Research article

Optimal harvesting in the presence of predation: An age-structured modelling approach

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ABSTRACT

Predation of wildlife and livestock by large carnivores takes place within many ecological and institutional settings. In this paper, moose predation by wolves is studied within a Norwegian institutional setting where the landowners obtain the moose harvesting value and where the wolf population is strictly controlled by the wildlife authorities. An age-structured model consisting of four categories of the moose population (calves, yearlings and adult females and males) is formulated, and both maximum yield (MY) and maximum economic yield (MEY) harvesting are studied. We find that the direct effect of higher predation pressure on an age-sex category works in the direction of higher harvesting pressure of that group. However, this direct effect is accompanied by indirect effects working through the stock abundance of all age-sex groups, and the net effect is ambiguous. In the numerical analysis, it is shown that harvest of the adult categories typically will be the optimal strategy, irrespective of the fact that calves are the main target of the wolves.

1. Introduction

Studying biomass predator – prey relationships has a long tradition within bioeconomic analysis. Hannesson (1983) is a well-known study analyzing the optimal exploitation of fish stocks, where it was demonstrated that the prey value loss versus the predation value gain was a crucial factor determining optimal management. Flåten and Stollery (1996) formulated a reduced form biomass model to assess the economic costs of a given level of predation pressure and used it to study the interaction between the mink whale and cod, without and with a harvesting value, respectively. On the other hand, there are few bioeconomic predator – prey studies modelled within an age-structured framework. One example is Bartram and Quaas (2017), who extended the model of Tahvonen et al. (2013) to a predator - prey model in a fishery economics setting. This analysis is mainly numerical. Age-structured bioeconomic papers in a terrestrial animal species context include Johannesen et al. (2019), who studied semi-domestic reindeer herding exposed to predation.

The present paper is follows up on Johannesen et al. (2019), but includes more theoretical reasoning as well as more numerical illustrations. The case considered is moose (*Alces alces*) predation by grey wolves (*Canis lupus*) within a Norwegian institutional setting. As the Scandinavian population of the grey wolf has increased significantly

during the last few decades, this predation problem has become a concern. The population was estimated to be 430 individuals in the winter of 2016–2017 (Wabakken et al., 2018). The wolf lives in small family groups as packs, or pairs, in the western-central part of Sweden and along the border area between Norway and Sweden. A minimum of 25 individuals were cross-boundary wolves, while 70–75 individuals are based in Norway only (as of December 2018). While the re-colonized Scandinavian wolf population is small and patchily distributed, the density of the moose population is generally high. It is the most important game species in Scandinavia, and about 35,000 animals are killed by hunters every year in Norway (Olaussen and Skonhoft, 2011). The hunting takes place mainly in September and October. The landowners hold the property rights to the hunting value and the traditional objective has been to maximize the meat value, possibly corrected for browsing damage to trees on the owner's own property (Sæther et al., 1992). Because the wolf population is strictly controlled by the wildlife authorities, it is assumed the wolf population does not respond numerically to changes in moose density. This reduced form model is a simplification of the more general predator – prey problem but represents a step in obtaining a better understanding of how various economic and biological factors, together with predation pressure, affect optimal harvest in an age-structured population model exposed to predation. This work has some similarities with the Flåten and Stollery (1996)

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study, but our analysis is more detailed as the main interest of our study is the loss of the prey population's different age classes and the accompanying costs.

In the ecological literature there are a large number of age-structured predator – prey studies. Some of these papers, like ours, analyze moose – predator (wolf, bear) relationships in Scandinavia. Nilsen et al. (2005) examined moose harvesting after the re-introduction of wolves, where the wolf population, as in the present study, does not respond numerically to changes in prey density. Not surprisingly, they found that using the same harvesting rates prior to the re-introduction of wolves will lead to a decline in the moose population when predators are present. However, by keeping a high density, female-biased moose population, the loss to the wolves was quite small. Another study is Jonzén et al. (2013), who used a quite detailed sex- and age-structured moose population model to examine optimal harvest strategies under predation, and to compare the resulting harvest composition with strategies commonly implemented in practice. Three alternative optimal strategies were considered, including maximizing the number of animals hunted and maximizing the yield biomass. One finding was that increased moose density and redistribution of the harvest toward bulls can compensate the harvest loss due to predation. However, this strategy builds on the assumption that fertility is not negatively affected by a skewed sex ratio. Another study from Sweden is Wikenros et al. (2015), who considered areas with detailed moose hunting data five years before and five years after wolf recolonization, as well as areas with wolves present continuously during the whole 10-year period. They documented how wildlife managers and hunters adjusted their harvest strategies to predation, and where wolf establishment lead to an instant reduction in harvest and a reduction in the number of females hunted. They found that the reduction in harvest over-compensated for the harvest loss caused by the wolves' presence.

Of these reported Scandinavian biological moose predation studies, our analysis is most comparable with Jonzén et al. (2013). The analysis here is based on a more detailed demographic model than what is included in the following analysis, and they also considered variations in the predation pressure over the year cycle, which is not the case in our analysis. However, compared to this work, we give a better explanation of how differences in the predation rates among the various age classes influence the harvest composition and the optimal utilization of the moose stock. Our framework includes two different value components of the moose population: the hunting value and the forest browsing damage costs. Optimal management both with and without browsing damage costs are considered, meaning that both maximum yield (MY) and maximum economic yield (MEY) harvesting are included. The population model is similar to Olaussen and Skonhoft (2011), but, in our case, predation is included as an additive source of mortality.

