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ANALYSIS

The costs and benefits of animal predation: An analysis of Scandinavian wolf re-colonization

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Abstract

After coming close to extinction, the grey wolf (*Canis lupus*) has re-colonized Scandinavia during the last two decades. The current population numbers some 100–120 individuals, and is distributed in small packs along the Swedish-Norwegian border. However, with wolf re-colonization, several conflicts have arisen. One conflict is due to wolf predation on livestock, especially sheep and reindeer. Another is predation on wild ungulates. As the wolves have shown a strong preference for moose (*Alces alces*) in this respect, a smaller moose population is available for game hunting. The cost of increased moose predation by wolves is examined using a two-step process. First, we analyse the costs to landowners, comprising the loss of animals potentially available for hunting less the reduction in browsing damage associated with a smaller moose population. Second, we examine the problem from a broader point of view, where costs external to landowners and local communities are included. By far the most important cost here is damage related to collisions between moose and motor vehicles.

Keywords: Bioeconomic analysis; Predation; Wolf; Moose

1. Introduction

In very many instances, wild animals provide benefits for humans. Quite frequently, however, we may also find that these species incur economic costs. Rodents damaging agricultural production are a typical example (see, e.g., Stenseth et al., 2003). In other instances, wild animals are simultaneously a nuisance and valuable. Large herbivores, for example, may cause grazing damage, but provide value through hunting or trapping (see, e.g., Zivin et al., 2000). Nuisance may also be channelled through ecological interaction. Some marine species are of this type, where whales, for example, prey upon or compete with commercially valuable species, like cod (Flaaten and Stollery, 1996). This also holds for terrestrial animal species, for example where bears and wolves prey upon wild ungulates in addition to livestock. Graham et al. (2005) provides an overview of these conflicts, making a distinction between predation–livestock conflicts and predator–game conflicts.

In the middle of the 1960s, the grey wolf (*Canis lupus*) was regarded as functionally extinct in Norway and Sweden (the Scandinavian peninsula). In the last

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part of the 1970s the first confirmed reproduction in 14 years was recorded. Since this first reproduction in northern Sweden, all new reproductions have been located in south-central parts of the Scandinavian peninsula (Wabakken et al., 2001). The re-colonized wolf population in Scandinavia now numbers some 100–120 individuals which live in small family groups, or packs, in the western-central part of Sweden and along the border area between Norway and Sweden (Wabakken et al., 2001). Although the population is still small in number, wolf re-colonization is already associated with several conflicts. One conflict is due to predation on livestock, including sheep and reindeer (Linell et al., 1996). While the total loss is quite modest, some farmers in a few areas have been seriously affected (Environmental Department, 2003). The predation on wild ungulates is another conflict, especially where the wolf shows a particularly strong preference for moose (*Alces alces*) (Milner et al., in press). As a consequence, a smaller moose population is available for hunting. The problem of moose predation also takes place in only a few areas, but has caused great concern in rural Scandinavia because moose is by far the most important hunting game species, with about 40,000 and 100,000 animals (with a mean body weight of about 190 kg for adult females and 240 kg for adult males) shot every year in Norway and Sweden, respectively (Gundersen, 2003). In addition, moose hunting in September/October is an important, if not the most important, social and cultural event taking place in many rural communities.

In this paper, the moose predation cost of the recent wolf re-colonization is analysed. The problem is examined using a two-step process. First, the cost to the *landowners* is studied. According to Scandinavian wildlife laws, landowners are given the hunting value of the moose. At the same time, when practicing forestry, they bear the cost of browsing damage, mostly taking place during the winter when young pine trees are the main food source for the moose (Storaas et al., 2001). The economic loss to the landowners due to wolf predation consists therefore of two components; the loss of animals potentially available for hunting minus the reduced browsing damage due to a smaller moose population. This loss, however, depends on the landowner's management goals and hunting practices. Next, we look at the problem from an *overall* point of view, which includes the cost due to moose–vehicle collisions. This cost is found to be considerable, and recent estimates indicate that it may be even higher than the meat value of the moose (Storaas et al., 2001). Both the landowners cost and the overall scheme is studied in ecological equilibrium.

The relationship between wolf and moose is highly interactive, mainly determined by the functional response of the wolf population to the moose population. There may also be a reverse numerical response if the moose population influences the wolf population growth. Wolf–moose ecology has been studied extensively in North America and to a lesser extent in Scandinavia (Nilsen et al., 2005). However, very few studies include any economic considerations. For exceptions, see Tu and Wilman (1992) and Boman et al. (2003). Tu and Wilman analyse the wolf–moose relationship using a Verhulst-Pearl type model. The aim of their study was to see how various predator control programs affected the dynamics of the ecological system when uncertainty was included. As mentioned, we are only concerned with ecological equilibrium. Boman et al. analysed bio-economic aspects of the dispersal pattern of wolf expansion in Sweden and where predation on moose was taken into account, but no moose population growth function was explicitly specified. In the present study, we focus on the moose population relationship, but ignore dispersal. Our analysis therefore draws more on the general bio-economic pest and nuisance literature (see, e.g., Zivin et al., 2000; Huffaker et al., 1992).

