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Predation costs and compensations in reindeer husbandry

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Conflicts often arise when large predators and free-ranging livestock share a common area. Various compensation schemes are used to attempt solving these conflicts, but the costs of predation to suffering stakeholders are often unknown. Semi-domesticated reindeer husbandry and large carnivores form one such system, where conflicts between predator conservation and the traditional livelihood are common. We apply an age- and sex-structured reindeer-lichen model to examine the effects of predation on reindeer management. Based on the previous studies we specify age- and sex-class-specific mortalities due to various predators, and study optimal reindeer husbandry under predation pressure and the costs of predation. We show that the costs of predation highly depend on the age-class-specific killing rates of reindeer by various predator species, but not on interest rate or pasture conditions. Regarding species that are more likely to kill adult reindeer in addition to calves, the total predation costs are clearly higher than the net slaughtering value of the predated animals. The decrease in steady-state yearly net income is highest for the gray wolf and lower for other predator species. Adapting to predation pressure includes increasing the size of the reindeer population in winter and changing the slaughtering age of males towards young adults, thus reducing the importance of calf harvesting. This result contrasts with the previous results from stage-structured models that do not fully include time lags related to long-living ungulate species. The costs of predation appear to be much higher in an ex post system than in a territorial compensation system, as in an ex post system herders have not adapted to the predation pressure and must search for the predated reindeer to gain compensations. Our results suggest that co-existence of a viable gray wolf population and profitable reindeer husbandry in the same area is not possible in most cases.

Keywords: adaption, age structure, bioeconomic model, compensation, optimization, predation, sex structure

Conflicts often arise when large predators and free-ranging livestock share a common area (Thirgood et al. 2005). As predator conservation programs intensify, various conflicting interest situations may become even more common in the future (Chapron et al. 2014). Cultural values and questions may also be connected to the conflicting interest, as a traditional herding livelihood forms the cultural basis for many indigenous people. Compensation schemes are a widely proposed solution for conflict solving (Dickman et al. 2011). However, costs relating to predation are often unknown, making it difficult to set fair compensation levels.

Semi-domesticated reindeer *Rangifer tarandus* herding in northern Fennoscandia and the large carnivore populations living in the same area are a prime example of a system where conflicts between predator conservation and traditional livelihood arise and are managed using various compensation schemes (Swenson and Andrén 2005). Reindeer herding differs greatly from typical livestock farming, as the productivity of the reindeer population is coupled with the dynamics of natural pastures. Therefore, adapting to predation requires considering the interactions between three trophic levels (pastures, herbivores, predators). In this study, we apply an existing age- and sex-structured reindeer–lichen model to examine the effects of predation caused by various predators on the productivity and economics of reindeer management. Our aim is to study how herders could adapt to the predation pressure by changing the management and slaughtering strategy of reindeer herds and what the costs of predation caused by various predators are. Based on our results, we then discuss the costs of predators under two compensation systems used in Fennoscandian reindeer husbandry.

The actual number of reindeer killed by predators in Fennoscandia (here Norway, Sweden and Finland) is difficult to estimate accurately, as for most of the year reindeer live freely on natural pastures and all reindeer killed by predators (especially calves) are impossible to document. Also, the regional pressure of predation on reindeer varies between the countries due to different-sized predator populations,

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availability of alternative prey, yearly snow and weather conditions, and landscape characteristics (Tablado et al. 2014). However, predator compensations are paid according to estimated damages in all Fennoscandian countries. Sweden is estimated to experience the greatest losses, with roughly 50 000 reindeer killed annually by predators (Swenson and Andrén 2005, Sami Parliament 2019). In Norway, herders have received predator compensation for roughly 20 000 reindeer killed annually during previous years (Swenson and Andrén 2005, Sønstebø 2018), although they have applied for compensations for much greater numbers (Sønstebø 2018). Losses have been estimated to be lowest in Finland, where compensation has been paid for roughly 10 000 annually killed reindeer (Reindeer Herders Association 2018). In addition to differences between the countries, there are huge differences in predator densities and the associated damages to reindeer herding within the countries.

The compensation systems also differ between the three countries and so do the methods for estimating the total predation rate. Compensation systems are typically dived into ex post systems and systems based on conservation performance (ex ante systems) (Zabel and Holm-Muller 2008). A territorial ex ante (conservation performance) compensation system is used in Sweden, and reindeer herders are compensated according to an evaluated number of predators and the predation pressure they cause (Zabel and Holm-Muller 2008). Ex post compensation systems are used in Finland and Norway, and reindeer killed by large carnivores must be found and compensation is paid according to observed or proven damages (Finlex 2009). Certain exceptions exist, for example a territorial system is used in Finland for calf losses caused by golden eagles *Aquila chrysaetos* and large carnivores from May (calf birth) to the end of November (Finlex 2009). Many difficulties have been associated with ex post compensation schemes that may be avoided with ex ante compensation schemes such as the territorial system that aims to pay according to the performance of predation conservation (Schwerdtner and Gruber 2007, Zabel and Holm-Muller 2008). Thus, developing a territorial compensation system is considered a one solution for reducing conflicts relating to the reindeer herding – predator problem in Finland and Norway (Heikkinen et al. 2011, Tveraa et al. 2014). However, experiences in Sweden have shown that conservation performance payment mechanisms also have their problems (Swenson and Andrén 2005), and reindeer herders argue that the territorial system does not work for the gray wolf *Canis lupus* in particular. However, for any well-working and equitable compensation system, understanding how various predation pressures affect the productivity and economy of reindeer husbandry is imperative.

Only a few studies have attempted evaluating the predation costs for reindeer herding livelihood in Nordic countries, and results appear inconsistent. Studies conducted in Norway have concluded that predation is not very problematic for reindeer herding in the area. Actually, Skonhoft et al. (2017) found that predation may even increase the net revenues of reindeer herders, when a 'tragedy of the commons' situation exists. Tveraa et al. (2014) consistently found that density-dependent food limitation is more important than predation for the productivity of reindeer herding in Norway. However, studies for Sweden and Finland emphasize opposite conclusions. According to Hobbs et al. (2012), predation reduces the growth rate of the reindeer population, and a biological basis exists for compensating predation damages for reindeer herders in Sweden. Heikkinen et al. (2011) and Kumpula et al. (2017) also found that calving and slaughtering percentages are lowered by intensified predation pressure in Finland. One important reason for this difference in conclusions appears to be the different predator abundances between countries and study areas. Also, differences in reindeer herding systems within Fennoscandia may explain these opposing results and conclusions. In addition, the differences in pasture conditions between the study areas also affect these solutions. For example, the conclusions by Skonhoft et al. (2017) are partly due to the overgrazing situation in Finnmark. Low pasture conditions are also common in Finland and Sweden, but supplementary feeding to balance the energy intake of reindeer is more commonly used in these areas. However, one important shortcoming of all the previous studies is that none have aimed to study optimal adaptation to predation or quantify the monetary costs to reindeer herding incurred by various predators.

Skonhoft (2008) included the effects of predation in his bioeconomic model of Scandinavian sheep farming. He found that predation decreases the total harvest but does not affect the harvesting strategy between stage classes (adult, lambs). However, according to Johannesen et al. (2019), high predation mortality causes calf slaughtering to become optimal in a reindeer husbandry system. As far as we know, Skonhoft et al. (2017) and Johannesen et al. (2019) are the only ones to study the economically sustainable or optimal adaptation of a reindeer management system to predation pressure. However, they did not include consumer–resource dynamics between reindeer and their pastures. In addition, they used a stage-structured model with only three stage variables, which is insufficient for describing time lags in the system that highly influence optimal harvesting decisions. Gervasi et al. (2012) included four age classes in their model of roe dear and moose predation and found that predation on various age classes produced very different demographic effects in a prey population. However, they did not study economically sensible harvesting strategies or include pasture dynamics.

