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Livestock and carnivores: Economic and ecological interactions

Abstract

Carnivores-livestock interactions cause human-wildlife conflicts worldwide. These interactions are present under a wide range of ecological and economic circumstances. This paper studies the relationship between predation mortality and natural mortality, when food availability affects natural mortality of the livestock. Semi-domestic Saami reindeer (*Rangifer t. tarandus*) herding in Norway is used as a case study. When predation affects reindeer density, food competition among reindeer changes, which changes weights and natural mortality in the reindeer population. An age-structured bio-economic model is presented, where this relationship is taken into account. While predation mortality may be additional to natural mortality in absence of food limitation, it can compensate for natural mortality in situations of food scarcity. Furthermore, due to density dependency in livestock weights, predation may increase the meat value of livestock. The paper analyzes how predation affects livestock production and economic performance under an optimized management scheme. One main result is that predation shifts the optimal harvesting composition towards calf harvesting and, therefore, the optimal stock composition among the different categories of animals. This contrasts findings in the existing bioeconomic literature. Furthermore, a changing harvesting pattern towards calf harvest is an important adjustment that highly limits the negative impact on profit of predation.

JEL Codes: Q2, Q24**Keywords:** livestock-predation model, food limitation, ecological and economic compensation mechanisms

1. Introduction

Throughout the world, interactions between carnivores and livestock can cause conflicts between humans and wildlife. Examples include wolf predation on sheep in North America and Europe (e.g. Berger 2006, Skonhoft 2006); bear, lynx, golden eagle, and wolverine predating on semi-domestic reindeer in Scandinavia (Nieminen 2010, Tveraa et al. 2003, Zabel et al. 2014); lion, leopard, spotted hyena, and cheetah killing livestock in Africa (Kolowski 2006); snow leopards and wolf killing livestock in the Himalayas (Mishra 1997); and tiger conservation and livestock predation in India (Zabel et al. 2011). See also Graham et al. (2005) for an overview. Over the last few years, predation control and various monetary compensation schemes, including PES (Payment for Environmental Services), have attracted an increasing interest as mechanisms to moderate these conflicts, and also to translate external, non-market environmental service values into economic incentives to provide environmental services (e.g., Berger 2006, Tveraa et al. 2014, and Zabel et al. 2014). For an overview, see Engel at al. (2008).

The interactions between carnivores and livestock take place under widely different ecological and economic circumstances. This paper considers the interaction between predation mortality and density-dependent natural mortality. Density dependence of natural mortality works through food limitation for livestock and may be caused by changing climate conditions, such as severe drought in semi-arid tropics and harsh winter conditions in alpine areas in northern Europe, but also by poor management of common pastures resulting in overgrazing as in the 'tragedy of the commons' (Hardin 1968). The relationship between predation mortality and food availability for prey has received considerable attention in the

ecological literature (e.g., Ballard et al. 2001, Boyce et al. 1999, Sinclair and Pech 1996, Tveraa et al. 2003, Vucetic et al. 2005, Wilmers et al. 2007). In general, it is more likely that predation is followed by density dependent weight increases resulting in reduced natural mortality and improved recruitment when ungulate density is high. On the other hand, when pastures are plentiful, predation has less impact on weights and therefore, is more likely to limit ungulate populations (e.g., Ballard et al. 2001). When livestock density increases, competition for food increases, leading to reduced livestock weight and increased natural mortality. That is, whether predation comes additionally to natural mortality (*additive* loss) or compensates for natural mortality (*compensatory* loss) depends on the significance of food limitation. A similar relationship has been demonstrated in semi-domestic reindeer herding in Norway, where reindeer rely on natural pastures throughout the year (Tveraa et al. 2003). Predation therefore affects the economics of livestock through changes in both livestock population size and weights, or the meat value per animal. To our knowledge, the latter is almost completely neglected in the natural resource economic literature. One exception is a descriptive analysis of such mechanisms found in Skonhoft et al. (2017).

In this paper, we analyze the carnivore-livestock relationship framed in an age-and sex-structured model. While optimal harvesting decisions in natural resource economics for years been analyzed within biomass models, (e.g., Clark 1990), it has been argued that such models have limited impact on actual management due to their overly simplifying properties (Wilen 2000). In a pioneering work, Tahvonen (2009) developed an analytical solvable age structure model for a fishery and demonstrated that the derived optimal harvesting might be significantly different from biomass models. Later contributors have applied age structure models to analyze e.g., several aspects of the optimal harvest among different age classes

and the role of gear and fishing selectivity (Skonhoft et al. 2012), and optimal harvesting in marine multi-species models (Bertram and Quaas 2017).

Age (and sex) structure models have also been introduced in the economics of terrestrial animal species. In case of wildlife management in Scandinavia, contributors have demonstrated how optimal harvesting decisions shift with changes in wildlife-imposed damages (Olaussen and Skonhoft 2011), when introducing trophy hunting (Naevdal et al. 2012), and when taking recreational values of hunting into account (Skonhoft et al. 2013). Tahvonen et al. (2014) developed a very detailed herbivore-plant model of semi-domestic reindeer-lichen interaction in Finland to analyze optimal harvesting of reindeer, and demonstrated recovery paths from overgrazed pastures. Other contributions include Elofsson et al. (2017) who analyzed hunting in a two species competing model. For a general modeling overview from a biological perspective, see Getz and Haight (1989) and Caswell (2001).

The present paper formulates a predator-prey model to analyze ecological and economic compensation effects caused by predation, and where semi-domestic reindeer (*Rangifer t. tarandus*) herding in Norway is used as a case study. Because the impact of predation typically differs between age categories of reindeer, the model includes age structure of the population. Furthermore, the age structure is of vital importance to understand how predation affects the optimal composition of harvest between age classes. A crucial characteristic of the model is to assume that reindeer weights are density dependent, which reflects that higher reindeer population levels mean less pasture per animal and hence, lower weights. We also assume density-dependency through the weight functions not only in the natural survival rates, but also in the recruitment rate. That is, while predation has a

direct negative effect on the size of the reindeer population, there is an indirect opposite effect present, working through higher weights, resulting in reduced natural mortality rates and increased recruitment rate. This is the ecological compensation effect.

As far as we know, with the exception of Skonhoft (2008) and Skonhoft el al. (2017), predation has never been included in an age structured bioeconomic terrestrial animal species model. However, contributions from fishery economics include Bertram and Quaas (2017), who extended the model in Tahvonen et al. (2013) to a predator-prey model. In contrast to the present analysis, they consider weights as fixed and hence, disregards any ecological, as well as economic, compensation effects. Just as in Bertram and Quaas (2017) we assume fixed (and exogeneous) predation rates, but we also include a situation where the rates vary with the reindeer density. The reindeer population may also influence the predator populations. However, this feedback effect (numerical response) is neglected as it is assumed the carnivores have alternative food sources (see, e.g., Boman et al. 2003 and Nilsen et al. 2005 for a discussion in somewhat other ecological settings in Scandinavia), and that the number of carnivores is strictly controlled with certain population goals for lynx and wolverine (see, e.g., Ekspertutvalget 2011). The carnivore population size is thus assumed independent of the size of the reindeer population.

The model presented is analyzed under an optimized management scheme, but this solution is also compared with a situation of severe overgrazing. The latter reflects the present management scheme in the major reindeer herding area in Norway and has clear signs of a 'tragedy of the commons' situation (Johannesen and Skonhoft 2009, Skonhoft et al. 2017). The novelty of our analysis is to include both age structure and ecological and economic compensation effects in a predator prey setting. One main result is that while predation

imposes an economic loss for sure in the optimized scheme, the loss may be significantly lower than expected due to the ecological and economic compensation effects involved. Another main result is that predation shifts the optimal harvesting composition among the different categories of animals.

The rest of the paper is structured as follows. In section 2, we start by giving a brief background of Saami reindeer herding in Norway and the prevailing problems related to food shortage and predation. Section 3 formulates the reindeer population model structured in three age classes, and where the weight-mortality, weight-fecundity and weight-density relationships are included. The effect of carnivore predation on total loss is also introduced here. This part of the model is based on Skonhoft et al. (2017). The considered reindeer population is assumed to be managed by a group of herders acting as a single agent and the economic benefit and cost functions for this management unit are formulated in section 4. The optimal management scheme follows in section 5. Section 6 presents the data and demonstrates the numerical results, and where we also compare with 'tragedy of the commons' case in Skonhoft et al. (2017). The same section also presents some results where the predation is assumed to be density dependent. Finally, section 7 concludes the study.

