Moose harvesting strategies in the presence of wolves

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Summary

1. Large carnivores are currently recolonizing areas where they have been extinct for decades. This poses considerable challenges for wildlife managers, partly because the optimal harvesting strategies of prey populations may be affected. If the carnivores in such areas are under strict management control (as in Scandinavia), the predator will not show a numerical response to changes in prey density. Consequently, the density of prey is mainly determined by the vital rates of the prey population and the predation pressure. In this study we modelled the optimal harvesting strategy for a prey population in which there was no numerical response by the predator.

2. Our model is an age-structured deterministic matrix model system. Optimal harvesting strategies are determined, measuring yield either as number of animals harvested or as mass of meat.

3. First, using a moose population in Hedmark in south-eastern Norway as a case study, we demonstrate that continuing to harvest at the rates used prior to wolf recolonization will lead to a decline in the moose population.

4. Secondly, harvesting quotas are specified by age and sex, usually with a high proportion of calves. Although wolves mainly kill juvenile moose (calves and yearlings), the relationship between harvest composition and yield is not affected by predation. Both in the presence and absence of predation, a high proportion of calves in the harvest gives the highest yield measured as the number of animals harvested, whereas a high proportion of adults maximizes the yield measured in terms of meat. Furthermore, a female-biased sex structure in the population gives a higher yield in both the presence and absence of the predator.

5. *Synthesis and applications.* We have shown that managers facing the new challenges presented by recolonizing populations of large predators such as wolves should reduce the size of harvest quotas in order to avoid decreases in prey populations. However, the general relationship between the harvesting strategy and yield maximization is not affected by wolf predation. The harvest yield from cervid populations is often important to local economies, and moose is the single most important game species in Scandinavia. It is therefore important to implement optimal harvesting strategies under these new conditions in order to prevent an unnecessary loss of yield, and success in this task may in turn affect local attitudes towards large carnivores.

Key-words: matrix models, population dynamics, recolonization, Scandinavia, wolf

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Introduction

Ungulate population dynamics may be influenced by the combined effects of predation (Vucetich, Peterson & Schaefer 2002), human exploitation (Solberg *et al.* 1999; Ericsson & Wallin 2001; Coulson *et al.* 2004),

density-dependent food limitation (Fowler 1987; Gaillard *et al.* 2000) and stochastic environmental factors (Sæther 1997; Georgiadis, Hack & Turpin 2003; Stenseth *et al.* 2004). The relative magnitude of the different mortality factors typically varies both spatially (Linnell, Aanes & Andersen 1995) and temporarily (Solberg *et al.* 2000; Coulson *et al.* 2001; Gula 2004; Smith *et al.* 2004). As large carnivores recolonize areas where they have been extinct for decades, such as the wolf *Canis lupus* (L.) in Yellowstone, USA (Ripple & Beschta 2002), and on the Scandinavian Peninsula (Wabakken *et al.* 2001), the potential effects of predation on the size of the surplus available for human exploitation present an intriguing question both for population biologists and wildlife managers. Although Errington (1946) stated that predation only removed a 'doomed surplus', published studies of the causes and levels of ungulate neonatal mortality show that juvenile mortality is typically higher in areas where predators are present (Linnell, Aanes & Andersen 1995; Hayes *et al.* 2000). This suggests that it might be necessary for managers to adjust harvesting quotas in areas with recolonizing carnivores.

In predator–prey relationships there is usually a feedback between the predator population size and the prey population size. The dynamics of these systems are generally determined by the growth rate of the herbivore population, and the functional and numerical response of the predator (Messier 1994). However, in areas with colonizing carnivore populations or carnivore populations under strict management control, the relationship will appear less interactive (i.e. the wolves are not able to respond numerically to variation in the prey population). In such areas the relationship will be determined mainly by the vital rates of the prey population and the predation pressure, without involving a numerically responding predator population. The Scandinavia wolf population is strictly controlled by management at a size far below the ecological capacity (Lande *et al.* 2003), and might as a result serve as an example of such a scenario. In this Scandinavian system the interaction between the wolf and its main prey, the moose *Alces alces* (L.), does not involve a numerical response to moose density under current political conditions. Rather, the local predation pressure on moose is determined by the presence or absence of a wolf pack and the size of the pack, both of which are at least partly determined by the carnivore management policy.

Because of sex and age dependency in mortality (Ericsson & Wallin 2001) and reproduction (Clutton-Brock, Guinness & Albon 1982; Ericsson *et al.* 2001) in ungulates, the age and sex composition of the harvest plays a crucial role in maximizing the yield (Sæther, Engen & Solberg 2001; Clutton-Brock *et al.* 2002). Currently there is general agreement on how to maximize the annual yield when large predators are absent, based both on deterministic (Sylvèn 1995) and stochastic (Sæther, Engen & Solberg 2001; Clutton-Brock *et al.* 2002) modelling studies. Generally, in harvesting regimes aiming to maximize the numbers of animals harvested, the harvest is dominated by calves and males (Sylvèn 1995; Solberg *et al.* 1999; Sæther, Engen & Solberg 2001), whereas a higher proportion of adults in the harvest is necessary to maximize the yield of meat (Sylvèn 1995). Furthermore, female-biased populations tend to give the highest yields (Caughley 1977; Cederlund & Sand 1991; Sylvèn 1995; Sæther, Engen & Solberg 2001; but see Clutton-Brock *et al.* 2002 in the case of trophy hunting). In contrast, very few studies have examined the combined effects of harvesting and predation. If predation acts mainly additively (Linnell, Aanes & Andersen 1995), a lower yield should be expected from the harvest when a predator is present than when it is not. However, little is known about how the age- and sex-specific harvest should be changed in the presence of a predator (Solberg *et al.* 2003).

