Consequences of harvesting on age structure, sex ratio and population dynamics of red deer Cervus elaphus in central Norway

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We explore some of the consequences of harvest on population growth rate, age and sex structure in a Norwegian population of red deer *Cervus elaphus*, using age-structured demographic models. Survival rates were estimated from individuals marked and monitored annually during 1977-1995, and information about reproduction patterns were obtained from hunting material in the same region. The population had an actual doubling time of 14 years, corresponding to a multiplication rate of 1.051. Harvesting led to a reduction of about 10% of the potential multiplication rate that equalled 1.166. Including stochasticity had only a small effect on the population multiplication rate. Due to a high hunting pressure, males had less than a 10% chance of reaching 4.5 years of age and the male-biased harvest strongly biased the sex ratio. Assuming that when the number of females per male increases above a given threshold some females would not manage to mate, we investigated at which level male harvesting could be maintained without having demographic consequences on the population growth rate. We concluded that the hunting pressure on males could probably be increased further but indirect consequences of a strongly biased sex ratio (e.g. on population genetic structure) remain to be studied. Variation in the multiplication rate mainly resulted from the variation in winter calf survival. In its present form the harvesting regime reduces the growth rate and biases the sex and age structure, but does not seem to threaten the population's viability and productivity.

Key words: age structure, harvesting, population dynamics, red deer, sex ratio

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The dynamics of wild populations result from the interplay between density-dependent and density-independent factors, and their combined effects on demographic parameters (Sæther 1997). For large mammals like ungulates, human harvesting is, in addition to natural processes, an important factor affecting population dynamics (Getz & Haight 1989, Solberg, Sæther, Strand & Loison 1998). Harvesting may have immediate consequences for population size, age composition and sex structure. Indirect consequences result from the impact of changing population size and structure on the demographic processes (Solberg et al. 1998). Mechanisms such as compensation (Sinclair & Pech 1996), oscillations (Solberg et al. 1998) and changes in life history traits (Skogland 1989) may eventually arise in the population dynamics as a result of harvesting.

When evaluating harvesting plans, managers should ideally take into account the current demographic processes as well as the consequences of particular harvesting regimes on future population dynamics and life history traits. Accordingly, a large body of theories and models have been considered for: 1) determining the sustainable yield in a short term context (Caughley 1977), 2) evaluating sustainable yields in an evolutionary context (Stokes, McGlade & Law 1993), and 3) optimising the harvest with reduced risk of extinction (Lande, Sæther & Engen 1997), both in deterministic and stochastic models (Getz & Haight 1989). However, even though our understanding of the relative role of density-dependent and density-independent factors on populations of large ungulates is rapidly improving (e.g. Sæther 1997, Gaillard, Festa-Bianchet & Yoccoz 1998), there is a gap between the theoretical basis and applied practice in wildlife management (Sinclair 1991).

Hence, models and ideal management strategies are seldom represented in practice. Application of such models would require long-term data sets (Caswell & Tuljapurkar 1997) on population size, age composition, sex ratios and demographic parameters and their variability through time, which are all difficult variables to estimate in the wild (Seber 1982, Lebreton, Pradel & Clobert 1993, McArdle, Gaston & Lawton 1990). In addition, because most populations of mammals are already harvested, the difference between the actual dynamics and the dynamics that would occur in the absence of harvest can be difficult to evaluate. The recent development of capture-mark-recapture models (Lebreton, Burnham, Clobert & Anderson 1992), which make it possible to separate hunting and natural mortality, has contributed to improving this situation.

In this study, we combined the results from a capture-mark-recapture project (Loison & Langvatn 1998) and data from a long-term monitoring project including information on reproductive performance of female red deer *Cervus elaphus* in central Norway (Langvatn, Albon, Burkey & Clutton-Brock 1996) to investigate the change in multiplication rate and the modification of age and sex structure, due to the current harvesting regime. We also explored the possible demographic consequences of a strongly sex biased harvesting regime to determine the level at which males could be harvested without depressing population growth rate.

