Erlend B. Nilsen · Erling J Solberg

Patterns of hunting mortality in Norwegian moose (*Alces alces*) populations

Abstract We used a simple life table approach to examine the age-specific patterns of harvest mortality in eight Norwegian moose populations during the last 15 years and tried to determine if the observed patterns were caused by hunter selectivity. The general opinion among local managers is that hunters prefer to shoot female moose not in company with calves to keep a high number of reproductive females in the population (and because of the emotional stress involved in leaving the calf/calves without a mother), and relatively large males because of the higher return with respect to meat and trophy. In support of the former view, we found the harvest mortality of adult females to be higher among pre-prime (1–3 years old) than prime-aged age classes (4–7 years old). This is probably because prime-aged females are more fecund and, therefore, more likely to be in company with one or two calves during the hunting season. As the season progressed, however, the selection pressure on barren females decreased, probably due to more productive females becoming 'legal' prey as their calf/calves were harvested. In males, we did not find any evidence of strong age-specific hunter se-lectivity, despite strong age-dependent variation in body mass and antler size. We suggest that this was due to the current strongly female-biased sex ratio in most Norwegian moose populations, which leaves the hunters with few opportunities to be selective within a relatively short and intensive hunting season. The management implications of these findings and to what extent the results are likely to affect the future evolution of life histories in Norwegian moose populations are discussed.

Keywords Hunter selectivity · Life table analysis · Moose · Mortality

E. B. Nilsen (✉)
Department of Forestry and Wildlife Management, Hedmark University College,
N-2480 Koppang, Norway
e-mail: erlend.nilsen@sue.hihm.no
Tel.: +47-624-30876
Fax: +47-624-30851

E. B. Nilsen
Centre for Ecological and Evolutionary Synthesis (CEES),
Department of Biology, University of Oslo,
P.O. Box 1066, N-0316 Blindern, Oslo, Norway

E. J. Solberg
Norwegian Institute for Nature Research,
Tungasletta 2, N-7485 Trondheim, Norway

Introduction

The life histories of animals are expected to have evolved to optimize the individual fitness under the prevailing selection pressure (Stearns 1992). Such selection pressure may be caused by resource availability (Palkovacs 2003), predation (Bronikowski et al. 2002; Palkovacs 2003) and, more recently, human harvest (Harris et al. 2002; for review, see also Reznick and Ghalambor 2005). Indeed, phenotype-based selective harvesting can have evolutionary consequences, if they target heritable traits (Coltman et al. 2003). During the last two decades, several commercial fish stocks have revealed significant evolutionary changes in life history traits caused by size-selective fishing (Ernande et al. 2004), sometimes leading to significant decreases in the annual harvest (Sutherland 1990). Similarly, age-selective harvesting may have long-term evolutionary consequences if they produce a mortality pattern that differs extensively from the pattern that shaped the present life history (Ginsberg and Milner-Gulland 1994; Olsen et al. 2004). Furthermore, intensive male-biased harvesting may distort normal population processes (Ginsberg and Milner-Gulland 1994; Solberg et al. 2002; Sæther et al. 2003) and possibly also reduce the genetic variability (Harris et al. 2002). However, few reports exist on the evolutionary and ecological consequences of

modern harvesting on terrestrial organisms, despite the potential for such (but see Harris et al. 2002; Coltman et al. 2003). Indeed, for most important large game species, we do not even know to what extent differential hunting mortality occur, indicating that documentation of its presence or absence may be a first approach to this important subject.

The moose (*Alces alces*) is the most important wildlife resource in Scandinavia (Storaas et al. 2001) and is intensively managed to maintain a high productivity to allow high annual harvest rates. This management goal is achieved by the use of sex- and age-specific harvest quotas, often by focusing the harvest mainly on calves and adult males to maintain a high proportion of adult reproductive females in the population (Solberg et al. 2000; Sæther et al. 2001). Although the quota system to some extent restricts what type of animals the hunters may shoot, indirect data suggest that hunters may still harvest age classes within quota categories by different intensities (Solberg et al. 2000; Ericsson and Wallin 2001). In a previous study, the occurrence and potential effects of sex- and age-specific harvesting have been described in the Vefsn moose populations in northern Norway (Solberg et al. 2000). It was shown how selective harvesting of males vs females may have biased the population sex ratio and influenced the age structure of both sexes (Solberg et al. 1999), potentially affecting the pattern of male body growth (Solberg and Sæther 1994). Similarly, Ericsson and Wallin (2001) and Solberg et al. (2000) show how hunter mortality may significantly differ among adult age classes, possibly because of hunter selectivity and/or differential hunting vulnerability. As a consequence, the present mortality pattern in intensively harvested moose populations may be very different from the pattern caused by carnivores like wolves (*Canis lupus*) and bears (*Ursus arctos*), potentially leading to short-term population dynamical and long-term evolutionary changes not foreseen when implementing the existing harvesting regime (Harris et al. 2002; Sæther et al. 2004).