We investigated the effects of a recolonizing predator under strict management control on a harvested ungulate population. More specifically, we examined the management implications of an early stage of wolf recolonization in Scandinavia on the optimal moose harvesting regime. Based on demographic parameters from Scandinavian moose populations and within the range of wolf kill rates reported in some recent empirical studies, we used age- and sex-structured matrix population models to explore the potential effect of wolf predation on a local moose population. First, we examined the consequences of continuing the harvest regime applied before the wolf recolonization. Secondly, we examined how the optimal composition of the harvest is affected by predation, and how this relates to the sex ratio and population size of the prey population. We did this for two measures of yield: the total number of individuals harvested and the total mass of meat.

Methods

THE SOCIO-ECOLOGICAL SYSTEM

The annual harvest of moose in Norway is around 35 000–40 000 individuals, with an estimated value of US$ 70–90 million (Storaas *et al.* 2001; Statistics Norway 2004), making it the most economically important game species. Natural mortality of moose is low (Sæther *et al.* 1996; Stubsjoen *et al.* 2000; Ericsson & Wallin 2001) and, because of the near absence of large carnivores for more than a century, most moose populations in Norway are strongly structured by human harvesting (Solberg *et al.* 1999, 2000; Stubsjoen *et al.* 2000). However, the situation where humans are the only major predator of wild ungulates in Norwegian forests is currently changing (Wabakken *et al.* 2001).

Persecution almost eradicated the wolf from Norway and Sweden in the late 19th and early 20th centuries, but since becoming protected by law in the 1970s there has been an increase in the population size of wolves (Wabakken *et al.* 2001). In Scandinavia, moose is the

main prey of wolves (Sand *et al.* 2005) and as a result the re-establishment of wolves in Norway is causing controversy. Consequently, there is an urgent need for scientifically based management plans. The size of the wolf population in Norway is strictly controlled, and occasionally managers decide to remove 'problem' individuals [mainly those taking domestic sheep *Ovis aries* (L.)] or even an entire pack. The current management aim is three breeding packs in Norway (Miljøverndepartementet 2004).

POPULATION MODEL

Ungulate populations are typically strongly structured according to age and sex (Gaillard, Festa-Bianchet & Yoccoz 1998), and consequently the dynamics are best explained when including age- and sex-specific vital rates. Population models based on matrix algebra (Caughley 1977; Caswell 2001) are well suited to studying how changes in demographic traits affect ungulate population growth rates. In these models, the starting point is a certain number of individuals in each age and sex class in the first year. The individuals are then transferred to the next class by rates defined by the elements of a transition matrix (Caswell 2001), representing age- and sex-specific birth and survival rates. The vector N_t is the number of individuals in the different age and sex classes at time t, and A_n is a population projection matrix, known as the Leslie matrix (Leslie 1945). A density-dependent matrix model in discrete time can be written as:

$$\vec{N}_{t+1} = A_n \vec{N}_t \qquad \text{eqn 1}$$

We consider three distinct time periods within a year: a summer period with neonatal mortality and predation, a harvesting period during autumn, and a winter period with natural non-predation mortality and predation. At the end of the winter, the females reproduce and individuals are moved from one age class to the next. We use an age- and sex-structured matrix with 16 age classes for each sex, where the last age class is a self-absorbing class for the older individuals (15+). For notational simplicity, this will be illustrated with only two age and sex classes, where $N_{t,0,f}$ and $N_{t,0,m}$ are the number of female and male calves at time t, respectively, and $N_{t,15+,f}$ and $N_{t,15+,m}$ are the number of females and males in age class 15+ at time t, and so on. The population vector N_t can thus be written as a matrix vector:

$$\vec{N}_t = \begin{bmatrix} N_{t,0,f} \\ N_{t,0,m} \\ . \\ . \\ . \\ N_{t,15+f} \\ N_{t,15+m} \end{bmatrix} \qquad \text{eqn 2}$$

We then write $A_n^{(\cdot)}$ for the season-specific Leslie matrix. The matrix entries are given by R_i, the age-specific fecundity, and $S_{(i,\text{sex})}^{(\cdot)}$, the season-, sex- and age-specific

survival. As no reproduction occurs during the summer and autumn seasons, these transition matrices only include survival probabilities on the diagonal:

$$A^{(\cdot)} = \begin{bmatrix} S_{(0,f)}^{(\cdot)} & 0 & . & . & 0 & 0 \\ 0 & S_{(0,m)}^{(\cdot)} & . & . & 0 & 0 \\ . & . & . & . & . & . \\ . & . & . & . & . & . \\ 0 & 0 & . & . & S_{(15+,f)}^{(\cdot)} & 0 \\ 0 & 0 & . & . & 0 & S_{(15+,m)}^{(\cdot)} \end{bmatrix} \qquad \text{eqn 3}$$