An economic–ecological context is required when studying sustainable and economically viable reindeer herding (Pekkarinen 2018), as the profitability of reindeer herding highly depends on winter pasture conditions (Pape and Löffler 2012), herding systems (Kumpula et al 2014, Pekkarinen et al. 2017), and on the predation pressure caused by large carnivores (Hobbs et al. 2012, Kumpula et al. 2017). However, the few studies that combine reindeer–pasture dynamics with the economics of reindeer herding do not take into account the effects of predation. In this study, we use the dynamic bioeconomic reindeer–lichen model in Tahvonen et al. (2014) and Pekkarinen et al. (2015), to which we include the effects on reindeer population of various predators. With a bioeconomic model it is possible to combine the ecological interactions of three trophic levels with the economy of reindeer herding. Our aim is to analyze the economically rational way of adapting to predation and to evaluate the costs of predation caused by various predator species. Based on our results, we then discuss the costs of predators under the two compensation systems used in Fennoscandian reindeer husbandry. As far as we know, this is the first study both assessing the economically rational adaptation of the management of an age- and sex-structured reindeer population to predation pressure and analyzing the predation costs caused by various predators in the reindeer–lichen management system.

Model and methods

Bioeconomic model for reindeer management

In this study, we expand the model in Tahvonen et al. (2014) and Pekkarinen et al. (2015) by including the estimated yearly mortality rates of reindeer caused by various predator species (for a mathematical description of the model, see Pekkarinen et al. 2015 and Supplementary material Appendix 1). We evaluate the mortality rates for winter and summer separately and also differentiate between adult females, adult males, young females, young males and calves. The reindeer population model includes 17 female and 13 male age classes and a detailed description of winter energy resource utilization by the reindeer population. Reproduction is specified by a modified harmonic mean mating system (Bessa-Gomes et al. 2010) and the diet choice between arboreal lichens, ground lichens and other cratered food (dwarf shrubs, mosses and graminoids) follows the principles of the optimal foraging theory (Stephens 1986). Winter food availability and the associated energy intake in relation to energy need during winter define an individual's weight decrease during winter and its consequences to mortality and reproduction. Lichen growth depends on the areas of lichen-dominated habitat types and their lichen biomass after consumption. The animals chosen for slaughter from the age and sex classes are the decision variables in the model (for objective function see Supplementary material Appendix 1). We use the formulation presented in Pekkarinen et al. (2015) with updated costs and prices, but without considering the effects of supplementary feeding. However, as a sensitivity analysis, we also examine the costs of predation by various predators in a situation where reindeer herding is based on intensive supplementary feeding.

To account for the total lichen reduction by grazing reindeer, the model also includes lichen wastage caused by reindeer in addition to what is ingested and converted into energy. This wastage is mainly generated by the reindeer trampling on and spilling of the lichen. Pekkarinen et al. (2017) estimated two wastage functions (constant and linear) to describe the situation in northernmost Finland. In this study, we use the constant wastage function, as it is simpler and reduces computing time compared to the linear wastage function.

Costs and prices

Finland and Norway both use an ex post compensation system. Thus, reindeer herders must prove that predators have caused damages to gain compensation for predation (including locating the reindeer carcass and any signs of predation). However, searching for killed reindeer can be very costly and time consuming. According to Järvenpää (2014), locating a killed reindeer costs 280–420€. However, according to Kumpula et al. (2017), reindeer herders reported that searching and locating a reindeer killed by predators takes 2.1–7.8 working days, meaning much higher costs than concluded by Järvenpää (2014). The difference between these findings is probably due to differing numbers of killed reindeer and the size of the area where killed reindeer have to be searched and located. In a study by Järvenpää (2014), the killing rate was much higher, probably leading to lower costs per located reindeer. In this study, we use the upper end (420€) of the results by Järvenpää (2014) when estimating the importance of searching costs. In addition, we include a sensitivity analysis with low (280€) and high (560€) searching costs. For computing the total searching costs, we assume that only 70% of all reindeer (adults and calves) killed during winter and 30% of adult reindeer killed during summer are found (Supplementary material Appendix 1). We also assume that calves killed by predators during summer (before the slaughtering season) are not searched for.

We computed the unit costs and producer meat prices for the 20 northernmost herding districts in Finland for years 2015 and 2016, based on data from the Reindeer Herder's Association. The estimated annual herding costs are 40.01€ (per reindeer in the winter population), slaughtering costs are 22.04€ (per slaughtered reindeer), and fixed costs are 1.56€ (per ha of total land area used by the reindeer herding cooperative). The estimated producer meat price is 10€ (per kg of meat).

Specifying mortality by various predators

Four large mammalian predators are present in the reindeer herding area of Fennoscandia: the gray wolf, wolverine *Gulo gulo*, brown bear *Ursus arctos* and Eurasian lynx *Lynx lynx* and one avian predator: the golden eagle, which can all cause remarkable losses for reindeer herding, at least locally (Nybakk et al. 2002, Nieminen et al. 2011). All three Nordic countries have conducted studies on the effects of predation pressure on reindeer herds. However, we can only roughly evaluate the killing rates, as it is not possible to obtain exact universal values for the annual killing rates of reindeer by various predators. This is because predation pressure and reindeer killing rates by a predator species are dependent on the densities of predators, reindeer and other prey species but also on local vegetation and landscape types, seasons, herding and grazing systems etc. Table 1 presents the kill rates for different predator species that we have evaluated based on semi-domesticated reindeer–predator statistic and previous research presented below.

Gray wolves are estimated to cause the greatest reindeer losses, and these losses are also relatively evenly divided between age and sex classes (Table 1). The analysis of wolf predation costs on Fennoscandian reindeer husbandry is important despite wolf packs not being allowed within the reindeer herding areas in Sweden or Norway and no permanent wolf territories existing within the reindeer herding area in Finland. Examining the costs of wolf predation may inform political decisions of whether or not wolf packs

Table 1. Average mortality rate estimates for reindeer caused by one individual of a predator species. Information is provided for different reindeer age and sex classes during different seasons. Estimations are based on existing literature.

	Wolverine	Gray wolf	Eurasian lynx	Brown bear	Golden eagle pair
Winter mortality					
Females	19	24	6	0	0
Males	2	4	0.9	0	0
Young females	2.5	8	4	0	0.8
Young males	0.5	2	1	0	0.2
Summer mortality					
Females	0	4	1	1	0
Males	0	1	0.1	0.1	0
Young females	0	2	2	0.8	0.4
Young males	0	1	1	0.1	0.1
Calves	2	20	14	16	14
Total mortality	26	66	30	18	15.5

Studies used in estimating the mortality rates by different predators: Brown bear: Karlsson et al. 2012, 2014, Åhman et al. 2015, Gray wolf: Kojola et al. 2004, 2009, Eurasian lynx: Pedersen et al. 1999, Mattisson et al. 2011, 2014, 2016, Hobbs et al. 2012, Wolverine: Mattisson et al. 2016, Golden eagle pair: Nybakk et al. 1999, Norberg et al. 2006, Nieminen et al. 2011, Predation in general: Nybakk et al. 2002, Nieminen et al. 2013.

could be allowed in a given area and what the associated costs would be.