In the following we are considering an area of fixed size with a moose population coexisting with a wolf population. One or more landowners manage the moose hunting in this area and if more landowners, they are in sum assumed to behave as a single agent. We start by formulating the ecological model in Section 2. The cost and benefit functions to the landowners follow in Section 3. In Section 4 we analyse the various moose management goals and assess the economic loss of wolf predation. Altogether, four harvesting scenarios are analysed. Section 5 provides a numerical illustration using a real life example from the Koppang area (located some 300 km north of Oslo). In Section 6, the cost of moose-vehicle collisions external to the landowner is included, and the wolf predation is then studied from a more overall perspective.

2. Moose–wolf interaction

While the recently re-colonized Scandinavian wolf population is small in number and patchily distributed, the density of the Scandinavian moose population is generally high. The main reasons for the latter are the previous near-absence of predators, the last decade's highly selective moose harvesting scheme focusing on young males and calves, and good growth conditions associated with changing forestry practices (Ostgard, 1987; Saether et al., 1992). The moose population size has accordingly increased significantly during the last 30 years or so in both Sweden and Norway. In Norway it increased from about 15,000 in the in the beginning of the 1970s to today's level of about 125,000. At the same time, the yearly number of moose hunted increased from about 6000 to close to 40,000 (Ostgard, 1987; Milner et al., in press).

Moose–wolf ecology has been subject to several intensive studies in North America. From these studies it appears clear that wolves, when present, influence the abundance of moose (Peterson, 1999; Hayes and Harestad, 2000). The Scandinavian ecosystem, however, differs from the North American system as the moose density is generally higher, the age and sex structures differ because of selective hunting schemes with a higher proportion of harvesting of calves and young males (Solberg et al., 2000) and harvesting accounts for a much higher proportion of total mortality (>85%; Saether et al., 1992). Wolf density in Scandinavia is also much lower, and more patchily distributed (Wabakken et al., 2001). The moose–wolf ratio is thus higher in Scandinavia, and the impact of wolf predation is likely to be of a more local nature. Wolf predation is focused on calves, yearlings, and older females, with calves as the main food source. The predation rates reported from Scandinavia also appear to be higher than those in North America, which may indicate that predation, for a given size of wolf pack, increases with moose density (Nilsen et al., 2005).

Based on the above cited studies, it is assumed that wolf predation represents an additional source of mortality for calves, yearlings, and older females. In our biomass framework, the natural growth of the moose population then translates into two terms; growth in the absence of wolves minus mortality through predation. 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 increases in the moose stock at low densities, but it is more unclear what happens at medium and high moose densities. In what follows a general functional form is used which may include a lower marginal predation effect at higher densities. A linear functional form, however, is applied in the numerical illustrations meaning that the predation rate is constant (Section 5 below).

While predation is determined by the size and number of wolf packs together with the size of the moose population, there may also be a feedback effect as the size of the moose population influences wolf population growth. However, in areas with colonizing carnivore populations, or carnivore populations strongly controlled, as in Scandinavia (Environmental Department, 2003), this relationship will appear less interactive meaning that the wolves are not able to respond numerically to variations in the moose population (Nilsen et al., 2005). Any numerical response of the wolf population is hence neglected and the size of the wolf population, or equivalently, the predation pressure, is determined outside the model. Our reduced-form ecological model has therefore the same structure as the Flaaten and Stollery (1996) model analysing the economic loss of the fisheries along the Norwegian coast and the Northeast Atlantic due to a given amount of minke whale predation.

When neglecting any stochastic variations in environment and biology, the equation

$$X_{t+1} - X_t = F(X_t) - G(W, X_t) - h_t \tag{1}$$

gives the growth of the moose population where X_t is the population size in year t, measured as the number of animals (or biomass), $h_t \geq 0$ is the harvest in the same year (also as the number of animals), and $F(X_t)$ is the density-dependent natural growth function in absence of wolf predation. $F(.)$ is assumed to be of the standard logistic type with $\partial F/\partial X_t = F' > 0$ for a 'small' population and $F' < 0$ when $X_t > X_{\text{msy}}$ (additional details provided below). $G(W,X_t)$ is the predation term where W is the size of the wolf pack, assumed exogenous throughout the analysis, with $G(0,X_t)$ and $\partial G/\partial W = G_W > 0$. The size of the moose stock generally influences predation as well,

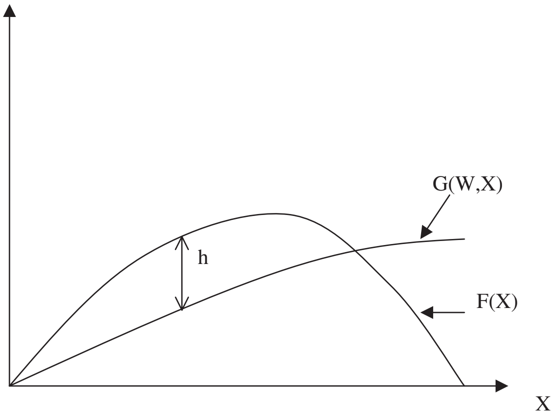

Fig. 1. Natural growth $F(X)$ and predation $G(W,X)$. Harvest h and ecological equilibrium.

