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Original article

Modelling the combined effect of an obligate predator and a facultative predator on a common prey: lynx *Lynx lynx* and wolverine *Gulo gulo* predation on reindeer *Rangifer tarandus*

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In conservation and management of large predators, effects of species are often considered separately. However, predators often interact with one another in different ways (e.g. interspecific competition, intra guild predation and kleptoparasitism) that may influence the total predation on a common prey. We estimated the total number of semi-domestic reindeer *Rangifer tarandus* killed by Eurasian lynx *Lynx lynx* and wolverine *Gulo gulo* at different relative abundances of the two species using a model based on diet, food requirements of lynx and wolverine and amount of food available on a reindeer. Our model suggests that total predation decreases by approximately 7.9% (± 4.8 SD) if wolverines scavenge on lynx-killed reindeer, compared to a model without scavenging. If the management goal is a constant number of predators, the model suggests that the total kill rate will be lowest in areas with only wolverines, as the estimated wolverine kill rate is much lower than the lynx kill rate. Our model showed that it is unlikely that the lowest number of reindeer killed per predator individual will be at a certain lynx-wolverine ratio, which would appear if lynx consumption of killed reindeer is low and wolverines are very efficient finding lynx-killed reindeer. However, if the management goal is a constant number of lynx and wolverines, the model suggests that the total predation is lower, if lynx and wolverines coexist in the same area compared to existing separately in different areas. The total predation by wolverine and lynx on reindeer is very important for the management of lynx and wolverine in the reindeer husbandry area in Sweden, as the current compensation scheme for predator-killed semi-domestic reindeer is based on the number of predators present within a reindeer herding district, and the compensation for wolverine and lynx is added independently of one another.

Key words: carnivore conservation, food requirement, Gulo gulo, kill rate, Lynx lynx, predator compensation system, Rangifer tarandus, reindeer, scavenging, wolverine

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The total predation on a common prey species by two or more predator species is not necessarily the sum of individual kill rates of the different predator species (Atwood et al. 2009). Predator species often interact with one another in different ways; i.e. in competition for food and direct predation on each other. Dominant predator species stealing food from subordinate predator species can have large effects on the subordinate predator species; e.g. on fitness or behaviour, and its kill rate. For instance, African wild dogs *Lycaon pictus* need to spend more time hunting prey in areas with lions *Panthera leo* and spotted hyenas *Crocuta crocuta*, as they lose killed prey to the two predator species (Gorman et al. 1998, Caro & Stoner 2003). Alternatively, one predator species can sometimes benefit from the presence of another species through scavenging; e.g. grizzly bears *Ursus arctos horribilis* take over kills from cougars *Puma concolor* (Murphy et al. 1998). On the other hand, a subordinate scavenger has to balance the risk of being killed at a carcass and the benefit from scavenging; e.g. the interaction between wolves *Canis lupus* and coyotes *Canis latrans* is complex. Coyotes benefit from scavenging on remains of prey killed by wolves (Atwood & Gese 2008). However, wolves often kill coyotes, and the coyote density is negatively related to wolf density (Berger & Gese 2007). Thus, interactions among predator species are important to the conservation and management of large predators (Ginsberg 2001, Chapron et al. 2008), as well as to the understanding of the effect of several predators on a common prey species (Atwood et al. 2007, 2009).