As reproduction is considered to occur at the end of winter, both survival and reproduction probabilities occur in the winter transition matrix:

$$A_n^{(\text{winter})} = \begin{bmatrix} 0 & 0 & 0 & . & . & S_{(15+,f)}^{(\cdot)}R_{(15+,f)}^{(\cdot)}/2 & 0 \\ 0 & 0 & 0 & . & . & S_{(15+,f)}^{(\cdot)}R_{(15+,f)}^{(\cdot)}/2 & 0 \\ S_{(0,f)}^{(\cdot)} & 0 & 0 & . & . & 0 & 0 \\ . & . & . & . & . & & . \\ . & . & . & . & . & & . \\ 0 & 0 & 0 & . & . & S_{(15+,f)}^{(\cdot)} & 0 \\ 0 & 0 & 0 & . & . & 0 & S_{(15+,m)}^{(\cdot)} \end{bmatrix}$$

$$\text{eqn 4}$$

DEMOGRAPHIC PARAMETERS

Fecundity

Moose, in common with most other large-sized ungulates, shows age-dependent patterns in reproductive output (Ericsson *et al.* 2001; reviewed in Gaillard, Festa-Bianchet & Yoccoz 1998). In our model, the reproductive part of the population is represented by cows ≥ 2 years and < 15 years. We used published age-specific estimates from Scandinavia (Ericsson *et al.* 2001). Reproductive output has been demonstrated to show density-dependent patterns (Sand *et al.* 1996; Ferguson, Bisset & Messier 2000), while Solberg *et al.* (2002) showed that in populations with a severely female-biased sex ratio the pregnancy rates among young females are reduced.

Let R_i be the age-specific fecundity, and r_i the fecundity rate at low population densities, when no crowding effects are acting, for age class i. To account for the density effect in reproduction, we used a density-dependence function suggested by Maynard Smith & Slatkin (1973) (i.e. a sigmoidal curve with an increasing degree of density dependence at high densities). Although the shape of the density dependence relationship in moose is poorly understood, empirical data suggest that the effect is rather moderate at a range of densities, but becomes quite strong once reaching a threshold. Consequently, the fecundity function for the prime-aged classes can be written:

$$R_i = \frac{r_i}{1 + (n/K)^b} \quad \text{when } i = 3\text{–}14 \qquad \text{eqn 5}$$

where *n* is the total population size, *K* is the inflection point in the function and *b* is the slope.

To adjust for the effect of the sex ratio on the pregnancy rates of young females, we multiply the reproduction function by $1 - \exp(-\gamma s)$ for the two youngest reproductive age classes (Sæther, Engen & Solberg 2001), where *s* is the number of mature males (≥ 2 years) divided by the numbers of sexually mature females ($1 \leq i < 15+$). The fecundity function for the second and third age classes can then be written:

$$R_i = \left[\frac{r_i}{1 + (n/K)^b} \right] (1 - \exp(-\gamma s)) \quad \text{when } i = 1-2 \qquad \text{eqn 6}$$

Mortality

For calves, we include two aspects of non-harvest natural mortality: neonatal mortality in summer and over-winter mortality (Stubsjoen *et al.* 2000). Although Eberhardt (2002) suggested that juvenile survival should be the first trait to be affected by density, the extensive review by Gaillard *et al.* (2000) suggested that, for the larger herbivores (> 50 kg, such as moose), primiparous fecundity may be more sensitive to density. There is no evidence for density dependence in juvenile survival in Scandinavian moose populations; indeed juvenile survival is very high (Ericsson 1999; Stubsjoen *et al.* 2000). Consequently, both summer and winter survival are unaffected by density in our model. In adults, non-predation natural mortality of large ungulates is generally low (reviewed by Gaillard, Festa-Bianchet & Yoccoz 1998; for Scandinavian moose, Stubsjoen *et al.* 2000; Ericsson & Wallin 2001) and there is little evidence that adult moose survival is affected by density within the range of densities observed in Scandinavia. Indeed, of all demographic parameters this component is generally the least affected by density (Gaillard, Festa-Bianchet & Yoccoz 1998; Eberhardt 2002; Festa-Bianchet, Gaillard & Cote 2003). We used estimates of adult moose winter mortality based on empirical data from Koppang, in Hedmark, eastern Norway (Gundersen 2003).

Wolf predation on moose is primarily focused on calves, yearlings and older females, with calves accounting for the bulk of the wolf kills (Gundersen 2003; Sand *et al.* 2005). We therefore restrict wolf predation to calves, yearlings and females of the oldest age class (15+ years) and allow the proportion of these classes in the kill to be proportional to their availability in the population. The functional response of the wolf to increasing moose densities has been a controversial topic (Messier 1994; Eberhardt 1997; Marshal & Boutin 1999; Hayes *et al.* 2000). However, this debate has mainly focused on the response at low moose densities. At medium to high moose densities, all studies seems to support the view that the kill rates are relatively unaffected by moose density. As we ran the model under predetermined management goals with medium to high moose densities (see below), the actual shape of the functional response at low moose densities does not affect our results. If we write α for the total number of moose killed in one season, the predation rate can then be expressed as:

$$P_i = 1 - \exp(-\alpha/\Sigma \, n_i) \quad \text{when } i = 0, 1 \quad \text{and } 15_{+f} \qquad \text{eqn 7}$$

The parameters and symbol values included in the population model are summarized in the Appendix and Table 1, respectively.

Although few studies have reported wolf kill rates of moose from Scandinavia, some recent studies by Sand *et al.* (2005) and Gundersen (2003) suggest that Scandinavian wolf kill rates may be considerably higher than most of those reported from North America. For instance, Sand *et al.* (2005) found a mean of 3·6–4·8 days between moose kills (i.e. 27·8–20·8 moose killed 100 days^{-1}) during winter with a mean wolf pack size of 3·3, while Gundersen (2003) estimated a total loss of 80–120 moose year^{-1}. The variation between sites and years may be caused by pack size (Hayes *et al.* 2000), snow conditions (Post *et al.* 1999) and methodology (Gundersen 2003; Sand *et al.* 2005). By allowing different levels of α in our model, we investigated the effects of different predation levels (Table 2). As we assumed the winter to be twice the length of the summer, we multiplied α by 2 in the winter predation expression (see Appendix 1 and Table 2).