$G(W,0)=0$ and $G_X \geq 0$, while the marginal effect may be reduced when the moose density becomes higher (see above), $G_{XX} \leq 0$. Finally, $G_{XW} \geq 0$ is assumed to hold. See Fig. 1.

The different management options are analysed only in ecological equilibrium. There are two reasons for this. First, equilibrium harvesting (of various types, see below) is the usually practice is Scandinavia. Moreover, as transitional dynamics and hence the time profile of the cost of predation depend on the chosen initial situation, nothing comparative can be said about the various harvesting schemes in a dynamic framework. In ecological equilibrium we have $F(X)-(W,X)-h=0$ which defines the prey isocline. The prey isocline is always assumed to be downward sloping. Under, say, a fixed quota harvesting scheme with h constant (see below), the slope reads $\mathrm{d}X/\mathrm{d}W=G_W/(F'-G_X)$. When negative, $G(W,X)+h$ therefore intersects with $F(X)$ from below. It is easily recognized that this implies dynamic stability.

3. The cost and benefit to landowners

The landowners receive the hunting value of the moose. Their net benefit is determined by hunting income minus the browsing cost due to the damage to young pine trees. The yearly hunting income is given as ph (the time subscript is dropped) where p is the hunting license price. In what follows, it is assumed that p is fixed and independent of the harvest and stock size. This is justified by the fact that there is competition among a large number of suppliers of hunting licenses in Scandinavia. Following the practice in Norway, a license allows the buyer to kill one animal, which is paid for only if the animal is killed. In reality, each hunter also pays a (small) fixed fee independent of whether any animal is shot or not, but this fee component is neglected.

The damage on young pine trees occurs mainly during the winter and varies with the quality of the timber stand and the productivity of the forest. The damage may take place immediately, and the damaged young pine trees may be replaced directly, but quite frequently there is a time lag between the occurrence of browsing and the economic loss of the damage. In such instances, however, discounting is not explicitly taken into account. A simple, but realistic, way to account for the browsing cost is to relate it to the size of the moose population, $D_t=D(X)$ with $D(0)=0$ and $D'>0$ (see also Zivin et al., 2000). The yearly net benefit, or profit, to the landowners in year t reads accordingly:

$$\pi(W) = ph - D(X). \tag{2}$$

The economic loss of the landowners due to predation is therefore the profit (2) in the absence of wolf predation minus the profit with wolf predation. The loss is then made up of two components; a change in the harvestable population and a change in the stock size causing browsing damage. The loss may also be negative, i.e. there is a gain, if the reduced browsing damage exceeds the reduced harvesting income. To account for the loss (or gain), however, the management goal of the landowners has to be specified as the harvest and stock size, and hence profit are related to the harvesting strategy employed.

4. The various management scenarios of landowners

According to Norwegian wildlife law, the State, through the Directorate for Wildlife and Nature Management (‘Direktoratet for Naturforvaltning’) in cooperation with the local wildlife authorities and the landowners, determines the number and composition (calves, juveniles, adult females, and adult males) of moose to be hunted within each management area. However, all the time the hunting value is obtained by the landowners (see above). The management goal is usually to maximize the meat value in an ecological equilibrium (Saether et al., 1992). Browsing damage may be taken into account, but often in an ad hoc manner. However, because of uncertainty of various types, lack of information, and so on, this management goal is generally implemented by landowners in a *pragmatic* manner, which in most instances, if not always, is reduced to simple goals concerning the equilibrium population size and/or the harvest (see Lande et al., 2003 for a general discussion and analysis in light of uncertainty).

The cost of predation is studied in light of such pragmatic harvesting strategies, and the following management options are analysed: (a) threshold harvesting (keeping a constant stock over time); (b) proportional harvesting (harvesting a fixed fraction of the population every year); and (c) harvesting a fixed number (quota) of animals every year. These three strategies are compared with a harvesting strategy giving the highest economic outcome for landowners: (d) maximizing the present value of profits. As mentioned, all management schemes are evaluated at the ecological equilibrium.

4.1. Threshold harvesting

Threshold harvesting, or keeping a constant stock level X^a, may typically be related to the maximum sustainable yield level, or other ‘sustainable’ population levels. In ecological equilibrium we have $F(X^a) - G(W,X^a) - h^a = 0$ where $h^a \geq 0$ indicates the threshold of harvesting. When $h^a > 0$ and X^a is constant, $dh^a/dW = -G_W < 0$ and any increased predation are exactly balanced by a reduced outtake. The economic loss due to wolf predation is then simply the reduced harvesting income:

$$\frac{d\pi^a(W)}{dW} = -pG_W(W,X^a) < 0. \tag{3}$$

The marginal profit loss is thus proportional to the harvesting price, and is non-decreasing in the threshold level X^a, as we have $G_{WX} \geq 0$.