In northern Sweden, where the reindeer husbandry area covers 230,000 km^2, several large predator species that prey upon semi-domesticated reindeer *Rangifer tarandus* coexist. The total number of reindeer after harvest in December has been between 220,000 and 260,000, and the yearly harvest has been between 47,000 and 74,000 during the last 10 years (official data from the Swedish Board of Agriculture and the Sámi Parliament). Eurasian lynx *Lynx lynx* and wolverine *Gulo gulo* are the most important predator species preying on reindeer (48 and 33% of the total compensation for predator-killed reindeer, respectively; Swedish Environmental Protection Agency and the Sámi Parliament). The estimated population size within the Swedish reindeer husbandry area during the last 10 years was 500-900 lynx (Andrén & Liberg 2008) and 350-550 wolverines (Swedish Environmental Protection Agency). Brown bear *Ursus arctos* and golden eagle *Aquila chrysaetos* are also common (estimated population sizes ca 2,000 bear individuals; Kindberg et al. 2009, and ca 550 pairs of breeding eagles; Tjernberg & Svensson 2007, within the Swedish reindeer husbandry area), but these two species mainly prey upon reindeer calves in late spring and early summer (Swenson & Andrén 2005, Norberg et al. 2006). According to the current Swedish large carnivore policy, there should be no occurrence of wolves in the reindeer husbandry area, so only a few individual wolves and no wolf packs are present in this area (Wabakken et al. 2009). Raven *Corvus corax* and red fox *Vulpes vulpes* are important scavenger species in the reindeer husbandry area (Haglund 1966) and may have a large impact on the available amount of food for all predator species (Vucetich et al. 2004). In our study we focus on the interaction between lynx and wolverine, as they are the most important year-round predator species preying on semi-domesticated reindeer (Swenson & Andrén 2005), and reindeer is the main prey for both species (Haglund 1966, Pedersen et al. 1999, Landa et al. 1997).

The lynx is an obligate predator (Pedersen et al. 1999, Mattisson 2011), whereas the wolverine is a facultative predator/scavenger that often scavenges on the remains of prey killed by other predators (van Dijk et al. 2008, Mattisson 2011). The rank of dominance between the lynx and the wolverine is unknown, but fatal interactions between the two species are very rare. According to Andrén et al. (2006), only one young male lynx was most likely killed by a wolverine out of 33 documented cases of mortality in lynx. No cases of a wolverine being killed by lynx were documented among 55 wolverine mortalities (Persson et al. 2009). Both the lynx and the wolverine are solitary species and the only groups formed are adult females with young of the year. Female wolverines reproduce on average every second year, but an increased food supply in late autumn to early spring can result in more frequent reproduction (Persson 2005). A lynx family group typically consumes around 60% of a killed reindeer (Pedersen et al. 1999), so the presence of lynx increase the supply of reindeer carcasses available for the wolverine. This may increase wolverine reproduction, which is important for wolverine management. On the other hand, wolverine scavenging might influence lynx kill rate on reindeer.

The Swedish Government compensates reindeer herders for damage caused by large predators (~ 60 million SEK or ~ 6 million € in 2008; Swedish Environmental Protection Agency and the Sámi Parliament). The current compensation scheme is based on the number of predators present within a reindeer grazing community and not on the documented losses (Swenson & Andrén 2005, Zabel & Holm-Müller 2008). There are no reliable estimates of the true losses of reindeer to predators, but locally the losses may be as large as the harvest. Thus, predators can have a large impact on reindeer management. The compensation for the different predator species is added independently of each other. Consequently, a reindeer-grazing community will benefit from having both wolverine and lynx in the same area, if the total number of reindeer kills per predator individual is reduced due to scavenging from wolverines on lynx-killed reindeer. As lynx and wolverine are very important predators on reindeer, even small changes in kill rate for the two species can have large consequences for reindeer management.

The aim of our study was to estimate the total kill rate on reindeer at different relative abundances of lynx and wolverine using published data on diet and food requirements for lynx and wolverine, taken together with the meat available on killed reindeer. In particular, we examined two different management scenarios. First, we estimated the total predation per individual given a constant number of predators but with different lynx-wolverine ratios. We were particularly interested in whether the lowest number of reindeer killed per predator individual would happen at a certain lynx-wolverine ratio. This could happen if, for example, the lynx consumption of killed reindeer is low and wolverines are efficient at finding lynx-killed reindeer to scavenge. Secondly, we estimated whether the total predation, given a constant number of lynx and wolverines, was lower when lynx and wolverine coexist in the same area compared to when lynx and wolverines exist separately. Both these scenarios are very important for the management of lynx and wolverine in the reindeer husbandry area in Fennoscandia.

Methods

Our model

We modelled the number of killed reindeer per predator individual with different relative abundances of lynx and wolverines, using a model based on kill rate (i.e. the number of reindeer killed/predator/time unit), diet and food requirement of lynx and wolverine. A basic unit in our model is the amount of reindeer meat (in kg) eaten by lynx and wolverines. To obtain a number of reindeer killed per predator we divided the estimated amount of reindeer consumed by either lynx or wolverine by the amount of available food on a reindeer. However, we had to take into account wolverine scavenging on lynx-killed reindeer. Scavenging depends on the amount of food available on the carcasses after the use by lynx and other scavengers, as well as the probability that the wolverine will find the lynx-killed reindeer.