In this study, we use kill-at-age data from 20,544 moose and a simple life table approach to examine the pattern of hunting mortality of moose in eight different populations in Norway. Based on previous reports (Solberg et al. 2000), the view of local wildlife managers and the current management practice in Norway, we hypothesise that hunters prefer to shoot females not in company with calves, as well as relatively large males, and that these preferences are reflected in the age structure of the male and female harvest. In moose, body mass and fecundity increase with age until prime (4–8 years; Solberg et al. 2004) and, accordingly, we expect higher hunting mortality of pre-prime vs prime-aged females and lesser hunting mortality of pre-prime vs prime-aged males. Shooting females in company with one or two calves is usually regarded as an accident and is generally not socially accepted among moose hunters. As such hunting preferences may also have positive effects on the reproductive potential of the population (Caughley 1977; Ericsson et al. 2000), they are also encouraged by most wildlife managers. In contrast, most hunters are assumed to prefer older and larger males as these provide more meat and larger antlers, despite the opposite strategy often being advocated by the management (Solberg et al. 2000).

Although such age-specific patterns in hunting mortality are previously documented in a Norwegian moose population (Solberg et al. 2000), less is known about the extent to which these patterns vary among populations. However, a large variation in harvest strategies, hunting pressure and population structure among populations suggests that both the level and the direction of hunter selectivity can be affected. For instance, large among-population-variation exists in the proportion of calves in the harvest, which in turn may affect the extent to which hunters are able to discriminate among females based on their reproductive status. We predict that hunters are less selective regarding pre-prime vs prime-aged females in populations with intensive harvesting of calves, as in such populations, a large proportion of prime-age females will loose their calf/calves during the hunting season and, thus, exposing themselves for being harvested later in the season. Moreover, high off-take of males during three decades have led to highly female-biased moose populations throughout most of Norway (Solberg et al. 2002; Sæther et al. 2003), with decreasing opportunities to both see and shoot an adult male. Thus, we predict that hunters would be less selective for old males when the proportion of males in the population is low, as this will imply few hunting opportunities for adult males in general and, hence, less opportunities to be selective. Also, the currently high hunting pressure in most populations to stabilise or decrease population size (Lavsund et al. 2003) is likely to affect the level of hunter selectivity. We predict that hunting selectivity of both sexes will be more pronounced in increasing than decreasing populations. This is because population decline is mainly due to over-harvesting following large quotas relative to the population size (Solberg et al. 1997, 1999). Indeed, as we assume the hunters to be highly motivated to fulfil their quota, we expect them to be less selective when it becomes difficult to find animals of preferred size or status (Solberg et al. 2000).

As an independent test of the age-specific variation in hunting mortality, we also estimated the change in the daily mean age of males and the reproductive status (indexed by the number of corpora rubra—see Materials and methods) of females throughout the hunting season. If hunters prefer older and larger males, or older males are more vulnerable for hunting, we expect male age to decrease as the hunting season progress. This is because the supply of older males decreases towards the end of the season if many old males are killed at the start of the season. Similarly, we expect the reproductive status of harvested females to increase as the hunting season progress because an increasing number of females that were in company with a calf at the start of the hunting season may have lost their calf due to hunting. According to our hypothesis, a calf acts as a life insurance for the female, and when it is gone, her chance of being killed increases.

Materials and methods

Study areas and material

The material was sampled from eight different populations in a gradient from north to south (Fig. 1), covering the most important moose regions in Norway. For further information on the study areas, see Solberg et al. (2002). These moose populations have been monitored annually since 1991 as part of the National Moose-Monitoring Program (Solberg et al. 1997), in which carcass mass (about 50% of total live body mass; Wallin et al. 1996), lower jaws, and ovaries were collected 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 from tooth replacement patterns in calves and yearlings (Peterson 1955) and from the number of layers in the secondary dentine of the incisors in adults (Haagenrud 1978). Furthermore, the reproductive status of a female was indicated by the number of corpora rubra in the ovaries. *Corpora rubra* (new pigmented scars) develops 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 number of corpora rubra in the ovaries of females harvested in the autumn is related to the number of calves produced during the preceding calving season (Sæther and Haagenrud 1985; Langvatn 1992; Langvatn et al. 1994). Because calves may be produced following ovulation in either of the two

ovaries, only females from which both ovaries were collected were included in the analysis regarding reproductive status. Owing to varying sampling procedures among regions during the period, and years with low sample size, varying number of sampling years from each region were included in the analyses depending on the variables examined (see below).

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 reported by the leader of each hunting team after the hunting season each year (Solberg and Sæther 1999). Data on moose observations existed for the complete study period in all regions, giving an average of 5,466 (range 2,735–8,689) moose observations per year and region, distributed over an average of 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 ($\geq$1-year-old) males per adult female, whereas the variation in population density was indexed by the number of moose seen per hunter-day. These indexes have been shown to quite reasonably reflect the variation in population structure and density within populations from year to year (Ericsson and Wallin 1999; Solberg and Sæther 1999; Solberg et al. 2002). However, among populations, the moose seen per hunter-day may be less precise in indexing variation in density because of local variation in observation conditions, hunting methods,