4.2. Proportional harvesting

Proportional harvesting follows as $h = \gamma X$, with $\gamma > 0$ as the fixed harvesting fraction. When inserted into the population equilibrium this yields $F(X^b) - G(W,X^b) - \gamma X^b = 0$, where X^b indicates the equilibrium stock. Differentiation gives $dX^b/dW = G_W/(F' - G_X - \gamma)$ and is negative when $[G(W,X) + \gamma X]$ intersects with $F(X)$ from below and we have dynamic stability (cf. Section 2). Following this harvesting rule, the moose stock is therefore lower with wolf predation than without predation. Accordingly, the equilibrium harvest, $h^b = \gamma X^b$, will be lower as well.

However, as both the number of animals harvested and the stock become lower, harvesting income and browsing damage decrease. Hence, the profit effect is ambiguous:

$$\frac{d\pi^b(W)}{dW} = \frac{[p\gamma - D'(X^b)]G_W(W,X^b)}{[F'(X^b) - G_X(W,X^b) - \gamma]}. \tag{4}$$

We therefore find that the presence of wolf predation, or equivalently, a larger wolf pack, reduces the profit of landowners if, and only if, the marginal harvesting income dominates the marginal browsing damage, such that $(p\gamma - D') > 0$. The moose population size is then above that of the static profit maximization condition, and an additional moose consumed by the wolf pack leads to an allocation further away from that maximum (see also below). In the opposite situation where $(p\gamma - D') < 0$, higher predation pressure increases the profit of the landowners as reduced marginal damage dominates the reduced harvesting income.

4.3. Fixed quota hunting

Following a fixed quota management rule, the ecological equilibrium condition is $F(X^c) - G(W,X^c) - h^c = 0$ where $h^c \geq 0$ indicates the fixed quota and X^c the accompanying stock level. Differentiating yields $dX^c/dW = G_W/(F' - G_X) < 0$ under the assumption of dynamic stability (again, see Section 2). The presence of wolf, or higher wolf predation pressure, will therefore unambiguously increase profit:

$$\frac{d\pi^c(W)}{dW} = -\frac{D'(X^c)G_W(W,X_c)}{[F'(X^c) - G_X(W,X^c)]} > 0. \tag{5}$$

At the cost of a smaller and less ‘sustainable’ moose population (but see the numerical results below), landowners will benefit from wolf predation.

However, the harvesting quota cannot be 'too large'. If the predation pressure is substantial, then there are simply not enough moose to sustain a harvest. We also find that a higher quota always means a smaller stock under the assumption of dynamic stability; that is $G(W,X)+h$ intersects with $F(X)$ from below (cf. above and Fig. 1). A higher quota, for any given predation pressure W, leads accordingly to reduced browsing damage. The profit therefore increases.

4.4. Maximizing present-value profit

The above harvesting schemes are now compared with a scenario of present-value profit maximization. This harvesting strategy hence follows by maximizing $\sum_0^{T-1} \rho^t[ph_t - D(X_t)]$ subject to the ecological growth equation (1), where T is the planning period and $\rho=1/(1+\delta)$ is the discount factor with $\delta \geq 0$ as the (annual) discount rate. The planning period, or number of years taken into account, is presumably long, or infinite, meaning that no scrap value, i.e., no final value of the moose population, is included in the objective function.

The current-value Hamiltonian of this problem (see, e.g., Conrad and Clark, 1987) is $H=ph_t - D(X_t) + \rho\lambda_{t+1}[F(X_t) - G(W,X_t) - h_t]$ where λ_{t+1} is the resource shadow price ('the value of the moose in the forest'). The first-order conditions for the maximum yield $p - \rho\lambda_{t+1}=0$ and $\rho\lambda_{t+1} - \lambda_t = D' - \rho\lambda_{t+1}(F' - G_X)$ when an interior solution is assumed to take place (a positive stock size and harvesting taking place at the steady state). The interpretations of these conditions are standard. The dynamics will typically be of the Most Rapid Approach Path (MRAP-dynamics) as the Hamiltonian is linear in the control. Suggested that the steady state is reachable from the initial position X_0 (see also the concluding section), the so-called 'golden rule condition' becomes:

$$F'(X^*) - \frac{D'(X^*)}{p} - G_X(W,X^*) = \delta. \tag{6}$$

This condition indicates that the net internal rate of return of the moose population should equal the external rate of return δ. Multiplying by p and rearranging, the golden rule condition also indicates that the net marginal value of the moose population 'in the forest', $p(F' - G_X) - D'$, should be equal to the marginal harvesting value 'in the bank', $p\delta$. Following condition (6), the stock size will always be below the maximum sustainable harvest level $F'(X^*)>0$, or $X^*<X_{\text{msy}}$. Discounting, as well as browsing damage and predation work in that direction. When the rate of discount is zero, $\delta=0$, it can easily be shown that solution (6) coincides with the solution of the problem of maximizing current profit (2) at ecological equilibrium.