2. Saami reindeer herding and food limitation

Reindeer husbandry in Norway is a traditional and culturally based livelihood of the Saami people. During the 15th century, entire herds of wild reindeer were domesticated and parts of the Saami people became herding nomads. The nomadic tradition has been preserved until today, where herds are relocated across huge areas between the summer- and winter

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grazing pastures. See Johannesen and Skonhoft (2011) for details. Reindeer herders rely on reindeer as their only source of agricultural production and reindeer meat is the main product (Johannesen and Skonhoft 2011). Reindeer herding is a small economic activity, comprising some 530 herding units keeping in total 230,000 animals (NRHA 2014)[1]. Some 2,000 tons of reindeer meat are produced yearly, which amounts to 1-2 percent of the total production of red meat in Norway (NRHA 2013b)[2].

Although small on a national scale, reindeer husbandry is of great importance to the Saami people both culturally and economically (Johannesen and Skonhoft 2009). It is an arena for sustaining and transferring Saami language, crafts, and knowledge and use of nature across generations. The importance with regard to sustaining Saami culture has also been emphasized by the Norwegian government, both in official statements (e.g., St. prp. Nr. 63 (2007-2008)) and through different types of subsidies. Interviews with Saami reindeer herders in the northernmost parts of Norway suggest that cultural values are important when choosing reindeer husbandry as a living, and herders seem to consider these values just as high as the income opportunities the industry provides (Johannesen and Skonhoft 2011).

The largest herding area in Norway is located in the northernmost part of the country, and constitutes about 70 % of the total reindeer activity in the country in terms of herd sizes and people involved (NRHA 2014). The climate conditions in this area are favorable for reindeer herding. The winter climate is dry, cold and stable, and a shallow and stable snow depth provides good access to food (Tveraa et al. 2007). Over the past decades, however, the herding communities in this area have been characterized by internal conflicts and strong

competition among herders over access to pastures (Hausner et al. 2012, Johannesen and Skonhoft 2009, Riseth and Vatn 2009). Lack of cooperation and coordination has resulted in increased herd sizes, by as much as 40% from 2002 to 2010 (Næss and Bårdsen 2015), and subsequent pasture degradation and food shortages (Johansen and Karlsen 2005), in short the 'tragedy of the commons' (Johannesen and Skonhoft 2009). At the same time, there has been a downward trend in animal weights in parts of the northernmost areas (Tveraa et al. 2012, figure 3), and ecological studies demonstrate a negative relationship between reindeer density and weights (Bårdsen et al. 2010, Bårdsen and Tveraa 2012). High population densities and low weights have also worked in the direction of reduced natural survival rates, especially for calves, as they are more prone to starvation than adult animals (Tveraa et al. 2013). Because females with lower weights are less likely to reproduce, lower fertility rates have also been observed (Bårdsen et al. 2010, Tveraa et al. 2003). For more details, see Skonhoft et al. (2017).

Hence, the effect of density dependence on population dynamics works through animal weights. Pasture quality and quantity also affects reindeer mortality due to predators, i.e. lynx (*Lynx lynx*), wolverine (*Gulo gulo*), and golden eagle (*Aquila chrysaetos*) (Tveraa et al. 2014), as small and weak reindeer, especially calves, are more vulnerable to predators than animals in good condition (Tveraa et al. 2003). Loss of reindeer to predators per area unit has increased substantially over the past few years in northernmost parts of Norway, also relatively to other reindeer herding areas in the country (Skonhoft et al. 2017). Accordingly, it has been suggested that the risk of losing reindeer to predators is dependent on reindeer's nutritional condition. Furthermore, it has been shown that various indicators of food limitation (i.e., reindeer density, climate, and plant productivity) are the most important variables explaining differences in losses to predators across reindeer herding areas (Tveraa

et al. 2014). When combined with findings showing that predators tend to kill weak animals (Tveraa et al. 2003), Tveraa et al. (2014) claim that losses to predators in the northernmost parts of Norway are highly compensatory. That is, a large fraction of animals killed would have died naturally due to their poor condition, even in the absence of predators.

3. Population model

As previously mentioned (section 2 above), there are clear indications of density dependent natural mortality in the reindeer population in northernmost Norway. The fecundity has also proven to be density dependent, working through food shortages (Tverraa et al. 2013). Therefore, the present model considers both the fertility- and natural mortality rates as density dependent through animal weights. Instead of using weight loss during winter as argument (Tahvonen et al. 2014), however, fertility- and natural mortality rates are related to the weights before the winter grazing season. Quality, size of the pasture, and weather conditions are assumed fixed (but see Tahvonen et al. 2014) and weights are associated with the grazing pressure through the number of grazing animals. That is, the density dependent fertility and natural mortality effects work through the number of animals, indirectly through animal weights (see also Borowik et al. 2016). Mortality rates generally differ between the different age classes, and are typically higher for calves than adults (Bårdsen et al. 2014). Within the range of actual reindeer densities, the sex composition seems to play a negligible fecundity role, and recruitment in our model is therefore steered by the number of adult females. However, an upper harvesting rate constraint is included for the male population to secure a minimum size of the male population. The predation rates are generally different for female and male adults, and both are generally lower than that of calves (Tveraa et al.

2003). As indicated, these predation rates are assumed fixed, but in section 6.5 we relax this assumption. All age classes have a slaughter value and are generally slaughtered.

The reindeer population managed by our considered group of herders at time (year) t is structured in three age classes: calves $X_{c,t}$ ($yr < 1$), adult females $X_{f,t}$ ($yr \geq 1$), and adult males $X_{m,t}$ ($yr \geq 1$). The population is measured in spring just before calving. As we neglect summer mortality and assume predation takes place after winter natural mortality, the events over the yearly cycle are then calving; slaughtering, which takes place in September – October; winter natural mortality (diseases, accidents, starvation); and predation[3]. The number of calves (recruitment) is first governed by:

(1) $\qquad X_{c,t} = f_t X_{f,t}$

where $f_t > 0$ is the fertility rate (number of calves per female). The fertility rate depends on food conditions/food shortages approximated by the (average) female weight $w_{f,t}$ (cf. section 1 above):

(2) $\qquad f_t = f(w_{f,t})$,

with $f' \geq 0$ and $f'' \leq 0$. The function is specified as:

(2') $\qquad f_t = \overline{f} \cdot (w_{f,t} / \overline{w}_f)^a$,

where $f_t = \overline{f}$ is the maximum fertility rate when the adult female weight reaches its maximum value, $w_{f,t} = \overline{w}_f$, while the parameter $0 < a < 1$ indicates that fertility is a concave function of the weight.

The natural survival rates $0 < s_{i,t} < 1$ also depend on the food conditions approximated by the weights and are generally different for the different age classes:

(3) $s_{i,t} = s_i(w_{i,t})$; $i = c, f, m$,

with $s_i' \geq 0$ and $s_i'' \leq 0$. It is specified as:

(3′) $s_{i,t} = \bar{s}_i \cdot (w_{i,t} / \bar{w}_i)^{b_i}$; $i = c, f, m$,

with $\bar{s}_i$ as the maximum survival rate for animal category i , and where the parameter $0 < b_i < 1$ generally differs among the animal categories.

The fixed predation rates $0 \leq m_i < 1$, $i = c, f, m$, also generally differ between sexes and age classes, and is typically lower for adults than calves $m_c > m_f \neq m_m$ (Mattisson et al. 2014, 2016, Tveraa et al. 2003). With these rates defined, the abundance of adult females and males are written as:

(4) $X_{f,t+1} = \psi(1 - h_{c,t})X_{c,t}s_{c,t}(1 - m_c) + (1 - h_{f,t})X_{f,t}s_{f,t}(1 - m_f)$

and

(5) $X_{m,t+1} = (1 - \psi)(1 - h_{c,t})X_{c,t}s_{c,t}(1 - m_c) + (1 - h_{m,t})X_{m,t}s_{m,t}(1 - m_m)$,

respectively, and where ψ is the fraction of female calves (usually about 0.5) and $0 \leq h_{i,t} < 1$ represents the harvest, or slaughter, rates.

The weight of the animals depends on food availability and the grazing pressure during the summer and fall, approximated by the total number of grazing animals[4]. We hence have:

(6) $w_{i,t} = w_i(X_{c,t} + X_{f,t} + X_{m,t}) = w_i(X_t)$; $i = c, f, m$,

with $w_i' \leq 0$. This weight-density relationships are specified as sigmoidal functions with an increasing degree of density dependence at high densities (Mysterud et al. 2001, Nielsen et al. 2005). This functional form is assumed for all categories of animals and reads:

(6′) $w_{i,t} = \dfrac{\overline{w}_i}{1 + (X_t / K)^\beta}$; $i = c, f, m$.