The rest of the paper is organized as follows. We start in section 2 by presenting the bioeconomic model. In sections 3, 4 and 5, the various exploitation schemes are formulated. We start with maximum biomass yield (MY) harvesting in section 3 and continue in section 4 with maximum economic yield (MEY) harvesting where the browsing damage costs also are included. In section 5, the optimization is carried out when also including a female – calf constraint to reflect the common code of conduct to never shoot an adult female without also shooting its calf. Section 6 gives a rather detailed numeric illustration of the exploitation schemes. Finally, section 7 sums up the main results and discusses some management implications.

2. The bioeconomic model

Wolf predation is focused on calves, yearlings, and older females, with calves as the main food source. A study of the prey selection of wolves during summer in a wolf-ungulate system in southern-central Scandinavia found that moose constituted about 95% of the total biomass killed (Sand et al., 2008, Zimmerman et al., 2015). While predation tends to increase with the size and number of the wolf packs,

there is controversy over how it is related to the size of the moose stock. It is generally accepted that the predation rate increases in the moose stock at low densities, but it is less clear what happens at medium and high moose densities (see, e.g., Nilsen et al., 2005). Because of this controversy, and for simplicity, we assume fixed predation rates independent of the size of the moose population. This assumption is in line with the Lotka – Volterra model (numerical section 6). The moose population may also influence the wolf population growth, but this feedback effect (numerical response) is as indicated not included as the Scandinavian wolf population is strictly controlled by the wildlife authorities (Stortingsmelding, 2015a, 2015b; Widman and Elofsson, 2018).

The population is structured in four stages, and includes calves $X_{c,t}$ ($yr < 1$), yearlings $X_{y,t}$ ($1 \leq yr < 2$), adult females $X_{f,t}$ ($yr \geq 2$) and adult males $X_{m,t}$ ($yr \geq 2$). t indicates time (year, yr). The population is measured in spring before calving. All stages are generally harvested, and the hunting, as mentioned, occurs in September–October. Natural mortality is assumed to take place during the winter, after the hunting season, as natural mortality throughout summer and fall is small and negligible. We also assume that predation takes place only during the winter, although in fact there is some predation, especially on calves, during spring and summer. The same natural mortality rate is imposed for males and females and these are lower than for the younger animals. Natural mortality is assumed to be density independent while fertility is density dependent.

The numbers of calves (recruitment) is first governed by:

$$X_{c,t} = r(X_{f,t}, X_{m,t})X_{f,t}, \tag{1}$$

with $r_t = r(X_{f,t}, X_{m,t})$ as the fertility rate (number of calves per female). The fertility rate generally depends on both female density (number of females) and male density, while the small fertility effect of yearlings is neglected. It decreases in female density $\partial r / \partial X_{f,t} = r\dot{}_f < 0$, and will also be reduced when the number of males becomes low, $r\dot{}_m > 0$. The number of yearlings follows next as:

$$X_{y,t+1} = s_c(1 - h_{c,t})(1 - m_c)X_{c,t} \tag{2}$$

where s_c is the fixed calf natural survival rate, $0 \leq h_{c,t} < 1$ is the calf harvesting rate and $0 \leq m_c < 1$ the fixed, and exogeneous, predation rate. Finally, the abundance of (adult) females and (adult) males becomes:

$$X_{f,t+1} = \omega s_y(1 - h_{y,t})(1 - m_y)X_{y,t} + s(1 - h_{f,t})(1 - m_f)X_{f,t} \tag{3}$$

and

$$X_{m,t+1} = (1 - \omega)s_y(1 - h_{y,t})(1 - m_y)X_{y,t} + s(1 - h_m)(1 - m_m)X_{m,t}, \tag{4}$$

respectively. ω is the female ratio of the yearlings when they enter the adult stage, s is the fixed natural survival rate, assumed to be identical for females and males, and s_y is the yearling survival rate. $0 \leq h_{y,t} < 1$, $0 \leq h_{f,t} < 1$ and $0 \leq h_{m,t} < 1$ are the harvesting rates of yearlings, females and males, respectively, and $0 \leq m_y < 1$, $0 \leq m_f < 1$ and $0 \leq m_m < 1$ are the predation rates. Notice that harvesting whole subpopulations is assumed not to be possible. When combining (1) and (2), we find:

$$X_{y,t+1} = s_c(1 - h_{c,t})(1 - m_c)r(X_{f,t}, X_{m,t})X_{f,t}. \tag{5}$$

Therefore, equation (3) – (5) provide a reduced form model in three stages. This form is used when studying exploitation below.

We will also include a female – calf harvest restriction in part of the analysis, because of the code of conduct mentioned above (Olaussen and Skonhoft, 2011). This restriction is given as:

$$h_{f,t}X_{f,t} \leq h_{c,t}X_{c,t}. \tag{6}$$

As indicated, there are two types of value components included in

the management problem, harvesting value and browsing damage costs, and both accrue to the landowner, or the group of landowners acting as a single agent through a landowner association. We start with the hunting value. Because both predation and natural mortality usually occur during the winter (after the hunting season) and because the population is measured in the spring before calving, the number of animals removed in the different categories in year t are defined as $H_{c,t} = h_{c,t}X_{c,t}$, $H_{y,t} = h_{y,t}X_{y,t}$, $H_{f,t} = h_{f,t}X_{f,t}$ and $H_{m,t} = h_{m,t}X_{m,t}$. The current hunting value is accordingly defined through:

$$Q_t = p\left(w_c h_{c,t} X_{c,t} + w_y h_{y,t} X_{y,t} + w_f h_{f,t} X_{f,t} + w_m h_{m,t} X_{m,t}\right), \quad (7)$$

with p (NOK/kg) as the hunting price, assumed to be similar for all stages (age-sex groups), and $w_c < w_y < w_f < w_m$ the (average) body slaughter weights of the different stages. These are assumed to be fixed and independent of the animal density. Density independent weights is a simplification, as the weights typically are lower with higher densities (e.g., Herfindahl et al., 2006). The unit hunting price is also assumed to be fixed and independent of the amount harvested as well as the stock sizes.