Differentiation of (6) yields $\mathrm{d}X^*/\mathrm{d}W = G_{XW}/(F'' - D''/p - G_{XX}) \leq 0$, as the numerator is negative because of the second-order conditions for a maximum. The steady-state harvest follows as $h^* = F(X^*) - G(W,X^*)$, and predation also reduces the harvest, $\mathrm{d}h^*/\mathrm{d}W = (F' - G_X)(\mathrm{d}X^*/\mathrm{d}W) - G_W < 0$. The profit $\pi^*(W) = ph^* - D(X^*)$ shifts accordingly as:

$$\frac{\mathrm{d}\pi^*(W)}{\mathrm{d}W} = \{p[F'(X^*) - G_X(W,X^*)] - D'(X^*)\}\frac{\mathrm{d}X^*}{\mathrm{d}W} - pG_W(W,X^*) < 0, \tag{7}$$

which is also negative because $[p(F' - G_X) - D'] \geq 0$ holds for the golden rule condition (6). Predation therefore lowers the profitability under this harvesting scheme because it represents one more constraint for the profit maximising landowner. As both harvesting income and browsing damage decrease, the reduced harvesting income dominates the reduced browsing damage. When $\delta=0$ and Eq. (6) coincides with current profit maximizing, condition (7) reduces to $\mathrm{d}\pi^*(W)/\mathrm{d}W = -pG_W < 0$, which may also be confirmed using the envelope theorem. The effect is then the same as in the threshold harvesting case (a), except that they generally occur at different stock levels.

5. Numerical illustration

5.1. Data and specific functional forms

The harvesting schemes are now numerically illustrated using data from the Koppang area, some 300 km north of Oslo, Norway. The intention is not to carry out an 'accurate' cost–benefit calculation as these simulations only mirror some qualitative aspects of wolf predation. A wolf pack settled in this region in 1997 in an area of about 600 km^2, with a moose population of about 1000 individuals. Since then the number of wolves has been between 5 and 12 individuals. The wolf population is strictly controlled (Environmental Department, 2003). The yearly predation, mainly calves and yearlings, has been difficult to assess, but Gundersen (2003) states it is in the range 0–18 moose/wolf/100 days. The number of moose harvested has decreased during the last years (Milner et al., in press) which may be consistent with a smaller population governed by a proportional harvesting strategy (see also below).

As mentioned, the natural growth rate of the moose population in the absence of predation is assumed to be of a standard logistic type $F(X_t)=rX_t(1-X_t/K)$ with r as the maximum specific growth rate and K as the carrying capacity. The functional response of the wolf population is specified as a Cobb-Douglas function, $G(W,X)=\alpha WX^{\beta}$ with $\alpha>0$ and $0<\beta\leq 1$. For simplicity, $\beta=1$ is used in the following calculations although there are good reasons to believe that there is some decreasing effect in the number of moose (Section 2 above). The predation rate, as a growth rate, is then fixed by αW. We also use a linear browsing-damage function $D(X)=aX$ with $a>0$ as the fixed damage cost per moose. For these functional forms, routine calculations yield ecological equilibrium profit under the various management schemes as: $\pi^{a}(W)=pX^{a}[r(1-X^{a}/K)-\alpha W]-aX^{a}$, $\pi^{b}(W)=(K/r)(p\gamma-a)\times(r-\alpha W-\gamma)$, $\pi^{c}(W)=ph^{c}-a(K/2r)\left[(r-\alpha W)+\sqrt{(r-\alpha W)^{2}-4rh^{c}/K}\right]$, and $\pi^{*}(W)=p(K/4r)[r^{2}-\delta^{2}-2(r-\delta)\alpha W-(a/p)^{2}+(\alpha W)^{2}]+a(K/2r)[r-\delta-(a/p)-\alpha W]$.

Under the fixed quota scheme (c), there will generally be two solutions for the stock size, and where the highest stock value is in accordance with dynamic stability (again, see above). Hence, π^{c} for obvious reasons (same harvesting income and lower grazing damage) yields a lower profit than the dynamically unstable solution.

The following parameter values are based on Skonhoft and Olaussen (2005), Gundersen (2003) and Nilsen et al. (2005). The maximum specific growth rate is given as $r=0.47$ while the carrying capacity is $K=3500$ (number of moose), which implies about 5.8 moose per square km. We study three alternative predation pressures with $\alpha W=0.05$ as the baseline value. This yields a yearly predation of somewhat below 90 individuals for a population size of, say, $X_{\mathrm{msy}}=K/2=1750$. The high predation pressure of $\alpha W=0.10$ and no predation at all, $\alpha W=0$, are contrasted with this baseline value. The hunting license price is fixed as $p=8000$ (NOK per moose, 2003 prices), while the marginal damage cost follows as $a=300$ (NOK per moose, 2003 prices). We assume no discount in the calculations reported below, $\delta=0$, meaning that the steady state of the present-value maximizing scenario (d) coincides with equilibrium harvesting profit maximizing (see above).

6. Results

Table 1 reports the results when there is no predation, $\alpha W=0$, and where the stock size under the threshold harvesting scenario (a) is $X^{a}=X_{\mathrm{msy}}=K/2=1750$ (number of moose), the harvesting fraction under the proportional harvesting scenario (b) is $\gamma=0.3$, and the harvesting quota under the fixed harvesting quota scenario (c) is $h^{c}=200$ (number of moose). The harvesting fraction under (b) is more or less in accordance with the most recent situation (Gundersen, 2003) while the fixed harvesting quota scheme (c) yields an outtake well below the harvest under the other schemes when there is no predation. The fixed harvesting fraction scheme (b) gives results quite close to the profit maximizing scenario (d), while the fixed quota scheme (c) yields a substantially higher stock. As a consequence, the browsing damage becomes substantial and depresses profitability.