Kojola et al. (2004) found that wolves predate reindeer during both the summer and winter seasons and wolf predation limits the growth of wild reindeer populations in central Finland. Kojola et al. (2009) showed that calf predation was high when wolf density was high. Thus, we assume that during the summer season the majority of wolf predation targets calves. However, during the winter season, after intensive calf slaughtering during autumn, predation more evenly affects all age classes. Still, we estimate that more than 25% of reindeer killed by wolves are young reindeer, although they only constitute ca 12% of the typical reindeer population in Finland. Our estimation of predation on adult reindeer is skewed towards females because more than 90% of adult reindeer are females in Finnish semi-domesticated reindeer populations. We use an estimate of 66 reindeer killed per one wolf in our model computations (Table 1). However, we also include a sensitivity analysis of the costs of predation assuming varying kill rates by wolves.

Although studies by Mattisson et al. (2011, 2016) indicate the lynx kill rate to be higher than that of wolverines, the analysis by Hobbs et al. (2012) suggested lynx and wolverines predation rates on semi-domesticated reindeer to be similar on average. Similarly, we estimate that wolverines and Eurasian lynx cause closely equal mortalities but lynx predation is more evenly divided between winter and summer seasons. We also assume that lynx predate more calves compared to wolverines. Indeed, Mattisson et al. (2014) found that more than half of the lynx predation targets calves. They also found that lynx kill rates differ considerably depending on season and reindeer population density. They showed that a single lynx killed ca 1–2 reindeer during the winter months with low reindeer densities, whereas ca 5–7 reindeer were killed during high reindeer densities. Kill rates averaged less during the summer season. However, we assume that the total kill rate during summer is slightly higher because the reindeer density and calf percentage are higher during summer. Pedersen et al. (1999) found that a lynx family group kills 30 reindeer during winter and that this predation targets especially adult females.

The mortalities caused by lynx and wolverines may also interact, as wolverines scavenge reindeer killed by lynx (Andren et al. 2011). However, in this study, we separate the predation of lynx and wolverines. Mattisson et al. (2016) found that wolverine kill rates varied highly similarly as with the lynx. However, the estimated average yearly kill rate was probably slightly more than 20 reindeer per wolverine. They also found that during summer, the majority of killed reindeer were calves whereas during winter wolverines mostly killed adult reindeer. Again, with both wolverines and lynx, our killing rate estimations for adult reindeer are skewed towards females because of the typical sex structure of winter herds.

As the estimated kill rates will have a high impact on our model solutions, it is imperative to acknowledge the uncertainties and variation associated with these estimations. Mattisson et al. (2011, 2014, 2016) estimated the uncertainty and the variation of the estimated kill rates in different conditions (low versus high reindeer abundance) for lynx and wolverine. The variation in predation rates between different conditions was very high, thus as a sensitivity analysis, we compute the costs of predation also with low and high kill rates for lynx and wolverine.

We estimate that brown bears and golden eagles have the lowest predation rates on reindeer, mostly killing calves during summer. Predation of reindeer by brown bear has been studied in Sweden using telemetric methods (Karlsson et al. 2012, 2014, Åhman et al. 2015). In the calving area, brown bears killed on average 0.4 (range 0.2–0.5) calves and 0.02 (range 0.004–0.03) females per day per bear during the period of 1 May–15 June. We use this average daily kill rate (0.4 calves) for the time between calf birth and mid-June, but as a sensitivity analysis, we examine the costs of predation also assuming low (0.2 calves) and high (0.5 calves) daily kill rates.

Golden eagles were observed to cause 3.0% mortality for calves tracked in the mountainous Käsivarsi reindeer herding cooperative between May and October while the same mortality for calves was 2.1% in the pine forest area of the Ivalo cooperative between June and October (Norberg et al. 2006, Nieminen et al. 2011). According to Norberg et al. (2006), predation by golden eagles caused 2.8–4.2% total mortality for calves between June and January. In a study conducted in mid-Norway, golden eagles caused 1.3% mortality for calves between 1 August and 20 December and 2.4% mortality between 6 August and 15 May (Nybakk et al. 1999). The same study observed that golden eagles may also kill older reindeer in rare situations.

The evaluated kill rates presented in Table 1 give the average number of reindeer killed by one individual of a certain predator species (for golden eagles we performed our calculations per nesting pair) in northernmost Finland. These kill rates are used in our bioeconomic model computations to evaluate how various predation pressures affect economically optimal solutions and the costs of predation. Thus, the model solutions are highly dependent on these estimated kill rates. These kill rates correspond relatively well with the available data on the observed losses of reindeer in different sex and age classes and with the evaluated number of various predators in the reindeer husbandry area (Statistics of Reindeer Herders' Association and Luke). However, because of a high variation in kill rates between environments, we include a sensitivity analysis to show how the costs of predation depend on the estimated kill rates. When defining how predation targets age and sex classes, we have assumed a typical herd structure in Finland (over 10 females per male, over 70% of calves slaughtered), which is also close to optimal model solutions (Tahvonen et al. 2014).

Winter predator mortality is assumed to occur evenly throughout the entire winter (i.e. daily winter mortality = total winter mortality/181 days). Similar assumptions are made for summer mortality (see Supplementary material Appendix 1 for how we extended the Pekkarinen et al. 2015 model by including predation mortality). In addition to direct losses, predation mortality also causes indirect effects in the model via changes in herd structure (the number of reindeer in different age and sex classes during different seasons). These indirect effects affect the number of females and males in different age groups, the mating success of females due to changes in adult male numbers, the calving rate and birth weight of calves, and also the consumption of lichens during different seasons. In this study, we only consider predation mortality and mortality from lack of winter food. Thus, mortality from other factors (mainly traffic) is assumed to be zero for adult reindeer and 2% for calves during their first summer.

We also assume that reindeer density is high and predator density is kept at a relatively low level by wildlife managers and is therefore not affected by reindeer population density. Thus, we do not take into account the numerical response for predator species, but instead assume that the predator population is strictly controlled by wildlife authorities. We assume that the high population density of semi-domesticated reindeer provides a steady energy resource for predators and thus wildlife management actions and legal and illegal hunting are the main factors affecting predator numbers.

Economic optimization

We use the Knitro optimization software (ver. 7.0.0 and 10.3) and AMPL programing language (Byrd et al. 2006) for all computations and optimizations. Our aim is to examine the optimal adaptation to predation and the costs of predation by various predators under optimal management. We assume a reindeer herding district where the growth rate of ground lichens is high and a seasonal pasture rotation system is used. To study how the costs of predation depend on the productivity of the herding system, we compute the results also assuming a lower lichen growth rate and without pasture rotation. We compute all the results for a herding district with a land area of 400 km^2, of which 100 km^2 is lichen pasture. This corresponds to a very small herding district, as the average district in Finland is roughly six times larger (Reindeer Herders Association 2018). However, as herding districts are composed of many reindeer owners, regional predation pressure may impact local livelihoods also in areas smaller than the district level.

We first compute the optimal steady-state solutions with various predator densities to study how kill rates by these predators affect the adaptation in a long-term situation with constant predation pressure. We compute the optimal steady-state solutions for a reindeer herding system with predator densities from zero to four predators (per 400 km^2 of land area) separately for each predator species. We also compute the steady-state costs of predation by different predators under an optimal management situation.

