

## **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. In this paper, predation mortality takes place due to food availability limiting the growth conditions for semi-domestic livestock. An age-structured bio-economic model is presented, where predation impacts livestock density, and thereby livestock weights and natural mortality. 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 slaughter value of livestock. The paper analyzes how predation affects livestock production and economic performance under different livestock management schemes. While predation may impose serious economic loss in an optimized scheme, it may be beneficial in situations with overgrazing and food limitations due to, e.g., common property problems.

**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 of such conflicts include wolf predation on sheep in North America and Europe (e.g. Berger 2006, Skonhøft 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 et al. (2008).

The interactions between carnivores and livestock take place under widely different ecological and economic circumstances. This paper considers the interaction between density-dependence of natural mortality and predation mortality. Density dependence 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 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 reductions in natural mortality and improved recruitment when ungulate density is high and more likely to limit ungulate populations when pastures are plentiful. See e.g., Ballard et al. (2001) who studied wild ungulates in North America, and found that ungulate density was detrimental to the relative importance of predation and food availability as factors limiting ungulate populations. 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 also been demonstrated in semi-domestic reindeer herding in Norway, where reindeer rely on natural pastures throughout the year (Tveraa et al. 2003). Food limitations may also have important economic consequences, as the meat value, or slaughter value, of the livestock can be severely influenced by predation. To our knowledge, this issue is almost completely neglected in the natural resource economic literature. One exception is a simple descriptive analyses of such mechanisms found in Skonhoft et al. (2017).

In this paper, we analyze the carnivore-livestock relationship framed in an age structured model. In natural resource economics, there is a small, but growing literature on the stage-, or age-structured models. The studies of moose harvesting in Scandinavia by Olausen and Skonhoft (2011) and Naevdal et al. (2012) are two examples, while the analysis of Skonhoft et al. (2013) on the cost and benefit of red deer management and the study by Tahvonen et al. (2014) on the lichen-reindeer system of Northern Finland are other examples. In the fishery economics literature, an early and important contribution is Reed (1980). See also the recent contributions by Tahvonen (2009) and Skonhoft et al. (2012). For a more general modeling overview from a biological perspective, see Getz and Haight (1989) and Caswell

(2001). By using an age structured model, it is possible to analyze the differences between additive and compensatory loss due to predation in a proper manner as predation has different effect among the different categories of animals. Second, it is important to take into account that calves are much more vulnerable to predation than adult animals when analyzing the livestock population growth. Third, since the setting here is a predator-prey relationship of carnivores and livestock, the age structure is of vital importance in order to understand how the optimal composition of harvest between age classes is affected by predation. With the exception of Skonhoft (2008) analyzing sheep farming in a Nordic context, predation has as far as we know, never been included in an age structured bioeconomic terrestrial animal species model. Important resource economic works on predator – prey models in a biomass framework include Hannesson (1983), Finnoff and Tschirhart (2003), and Tschirhart (2009).

In the age-structured bio-economic model formulated here, we analyze how food limitation influences the impact of predation on animal density and economic performance in semi-domestic livestock keeping. Saami reindeer (*Rangifer t. tarandus*) herding in Norway is used as a case study. The major focus of the paper is to study how predation affects the livestock population and economics of livestock keeping, and also to identify the economic and ecological compensation mechanisms involved. The model is analyzed under an optimized management scheme, and 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. The main results are that predation may impose a serious economic loss in the optimized scheme, while it

may be beneficial in the case of severe overgrazing. Our study and analysis should also have relevance for other herding communities relying on natural pastures for their livestock, such as the various pastoral communities in Africa and Asia, and transhumance livestock keeping in the Alps in Europe.

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 mortality is also introduced here. The considered reindeer population is assumed to be managed by a group of herders and the economic benefit and cost functions for this management unit are formulated in section 4. In section 5, data and functional forms are presented while the results of the optimized management scheme are demonstrated in section 6. In section 7, the results are discussed and compared with the present management situation of overgrazing. Finally, section 8 concludes the study.

## **2. Saami reindeer herding and food limitation**

Reindeer husbandry is a traditional and culturally based livelihood of the Saami people in Norway, Sweden, Finland, and Russia, and can be traced back to the fifteenth century when the Saami people domesticated entire reindeer herds, and parts of the Saami people became herding nomads (e.g., Riseth 2006). This tradition has been preserved until today. In Norway, reindeer husbandry is an exclusive right of the Saami people. It is a small economic activity, comprising some 530 herding units keeping a total of 230,000 animals (NRHA 2014).

The industry produces some 2,000 tons of reindeer meat yearly, which amounts to 1-2 percent of the total production of red meat in Norway (NRHA 2013b). Income from reindeer meat production was about 15 million NOK in 2011 (NRHA 2013b).<sup>1</sup> Although small on a national scale, reindeer husbandry is of great importance to the Saami people both culturally and economically (Johannesen and Skonhoft 2009). In fact, to many herders, cultural values are important when choosing reindeer husbandry as a living, and these values seem to be valued just as highly as the income opportunities the industry provides (Johannesen and Skonhoft 2011).

Reindeer graze on open natural pastures throughout the year, and the pastures are utilized as common properties. 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 climatic 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, relatively to the reindeer herding areas further south (Tveraa et al. 2007). Over the past decades, the herding communities in the northernmost part of the country 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 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

---

<sup>1</sup> Exchange rate: 1 EUR =9.25 NOK (Sept. 2016).

negative relationship between animal weights and density (Bårdsen et al. 2010, Bårdsen and Tveraa 2012).

Figure 1, panels (a) and (b), compare density and weight time series in this area with the best performing reindeer herding area in Norway (south), where weight is illustrated by the average slaughter weight of calves over all districts in the respective herding area. Herders in south have managed to coordinate their activity and restrict the reindeer density to avoid pasture degradation<sup>2</sup>. Although pastures are exploited as common properties in both northern and southern Norway, increased herd sizes and overgrazing problems are not observed in the south. The reason may be that the northernmost areas are characterized by more open landscapes with few natural borders, longer migration routes between the summer and winter pastures, and a larger number of herders, which leaves herding communities in the north with more severe challenges related to cooperation and coordination than in the south (Riseth and Vatn 2009). On the other hand, it may be argued that the sharing of large pastures by several herders, or groups of herders, may add flexibility to cope with climate variability. However, in a study of the northernmost reindeer herding areas in Norway, Hausner et al. (2012) find that the size of the winter pastures (where the largest pastures encompasses a large number of herding groups) has a negative effect on various outcomes indicating sustainability (e.g., calf body mass, proportion of calf

---

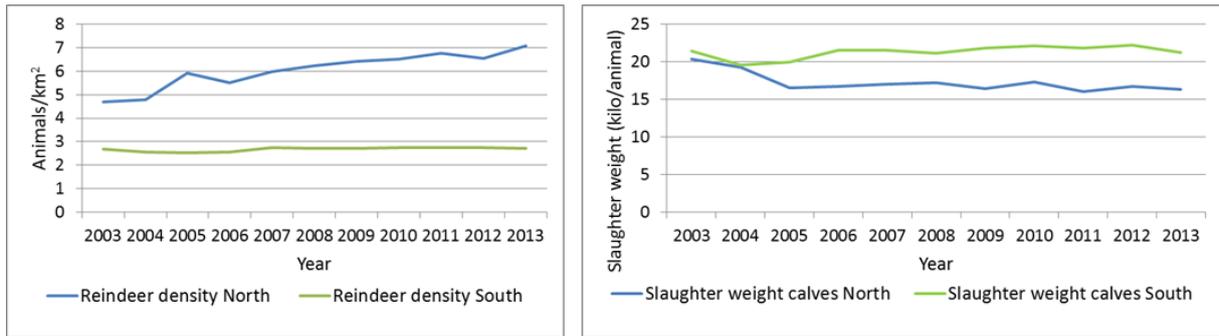
<sup>2</sup> Although pastures are exploited as common properties in both northern and southern Norway, increased herd sizes and overgrazing problems are not observed in the south. The reason may be that the northernmost areas are characterized by more open landscapes with few natural borders, longer migration routes between the summer and winter pastures, and a larger number of herders, which leaves herding communities in the north with more severe challenges related to cooperation and coordination than in the south (Riseth and Vatn 2009). On the other hand, it may be argued that the sharing of large pastures by several herders, or groups of herders, may add flexibility to cope with climate variability. However, in a study of the northernmost reindeer herding areas in Norway, Hausner et al. (2012) find that the size of the winter pastures (where the largest pastures encompasses a large number of herding groups) has a negative effect on various outcomes indicating sustainability (e.g., calf body mass, proportion of calf slaughter, and gross income).

slaughter, and gross income). As seen, the reindeer density in northern Norway is currently more than twice the density in south, and the average slaughter weight is significantly lower<sup>3</sup>. The per animal slaughtering value is therefore significantly lower in the north (NRHA 2013b). The high population density in northern Norway and the 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. 2013a). 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).

**Figure 1:** Reindeer density, weight of calves, and losses of calves to predators 2003 – 2013  
(Source: <http://www.reinbase.no> and <http://www.rovbase.no>).