Material and methods

Study area and population

Our study was carried out in the Trøndelag region of central Norway (63°30'N, 9°30'E). In this region, red deer traditionally undertake seasonal migrations between summer ranges, usually located in the mountains, and low-land winter ranges located on the coast (Albon & Langvatn 1992). During the hunting season which lasts from 10 September to 15 November, hunters are required to send in samples and data on shot animals, including marked individuals. Marking of red deer took place during winter between January and April on four marking sites, close to farmhouses where hay and silage were provided so that red deer could be approached. Red deer were darted at ranges of up to approximately 40 m, using a double-barrel rifle 'Injecta' (Øen 1982) and M-99, etorphine-hydrochloride or 'Large Animal Immobilon' (C-vet. Ltd). All animals were marked with large, numbered plastic ear tags in different colours referring to cohort and marking place. All animals were weighed, measured and sampled for various purposes.

Demographic parameters and hunting statistics

To study the difference between the actual dynamics of harvested populations and the population dynamics that might be observed without harvesting, estimates for reproductive performance in females, natural survival rates, and specific mortality rates due to hunting are required. These estimates were calculated in earlier studies by Langvatn et al. (1996) and Loison & Langvatn (1998). Below we briefly summarise the data, methods and results of these studies. We also explain how we calculated the annual survival rates according to age, sex and year.

The calving rates of females were based on a time series of females shot during the hunting seasons from 1968 to 1990 (Langvatn, Bakke & Engen 1994, Langvatn et al. 1996). The ages of females were determined by counting cementum layers in the incisors (Reimers & Nordby 1968), and the reproductive history and status were determined from analyses of uteri and ovaries (Langvatn 1992, Langvatn et al. 1994, 1996). Calving rates of females 3-18 years of age were very high (0.98, SD = 0.006, N = 558) for the region of Trøndelag, and stable from year to year (Langvatn et al. 1996). The mean calving rate of 2-year-old females was 0.71 (SD = 0.032, N = 203, range: 0.57-0.85), and depended on the May-June day-degrees experienced by females during their second year of life. The vari-

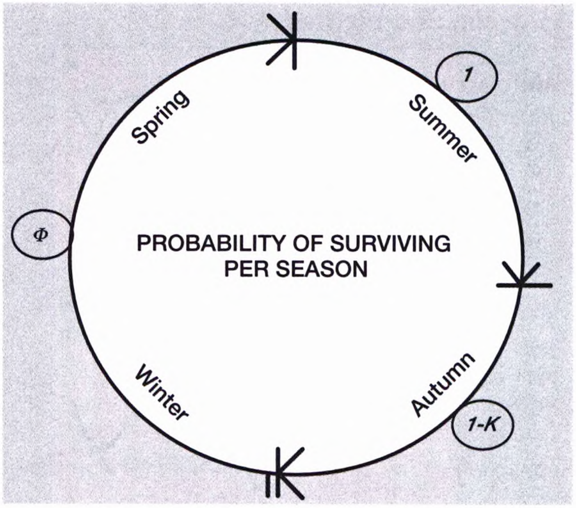

Figure 1. Graphical presentation of the three components of annual survival: winter-spring survival (Φ), summer survival (equal to 1), and autumn survival (1-K).

ance over time for the calving rate of 2-year-old females was 0.0052 (SD = 0.072).

Survival rates and probabilities of being harvested were estimated from a sample of 367 males and 311 females of known age marked individually and monitored during 1977-1995. Individuals were captured, marked and recaptured or resighted each year between January and April (Loison & Langvatn 1998). Most red deer were caught and marked as 6-8 month-old calves. Hunters reported and provided samples from marked individuals shot during the hunting season. Based on resighting/recapture and recovery data, we analysed the natural survival, the probability of being harvested in the autumn and the probability of being recaptured/resighted during winter, according to age, sex and year, using recent developments of capture-mark-recapture models (Loison & Langvatn 1998). The principle of this analysis was to decompose the yearly survival into winter-spring survival, summer survival and autumn survival (Fig. 1). Winter-spring survival (coded Φ) corresponds to the natural survival component, winter and spring being seasons during which red deer may only die from natural causes. We assumed that all red deer survived the summer (summer survival equal to 1) and that the only cause of mortality during autumn was hunting (with the probability of being harvested coded K). Capture-mark-recapture analyses allowed the fitting of models that include the effects of different factors assumed to affect survival rates, probabilities of being harvested and probabilities of being recaptured, and to select a parsimonious model giving the best description of the data (see Lebreton et al. 1992, Burnham, White & Anderson 1995 for details on the principle of capture-recapture modelling and model selection). Details on the analysis concerning the red deer population studied are available in Loison & Langvatn (1998). This analysis led to estimates of natural survival rates and probabilities of being harvested, without requiring estimates of population size. Below, we sum up the main results of interest in the context of the analysis performed here (Table 1). Survival rates were age-class dependent in males and females (three age classes: 0.5 years old, 1.5 years old and ≥ 2.5 years old). Most of the variability in survival over time was found for calf winter survival in relation to winter severity (Loison & Langvatn 1998). The probability of being harvested was age dependent for males and, irrespective of age class, higher for males (yearlings: K = 0.30 ± 0.03; ≥ 2.5 years old: K = 0.42 ± 0.09) than for females (K = 0.12 ± 0.02). In addition, we found that the probabilities of being harvested showed a trend over time that could be modelled using a quadratic function of these probabilities with time for males that revealed an increase of the probabilities of being hunted until the mid 1980s that levelled off in the 1990s (Fig. 2, Loison & Langvatn 1998). No similar trend was detected in females ($\chi^2 = 5.06$, df = 2, P = 0.08) for which the probabilities of being harvested could be considered as constant over the study years.