The forest browsing damage on young pine trees occurs during winter when other food sources are limited. The cost is assumed to be related to the number of animals, determined by the population during the winter and approximated by the population size after the hunting season, but before natural mortality. The cost is generally different for the various age-sex categories, $D_{i,t} = D_i((1-h_{i,t})X_{i,t})$ ($i = c,y,f,m$), and where more animals mean higher costs, $D_i(0) = 0$ and $D_i' > 0$. With linear functions (as in Olaussen and Skonhoft, 2011), the current browsing damage cost for animal category i becomes $D_{i,t} = d_i(1-h_{i,t})X_{i,t}$ with d_i as the per animal (NOK per animal) cost, and with the typical pattern as $d_c < d_y < d_f = d_m$. The total browsing damage function is accordingly defined through:

$$D_t = d_c\left(1-h_{c,t}\right)X_{c,t} + d_y\left(1-h_{y,t}\right)X_{y,t} + d_f\left(1-h_{f,t}\right)X_{f,t} + d_m\left(1-h_{m,t}\right)X_{m,t}. \quad (8)$$

3. Exploitation I: maximum yield (MY) harvesting

We start by analysing the exploitation of the moose population when only including the hunting value, and where we neglect the calf – cow constraint (6). As the meat price p (NOK/kg) is assumed to be similar for all categories of animals it has no allocation effect, and this exploitation scheme therefore coincides with maximum yield (MY) optimization. The problem is stated as $\max_{h_{c,t}, h_{y,t}, h_{f,t}, h_{m,t}} \sum_{t=0}^{t=\infty} \rho^t Q_t$ subject to the growth equation (3) – (5) and known initial size of the population. $\rho = 1/(1+\delta)$ is the discount factor with $\delta \geq 0$ as the (yearly) discount rate, assumed to be fixed. The Lagrangian of this problem is written as

$$L = \sum_{t=0}^{\infty} \rho^t \left\{ \left[p\left(w_c h_{c,t} r(X_{f,t}, X_{m,t}) X_{f,t} + w_y h_{y,t} X_{y,t} + w_f h_{f,t} X_{f,t} + w_m h_{m,t} X_{m,t}\right) \right] \right.$$
$$-\rho\eta_{t+1}\left[X_{y,t+1} - s_c(1-h_{c,t})(1-m_c)r(X_{f,t}, X_{m,t})X_{f,t}\right]$$
$$-\rho\lambda_{t+1}\left[X_{f,t+1} - \omega s_y(1-h_{y,t})(1-m_y)X_{y,t} - s(1-h_{f,t})(1-m_f)X_{f,t}\right]$$
$$\left. -\rho\mu_{t+1}\left[X_{m,t+1} - (1-\omega)s_y(1-h_{y,t})(1-m_y)X_{y,t} - s(1-h_{m,t})(1-m_m)X_{m,t}\right] \right\}$$

where $\eta_t > 0$, $\lambda_t > 0$ and $\mu_t > 0$ are the shadow prices (in NOK/animal) of the yearling, female and male populations, respectively.

All the first-order control conditions of this maximizing problem are stated with the corresponding complementary slackness conditions and where the possibility of keeping each of the stages unexploited is possible, while harvesting whole sub-populations is not possible. These control conditions then read:

$$\frac{\partial L}{\partial h_{c,t}} = rX_{f,t}[pw_c - \rho\eta_{t+1}s_c(1-m_c)] \leq 0; \ 0 \leq h_{c,t} < 1, \quad (9)$$

$$\frac{\partial L}{\partial h_{y,t}} = X_{y,t}\left\{pw_y - \left[\rho\lambda_{t+1}\omega s_y(1-m_y) + \rho\mu_{t+1}(1-\omega)s_y(1-m_y)\right]\right\} \leq 0; \ 0$$
$$\leq h_{y,t} < 1, \quad (10)$$

$$\frac{\partial L}{\partial h_{f,t}} = X_{f,t}\left[pw_f - \rho\lambda_{t+1}s(1-m_f)\right] \leq 0; \ 0 \leq h_{f,t} < 1 \quad (11)$$

and

$$\frac{\partial L}{\partial h_{m,t}} = X_{m,t}[pw_m - \rho\mu_{t+1}s(1-m_m)] \leq 0 \ ; 0 \leq h_{m,t} < 1. \quad (12)$$

The portfolio conditions are not stated here but are found in Olaussen and Skonhoft (2011).

Condition (9) states that the calf harvest should take place up to the point where the marginal harvest income, pw_c, is equal to, or below, the marginal cost in terms of the reduced population of the yearlings, $\rho\eta_{t+1}s_c(1-m_c)$. The marginal cost takes biological, s_c, and economic ρ, discounting into account, and is evaluated by the yearling shadow price, η_{t+1}. In addition, predation, m_c, influences the marginal cost. When the marginal income is below that of the marginal cost and condition (9) is strictly negative, harvesting is not profitable, $h_{c,t} = 0$. On the other hand, when condition (9) holds as an equation, calf harvesting is profitable and $0 < h_{c,t} < 1$. In a parallel manner, condition (10) indicates that harvesting of the yearlings should take place up to the point where the marginal benefit is equal to, or below, the marginal cost in terms of the sex-weighted reduced population of males and females evaluated by their respective shadow prices. The female and male conditions (11) and (12) are simpler, as reduced stock growth works only through its own stage, but the marginal income and marginal cost considerations are parallel.