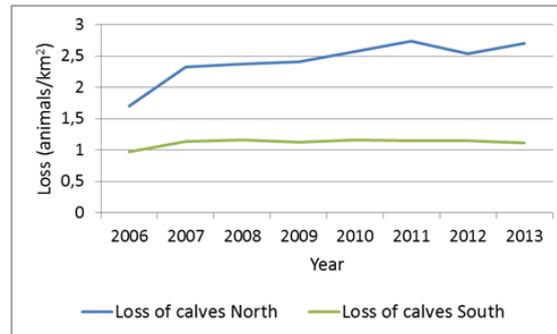
---

<sup>3</sup> Empirical evidence shows that increased harvest rates, and hence reduced density, increases weights in the northernmost area (Tveraa et al. 2007, Bårdsen et al. 2014). This suggests that a top-down control (i.e., increased harvest rates) is needed to avoid food limitation in this area (Tveraa et al. 2007). For instance, ecological studies suggest that the density in the northernmost area should be reduced to approximately 3 animals per km<sup>2</sup> in order to achieve similar weight of calves as in south (Bårdsen et al. 2014). Note, however, that some of the difference in weights may also be explained by differences in plant productivity between the areas. Some measures of plant productivity are higher in south than in the northernmost part of Norway (Tveraa et al. 2013b, figure 3) and evidence shows that these have a positive impact on weights (Tveraa et al. 2007).



(a)

(b)



(c)

Figure note: The North and South curves are based on data from the western Finnmark and Sør-Trøndelag/Hedmark herding areas, respectively.

Since reindeer graze on natural pastures throughout the year, they are prone to a risk of being killed by predators such as lynx (*Lynx lynx*), wolverine (*Gulo gulo*), and golden eagle (*Aquila chrysaetos*) (Tveraa et al.

2014). Small and weak reindeer, especially calves, are more vulnerable to predators than animals in good condition (Tveraa et al. 2003). Figure 1 panel (c) shows that the loss of calves to predators per km<sup>2</sup> has increased substantially over the past few years in the north, while it has remained stable and at a lower level in the south. Although differences in predation densities may explain some of this variation, Tveraa et al. (2014) demonstrated that various indicators of food limitation (i.e., reindeer density, climate, and plant productivity) are the most important variables explaining differences in predator losses.

Furthermore, when combined with the previous 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), the present natural mortality and predation rates are generally high in northernmost Norway, and there are clear indications of density dependent natural mortality. Mortality rates generally differ between the different age classes of the reindeer population, and are typically higher for calves than adults (Bårdsen et al. 2014). The fecundity has also proven to be density dependent, working through food shortages (Tveraa et al. 2013). 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 (but see Tahvonen et al. 2014, where recruitment depends on the sex composition of the stock). Both the fertility and natural mortality rates are related to animal weights in our model. However, instead of weight loss during winter (e.g., Tahvonen et al. 2014), these rates are related to the weight before the winter grazing season. The animal weights are in turn associated with the grazing pressure through the number of grazing animals. Therefore, the density dependent fertility and natural mortality effects do not work directly through the number of animals, but rather indirectly through food availability and animal weights. The predation rates are generally different for female and male adults, and both are generally lower than that of calves (Tveraa et al. 2003). All age classes have a slaughter value and are generally slaughtered.

### 3.1 The model

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<sup>4</sup>. The number of calves (recruitment) is first governed by:

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

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 2 above):

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

with  $f' \geq 0$  and  $f'' \leq 0$ .

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:

---

<sup>4</sup> 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 traceable. 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.

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

with  $s_i' \geq 0$  and  $s_i'' \leq 0$ . The predation rate associated with the carnivores  $0 \leq m_{i,t} < 1$ ,  $i = c, f, m$ , differs between sexes and age classes, and is typically lower for adults than calves  $m_{c,t} > m_{f,t} \neq m_{m,t}$  (Mattisson et al. 2014, Tveraa et al. 2003). With these rates defined, the abundance of adult females and males are written as:

$$(4) \quad X_{f,t+1} = \psi(1-h_{c,t})X_{c,t}S_{c,t}(1-m_{c,t}) + (1-h_{f,t})X_{f,t}S_{f,t}(1-m_{f,t})$$

and

$$(5) \quad X_{m,t+1} = (1-\psi)(1-h_{c,t})X_{c,t}S_{c,t}(1-m_{c,t}) + (1-h_{m,t})X_{m,t}S_{m,t}(1-m_{m,t}),$$

respectively, and where  $\psi$  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<sup>5</sup>. We hence have:

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

with  $w_i' \leq 0$ . Typically, this density effect will be small on the margin when the density is 'low', but more substantial when the density becomes higher. In the numerical analysis (section 5 below) a sigmoidal function is used. From Eq. (6) we find that the total animal

---

<sup>5</sup> Instead of using the total number of animals as density measure, we could weight 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 investigating factors affecting animal weights (e.g., Bårdsen et al. 2010) or vegetation biomass (e.g., Kumpula et al. 2014).

density feeds back to the fertility rate through Eq. (2) and the natural survival rates through Eq. (3).

It is also recognized that predation and natural mortality are interacting. When treating the predation rates exogenously, as independent of the reindeer population sizes (more details section 5 and Appendix A), and when the first order predation mortality effect works in the direction of less animals, we have  $X_t = X(m_{c,t}, m_{f,t}, m_{m,t})$  with  $\partial X / \partial m_{j,t} < 0$  ( $j = c, f, m$ ).

As a consequence, the animal weights increase through Eq. (6),  $w_{i,t} = w_i(X(m_{c,t}, m_{f,t}, m_{m,t}))$ , with  $\partial w_{i,t} / \partial m_{j,t} = (\partial w_i / \partial X)(\partial X / \partial m_{j,t}) \geq 0$ . This again feeds into higher natural survival rates through Eq. (3),  $s_{i,t} = s_i(X(m_{c,t}, m_{f,t}, m_{m,t}))$ ,  $i = c, f, m$ , with

$\partial s_{i,t} / \partial m_{j,t} = (\partial s_i / \partial w_i)(\partial w_i / \partial X)(\partial X / \partial m_{j,t}) \geq 0$ . Therefore, predation mortality generally *compensates* natural mortality; that is, higher predation pressure shifts up the natural survival rates<sup>6</sup>. 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

$$f_t = f(w_{f,t}(X(m_{c,t}, m_{f,t}, m_{m,t}))) \text{ with } \partial f_t / \partial m_{j,t} = (\partial f_t / \partial w_f)(\partial w_f / \partial X)(\partial X / \partial m_{j,t}) \geq 0.$$

We may also consider the above compensatory effects in terms of mortality 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  $M_{i,t} = (1 - h_{i,t})X_{i,t}s_{i,t}m_{i,t}$ , the total of natural- and predation mortality of category  $i$  becomes  $N_{i,t} + M_{i,t} = (1 - h_{i,t})X_{i,t}(1 - s_{i,t}) + (1 - h_{i,t})X_{i,t}s_{i,t}m_{i,t}$ . The total mortality rate (after harvest) may therefore be written as

---

<sup>6</sup> Notice also that harvesting mortality has the same compensatory effect as predation mortality.

$(N_{i,t} + M_{i,t}) / ((1 - h_{i,t})X_{i,t}) \equiv g_{i,t} = (1 - s_{i,t}) + s_{i,t}m_{i,t}$ . Changing mortality rates due to increased predation reads now  $\partial g_{i,t} / \partial m_{i,t} = s_{i,t} - (1 - m_{i,t})(\partial s_{i,t} / \partial m_{i,t})$  with  $\partial s_{i,t} / \partial m_{i,t} \geq 0$ . The first order effect is therefore captured by the term  $s_{i,t}$ . The second order effect is captured by  $-(1 - m_{i,t})(\partial s_{i,t} / \partial m_{i,t})$ , 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.

### 3.2 Steady state

As there are strong density dependent effects in the present model, we expect the population equilibrium to be stable both with fixed harvesting rates as well as in an optimized management scheme. This is confirmed by the numerical analyses, which demonstrate that the equilibrium is stable and unique with the given functional forms and under a wide set of parameter values under the optimized scheme (see Appendix B) as well as when the harvesting rates are kept fixed.<sup>7</sup> In an equilibrium, or steady state,

$X_{i,t+1} = X_{i,t} > 0$  ( $i = c, f, m$ ), we now find that Eqs. (4) and (5) can be written as:

$$(7) \quad 1 = \psi(1 - h_c)fs_c(1 - m_c) + (1 - h_f)s_f(1 - m_f)$$

and

---

<sup>7</sup> The optimized 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.

$$(8) \quad X_m = (1-\psi)(1-h_c)fX_f s_c(1-m_c) + (1-h_m)X_m s_m(1-m_m),$$

respectively, when inserting Eq. (1) and dropping the time subscript.

As the total stock  $X$  determines the natural survival rates and the fertility rate through Eqs. (3), (2) and (6), Eq. (7) defines  $X$  as a function of the female and calf predation rates for the given harvest rates. This means that we assume there are always enough males, and hence male predation does not affect the total stock.