Fig. 1 Locations of the eight moose monitoring areas in Norway from which data were derived
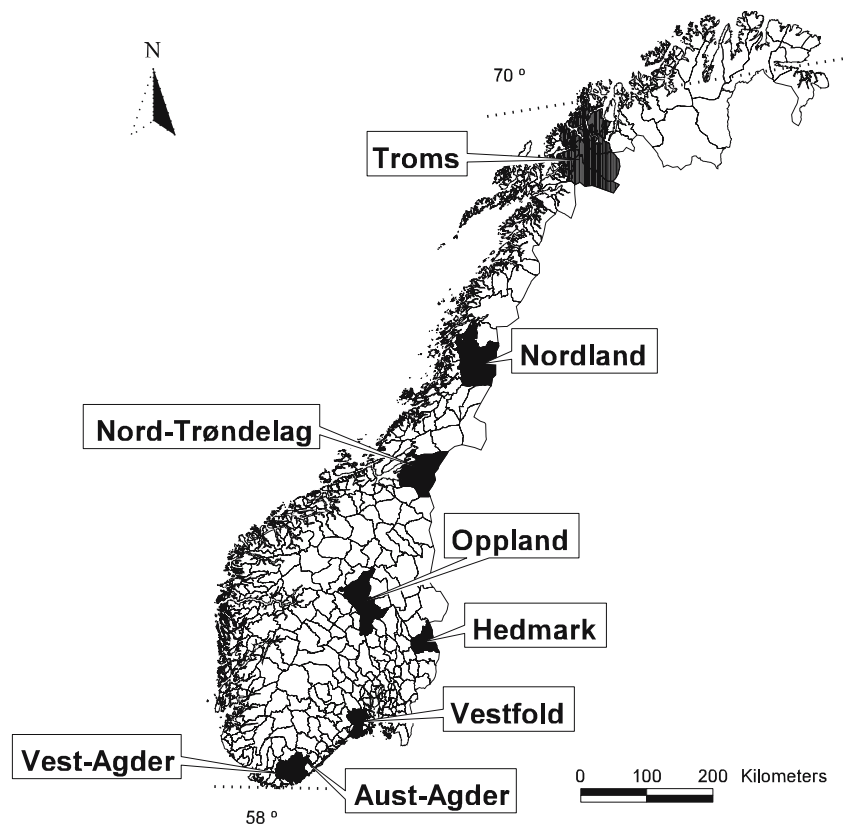
etc. (Ericsson and Wallin 1999), and may only give a rough indication of the variation in density. For the use and precision of indexes based on moose observations, we refer to Solberg and Sæther (1999) and Ericsson and Wallin (1999). Based on the moose observation data, we estimated the population growth rates (r) as the geometric mean of the annual increase in moose seen per hunter-day (n_t), $\lambda=n_{t+1}/n_t$, $r=\ln(\lambda)$ (Caughley 1977) for the particular period and region considered. We used the geometric mean rather than the arithmetic mean because population growth is a geometric process (Case 2000). The growth rate in hunter observations ranged between $r=0.14$ and $r=-0.07$ for the different periods and regions. Trends in the number of observed moose per day for the different regions throughout the study period are illustrated in Fig. 2.

Analyses of age-specific harvest mortality

To examine the variation in hunting mortality, we used a simple life table analysis to evaluate the extent by which pre-prime age classes (1–3 years) differed in hunting mortality from prime age classes (4–7 years). We defined the prime age classes based on the variation in carcass mass, number of antler points (males) and proportion of females that produced calf/calves in relation to age. In both males and females, these values tend to level off at about 4 years of age and show relatively little variation between age classes for older individuals (Fig. 3, Solberg et al. 1997; Solberg et al. 2004). Accordingly, we assumed the hunters to be unable to discriminate among moose 4–7 years of age. Then, given that the population have a reasonably stable age structure and no age-dependent natural mortality, the relative survival rate of the prime age classes can be estimated by the slope of the linear regression of the logarithm of the proportion of each age group in the harvest (4–7 years old) on age (Boer 1988; Caughley 1977). However, because most populations were either increasing or decreasing during the study period, we first corrected the age frequencies for the population growth rate, by multiplying the age-specific frequencies by e^{rx}, where r is the population growth rate (see above) and x is age (Caughley 1977; Krebs 1999). Moreover, to facilitate the comparison of relative mortality rates among areas and