When again studying the calf control condition (9), it is observed that the *direct* effect of increased predation pressure and higher predation rate m_c represents a marginal cost reduction. Increased calf predation pressure thus works in the direction of calf harvesting being an optimal option. We find similar direct marginal cost reduction effects through predation and higher predation pressure in the other control conditions (10)–(12). However, *indirect* effects working through the various shadow prices are also apparent. For example, it is observed that a higher yearling shadow price η_{t+1}, indicating a higher yearling value 'in the forest', increases the marginal cost of hunting calves and hence works in the direction of reduced harvesting pressure. The yearling shadow price and the other shadow prices yield the interaction between the control conditions, the portfolio conditions and the biological constraints. Altogether, this comprises a complex system with eleven unknowns and eleven equations, and it seems difficult, if not impossible, to assess analytically the net effect of predation among the various animal categories. However, by combining the control conditions for the yearlings and adults, the shadow prices can be omitted, and something more distinct can be said about the working of predation among these age categories.

Assume first that yearling harvest is not optimal, while harvesting both adult categories is optimal. With positive stock sizes, condition (10) then holds as an inequality, while conditions (11) and (12) hold as equations. Therefore, when eliminating the shadow prices, we find after some small rearrangements $\frac{w_y}{s_y(1-m_y)} < \frac{\omega w_f}{s(1-m_f)} + \frac{(1-\omega)w_m}{s(1-m_m)}$. With the meat value, and hence the marginal harvest income, higher for the adults than the yearlings, and with survival rates that not differ too much (see numerical section), this inequality will definitely hold without predation, and $m_i = 0$ ($i = y,f,m$). Accordingly, harvest of both adult groups and no yearling harvest is then a possible outcome. However, with a substantially higher predation rate for yearlings than adults, this inequality may be reversed to $\frac{w_y}{s_y(1-m_y)} > \frac{\omega w_f}{s(1-m_f)} + \frac{(1-\omega)w_m}{s(1-m_m)}$. In this case, yearling harvest together with harvest of one of the adult categories, but not both, may

thus represent the optimal harvest strategy responding to predation.

These considerations give some indications on how predation and different predation pressures among the different categories of animals may affect the optimal harvesting scheme. Accordingly, with a high predation pressure of a certain age and sex category, harvesting of that animal category may be beneficial. The intuition is simple; it is more beneficial for the landowner to obtain the hunting value instead of losing the animals to the wolf. However, from this discussion, nothing can be inferred about how predation and changing predation pressure influence the number of animals hunted and changes in the population sizes. We come back to this in the numerical analysis (section 6 below).

We will also look at MY harvesting when the management goal is to maximize the offtake; that is, the number of animals harvested. The current objective function then reads simply $H_t = h_{c,t}X_{c,t} + h_{y,t}X_{y,t} + h_{f,t}X_{f,t} + h_{m,t}X_{m,t}$, with the optimal control conditions as in the above Eqs. (9)–(12), except that the animal weights (and the hunting price) are not included. For example, for the calf population we then find:

$$\frac{\partial L}{\partial h_{c,t}} = rX_{f,t}[1 - \rho\eta_{t+1}s_c(1-m_c)] \leq 0; \ 0 \leq h_{c,t} < 1. \tag{13}$$

The marginal harvesting income is accordingly similar among all stages, and this works for certain in the direction that calf harvesting, and also yearling harvesting, will be more beneficial. Therefore, with a higher predation pressure on these animal categories than on the adults, the optimal response to predation may be a substantial harvest of young animals. However, the picture is still quite complex because of the indirect effects working through the animal shadow prices.

4. Exploitation II: maximum economic yield (MEY) harvesting

When also including the browsing damage, and hence maximizing the present value landowner profit, the optimization problem is $\max_{h_{c,t},h_{y,t},h_{f,t},h_{m,t}} \sum_{t=0}^{t=\infty} \rho^t (Q_t - D_t)$ subject to the biological growth equations (3) – (5). When illustrating the optimality by again looking at the calf control condition, we now find:

$$\frac{\partial L}{\partial h_{c,t}} = rX_{f,t}\left[pw_c + d_c - \rho\eta_{t+1}s_c\left(1-m_c\right)\right] \leq 0; \ 0 \leq h_{c,t} < 1; \tag{14}$$

Therefore, the only difference in this MEY problem compared to the MY problem is that the marginal income also includes the harvest gain of a reduced number of animals leading to lower browsing damage. Therefore, the marginal income shifts up for all age classes, and clearly indicates a more aggressive exploitation of the moose population compared to MY harvesting. Additionally, as we have $d_c < d_y < d_f = d_m$ in addition to $w_c < w_y < w_f < w_m$ (see numerical section 6), the MEY problem makes harvesting of the adult stages potentially even more beneficial than in the MY problem. It is also now obvious that the harvest price p has an allocative effect, because there will be a trade-off between the harvest value and the browsing damage; we may then expect that a higher harvest price will dampen the exploitation pressure as the damage costs become relatively less important. Because the marginal harvesting income increases while the cost side is unaffected, predation and a changing predation pattern may potentially have a smaller effect on the optimal harvest response in the MEY problem than in the MSY problem.