#### 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 Skonhøft 2011). As natural mortality and predation are assumed to take place during the late fall and winter, after the slaughtering, the number of animals removed year  $t$  through slaughtering simply writes  $H_{i,t} = h_{i,t} X_{i,t}$ ,  $i = c, f, m$ . The current slaughter, or meat value, for our considered group of herders is accordingly:

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

and where  $p$  is the net meat price (NOK/kg), i.e., the slaughter value corrected for slaughter costs. The meat price is assumed to be fixed and similar for all categories of animals (but see footnote 10, section 6).

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:

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

With  $C' > 0$  and  $C'' \geq 0$ , 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:

$$(11) \quad \pi_t = I_t - C_t$$

In steady state, the profit reads:

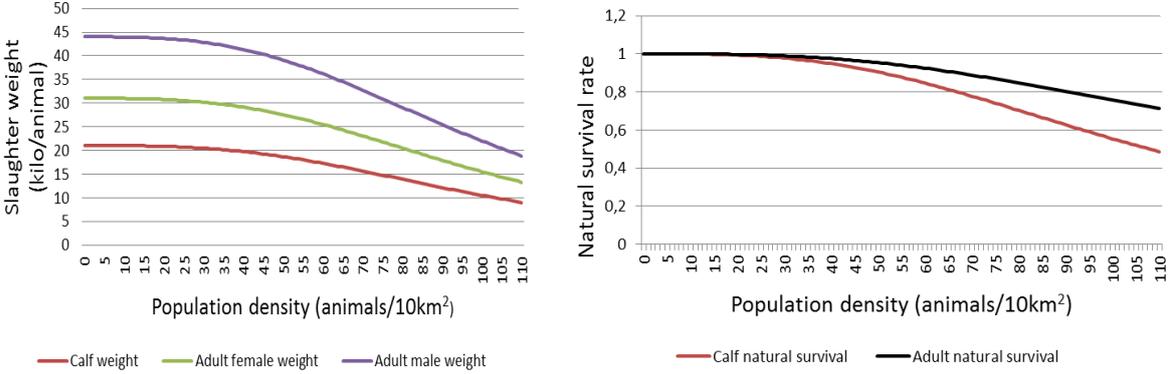
$$(12) \quad \pi = p(w_c h_c X_c + w_f h_f X_f + w_m h_m X_m) - C(X_c + X_f + X_m)$$

More aggressive predation for *given* harvesting rates will generally reduce the stock sizes and thereby work in the direction of reduced slaughter income. 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 (but see section 7), more aggressive predation therefore has an ambiguous effect on profitability through both ecological and economic forces.

## 5. Data and functional forms

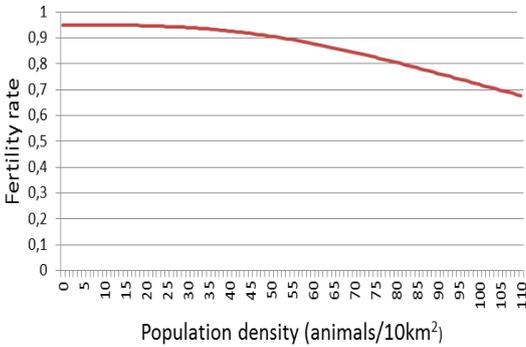
The specific functional forms and parameter values applied in the numerical analysis are presented in detail in Appendix A. The assumed functional forms for the survival- and recruitment (fertility) rates and animal weights, and also the functional forms between the weights and population density, lead to a sigmoidal relationship between the survival- and recruitment rates and total animal density. See Figure 2. Ecological evidence suggests a negative relationship between density and body mass, and that the negative effect is less profound in presence of good pasture conditions (Bårdsen and Tveraa 2012). We therefore specify (slaughter) weights as less responsive to increased population density for low density levels, but more responsive for higher densities. 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.

**Figure 2:** Natural survival-, recruitment, and weight functions. Baseline parameter values (Table A1 Appendix A).



(a)

(b)



(c)

The specified functional forms and parameter values fit well with the present ‘tragedy of the commons’ situation in the northern part of Norway. The reindeer density in this area was 70 animals/10km<sup>2</sup> in 2012 and the average (slaughter) weight of calves was 17 kilo/animal (NRHA 2014). See also section 2. Figure 2 also clearly indicates that changing total stock size in the domain of a high animal density of, say, 80 (animals/10km<sup>2</sup>) 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. Therefore, depending on the population density, a given as well as a shifting predation pressure will have different effects on natural survival, and fertility.

We assume that the predation loss increases linearly with reindeer density, and that reindeer density does not affect the predation rates  $m_{i,t}$  ( $i = c, f, m$ )<sup>8</sup>. Feedback effects may also be present, as the size of the reindeer population can influence the population growth of the predator population. However, any 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 regulated with certain population goals for lynx and wolverine (see, e.g., Ekspertutvalget 2011). The carnivore natural growth is thus assumed independent of the size of the reindeer population, and the predation rates are exogenous in our analysis (see also section 3.1 above). The maintenance cost function is assumed to be linear. Appendix A gives more details.

The parameter values are mainly based on the annual reports from the herders to the government (NRHA 2014), and official statistics on losses to predators ([www.rovbase.no](http://www.rovbase.no)). See Appendix A Table A1. We lack data for some parameter values indicating the exact functional forms of the fertility, survival, and weight functions. These values are partly assumed and partly calibrated, and are hence also due to sensitivity analysis (section 7.3 below). Most of the parameter values are either dimensionless or per animal basis (i.e., kg/animal). An important exception is the parameter indicating the carrying capacity in the weight – density relationships which has the dimension of animals/10 km<sup>2</sup>. For this reason, all stock values and the number of animals slaughtered and lost to predation, and also economic values, are related to per 10 km<sup>2</sup>.

---

<sup>8</sup> Note that this assumption is standard in classical predator-prey models such as the Lotka-Volterra model.

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 Appendix B Figure B1)<sup>9</sup>. In the remaining parts of the paper we therefore concentrate on demonstrating steady state results.

Sections 6 present ecological and economic effects of varying predation rates. The baseline predation rates represent the average of claimed and compensated losses in northernmost Norway for the past few years. We also present a high predation scenario, which simply represents a 25 per cent increase in the baseline predation rates; however, this is still below maximal claims. A scenario with no predation is also included. We start in section 6 with the optimized management situation, and compare with the present management situation in the northernmost part of Norway where low harvesting rates and a high animal density has caused overgrazing, i.e. the ‘tragedy of the commons’ outcome (see section 2) in section 7.

## 6. Optimal management scheme

### 6.1 The maximization problem

We now study a 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. The

manager hence aims to 
$$\max_{h_{c,t}, h_{f,t}, h_{m,t}, X_{c,t}, X_{f,t}, X_{m,t}} PV = \sum_{t=0}^{\infty} \rho^t (I_t - C_t)$$
 subject to the biological

---

<sup>9</sup> Note that the dynamic figures presented in the Appendix B are for the optimized scheme, but the dynamic patterns for the fixed harvest rates are very much similar (available on authors’ request).

constraints (1), (4), and (5). In addition, a constraint is added to avoid a too skewed male/female ratio  $h_{m,t} \leq \bar{h}_m$ , and where  $\bar{h}_m$  is the upper limit male harvest level (see Skonhøft et al. 2013). The discount factor is  $\rho = 1/(1 + \delta)$  with  $\delta \geq 0$  as the discount rent.

The current value Hamiltonian of this problem may be written as:

$$\begin{aligned}
(13) \quad H = & p(w_{c,t}h_{c,t}X_{c,t} + w_{f,t}h_{f,t}X_{f,t} + w_{m,t}h_{m,t}X_{m,t}) - C(X_{c,t} + X_{f,t} + X_{m,t}) - \lambda_t(X_{c,t} - f_tX_{f,t}) \\
& - \rho\mu_{t+1}(X_{f,t+1} - \psi((1-h_{c,t})X_{c,t}s_{c,t}(1-m_{c,t}) - (1-h_{f,t})X_{f,t}s_{f,t}(1-m_{f,t}))) \\
& - \rho\eta_{t+1}(X_{m,t+1} - (1-\psi)((1-h_{c,t})X_{c,t}s_{c,t}(1-m_{c,t}) - (1-h_{m,t})X_{m,t}s_{m,t}(1-m_{m,t}))) \\
& - \varpi_t(h_{m,t} - \bar{h}_m)
\end{aligned}$$

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. These control conditions with  $X_{i,t} > 0$  ( $i = c, f, m$ ) are:

$$(14) \quad \frac{\partial H}{\partial h_{c,t}} = X_{c,t} [pw_{c,t} - s_{c,t}(1-m_{c,t})\rho(\mu_{t+1}\psi + \eta_{t+1}(1-\psi))] \begin{matrix} \geq 0 \\ < \end{matrix} ; 0 \leq h_{c,t} \leq 1,$$

$$(15) \quad \frac{\partial H}{\partial h_{f,t}} = X_{f,t} [pw_{f,t} - \rho\mu_{t+1}(s_{f,t}(1-m_{f,t}))] \begin{matrix} \geq 0 \\ < \end{matrix} ; 0 \leq h_{f,t} \leq 1,$$

and

$$(16) \quad \frac{\partial H}{\partial h_{m,t}} = pw_{m,t}X_{m,t} - \rho\eta_{t+1}(X_{m,t}s_{m,t}(1-m_{m,t})) - \varpi_t \leq 0 ; 0 \leq h_{m,t} \leq \bar{h}_m.$$

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 (see Appendix B) and are not discussed here.