In addition to the steady-state solutions, we also compute the dynamic solutions for the system, as optimal steady states with positive interest rate cannot be solved without the transition phase. We use dynamic optimization solutions to also examine the effects of unanticipated predation. We study how much higher the costs of predation are if it suddenly occurs for a one-year period for which no preparations have been made to account for abrupt predation losses.

We then perform a sensitivity analysis to study how input variables affect the model solutions and the costs of predation. We compute the costs of predation by different predators and predator densities with different interest rates, pasture conditions, herding district sizes, searching costs, kill rates, and with and without supplementary feeding.

Finally, with these model solutions in mind, we evaluate and discuss the costs of predation under different compensation schemes. For an ex post compensation scheme, we assume that herders do not anticipate predation and therefor have not adapted to it beforehand. We compute the costs of the unanticipated one-year predation and assume that the predators will be removed after one year. In addition, we assume that in an ex post system herders search for the killed reindeer to gain compensation. On the other hand, no searching costs are included for a territorial ex ante compensation system, and we assume that the predation pressure is constant over a long time and that the herders have adapted to this constant predation pressure.

Results

Optimal steady-state solutions

First we compute economically optimal long-run steady-state solutions with 0% interest rate and different predator densities. Figure 1 shows that without predation in a herding district with highly productive lichen pastures, the

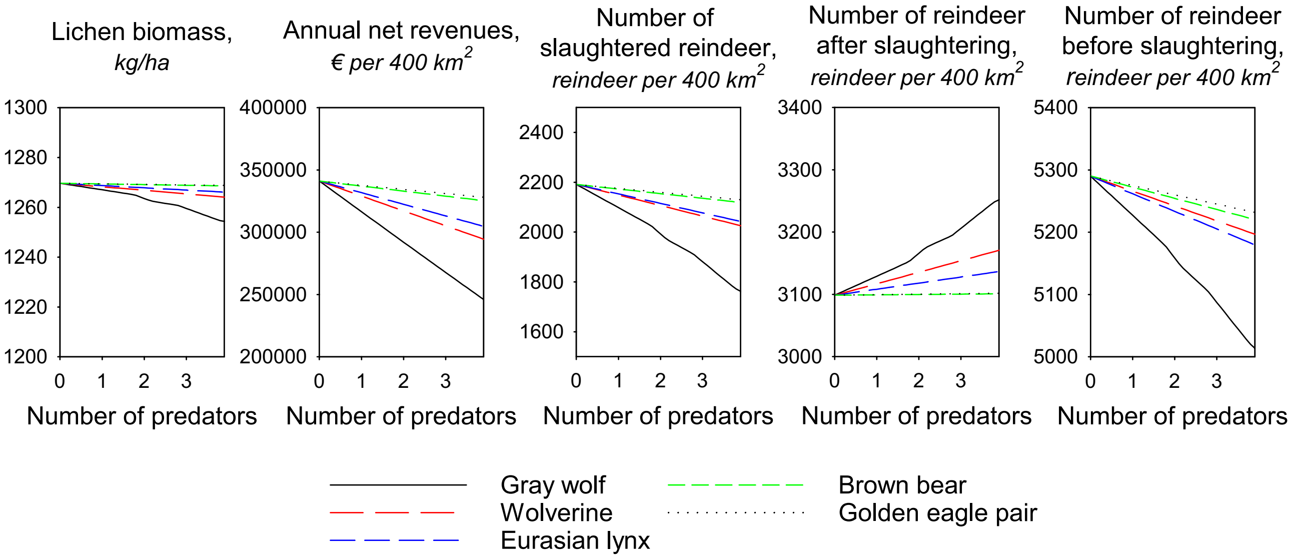

Figure 1. The optimal steady-state lichen biomasses, annual net revenues, number of slaughtered reindeer, and the sizes of the reindeer population after and before slaughtering corresponding to predator densities from zero to four predators per 400 km^2.

steady-state lichen biomass is 1269 (kg ha^{-1}), yearly net revenues are 341 141€ (per 100 km^2 of lichen pasture), the number of slaughtered reindeer is 2191 (per 100 km^2 of lichen pasture), and the number of reindeer left alive after autumn slaughtering is 3099 (per 100 km^2 of lichen pasture). These solutions are in line with results by Tahvonen et al. (2014), when updated prices, costs and wastage are taken into account.

Increasing predator density decreases the steady-state number of reindeer before slaughtering along with the number of slaughtered reindeer. However, the size of the reindeer population left alive in autumn and early winter slaughtering increase with increasing predator pressure. This happens because it is optimal to prepare for upcoming predation pressure by leaving more reindeer alive. The steady-state lichen biomass slightly decreases due to an increase in winter grazing pressure caused by these reindeer. Also, the yearly net revenues decrease, as the number of slaughtered reindeer is lower than without predation. The decrease in yearly net revenues is nearly linear and thus the costs of predation are proportional to the total number of predators of different predator species in the area of herding district. In a long-term steady state, one gray wolf causes approximately 25 000€ in losses per year and a wolverine causes 12 000€ per year. Eurasian lynx, brown bear and one golden eagle pair cause approximately 9000€, 4000€ and 3000€ losses per predator per year, respectively.

Table 2 shows the steady-state annual net income and loss of net income due to predation by different predators in a constant predation situation. The solutions are computed with 0% interest rate for a herding district with a high growth rate of ground lichens and seasonal pasture rotation. In addition, the table shows the slaughtering values of the predated reindeer. The slaughtering values are computed by considering the value of the meat of the killed reindeer and the slaughtering costs. The slaughtering values of reindeer predated by brown bear and golden eagle are close to the net revenue decrease in reindeer herding due to these predators. This is because these predators mostly kill calves, ca 80% of which would have been slaughtered in any case during the following slaughtering season. The slaughtering value can even be higher than the annual net revenue loss in an optimal steady state (golden eagle pair in Table 2) because the adaption can be optimized beforehand to the known upcoming predation pressure. However, as gray wolves, wolverines and Eurasian lynx also kill adult reindeer in addition to calves, affecting the reproduction and production rates of the population, they have clearly higher effects on the net income decrease than the slaughtering value of killed reindeer.

Table 2. The steady-state annual net income (0% interest rate), losses due to predation by a single predator (and a golden eagle pair), and the slaughtering values of predated reindeer. Slaughtering values are computed by taking into account the price of meat (10€ per kg) of the killed reindeer and the slaughtering costs (22.04€ per slaughtered reindeer).

Predator	Annual net revenues, €	Loss of annual revenues due to predation, €	Slaughtering value of predated reindeer, €	Slaughtering value compared to total loss, %
No predation	341 141			
Gray wolf	316 516	24 625	20 450	83
Wolverine	329 134	12 007	9062	75
Eurasian lynx	331 800	9341	8272	89
Brown bear	337 102	4039	4010	99
Golden eagle pair	337 814	3327	3364	101