Harvesting

Harvesting was simulated by applying the Norwegian quota system, whereby quotas are assigned for either calves, cows (≥ 1 year) or bulls (≥ 1 year) (Solberg *et al.* 1999). We assume that the population size is known, and that the quotas assigned are actually harvested (i.e. hunting success equals 100%). Typically, more than 85% of the quota is harvested across Norway, with an even higher percentage taken in most of the countries now recolonized by wolves (Statistics Norway 2004). We write h_c, h_f and h_m for the harvesting rates for calves, females and males, respectively. We calculate the annual yield based on the pre-harvest population size (i.e. after summer mortality). Consequently, the total annual harvest is $\Sigma \, n_i h_i$, summed across all age and sex classes, where n_i is the pre-harvest population size of age class *i*.

POPULATION TRAJECTORIES

To evaluate whether the current harvesting regime in Scandinavia could be sustained in the presence of wolves, we ran the model with the harvesting rates reported from the Koppang area (Gundersen 2003). A wolf pack settled in this area in 1997, utilizing *c.* 600 km^2, with about 600–800 moose inside the wolf territory (Gundersen 2003). The demographic rates of the Koppang moose population are well known, and closely approximate those in our model (Gundersen 2003). However, estimates of wolf predation rates for the area vary widely between years and method of estimation (Gundersen 2003). We therefore ran the model with

Table 1. Definitions and parameter values in the population model

Parameter	Symbol	Age class	Value	
Reproduction				
Intercept of the age-specific reproduction function*	r_i	$i = 1$	0·1	
		$i = 2$	0·8	
		$i = 3, 4$	1·0	
		$i = 5, 6 \ldots 10, 11$	1·3	
		$i = 12, 13, 14$	1·1	
		$i = 15+$	0·0	
Coefficient in the reproduction function	b	$i = 1, 2 \ldots 13, 14$	3	
Population size at which R_i is half of r_i	K	$i = 3, 4 \ldots 14, 15$	2000–3000–4000	
		$i = 1, 2$	1/3 of the value for $i = 3, 4 \ldots 13, 14$	
Constant in the sex ratio expression	γ	$i = 1, 2$	10·0	
			Females	Males
Non-predation mortality				
Summer mortality†	$q_{\mathrm{summer},i,\mathrm{sex}}$	$i = 0$	0·10	0·10
		$i > 0$	0·00	0·00
Winter mortality	$q_{\mathrm{winter},i,\mathrm{sex}}$	$i = 0, 1 \ldots 8, 9$	0·05	0·05
		$i = 10, 11, 12, 13$	0·10	0·10
		$i = 15+$	0·50	0·50
Predation				
	α	$i = 0, 1$	0–20–40	0–20–40
		$i = 15+$	0–20–40	
Carcass mass‡	$C_{i,\mathrm{sex}}$	$i = 0$	71	74
		$i = 1$	143	149
		$i = 2$	174	187
		$i = 3, 4 \ldots 14, 15+$	183	240

*Numerical values based on Ericsson *et al.* (2001).
†Numerical values based on Stubsjoen *et al.* (2000).
‡Numerical values based on Solberg *et al.* (1997).

Table 2. Different levels of predation used in the simulations. The α-level refers to the total number of animals killed by the wolf pack in one time step. In winter, α is multiplied by 2 in the predation expression to account for the longer duration of the winter. Consequently, a maximum of three times α is killed in 1 year. Note that empirical estimates of predation rates from Scandinavia are higher than those reported from North American studies (see text)

Predation level	α-level	Numbers of animals killed year^{-1}
No predation	0	0
Low predation	20	60
High predation	40	120

different levels of predation, within the range reported from these studies (Table 2).

SENSITIVITY TO THE PROPERTIES OF THE MODEL

We developed the simulation model to assess the consequences of wolf predation on moose harvesting strategies. We used numerical examination to identify population performances at different harvesting strategies under different predetermined management goals. As most moose populations in Scandinavia are considered to be below the ecological carrying capacity (if this even exists for moose; Peterson 1999), with very little natural mortality, management goals were chosen that kept the population within predetermined limits of operational

sex ratio and population size. We assumed an area of *c.* 1000 km², as this is approximately the mean size of a wolf territory in Scandinavia. The baseline population size was 1000 moose (i.e. 1·0 moose km^{-2}) and the baseline sex ratio was 1 : 2 (one male to two females), which is close to the mean in Scandinavia (Hörnberg 2001; Solberg *et al.* 2005). However, we also evaluated the effects of changing the sex ratio and population size. The baseline predation level was low predation (cf. Table 2), but we also ran the model with a high level of predation. Finally, we evaluated the robustness of the results to changes in the strength of density dependence of reproduction.

To reach the predetermined management goals regarding sex ratio and population size, each cow harvest rate had to be combined with a specific calf and bull harvest rate. In the programme we first selected the cow harvest rate and then searched for the corresponding calf and bull harvest rate necessary to reach the predetermined management goal. When we had found the combination of harvesting rates that met the management goals, we measured the yield in a single year. The yield was measured as total mass of meat (Table 1) but we also compared this with the total number of animals harvested.