The annual survival rate (denoted AS) is the probability of surviving the winter/spring and not being shot in the autumn (see Fig. 1). Hence, it can be calculated as AS = Φ*(1-K). These annual survival rates were estimated separately for each sex, age class and

Table 1. Mean values and standard deviation (SD) over time for natural survival according to age class and sex, given for the scenarios corresponding to the 'potential dynamics' (only natural survival considered) and to the 'actual dynamics' (natural survival and survival from hunting considered). Standard deviation for calf (age class 0-0.5) summer survival rate is not available.

Age-class (years of age)		Potential dynamics		Actual dynamics	
		♂	♀	♂	♀
0-0.5	Mean	0.75	0.75	0.75	0.75
	SD	-	-	-	-
0.5-1.5	Mean	0.80	0.80	0.62	0.71
	SD	0.150	0.150	0.130	0.100
1.5-2.5	Mean	0.87	0.92	0.52	0.81
	SD	0.065	0	0.110	0.020
>2.5	Mean	0.93	0.93	0.55	0.82
	SD	0.070	0	0.105	0.020

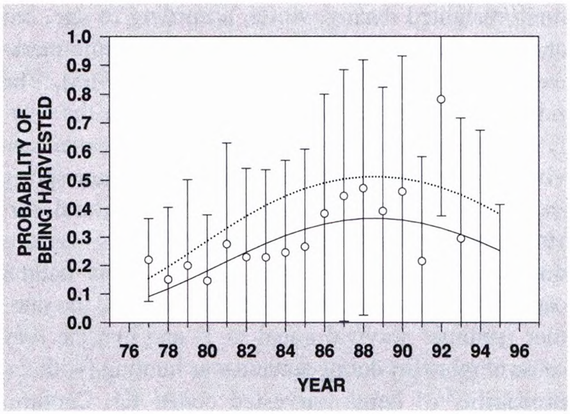

Figure 2. Annual probability of being harvested during 1977-1995 for red deer males. The probability of being harvested is age class dependent. Estimates obtained from the capture-recapture models including annual variation are given with their standard errors (see Loison & Langvatn 1998). For the sake of clarity, only annual estimates of 1.5-year-old males are presented (○). The lines correspond to the model estimates for the trend across years for the probability of being harvested, modelled as a quadratic-logistic function of time for both 1.5- (solid line) and >1.5-year old males (punctuated line).

year. We used the values of the probabilities of being harvested derived from the capture-mark-recapture model, modelling the probabilities of being harvested as a quadratic function of time, both in males and females. Because of the variability over time in natural survival rates and/or the probability of being harvested, the total mortality rates varied over time for all sex and age classes (Fig. 3). We could therefore estimate mean values and standard deviations across years for the annual survival rates (AS) and the natural survival rates only (Φ, see Table 1).

The natural survival from birth to winter and the probability for calves of being harvested during the hunting season has not been investigated using capture-mark-recapture methods. No data are available regarding the inter-annual variability of the survival of calves during summer. We therefore based such values included in the models on the data published by Wegge (1975). We considered survival from birth to winter to be 0.75, on average. However, we repeated the analysis by running models with this parameter ranging from 0.5 to 0.9.