Control condition (14) says that calf harvesting should take place up to the point where the marginal harvest value is equal to, or below, the cost in terms of reduced populations of both females and males, when evaluated at their respective shadow prices, while also taking discounting into account. 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. In a similar manner, control condition (15) says that females should be harvested up to the point where marginal meat income 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 (16) is analogue to the female harvest condition, but with the additional shadow price  $\varpi_t$  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. As mentioned, this harvest restriction is imposed in order to avoid a too skewed adult male-female ratio, and when binding it hence comes with a cost imposed by the shadow price.

When the predation pressure  $m_i$  increases, it is difficult to assess the effects from the above control conditions due to the density dependency affecting the fertility, natural survival, and

weight functions. The direct effect of increased predation is that the stock size decreases. The indirect effect is that lower stock size works in the direction of higher weight of each animal category, and hence shifts up the natural survival rates and the fertility rate. If we neglect these indirect effects, or assume that the direct effects dominate the indirect effects, the direct effect pulls in the direction of increased harvesting to keep the predation and natural mortality down. The direction and magnitudes of these ecological compensation effects are studied detailed numerically below.

## *6.2 Results*

We start by comparing the optimal steady state management scheme under the baseline predation pressure with the present management situation (Table 3 versus Table 1). First, the slaughter rate of calves is shifted down from 0.2 to 0.0 when moving from the present management situation to optimal management, while the adult slaughter rates are increased from 0.05 to 0.25 for females and from 0.21 to 0.70 for males (column one Table 3). Consequently, the total animal density reduces with optimal management from 70 (animals/10km<sup>2</sup>) to 47 (column one Tables 1 and 3, respectively), or by about 33 %. The survival- and fertility rates are therefore significantly higher under optimal management. For example, the adult survival rates shift up from 0.89 to 0.96 (columns four), and the fertility rate shifts up from 0.84 to 0.91 (columns three). Note also that the natural mortality (columns five) drops dramatically. Hence, the yearly number of animals lost due to natural mortality reduces from 8.8 (animals/10km<sup>2</sup>) to 2.1, while the combined natural and predation mortality reduces from 14.4 to 7.4 (animals/10km<sup>2</sup>). Therefore, we find that the number of animals lost to natural mortality and predation reduces significantly when

compared to the present management situation. Total mortality as a proportion of the stock level reduces as well, from about 21% to 16%.

Much of the same pattern is observed under the High predation pressure scenario. However, important differences regarding the harvest rates are noticed, as the optimal harvest rate of calves increases from 0 to 0.7. On the other hand, the optimal female harvest rate drops from 0.25 to 0. The differences occur because the harvest rates are adjusted to changes in the predation pressure in the optimal management situation (cf. the above conditions 14-16). As the predation pressure increases, it is optimal to start harvesting calves and reduce the harvest rate of adult females. The reason is that a lower female harvesting rate ensures recruitment, while a higher calf harvest rate transfers calves that would otherwise be lost to predators to slaughtering income. 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 an adult harvest. This is indeed an interesting effect and highlights the importance of analysing the complexity of this problem 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.

We now turn to the ecological compensation effects of predation under optimal management. First, it is observed that as the predation rates shift up from zero to the baseline levels (column six Table 1), losses to predators increase for all age classes. This effect is dampened by the ecological compensation mechanisms (column five), though this is not enough to offset an increase in total mortality for calves and adult females (column seven). However, the ecological compensation is strong enough to ensure unchanged total mortality for adult males.

**Table 1:** Steady state biological effects. Optimal management.

Predation pressure <sup>1)</sup>	Animal density (# of animals/10km <sup>2</sup> ) and harvest rates (in parenthesis)		Fertility rate $f$	Survival rates $s_c, s_f, s_m$	Mortality (# of animals/10km <sup>2</sup> )		
	$X$	$X_c, X_f, X_m$  ( $h_c, h_f, h_m$ )			Natural <sup>2)</sup>	Predation <sup>3)</sup>	Total
Zero	50.7	18.5, 20.5, 11.7  (0.0, 0.38, 0.70)	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  (0.0, 0.25, 0.70)	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  (0.70, 0.0, 0.70)	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: <sup>1)</sup> Baseline predation pressure;  $m_c = 0.27$ ,  $m_f = m_m = 0.04$ . High predation pressure;  $m_c = 0.34$ ,  $m_f = m_m = 0.05$ . <sup>2)</sup> Natural mortality (after harvest) equals  $N_i = (1-h_i)(1-s_i)X_i$ ,  $i = c, f, m$ . <sup>3)</sup> Loss of animals to predators equals  $M_i = (1-h_i)s_iX_im_i$ ,  $i = c, f, m$ .

With a further increase in the predation rates to the High level, the density effect in total number of animals is negligible, and consequently, the recruitment and natural survival rates remains unchanged. The observed changes in total mortality are now due to changes in the optimal harvest rates, and hence the stock composition, all of which lead to the mixed results. Nevertheless, for all predation levels and age classes, the proportion of animals lost to natural mortality and predation is substantially below the present management scheme scenario presented in section 7 below.

Table 2 reports the economic results. The clear economic gain of optimal management compared to the present management situation (Table 2) is first notified. With no predation, the yearly profit under the optimized scenario is 2,546 (EUR/10km<sup>2</sup>), while it was just 458 in the present 'tragedy of the commons' situation (columns five). This difference is lower under the baseline and high predation scenarios. It is also a profound difference when considering only the slaughter income (column three), where the higher number of animals slaughtered as well as higher weights and more valuable animals (column two) both contribute. More importantly, it is recognized that the annual profit reduces with any increase in the predation pressure under the optimal management scheme. The reason is obvious; predation works by constraining the feasibility set of the optimizing problem. Even if the ecological and economic compensation is weaker under the optimal scheme than under the present management scheme, the effects are still quite strong. For example, the increased predation pressure from the baseline to the high predation scenario, which represents a 25% increase, is accompanied by a profitability reduction of just 8%. The modifying effect is the increased weight of each category (calf, female, male), while the changed harvest pattern shifting from female to calf harvest also plays an important role.

**Table 2:** Steady state economic effects. Optimal management.

Predation Pressure <sup>1)</sup>	Harvesting (# of animals/10km <sup>2</sup> ) $H_c, H_f, H_m$	Weight (kg/animal) $w_c, w_f, w_m$	Income (EUR/10km <sup>2</sup> )	Cost (EUR/10km <sup>2</sup> )	Profit (EUR/10km <sup>2</sup> )
Zero	0.0, 7.7, 8.2	18.6, 27.4, 38.9	3,079	533	2,546
Baseline	0.0, 5.0, 5.9	19, 28.1, 39.9	2,188	491	1,697
High	14.4, 0.0, 1.8	19.1, 28.2, 40.1	2,041	485	1,556

Table notes: <sup>1)</sup> Baseline predation pressure;  $m_c = 0.27$ ,  $m_f = m_m = 0.04$ . High predation pressure;  $m_c = 0.34$ ,  $m_f = m_m = 0.05$ . <sup>2)</sup> Exchange rate: 1 EUR =9.25 NOK (Sept. 2016).

