose harvested in the Vefsn valley during 1967-1995 in relation to age. The pregnancy rate (upper curve, right axis) refers to the proportion of females that were pregnant the current year (presence of one or two *corpora rubra*), whereas the twin pregnancy rate (lower curve, right axis) refers to the proportion of pregnant females having two *corpora rubra*; N = 332.

have no reasons to believe that there have been large variations in the net dispersal during the study period.

The age-specific harvest mortality was calculated as the annual number of moose harvested divided by the annual number of moose present in the respective age groups. Because of the low annual number of old individuals harvested, and the associated large fluctuations in the age-specific harvest mortality, we averaged the harvest mortality for females 6-9 years old and for females 10-14 years old. The former age group corresponds to the most fecund age groups in the population (prime females) according to the number of new pigmented scars, *corpora rubra*, (Langvatn 1992, Langvatn, Bakke & Engen 1994, see also Sæther & Haagenrud 1985, Sand 1998) in ovaries from harvested females in the area (Fig. 3), whereas the latter age group corresponds to post-prime females showing reduced fecundity (see Fig. 3), probably due to senescence (Bell 1984). Among males we averaged the harvest mortality values for individuals 5-7 years old.

Based on the cohort analysis, we also estimated total population size (n_t) just prior to the hunting season and calves per adult female prior to the hunting season during the study period (see Table 1). We used the quota size (q_t) in relation to the pre-harvest population size, as an estimate of hunting pressure (q_t/n_t). Hence, during years with high hunting pressure, we expected a large proportion of the population to be harvested (see Table 1).

Cohort analysis has previously been used in sever-

al studies of ungulate population dynamics, e.g. red deer *Cervus elaphus* (Lowe 1969), white tailed deer *Odocoileus virginianus* (McCullough 1979, Fryxell et al. 1991) moose (Fryxell et al. 1988, Ferguson 1993, Ferguson & Messier 1996) and caribou *Rangifer tarandus* (Eberhardt & Pitcher 1992), and has been found adequate for determining age-specific differences in mortality in moose (Fryxell et al. 1988). We refer to Solberg & Sæther (1994, 1999) and Solberg et al. (1999) for a more complete description of the study area, the data, and the use of cohort analysis in reconstructing the Vefsn moose population.

Hunting regulations

After being introduced in 1971 (Østgård 1987), selective hunting of specific sex and age groups is now being utilised in all Norwegian moose populations (Østgård 1987, Haagenrud, Morow, Nygren & Stålfelt 1987, Cederlund & Markgren 1987) by assigning specific quotas for calves and adults (≥ 1 -year old) of both sexes. In general, more permits are given for adult males, and less for adult females (Østgård 1987). The selective-hunting system was introduced to increase the reproductive potential of the populations (Østgård 1987). Calves can be harvested on whatever type of permit. Because of reluctance among hunters to shoot calves, the proportion of the quota attributed to calves has been gradually increased in most areas. In the Vefsn valley, specific quotas on calves were only introduced in 1977 (see Table 1), because hunters' reluctance to shoot calves was particularly strong. Accordingly, the proportion of calves in the Vefsn valley harvest is still lower than the national average (18 vs 32% of the harvest in 1996). To compensate for the unwillingness to shoot calves, the hunters have been encouraged to utilise more of their adult quota to shoot yearlings of both sexes (M. Håker, pers. comm.). Usually it is possible to recognise yearlings by their smaller body size and antler size (males) and therefore it is possible to separate them from older individuals during the hunt. Thus, although not separated as a unique quota category, yearling hunting mortality may still vary depending on the recommendations of local wildlife managers. To avoid the possible influence of these recommendations (which we could not quantify) we analysed the harvest mortality at two levels: 1) the variation among calves, yearlings and adults (≥ 2 years old) of both sexes, and 2) the age-specific variation within adults (≥ 2 years old) of both sexes. In the first analysis, both quota allocation and recommendations may affect the mortality pattern, whereas

the age-specific differences in harvest mortality within adults should be unrelated to permit allocation.