Tables 2 and 3 present the effects under the baseline predation pressure (Table 2) and when the predation pressure is high (Table 3). When compared with

Table 1
Landowner management (no predation $\alpha W=0$)

Management scheme	Population size X	Harvest h	Profit π
(a) Threshold harvesting ($X^{a}=1750$)	1750	411	2765
(b) Proportional harvesting ($\gamma=0.3$)	1266	380	2659
(c) Fixed quota harvesting ($h^{c}=200$)	3004	200	699
(d) Profit maximising[a]	1610	409	2786

Population size (number of moose), harvest (number of moose) and profit (1000 NOK).

[a] Steady-state and no discounting ($\delta=0$).

the no predation scenario, it can be seen that the cost of predation is substantial under the threshold harvesting scheme (a) as the surplus stock available for harvesting decreases significantly with higher predation. The loss is 25% and 51% under the baseline predation and the high predation assumption, respectively. The relative loss is even higher under the fixed harvesting fraction scenario (b) which is somewhat surprising as the profitability effect of predation here is generally unclear. However, because $(p\gamma - D')=(p\gamma - a)=(8000\times 0.3-300)>0$ (cf. Section 4), higher pressure also reduces the profit under this management strategy. The predation cost according to the profit maximizing scheme (d) follows very much the same pattern, with the more modest loss of 12% and 41% under the baseline alternative and high predation pressure, respectively. On the contrary, and in line with the analytical exposition, profitability improves with predation under the fixed quota scenario (c), and increases 20% under the baseline predation pressure compared with no predation.

Sensitivity analysis for the management schemes (a), (b), and (c) is also conducted with different values for the stock threshold level, harvesting fraction, and harvesting quota, respectively. When the threshold stock level is lowered, we find that the economic viability under the threshold scheme (a) worsens as reduced harvesting income dominates reduced browsing damage. However, the cost of predation also becomes less significant. With, say, $X^{\mathrm{a}}=X_{\mathrm{msy}}/2=875$ (number of moose), we find $\pi^{\mathrm{a}}=2205$ (1000 NOK) without predation, which reduces to $\pi^{\mathrm{a}}=1855$ under the baseline predation pressure. The loss is therefore somewhat lower than the previous high threshold level case; just 16% compared to a previous loss of 25% (Table 2). When the harvesting fraction under scenario (b) is reduced, more or less the same picture emerges so long as $(p\gamma - a)>0$ holds (see above).

Table 2
Landowner management (baseline predation $\alpha W=0.05$)

Management scheme	Population size X	Harvest h	Profit π
(a) Threshold harvesting ($X^{\mathrm{a}}=1750$)	1750	324 (−21)	2065 (−25)
(b) Proportional harvesting ($\gamma=0.3$)	894 (−29)	268 (−29)	1877 (−29)
(c) Fixed quota harvesting ($h^{\mathrm{c}}=200$)	2542 (−15)	200	837 (+21)
(d) Profit maximising[a]	1424 (−12)	326 (−20)	2179 (−12)

Population size (number of moose, harvest (number of moose) and profit (1000 NOK).

[a] Steady-state and no discounting ($\delta=0$) In brackets: Deviation from no predation alternative (in %).

Table 3
Landowner management (predation $\alpha W=0.10$)

Management scheme	Population size X	Harvesting h	Profit π
(a) Threshold harvesting ($X^{a}=1750$)	1750	236 (−43)	1365 (−51)
(b) Proportional harvesting ($\gamma=0.3$)	521 (−59)	156 (−59)	1095 (−59)
(c) Fixed quota harvesting ($h^{c}=200$)	2017 (−33)	200	995 (+42)
(d) Profit maximising[a]	1238 (−23)	252 (−38)	1647 (−41)

Population size (number of moose), harvesting (number of moose) and profit (1000 NOK).

[a] Steady-state and no discounting ($\delta=0$) In brackets: Deviation from no predation alternative (in %).

7. The social planner solution and the social benefit of predation

So far landowners have determined the harvest and moose population for a given wolf predation pressure. This may be considered as an institutional outcome where the landowners have property rights (hunting rights) over the moose population, while being corrected for one externality, the public good value of the wolf population (see, e.g., Bromley, 1991). The in-situ value of the wolf population that just balances the predation cost may also be calculated under his property rights scheme, and is indicated by VW.[1] When adding VW and illustrating by using harvesting scheme (d), we find that the social surplus is $S(W)=\pi(W)+VW=2179+VW$ under the baseline predation pressure assumption, and where the first term is the landowner profit (again, see Table 2). Comparing the landowner profit in the absence of predation, and hence neglecting the wolf value, $S(0)=\pi(0)=$

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[1] It should be emphasised that this represents no intention to try to calculate the existence money value of the Scandinavian wolf. This is difficult, if not meaningless, but see Boman and Bostedt (1999) and Dahle et al. (1987) for serious attempts.