Results

POPULATION TRAJECTORIES

Our simulations clearly demonstrated that wolf predation negatively affected the population trajectories of a

Table 3. Stable (+) and unstable (–) equilibrium points under different conditions

	Sex ratio	K = 2000			K = 3000			K = 4000		
		1 : 4	1 : 2	1 : 1	1 : 4	1 : 2	1 : 1	1 : 4	1 : 2	1 : 1
n = 500	α = 0	+	+	+	+	+	+	+	+	+
	α = 20	–	–	–	–	–	–	–	–	–
	α = 40	–	–	–	–	–	–	–	–	–
n = 1000	α = 0	+	+	+	+	+	+	+	+	+
	α = 20	+	+	+	–	–	–	–	–	–
	α = 40	–	–	–	–	–	–	–	–	–
n = 1500	α = 0	+	+	+	+	+	+	+	+	+
	α = 20	+	+	+	+	+	+	+	+	–
	α = 40	+	+	+	+	+	–	–	–	–

moose population if subjected to the same harvesting regime as prior to the wolf recolonization (Fig. 1). In the absence of wolf predation, all populations increased except when a starting population size of 1200 moose was combined with strong density-dependent reproduction. In this case the population size was stable. However, in the presence of wolves all populations decreased in size, with a steeper decline under higher predation pressure. This pattern occurred regardless of the starting population size or strength of density dependence, although with a low predation level and weak density dependence ($K = 3000$) the decline was very slight.

SENSITIVITY TO THE PROPERTIES OF THE MODEL

A high proportion of calves in the harvest gave the highest yield measured as the number of animals harvested, whereas a high proportion of adults in the harvest gave the highest yield of meat (Fig. 2). This finding was general, regardless of the presence and absence of predation, and did not change as predation pressure, strength of the density dependence, target sex ratio or target population size varied. When predation was included in the model the calf harvest rate corresponding to a given cow harvest rate was lower, whereas the bull harvest rate for a given cow harvest was unaffected (Fig. 3a). This reduction in the calf harvest rate for a given cow harvest rate consequently led to a reduction in the total yield (Fig. 3b). The level of predation (high and low; Table 3) affected the calf harvest rate corresponding to a given cow harvest rate, but did not affect the functional form of the relationships.

As moose density increased, the proportional reduction in the yield following the introduction of the predator decreased (Fig. 4). Also, the proportional loss from the harvest was lower when the sex ratio was more female biased. Our findings did not appear to be very sensitive to the strength of the density dependence, as varying K from 2000 to 4000 did not change the functional form of the relationships. Furthermore, changing the target sex ratio did not affect the shape of the relationship between cow and calf harvests necessary to reach the predetermined management goal (Fig. 5a,b).

When predation was not included in the model, the sex ratio did not affect the size of the calf harvest that had to be combined with a given cow harvest rate to reach the management goal. In contrast, when we ran the model with predation, the calf harvest rate for a given cow harvest also had to be changed when the target sex ratio was changed. In general, a more female-biased population allowed for a higher calf harvest rate at a given cow harvest rate. Both in the absence (Fig. 5b) and presence (Fig. 5d) of predators, a more female-biased population gave a higher yield.

Predation also affected the stability of the system. In situations without predation, all combinations of target sex ratios and populations sizes could be met, whereas in situations with predation many of the combinations were unstable (Table 3). In the unstable combinations, a small change in the harvesting rates would lead the population far from the predetermined management goals. Generally, instability increased both when the level of predation increased and when the strength of the density dependence decreased (i.e. increasing K-value), whereas at higher population sizes and in populations with more female-biased sex ratios, populations were more stable.

Discussion

Our simulations demonstrate that if managers do not adjust the size of their harvest in areas where large predators are recolonizing, then ungulate populations will decline. This is not surprising, given that wolf predation acts as a significant and mainly additive mortality factor where present. However, the composition of the harvest in terms of sex and age need not change. Both in the presence and absence of predation, there was an inverse relationship between the number of animals harvested and the yield measured by the mass of the meat for a given combination of sex ratio and population size. This is because harvesting strategies that yield a high number of animals must contain a large proportion of calves. In moose, an adult male weighs about three times that of a calf. In line with this, Sylvèn (1995) found that maximizing the number of animals harvested required a large proportion of calves in the
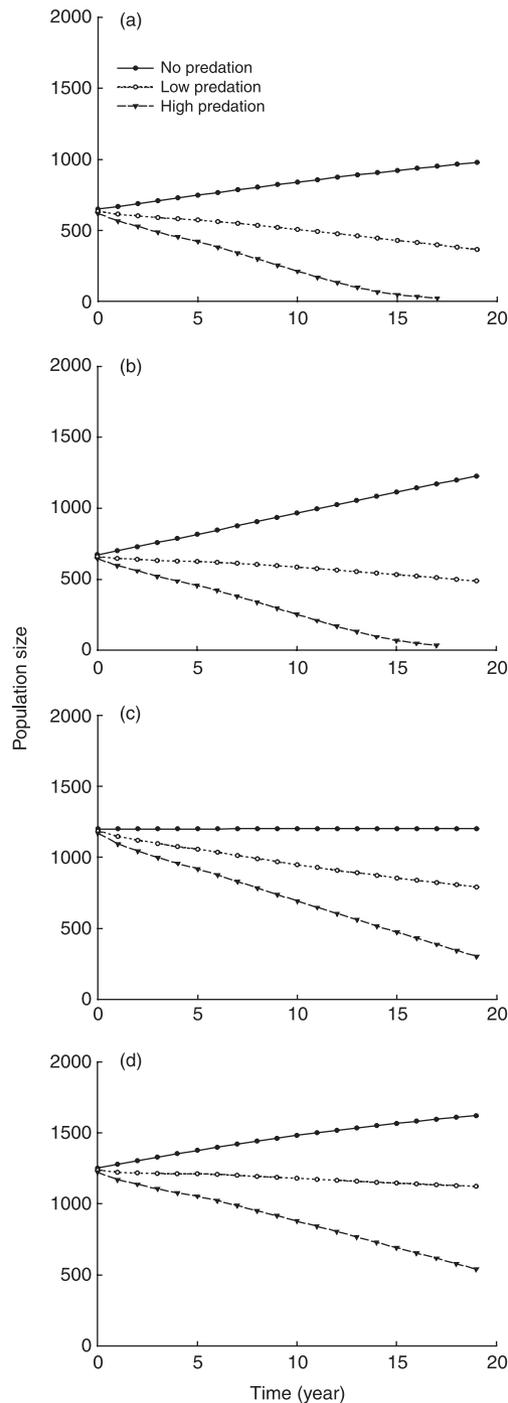
Fig. 1. Population trajectories under different predation pressures with harvesting rates of 11% for cows, 18% for calves and 28% for bulls (Gundersen 2003). In (a) and (c) we assume strong density dependence ($K = 2000$), with starting population sizes of 600 (a) and 1200 (c) individuals, respectively. In (b) and (d), we assume weaker density dependence ($K = 3000$), again with starting population sizes of 600 (b) and 1200 (d) individuals, respectively.