Hunting selectivity

We were particularly interested in examining the potential influence of hunter selectivity on the age-specific differences in mortality. In Norway, most hunting areas are easily accessible, which, combined with hunters hunting in teams and extensive use of radios and elkhounds, may provide many shooting opportunities and lead to a generally high hunting success (on average 73% in Vefsn during the study period; Solberg & Sæther 1999). The popular belief is that hunters prefer to shoot large males for the meat and trophy and adult females unaccompanied by calves for the mass of meat compared to that of younger animals and due to the hunters' emotional reservations against shooting calf-rearing females. The fact that both male body mass and antler size increase with age (Solberg & Sæther 1993, 1994) implies that hunters will prefer shooting the oldest age classes in males, whereas in females the mortality may be biased towards young less productive or potentially older post-reproductive females (e.g. Wallin 1992). However, if hunting selectivity was important, we would expect the mortality pattern to vary with selection criteria. Accordingly, we would expect the selectivity to decrease with: 1) increasing use of quotas attributed to calves as this seriously would restrict the hunters from shooting their preferred animals, 2) increasing hunting pressure or decreasing population size as this would reduce the proportion and absolute number of preferred moose available within a short hunting season (2–4 weeks; Solberg & Sæther 1999), and 3) the number of calves per female in the population, either because of a high off-take of calves during the hunt or because of a low recruitment rate. This would affect the possibility of discriminating between reproducing and non-reproducing females.

Analyses

Harvest mortality of calves, yearlings and adult males and females related to hunting pressure and hunting policy

We first investigated how harvest mortality in the different age classes (calves, yearlings, adults) responded to variation in hunting pressure and the proportion of quota attributed to calves. Population size was not included in this model as this variable was highly correlated with the proportion of the quota attributed

to calves ($r = 0.82$, $P < 0.001$) and therefore may be considered represented by this variable (see Discussion). Because of the different lengths of the time series for males and females, we analysed each sex separately. We used ANCOVA to analyse the harvest mortality according to one category variable (age class) and the two covariates: hunting pressure and proportion of the quotas attributed to calves (which we used as an index of the change in hunting policy). Because harvest mortality is a proportion estimated with varying precision from year to year, we used generalised linear models (logistic regression with binomial error models; Crawley 1993). From a global model including age class, hunting pressure, the percentage of the quotas attributed to calves, population size, and the two-way interactions involving age class, we tested whether the interaction between age class and hunting pressure or the proportion of the quotas attributed to calves were significant. Based on the hypothesis that hunters are given less chances to be selective (e.g. shoot only adults) when the hunting pressure is high and a large part of the quota is attributed to calves only, we predicted that the difference in harvest mortality between adults and calves and yearlings would decrease when 1) the hunting pressure increased, and 2) the proportion of the quotas attributed to calves increased.

Patterns of harvest mortality in relation to age in adults

We investigated patterns of harvest mortality of different age groups among adults in relation to population demography. For males, we performed an ANCOVA of the harvest mortality according to age class (2, 3, 4, 5-7), hunting pressure and population size, whereas for females we used age class (2, 3, 4, 5, 6-9, 10-14), hunting pressure, population size, calves per female in the population (derived from the cohort analysis) and calf harvest (calves per female in the harvest). We then tested for a general effect of age (see hypotheses above) and for a significant interacting effect of age class and the covariates on harvest mortality. If present, this would indicate different age-specific mortality depending on hunting pressure, population size or in females only, calves per female and calf harvest. As previously, we used logistic regressions. All logistic ANCOVAs were performed using Proc Genmod in SAS (SAS Institute 1996). We used the Akaike Information Criterion (AIC) to select the 'best' model (Collet 1994). The model with the lowest AIC was considered to be the most appropriate. All other statistics were performed using SPSS (SPSS 1997).

Results

Harvest mortality of different age and sex classes in relation to hunting pressure and hunting policy

Over the years there were large differences in harvest mortality among male age classes (Fig. 4) with low calf mortality (mean = 0.07, SD = 0.07), intermediate mortality in yearlings (mean = 0.33, SD = 0.09) and high mortality in adults (mean = 0.43, SD = 0.04). The variation in mortality was explained by both the variations in age, hunting pressure, the proportion of the quotas attributed to calves and the interaction effects (Table 2). The harvest mortality of calves increased more with the relative calf quota (slope = 4.12, SE = 1.06) than the harvest mortality of yearlings and adults. Similarly, the harvest mortality of calves (slope = 2.45, SE = 0.87) and yearlings (slope = 1.76, SE = 0.69) increased more with hunting pressure, than the harvest mortality of adults (see Table 2, Fig. 5), indicating that hunters turned their attention towards calves and yearlings when the hunting pressure increased. The hunting pressure and the proportion of quota attributed to calves were only moderately correlated ($r = 0.52$, $N = 24$, $P = 0.009$).