### 6.3 Sensitivity analysis

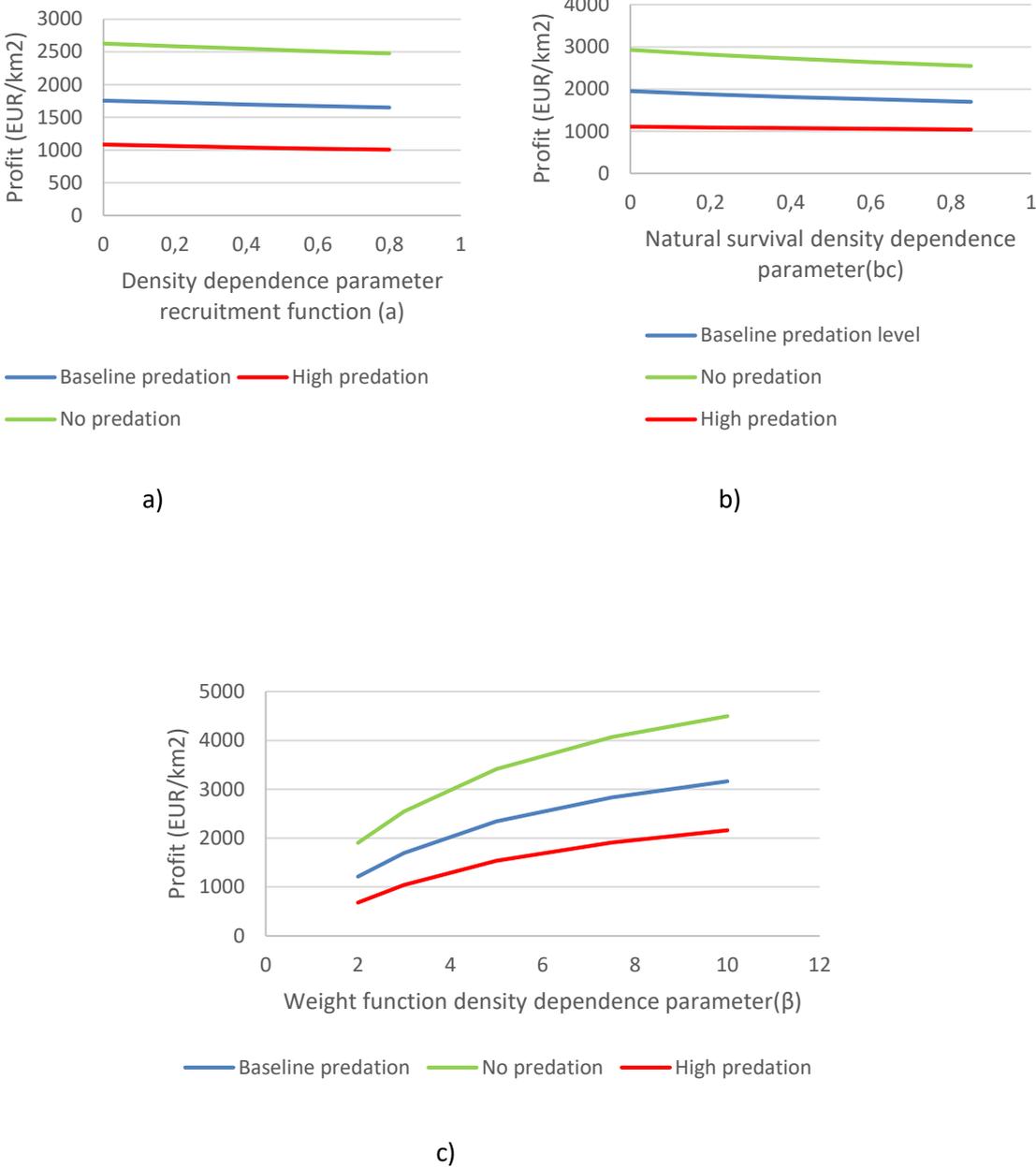
#### 6.3.1 Varying density dependency in recruitment, natural survival, and weights

We analyse now how changes in the density dependency parameters in recruitment, natural survival, and weights affect the economic outcome under optimal management. The results are demonstrated in Figure 3.

A partial increase in the density dependency in the recruitment function (increased  $a$ ) or the natural survival functions (increased  $b_i$ ,  $i = c, f, m$ ; see Appendix A for details) 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. A lower stock

density means fewer animals slaughtered, and works in the direction of reduced slaughtering profit. It is equally important to note that changing the density dependency in recruitment and natural survival rates result in quite similar economic effects due to increased predation as in the baseline scenarios. However, as illustrated in Figure 3 (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 2.

**Figure 3:** Steady state profit under varying predation pressure. Changing density dependency in recruitment ( $a$ ) (Panel a), natural survival of calves ( $b_c$ ) (Panel b), and weights ( $\beta$ ) (Panel c)\*.



\* See note 1, Table 1.

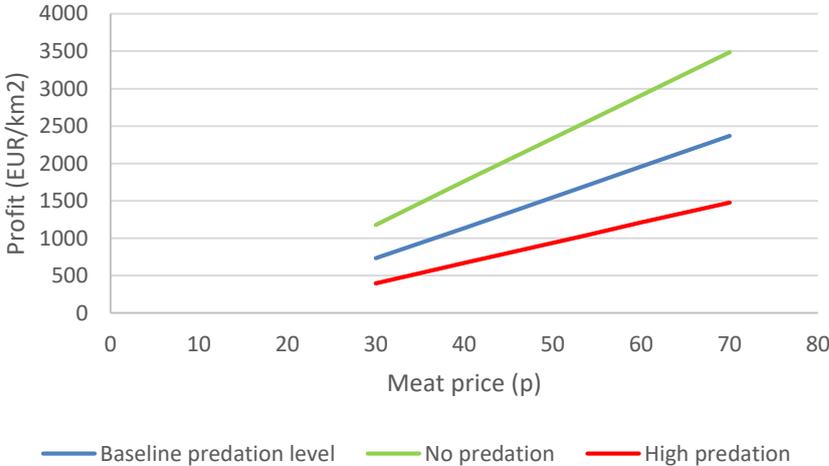
Next, it is recognized that partial increases in the density dependent parameter in the weight functions ( $\beta$ ) increases the profits under all predation levels (Figure 3, panel (c)). A higher density effect makes weights more sensitive to changes in stock density along the downward

sloping part of the sigmoidal functions (see Section 5 and Figure 2a). 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. As in the case of changes in density dependence effects in recruitment and natural survival ( $a$  and  $b_c$ ), the profit changes more with higher density dependence when there is a lower 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 2.

### 6.3.2 Varying the meat price or herding cost

Any increase in the slaughter price  $p$  (or reduced per unit herding cost) shifts, not surprisingly, the profit up under all predation rates (Figure 4). Again, the resulting profit shift is stronger the lower the predation rate is. However, in this case, the explanation is slightly different. As a higher meat price gives incentives to increase the harvesting pressure and reduce the stock of all categories of animals, the density dependent effects at work are weaker the higher the meat price is. As discussed above, predation works in the same direction, since higher predation reduces the stock sizes, and hence pulls in the direction of weaker density dependence effects. Moreover, density dependence generally means that higher predation is partly compensated by weaker density effects. When the meat price increases, the total stock therefore decreases, though the effect through weaker density dependent effects in survival, and recruitment is not so strong since the stock is already lower due to predation. In other words, because the slaughter volume reduces with increased meat prices along every profit schedule, profit will increase at a slower rate depending on how high the predation is.

**Figure 4:** Steady state profit under varying meat price and predation pressure\*.



\*See note 1, Table 1.

**7. Present management situation: ‘Tragedy of the commons’**

We now present the main results under the present management situation in the northernmost part of Norway, i.e. the ‘tragedy of the commons’ outcome.<sup>10</sup> As described in Section 2, conflicts over the utilization of common property pastures in this area has resulted high reindeer densities and poor vegetation conditions. The present harvesting rates are therefore relatively low compared to, for example, the best performing area, and are also low compared to the optimal harvesting rates derived in Section 6.2 above.

We compare the optimal steady state management scheme under the baseline predation pressure with the present management situation. First, the slaughter rate of calves is shifted up from 0.0 to 0.2 when moving from the optimal management situation to present management, while the adult slaughter rates are reduced from 0.25 to 0.05 for females and

<sup>10</sup> A comprehensive description of the tragedy of the commons case is found in Skonhoft et al. (2017).

from 0.70 to 0.21 for males. Consequently, the total animal density decreases with present management from 70 (animals/10km<sup>2</sup>) to 47, or by about 33 %. The survival- and fertility rates are therefore significantly lower under present than optimal management. For example, the adult survival rates shift down from 0.96 to 0.89, and the fertility rate shifts up down from 0.91 to 0.84. Accordingly, the natural mortality drops. Hence, the yearly number of animals lost due to natural mortality increases from 2.1 (animals/10km<sup>2</sup>) to 8.8, while the combined natural and predation mortality increases from 7.4 to 14.4 (animals/10km<sup>2</sup>). Therefore, we find that the number of animals lost to natural mortality and predation increases significantly when compared to the optimal management situation. Total mortality as a proportion of the stock level increases as well, from about 16% to 21%.

As seen in the optimized scheme, increased predation pressure reduces the steady state stock and, not surprisingly, losses to predators increase for all animal categories. However, the ecological compensation effect working through increased natural survival, and hence, reduced natural mortality loss, dampens the effect on total mortality. For instance, when shifting from the no predation scenario to the baseline level, while also keeping the survival rates fixed at their no predation level, we find that the total mortality of adult females (males) reduces from 5.7 animals (2.9 animals) to 5.6 animals (2.7 animals). However, because food limitation reduces and the animal weight increases, the natural survival rates increase as well. Therefore, when including the ecological compensation mechanism, the natural mortality for females (males) is further drawn down to 3.0 animals (1.5 animals) under the baseline predation level. In this case, the compensation effect is so strong that the

total mortality for adult animals actually reduces under the baseline predation situation as compared to the no predation scenario. It is also recognized that the natural mortality compensation mechanism is strong for the calf population, though it is not sufficient enough to offset the increased predation. Therefore, the total mortality increases from 7.3 to 8.4 animals for this category when moving from no predation to the baseline predation scenario. When moving from the baseline predation scenario to high predation pressure, much of the same picture emerges, and the total mortality rates are lower for both categories of adult animals when the predation pressure is high. See Appendix A.2 Figure A1 for the impact on total losses for a wider range of predation pressures.