Fig. 2. In (a) the proportion of calves in the harvest is plotted against the cow harvest rate; (b) shows the relationship between the yield measured as meat and the yield measured as number of animals harvested. The relationship is shown in a case without predation (the upper line in both cases) and with predation (the lower line in both cases). Population size is 1000, sex ratio 1 : 2, $K = 2000$ and $\alpha = 0$ and 20, respectively.

harvest (82%) compared with that required to maximize the yield of meat (28%). However, few studies have evaluated how the harvesting strategies, in terms of sex and age structure of the harvest, must be changed in the presence of predators. Most studies from North America that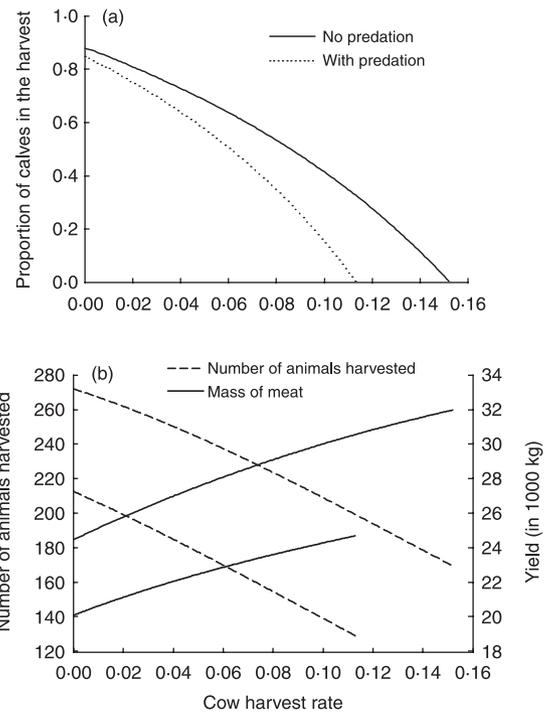 focus on wolf–moose population dynamics have excluded harvesting (Messier 1994), whereas the harvesting models developed in Scandinavia have examined situations without wolves (Sylvèn 1995; Sæther, Engen & Solberg 2001). We have demonstrated for the first time that the general relationships between the age and sex composition of the harvest and yield, in terms of animals harvested or mass of the meat, are similar both in the presence and absence of predation. Consequently, a high proportion of calves in the harvest gives the highest yield measured as the number of animals harvested, whereas a high proportion of adults in the harvest gives the highest yield of meat, regardless of predation.

Overexploitation is a common cause of population decline and species extinction (Groomberg 1992), and it is crucial that knowledge about the ecology of the species (Marboutin *et al.* 2003; Stephens *et al.* 2003) as well as the environment that the species inhabits (Georgiadis, Hack & Turpin 2003) is included in management plans for sustainable exploitation (Ticktin 2004). Here we have shown that the human exploitation rates of game species should be decreased when large carnivores recolonize an area, to avoid population decline. The necessity of reducing the size of the annual harvest in the presence of predation has also been demonstrated for elk *Cervus elaphus canadensis* (L.) in Yellowstone National Park, where harvest rates applied prior to wolf recolonization were no longer sustainable once the
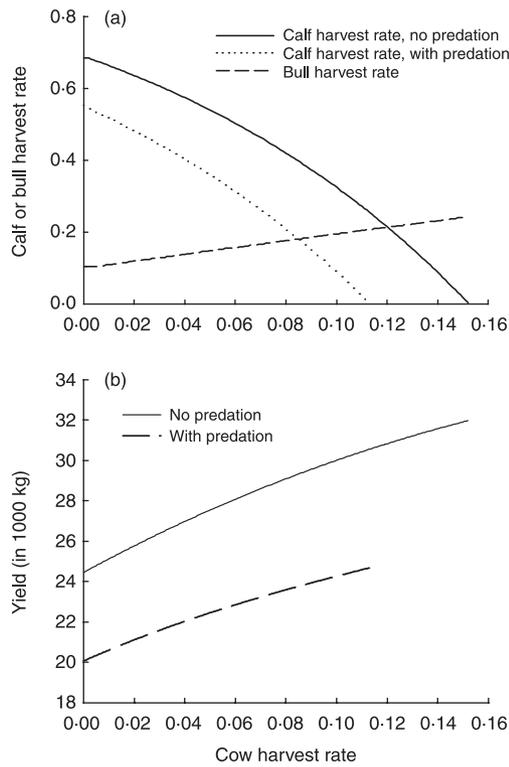
Fig. 3. In (a) the relationship between a given cow harvest and the calf harvest rate necessary to meet the predetermined management goals is given for a situation without wolf predation and with wolf predation; (b) shows the corresponding yield by combining the cow, bull and calf harvest rate from (a). Population size is 1000, sex ratio 1 : 2, $K = 2000$ and $\alpha = 0$ and 20, respectively.
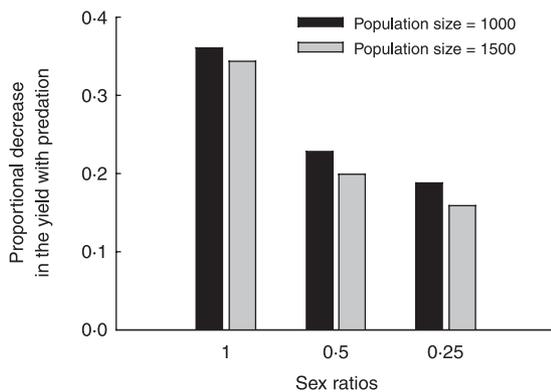