The parameter $K > 0$ is the stock size for which the density-dependent weight effect is equal to density-independent weight effect. This parameter scales the population sizes, and its value is contingent upon factors like the size of the grazing area and the productivity of the grazing resources (i.e., lichen). The parameter $\beta > 0$ indicates to what extent density-independent factors compensate for changes in the stock size. From Eq. (6) we find that the total animal density feeds back to the fertility rate through Eq. (2) and the natural survival rates through Eq. (3). For the above specified functional forms this yields

$f_t = \overline{f} \cdot (\dfrac{1}{1 + (X_t / K)^\beta})^a$ and $s_{i,t} = \overline{s}_i \cdot (\dfrac{1}{1 + (X_t / K)^\beta})^{b_i}$, respectively. Therefore, both the

fertility rate and the survival rates are sigmoidal functions of the total animal stock.

It is also recognized that predation and natural mortality are interacting. When the predation rates are exogenous, and when the first order predation mortality effect works in the direction of less animals, we have $X_{t+1} = X(m_c, m_f, m_m)$ with $\partial X_{t+1} / \partial m_j < 0$ ($j = c, f, m$). As a consequence, the animal weights increase through Eq. (6), $w_{i,t+1} = w_i(X(m_c, m_f, m_m))$, with $\partial w_{i,t+1} / \partial m_j = (\partial w_i / \partial X)(\partial X / \partial m_j) \geq 0$. This again feeds into higher natural survival rates through Eq. (3), $s_{i,t} = s_i(X(m_c, m_f, m_m))$, $i = c, f, m$, with

$\partial s_{i,t+1} / \partial m_j = (\partial s_i / \partial w_i)(\partial w_i / \partial X)(\partial X / \partial m_j) \ge 0$. Therefore, predation mortality generally *compensates* natural mortality; that is, higher predation pressure shifts up the natural survival rates[5]. This compensatory effect will typically be stronger in the presence of a severe food shortage and also in situations where weights are more sensitive to changes in animal density. There is also a compensating effect present through the fertility rate, as we find

$f_t = f(w_{f,t}(X(m_c, m_f, m_m)))$ with $\partial f_{t+1} / \partial m_j = (\partial f_t / \partial w_f)(\partial w_f / \partial X)(\partial X / \partial m_j) \ge 0$.

We may also consider the above compensatory effects in terms of morality rates. With natural mortality of category i (after harvest) given as $N_{i,t} = (1 - h_{i,t})X_{i,t}(1 - s_{i,t})$ and predation as $M_{i,t} = (1 - h_{i,t})X_{i,t}s_{i,t}m_i$, the total of natural- and predation mortality of category i becomes $N_{i,t} + M_{i,t} = (1 - h_{i,t})X_{i,t}(1 - s_{i,t}) + (1 - h_{i,t})X_{i,t}s_{i,t}m_i$. The total loss rate (after harvest) may therefore be written as $(N_{i,t} + M_{i,t}) / ((1 - h_{i,t})X_{i,t}) \equiv g_{i,t} = (1 - s_{i,t}) + s_{i,t}m_i$. Changing mortality rates due to increased predation reads now

$\partial g_{i,t+1} / \partial m_i = s_{i,t} - (1 - m_i)(\partial s_{i,t+1} / \partial m_i)$ with $\partial s_{i,t+1} / \partial m_i \ge 0$. The first order effect is therefore captured by the term $s_{i,t}$. The second order effect is captured by $-(1 - m_i)(\partial s_{i,t+1} / \partial m_i)$, and this represents the feed-back, or compensatory effect. Again, this effect is supposed to be stronger under the present management situation than under the optimized management scheme.

4. Cost and benefit functions

In this paper, we are only concerned with the slaughtering value and the maintenance costs of the animals. Therefore, any positive stock values are neglected (but see Johannesen and Skonhoft 2011). As natural mortality and predation are assumed to take place during the late fall and winter, after the slaughtering (section 3 above), the number of animals removed through slaughtering is $H_{i,t} = h_{i,t}X_{i,t}$, $i = c, f, m$. The current slaughter revenue, or meat value, R_t for our considered group of herders is accordingly:

(9) $R_t = p(w_{c,t}h_{c,t}X_{c,t} + w_{f,t}h_{f,t}X_{f,t} + w_{m,t}h_{m,t}X_{m,t})$,

and where p is the net meat price (EUR/kg), i.e., the unit slaughter value corrected for slaughter costs. The justification for the fixed unit price is that meat production from the considered group of herders constitutes only a limited part of the supply of reindeer meat to the Norwegian market. The same assumption is recently applied by Tahvonen et al (2014), Pekkarinen et al. (2015), and Pekkarinen et al (2017) analyzing reindeer herding in Finland.

The operating costs are generally different between winter and summer seasons. There are also costs included in the moving of animals from the winter grazing to the summer grazing area, and *vice versa*. However, such differences in seasonal costs are neglected, and we simply relate the operating costs to the total size of the summer stock:

 (10) $C_t = C(X_{c,t} + X_{f,t} + X_{m,t})$,

According to NRHA (2014) this cost function is typically strictly concave for rather small stock sizes, and then more or less linear. As we consider a group of herders (acting as a single agent) with a herd size that may be rather large, we assume the cost function to be linear, and thus $C' > 0$ and $C'' = 0$, and $C(0) = 0$. In this paper, the possible costs of protective

effort with respect to predation, and also any compensation benefits for the predation losses offered by the State are not taken into account. Therefore, Eq. (10) represents the total variable costs. As any possible positive stock value is not included (see above), the current net benefit, or profit, is thus given by:

(11) $\quad \pi_t = R_t - C_t = p(w_{c,t}h_{c,t}X_{c,t} + w_{f,t}h_{f,t}X_{f,t} + w_{m,t}h_{m,t}X_{m,t}) - C(X_{c,t} + X_{f,t} + X_{m,t})$

More aggressive predation for *given* harvesting rates will generally reduce the stock sizes and thereby work in the direction of reduced slaughter revenue. However, in addition to counteracting ecological forces in terms of reduced natural mortality and increased fertility, there are also important counteracting economic forces, as smaller stock sizes feed back into higher animal weights, and thus higher per animal meat values. Additionally, the operating costs will be reduced. Generally, when keeping harvesting rates fixed and ignoring any adjustment via optimization (see section 6.4), more aggressive predation therefore has an ambiguous effect on profitability through both ecological and economic forces. On the other hand, under optimizing behavior, increased predation will affect the profitability if it influences harvest rates and stock sizes. The feasible solution space then reduces and profitability will be lowered.

5. Optimal management scheme

The management scheme where a unified manager chooses harvest rates and stock sizes optimally in order to maximize the present value profit of the reindeer stock is now

analyzed. The manager hence aims to $\max\limits_{h_{c,t},h_{f,t},h_{m,t},X_{c,t},X_{f,t},X_{m,t}} PV = \sum\limits_{t=0}^{\infty} \rho^t \pi_t$ subject to the

biological constraints (1), (4), and (5). In addition, as indicated, a constraint is added to avoid

a too skewed male/female ratio as males is not explicitly included in the recruitment

function Eq. (1), $h_{m,t} \leq \overline{h}_m$, and where $\overline{h}_m$ is the upper limit male harvest level (see also

Skonhoft et al. 2013). The discount factor is $\rho = 1/(1+\delta)$ with $\delta \geq 0$ as the discount rate.

The current value Hamiltonian of this problem is written as:

$$
\begin{aligned}
H = {} & p\left(w_{c,t}h_{c,t}X_{c,t} + w_{f,t}h_{f,t}X_{f,t} + w_{m,t}h_{m,t}X_{m,t}\right) - C\left(X_{c,t} + X_{f,t} + X_{m,t}\right) - \lambda_t\left(X_{c,t} - f_t X_{f,t}\right) \\
& - \rho\mu_{t+1}\left(X_{f,t+1} - \psi\left((1-h_{c,t})X_{c,t}s_{c,t}(1-m_c) - \left((1-h_{f,t})X_{f,t}s_{f,t}(1-m_f)\right)\right)\right) \\
& - \rho\eta_{t+1}\left(X_{m,t+1} - (1-\psi)(1-h_{c,t})X_{c,t}s_{c,t}(1-m_c) - (1-h_{m,t})X_{m,t}s_{m,t}\left(1-m_m\right)\right) \\
& - \varpi_t\left(h_{m,t} - \overline{h}_m\right).
\end{aligned}
$$
(12)

Here, $\lambda_t > 0$, $\mu_t > 0$, and $\eta_t > 0$ are the shadow prices of the calf population constraint (1),

the female constraint (4), and the male population constraint (5), respectively, while $\varpi_t \geq 0$

is the shadow price of the male harvest rate constraint.