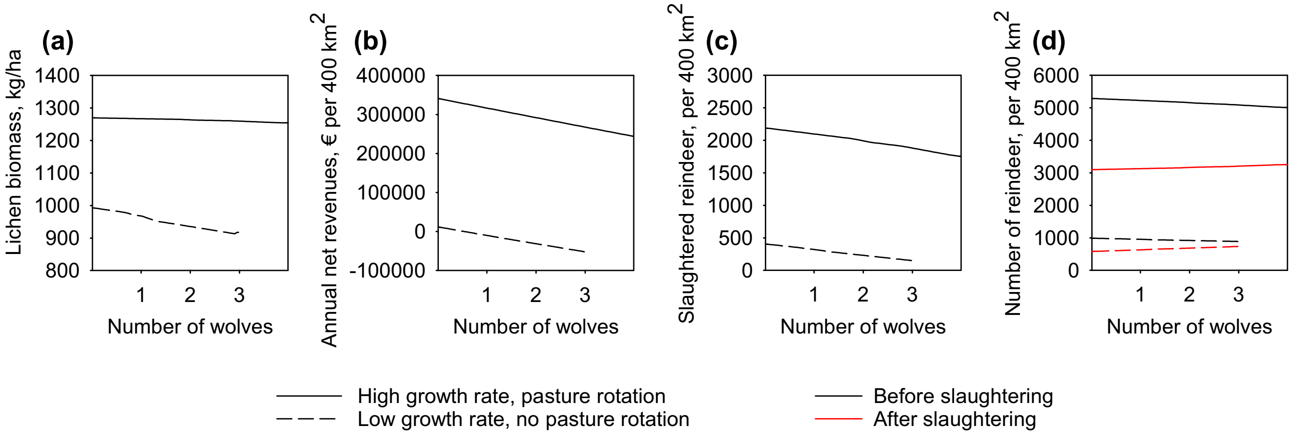

Figure 2. The optimal steady-state lichen biomasses (a), annual net revenues (b), number of slaughtered reindeer (c), and the sizes of the reindeer population before (black lines d) and after slaughtering (red lines d) corresponding to gray wolf densities from zero to three gray wolves per 400 km². Solid lines represent the solutions for a herding district with good pasture conditions (ground lichen growth rate is high and pasture rotation is used). Dashed lines represent a herding district with a lower growth rate of ground lichens and no pasture rotation.

Figure 2 shows the optimal steady-state solutions corresponding with gray wolf densities from zero to three individuals per 400 km² of land area for two different hypothetical herding districts. Solutions show that both pasture quality and gray wolf density have a large effect on the optimal solutions. In the herding district with a lower ground lichen growth rate and no seasonal pasture rotation system, the number of reindeer, annual revenues and lichen biomass are all lower than in the herding district with a high ground lichen growth rate and seasonal pasture rotation system. These management conditions (the quality of lichen pastures and grazing system) affect the optimal steady-state lichen biomass and reindeer number much more strongly than the number of gray wolves. However, the number of gray wolves and pasture quality both have a strong effect on annual net revenues. The combined effect of low pasture quality and high predation pressure leads to a situation where no sustainable solution is found if the number of gray wolves increases to above three wolves per 400 km². Annual net revenues become negative even sooner, at a gray wolf density of one wolf per 400 km². For an average size Finnish reindeer herding district, this translates into approximately five to six wolves per district being enough to collapse the economic sustainability of reindeer husbandry in the area.

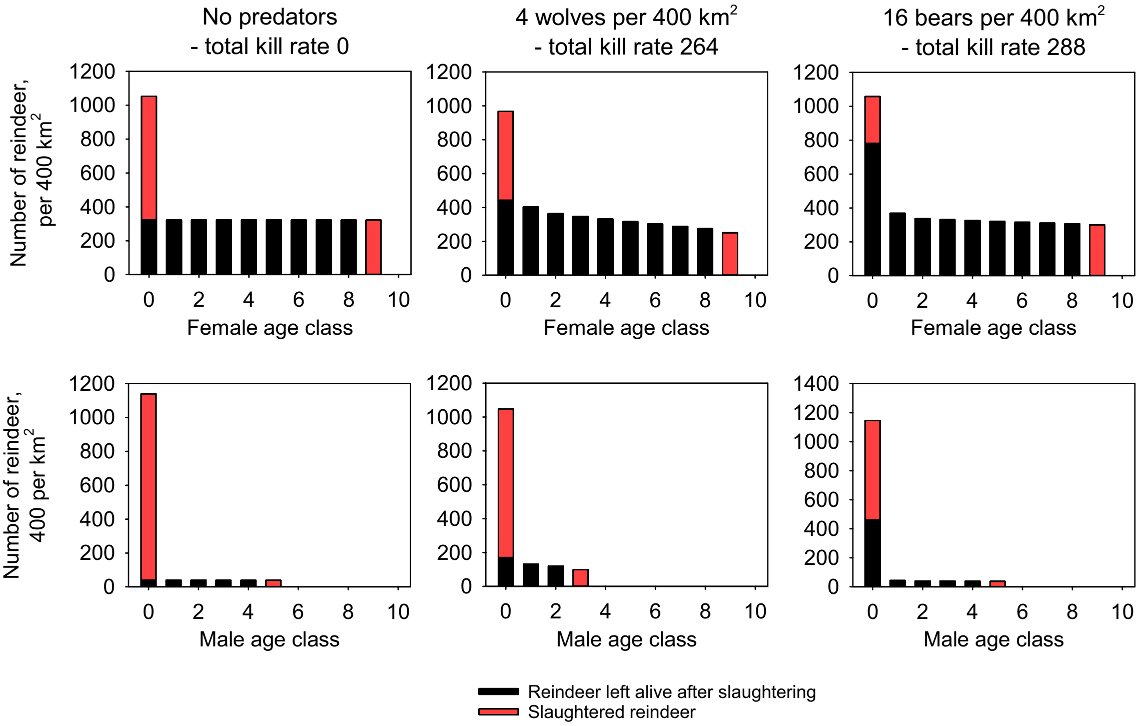

Figure 3. The optimal structure and harvesting strategy for a reindeer population in steady states without predation, with high gray wolf density and with very high brown bear density.

Optimal slaughtering strategy and population structure

Figure 3 shows the optimal structure and harvesting strategy for a reindeer population in steady states without predation, with a high gray wolf density and with a very high brown bear density. Although the slaughter weight of calves (22–24 kg) is only half that of a prime-aged male (59 kg) or female (39 kg), it is not economically rational to maximize the average size of slaughtered animals but also to take the effects on winter pastures into account. Thus, without predation, slaughtering is highly concentrated on calves because they do not consume the scarce winter pastures, as they are slaughtered before the first winter.

With very high predation by brown bear, the optimal age structure of the reindeer population does not change a lot, although the relative importance of calf harvesting decreases. However, with high predation pressure by gray wolves, the age structure of adult females is skewed towards younger age classes. The age structure of adult males changes even more, as it becomes optimal to slaughter them at a younger age than in a situation with no predation. This ensures that fewer adult males die before they reach the slaughter age. However, the total number of males needs to be higher to ensure high calf production, as younger males have lower reproductive efficiency (smaller harem size).

The difference between the effects of brown bear and gray wolf predation is caused by the different mortality rates of reindeer in various age classes caused by these predators. Brown bears mostly attack calves whereas gray wolves more evenly predate all age and sex classes. This is also the reason why the economic loss caused by very high brown bear predation (ca 65 000€) is lower than losses caused by a high wolf density (ca 99 000€), even though the total kill rate by 16 brown bears (288 reindeer killed) is higher than the total kill rate of four gray wolves (264 reindeer killed).

As our analysis focuses on economically rational solutions, the mortality due to insufficient energy intake during winter is minor, as it is not economically sensible to let adult reindeer die in starvation. Thus, the lichen biomass in the optimal steady states is kept at a level that satisfies the energy need of the reindeer population. However, in reality this is not always the case and mortality due to starvation may affect the age structure of a reindeer population, especially in areas where supplementary feeding is not used. Traffic, diseases and other factors besides predation and starvation additionally cause mortality, but they were excluded from this analysis.