Fig. 4. Proportional reduction in the yield (measured as meat) when predation is added to the model ($K = 2000$ and $\alpha = 20$) with varying target sex ratios and population sizes.

Fig. 5. Effects of the operational sex ratio in the population. (a) and (c) show the combinations of harvesting rates that give the desired sex ratio when the model is run (a) without and (c) with predation, respectively. (b) and (d) shows the corresponding yield, (b) without and (d) with predation, respectively ($K = 2000$, $\alpha = 20$ in the case with predation).

wolf had re-established (P.J. White, R. Garrott & L. Eberhardt, unpublished). Similarly, Mech & Nelson (2000) demonstrated that white-tailed deer *Odecoileus virginianus* (L.) buck harvests were affected by wolf predation. However, in a recent review of deer–predation relationships and the effects on the harvest (Ballard *et al.* 2001), a small number of studies reported positive effects of predator removal on deer population size, but in only one of these did this increase in prey population size result in a higher harvest. The authors' main conclusion
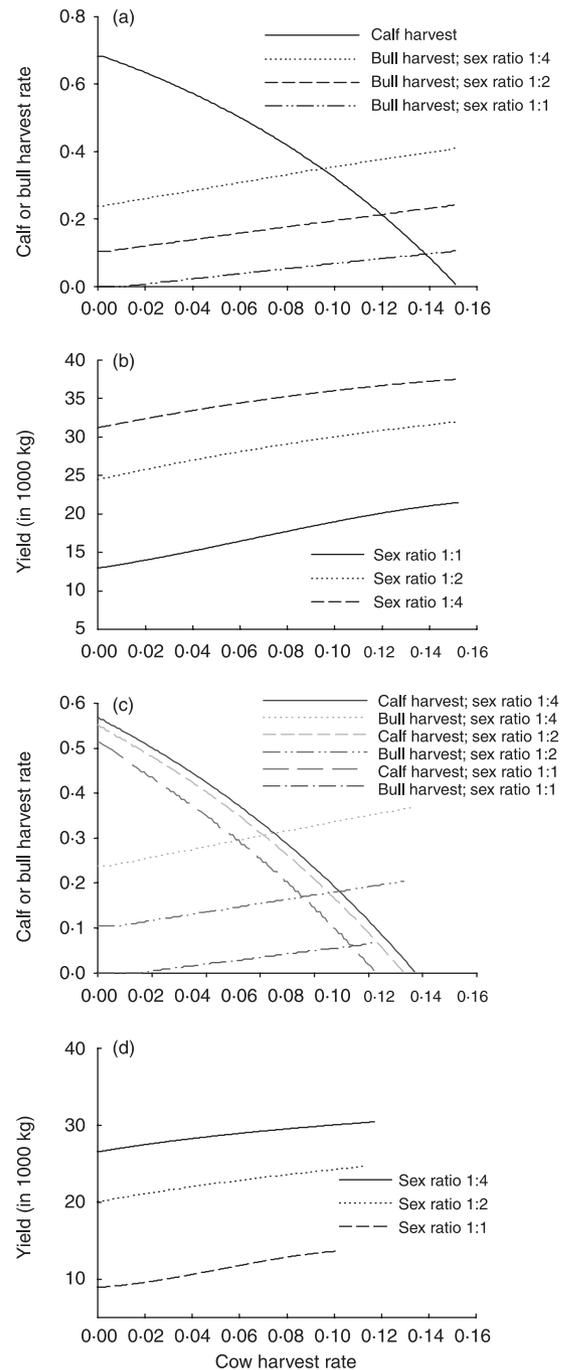
was that the deer population density in relation to habitat carrying capacity was crucial in determining the impact of predation. When the deer population was food limited at or near ecological carrying capacity, the population responded little to predator removal, as predation was mainly compensatory to other mortality factors. In Scandinavia, most moose populations are expected to be well below such densities (Hörnberg 2001).