Fig. 2 Trends in the observed number of moose per hunter-day for the different regions throughout the study period
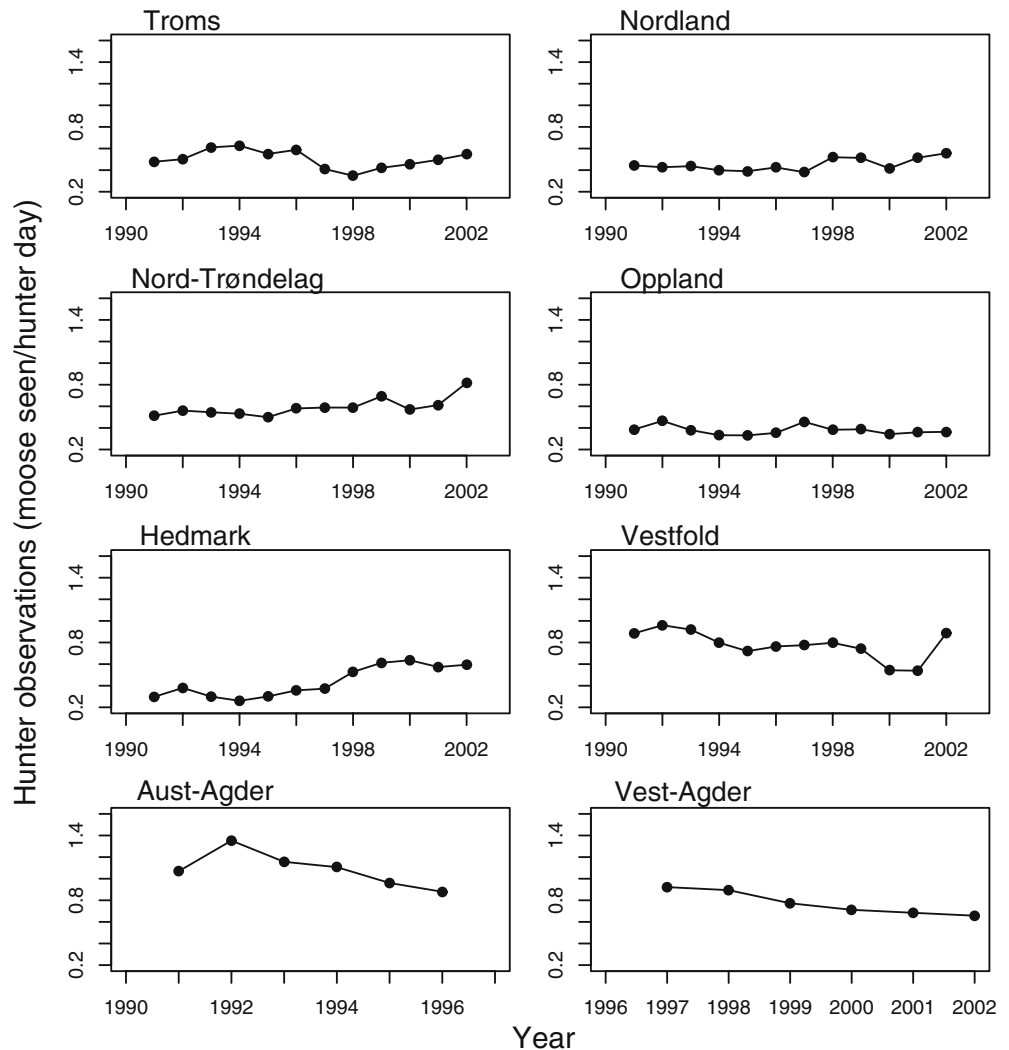
Fig. 3 Variation in mean male carcass mass (*filled circles*, ±2 SE, *n*=7981) and number of antler points (*open squares*, ±2 SE, *n*=8162, *top panel*), and mean female carcass mass (*filled circles*, ±2 SE, *n*=9654) and proportion of females with calf/calves (*open squares*, ±2 SE, *n*=3401, *lower panel*) in relation to age in all study areas combined during the study period. Carcass mass is about 50% of live body mass (Wallin et al. 1996). Calf production is based on the proportion of harvested females with corpora rubra in their ovaries. The presence of corpora rubra indicates that the female gave birth to at least one calf in the year she was killed (see Materials and methods)
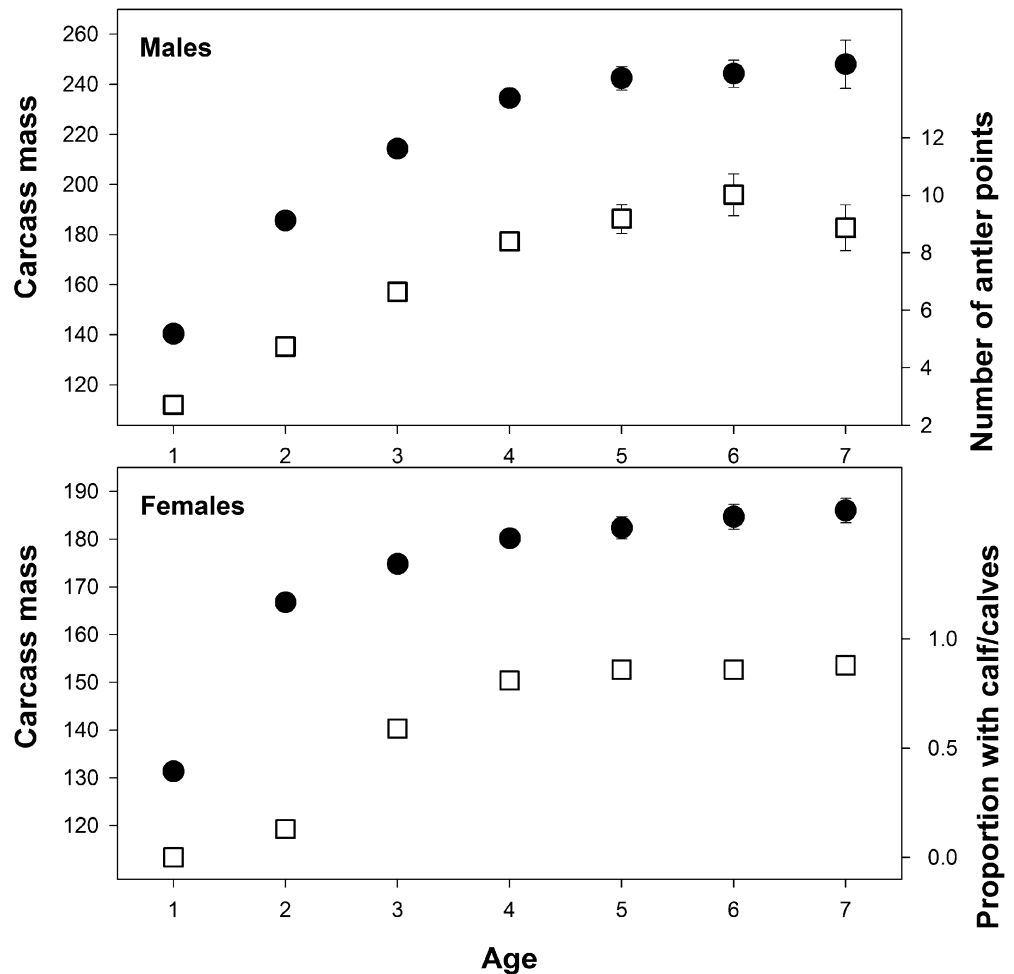
periods, we estimated the regression slope based on the ln-proportions rather than the ln-frequencies of each age group in the harvest. From this slope, we deduced the relative hunting mortality rate on the younger age classes by comparing their ln-age-proportions relative to the slope.