As in the optimized regime, the number of animals slaughtered decreases when the predation pressure shifts up, simply because of reduced stock sizes. The slaughter weights increase, though this is not sufficient enough to offset the impact of the reduced number of slaughtered animals on the slaughter income. The slaughter income reduces only slightly from 1,343 (EUR/10km<sup>2</sup>) with zero predation to 1,309 under the baseline scenario (2.6% reduction). In comparison, it was reduced from 3079 to 2188 (EUR/10km<sup>2</sup>) in the optimized scheme (29% reduction). However, when also taking into account the reduced maintenance cost following the reduced flock size, we find that the economic compensation of increased weights is strong enough to make the herders economically better off with predation than without predation. In fact, the annual steady state slaughter value net of maintenance costs increases from 458 (EUR/10km<sup>2</sup>) to 569 in the baseline scenario, and when increasing the

predation to the high level, the profit increases even further to 585 (EUR/10km<sup>2</sup>).<sup>11</sup> This will of course never happen under the optimized management scenario, where the accompanying profit levels under the three predation scenarios are 2546 (no predation), 1697 (baseline), and 1556 (high predation) (EUR/10km<sup>2</sup>).

## **8. 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 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 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.

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 in detail 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,

---

<sup>11</sup> Notice that an alternative formulation of the meat price taking into account that animals in good conditions (i.e., higher weight) may be valued more, would strengthen the positive impact on profit of increased predation.

and also through the number of animals influencing the operating costs of the herders. The novelty of our analysis is to include both age 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 the bioeconomic literature.

By first focusing on the economically optimal management scheme, we find that the ecological effect of increased predation is dampened by a compensating change in natural mortality. However, in this case, profit decreases unambiguously with an increased predation pressure as predation constraints the behavior of optimizing herders.

Furthermore, the presence of density dependent ecological and economic compensation mechanisms may cause the optimal harvest composition to change dramatically across age classes in response to changed predation pressure.

When we next compare with the present management scheme where slaughtering rates are fixed at their present levels in accordance with a 'tragedy of the commons' outcome, we highlight the density dependent relationships at work; that is, the ecological- and economic compensation mechanisms of predation. We find that the degree of ecological compensation may be significant, and may even cause reindeer total mortality to be lower, albeit with a higher predation pressure. Furthermore, the economic compensation mechanism may cause the slaughter profit to increase in the presence of increased predation pressure.



## References

- Ballard, W. B., D. Lutz, T. W. Keegan, L. H. Carpenter, and J. C. deVos, Jr., 2001. Deer-predator relationships: a review of recent North American studies with emphasis on mule and black-tailed deer. *Wildlife Society Bulletin*. 29, 99-115.
- Berger, K. M., 2006. Carnivore-livestock conflicts: Effects of subsidized predator control and economic correlates in the sheep industry. *Conservation Biology*. 20, 751-761.
- Boman, M., G. Bostedt and J. Persson, 2003. The bioeconomics of the spatial distribution of an endangered species. The case of the Swedish wolf population. *Journal of Bioeconomics*. 5, 55 - 74
- Boyce, M. S., A. R. E. Sinclair, and G. C. White, 1999. Seasonal compensation of predation and harvesting. *Oikos*. 87, 419-426.
- Bårdsen, B. J., H. Berglann, A. Stien, and T. Tveraa, 2014. The effect of harvest on the productivity within the reindeer husbandry (in Norwegian). NINA report. 999, Tromsø.
- Bårdsen, B. J., T. Tveraa, P. Fauchald, and K. Langeland, 2010. Observational evidence of risk-sensitive reproductive allocation in a long-lived mammal. *Oecologia*. 162, 627-639.
- Bårdsen, B. J. and T. Tveraa, 2012. Density-dependence vs. density-independence – linking reproductive allocation to population abundance and vegetation greenness. *Journal of Animal Ecology*. 81, 364-376.
- Caswell, H., 2001. *Matrix population models: Construction, analysis and interpretation*. 2th ed. Sinauer, Boston.
- Clark, C., 1990. *Mathematical bioeconomics*. Wiley Interscience, New York.

Ekspertutvalget, 2011. Innstilling fra ekspertutvalg vedrørende endringer i erstatningsordningen for rovviltskade på husdyr. Direktoratet for Narturforvaltning, Trondheim.

Engel, S., S. Pagiola and S. Wunder, 2008. Designing payment for environmental services in theory and practice: an overview of the issues. *Ecological Economics*. 85, 663 – 674.

Finnoff, D. and J. Tschirhart, 2003. Protecting and endangered species while harvesting its prey in a general equilibrium ecosystems model. *Land Economics*. 79, 160-180.

Getz, A. and R. G. Haigh, 1989. *Population harvesting*. Princeton University press, Princeton.

Graham, K., A. P. Beckerman, and S. Thirgood, 2005. Human-predator-prey conflicts: ecological correlates, prey losses and patterns of management. *Biological Conservation*. 122, 159-171.

Hannesson, R., 1983. Optimal harvest of ecologically interdependent fish species. *Journal of Environmental Economics and Management*. 10, 329-345.

Hardin, G., 1968. The tragedy of the commons. *Science*. 162, 1243-1248.

Hausner, V. H., P. Fauchald, and J-L Jernsletten, 2012. Community-based management: Under what conditions do Sámi pastoralists manage pastures sustainably? *PLoS ONE*. 7, e51187. doi:10.1371/journal.pone.0051187.

Johannesen, A. B. and A. Skonhoft, 2011. Livestock as insurance and social status: Evidence from reindeer herding in Norway. *Environmental and Resource Economics*. 48, 679-694.

Johannesen, A. B. and A. Skonhoft, 2009. Local common property exploitation with rewards. *Land Economics*. 85, 637-654.

Johansen, B. and S. R. Karlsen, 2005. Monitoring vegetation changes on Finnmarksvidda, Northern Norway, using Landsat MSS and Landsat TM/ETM+ satellite images.

*Phytocoenologia*. 35, 969-984.

Kolowski, J. M. and K. E. Holekamp, 2006. Spatial, temporal, and physical characteristics of livestock depredations by large carnivores along a Kenyan reserve border. *Biological Conservation*. 128, 529-541.

Kumpula, J., M. Kurkilahti, T. Helle, and A. Colpaert, 2014. Both reindeer management and several other land use factors explain the reduction in ground lichens (*Cladonia* spp.) in pastures grazed by semi-domesticated reindeer in Finland. *Regional Environmental Change*. 14, 541-559.

Mattisson, J., G. B. Arntsen, E. B. Nilsen, L. E. Loe, J. D. C. Linnell, J. Odden, J. Persson, and H. Andrén, 2014. Lynx predation on semi-domestic reindeer: do age and sex matter? *Journal of Zoology*. 292, 56-63.

Mishra, C., 1997. Livestock depredation by large carnivores in the Indian trans-Himalaya: conflict perceptions and conservation prospects. *Environmental Conservation*. 24, 338-343.

Mysterud, A., N.G., Yoccoz, N.C. Stenseth., R. Langvatn, 2001. Effects of age, sex and density on body weight of Norwegian red deer: evidence of density-dependent senescence. *Proc. R. Soc. Lond. B*. 268, 911-919.

Naevdal, E., J.O. Olausson, and A. Skonhøft, 2012. A bioeconomic model of trophy hunting. *Ecological Economics*. 73, 194-205

Nieminen, M., 2010. The impact of large carnivores on the mortality of semi-domesticated reindeer (*Rangifer tarandus tarandus* L.) calves in Kainuu, southeastern reindeer region in Finland. *Rangifer*. 30, 79-87.

Nilsen, E., Pettersen, T., Gundersen, H., Mysterud, A., Milner, J., Solberg, E., Andreassen, H., Stenseth, and N.C., 2005. Moose harvesting strategies in the presence of wolves. Spatially structured populations. *Journal of Applied Ecology*. 42, 389–399.

Norwegian Reindeer Husbandry Administration (NRHA), 2013a. Ressursregnskap for reindriftnæringen (in Norwegian), Alta.

Norwegian Reindeer Husbandry Administration (NRHA), 2014. Ressursregnskap for reindriftnæringen (in Norwegian), Alta.

Norwegian Reindeer Husbandry Administration (NRHA), 2013b. Totalregnskap for reindriftnæringen (in Norwegian), Alta.

Olaussen, J.O., and A. Skonhoft, 2011. A cost benefit analysis of moose harvesting in Scandinavia. A stage structured modelling approach. *Resource and Energy Economics*. 33, 589-611.

Pekkarinen, A-J, J. Kumpula, and O. Tahvonen, 2015. Reindeer management and winter pastures in the presence of supplementary feeding and government subsidies. *Ecological Modelling*. 312, 256-271.

Reed, W., 1980. Optimal age-specific harvesting in a nonlinear population model. *Biometrics*. 36, 579-593.

Riseth, J. Å., 2006. Sami reindeer herd managers: Why do they stay in low-profit business? *British food journal*. 108, 541-559.

Riseth, J. Å. and A. Vatn, 2009. Modernization and pasture degradation: A comparative study of two Sami reindeer pasture regions in Norway. *Land Economics*. 85, 87-106.