Dynamic solutions

Next we computed the optimal solutions from various initial states outside a steady state with and without predation mortality using zero and positive interest rates. Tahvonen et al. (2014) demonstrated that the model solution leads to a long-term steady state or to a cycle around the steady state. Also in this study, with constant predation pressure and optimal adaptation to it, the system goes into a steady state (or a cycle around the steady state) after the transition phase, even if the initial state is far outside the steady state. This enables us to compare the average annual net revenues in the predator-free steady state with the net revenues in a steady state with constant predation pressure (Fig. 4).

Figure 4 shows an example of a dynamic solutions for the system starting from a predator-free optimal steady-state situation. If no predators are present, the system remains in the same steady state. However, if a constant predation pressure (dotted green line) is introduced, the system converges in to a new steady state after a transition phase. Similarly, as shown in Fig. 1 and 2, the number of reindeer after slaughtering is higher in this new steady state, but lichen biomass and the yearly net revenues are lower than in the predator-free steady state. However, an unanticipated abrupt predation pressure can cause higher losses than losses experienced in the constant predation steady state. Figure 4 shows an example of the effect of introduced one-year predation pressure by ten gray wolves (dashed line) on a 400-km^2 herding district. With 0% interest rate, the one-year predation by one gray wolf causes a total loss of approximately 29 000€ over the adaptation period (Table 3).

Effects of the searching costs

Table 4 shows the steady-state annual net revenues with and without searching costs with 0% interest rate. Taking into account the costs of searching for reindeer killed by predators (420€ per one searched and located reindeer, Järvenpää 2014), the annual net income further decreases, especially when predators kill adult reindeer (as calves are not searched for). Considering the costs of searching for reindeer killed by predators is clearly very important with wolverines, gray wolves and Eurasian lynx, as they increase the net losses by 43–59%.

Sensitivity analysis and the effects of input variables

Figure 5 shows that the costs of predation are nearly independent of pasture conditions. The predator species in question and the individual number of that species in the area of the herding district explain the decrease in annual net revenues. Also, the costs of predation per one predator are independent of the size of the herding districts (40 km^2 versus 400 km^2). This shows that predator density does not affect the costs of predation per individual in this type of a model formulation. Thus, it is the actual number of predators within a herding district that has the major effect on the solution.

We also computed the costs of predation in a situation where reindeer herding is based on intensive supplementary feeding. The intensive use of supplementary feeding in the optimal model solution was achieved by assuming the costs of feeding to be very low (0.05€ per kg of supplementary food delivered to pastures). Figure 5 shows that whether or not supplementary feeding is used does not affect the costs of predation in the model solutions. In addition, we found that the interest rate level does not appear to affect the annual costs of predation in a steady state.

Although interest rate and management conditions do not significantly influence the computed costs of predation, the estimated kill rate and searching costs do. Mattisson et al. (2014, 2016), Karlsson et al. (2012, 2014) and Åhman et al. (2015) showed a very high variation in the kill

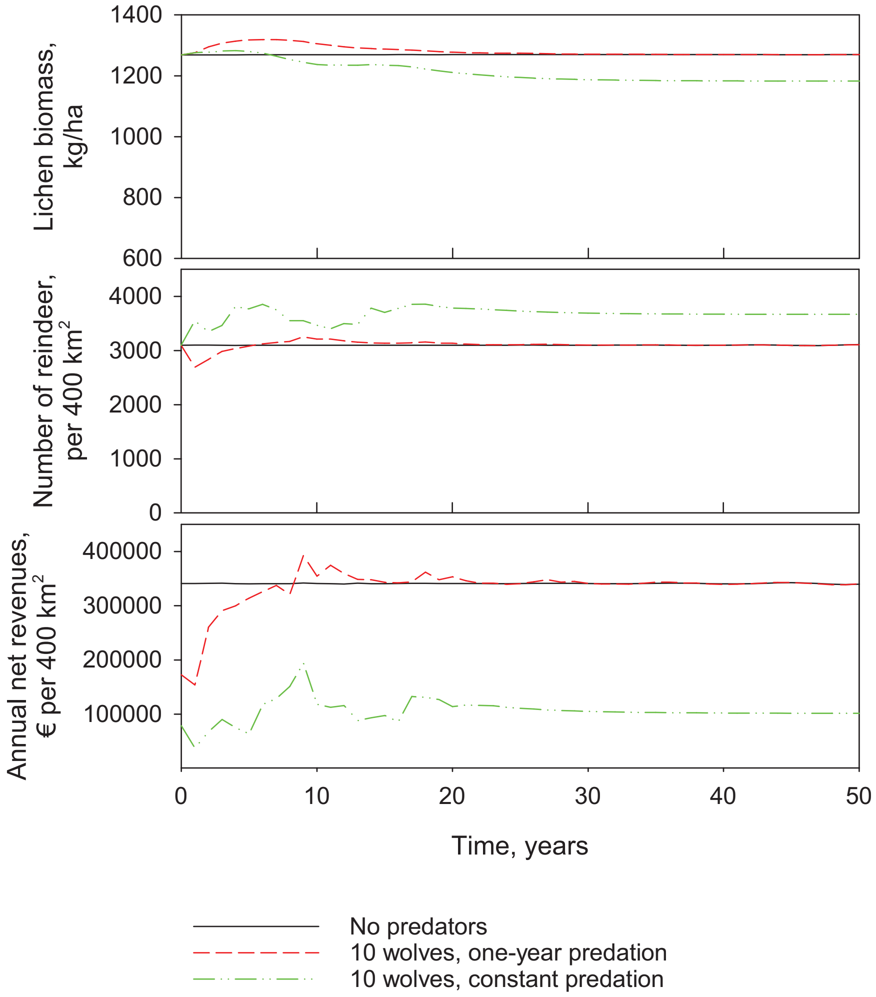

Figure 4. Example of optimal solutions with different predation pressures starting from the (predator-free) optimal steady state. The solid line represents a solution without predators and the green dotted line a solution where constant predation pressure by ten gray wolves per 400 km^2 is introduced. The red dashed line represents a solution with the same predation pressure, but only during the first year (t=0) and not after that.

rates by wolverines, Eurasian lynx and brown bears in various situations and areas. We have included the variation in kill rates from these studies in Table 5. We also varied searching costs and computed the solutions for both constant steady-state predation and for unanticipated abrupt predation pressure for one year. These solutions show that the level of predation costs by wolverine and Eurasian lynx are similar and that the variation in costs is very high between different situations. The costs caused by brown bear predation also vary greatly but are lower in most situations compared to the wolverine and lynx.

Figure 6 shows that the costs of predation by a wolf pack are high even if the estimated kill rate would be half of the 66 assumed in this study. It also demonstrates the importance of accurate estimates for kill rates and searching costs for defining the costs of predation. Figure 6 and Table 5 also show that the annual costs of predation are clearly lower in a territorial ex ante system if predation pressure remains constant and herders have adapted to it. In an ex post system, however, costs may increase to a very high level if predation is unanticipated (one-year predation) and searching costs are high.

Table 3. Loss of net revenues due to predation calculated per one single large predator or golden eagle pair during one year in an unanticipated (one-year predation) and in a predictable (steady-state) situation.

	Loss of net revenues		
Predator	Steady state, €	One-year predation, €	Increase in losses due to unanticipated predation, %
Gray wolf	24 625	29 292	19
Wolverine	12 007	13 146	9
Eurasian lynx	9341	9916	6
Brown bear	4039	4092	1
Golden eagle pair	3327	3332	0

Table 4. Optimal steady-state solutions with (420€/located killed reindeer) and without searching costs.