Populations with a female-biased sex ratio were more productive regardless of population size and predation, as also shown in other studies (Caughley 1977; Sæther, Engen & Solberg 2001). This was despite the fact that females in the two youngest reproductive classes were negatively affected by a female-biased sex ratio in our model. Clutton-Brock *et al.* (2002), on the other hand, derived a very different result when modelling the optimal harvest of red deer in Scotland. Because of stronger density dependence in male survival and dispersal, a high female population density and a female-biased sex ratio will reduce the number of males in the harvest. As their aim was for trophy animals, fewer males in the harvest resulted in reduced income. In contrast, in our study the aim was to maximize the yield measured as number of animals or mass of meat (as is common in Scandinavia). Also, we are not aware of any studies indicating that survival and dispersal in male moose are more sensitive to density than in females. Consequently, the very different results are caused by differences in both the biology of the species and the socio-economical settings. However, although Solberg *et al.* (2002) found that only primiparous moose were affected by biased sex ratios, a lack of old bulls could also have consequences for the demography of the moose population (Sæther *et al.* 2004). Thus, the potential effect of males should not be ignored (Mysterud, Coulson & Stenseth 2002).

We have assumed that predation is additive, which seems to be the case at least for juveniles (Linnell, Aanes & Andersen 1995). Moose cows that lost their calves to brown bears *Ursus arctos* (L.) showed compensation by producing a larger litter the subsequent spring (Swenson, Dale & Sandegren 2001). This would only have a marginal effect on the dynamics, and as yet there is no indication that compensation occurs in the case of wolf predation (E. J. Solberg, unpublished data). This could be because wolf predation on moose is more evenly distributed throughout the year, whereas bear predation is more focused around the calving season. Furthermore, no data from Scandinavia support the view that wolves kill sick and weakened individuals (Sand *et al.* 2004). Thus, it is unlikely that the assumption of additivity biases our results. Lastly, both density-dependent and stochastic factors affect the population dynamics of large herbivores (Sæther 1997; Lande, Engen & Sæther 2003). In our simplified approach, we have not included stochasticity, but consider a range of different parameter combinations. In stochastic environments, however, the population growth rate, and therefore the potential harvestable surplus, tends to be lower than that predicted from purely deterministic models (Lande, Engen & Sæther 2003). Therefore, the harvesting rates presented in this study should be considered upper limits rather than mean values.

We have evaluated how managers can optimally adapt the harvest of a large herbivore to a situation in which a predator is recolonizing. For a given population size, the harvestable yield will always be reduced in the presence of wolves, except maybe for moose populations at or near ecological carrying capacity (Ballard *et al.* 2001; but see Peterson 1999). However, when the predator population is not allowed to respond numerically to the prey population size, the proportional reduction in the yield will be less as the herbivore population density increases, because of the functional response of the predator. Furthermore, we have shown that wolf recolonization could lead to a population decline for moose populations within a wolf territory, if the managers do not adjust the quotas accordingly. Of particular interest for the managers is that the harvesting strategies (in terms of composition of the harvest) that optimize the yield in situations without predation also optimize the yield in the presence of predators. However, the calf harvest rate corresponding to a given cow harvest rate should be reduced in the presence of predation. How much the rates must be reduced depends on the number of animals removed by the predator. So far, the estimates of wolf kill rates from Scandinavia have been quite variable between years and between different methods used to estimate the rates (Gundersen 2003; Sand *et al.* 2005).

In a situation in which a predator population is strictly regulated, the proportional effect of predation will be less profound at high population sizes, because of the functional response of the predator. The system was also more stable when kept at high population sizes, as the proportional effect of a fixed number of predators became stronger as the population size decreased. Thus, keeping a high-density female-biased moose population should be a goal for managers within wolf territories if they want to reduce the proportional loss to the wolf and manage a stable population.

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Appendix 1

Components of the population model

Parameter	Symbol	Expression	Conditions
Fecundity	R_i	$[(r_i/(1 + (n/K)^b))](1 - \exp(-\varepsilon s))$	$i = 1, 2$
		$(r_i/(1 + (n/K)^b))$	$i = 3, 4, \ldots 14, 15+$
Non-predation natural mortality			
Summer	$q_{\text{summer},i,\text{sex}}$		$i = 0, 1 \ldots 14, 15+$
Winter	$q_{\text{winter},i,\text{sex}}$		$i = 0,1 \ldots 14, 15+$
Predation rate			
Summer	$P_{(\text{summer},i,\text{sex})}$	$1 - \exp(-\alpha/\Sigma\, n_i)$	$i = 0, 1 \text{ and } 15+(f)$
Winter	$P_{(\text{winter},i,\text{sex})}$	$1 - \exp(-2\alpha/\Sigma\, n_i)$	$i = 0, 1 \text{ and } 15+(f)$
Harvest rate	$h_{i,\text{sex}}$		$i = 0, 1 \ldots 14, 15+$
Survival	$S_{(i,\text{sex})}^{(\cdot)}$		
Summer	$S_{(i,\text{sex})}^{(\text{summer})}$	$1 - ((1 - q_{\text{summer},i,\text{sex}})(1 - P_{(\text{summer}, i, \text{sex})}))$	$i = 0, 1 \ldots 14, 15+$
Autumn	$S_{(i,\text{sex})}^{(\text{fall})}$	$1 - h_{i,\text{sex}}$	$i = 0, 1 \ldots 14, 15+$
Winter	$S_{(i,\text{sex})}^{(\text{winter})}$	$1 - ((1 - q_{\text{winter},i,\text{sex}})(1 - P_{(\text{winter}, i, \text{sex})}))$	$i = 0, 1 \ldots 14, 15+$