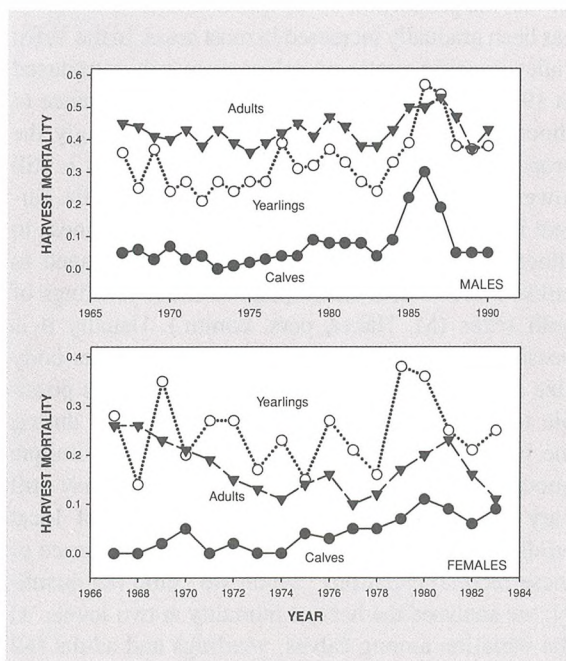


Figure 4. Annual variation in harvest mortality rate of calves, yearlings and adults (≥ 2 years old) of both sexes during the period 1967-1990 for males (upper figure) and 1967-1983 for females (lower figure). Note differences in axes.

Table 2. Combined effects on the sex-specific variation in harvest mortality of calves, yearlings, adults (≥ 2 -years old), and of adult age classes, only. Only the best models (according to the AIC) explaining the variation in each dependent variable are presented.

Dependent variable	Independent variables	χ^2	P-value
Male harvest mortality (calves, yearlings, adults)	Age	183.77	0.001
	Hunting pressure	66.36	0.001
	Proportion of quota attributed to calves	19.01	0.001
	Age * hunting pressure	10.85	0.004
	Age * quota attributed to calves	16.66	0.001
Female harvest mortality (calves, yearlings, adults)	Age	100.53	0.001
	Hunting pressure	22.64	0.001
	Proportion of quota attributed to calves	5.17	0.023
	Age * quota attributed to calves	12.79	0.002
Adult male harvest mortality	Age	19.79	0.001
	Hunting pressure	72.02	0.001
Adult female harvest mortality	Age	15.07	0.001
	Hunting pressure	11.24	0.010
	Age * hunting pressure	11.76	0.038

In females, yearlings and adults showed higher harvest mortality (yearling mean = 0.24, SD = 0.07, adult mean = 0.17, SD = 0.05) than calves (mean = 0.04, SD = 0.04) over the years. In females, yearling and adult harvest mortalities were lower than for similar age classes in males (see Fig. 4). The best model included age, hunting pressure and the proportion of the quotas attributed to calves, as well as the interac-

tion between female age and the proportion of the quotas attributed to calves (see Table 2). As with males, the harvest mortality of calves increased with the proportion of the quota attributed to calves (slope = 7.97, SE = 2.25), whereas no significant change occurred in yearlings and adults ($P > 0.10$). In contrast, there was no significant interaction between age and hunting pressure ($P > 0.10$, see Table 2), despite a slightly stronger increase in the mortality of adult females with hunting pressure (see Fig. 5). Accordingly, the change of quotas to include an increasingly larger proportion of calves could to some extent explain the change in harvest mortality among females of different age categories, whereas the variation in hunting pressure had no similar strong effect. The latter could possibly be ascribed to the smaller variation in hunting pressure found during the time span with hunting mortality data of females (see Fig. 5 and Table 1).

Patterns of harvest mortality in relation to age in adults

The harvest mortality of adult males differed significantly among age classes and increased with hunting pressure (see Table 2), whereas no significant effect of population size or interaction between age class and hunting pressure was detected ($P > 0.10$). The highest harvest mortality was found among the older age groups and the lowest among two-year-old males (Fig. 6).