The first-order necessary control conditions of this maximizing problem are stated with the

actual complementary slackness conditions and where the possibility for keeping each of the

age classes unexploited is considered. Additionally, the possibility for harvesting all calves

and females is also taken into account. These control conditions with $X_{i,t} > 0$ ($i = c, f, m$)

are then:

(13) $\quad \dfrac{\partial H}{\partial h_{c,t}} = X_{c,t}\left[pw_{c,t} - s_{c,t}(1-m_c)\rho\left(\mu_{t+1}\psi + \eta_{t+1}(1-\psi)\right)\right] \mathrel{\overset{\geq}{\underset{<}{=}}} 0 \; ; 0 \leq h_{c,t} \leq 1,$

(14) $\quad \dfrac{\partial H}{\partial h_{f,t}} = X_{f,t}\left[pw_{f,t} - \rho\mu_{t+1}\left(s_{f,t}(1-m_f)\right)\right] \gtreqless 0 \quad ; 0 \le h_{f,t} \le 1,$

and

(15) $\quad \dfrac{\partial H}{\partial h_{m,t}} = pw_{m,t}X_{m,t} - \rho\eta_{t+1}\left(X_{m,t}s_{m,t}(1-m_m)\right) - \varpi_t \le 0 \quad ; 0 \le h_{m,t} \le \bar{h}_m .$

The portfolio conditions $-\partial H / \partial X_{c,t} = \rho\lambda_{t+1} - \lambda_t$, $-\partial H / \partial X_{f,t} = \rho\mu_{t+1} - \mu_t$, and

$-\partial H / \partial X_{m,t} = \rho\eta_{t+1} - \eta_t$ are rather messy. For the calves, it reads:

$$-\dfrac{\partial H}{\partial X_{c,t}} = -p(w_{c,t}h_{c,t} + h_{c,t}X_{c,t}w'_{c,t} + h_{f,t}X_{f,t}w'_{f,t} + h_{m,t}X_{m,t}w'_{m,t}) + C' + \lambda_t - \lambda_t f'_t w'_{f,t} X_{f,t}$$

$$-\rho\mu_{t+1}\psi(1-h_{c,t})(1-m_c)(s_{c,t} + X_{c,t}s'_{c,t}w'_{c,t}) - \rho\mu_{t+1}(1-h_{f,t})(1-m_f)X_{f,t}s'_{f,t}w'_{f,t}$$

(16)

$$-\rho\eta_{t+1}(1-\psi)(1-h_{c,t})(1-m_c)\left(s_{c,t} + X_{c,t}s'_{c,t}w'_{c,t}\right)$$

$$-\rho\eta_{t+1}(1-h_{m,t})(1-m_m)X_{m,t}s'_{m,t}w'_{m,t} = \rho\lambda_{t+1} - \lambda_t$$

For the other categories of animals, the portfolio conditions follow similar patterns (available from authors upon request).

Control condition (13) states that calf harvesting should take place up to the point where the marginal harvest value is equal to, or below, the marginal cost in terms of the sex weighted reduced populations of adults, when evaluated at their respective shadow prices, while also taking biological ($s_{c,t}$) and economic (ρ) discounting into account. Additionally, predation influences the marginal cost. When this condition is strictly negative, the marginal benefit is below the marginal cost and harvesting is thus not profitable, i.e., $h_{c,t} = 0$. On the other hand, when it is strictly positive, it indicates that the whole calf population should be slaughtered. However, this is not likely to show up as an optimal option over a long

sequence of years as the whole population then goes extinct. Notice that the *direct* effect of higher predation rate m_c is reduced marginal cost, and hence works in the direction of more aggressive harvesting.

In a similar manner, control condition (14) states that females should be harvested up to the point where marginal meat revenue is equal, below or higher than the marginal cost in terms of reduced growth evaluated at the discounted female shadow price. The male control condition (15) is analogue to the female harvest condition, but with the additional shadow price ϖ_t associated with the male upper limit harvest constraint. With $\varpi_t > 0$ the upper male harvest restriction is binding, and we have $h_{m,t} = \bar{h}_m$. This means that there is potentially a cost in terms of reduced profit associated with the harvest limit.

While the direct harvesting effect of increased predation pressure m_i ($i = c, f, m$) works in the direction of lower marginal costs and more aggressive harvesting for all categories of animals, it is difficult to assess the total effect due to the density dependency affecting the fertility, natural survival, and weight functions. These *indirect* effects, or ecological compensation effects, working through lower stock sizes and higher shadow prices, pull in the direction of higher weight of each animal category, and hence shifts up the natural survival rates. Accordingly, the marginal harvest costs are shifted up. Therefore, depending on the magnitude of the ecological compensation effects, more predation may either increase or reduce harvesting rates. The direction and magnitudes of these effects are studied in detail numerically below.

6. Numerical analysis

6.1 The data

This section presents numerical ecological and economic results. The baseline values used fit well with the present 'tragedy of the commons' situation in the northern part of Norway (see also section 2), which was analyzed in Skonhoft et al. (2017). Table 1 presents the baseline parameter values. The main source is the annual reports from herders in western Finnmark to the government (NRHA 2014) and official statistics on losses to predators (http://www.rovbase.no). Our baseline fixed predation rates are as in Skonhoft et al. (2017), where losses to predators are based on a combination of losses reported by herders yearly when applying to the State for compensation for losses and the number of losses considered as likely by the State when offering compensation (http://www.rovbase.no). Due to the characteristics of the compensation system, there is a tendency of overstating losses to predators and understating natural mortality accordingly in order to increase the compensation payment received (see Tveraa et al. 2014). Hence, it is difficult to determine the exact baseline loss to predators. The baseline predation rates in Table 1 are therefore specified based on the average of claimed and compensated losses in 2013 and suggest that, after harvesting and natural mortality 27% of the calve population and 4% of the adult population and lost to predators. The baseline predation scenario is compared with two other scenarios; no predation at all and a high predation pressure.

Table 1 about here

The reindeer density in northern part of Norway was 70 animals/10km^2 in 2012 and the average (slaughter) weight of calves was 17 kilo/animal (NRHA 2014). The slaughter weights and calving rate in the best performing reindeer herding area in Norway, where the vegetation cover is intact, are used as proxies for maximum weights and calving rate, respectively. Then, Figure 1 showing the weight, natural survival, and recruitment functions, clearly indicates that changing total stock size in the domain of a high animal density of, say, 80 (animals/10km^2) has a more profound effect on the animal weights, and hence also the survival- and recruitment rates, than a low animal density of, say, 40 animals. This is in line with ecological evidence suggesting a negative relationship between density and body mass, but less a profound relationship in presence of good pasture conditions (Bårdsen and Tveraa 2012). The concave-convex form is also in accordance with the model developed by Pekkarinen et al. (2015), although their functional arguments differ from the present ones. Therefore, the effect of a given as well as a shifting predation pressure on natural survival and fertility, depends on the population density. The male harvest constraint is set to 0.7. For more details on the parametrization of the model, see Skonhoft et al. (2017).

Figure 1 about here

6.2 Results

The change in the population size over time depends on the strength of the density dependency in weights, natural survival, and recruitment; also, a steep sigmoidal weight

function may typically render the system unstable. However, within a reasonable range of predation pressures (see below), the system approaches a steady state relatively rapidly, and without any overshooting/undershooting, see Figure 2. In the remaining parts of the paper, we therefore concentrate on demonstrating steady state results[6].

Figure 2 about here

Table 2 presents the steady state biological results under the various predation pressures, while Table 3 gives the harvest and economic results. First, as the predation rates shift up from Zero to the Baseline scenario, the steady state stock reduces (column two and three, Table 2). For all age classes, the total loss of animals (last column) is dampened by the ecological compensation mechanisms working through higher weights (column four, Table 3) and increased natural survival rates (column four, Table 2). However, this is not enough to offset an increase in total loss of calves and adult females (last column). Still, the ecological compensation is strong enough to ensure unchanged total loss for adult males.

Table 2 about here

With a further increase in the predation rates to the High level scenario, the density effect in total number of animals, and hence weights (Table 3), is negligible. Consequently, the natural survival rates remain unchanged for all classes. Still, total loss now starts to reduce

for calves, and the reason is that the optimal harvest rate has increased (Table 3). That is, it becomes optimal to harvest a higher fraction of calves before natural and predation mortality occur. In contrast, female total loss increases further (Table 2), mainly because the fraction of females harvested reduces (Table 3).