In the absence of any differential hunting mortality (due to hunter selectivity or differential hunting vulnerability), the ln-age-proportions of yearlings, 2- and 3-year-olds, were expected to fit the slope, whereas deviations from the slope were interpreted as higher (above the slope, see Fig. 4a) or lower (below, see Fig. 4b) hunting mortality rate relative to the prime-age age classes (Crete et al. 1981; Boer 1988). However, because some deviations from the slope may also be expected by chance or violations of the assumptions (see below), we subjectively determined that differential hunting mortality rates were present only to the extent that the mean sum of squares of the ln-age-proportions of the younger age classes (1–3 years old) more than doubled the mean sum of square of the ln-age-proportions of the prime age classes. By this procedure, we minimised the risk that extreme values (outliers) were interpreted as differential hunting mortality. Also, we excluded the populations whose linear regression of the ln-age-proportions in the harvest for the prime-aged age

classes on age showed a poor fit, indicating that the assumptions were clearly violated. As we have no statistical, rigorous way of detecting a poor fit (as the slope of linear regression is expected to be significantly negative in all populations), we subjectively selected $R^2 < 0.60$ to be a poor fit.

This method may give reasonable estimates of the variation in hunting mortality rate given that the assumptions are not seriously violated. For instance, if large variation exists in the natural mortality rate among adult age classes, this may seriously affect both the slope and the hunting mortality estimates. However, because of the very low densities of large carnivores like wolves and bears in Norway (Swenson et al. 1994; Wabakken et al. 2001), the natural mortality of adult moose is generally low (<5% annually, Stubsjøen et al. 2000; Ericsson and Wallin 2001, Solberg et al. 2005). This suggests that a large annual variation in mortality rate among adult age classes is rather unlikely. Moreover, although changes in survivorship with age most often is a nonlinear process (Sibly et al. 2005), earlier studies have shown that senescence in moose survival does not occur before about 10 years of age (Ericsson and Wallin 2001). Because we only included age classes up to 7 years in our analyses, we therefore assume
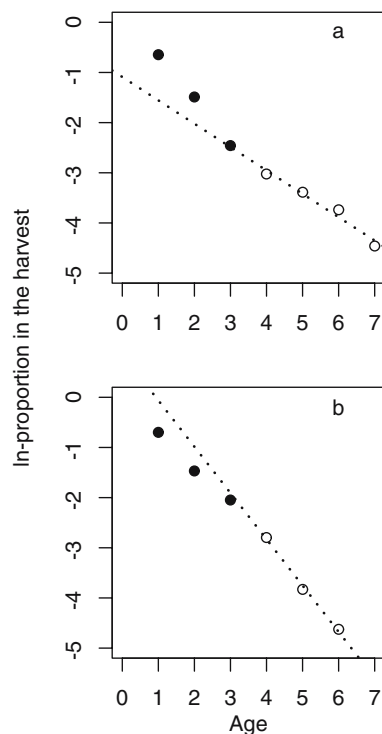
Fig. 4 The expected pattern of age-specific hunting mortality in females (a) and males (b). The data presented are from Nordland (early) where the expected patterns occurred

that the variation in survival observed in our study is solely an effect of differential hunting mortality.

Erroneous estimates of hunter selectivity may also appear if annual variations in natural mortality or recruitment rates have destabilised the age structure (Caughley 1977; Case 2000; see also Coulson et al. 2004). This has probably occurred in most populations, although the extent is unknown. However, as we averaged age proportions over several years with data (Table 1), we believe that at least part of the short-term fluctuations in age structure was cancelled out in the mortality estimates. Moreover, because we only possessed observation data back until the mid-1980s (at the maximum), and to minimise the effect of variation in age structure over time, we restricted the analyses to include only age classes up to 7 years.

We divided the period into an early (years≤1996) and late (years≥1997) period for regions from which data were available for the whole period, whereas years were pooled across this cut-off for regions from which data for only a few years were available (Table 1). The reason for the split was to be able to test for changes in relative hunting mortality rates during the study period.

Statistical analyses

To test our hypotheses about the between-population variation in hunter selectivity, we used the mean residual variation of pre-prime ln-age-proportions from the expected values based on the slope of the linear regression of the ln-age-proportions of prime individuals (4–7 years old) on age as the dependent variable (as a measure of selectivity). We then fitted linear models, with population growth rate and proportion of calves in the harvest as independent variables for the females, and population growth rate and population sex ratio for the males. The model selection was guided by the corrected Akaike's Information Criterion (AICc) (Burnham and Anderson 2002), comparing the model deviance with the number of parameters used (the lowest value of AICc represents the most parsimonious model). We next tested our expectation that there was a decrease in the mean age of males and an increase in the mean reproductive status of females with increasing kill date. Variation in reproductive status in females was analysed by fitting Poisson regression models (Venables and Ripley 2002) to the data, as the response variable (number of corpora rubra) follows a Poisson distribution (0, 1 or 2 corpora rubra), whereas variations in male age were analysed by linear least-square regressions. The models included killing date and region as independent variables for males, and killing date, region and proportion of calves in the harvest for females.