5. Exploitation III: including the calf – female constraint

Condition (6) represents the calf – female constraint. The Lagrangian when including this constraint and when considering the MY problem then reads:

$$L = \sum_{t=0}^{\infty} \rho^t \Big\{ \big[p\big(w_c h_{c,t}r\big(X_{f,t},X_{m,t}\big)X_{f,t} + w_y h_{y,t}X_{y,t} + w_f h_{f,t}X_{f,t} + w_m h_{m,t}X_{m,t}\big) \big]$$
$$-\rho\eta_{t+1}\big[X_{y,t+1} - s_c\big(1-h_{c,t}\big)\big(1-m_c\big)r\big(X_{f,t},X_{m,t}\big)X_{f,t}\big]$$
$$-\rho\lambda_{t+1}\big[X_{f,t+1} - \omega s_y\big(1-h_{y,t}\big)\big(1-m_y\big)X_{y,t} - s\big(1-h_{f,t}\big)\big(1-m_f\big)X_{f,t}\big]$$
$$-\rho\mu_{t+1}\big[X_{m,t+1} - (1-\omega)s_y\big(1-h_{y,t}\big)\big(1-m_y\big)X_{y,t} - s\big(1-h_{m,t}\big)\big(1-m_m\big)X_{m,t}\big]$$
$$-\rho\psi_{t+1}\big[h_{f,t}X_{f,t} - h_{c,t}r\big(X_{f,t},X_{m,t}\big)X_{f,t}\big] \Big\}$$

with $\psi_t \geq 0$ as the shadow price of this new constraint. We find that the control conditions for the yearling and adult male categories are unaffected by this new constraint. On the other hand, the control conditions for the calf and adult female categories change and now become:

$$\frac{\partial L}{\partial h_{c,t}} = rX_{f,t}[pw_c - \rho\eta_{t+1}s_c(1-m_c) + \rho\psi_{t+1}] \leq 0; \ 0 \leq h_{c,t} < 1. \tag{15}$$

and

$$\frac{\partial L}{\partial h_{f,t}} = X_{f,t}\big[pw_f - \rho\lambda_{t+1}s\big(1-m_f\big) - \rho\psi_{t+1}\big] \leq 0; \ 0 \leq h_{f,t} < 1, \tag{16}$$

respectively.

When this constraint is binding and $\psi_t > 0$, it thus works partially in the direction of reducing the marginal cost of calf harvesting and increasing it for adult female harvesting. Therefore, if adult female harvesting is potentially beneficial and the cost of giving up the female harvest is high, the optimal programme should include calf harvest as well. On the other hand, if the cost of giving up female harvest is modest, the result may be zero female as well as zero calf harvest, still with a binding female – calf constraint. If female harvest is not potentially beneficial, we may also end up with zero female and calf harvest without the binding constraint and $\psi_t = 0$. More profitable calf harvesting through high calf predation pressure may also work in the direction of a non-binding constraint. However, it is now much more complicated to assess how predation and different predation pressures among the different age classes influence the harvest pattern. Indeed, in the numerical analysis it is shown that predation may change the optimal harvest pattern in unexpected ways.

6. Numerical analysis[1]

6.1. Data and specific functional forms

The various exploitation schemes and the effect of predation will now be illustrated numerically. Our illustration is motivated by the northern part of Hedmark County in Norway, some 250 km north of Oslo. This has been a traditional moose hunting region, and a wolf pack was established there in the 1990's. Both moose hunting and wolf predation have been studied in this area, and predation data is based on Zimmerman et al. (2015). Our specification of the moose fertility rate is adopted from Nilsen et al. (2005). It is a sigmoidal function with an increasing degree of density dependence at high densities, and reads:

$$r_t = r\big(X_{f,t},X_{m,t}\big) = \frac{\bar{r}}{1 + \big(X_{f,t}/K\big)^b}\big(1 - e^{-aX_{m,t}/X_{f,t}}\big). \tag{17}$$

$\bar{r} > 0$ is the intrinsic growth rate (maximum number of calves per female), and $K > 0$ is the female stock for which density-dependent fertility is equal to density-independent fertility. This parameter scales the population sizes. The fertility rate *ceteris paribus* shifts up with a higher male– female population ratio, and $a > 0$ yields the strength of this composition effect. Finally, the compensation parameter $b > 0$ indicates to what extent density-independent effects compensate for

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[1] The optimization was performed by using the 9.4 version of MATLAB R2018a.

changes in the female stock size. With $b > 1$, which is assumed in the calculations, this fertility rate implies a peak-valued recruitment function in the female density (Ricker version).

As predation is assumed to take place after hunting, but before natural mortality, $X_{i,t}(1 - h_{i,t})$ $(i = c, y, f, m)$ yields the number of animals exposed to predation. Predation in the number of animals with the Lotka – Volterra functional form (section 2 above) is then given as $M_{i,t} = X_{i,t}(1 - h_{i,t})\xi_i W$, where W is the exogeneous number of predators (wolves) and where ξ_i indicates the predation pressure for the different categories of animals. The predation rate is then defined as $m_i = \xi_i W$, and is thus independent of the prey (moose) density.

Table 1 gives the parameter values. We are assuming zero discount rate as the baseline value. This indicates that the landowners consider the moose only as natural capital, not financial capital, which fits with anecdotal evidence from Norway (Skonhoft and Solstad, 2020). The steady state of the optimized programs then coincides with the goal of maximizing the equilibrium harvest value or economic yield (see, e.g., Clark, 1990, Ch. 2.5). However, we will also carry out sensitivity analysis of the discount rate.

6.2. Results

Due to the strong degree of linearity in the model, together with density-dependent regulating through the recruitment function, we find that the dynamics share similarities with the Most Rapid Approach Path (MRAP). Within a reasonable range of predation pressures and initial conditions, the system approaches steady state relatively rapidly. See also Olaussen and Skonhoft (2011). We therefore demonstrate only steady state results.