From Table 3 we also notice that the optimal harvest rate of calves remains zero when moving from Zero to Baseline predation pressure (column one). This happens irrespective of the fact that the direct effect through optimality condition (13) (section 5 above) works in the direction of reduced marginal cost. Therefore, the indirect effects working through the ecological compensation mechanisms offset the direct effect. Perhaps more surprisingly, the optimal female harvest rate drops from 0.38 to 0.25. As the predation pressure increases from no predation to the Baseline scenario, it is thus optimal to reduce the harvest rate of adult females. The reason is that a lower female harvesting rate increases recruitment, and that this effect dominates the direct marginal cost effect working in the direction of more aggressive harvesting through condition 14 (section 5). However, when the predation pressure further increases from the Baseline to the High level scenario, the harvest rate of calves increases from 0.0 to 0.7, indicating that the direct marginal cost effect dominates the indirect effects. On the other hand, it becomes optimal to harvest no females at all. The reason why the optimal harvest rates shift in opposite directions is that a higher calf harvest rate transfers calves that would otherwise be lost to predators to slaughtering revenue, while it becomes optimal to reduce the female harvest rate and increase the female stock to ensure increased recruitment and a larger stock of calves. Therefore, as the predation rate is higher for calves than for adults, an increased calf harvest mitigates the higher predation pressure more effectively than that of adult female harvest. This is indeed an interesting effect and highlights the importance of analysing the complexity of predation in an age-

structured setting, as the compensation effects of predation clearly affects the optimal composition of harvest between different age classes of the population.

Table 3 about here

Table 3 also demonstrates that the number of animals harvested decreases (column two) when moving from Zero to the Baseline predation scenario. The reason is that the stock sizes reduce, as well as the female harvest rate (column one). On the other hand, as already indicated, the slaughter weights increase (column three), which dampens the negative effect on harvesting revenue of increased predation (column four). This is the economic compensation effect. In addition, the operating cost reduces as the stock size reduces, which further dampens the negative impact on the profit. Still, profit reduces by 33% (1,697/2,546). Hence, it is more interesting to note that increased predation pressure from Baseline to the High scenario is accompanied by a profitability reduction of just 8% (1,556/1,697). Again, one modifying effect is the increased weight of each category of animals (calf, female, male). However, the changed harvest pattern shifting from female to calf harvest is an important adjustment, highly limiting the negative impact on profit of increased predation.

Figure 3 further explores the changes in harvest (panel a) and total loss (panel b) due to predation. Both the harvest rate and total loss of calves peak around the High predation pressure scenario, representing a 25 percent increase in the predation pressure compared to Baseline scenario, and then decreases. Accordingly, for a further increase in the predation

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pressure the harvest of calves must be reduced to compensate for the predation loss in all categories of the reindeer population. It is also observed that it is optimal with zero female harvesting around this 25 percent increase in predation compared to Baseline scenario. The male harvest rate remains constant as given by the upper constraint $\bar{h}_m = 0.70$ for all predation pressures presented.

Figure 3 about here

6.3 Sensitivity analysis

We demonstrate now how changes in the density dependency parameters regulating recruitment, natural survival rates, and weights affect the economic outcome. First, a partial increase in the density dependency in the recruitment function (increased a; Eq. 2') implies that the sum of natural-, predation-, and harvesting mortality increases relatively to stock growth. The animal density therefore reduces, which causes weights, and hence, natural survival and recruitment to increase until a new steady state is approached. In the numerical examples we find that the impact on profit is negative or zero as the effect via higher weights never dominates a lower stock density, and hence fewer animals harvested. See Figure 4, panel a). The effect on profit of increased density dependency in the natural survival functions (increased b_i, $i = c, f, m$; Eq. 3') is next considered, and we find it to be quite similar (panel b). It is equally important to note that changing the density dependency in recruitment and natural survival rates result in more or less similar profitability effects

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irrespective of the predation pressure. However, as illustrated in Figure 4 (a) and (b), the strength in these effects changes. The profit reduces more with higher density dependence (both a and b_c) when there is a lower predation pressure. The reason is that as higher predation drives the stock density down, the weight gain of further reductions due to stronger density dependent effects declines along the sigmoidal weight function. See Figure 1.

Figure 4 about here

Finally, as shown in Figure 4, panel c), we find that larger values of the density dependent parameter in the weight functions (increased β; Eq. 6') increases the profit under all predation scenarios. A higher density effect makes weights more sensitive to changes in stock density along the downward sloping part of the sigmoidal functions (see Figure 1, panel a). However, at the same time, the system tolerates a higher stock density before weight reductions set in, and hence, implies an outward shift in the curve. Just as when considering changes in the density dependence effects in recruitment and natural survival (a and b_c), the profit seems to change more with more profound density dependence when there is no or low predation pressure. Again, the reason is that as higher predation drives the stock down, the weight gain of further reductions due to stronger density dependent effects declines along the sigmoidal weight function, see Figure 1.

We have also run sensitivity analysis with changing economic parameter values, and where Figure 5 reports the effects of price changes. Any increase in the given slaughter price p

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(EUR/kg) shifts, not surprisingly, the profit up under all three predation scenarios. More importantly, the resulting shift in profit is again stronger the lower the predation pressure is. The reason is that the stock size is higher and hence, the density dependent effects are stronger (see Figure 1), along profit schedules with lower predation rates. This clearly demonstrates the effect of the ecological density mechanisms as the weight gain is stronger, and consequently, the profit increase is stronger along profit schedules with lower predation rates.

Figure 5 about here

6.4 Comparing optimal management with the 'tragedy of the commons' outcome

So far, we have analyzed ecological and economic effects of predation when the present value harvesting profit is maximized. That is, when our group of herders behaves as if they manage to internalize any reciprocal grazing externalities involved. However, as described in Section 2, reindeer herders frequently fail to coordinate their herd sizes, especially in the northernmost part of Norway where conflicts over the utilization of common property pastures has resulted high reindeer densities and poor vegetation conditions, the so called 'tragedy of the commons' outcome. Skonhoft et al. (2017) analyzed the impact of predation under a tragedy of the commons scenario in this area. They apply the current harvesting rates in this area, which are $h_c = 0.20$, $h_f = 0.05$, and $h_m = 0.21$, which differ substantially compared to the above harvesting rates resulting from optimal management (Table 3).

Furthermore, Skonhoft et al. (2017) assume that herders fail to adjust the harvesting rates to a changing predation pressure, but instead keep the harvesting rates fixed. Table 4 compares the main findings therein with the above optimal management.

Table 4 about here

First, the optimal management scheme results in a lower total animal density compared with the 'tragedy of the commons' outcome. In the Baseline scenario, optimal management reduces the stock from 70 (animals/10 km^2) to about 47, or by about 33 %. Therefore, the weights and survival- and fertility rates are significantly higher under optimal management. The yearly number of total animals lost due to natural mortality is 2.1 (1.4 + 0.6 + 0.1 animals/10km^2) under optimal management as opposed to 8.8 (4.3 + 3.0 + 1.5) in the 'tragedy of the commons' outcome. The combined natural and predation mortality reduces from 14.4 to 7.4 (animals/10km^2) with optimal management. Therefore, the number of animals lost to natural mortality and predation reduces significantly when compared to the 'tragedy of the commons' situation. Total loss as a proportion of the stock level reduces as well, from about 21% to 16%. Second, the profit is about three times higher (1,697/568) following optimal management under the Baseline predation scenario. When coordinating and restricting the total stock size, weights increase and this results in a 67% increase in revenue. Furthermore, the operating cost becomes lower as the herd size reduces which strengthens the impact on overall profit.

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One main finding in Skonhoft et al. (2017) is that when herdsmen fail to internalize reciprocal grazing externalities, they may be better off with a higher predation pressure. This finding is indicated by the profitability figures in Table 4 where the profit is highest under the High predation scenario. That is, in the 'tragedy of the commons' scenario, predation corrects to some degree the institutional failure where herders fail to internalize externalities and hence, keep too many animals. Therefore, the deviation in profit between the optimal management scheme and the 'tragedy of the commons' outcome reduces with increased predation.

6.5 Density dependent predation

In the above theoretical reasoning as well as numerical analysis, we have assumed that the predation rates are fixed and independent of the livestock density. This is generally a simplification of reality. The predators of reindeer are wolverine, lynx and golden eagle (Section 2). Since these predators may be both hunters and scavengers, the influence of abundance of prey on the kill rate is not straightforward. High reindeer density, resulting in poor body condition, may increase their accessibility for predators. On the other hand, increased natural mortality due to individuals being in poorer condition will increase the scavenging opportunities, thereby reducing the need for hunting (Mattisson et al. 2016). Moreover, the density dependence effect seems to depend on both the type of predator and the season of the year. Mattisson et al. (2016) found a density dependence effect for wolverine calf predation in the summer, but no density dependence throughout the rest of

the season, while Mattisson et al. (2011) reported that the highest kill rates for lynx are in winter in areas where the reindeer density is high.

The evidence therefore seems to be some mixed, but in what follows we illustrate density dependent predation rates by assuming that these reduce with the reindeer density. With $s_{i,t}X_{i,t}(1-h_{i,t})=Y_{i,t}$ as the stock size of reindeer category i after slaughtering and winter natural mortality; that is, the stock size exposed for predation (cf. section 3), we specify the predation function in number of lost animals as $P_{i,t}=\dfrac{d_iY_{i,t}}{\omega_i+Y_{i,t}}W$. $d_i>0$ and $\omega_i>0$ ($i=c,f,m$) are parameters determining the magnitude and strength of the density dependence, and W is the number of predators. Accordingly, $\dfrac{d_iY_{i,t}}{\omega_i+Y_{i,t}}$ yields the consumption, or kill, per predator, while $m_{i,t}=P_{i,t}/Y_{i,t}=\dfrac{d_iW}{\omega_i+Y_{i,t}}$ yields the predation rates, decreasing in the livestock density.