All statistical analyses were run using R 2.1.0 under windows (R Development Core Team 2004), and all significance levels were two-tailed.

Table 1 Data used in the analyses of age-specific hunting mortality in female and male moose in Norway in eight regions

County	Females		Males	
	Early	Late	Early	Late
Nordland	1991–1996	1997–2002	1991–1996	1997–2003
Oppland	1991–1996	1997–2002	1991–1996	1997–2003
Hedmark	1991–1996	1997–2002	1991–1996	1997–2003
Troms	1991–1996	1997–2002	1991–1992	
Nord-Trøndelag	1991–1996	1997–2002	1991–1992+2000[a]	
Vestfold	1991–1996	1997–2002	1991–1992+2000–2002[a]	
Aust-Agder	1991–1995		1991–1992	
Vest-Agder		1997–2002		1997+2000

[a]Data pooled across periods in the analyses, due to data being available for a limited number of years

Results

Age-specific hunting mortality

The ln-age-proportions of prime-aged females in the harvest revealed a relatively close linear relationship with age in most regions (R^2=0.65 to 0.99). However, in Hedmark (early and late), the fit was rather poor (R^2=0.25 and 0.03, respectively), suggesting that one or more of the assumptions were seriously violated. Based on the extension of the regression slope, young females were found to have consistently higher hunting mortality rates than prime-aged females in all regions (Fig. 5a). However, in Nordland (late), Nord-Trøndelag (early) and Oppland (early), the ln-age-proportions of 3-year-old females were slightly below the slope, although there were clearly elevated mortality rates for the two younger age classes. When comparing the early and late periods for the regions from which we had data for both periods (see Table 1), there was a clear trend towards an increasing difference in relative hunting mortality rates of pre-prime vs prime females (t=4.30, df=4, p=0.012, paired t-test).
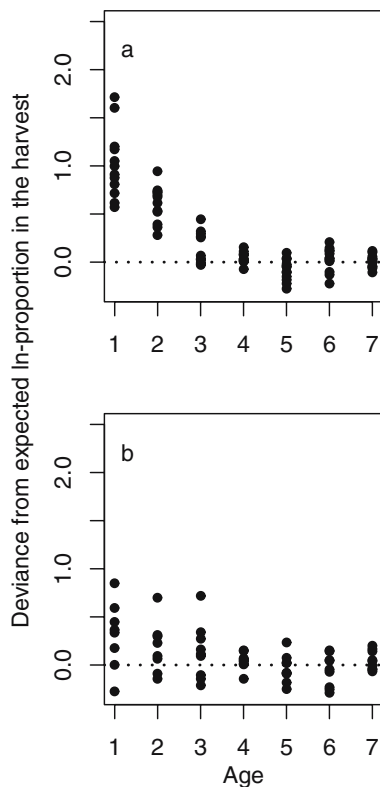

Fig. 5 Evidence of age-specific harvest mortality for female (a) and male (b) moose in eight different moose regions in Norway. The relationship between age and the ln-proportion of each age group in the harvest for the prime-aged age classes are scaled down to zero, and the y-axis indicates the deviance from this relationship for the different age classes. Accordingly, points *above the line* indicate higher hunting mortality than expected whereas points *below the line* indicates lower hunting mortality. Each point represents the mean ln-age-proportion within one population during 2 to 6 years (see Table 1)

Also, in males, the ln-age-proportions of prime-aged individuals in the harvest revealed a relatively close linear relationship with age in most regions (R^2=0.64 to 0.99), whereas the assumptions were probably seriously violated in Hedmark (late) where the fit was poor (R^2=0.03). Our expectation of lower hunting mortality rates among pre-prime males was generally not supported (Fig. 5b.), as we only found the predicted lower hunting mortality rate of pre-prime vs prime-aged classes in Nordland (early) and to some extent in Aust-Agder. A trend in the opposite direction was evident in Troms, Nord-Trøndelag, Oppland (early) and Vestfold, whereas no significant differences in hunting mortality rate were found in the other regions.

For a full summary of the patterns of age-specific mortality in the different populations, we refer to the S1.

Correlates of age-specific hunting mortality

In females, neither the hypothesis that the hunters become more selective when the population growth is high nor when the proportion of calves in the harvest is low was supported (Table 2) based on the AICc values. However, we call for a cautious interpretation of these results, as there was a strong positive correlation between the two independent variables (r=0.61, n=12, p=0.037). As we expected, opposite effects of population growth rate and calf proportion in the harvest might potentially have cancelled each other out.

In males, neither prediction was supported (Table 2), as the strength of selection was neither associated with variation in population growth rate nor with variation in population sex ratio.

Reproductive status and male age in relation to kill date

Regarding the daily variation in mean number of corpora rubra (females), we found an increase as the hunting season progressed (β=0.009 (SE 0.001), $\chi^2_{[1, 6650]}$=39.1, p<0.001), after controlling for the effect of region ($\chi^2_{[7, 6650]}$=102.1, p<0.001). There was no interaction between region and kill date ($\chi^2_{[7, 6643]}$=8.0, p=0.300) suggesting that the patterns were similar in the different regions. Furthermore, there was no interaction between kill date and the proportion of calves killed in a population ($\chi^2_{[1, 6655]}$=2.0, p=0.200), indicating that the pattern did not become stronger in populations where more females lost their calves. Hence, we found support for the prediction that more fecund females were harvested at the end compared to the start of the season, which was expected if hunters were actively selecting females without calves, but not that this pattern became stronger when a higher proportion of calves were shot.