Demographic scenarios

The demographic models were applied under two sets of scenarios, differing in the survival rates included in the models. In the first set of scenarios, we studied the actual dynamics of the population by considering the annual survival (AS) calculated from both the natural survival and the probability of surviving the hunting period. We called these scenarios the 'actual dynamics' scenarios. In the second set of scenarios, we considered only the natural survival (Φ). This assumes that mortality from natural causes only occurred during winter and spring. With this second type of scenarios, we studied the current potential dynamics of the population. We therefore called this type of scenarios the 'potential dynamics' scenarios.

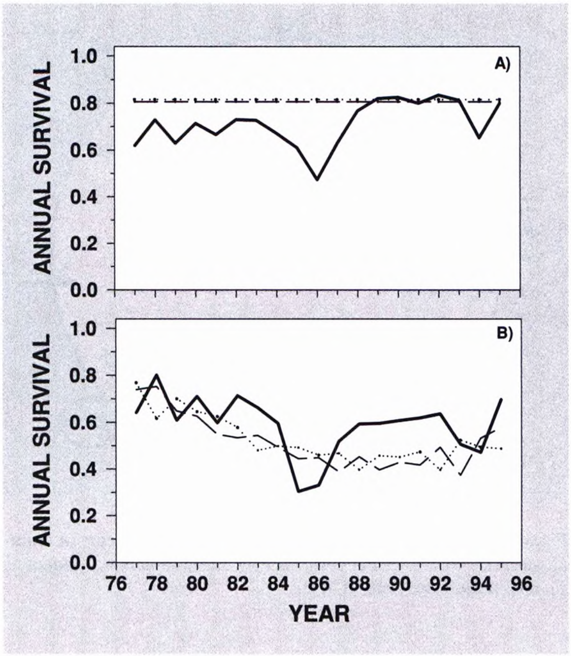

Figure 3. Annual survival during 1977-1995 for female (A) and male (B) red deer according to the age groups: 0.5-1.5 years of age (solid line), 1.5-2.5 years of age (dashed line), and >2.5 years of age (punctuated line). The annual survival corresponds to the probability of surviving both the natural causes of mortality and harvest.

Statistical analyses

We used age-structured models in discrete time (Leslie 1945, Caswell 1989). For simplicity, we hereafter used Leslie matrices as a generic name for all the age-structured models considered. We built Leslie matrices including both males and females, and specified three age classes for females (0.5, 1.5 and 2.5-year-old individuals) and four age classes for males (0.5, 1.5, 2.5 and ≥ 3.5-year-old individuals). We examined the population dynamics from winter to winter, first in the deterministic case and then in the stochastic case.

The population vector, N, was:

$$\mathbf{N}=\begin{pmatrix} nf_1 \\ nf_2 \\ nf_3 \\ nm_1 \\ nm_2 \\ nm_3 \\ nm_4 \end{pmatrix},$$

where nf_i is the number of females in age class i and nm_i is the number of males in age class i. Then, the Leslie matrix, A, with both male and female sections of the population, was defined as:

$$\mathbf{A}=\begin{pmatrix} 0 & S_0 * F_1{*}0.5 & S_0 * F_2{*}0.5 & 0 & 0 & 0 & 0 \\ S_1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & S_2 & S_3 & 0 & 0 & 0 & 0 \\ 0 & S_0 * F_1{*}0.5 & S_0 * F_2{*}0.5 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & S'_1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & S'_2 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & S'_3 & S'_4 \end{pmatrix},$$

where S_i is the survival for females in age class i, S'_i the survival for males in age class i, F_1 the calving rate of 2-year-old females and F_2 the calving rate of older females. Survival rates S_3 and S_4 had the same values as we did not detect any difference in survival between males 2.5 years old and older males (Loison & Langvatn 1998).

In the stochastic case, we assumed that the variability of demographic parameters from year to year was an effect of climatic variation. Hence, we assumed that the variation of all demographic parameters was correlated. The standard deviation obtained from empirical data (Langvatn et al. 1994,1996, Loison & Langvatn 1998) determined the response of each parameter to these temporal variations (see Table 1 for values). We performed all demographic analyses using ULM software (Legendre & Clobert 1995).