In our model, we kept the total number of lynx and wolverines constant and the outcome of the model is presented as the number of killed reindeer per predator at different relative abundances of lynx and wolverine. We used lynx-wolverine ratios from 0 to 2, (0=only wolverines, 1=equal number of lynx and wolverines and 2 = twice as many lynx as wolverines). This represents the common relative abundances of lynx and wolverines in Sweden (national survey; Swedish Environmental Protection Agency, and ongoing research in northern Sweden have measured lynx-wolverine ratios between 0.14 and 0.5; Danell et al. 2006, Persson et al. 2006).

First, we estimated the number of lynx-killed reindeer (R_{lynx}), which depends on the number of lynx in the area (L_{number}) and lynx kill rate ($L_{kill\ rate}$). In addition, we made it possible to have lynx kill rate dependent on the number of wolverines in the area (A). The number of lynx-killed reindeer was:

$$R_{lynx\ killed} = L_{number} \times L_{kill\ rate} \times (1 + A \times (W_{lumber}/L_{lumber})).$$

This means that the lynx kill rate is not affected by wolverines when $A = 0$, whereas with an $A = 0.25$, the lynx kill rate increases by 25% when the wolverine-lynx ratio is 1, and by 50% when the wolverine-lynx ratio is 2. Thus, the parameter A is the proportion of increase in the lynx kill rate when going from areas with only lynx to areas with both lynx and wolverine. We used an A between 0 and 0.25, a range that includes a quite strong effect on kill rate by another predator (Creel et al. 2001, Krofel & Kos 2010). Mattisson (2011) reported some effects of wolverine presence on lynx use of reindeer carcasses.

Secondly, we needed to estimate the number of wolverine-killed reindeer ($R_{wolverine\ killed\ (total)}$). With the current lack of data on wolverine kill rate, we assumed that it depends on the wolverine food requirement ($W_{food\ requirement}$), proportion of reindeer in the wolverine diet (W_{diet}), amount of food available on a reindeer (R_{mass}) and the proportion of a self-killed reindeer consumed by a wolverine ($W_{reindeer\ use}$). However, the kill rate should be reduced by the intake from scavenging on lynx-killed reindeer. We estimated the intake from scavenging as the available biomass of lynx-killed reindeer ($R_{carcass}$) and the proportion of a lynx-killed reindeer consumed by a wolverine after lynx consumption ($W_{carcass\ use}$). Furthermore, we added the possibility that wolverines will have a minimum kill rate on reindeer, i.e. they will always kill some reindeer irrespective of the carcass availability. This we described as the proportion of their food requirement that is self-killed ($W_{minimum}$). Consequently, the number of reindeer killed by wolverines has to be estimated in several steps.

We estimated the minimum number of wolverine-killed reindeer ($R_{wolverine\ killed\ (min)}$), which depends on the number of wolverines in the area (W_{number}), their food requirements ($W_{food\ requirement}$), the proportion of reindeer in the wolverine diet (W_{diet}), the minimum proportion of their food requirement that were from self-killed reindeer ($W_{minimum}$), the amount of food available on a reindeer (R_{mass}) and the proportion of a self-killed reindeer consumed by a wolverine ($W_{reindeer\ use}$). Consequently, the minimum number of wolverine-killed reindeer was:

$$R_{wolverine\ killed\ (min)} = (W_{number} \times W_{food\ requirement} \times W_{diet} \times W_{minimum})/(R_{mass} \times W_{reindeer\ use}).$$

We then compared the amount of food available to wolverines from lynx-killed reindeer with the food requirement for wolverines after they have killed a minimum number of reindeer. The amount of food available from lynx-killed reindeer ($R_{carcass}$) depends on the number of lynx-killed reindeer ($R_{lynx\ killed}$), the amount of food available on a reindeer (R_{mass}), number of lynx (L_{number}), food requirements for lynx ($L_{food\ requirement}$) and the proportion of reindeer in the lynx diet (L_{diet}). The amount of food available for wolverines from lynx-killed reindeer then is:

$$R_{carcass} = R_{lynx\ killed} \times R_{mass} - L_{lumber} \times L_{food\ requirement} \times L_{diet}.$$

If the food requirement for wolverines is fulfilled after they have killed a minimum number of reindeer and accessed the amount of food available for wolverines from lynx-killed reindeer, then the wolverines do not need to kill more reindeer.