Among adult females, pre- and post-prime females showed higher harvest mortality over the years than prime age females (see Fig. 6). The best model included age, hunting pressure and the interaction term (see Table 2). The significant interaction was caused by

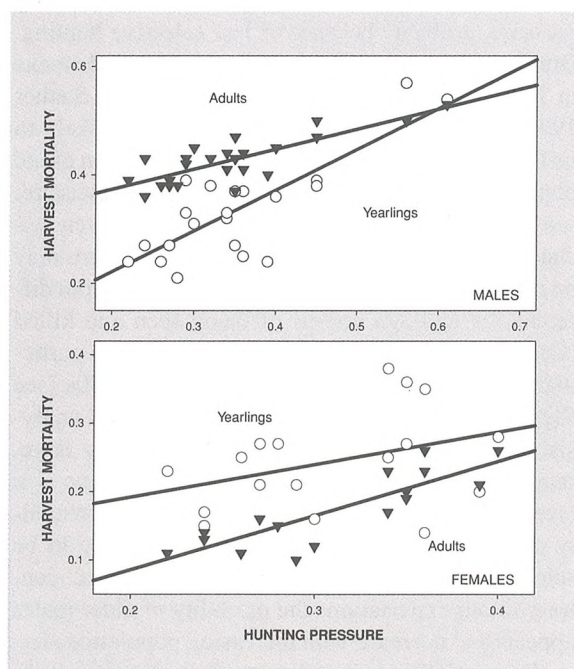


Figure 5. Harvest mortality rate of yearlings and adults (≥ 2 years old) of both sexes in relation to hunting pressure (the proportion of the population size given as hunting permits) during the period 1967-1990 for males (upper figure) and 1967-1983 for females (lower figure). Note differences in axes.

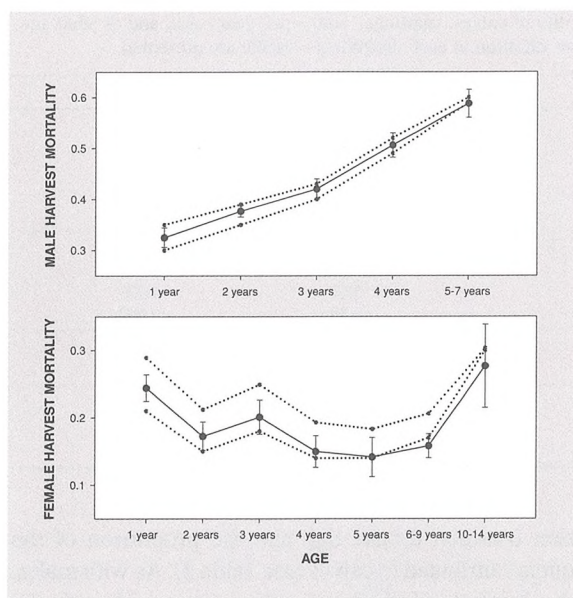


Figure 6. Annual age-specific harvest mortality rate (\pm SE) of male and female moose in the Vefsn valley during 1967-1990 for males and 1967-1983 for females. The dotted curves represent the age-specific harvest mortality of males and females when reconstructing cohorts without natural mortality (upper curves) and with the inverse of the age-specific natural mortality estimates (bottom curves, see Material and methods).

the hunting mortality of post-prime females increasing with a lower rate than that of the younger females ($P < 0.05$) with increasing hunting pressure. Contrary to our expectations, this suggests that the age-specific harvest mortality becomes less similar with increasing hunting pressure. However, there was also a significant interaction between age class and the frequency of calves in the population ($\chi^2 = 11.66$, $df = 5$, $P = 0.039$) if hunting pressure was removed from the model. This was mainly due to increasing differences in hunting mortality between post-prime and younger female age classes with increasing number of calves per female in the population ($P < 0.05$), possibly because less prime females were available for selective hunters in years with high recruitment rates. Because hunting pressure and calves per female were highly correlated ($r = -0.75$, $N = 17$, $P = 0.001$), this model could be considered an alternative explanation, despite the fact that it was found less important based on the AIC. No interaction existed between age class and the proportion of calves in the harvest ($P > 0.10$), suggesting that the harvest mortality of prime aged females compared with pre-prime females was unaffected by the frequency of females losing their calf during the hunting season. Similarly, there was no significant effect

of population size or the interaction effect including age, which coincides with the fact that population size was highly correlated with the proportion of calves in the harvest ($r = 0.80$, $N = 17$, $P < 0.001$).