The asymptotic multiplication rate corresponds to the largest eigenvalue of the Leslie matrices in the deterministic case (Caswell 1989), denoted λ_d. It is the multiplication rate of the population once the population has reached a stable age structure. In the stochastic case, we used the long-term approximation of the multiplication rate given in Tuljapurkar (1990), denoted λ_s. From these estimates of the multiplication rate, we calculated the doubling time of the population, which corresponds to the mean length of time required for the population size to double. It can be calculated as $DT = \ln\lambda/\ln 2$.

We calculated the asymptotic age structure of the population from the Leslie matrices, which corresponds to the first eigenvector of the matrix (Caswell 1989). Based on the proportion of individuals in each sex and age class in the population, we calculated the sex ratio. We estimated two sex ratios: 1) the number of females ≥ 2.5 years of age per male ≥ 2.5 years of age, and 2) the number of females ≥ 2.5 years of age per male ≥ 3.5 years of age.

We also calculated the elasticity of the multiplication rate (De Kroon, Plisier, van Groenendall & Caswell 1986) to female demographic parameters. The elasticity corresponds to the first partial derivate of the multiplication rate (ln-transformed) with respect to each single demographic parameter (ln-transformed). This gives a measure of the response of the multiplication rate to a change of a given demographic parameter (Caswell 1997). Thereafter, we deduced the contribution of the variability of each demographic parameter to the variability of the annual multiplication rate, which was estimated as the product of the coefficient of variation of a demographic parameter and its elasticity ('actual elasticity coefficient' in Steen & Erikstad 1996; see Tuljapurkar 1990, Caswell 1997 for theoretical consideration and Gaillard et al. 1998 for an application in a life history context): $AE = CV *$ elasticity, where CV is the coefficient of variation.

Predicting the level of male harvesting that would lead to a decrease in population growth rate

We investigated which level of male harvesting would lead to a bias in sex ratio that could negatively affect female fecundity. To approach this problem, we assumed that when the number of females per adult male exceeded a certain threshold, not all females would mate and conceive. Although there is little evidence that strong bias in sex ratio affects female fecundity, it has been shown that the lack of males older than three years of age associated with a large number of females per male could negatively affect the timing of breeding, and thereby calf survival (Noyes, Johnson, Bryant, Findholt & Thomas 1996). At the high latitude of this Norwegian population, the timing of breeding may be more important than in other populations where red deer or wapiti *Cervus canadensis* have been studied before (Noyes et al. 1996, Squibb 1985, Pemberton, Albon, Guinness, Clutton-Brock &

Dover 1992), such that the probability of a negative effect of a female biased sex ratio and young male age structure could be larger. We calculated the multiplication rate for different threshold values and for different male mortality rates. We assumed that either the proportion of males ≥ 2.5 years of age or the proportion of males ≥ 3.5 years of age would be critical for female conception. We therefore considered threshold values ranging between two and four females per male ≥ 2.5 years of age, and then threshold values ranging between four and eight females per male ≥ 3.5 years of age. These values are above the natural sex ratio which is assumed to be 1.5-2 females per male ≥ 2.5 years old (Clutton-Brock, Guinness & Albon 1982, Clutton-Brock & Lonergan 1994). Mortality rates of males ≥ 2.5 years of age were varied between 0.20 and 0.80.

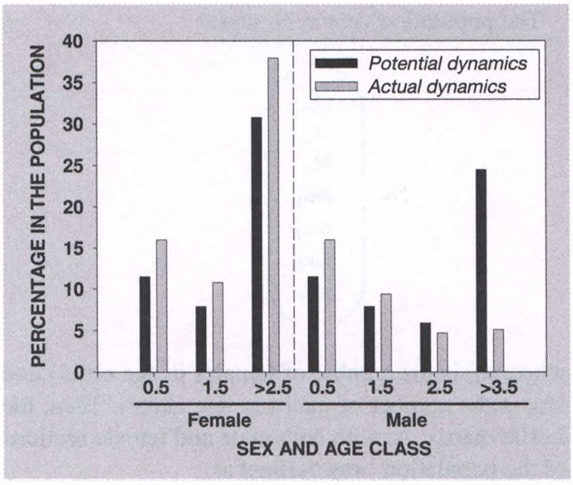

Figure 4. Sex and age structure of the population depending on the two demographic scenarios.