The parameter values d_i, W , and ω_i are first calibrated to correspond with the Baseline fixed predation rates, and next adjusted to fit the High predation scenario (Table 1). The Baseline scenario yields stock sizes and a dynamic pattern quite close to the results shown in Figure 2 panel b). Hence, when introducing density dependent predation under this scenario and comparing the dynamics and the steady state harvest rates, population sizes and also the economic outcome, there are small and negligible differences with the fixed predation case. However, when comparing the High predation scenario under density dependent predation, depicted in Figure 6, with the case of fixed predation rates under the same scenario, there is one striking difference as the dynamic pattern becomes quite different from the smooth pattern described in Figure 2 panel c). With density dependent predation

rates there are now oscillations for all categories of livestock over the whole period. This seems to be no coincidence as further sensitivity analysis suggest that the oscillations seems to increase the higher the predation pressure is. This is rather counterintuitive, as one would expect density dependency to dampen fluctuations. The explanation may be that as the reindeer density increases, the weight of the animals decrease and survival rates generally decrease as well. However, in the case of a density dependent predation, the weight reduction is less due to increased predation, and this effect is then reinforced by the fact that the natural survival rate will decrease as well. Accordingly, we now have two effects working in the same direction through the weight of the reindeer. The effect of predation is hence stronger than in the constant predation case, which may induce the observed oscillations.

Figure 6 about here

7. Concluding remarks

This paper studies a bioeconomic model of a livestock population subject to predation, and where food limitation influences the impact of predation on livestock recruitment, survival rates, and weights. The predation rates are assumed fixed and exogenous, but we also briefly include density dependent effects in the predation. The analysis is exemplified by semi-domestic reindeer herding in the northernmost parts of Norway, where the plant cover has declined significantly during the last few decades, presumably due to common property

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conflicts and overgrazing. Because animals with low weights also are at greater risk of being lost to predators, reindeer predation in this area largely compensates for natural mortality. Our study and analysis should also have relevance for other herding communities relying on natural pastures for their livestock, and where livestock co-exist with predators, such as the various pastoral communities in Africa and Asia, and transhumance livestock keeping in the Alps in Europe.

The model studied considers recruitment- and natural survival rates as density dependent in an age-structured setting. That is, changes in reindeer density affect animal weights, which in turn affect recruitment- and natural survival rates for all categories of animals. In this way, the model captures quite detailed the ecological compensatory mechanism of increased predation, as reduced reindeer density increases the animal weights and therefore reduces natural mortality. However, the model also captures economic compensation mechanisms of predation working through increased reindeer weights, and hence higher slaughter values, but also through the number of animals influencing the operating costs of the herders. The novelty of our analysis is to include both age and sex structure and ecological and economic compensation effects in a predator prey setting. Our results suggest that such effects, well known from the ecological literature, also should be taken into account in bioeconomic modelling.

We focus on the economically optimal management scheme, and find that the ecological effect of increased predation is dampened by a compensating change in natural mortality. However, profit decreases unambiguously with an increased predation pressure as predation constraints the feasibility room for the management of the optimizing herders. Furthermore, the presence of density dependent ecological and economic compensation

mechanisms may cause the optimal harvest composition to change quite dramatically across the different animal categories in response to changed predation pressure. For instance, in contrast to findings in the existing bioeconomic literature, we find that calf harvest may be optimal in presence of predation. In fact, we demonstrate that a changing harvesting pattern towards calf harvest is an important adjustment that highly limits the negative impact on profit of increased predation.

We have also compared the optimal management scheme with the present management scheme in northernmost parts of Norway, where management bears clear signs of a 'tragedy of the commons' situation. We have seen that the degree of ecological compensation may be significant, and may even cause reindeer total loss to be lower and profits to be higher, albeit with a higher predation pressure. Still, there are significant profits to gain by coordinating the herd size so as to maximize overall profit. Finally, we have briefly included density depend effects in predation and find that this may cause oscillations in the population evolvement when the predation rates increase. One important policy implication from the present study is that curbing predation may have significant economic effects for the reindeer herders at a low and moderate predation level under the optimized management scheme. On the other hand, the effects seem to be more moderate at a higher level. However, to fully assess the policy implications and the possibly use of policy instruments, the existence value of the predators (lynx, wolverine and golden eagle) should also be taken into account.

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[1] One management unit typically covers several reindeer owners, usually relatives of the unit manager. In western Finnmark, our case study area, there are on average 6 owners per management unit (Johannesen and Skonhoft 2010).

[2] Exchange rate: 1 EUR =9.25 NOK (Sept. 2016).

[3] In reality, predation and natural mortality generally take place simultaneously. However, by sequencing the events over the annual cycle the model becomes analytically and numerically tractable. We have also studied the model when predation takes place before natural mortality. This causes a change in the distribution of losses from natural mortality to predation mortality, but has a negligible impact on the remaining results, as long as (slaughter) weights, and hence, the fertility rate and natural survival rates, depend on the autumn stock size.

[4] Instead of using the total number of animals as density measure, we could weigh calves and adults according to, e.g., their energy intake. However, ecological studies frequently also use the total number of animals as a density measure when analyzing factors affecting animal weights (e.g., Bårdsen et al. 2010) or vegetation biomass (e.g., Kumpula et al. 2014).

[5] Notice also that harvesting mortality has the same compensatory effect as predation mortality.

[6] The model is solved using the Knitro solver engine (version 10.0) bundled with the Premium solver platform from Frontline systems. The stability and uniqueness of the steady states are checked by the global optimization tool Multistart. The Multistart runs the nonlinear solver a series of times, and the Multistart method`s Bayesian test determines that all locally optimal solutions are probably found. In addition, the Interval Global Solver is used to check that the baseline steady state found is a global optimum.
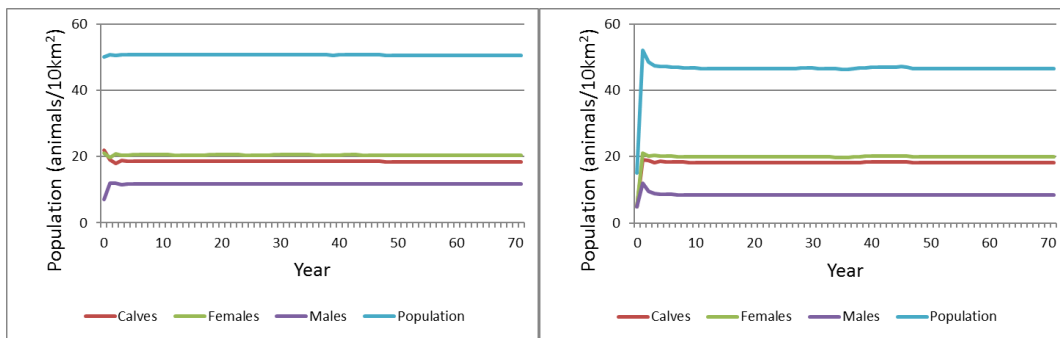
Figures

(a)

(b)