We start with MY and MEY harvesting without the female – calf constraint. Table 2 first presents the biological results with both baseline predation and zero predation. With MY harvesting, it is first observed that only adult harvesting is optimal both under the baseline predation assumption and without predation. Adult harvesting in the absence of predation is as expected because the marginal harvest values are substantially higher for these animal categories than for yearlings and calves (section 3). With predation, reduced harvest rates take place for both adult categories, while there is still no calf harvest, even though the predation rate, which drives down the marginal harvesting cost, is quite substantial. Therefore, this direct marginal cost effect, working through control condition (9), is not strong enough to encourage calf harvesting. The absence of yearling harvest is as expected because the yearling predation rate is quite moderate. The number of all categories of animals reduces with predation and the harvest reduces as well. A smaller stock size of all categories of animals together with lower harvest are therefore

the optimal answers to predation under the present MY harvesting scheme.

When browsing damage is included (lines three and four) and we consider MEY harvesting, it is first observed that adult harvesting continues to be the only optimal strategy, both without and with predation. Based on the observed outcome from MY harvesting, this is as expected, because the marginal damage cost is highest for the adult animals. See condition 14 above. Moreover, also as expected (section 4), the harvest rates shift up for both male and female adults compared to the MY scenario and the stock sizes reduce for all categories of animals, both with and without predation. The harvest in absolute number is reduced as well, even though the harvest rates increase. Reduced harvest therefore goes hand in hand with lower predation in number of animals under MEY harvesting compared to MY harvesting. However, when predation is introduced, the relative reduction in number of animals harvested (and the stock) is about the same under the MY and MEY schemes.

Table 3 demonstrates the economic results. The cost of predation is quite significant under both management schemes, and the harvest value (or biomass harvested) is reduced by about 16% (4484/5305) under MY harvesting. With MEY harvesting, the baseline predation scenario optimized economic loss is about 18% (3565/4365). Notice that the browsing damage cost is higher under MY optimization than MEY optimization, both without and with predation.

It is also of interest to compare optimal harvest with the situation when the harvest rates are not optimally adjusted to the predation pressure. Table 4 reports results from both MY and MEY management in this situation. Somewhat surprisingly, we find that the harvest as well as stock sizes are very much in line with the optimized scheme, and that smaller stocks to a large extent are balanced by higher harvesting rates when predation is ignored. Accordingly, the harvest value economic loss of not adjusting harvesting to the baseline predation pressure turns out to be quite small. Under the MEY scheme, the economic loss of not taking predation into account is just 2% (3492/3565).

Next, Table 5 shows the outcome when the number of animals hunted is maximized. As expected, the exploitation changes in the direction of the non-adults, and calf harvesting becomes optimal. It is also optimal to harvest a small number of adult males, both with and without predation. The reason behind this strong bias in the direction of calf harvesting is that the marginal cost side now is the only decisive factor affecting optimal management (cf. Condition 13). Accordingly, it becomes important to harvest when the animals are young, in order to lower the total natural mortality over the life cycle. Notice that the harvest rate for the calves reduces with predation. On the other hand, a somewhat higher harvest is the optimal response to predation for adult

Table 1
Baseline biological and economic parameter values.

Parameter	Description	Value	Reference/Source
$\bar{r}$	Maximum specific growth rate	1.15 (1/year)	Nilsen et al. (2005)
K	Female stock level where density factors dominate density independent factors	1000 (# of animals)	Calibrated
a	Male density recruitment factor	10	Nilsen et al. (2005)
b	Density compensation parameter	2	Nilsen et al. (2005)
s_c, s_y, s	Natural survival rate calves, yearlings, adults	0.90, 0.95, 0.95	Nilsen et al. (2005)
ω	Sex ratio yearlings	0.50	Olaussen and Skonhoft (2011)
w_c w_y, w_f, w_m	Weight calves, yearlings, female adults, male adults	65, 135, 150, 170 (kg/animal)	SSB (2009)
m_c m_y, m_f, m_m	Predation rate calves, yearlings, female adults, male adults	0.103, 0.017, 0.013, 0	Zimmermann et al. (2015)
p	Meat price	75 (NOK/kg)	Olaussen and Skonhoft (2011)
d_c, d_y, d_f, d_m	Marginal browsing cost calves, yearlings, female adults, male adults	250, 500, 750, 750 (NOK/animal)	Olaussen and Skonhoft (2011)
δ	Discount rate	0 (1/year)	Assumed

Table note: 2010 price level. Exchange rate: 9.90 NOK/Euro (August 2019).

Table 2
Steady state biological results.

Exploitation scheme	Predation pressure	$H_c(h_c)$	$H_y(h_y)$	$H_f(h_f)$	$H_m(h_m)$	$X_c(M_c)$	$X_y(M_y)$	$X_f(M_f)$	$X_m(M_m)$
MY harvesting (max Q)	Zero	0 (0)	0 (0)	208 (0.24)	233 (0.59)	564 (0)	507 (0)	871 (0)	396 (0)
	Baseline	0 (0)	0 (0)	169 (0.20)	202 (0.54)	560 (58)	452 (8)	839 (9)	374 (0)
MEY harvesting (max $\pi = Q - D$)	Zero	0 (0)	0 (0)	205 (0.26)	230 (0.76)	546 (0)	492 (0)	782 (0)	302 (0)
	Baseline	0 (0)	0 (0)	167 (0.23)	199 (0.71)	538 (55)	434 (7)	743 (7)	280 (0)

H_i harvest in # of animals, h_i harvest rate, X_i stock size in # of animals, M_i predation in # of animals.
($i = c$ calves, $i = y$ yearlings, $i = f$ adult females, $i = m$ adult males). Baseline predation pressure; $m_c = 0.103$, $m_y = 0.017$, $m_f = 0.013$, $m_m = 0$.