Sinclair, A. R. E. and R. P. Pech, 1996. Density dependence, stochasticity, compensation and predator regulation. *Oikos*. 75, 164-173.

Skonhoft, A., 2006. The costs and benefits of animal predation: An analysis of Scandinavian wolf re-colonization. *Ecological Economics*. 58, 830-841.

Skonhoft, A., 2008. Sheep as capital and farmers as portfolio managers: a bioeconomic model of Scandinavian sheep farming. *Agricultural Economics* 38, 193-200

Skonhoft, A., A.B. Johannesen, and J.O. Olausen, 2017. On the tragedy of the commons: When predation and livestock loss may improve the economic lot of herders.

*Ambio*

Skonhoft, A., V. Veiberg, A. Gauteplass, J. O. Olausen, E. Meisingset, and A. Mysterud, 2013. Balancing income and cost in reindeer management. *Journal of Environmental Management*. 115, 170 – 188.

Skonhoft, A., N. Vestergaard and M. Quaas, 2012. Optimal harvest in an age structured model with different fishing selectivity. *Environment and Resource economics*. 51, 525 – 544.

Tahvonen, O., 2009. Economics of harvesting age-structured fish populations. *Journal of Environmental Economics and Management*. 58, 281-299.

Tahvonen, O., J. Kumpula, and A-J Pekkarinen, 2014. Optimal harvesting of an age-structured, two-sex herbivore-plant system. *Ecological Modelling*. 272, 348-361.

Tschirhart, J., 2009. Integrated Ecological-Economic Models. *Annual Review of Resource Economics*. 1, 381 – 407.

Tveraa, T., A. Stien, B-J Bårdsen, and P. Fauchald, 2013a. Population densities, vegetation green-up, and plant productivity: Impact on reproductive success and juvenile body mass in reindeer. *PLoS ONE*. 88, e56450. doi:10.1371/journal.pone.0056450.

Tveraa, T., A. Stien, H. Brøseth, and N. G. Yoccoz, 2014. The role of predation and food limitation on claims for compensation, reindeer demography and population dynamics. *Journal of Applied Ecology*. 51, 1264-1272.

Tveraa, T., M. Ballesteros, B-J Bårdsen, P. Fauchald, M. Lagergren, K. Langeland, E. Pedersen, A. Stien, 2013b. Estimation of productivity and losses within the reindeer husbandry (in Norwegian). NINA report. 938, Tromsø.

Tveraa, T., M. Ballesteros, B-J Bårdsen, P. Fauchald, M. Lagergren, K. Langeland, E. Pedersen, A. Stien, 2012. Predators and reindeer husbandry – current knowledge in Finnmark (in Norwegian). NINA report. 821, Tromsø.

Tveraa, T., P. Fauchald, C. Henaug, and N. G. Yoccoz, 2003. An examination of a compensatory relationship between food limitation and predation in semi-domestic reindeer. *Population Ecology*. 137, 370-376.

Tveraa, T., P. Fauchald, N. G. Yoccoz, R. A. Ims, R. Aanes, and K. A. Høgda, 2007. What regulate and limit reindeer populations in Norway? *Oikos*. 116, 706-715.

Vucetich, J. A., D. W. Smith, and D. R. Stahler, 2005. Influence of harvest, climate and wolf predation on Yellowstone elk, 1961-2004. *OIKOS*. 111, 259-270.

Wilmers, C. C., E. Post, A. Hastings, 2007. The anatomy of predator-prey dynamics in a changing climate. *Journal of Animal Ecology*. 76, 1037-1044.

Zabel, A., G. Bostedt, and S. Engel, 2014. Performance payments for groups: The case of carnivore conservation in northern Sweden. *Environmental and Resource Economics*. 59, 613-631.

Zabel, A., K. Pittel, G. Bostedt, and S. Engel, 2011. Comparing conventional and new policy approaches for carnivore conservation: Theoretical results and application to tiger conservation. *Environmental and Resource Economics*. 48, 287-301.

## Appendix A. Specific functional forms and numerical specification

### A.1 Specific functional forms

We start to specify the functional forms. The fertility rate, increasing in the female weight, is first specified as:

$$(A.1) \quad f_t = \bar{f} \cdot (w_{f,t} / \bar{w}_f)^a .$$

Here,  $f_t = \bar{f}$  is the maximum fertility rate when the adult female weight reaches its maximum value,  $w_{f,t} = \bar{w}_f$ . The parameter  $0 < a < 1$  indicates that fertility is a concave function of the weight. The next equation:

$$(A.2) \quad s_{i,t} = \bar{s}_i \cdot (w_{i,t} / \bar{w}_i)^{b_i} ; i = c, f, m$$

yields the same functional form for the natural survival rates. Here,  $\bar{s}_i$  is the maximum survival rate for animal category  $i$ , and the parameter  $0 < b_i < 1$  is generally different among the different categories.

The weight-density relationships, where weights decrease in the total number of animals, are specified as sigmoidal functions with an increasing degree of density dependence at high densities (Myerud et al. 2001, Nielsen et al. 2005). The same functional form is assumed for all categories of animals and reads:

$$(A.3) \quad w_{i,t} = \frac{\bar{w}_i}{1 + (X_t / K)^\beta} ; i = c, f, m .$$

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 compensation parameter  $\beta > 0$  indicates to what extent density-independent factors compensate for changes in the stock size.

Combining Eqs. (A.1) and (A.3) yields  $f_t = \bar{f} \cdot \left(\frac{1}{1 + (X_t / K)^\beta}\right)^a$ , while Eqs. (A.2) together with

(A.3) yield  $s_{i,t} = \bar{s}_i \cdot \left(\frac{1}{1 + (X_t / K)^\beta}\right)^{b_i}$ . Therefore, both fertility and survival rates are sigmoidal

functions of the total animal stock. It is furthermore recognized that with these functional forms, the ratio of the natural survival rates between the two adult categories of animals in equilibrium as well as outside steady state will be proportional to the maximum survival rates  $\bar{s}_i$  under the assumption of  $b_f = b_m$ . Because of  $\bar{s}_f = \bar{s}_m$  (see Table A1), we therefore find that the natural survival rates of the adult categories all the time will be similar.

For simplicity, and as already indicated, we assume that all predation takes place after the winter natural mortality, which reflects the fact that the late winter population is the most vulnerable to predation. With a Lotka – Volterra type of predator – prey relationship (see, e.g., Clark 1990), the predation loss in the number of animals of the various animal

categories reads  $M_{i,t} = \theta_i s_{i,t} (1 - h_{i,t}) X_{i,t} Q_t$ . Here,  $Q_t$  is the number of predators, and  $\theta_i > 0$

is a parameter indicating the strength of the predation pressure, depending on, among

others, the type and mix of predators in our considered area, weather conditions, and so

forth. The predation rate and the number of animals lost relatively to the size of the standing

population may then be written as:

$$(A4) \quad m_{i,t} = M_{i,t} / (s_{i,t} (1 - h_{i,t}) X_{i,t}) = \theta_i Q_t; \quad i = c, f, m.$$

The predation coefficient is generally higher for the calves than for adults,  $\theta_c > \theta_f$  and  $\theta_c > \theta_m$  and hence,  $m_{c,t} > m_{f,t}$  and  $m_{c,t} > m_{m,t}$ . Therefore, the predation rates are independent of the reindeer population, given our assumptions (see section 5.1 and 3.1).

Finally, the maintenance cost function is specified as linear:

$$(A.5) \quad C_t = c \cdot (X_{c,t} + X_{f,t} + X_{m,t}),$$

such that  $c > 0$  is the constant marginal maintenance cost.

## *A.2 Parameter values*

Table A1 presents the baseline parameter values, mainly based on the annual reports from herders in western Finnmark to the government (NRHA 2014) and official statistics on losses to predators ([www.rovbase.no](http://www.rovbase.no)). Our baseline predation rates are set based on data on losses to predators, as reported by herders yearly when applying to the State for compensation for losses to predators and the number of losses considered as likely by the State when offering compensation. 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 are specified based on the average of claimed and compensated losses in 2013. The baseline harvesting rates are the same as the current rates in the northernmost part of Norway.

**Table A1:** Baseline parameter values

Description	Parameter	Value	Unit	Reference
Sex ratio	$\psi$	0.5		Assumed
Maximum fertility rate	$\bar{f}$	0.95	Calves/females	NRHA (2014)
Maximum weights	$\bar{w}_c, \bar{w}_f, \bar{w}_m$	21, 31, 44	kg/animal	NRHA (2014)
Parameter fertility rate	$a$	0.4		Calibrated
Maximum survival rates	$\bar{s}_c, \bar{s}_m, \bar{s}_m$	1, 1, 1		Assumed
Parameter survival rates	$b_c, b_f, b_m$	0.85, 0.4, 0.4		Calibrated
Weight parameter	$\beta$	3		Assumed
Carrying capacity	$K$	100	Animals/10 km <sup>2</sup>	Assumed
Predation rates	$m_c, m_f, m_m$	0.27, 0.04, 0.04		www.rovbase.no
Harvesting rates <sup>1)</sup>	$h_c, h_f, h_m$	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	$\delta$	0.03		Assumed

<sup>1)</sup> Harvesting rates used in section 5. Fixed at the present level in the northernmost part of Norway.