If $W_{number} \times W_{food\ requirement} \times W_{diet} - R_{wolverine\ killed\ (min)} \times R_{mass} \times W_{reindeer\ use} - R_{carcass} \times W_{carcass\ use} < 0$, then $R_{wolverine\ killed\ (extra)} = 0$.

However, if this was not true, we estimated the number of extra wolverine-killed reindeer. This depends on the amount of food needed for wolverines after they have used the minimum number of self-killed reindeer and the amount of food available for wolverines from lynx-killed reindeer, the amount of food available on a reindeer and the proportion of a self-killed reindeer used by wolverines, i.e. $R_{wolverine\ killed\ (extra)} = (W_{number} \times W_{food\ requirement} \times W_{diet} - R_{wolverine\ killed\ (min)} \times R_{mass} \times W_{reindeer\ use} - R_{carcass} \times W_{carcass\ use})/(R_{mass} \times W_{reindeer\ use})$.

The total number of wolverine-killed reindeer was: $R_{wolverine\ killed\ (total)} = R_{wolverine\ killed\ (min)} + R_{wolverine\ killed\ (extra)}$.

We then estimated the predation on reindeer per predator individual, as the total number of lynx- and wolverine-killed reindeer divided by the number of lynx and wolverines in the following way: $T_{loss\ per\ predator} = (R_{lynx\ killed} + R_{wolverine\ killed\ (total)}/(L_{number} + W_{number})$.

Input into the model

We used published data on diet and food requirements for lynx and wolverine together with food available on reindeer as input values in the model (Table 1).

Table 1. The variables used in the model and the mean and range of the values used in the sensitivity simulations. See model section for references and more explanations of the variables.

Variable	Mean	Range	Quality
R_{mass} (food available on a reindeer, in kg)	28[a]	18-38	Good
$L_{kill\ rate}$ (lynx kill rate without wolverines, number of reindeer/lynx and month)	4[b]	3-5	Fairly good
A (effect of number of wolverine on lynx kill rate)	0.125	0-0.25	Unknown
$L_{food\ requirement}$ (lynx food requirement, in kg/day)	1.7[c]	1.4-2.0	Good
L_{diet} (proportion of reindeer in lynx diet)	0.9[b,d]	0.85-0.95	Good
$W_{food\ requirement}$ (wolverine food requirement, in kg/day)	1.2[c]	1.0-1.4	Good
W_{diet} (proportion of reindeer in wolverine diet)	0.80[d]	0.7-0.9	Good
$W_{reindeer\ use}$ (proportion of a self-killed reindeer consumed by a wolverine)	0.70[d,e]	0.6-0.8	Poor
$W_{carcass\ use}$ (proportion of a lynx-killed reindeer consumed by a wolverine after lynx consumption)	0.30[d,e]	0.2-0.4	Poor
$W_{minimum}$ (minimum proportion of wolverine food requirement based on self-killed reindeer)	0.20	0.1-0.3	Unknown

[a] Reindeer Husbandry in Sweden 1999
[b] Pedersen et al. 1999
[c] Golley et al. 1965, Munoz-Garcia & Williams 2005
[d] Haglund 1966
[e] own observation

The amount of food available on a reindeer was taken from carcass weight measured at harvest, i.e. total body mass minus head, skin, lower legs, blood and viscera, and it constitutes on average 55% of the total body mass. The mean carcass masses in winter were 18, 29 and 40 kg for calves, adult females and adult male, respectively (Reindeer Husbandry in Sweden 1999). The reindeer winter herd was heavily skewed towards adult females, with the approximate percentages of adult males, adult females and calves after the autumn (September) and winter (December) harvest being 10, 70 and 20%, respectively (Reindeer Husbandry in Sweden 1999). Weighted by the proportions and mean slaughter masses, an average reindeer weighed 28 kg. In the simulations we used a mean of 28 kg (see Table 1). Consequently, we assumed that both lynx and wolverine kill reindeer in relation to their availability.