Table 3
Yearly steady state economics (in 1000 NOK).

	MY harvesting (max Q)		MEY harvesting (max $\pi = Q - D$)	
	Zero predation	Baseline predation	Zero predation	Baseline predation
Hunting value Q	5305	4484	5235	4410
Browsing damage D	1015	997	869	845
Profit π	4290	3487	4365	3565

Table 4
Yearly steady state economics and loss of predation when not taking predation into account (in 1000 NOK).

	MY harvesting (max Q)		MEY harvesting (max $\pi = Q - D$)	
	Optimized harvesting[a]	Ignoring predation[b]	Optimized harvesting[c]	Ignoring predation[d]
Hunting value Q	4484	4398	4410	4208
Browsing damage D	997	859	845	716
Profit π	3487	3538	3565	3492

[a] Harvest rates $h_c = 0$, $h_y = 0$, $h_f = 0.20$, $h_m = 0.54$.
[b] Harvest rates $h_c = 0$, $h_y = 0$ $h_c = 0.24$ and. $h_{cm} = 0.59$
[c] Harvest rates $h_c = 0$, $h_y = 0$, $h_f = 0.23$, $h_m = 0.71$.
[d] Harvest rates $h_c = 0$, $h_y = 0$, $h_f = 0.26$, $h_m = 0.76$.

males. Notice also that omitting female harvest is crucial to keep the recruitment as high as possible, since the goal is to maximize the number of animals harvested. The loss of predation now accounts for about 7% (456/487).

Table 6 demonstrates the outcome when the calf – female constraint is included, and where MY harvesting is first considered. Because adult female harvesting is beneficial both with and without predation (Table 2), this constraint will bind. This means higher female marginal harvesting cost, while the opposite happens for the calf harvesting cost (conditions 15 and 16). Without predation, however, this marginal cost reduction for the calf population is not strong enough to encourage harvesting and we therefore also find zero female harvest. On the other hand, it becomes highly beneficial to harvest yearlings, while a modest amount of male harvest is apparent. The harvest pattern changes dramatically when predation is included; now, both calf harvest and adult female harvest take place (line two). Additionally, the yearling harvest is reduced to zero, while the adult male harvest become quite significant. Under MEY management (lines three and four), the pattern is somewhat different, as calf and adult female harvest also become profitable in the absence of predation.

Table 5
Steady state harvest maximizing (max H).

Predation pressure	$H_c(h_c)$	$H_y(h_y)$	$H_f(h_f)$	$H_m(h_m)$	H
Zero	463 (0.82)	0 (0)	0 (0)	24 (0.24)	487
Baseline	423 (0.76)	0 (0)	0 (0)	33 (0.09)	456

See Table 2 for notation.

6.3. Sensitivity results

Some sensitivity results without the calf – female constraint will now be demonstrated. We start with changing predation pressure. Under MY harvesting, we find that only adult harvesting is optimal under all predation assumptions, except that calf harvesting is optimal when predation becomes very high. Fig. 1 demonstrates what happens under MEY optimization; again, only adult harvesting is optimal for low and medium predation pressure. The harvesting rates reduce gradually with higher predation pressure. When that pressure reaches five, indicating that the calf predation rate is about 0.52 (5*0.103; see Table 1), calf harvesting starts to become optimal. At this predation level, the adult female harvesting is quite small; female harvest is no longer optimal when the predation pressure reaches about 6. The economic surplus reduces gradually with increasing predation, and we find the MSY to be reduced by about 30% when the baseline predation pattern is doubled.

Finally, Table 7 reports some other sensitivity results. Increased discount rate (line two) leads, as expected, to higher steady state exploitation pressure and lower stock sizes. This is the standard outcome in bioeconomic models. On the other hand, increasing the harvest price leads to a somewhat lower exploitation pressure under MEY optimization, while the exploitation and harvest pattern under the MY scheme is unchanged. Doubling the unit damage cost for all categories of animals (line four) means that harvesting becomes more profitable, and the adult harvest rates increase significantly. Finally, the last line in this table shows the effects of reduced weights for all categories of animals. This scenario may hence illustrate a situation where hunting, *ceteris paribus*, take place in a less productive moose area. Because the weights are reduced proportionally, this will not affect the MY optimization. Under MEY optimization, on the other hand, the harvest rates increase, and the stocks reduce compared to the baseline situation. Indeed, the proportional weight reduction works in a similar manner as a reduction in the harvest price. Notice that the 20% reduction in the weights has a quite significant economic effect, as the profitability reduces by 25% (2688/ 3567).

7. Concluding remarks

In a Norwegian institutional setting where the hunting value of the moose belongs to the landowners and where the size of the wolf population affects the moose population growth, but not *vice versa*, we have analyzed how wolf predation influences optimal moose hunting management. Both maximum sustainable yield harvesting (MY), and maximum economic yield harvesting (MEY) are considered. It is demonstrated that predation has a two-tiered effect on the optimal harvesting decision. The direct effect influences the marginal harvesting

Table 6
Steady state biological results with calf – female harvesting constraint.