(c)
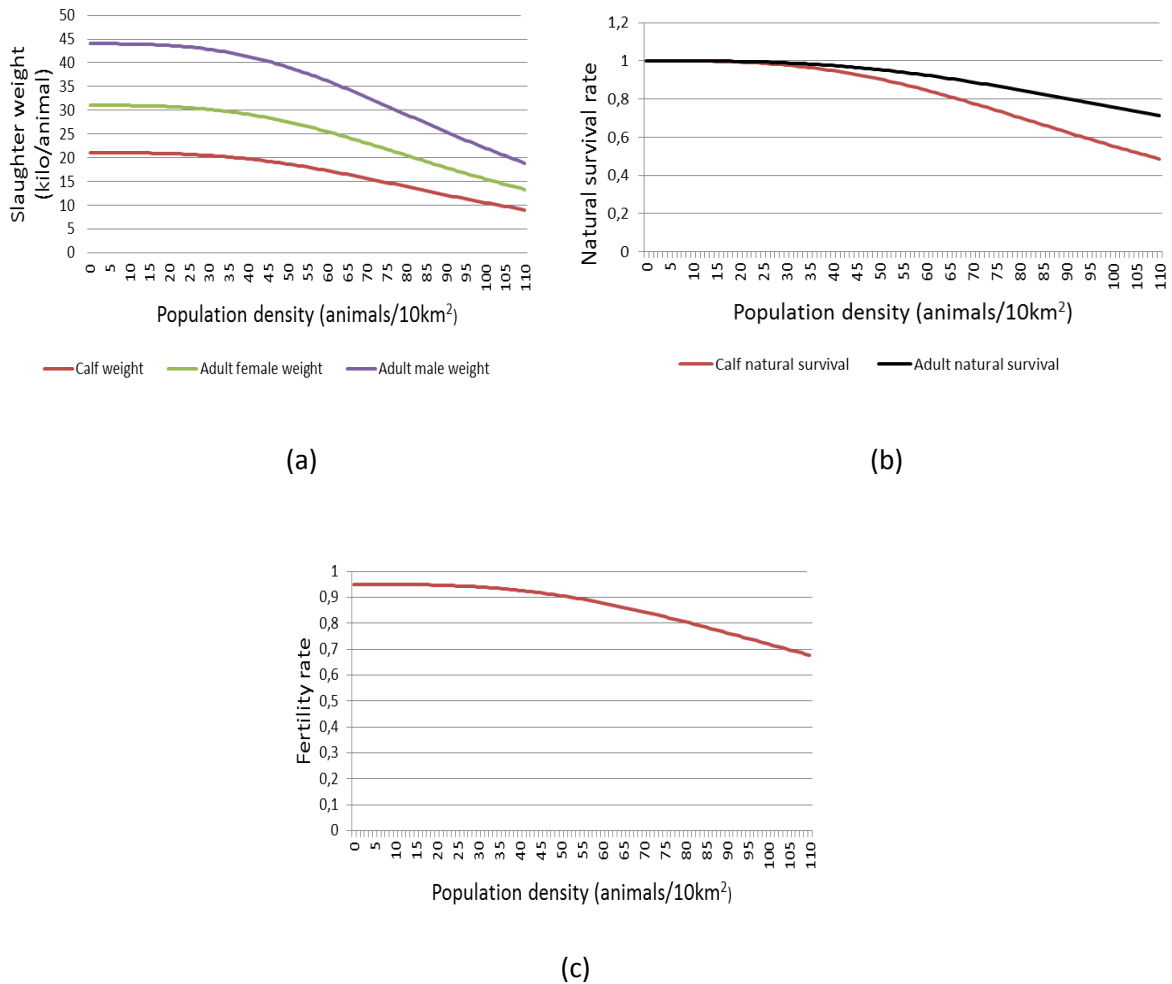
Figure 1: Natural survival-, recruitment, and weight functions. Baseline parameter values (Table 1).
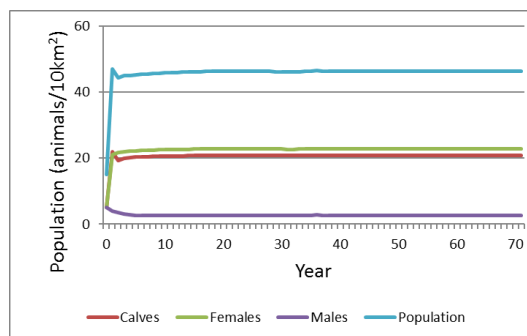
Figure note: All the functions are sigmoidal. But due to the scaling, this pattern is not observed in panel (b) and (c).
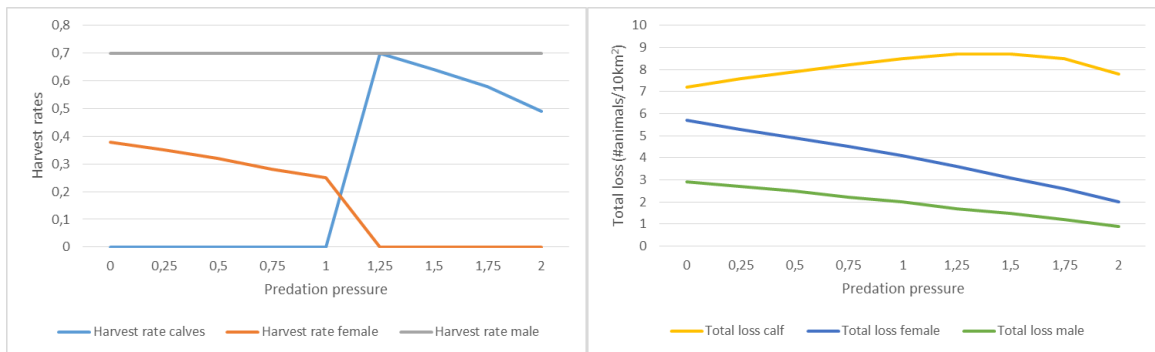
1

a) No predation

b) Baseline predation

c) High predation

Figure 2: Population dynamics. Optimal management scheme.
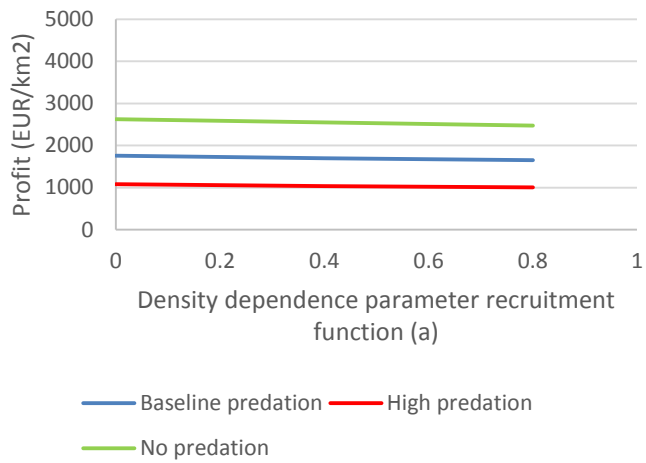
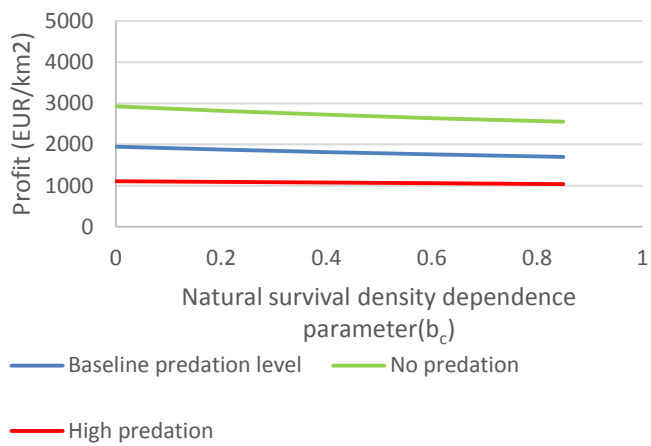a)   b)

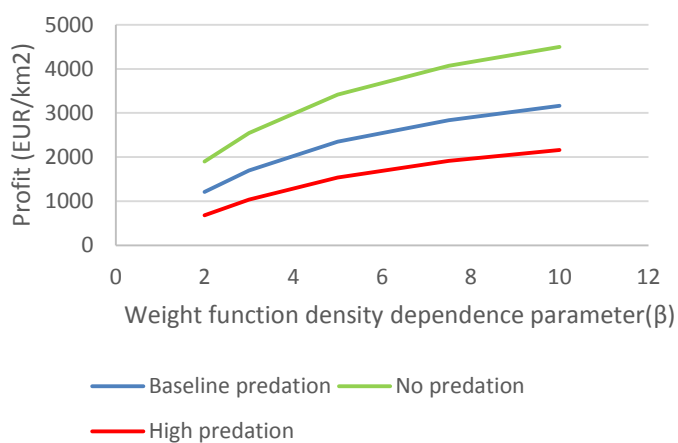**Figure 3.** Harvest rates, total loss and predation.