Results

Multiplication rate and doubling time

The potential deterministic multiplication rate was λ_d = 1.166, which corresponds to a population doubling time of about 4.5 years. In the case of the 'actual dynamics' scenario including harvest, the multiplication rate was reduced by 10% (λ_d = 1.051) and the population doubling time increased by 310% to 14 years. Stochasticity only affected calf survival during winter and had a rather low impact on the population multiplication rate. In the case of the 'potential dynamics' scenario, the stochastic multiplication rate was λ_s = 1.164, and in the case of the 'actual dynamics' scenario, λ_s = 1.049. When varying the summer survival rate of calves from 0.5 to 0.9, the multiplication rate remained over 1 in the 'potential dynamics' scenario, but dropped below 1 in the 'actual dynamics' scenario if the summer survival rate was less than 0.55.

Age structure and sex ratio

Sex and age structure of the population were clearly affected by the harvesting regime (Fig. 4). With only the natural causes of mortality, the population would have consisted of more equal numbers of males and females one year and older. With the current sex and age-biased hunting practice, only 1/3 of the population consisted of males (35%). The sex ratio calculated as the number of females per male among animals ≥ 2.5 years old increased nearly fourfold from a non-harvest to a harvest situation (from 1.01 to 3.9). Similarly, when the sex ratio was calculated as the number of females ≥ 2.5 years of age per male ≥ 3.5 years of age, the increase was even larger (from 1.3 to 7.4).

Elasticity analysis

The multiplication rate was most sensitive to the survival rates of adult females (Table 2). The elasticity of λ to adult survival rate was 3.4 times larger than the elasticity of λ to juvenile survival rates, and 3.9 times larger than the elasticity to adult fecundity or yearling survival rate. In addition, λ appeared to be particularly insensitive to the fecundity of 1.5-year-old females. The elasticity values in the female segment were very similar in the scenarios of the actual and the potential dynamics, both with or without stochasticity. The relative elasticity values allow us to conclude that a given proportional increase in the harvest pressure in one age class would lead to the largest reduction in population growth rate if it occurs for the adult segment of the population.

The first winter survival rate (S_1) contributed most to the variation in λ. The AE coefficient of S_1 was, for instance, about 10 times the AE coefficient of the fecundity of 1.5-year-old females.

Possible consequences of a biased sex-ratio

For low values of male mortality rates, the annual multiplication rate was at its maximum value (λ = 1.05), because the number of males was not limiting (Fig. 5). The current level of mortality of males (0.45) would lead to a reduction in population growth rate if the threshold was below five females per male

Table 2. Coefficient of variation (CV), elasticity of the annual multiplication rate and actual elasticity coefficient (AE) for female demographic parameters: S_0 is survival from 0.5 to 1.5 years of age, S_1 from 1.5 to 2.5 years, S_2 from 2.5 to 3.5 years and S_3 from 3.5 years of age and onwards. F_1 and F_2 refer to fecundity of 1.5 and ≥ 2.5-year-old females, respectively.

	Demographic parameter					
Senario	S_0	S_1	S_2	S_3	F_1	F_2
Potential dynamics						
CV	0	0.188	0	0	0.101	0
Elasticity	0.16	0.16	0.14	0.54	0.025	0.14
AE coefficient	0	0.0301	0	0	0.0025	0
Actual dynamics						
CV	0	0.141	0.025	0.024	0.101	0
Elasticity	0.17	0.17	0.19	0.51	0.030	0.14
AE coefficient	0	0.0240	0.0048	0.0122	0.0030	0

≥ 3.5 years of age or three females per male ≥ 2.5 years of age. The observed sex ratio values were 7.4 and 3.9 females per male 3.5 years of age and ≥ 2.5 years of age, respectively, without reducing calving rates. In this population, threshold values are therefore either equal to or above the observed values. In case these values should correspond to threshold values, the hunting pressure of males could increase without reducing the population growth rate. Assuming a threshold of four females per male ≥ 2.5 years of age and that 2.5-year-old males participate in the rut, the hunting pressure could be increased by more than 15%. Assuming a threshold of 7.5 females per male ≥ 3.5 years of age and that males 2.5 years old would not participate in the rut, the hunting pressure could be increased by about 7% (see Fig. 5).