Discussion

Our results revealed large variation in the age-specific harvest mortality of both sexes over the study period, including a generally high mortality of adults. Particularly at the start of the study period, before specific quotas attributed to calves were implemented in the area, the preference for old-age individuals was pronounced (see Fig. 4). This was more apparent in males than in females, and may be explained by the large age-specific growth in males (Solberg & Sæther 1994), giving the hunters a wide range of body sizes to select from. During the whole period, calves were selected against, despite the fact that calves could be harvested on all sex and age permits. However, as an increasing proportion of the hunting quota was given as calves only, hunters were forced to shoot more calves and the harvest mortality of calves relative to older age classes increased. This effect was further intensified during years of high hunting pressure, probably because of less selective hunting. During the short moose season in Norway (2-4 weeks in late September and October; Solberg & Sæther 1999), searching time (and hunting area) is likely to be limited, particularly when a large proportion of the population is to be harvested (high hunting pressure; see Fig. 5). During such years, hunters are given less chance to be selective and the mortality pattern may be more a question of the risk of individuals from different sex and age groups of being seen and killed (Caughley 1966, Crête et al. 1981). This was particularly apparent among males in the mid-1980s (see Figs. 4 and 5), when, according to the cohort analysis, the relative number of permits was very large, ranging between 45 and 61% of the population size (see Table 1). A large population size could potentially also increase the opportunities for hunters to be selective, but we found no such effects. Indeed, contrary to our expectations the mortality of older males appeared to decrease with increasing population size, as the population size and proportion of quota attributed to calves were strongly positively related. Thus in the present case, we rather believe that the predicted effect of changing calf quota was the cause of the change in harvest mortality.

In adult males, the general increase in harvest mortality with age supported our prediction that body size and antler size are important criteria for the hunters' preferences. In the oldest age group, as many as 59% (on average) of the males were harvested each year, increasing to > 80% during some peak years. The high mortality of prime males, was opposite to what was expected based on previous studies showing that the hunting susceptibility of pre-prime individuals is higher than that of prime individuals within both sexes (e.g. Crête et al. 1981, Boer 1988, Fryxell et al. 1988, Cederlund & Sand 1991). In a study of harvest mortality in several moose populations with high hunting pressure (assumed to lead to no hunter selectivity), Crête et al. (1981) found that yearlings and 2-year-old moose of both sexes were more susceptible to hunting than older individuals. Similar results were found in other studies in North America (Fryxell et al. 1988, Boer 1988) and Sweden (Cederlund & Sand 1991, but see Ericsson 1999), possibly because young independent individuals have a tendency to move more and have larger home ranges (e.g. Fryxell et al. 1988).

Among adult females, less fecund age groups appeared more vulnerable to hunting than prime age females (see Fig. 6), suggesting that hunters prefer females without calves or that individuals from these age groups have a higher risk of being seen and shot. The mortality was particularly high among post-prime females, possibly a consequence of the combined effect of both hunter selectivity and the fact that these age groups are more prone to be seen because of senescence infirmities (e.g. reduced hearing and vision; Ericsson 1999). Significant effects of senescence, including reduced fecundity, has been found in ungulates (Gaillard, Allaine, Pontier, Yoccoz & Promislow 1994, Loison et al. 1999), and assuming that such effects also exist in moose, old females may more often be barren compared to prime females. In a recent study, Ericsson (1999) found that the calves of older females suffered higher summer mortality than the calves of younger females, indicating that older females may be followed by calves at the onset of the hunting season less frequently than predicted by their ovaries. Moreover, because old females may be larger than younger individuals (Solberg & Sæther 1994), the combination of large size and no accompanying calf may have made them particularly vulnerable to hunting. To some extent the mortality of post-prime females may also be an artefact produced by the cohort analysis as we, by truncating the age-distribution at age 14, ignored a small number of older moose, which if present,

would have inflated the number of older females in the population (Fryxell et al. 1988).

Another factor supporting the effect of hunter selectivity was the general decreasing difference in harvest mortality among adult female age groups with decreasing recruitment rates. An explanation of this could be that hunters become less selective when the number of females accompanied by calves decreases. Although a better model was found by including hunting pressure (based on AIC), the close correlation between hunting pressure and calves per female makes it almost impossible to separate these two models. Why only post-prime females suffered increased mortality during high hunting pressure or low recruitment years is difficult to determine. However, if these females were also plagued by other senescence related infirmities (e.g. Gaillard et al. 1994, Ericsson 1999), they may simply have been more susceptible to hunting than younger less fecund females. Thus to conclude, both the sex- and age-specific hunting system, as well as the combined effect of hunter selectivity and differential risk of being seen and shot may explain the mortality pattern observed among moose in our study population.