Exploitation scheme	Predation pressure	$H_c(h_c)$	$H_y(h_y)$	$H_f(h_f)$	$H_m(h_m)$	$X_c(M_c)$	$X_y(M_y)$	$X_f(M_f)$	$X_m(M_m)$
MY harvesting (max Q)	Zero	0 (0)	413 (0.81)	0 (0)	27 (0.07)	564 (0)	508 (0)	898 (0)	389 (0)
	Baseline	120 (0.21)	0 (0)	120 (0.14)	155 (0.43)	560 (45)	355 (6)	850 (9)	365 (0)
MEY harvesting (max $\pi = Q - D$)	Zero	140 (0.26)	0 (0)	140 (0.19)	165 (0.59)	539 (0)	359 (0)	751 (0)	282 (0)
	Baseline	118 (0.22)	0 (0)	118 (0.17)	150 (0.57)	531 (43)	333 (6)	717 (8)	265 (0)

See Table 2 for notation.
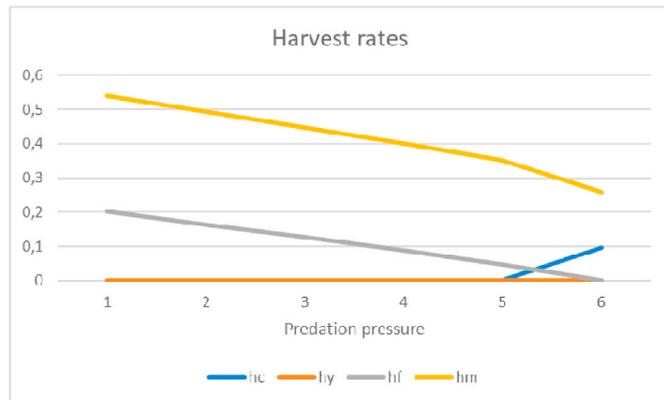
Fig. 1. Steady state harvesting rates. MEY harvesting (max $\pi = Q - D$) Predation pressure equal to 1 represent the Baseline predation pressure (see Table 2) while, say, 2 indicates a doubling of the rates for all categories of animals.

cost and an indirect effect works through the stock abundance and the animal shadow prices.

Wolf predation is focused on calves, yearlings, and older females, with calves as the main food source. Our predation data indicates a predation rate of about 10% for the calves and 1% for yearlings and adult females, while there is no predation of adult males. With these baseline predation rates, we find that harvesting of adult females and males, but not calves and yearlings, is optimal under both MY and MEY harvesting. When comparing to the situation without predation, it is shown that the optimal answers to predation are smaller stock of all categories of animals combined with lower harvest. In line with the theoretical reasoning, we also find that the exploitation pressure will be higher under MEY than MY management, both with and without predation. We have also analyzed how predation influences the outcomes when the harvest offtake is maximized and when a calf – female constraint is included, reflecting the code of conduct to never shoot an adult female without the calf. We find here that both calf and yearling harvest may be the optimal answer to predation.

The economic loss of predation with the baseline predation pressure is in the range 15–20%, and somewhat higher under MEY than MY management. However, while the economic loss of predation is significant, an important management implication seems to be that the economic loss of not taking the predation into account turns out to be quite small. Under MEY harvesting with the baseline predation rates, but utilizing the optimized harvesting rates as without predation, the economic loss is just 2% compared to the situation when adjusting the harvest to the actual predation pattern. Another important management implication seems to be that Ignoring the forest damage cost gives more or less similar small landowner loss (about 2%) both with and without predation. However, the optimal harvest rates are significantly different under MY and MEY harvesting both without and with predation.

The analysis presented here contributes both to the more general, but rather scant, literature on how predation works in age-structured models, and to the more specific literature analyzing moose – predator (wolf, bear) relationships in Scandinavia. Our modelling is based on certain simplifications, of which the assumption of fixed predation rates, irrespective of the size of the moose population, possibly is of most importance. For a critical discussion, see Johannesen at al. (2019). It should also be noted that traffic damage costs due to moose – vehicle and moose railway collisions are not included in the present analysis. These costs, external for the landowners, are often of large importance (see Solberg et al., 2009) with crucial management implications as it will be optimal to keep a smaller moose stock of the various age classes from an overall point of view (social planner solution) than from the perspective of the landowners. Typically, we then find that the wolf predation will reduce these external costs, but differently for the various categories of the moose population. For an analysis within a biomass model, see Skonhoft and Solstad (2020).

Credit author contribution statement

Anders Skonhoft: Conceptualization, Methodology, Writing - original draft. **Veronika Friberg:** Formal analysis.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Table 7
Steady state sensitivity results. MY Harvesting and MEY harvesting in brackets. Benefit and costs in 1000 NOK.

	h_c	h_y	h_f	h_m	Q	D	π
Baseline	0 (0)	0 (0)	0.20 (0.23)	0.54 (0.71)	4484 (4394)	997 (828)	3487 (3566)
Increased discount rate, $\delta = 0.05$	0 (0)	0 (0)	0.22 (0.25)	0.67 (0.83)	4439 (4254)	881 (732)	3558 (3522)
Increased hunting price, $p = 100$ (NOK/kg)	0 (0)	0 (0)	0.20 (0.22)	0.54 (0.67)	5979 (5904)	997 (864)	4982 (5040)
Doubling damage costs, $d_i* 2$ (NOK/animal)	0 (0)	0 (0)	0.20 (0.25)	0.54 (0.85)	4484 (4206)	997 (1416)	3487 (2790)
Reduced weights, $w_i*0.8$ (kg/animal)	0 (0)	0 (0)	0.20 (0.24)	0.54 (0.75)	4484 (3483)	997 (795)	3487 (2688)

See Tables 2 and 3 for notation.

Acknowledgements

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