	Annual net revenues		Loss of annual revenues due to predation		
Predator	Without searching costs, €	With searching costs, €	Without searching costs, €	With searching costs, €	Increase in losses due to searching costs, %
No predation	341 141	341 141			
Gray wolf	316 516	304 336	24 625	36 805	49
Wolverine	329 134	322 078	12 007	19 063	59
Eurasian lynx	331 800	327 786	9341	13 355	43
Brown bear	337 102	336 850	4039	4291	6
Golden eagle pair	337 814	337 457	3327	3684	11

Discussion

Our study shows that large predators can have major effects on a reindeer herding system and on the economically optimal herding strategy. We first studied the economically rational way of adapting to predation by using a bioeconomic age- and sex-structured model of a reindeer husbandry system. With domestic livestock, keeping the animals in corrals during their most vulnerable times is often sensible to protect them from predation (Schiess-Meier et al. 2017). However, this is often impossible with semi-domesticated or wild animals, so other methods must be used for the adaptation, for example by adjusting the size and structure of the population via harvesting. We found that the number of reindeer left alive in the optimal solutions after autumn slaughtering increases with increasing predation pressure. This happens because it is optimal to prepare for upcoming predation pressure by leaving more reindeer alive. This compensates for the increased mortality by predators and ensures good calf production during spring. However, due to predator mortality, the higher number of reindeer left alive after autumn slaughtering does not significantly reduce pasture growth. With optimal adaptation the numbers of calves born in spring and slaughtered during next autumn are higher than without adaption and pasture conditions (lichen biomass in our model) remain at an optimal level.

Adapting to predation can also change the optimal slaughtering strategy and structure of a reindeer herd. Johannesen et al. (2019) found that high predation mortality causes calf slaughtering to become optimal. However, they used a stage-structured model structure that does not include the time lags associated with changing fecundity or the weight of adult reindeer as they get older. Thus, the model they used is unable to describe economically rational calf harvesting strategies in the absence of predators. In addition, in their model, calf harvesting does not affect the consumption rate of winter pastures by calves. We included pasture dynamics and a full description of the age- and sex-structured reindeer population and found that calf slaughtering may actually fall to a very low level because of predation. This may be caused by direct predation on calves or by predation targeting adults. When adults are predated, it is economically sensible to leave more calves alive to compensate the loss of older animals.

In addition to the effects on the optimal level of calf harvesting, our model solutions show that high predation pressure may shift the slaughtering of adult males towards younger age classes. However, this happens only if predation targets adults in addition to calves. Gervasi et al. (2012) found that age class-specific mortality rates due to predation are important in determining the demographic effects on the prey population, and in this study, we showed that the same applies for optimal slaughtering strategies when adapting to predation pressure.

Table 6 shows the benefits of adapting to predation by leaving more reindeer alive after slaughtering and by changing the slaughtering strategy. Without this change in adaptation, the lichen biomass would be much higher and annual

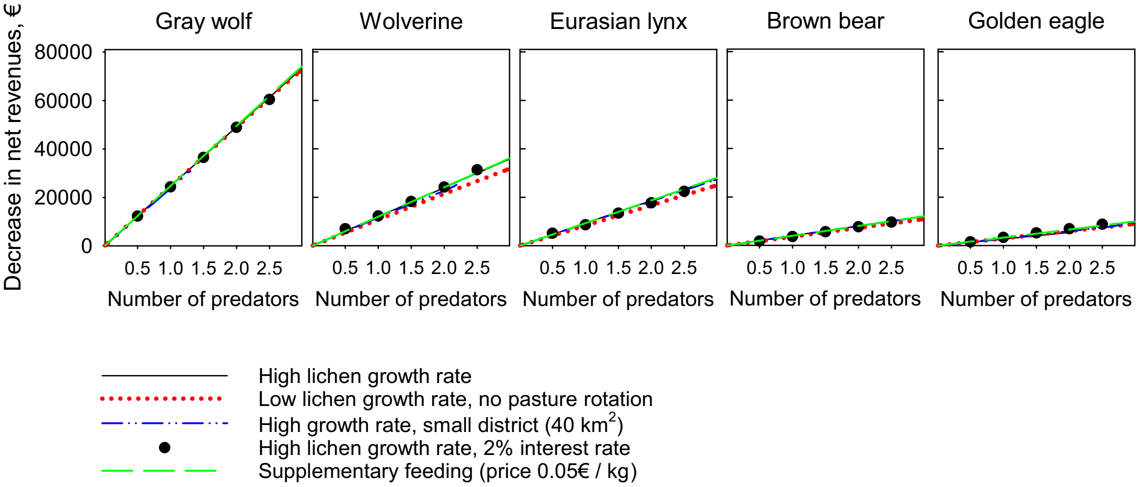

Figure 5. Costs due to predation caused by different predator species. The decrease in net revenues is mainly affected by the predator species and number of predators, but not much by interest rate, pasture conditions, use of supplementary feeding, or size of the herding district.

Table 5. Total costs due to predation caused by a single predator (wolverine, Eurasian lynx or brown bear) with different estimated kill rates and searching costs. Constant predation represents a situation where predation pressure is known beforehand and reindeer herders have adapted to it optimally. One-year predation gives the costs of an unanticipated abrupt predation pressure lasting for one year with different searching costs for located killed reindeer.

Predator	Estimated mortality rate	Constant predation, searching costs: 0 €	One-year predation, searching costs: 280 €	One-year predation, searching costs: 420 €	One-year predation, searching costs: 560 €
		Costs of predation, €	Costs of predation, €		
	10	4618	6860	7780	8680
Wolverine	26	12 007	17 930	20 300	22 660
	50	23 090	34 620	39 160	43 710
	12	3736	5180	5720	6060
Eurasian lynx	30	9341	12 970	14 500	15 670
	60	18 682	26 070	28 855	31 340
	7	785	1695	1730	1765
Brown bear	18	4039	4340	4350	4510
	23	5161	5451	5555	5670

net revenues lower. Thus, according to our model solutions with high predation pressure, optimal adaptation can decrease the costs of predation by approximately 4000€ per gray wolf.

Secondly, we evaluated the costs of predation on reindeer herding economy. The analysis by Skonhoft et al. (2017) suggests that in a 'tragedy of the commons' situation predation may actually benefit reindeer herders. This could apply to very specific circumstances, where herd size is continuously kept at a high level and thus lichen biomass and the long-term harvesting rate remain very low. In addition, Skonhoft et al. (2017) assumed that the harvesting rate does not adapt to changing predation pressure. However, it is reasonable to assume that even in a 'tragedy of the commons' situation herders will react to changing predation pressure. Furthermore, although lichen pastures may have low lichen biomasses, the 'tragedy of the commons' situation does not represent the actual circumstances in most parts of the reindeer herding area in Fennoscandia. In contrast, Tahvonen et al. (2014) found that reindeer herders in Finland use slaughtering strategies that are very close to economically optimal solutions. Our results show that when the reindeer population is managed in an economically rational way, predation can cause major economic losses.