We found no general increase in the mean age of harvested males as the hunting season progressed ($F_{[1,9248]}$= 0.279, p=0.597) after controlling for the effect of region

Table 2 AICc values for the models fitted to explain the between-population variation in the strength of hunter selectivity in female and male moose ($n=12$ populations in females and $n=10$ populations in males)

Dependent variable	Model	AICc	ΔAICc	R^2
Age-specific hunting mortality in females	Intercept only	−0.65	–	–
	Proportion of calves	2.37	3.02	0.05
	Growth rate	2.71	3.36	0.02
	Proportion of calves + growth rate	7.08	7.73	0.05
	Proportion of calves * growth rate	13.04	13.69	0.07
Age-specific hunting mortality in males	Intercept only	10.76	–	–
	Growth rate	13.74	2.98	0.13
	Sex ratio	14.09	3.33	0.10
	Sex ratio + growth rate	18.18	7.42	0.27
	Sex ratio * growth rate	27.06	16.30	0.28

ΔAICc is the change in AICc compared with the most parsimonious model

($F_{[7, 9248]}=18.571$, $p<0.001$). Nor were there any interaction between region and kill date ($F_{[7, 9241]}=1.109$, $p=0.354$). Thus, contrary to our predictions, we found little support for the expectations that males are systematically selected based on age and size, or experience any age-specific variation in hunting vulnerability.

Discussion

The study partly confirmed previous results on the Vefsn moose populations (Solberg et al. 2000) that harvest mortality was higher for pre-prime than prime-aged females, but to a lesser extent that older males were harvested more frequently than younger males. The difference in mortality between pre-prime and prime-aged females also decreased as the hunting season proceeded. In the following, we discuss these patterns with respect to hunting selectivity and vulnerability, and evaluate to what extent confounding variables may have affected the results. Finally, we discuss the potential short- and long-term ecological and evolutionary effects of the observed age-specific hunting mortality and its management implications.

In females, there was a strong indication of differential harvest mortality between age groups. Indeed, there was an overwhelming pattern that the pre-prime females had higher hunting mortality than prime-aged females, as evidenced by the life table analyses and the increase in number of corpora rubra in females shot as the harvest season progressed. The general opinion among moose managers is that this pattern occurs because hunters dislike shooting the mother from the calf/calves, and because hunters support the use of this hunting strategy to increase the productivity of the population. As indicated in several harvesting models (e.g. Ericsson et al. 2000), the short term growth rate can be substantially improved by harvesting barren females compared to a strategy of random harvesting of females with respect to litter size. However, although our results partly support the prediction that hunters are selective in their choice of prey, variation in hunting vulnerability (susceptibility) may as well have influence on this pattern.

Several studies have indicated differential hunting (e.g. Chamberlain et al. 1999) and trapping vulnerability (e.g. Noyce et al. 2001) among sex and age groups in different mammal species, and this may also occur in moose. Data from North American moose populations (Crete et al. 1981; Boer 1988), for instance, indicate higher susceptibility to hunting among younger individuals of both sexes, possibly due to higher movement rates (Courtois et al. 1998). In contrast, Ericsson and Wallin (2001) reported increasing hunting mortality with age for moose females in Sweden, and as the pattern was mainly due to high hunting mortality among senescent individuals (>12 year of age), they speculated that reduced mobility could make them more susceptible for hunting. Alternatively, hunter selectivity of barren females may have generated the pattern, as moose showed reproductive senescence in the same populations (Ericsson et al. 2001), and females that gave birth in a given year showed significantly lower hunting mortality than those that did not (Ericsson and Wallin 2001). In the present study, the fact that the frequency of females with increasing number of corpora rubra increased as the hunting season progressed also suggests that active hunter selectivity for barren females contributed to the age-specific patterns of hunting mortality reported here. Although the same pattern might have occurred if pre-prime females were more vulnerable to be seen and shot at the start of the season (leaving less young females available later in the season), the relatively dense and female-biased moose populations in Norway suggest that a high proportion of pre-prime females would also be available at the end of the season. Thus, we suggest that the difference in hunting mortality rate between pre-prime and prime-aged females reported here was at least partly caused by active hunter selectivity.

Surprisingly, we did not find the strength of selection to be affected by population growth rate to any detectable extent after we controlled for the variation in the proportion of calves in the harvest. This indicates that the hunters are able to maintain their selectivity even when the harvesting pressure is high. However, the expected relationship may have been cancelled by the opposite effect of variation in the proportion of calves in the harvest (see Results).

Indeed, given the low sample size (12 populations) and our relatively rough index of selection, it was impossible to test the independent effects of variation in both hunting pressure and proportion of calves in the harvest with an adequate statistical power. Another possible explanation could be that the population size per se rather than the hunting pressure determines the opportunity to be selective. This is particularly relevant with respect to the hunting pressure on adult females, as most Norwegian moose populations are strongly sex-biased in the direction of females (Solberg et al. 2002, 2005; Lavsund et al. 2003). Thus, even in populations under heavy hunting pressure, there are probably a large number of adult females available to select among. By using the number of moose shot per square kilometer as a proxy of population density (see Solberg and Sæther 1999 for a discussion), however, we did not find such a relationship ($t=0.575$, $n=12$, $p=0.578$, linear regression).