2786 (Table 1), we find that $S(W)>S(0)$ implies $VW>(2786-2179)=607$ (1000 NOK). The in-situ social value of the wolf population must therefore be at least 607 to yield a positive social gain of predation under the baseline predation pressure and the profit maximizing harvesting scheme (d). Likewise, we find that under the high predation pressure (Table 3), $VW>(2786-1647)=1139$ (1000 NOK) must hold if predation, on this premise, should be socially desirable.

However, to better assess the social cost or gain of predation, more cost and benefit components should be included. The single most important of these is the damage related to moose–vehicle and moose–railway collisions. These costs can be considerable (see the introductory section) and are, to a large extent, experienced by people living outside the various 'moose areas'. This is also the case in the chosen study area as the traffic damage mostly occurs on the highway and railway connecting Norway's main cities, Oslo and Trondheim, which run through the area. For landowners (as well as the local community) in the Koppang area, the cost related to moose–vehicle collisions is therefore basically external.

A simple, yet realistic, way to account for the moose–vehicle damage is, as for the browsing damage, to relate it to the population size as more moose, *ceteris paribus*, mean more damage (Gundersen, 2003) and a higher yearly cost. That is:

$$T_t = T(X_t) \tag{8}$$

with $T(0)=0$ and $T'>0$. Neglecting further cost and benefit components (but see below), the yearly social benefit of the moose population is $[ph_t-D(X_t)-T(X_t)]$. When assuming that W reflects the socially desirable size of the wolf pack (more on this below), present-value maximizing $\sum_0^{T-1}\rho^t[ph_t-D(X_t)-T(X_t)]$ yields the golden rule of the social planner solution as:

$$F'(X^{\mathrm{s}}) - \frac{D'(X^{\mathrm{s}})+T'(X^{\mathrm{s}})}{p} - G_X(W,X^{\mathrm{s}}) = \delta, \tag{9}$$

where superscript 's' indicates the social planner solution. Compared to the golden rule of the present-value profit maximization scheme of the landowners (6), we find $X^{\mathrm{s}}<X^*$, and hence also $h^{\mathrm{s}}<h^*$ because X^* as well as X^{s} are below that of X_{msy}. Compared to the other management schemes not very much more can be said, as the differences hinge on the parameterization of these models. We therefore concentrate on comparing the steady state of harvesting scheme (d) with the social planner solution.

The social gain (or loss) of predation when traffic damage cost is included is examined using the same functional forms and parameter values as above. In addition, and in line with the application of a linear browsing-damage function, we also introduce a linear traffic-damage function, $T(X_t)=tX_t$ with $t>0$ as the fixed damage cost per moose. Based on Storaas et al. (2001), $t=1000$ (NOK per moose, 2003 prices) is used as a baseline value. $\alpha W=0.05$ first illustrates the predation pressure representing the socially desirable size of the wolf population (Table 4).

Harvesting scheme (d) implemented when the social value of the wolf population is neglected and the traffic damage costs are not taken into account, yields a landowner profit of $\pi(0)=2786$ (1000 NOK) (Table 1). When subtracting the traffic damage cost, the social surplus becomes $S(0)=\pi(0)-T(X)=2786-1610=1176$. On the other hand, profit maximization implemented when correcting for the external traffic damage cost, but still not accounting for the public good value of the wolf population, yields a significantly lower stock (and offtake), and reduces the landowner profit to $\pi(0)=2553$. The social surplus, however, increases to $S(0)=\pi(0)-T(X)=2553-1145=1408$. Finally, the social surplus of the social planner solution becomes $S(W)=\pi(W)-T(X)+VW=1947-959+VW=988+VW$. Under the baseline predation pressure of $\alpha W=0.05$, we hence find that $S(W)>S(0)$, which means that $VW>(1408-988)=420$ (1000 NOK) to yield a positive social value of predation. This in-situ value is well below what was found when the traffic damage cost was not included.

We have also studied what happens under other predation pressure assumptions, and shifting the pressure from $\alpha W=0.05$ to $\alpha W=0.10$ increases this break-even VW value from 420 to 767 (1000 NOK). See also Fig. 2 where break-even VW values are calculated for a whole range of predation rates under the baseline economic conditions. The break-even values may also be calculated under other price and cost assumptions, and not surprisingly they shift upward when the hunting becomes more valuable, and downward with a higher traffic damage cost (Fig. 2). For example, when

Table 4
Social planner solution (steady-state) and landowner management harvesting scheme d), profit maximising (steady-state)

	Population size X	Harvesting h	Landowner profit π	Traffic damage T	Social value wolf population	Social surplus S
Profit maximising	1610	409	2786	1.610	–	1176
Profit maximising, taking traffic damage into account	1145	362	2553	1145	–	1408
Social planner solution	959	279	1947	959	VW	$988+VW$

Population size (number of moose), harvesting (number of moose), profit, traffic damage, social value wolf population and social surplus (all values in 1000 NOK).
Steady-state and no discounting ($\delta=0$). Baseline predation pressure ($\alpha W=0.05$) social planner solution.

the traffic damage cost shifts from 1000 to 1500 (NOK per moose), we find that the break-even *VW* value decreases from 420 to 327 under the baseline predation pressure assumption.