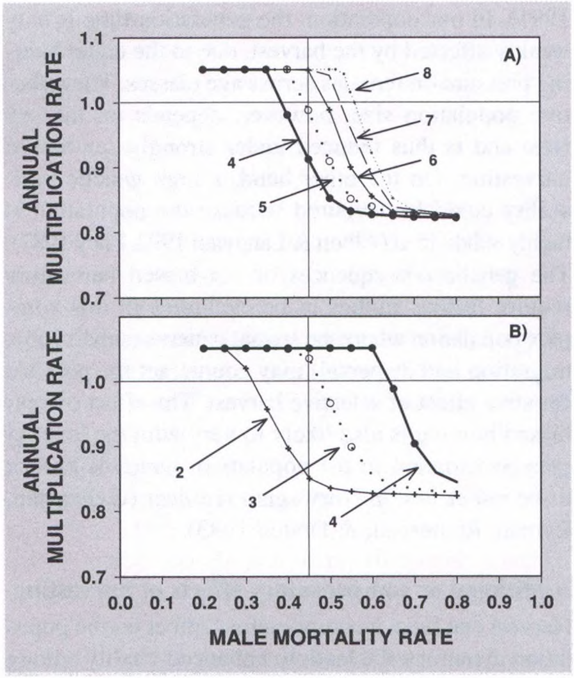

Figure 5. Annual multiplication rate of the population according to male mortality rates with different threshold values, i.e. maximum number of females that a male can mate with during a breeding season. Arrows and numbers indicate the threshold value used for each curve; A) threshold calculated as the number of females per males ≥ 3.5 years old; B) threshold calculated as the number of females per male ≥ 2.5 years old.

Discussion

The above evaluation of the impact of hunting on multiplication rate, age and sex structure of a red deer population included figures for natural mortality, reproductive performance and the probability of being harvested that have been estimated elsewhere (Langvatn et al. 1996, Loison & Langvatn 1998). Although no information about population size was available, we could evaluate the percentage of the production culled through the annual harvest. In agreement with previous studies, we found that including stochasticity in the demographic parameters had a limited impact on the annual multiplication rate (Benton, Grant & Clutton-Brock 1995, Dixon, Friday, Ang, Heppell & Kshaitriya 1997). In the following, we discuss the usefullness of the 'potential dynamics' scenario, and possible consequences of sex-biased harvesting on the demographic processes of the population.

Comparing current demographic processes with and without hunting: insights and limitations

Our study population has been hunted for more than 30 years. Therefore, demographic processes operating in our population are those of a population maintained at a relatively low density and slow growth rate. If the population was not hunted and was growing at the rate determined by natural demographic parameters alone, it could increase much faster, and demographic processes would rapidly change. Indeed, previous studies have shown that density-dependence was gradual and common in red deer population reaching high densities (Clutton-Brock Albon & Guinness 1985,1987, Coulson, Albon, Guinness, Pemberton & Clutton-Brock 1997, Singer, Hartings, Symonds & Coughenour 1997). Among the main expected response to density would be reduced male survival, decreasing calving rates, delayed age at maturity and lower calf winter survival (Clutton-Brock et al. 1987). In our case, the use of the 'potential dynamics' scenarios is therefore restricted to ranges of density below which density-dependence responses arise and mainly serves as a reference point to quantitatively assess the current impact of hunting on the dynamics of the population.

The multiplication rate obtained with the natural demographic parameters ('potential dynamics' scenario) would lead to a population increase of about 16% per year. This is lower than the maximum rate of increase found for wapiti under favourable conditions (Gogan & Barrett 1987, McCorquodale, Eberhardt, Eberhardt, Tiller & Cadwell 1996), which have the potential for increasing by more than 30% every year. However, the latter value implies adult survival rates of 0.98, which are above the natural survival rates observed in Norway, even at low density. Differences in winter conditions and/or population density may explain the differences in these adult survival rates.