Figure note: Predation pressure equal to 1 represents the Baseline predation pressure (see Table 1) while, say, 1.25 indicates 25% higher rates for all categories of animals.
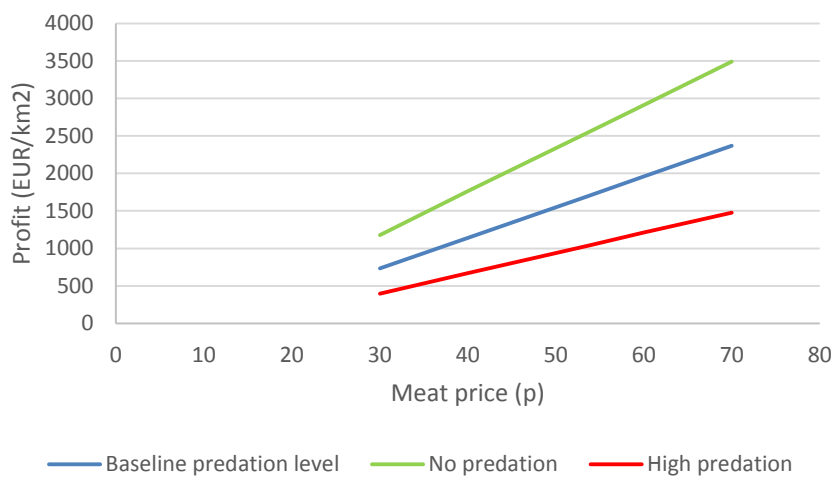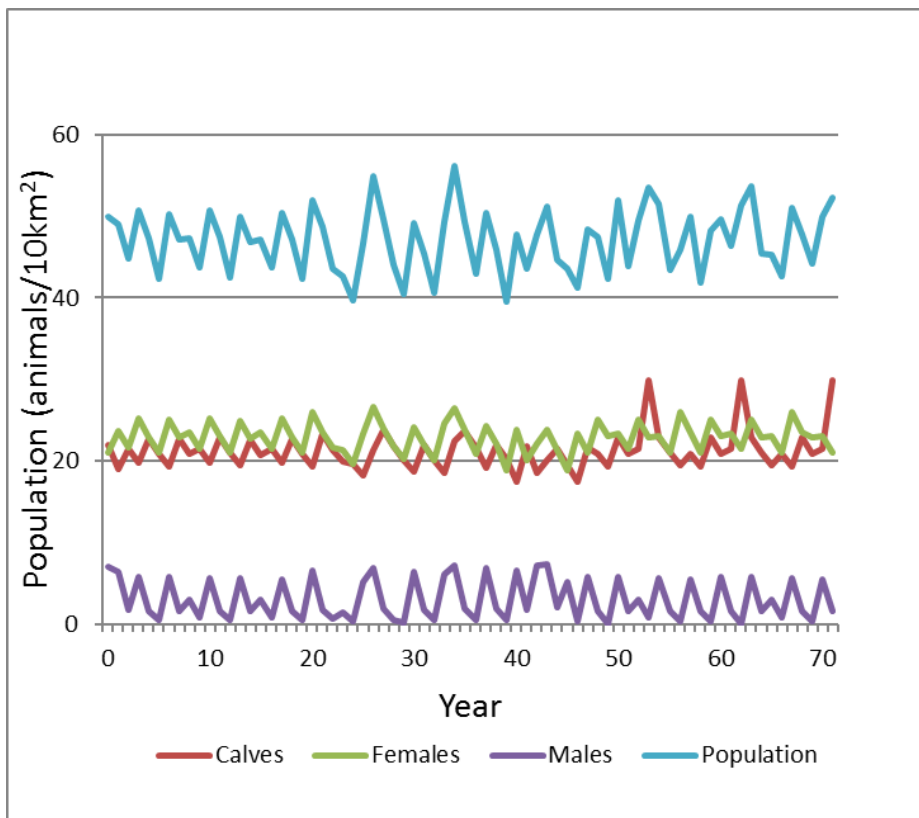
a)

b)

c)

Figure 4: Steady state profit under the various predation scenarios. Changing density dependency in recruitment (a ; panel a), natural survival of calves (b_c ;panel b), and weights (β ;panel c)*.

Figure 5: Steady state profit under varying meat price (p) and predation pressure.

Figure 6: Population dynamics. High density dependent predation pressure.

Figure note: Calibrated so that the average predation pressure is in accordance with the High predation scenario with constant predation rates; $m_c = 0.34$, $m_f = m_m = 0.05$.

Tables

Table 1: Baseline parameter values

Description	Parameter	Value	Unit	Reference
Sex ratio	ψ	0.5		Assumed
Maximum fertility rate	$\overline{f}$	0.95	Calves/females	NRHA (2014)
Maximum weights	$\overline{w}_c$, $\overline{w}_f$, $\overline{w}_m$	21, 31, 44	kg/animal	NRHA (2014)
Parameter fertility rate	a	0.4		Calibrated
Maximum survival rates	$\overline{s}_c$, $\overline{s}_m$, $\overline{s}_m$	1, 1, 1		Assumed
Parameter survival rates	b_c , b_f , b_m	0.85, 0.4, 0.4		Calibrated
Weight parameter	β	3		Assumed
Carrying capacity	K	100	Animals/10 km^2	Assumed
Predation rates	m_c , m_f , m_m	0.27, 0.04, 0.04		www.rovbase.no
Harvesting rates[1]	h_c , h_f , h_m	0.20, 0.05, 0.21		NRHA (2014)
Meat price	p	5.8	EUR/kg	NRHA (2013b)
Maintenance cost	c	10.5	EUR/animal	Calibrated
Discount rate	δ	0.03		Assumed
Male harvest constraint	$\overline{h}_m$	0,7		Skonhoft et al (2013)
Dens. dep. predation	d_c, d_f, d_m	0.19, 0.03, 0,03		Calibrated
Dens. dep. predation2	$\omega_c, \omega_f, \omega_m$	61, 60, 70		Calibrated
Predation pressure	W	100 (high=125)		Calibrated

[1] Harvesting rates used in section 5. Fixed at the present level in the northernmost part of Norway.

Table 2: Steady state biological results. Optimal management.

Predation pressure[1]	Animal density (# of animals/10km²)		Fertility rate	Survival rates	Mortality (# of animals (c, f, m)/10km²)		
	X	X_c , X_f , X_m	f	s_c , s_f , s_m	Natural[2]	Predation[3]	Total
Zero	50.7	18.5, 20.5, 11.7	0.90	0.90, 0.95, 0.95	1.8, 0.6, 0.2	0.0, 0.0, 0.0	1.8, 0.6, 0.2
Baseline	46.6	18.2, 19.9, 8.5	0.91	0,92, 0.96, 0.96	1.4, 0.6, 0.1	4.6, 0.6, 0.1	6.0, 1.2, 0.2
High	46.1	20.8, 22.7, 2.6	0.91	0.92, 0.96, 0.96	0.5, 0.8, 0.0	2.0, 1.1, 0.0	2.5, 1.9, 0.1

Table notes: [1] Baseline predation pressure; $m_c = 0.27$, $m_f = m_m = 0.04$. High predation pressure; $m_c = 0.34$, $m_f = m_m = 0.05$. [2] Natural mortality (after harvest) equals $N_i = (1-h_i)(1-s_i)X_i$, $i = c, f, m$. [3] Loss of animals to predators equals $M_i = (1-h_i)s_i X_i m_i$, $i = c, f, m$.

Table 3: Steady state harvest and economics. Optimal management.

Predation Pressure	Harvesting rates h_c , h_f , h_m	Harvesting (# of animals/10km²) H_c , H_f , H_m	Weight (kg/animal) w_c , w_f , w_m	Revenue (EUR/10km²)	Cost (EUR/10km²)	Profit (EUR/10km²)
Zero	0.0, 0.38, 0.70	0.0, 7.7, 8.2	18.6, 27.4, 38.9	3,079	533	2,546
Baseline	0.0, 0.25, 0.70	0.0, 5.0, 5.9	19.0, 28.1, 39.9	2,188	491	1,697
High	0.70, 0.0, 0.70	14.4, 0.0, 1.8	19.1, 28.2, 40.1	2,041	485	1,556

Table 4: Steady state results under the 'tragedy of the commons' outcome in northernmost Norway (Skonhoft et al. 2017) and the optimal management scheme. Identical economic and biological parameter values.

	Predation pressure		
	Zero	Baseline	High
Tragedy of the commons			
Animal density (# of animals/10km^2)	84.1	70.4	65.7
Weight (kg/animal) w_c , w_f , w_m	13.2, 19.4, 27.6	15.6, 23.0, 32.6	16.4, 24.1, 34.3
Natural mortality (# of animals/10km^2)	7.3, 5.7, 2.9	4.3, 3.0, 1.5	3.6, 2.4, 1.2
Predation mortality (# of animals/10km^2)	0.0,0.0,0.0	4.1, 1.0, 0.5	5.1, 1.2, 0.6
Total loss (# of animals/10km^2)	7.3, 5.7, 2.9	8.4, 4.0, 2.0	8.7, 3.6, 1.8
Profit (EUR/10km^2)	458	568	585
Optimal management			
Animal density (# of animals/10km^2)	50.7	46.6	46.1
Weight (kg/animal) w_c , w_f , w_m	18.6, 27.4, 38.9	19.0, 28.1, 39.9	19.1, 28.2, 40.1
Natural mortality (# of animals/10km^2)	1.8, 0.6, 0.2	1.4, 0.6, 0.1	0.5, 0.8, 0.0
Predation mortality (# of animals/10km^2)	0.0,0.0,0.0	4.6, 0.6, 0.1	2.0, 1.1, 0.1
Total loss (# of animals/10km^2)	1.8, 0.6, 0.2	6.0, 1.2, 0.2	2.5, 1.9, 0.1
Profit (EUR/10km^2)	2,546	1,697	1,556