Despite the strong age-specific growth and antler size in males (Fig. 3; see also Solberg and Sæther 1994), we found little evidence for age-specific variation in hunting mortality rate in males, except for a few regions and periods. This is in contrast to previous studies in Norway (Solberg et al. 2000) and Sweden (Ericsson and Wallin 2001), where older males were found to have significantly higher hunting mortality rates than the younger males. We speculate that this may be due to the low proportion of males in all regions, as most Norwegian moose populations are strongly female biased (Solberg et al. 2002, 2005). Indeed, for Norway as a whole, Solberg et al. (2005) estimated the males to constitute less than one third of the adult (≥ 1 year) population, although with large variation among regions (Solberg et al. 2002). With hunters highly motivated to fulfil their quotas, a limited encounter rate is likely to cause limited possibilities to be selective during the short moose hunting season in Norway (3–4 weeks in late September–late October). Moreover, as much focus in the national media has been directed lately at the low proportion and age of males in Norwegian moose populations because of the possible effects on reproduction (Solberg et al. 2002; Sæther et al. 2003) and calf sex ratios (Sæther et al. 2004), it is likely that hunters are also getting more disciplined with respect to what animal they harvest from the populations.

In Scandinavian moose populations, human exploitation is considered to be one of the driving factors shaping the population dynamics (Solberg et al. 1999), and harvest mortality is generally regarded the most important mortality factor (Stubsjøen et al 2000; Solberg et al. 2000; Ericsson and Wallin 2001). If the mortality patterns shaped by human off-take differ from the patterns observed in non-hunted populations, selective hunting could potentially have long-term evolutionary effects on life history characteristics (see Harris et al. 2002 for a discussion), given that these traits show heritable variation. The evolution of life history traits are often affected by trade-offs (Stearns 1992), e.g. current reproduction vs future reproduction and survival probabilities. For instance, Testa (2004) reported that a female moose accompanied by calf/calves experienced higher mortality rates due to predation in a pop-

ulation in south-central Alaska, with no female harvest, indicating a reproduction–survival trade off (see also Tavecchia et al. 2005 and Koivula et al. 2003 for examples of reproduction–survival trade-offs for mammals in predator-free areas). Similarly, moose females with their first litter have been reported to have increased hunting vulnerability in a Canadian population (Ferguson 2002). This pattern differs from the pattern reported in the present study, in which pre-prime females experienced higher hunting mortality than the prime-aged females. Given that this pattern is related to the presence of a calf/calves or not, also large pre-prime females that tend to mature earlier (Sæther and Heim 1993) may experience increased survival. Moreover, to the extent that the relative allocation of resources to reproduction varies among females, hunting may indeed select for decreasing age at maturity. This is because, in Norwegian moose populations, young individuals reduce their risk of being harvested by maturing at an early age (see also Ericsson 2001). The long-term outcome may be more females maturing as yearlings at a lower body mass, despite the likely opposing natural selection pressure. Decreasing age at maturity could in turn result in prime-aged females with lower body mass (as reproduction is generally costly in terms of future body growth, see Sæther and Haagenrud 1985; Sand 1998), and potentially increased natural mortality and decreased reproductive output later in life.

The present results may also have management implications as, in Norway, data from hunter-killed moose traditionally have been used extensively for monitoring purposes. For instance, each year, data from more than 3000 hunter killed moose are collected from seven different populations as part of the national monitoring program for moose (Solberg et al. 1997). Data include age, carcass mass as well as reproductive measurements based on ovary sectioning. As indicated by our results, however, such data may not necessarily be a random sample of the population, and as the level of harvest mortality varies among populations and years, such data may not even be a very precise index of variation in, e.g., age structure or mean reproductive rates. This may also to some extent account for the distribution of animals within age groups, in particular if the variation in harvest mortality is caused by active hunter selectivity. If, for instance, hunters are selecting female moose based on calving status, both the age-specific mean reproductive rates and body masses are likely to be underestimates because age at maturity and fecundity in moose are correlated with body mass (Sæther and Heim 1993; Sand 1996). Similarly, age-specific body masses of males may be overestimates in populations where hunters are selecting on male size (e.g. through antler size or directly on body size). Under such conditions, the variation in population condition (sensu Hanks 1981) is probably best indexed by the variation in body mass of calves and yearlings, and the ovulation rates of yearling females, as these groups have low status as trophy animals and because yearling females, independent of size, have not yet produced their first calf/calves.

The life table approach applied here rests on several assumptions that to some extent could have been violated (see Materials and methods). However, we have no reasons to believe that this has influence on the general direction of our results. This is further supported by the contrasting patterns observed in males and females, which usually are found to have quite similar natural mortality rates in Scandinavia (e.g. Ericsson and Wallin 2001; Solberg et al. 2005). If our results were simply a spurious result of the method employed, we would have expected similar harvest mortality patterns in both sexes. Moreover, as the predicted direction in calving status (number of corpora rubra) with kill date was found in females, but with no relationship found between age and kill date in males, we believe this further corroborates the pattern of differential age-specific hunting mortality in females, but only to a small extent in males. Despite our relatively rough approach, we thus conclude that age-specific variation in harvest mortality occurs in many Norwegian moose populations, in particular among adult females.

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