The social gain or cost of predation may also be found under the other management schemes but, as already indicated, nearly everything depends on the parameterization of these models. We therefore just briefly examine the fixed fraction harvesting scheme (b) when $\gamma=0.3$. When the public good value of the wolf population is disregarded and there is no predation, this scheme yields the social surplus of $S(0)=\pi(0)-T(X)=(1659-1266)=1393$ (again, see Table 1). When compared with the social planner solution of $S(W)=\pi(W)-T(X)+VW=(988+VW)$, we find that $VW>405$ to yield a positive social value of predation. This result is therefore very much the same as e found under the profit maximisation scenario (d).

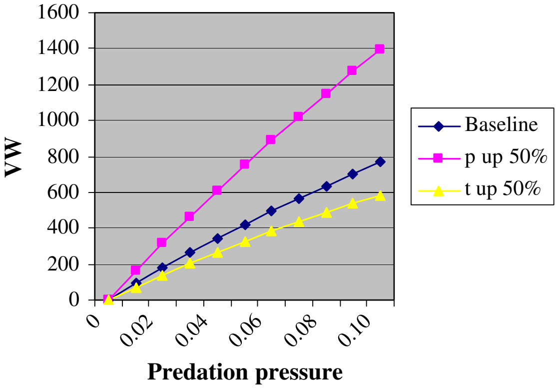

Fig. 2. Break-even in-situ wolf value *VW* (1000 NOK) social planner solution. Baseline parameter values, increased hunting price (*p* shifts from 8000 to 12,000 NOK per moose) and increased traffic damage cost (*t* shifts from 1000 to 1500 NOK per moose).

These calculations are, as noted, only of an illustrative character, as additional value components should be included in a more complete cost–benefit analysis. Such values may include, amongst other things, a positive non-consumptive moose population stock value (viewing value, etc.) and the cost of the wolf pack due to livestock predation. However, because of the large number of moose in Scandinavia, the in situ value of moose is expected to be quite small, if not negligible, at the *margin*. The livestock predation cost of the wolf is also thought to be quite small, but could be of significance in a few local areas (cf. Section 1).

8. Concluding observations

In this paper we have studied a reduced form moose–wolf ecological model where the size of the wolf population affects the moose population growth, but not vice versa, as the wolf population is controlled. Within this framework and in ecological equilibrium, it is demonstrated that the cost to landowners of moose predation strongly depends on their management goals. Two of the moose harvesting schemes considered yield reduced profit while the proportional scheme yields no clear conclusion. In addition to prices and costs, the critical factor here is the size of the harvested fraction. On the other hand, the fixed harvesting quota scheme yields always higher profit in the presence of predation. The reason for this is straightforward as predation reduces the moose stock, and hence browsing damage, while the number of animals harvested, and therefore the harvesting income, remains unchanged. Numerical examples from the Koppang area in Norway indicate that the recent predation pressure may reduce landowner profit by somewhat above 10% under the profit maximizing scheme. The loss may be higher under a proportional harvesting scheme. These results may be readily compared to Flaaten and Stollery (1996), who found that the reduced prey harvest in the Norwegian fisheries because of minke whale predation was somewhere between 3% and 7% of the gross profit of the cod and herring fisheries, respectively.

The assessment of the landowner loss may be considered as an institutional situation where the landowners have property rights (hunting rights) over the moose population while being corrected for one externality, the public good value of the wolf population. When also correcting for the external cost of moose–vehicle collisions, a form of social planner solution is studied. The break-even value of the wolf population alongside the social value of the moose population with and without predation may then be found. Under the baseline price and cost assumptions and a baseline predation pressure of 5%, we find this to be about 420 (1000 NOK) when the landowner's management plan is steered by profit maximization. Hence, on the given premises, if the in situ value of the wolf pack representing such a predation pressure is above 420, there is a social gain in predation. If represented by a wolf pack of, say, four to five individuals (which may be realistic), the per unit wolf value is quite modest. The break-even value increases under improved economic conditions for moose harvesting, while it decreases with a higher cost of traffic damage. These values may be compared to the Scandinavian contingent valuation studies (Dahle et al., 1987; Boman and Bostedt, 1999) which indicates a much higher willingness-to-pay for the wolf existence value (but see footnote 1). The outcomes may also be seen in light of today's harvesting practice in the Koppang area. Assuming that proportional harvesting represents the actual harvesting strategy with the harvesting fraction fixed as 0.3 (Section 5), we find very much the same results as was found under the profit maximisation scheme.

The analysis has been carried out assuming ecological equilibrium. Generally, this fits actual moose management practices in Scandinavia under all the harvesting strategies considered. Despite this, it may make sense to analyse the various management schemes within a dynamic framework. For example, it may be of interest to analyse if, and under what economic and ecological conditions, the proportional harvesting scheme may cause oscillations in the moose population. However, little comparative information about the various management schemes can be inferred from dynamic analysis as the cost of predation, not least because of discounting, critically hinges on the initial size of the moose population.

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