Differential harvest mortality of age and sex classes may have direct management implications as well as long-term evolutionary and ecological consequences (Stokes, McClade & Law 1993). Given the large impact of hunting on many moose populations, variation in the age-specific harvest mortality may affect our ability to predict the outcome and demographic consequences of harvesting. In large mammals, age- and size-structured fecundity is the rule (Caswell 1989) and moose is no exception (Sæther & Haagenrud 1983, Sand 1998, Solberg et al. 1999). By affecting the variation in the mortality rates of females, hunters may modify the mean fecundity of the population and in turn the population growth rate. Moreover, the impact of hunter selectivity may affect the use of harvest data in monitoring moose populations, if there is a predominance of less fecund females in the harvest. Age-specific fecundity rates based on ovary analyses will therefore be an underestimate of the fecundity rates in the population. Similarly, because of size-dependent fecundity in moose (Sæther & Haagenrud 1983, Sand 1996), body mass data from harvested females may underestimate the age-specific body mass in the population. However, as long as hunter selectivity is reasonably constant from year to year, both the age-specific fecundity and body mass may be valid indices of the annual variation in both characters (Hanks 1981).

The evolutionary consequences of hunter selectivity and age- and sex-specific hunting systems in ungulates have only been evaluated to a lesser extent (but see Ryman, Baccus, Reuterwall & Smith 1981, Hartl, Lang, Klein & Willing 1991, Ginsberg & Milner-Gulland 1994, Fitzsimmon, Buskirk & Smith 1995, Ericsson 1999). However, to the extent hunting inflicts a mortality pattern that differs substantially from natural mortality, and that the selected traits show heritable variation, we would expect an evolutionary response to hunter selection (Endler 1986, Williams 1992). Life history theory assumes a trade-off among life history characters as the amount of available resources an individual can allocate to different characters in most cases are fixed (Stearns 1992). Accordingly, the lower fecundity of young female moose can be explained as a trade off between current reproduction and future reproduction and survival to optimise life-time reproductive success (Sæther & Haagenrud 1983, 1985, Sand 1998). By increasing the mortality of pre-prime females (because they are not accompanied by calves) compared to prime age females, we may change the optimal strategy towards earlier reproduction, with possible increased natural mortality and reduced reproduction at older age as a consequence.

Among males, the large variation in mortality may result in evolutionary changes to the extent hunter selection on body size is the cause of the pattern. By regressing the mean age-specific carcass mass (assumed to be 55% of total mass; Markgren 1982) on the age-specific hunting vulnerability, this suggested that harvest mortality increased by 0.2% (SE = 0.04) for each kilogram increase in carcass mass. Thus, considering the often large within age class variation in body mass found in male moose (e.g. 5-year olds; mean = 264 kg, SD = 33, which may already be a truncated sample; Solberg & Sæther 1994), a certain potential for selection also exist within age group. In turn this may increase the relative genetic contribution of small-sized individuals, which may affect male size over time. Selective hunting of males with large horns and antlers are suggested to account for reduced genetic variability in populations of red deer (Hartl et al. 1991) and bighorn sheep *Ovis canadensis* (Fitzsimmon et al. 1995), suggesting that the potential evolutionary consequences of selective harvesting may be present even within a short time span. To what extent selective harvesting of moose will also affect the future yield of meat or trophies will depend on forthcoming regulations controlling the hunt. During the last two decades fishery ecologists have re-

vealed evolutionary changes in life history traits of commercial fish stocks caused by selective fishing, and despite the fact that selective fishing was used as part of a strategy intended to increase the yield, the long-term effect may be quite the opposite (Sutherland 1990). Although no such scenario is suggested here, we advocate more modelling and experimentation to examine the long-term evolutionary effects of selective harvesting of large game species.

Acknowledgements - we wish to thank all the hunters in the Vefsn valley who made this study possible through their sampling of data from the moose harvested, H. Haagenrud who initiated the study and M. Håker who organised the collection of data. We are also grateful to K. Jerstad and J.E. Skåtan for valuable discussions about hunter selectivity, and to J. Linnell and two anonymous referees who provided constructive comments on an earlier draft. The study was funded by the Norwegian Research Council (Use and management of outlying fields), the Directorate for Nature Management (DN) and the Norwegian Institute for Nature Research (NINA).

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