Possible consequences of the sex-biased population structure

Harvest obviously changes the age structure and the sex ratio of our study population, which in turn may have complex consequences for the population's dynamics (Caughley 1977, Ginsberg & Milner-Gulland 1994, Clutton-Brock & Lonergan 1994, Lindström 1998). The consequences may depend on the mating system, the timing and synchrony of oestrus, the age of males and the sensitivity of male survival rate to male and/or female density. A too high number of females per male during the rutting season may lead to a decrease in productivity of the population through a decrease in pregnancy rates and/or a delay in parturition (Noyes et al. 1996). In red deer and elk *Alces alces*, the natural sex-ratio appears to be between 1.5 and 2 females per male (Clutton-Brock et al. 1982, Clutton-Brock & Lonergan 1994), but a bias as high as five females per male have not been found to affect pregnancy rate (Pemberton et al. 1992, Squibb 1985), unless most of the males are too young (Noyes et al. 1997). In our population, the sex ratio including all males over 2.5 years of age lies within the range where no effect on the pregnancy rate is expected (approximately 3.5 females per male), and accordingly, high reproductive performance of females was found in our study population (Langvatn et al. 1996). Further studies are nevertheless required to investigate whether the age structure of the male segment may affect the timing and synchrony of birth, which may be of extreme importance for calf survival at this high latitude (Rutberg 1987).

Although available data suggested that the sex-biased culling had no impact on the natural demographic processes, theoretical models suggest that sex-biased harvesting may lead to complex dynamics in polygynous species when associated with sex specific survival and density dependence (Lindström & Kokko 1998). In addition, it could reduce the effective population size and the generation time (Ryman, Baccus, Reuterwall & Smith 1981) which is related to the amount of genetic variation. Selective harvesting has been shown to modify the allele frequencies in a French population of red deer (Hartl, Lang, Klein & Willing 1991). In our population, the generation time is only weakly affected by the harvest, due to the equal hunting pressure on females across age classes. The effective population size, however, depends on the sex ratio and is thus reduced under strongly sex-biased harvesting. On the other hand, a high genetic variability could be favoured because the population is highly subdivided (Albon & Langvatn 1992, Lacy 1987). The genetic consequences of sex-biased harvesting require further studies to be evaluated in this complex population where the spatial patterns (subdivision, migration and dispersal) may counteract the possible negative effect of selective harvest. The effect of sex-biased hunting is also likely to vary with the level of genetic variation in the population, which is known to be rather low in Norwegian red deer (Gyllensten, Ryman, Reuterwall & Dratch 1983).

Additional or compensatory effects of harvesting

Harvest can have a compensatory effect on the population dynamics if it leads to enhanced vitality among individuals and reduction in natural mortality, and/or increased reproductive performance (Williams, Johnson & Wilkins 1996). Otherwise, hunting mortality is additive to natural mortality. In our population, no effects of density on survival rates and reproductive performance have been demonstrated. Rather, the population appears to be currently limited by stochastic fluctuation in recruitment parameters (juvenile survival and age at first breeding, Langvatn et al. 1996, Loison & Langvatn 1998). Therefore, it is reasonable to conclude that harvest is additive to natural mortality and does not have any direct positive consequence on demographic parameters with the current densities of red deer. However, if harvesting maintains a sex ratio that reduces inter male competition, a possible compensatory effect of hunting could act through an increase in male survival rates with an ultimate effect on sex and age structure.

Temporal stochasticity and management strategies for red deer in Norway

The present level of harvesting in our study population does not seem to pose any threats to the population future viability and productivity, even when stochasticity of demographic parameters is added into the analysing models. In addition, we did not find any evidence of negative effects of sex-biased harvest at its current level on the reproductive performance of females. Our investigation of the relationships between growth rate, male mortality and bias in sex ratio allowed us to determine a lower limit for bias of sex ratio that does not lead to a reduced population growth rate and to predict levels of mortality rates that could be sustained in the population.

Wildlife managers may aim at optimising the number of individuals culled (Sylvén 1995), the amount of meat produced (Fairall 1985, Sylvén 1995), the number of adult stags which can be culled (Clutton-Brock & Lonergan 1994, Buckland, Ahmadi, Staines, Gordon & Youngson 1996) or the size of trophies (Jorgenson, Festa-Bianchet & Wishart 1993). However, such strategies should acknowledge constraints like acceptable population size, population demography, viability and the objective of long-term sustainability (Getz & Haight 1989, Sæther, Engen & Lande 1996). To be able to determine the 'best' harvesting strategies, the first step is to obtain information about the demographic patterns of the population. In the case of the red deer in Norway, this study is a preliminary analysis of information which can allow future optimisation of management strategies.

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