In spring 2012, after slaughtering and losses, herders in the northernmost part of Norway (i.e., western Finnmark) kept in total 104 200 animals, of which 75% were females and 25% males (NRHA 2013a, 2014). During the following summer, 65 800 calves were born, which gives a recruitment rate of 0.84 calves per female (NRHA 2014). The model is specified at a scale of 10 km<sup>2</sup>, and when given a total area of 24,400 km<sup>2</sup>, the stock density is 70 animals (10<sup>-1</sup>km<sup>-2</sup>).

The baseline parameter values reported in Table A1 are determined as follows. The slaughter weights in the best performing reindeer herding area in Norway (south), where the vegetation cover is intact, were used as proxies for maximum weights. When using these values together with the baseline stock density in the weight functions, and when assuming that  $\beta = 3$  and  $K = 100$ , the weights in steady state (Table 2) correspond reasonable well with the actual weights observed in the northernmost part of Norway (NRHA 2014).

The slaughtering price was 5.8 EUR per kilo in 2012 (NRHA 2013b). With the current stock composition ( $X_c = 27$ ,  $X_f = 31$ ,  $X_m = 12$ ), and slaughtering composition ( $h_c = 0.2$ ,  $h_f = 0.05$ ,  $h_m = 0.21$ ), this gives a gross slaughtering income of 1,177 EUR per 10 km<sup>2</sup>. Net income in the northernmost part of Norway was 568 EUR per 10km<sup>2</sup> in 2012 (NRHA 2013b).

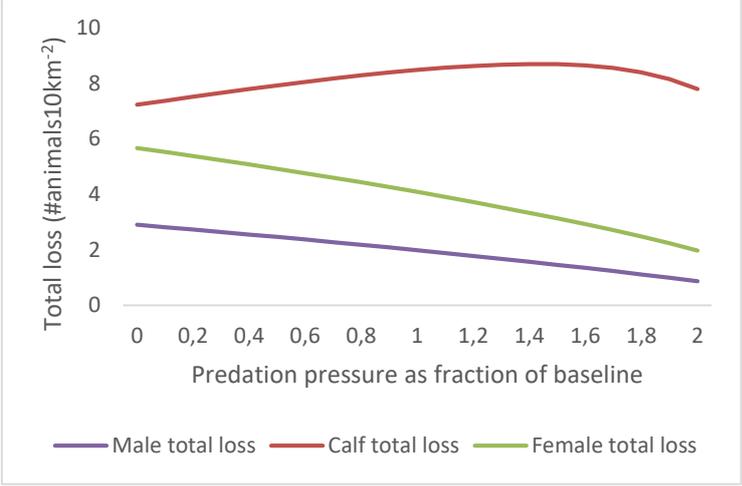
The per animal herding cost  $c$  is calibrated so that the same slaughtering rates give the same yearly profit level in our model in steady state.

We use the calving rate in the best performing reindeer herding area as a proxy for the maximum calving rate  $\bar{f}$ . The recruitment parameter  $a$  is calibrated to give a baseline calving rate similar or equal to the observed calving rate of 0.84 calves per female in the north (NRHA 2014).

The maximum natural survival rates are set equal to unity. When determining the baseline survival parameters  $b_c$ ,  $b_f$ , and  $b_m$ , we assume that  $b_f = b_m$  and that the survival rate of calves is more sensitive to changes in stock density so that  $b_c > b_f = b_m$ . Finally, we calibrate  $b_c$ ,  $b_f$ , and  $b_m$  so that the ecological values fit reasonable well with actual values in north.

Figure A1 shows the impact of a changing predation pressure on total loss. Without any ecological compensation effect, the total loss would increase with a higher predation pressure for all categories of animals. However, for adult animals the ecological compensation effect is strong enough to reduce the total loss for all predation pressures illustrated. Calf predation on the other hand, increases the total loss of calves up to a certain predation pressure (40% above baseline) before the ecological compensation effect starts dominating so that a further increase in the predation pressure decreases total loss.

**Figure A1:** Total loss\*



\*The range on the horizontal axis represent fractions of the baseline predation rates  $m_c = 0.27$  and  $m_f = m_m = 0.04$ . Therefore, 1 represent the baseline predation pressure while, say, 2 represents a doubling of (all) the baseline rates.

**Appendix 2. Portfolio conditions and population dynamics**

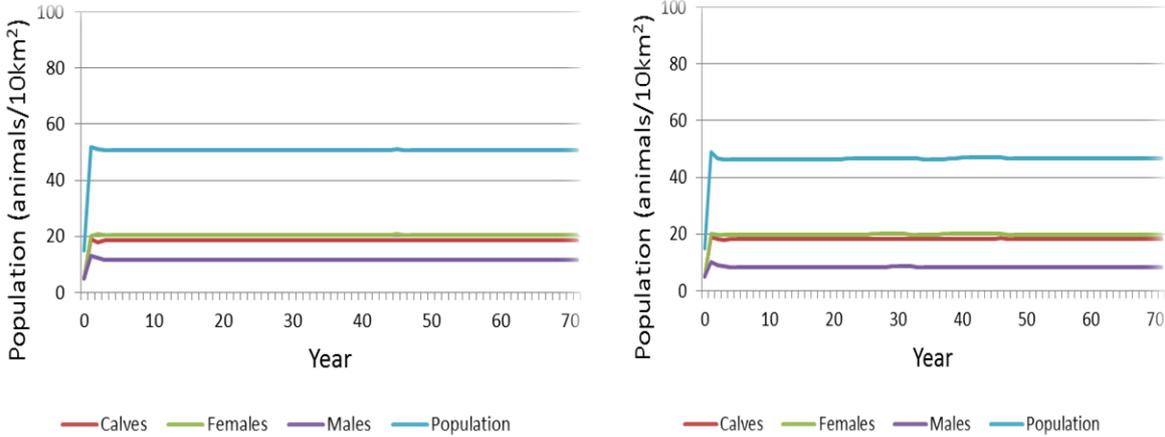
The portfolio conditions  $-\partial H / \partial X_{i,t} = \rho \lambda_{i+1} - \lambda_t$ ,  $i = (c, f, m)$  are rather messy due to the various density dependence and compensation effects. For example, the calf portfolio condition is written as:

$$\begin{aligned}
-\frac{\partial H}{\partial X_{c,t}} &= -p(w_{c,t}h_{c,t} + h_{c,t}X_{c,t}w'_{c,t} + h_{f,t}X_{f,t}w'_{f,t} + h_{m,t}X_{m,t}w'_{m,t}) + C' + \lambda_t - \lambda_t f'_t w'_{f,t} X_{f,t} \\
&- \rho\mu_{t+1}\psi(1-h_{c,t})(1-m_{c,t})(s_{c,t} + X_{c,t}s'_{c,t}w'_{c,t}) - \rho\mu_{t+1}(1-h_{f,t})(1-m_{f,t})X_{f,t}s'_{f,t}w'_{f,t} \\
\text{(A.6)} \quad &- \rho\eta_{t+1}(1-\psi)(1-h_{c,t})(1-m_{c,t})(s_{c,t} + X_{c,t}s'_{c,t}w'_{c,t}) \\
&- \rho\eta_{t+1}(1-h_{m,t})(1-m_{m,t})X_{m,t}s'_{m,t}w'_{m,t} = \rho\lambda_{t+1} - \lambda_t
\end{aligned}$$

$$-\frac{\partial H}{\partial X_{f,t}} \text{ and } -\frac{\partial H}{\partial X_{m,t}} \text{ follows similar patterns (available on authors request).}$$

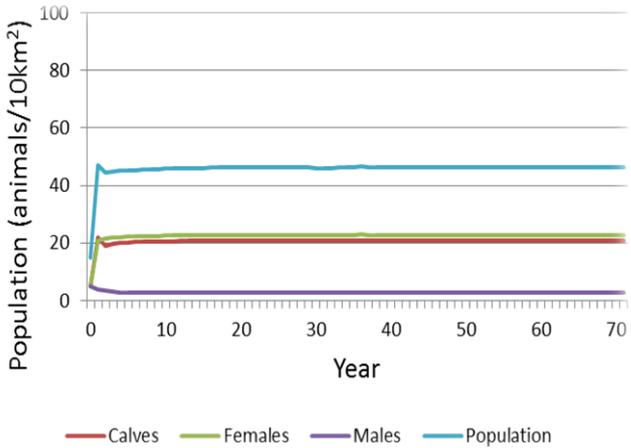
Figure B1 demonstrates population dynamics under no predation, baseline predation, and high predation pressure in the optimized management harvesting regime. As the figures demonstrate, the different population age classes approaches their stable equilibrium paths quite fast. We solve the model over 100 years. This long horizon ensures that the reported solutions will be numerically indistinguishable from the infinite horizon solution over the reported period of 70 years.

**Figure B1:** Population dynamics. Optimal management scheme.



a) No predation

b) Baseline predation



c) High predation