We found that the productivity of a reindeer population and annual net revenues are strongly affected by both high predation pressure and pasture conditions. Especially high predation pressure combined with less-productive pastures can lead to a difficult economic situation in reindeer herding. Our results suggest that with a lower growth rate of ground lichens and without pasture rotation a constant gray wolf density of three individuals per 400 km^2 leads to the total collapse of the reindeer herding livelihood. The economic profitability and annual net revenues of reindeer management become negative already at a gray wolf density of one individual per 400 km^2. This shows that the coexistence of a viable gray wolf population and productive reindeer management would be very difficult. In Finland, 35% of the reindeer herding districts are smaller than 2000 km^2. Also, the availability of good condition or highly

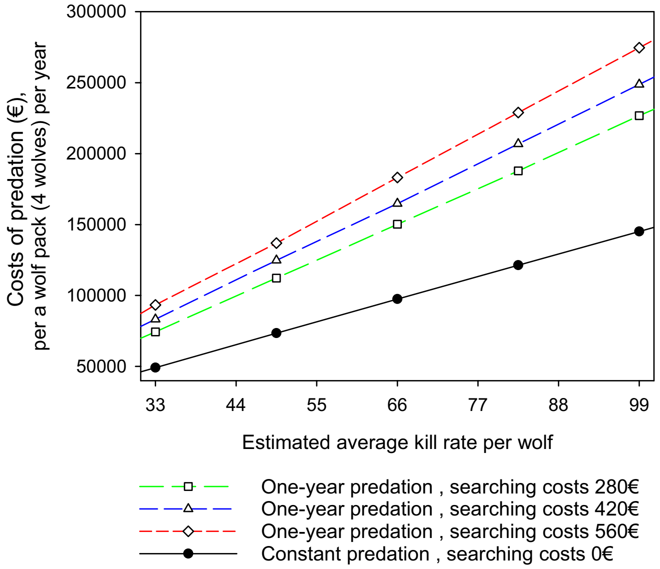

Figure 6. Total costs due to predation caused by a single wolf pack (four wolves) with different estimated kill rates. The solid black line represents a situation where predation pressure is known beforehand and reindeer herders have adapted to it optimally. The dashed lines show the costs of an unanticipated abrupt predation pressure during one year with different searching costs for located killed reindeer.

Table 6. Adaptation of slaughtering strategy reduces the costs of predation. With restricted adaptation the annual net revenues are lower and lichen biomass higher than with full adaptation. In restricted adaptation slaughtering is targeted at the same age classes as in the 'No predation' – situation. The number of reindeer left alive is also the same.

		Predation (10 gray wolves)		Predation (4 gray wolves)	
	No predation	Full adaption	[a]Restricted adaptation	Full adaption	[a]Restricted adaptation
Annual net revenues, €	341 141	101 710	58 635	243 651	228 015
Number of reindeer	3099	3443	3099	3255	3099
Lichen biomass, kg ha^{-1}	1270	1237	2556	1254	1944

[a] Fixed slaughtering percentages from age classes and fixed number of reindeer left alive after slaughtering.

productive lichen pastures are low due to the current state of forest structure in most of the herding districts. Thus, our results imply that even one gray wolf pack could collapse the economic viability of reindeer herding in these districts. This supports the economic rationale behind the policies adopted in Fennoscandian countries where wolf packs are not allowed in the reindeer herding area.

Tveraa et al. (2014) and Heikkinen et al. (2011) suggested that changing the compensation system towards a territory-based ex ante system could help reduce conflicts between predation protection and reindeer herding in certain cases. Skonhoft (2017) studied predator compensations for sheep farming in Scandinavia and found that it is beneficial for natural resource managers to use an ex ante system compared to an ex post system. Also, our model solutions suggests that compensations need to be clearly higher in a system based on documented losses due to the costs of searching for reindeer carcasses. In addition, the costs are even higher if predator numbers are unknown and anticipating and preparing beforehand for predation is not possible. Combining the searching costs with the costs of unanticipated predation may nearly double the costs of predation compared to a constant predation situation (Table 5, Fig. 6), where herders have adapted to predation pressure and are assumed to not search for killed reindeer. This suggests that the territorial system could be much more inexpensive than the current system in Finland and Norway.

However, expenses in the territorial system may increase considerably due to the need for real-time documentation and information about predator densities and estimating the average number of reindeer killed by one predator. Furthermore, using the territorial system may be very difficult with gray wolves (and possibly also with wolverines), as even one gray wolf pack could in many cases collapse the economic profitability of reindeer herding in the area. The distribution of the compensation benefits between reindeer herders is also a problem in ex ante systems (Zabel et al. 2014). Dividing the compensation money fairly between the reindeer herders according to the true losses they have each faced is clearly problematic if killed reindeer are not searched for and documented.

In 2015, an estimated 10 gray wolves, 120 wolverines, 80 Eurasian lynx, 270 brown bears and 350 golden eagle pairs inhabited the Finnish reindeer herding area (Reindeer Herders Association 2018). Combining this with the modeled costs of predation by the different species addressed in this study, allows us to evaluate the total predation costs for reindeer herding during 2015 in Finland. If a territorial system had been in use and the number of predators had been known and their killing rates correspond to our estimates, the estimated loss of net revenues would have been 4.7 million euros. However, taking into account the searching costs and unanticipated predation, the estimated total predation costs increase to 6.3 million euros. The total quantity of predation compensations paid for reindeer herders in Finland in 2015 was approximately 6.5 million euros (Reindeer Herders Association 2018). Thus, the paid predator compensations appeared to cover the costs of predation for that year. However, the number of predator-killed reindeer and the associated compensation levels have varied strongly during the past 15 years. Compensations were less than one million per year prior to 2003, but had risen to over 10 million euros per year by 2016 and again dropped to 7 million euros in 2018. The number of predators and the market price of reindeer meat have increased during that time, both of which have affected the compensation level. In addition to predator density, the actual number of reindeer killed and the efficiency of finding killed reindeer along with the annual costs and prices relating to reindeer herding affect how much compensation is paid and what the true costs of predation are. The predator numbers and modeled predation costs also reveal that although the costs per predator are highest for wolf, the impact of wolf is only local. At the country level, the costs by wolves are by far the lowest of all the studied predator species, as the total population size in the Finnish reindeer herding area is only approximately 10 wolves. According to our solutions, wolverines cause the highest country-level total costs.

Conclusions

This study shows that predation can cause high losses to reindeer herding, giving clear basis and justification for paying compensations to herders. In addition, results from our model suggest that the ex post compensations paid out in Finland during the past years have roughly covered the direct net losses from predation and the expenses of searching for predated reindeer. However, more detailed empirical data and analysis of the costs and predator numbers are still required. Compensation levels could, however, be smaller if a territorial system was used for all predators, but that would require costly accurate information on predator numbers. In addition, clearly more research on age- and sex-class-specific predation rates of different predation species and how predation rates change in varying situations is needed.

Results of our study also show that adaptation to predation pressure in the management of free-ranging herbivores can partly be accomplished via changes to slaughtering strategy. Economically sensible adaptation ensures that the body condition of herbivores and calf production remain high and natural pastures remain at the optimal state. Adaptation reduces the losses caused by predation, but costs to herders still remain high in most situations. In addition, losses can be very high with efficient predator species that depredate adults in addition to calves. Our results suggest that combining a viable gray wolf population and profitable reindeer management in the same area would be very difficult. This supports the economic rationale behind the policy adopted in Fennoscandian countries where wolf packs are not allowed in the reindeer herding area. Although, according to our results, continuing reindeer husbandry in average-sized districts would be possible even with one to three wolf pack territories, the economics of reindeer husbandry would then be based solely on predation compensations. This would clearly be an economically and culturally unsustainable situation for local reindeer herders.

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Supplementary material (available online as Appendix wlb-00684 at <www.wildlifebiology.org/appendix/wlb-00684>). Appendix 1–3.