We estimated the daily food requirement for lynx based on the metabolic relationship between body mass and food intake (Golley et al. 1965, Munoz-Garcia & Williams 2005). Golley et al. (1965) found a negative linear relationship between food intake and body mass for felids; food intake (g/kg body mass) = 150 - 58 log(body mass in kg). The mean adult body mass of female lynx was 16.4 kg ($\pm$ 0.55 SE; N = 30) and for males 22.1 kg ($\pm$ 0.51 SE; N = 21; H. Andrén, unpubl. data), which will result in a daily food requirement of about 1.7 kg/day (range: 1.4-2.0 kg/day). This also corresponds to the daily food given to lynx in zoos (pers. com. Nordens Ark). Reindeer make up about 90% of the food intake by female lynx and their kittens in winter, and a family group kills on average 5.9 reindeer ($\pm$ 1.1 SE) per month in winter (Pedersen et al. 1999). This corresponds to a kill rate of about three reindeer per month and lynx, as a family group consists of an adult female and one or two kittens. However, male lynx have a higher kill rate on roe deer *Capreolus capreolus* than females (Breitenmoser & Haller 1993, Okarma et al. 1997, Nilsen et al. 2009). This relationship presumably also exists for kill rate on reindeer. Consequently, it is likely that the mean kill rate for an average lynx on reindeer is higher, and we therefore assumed a kill rate of four reindeer per month in winter for an average lynx (see Table 1). Given the mean value and range (see Table 1), an estimated average lynx consumes 41% ($\pm$ 12 SD) of a killed reindeer ((1.7 kg/day $\times$ 30 days $\times$ 90% reindeer in the diet)/(28 kg reindeer $\times$ 4 reindeer/month)), if wolverines do not influence the kill rate (i.e. A = 0; see Table 1).

The daily food requirement for wolverines was estimated using the same equation as used for lynx (see above; Golley et al. 1965). The mean adult body mass for female wolverines is 10.2 kg ($\pm$ 0.11 SE; N = 67) and for males 14.5 kg ($\pm$ 0.18 SE; N = 48; J. Persson, unpubl. data), which will result in a daily food requirement of about 1.2 kg/day (range: 1.0-1.4 kg/day). This also corresponds to the daily food given to wolverines in zoos (pers. com. Nordens Ark). Reindeer is the main prey of wolverines (Haglund 1966), but wolverine consumption of self- or lynx-killed reindeer is unknown. However, it is likely that wolverines consume a higher proportion of self-killed reindeer than of lynx-killed reindeer, as the latter scenario includes that the lynx-killed reindeer will be both found and consumed by the wolverine. Furthermore, other scavengers may have eaten parts of the lynx-killed reindeer before the wolverine discovers it; e.g. if wolverines find 50% of the lynx-killed reindeer and consume 60% of the meat available after lynx consumption, then wolverine use of lynx-killed reindeer is 30% (= 0.50 $\times$ 0.60). Therefore, in the model, the proportion of lynx-killed reindeer used by wolverines will always be lower than the proportion of wolverine-killed reindeer used. We used a higher consumption rate for wolverines on self-killed reindeer (mean: 70%; see Table 1) than for lynx, as wolverines make food caches, often inaccessible for other scavengers and use the carcass over a longer period (Haglund 1966). The estimated mean consumption was 41% for lynx (see above).

Input values were selected to cover the possible range and uncertain values had larger ranges than more certain values (see Table 1). The time frame for all calculations was one month. Consequently, the daily food requirements given in Table 1 were multiplied by 30.

Testing the effects of different variables

Our knowledge about the value of the different variables in the model varies greatly (see Table 1). Therefore, we tested the effect of this uncertainty on the outcome of the simulations. We randomly selected values for 10 different variables from a uniform distribution given by their mean and range, to test the effect of different variables on total kill rate. We ran simulation 5,000 times and estimated the total number of killed reindeer per predator individual for each set of different lynx-wolverine ratios in each simulation. We explored the outcome of the simulations using multiple regressions. This corresponds to a sensitivity analysis by simulations.

We estimated the effect of wolverine scavenging on total predation on reindeer by comparing the total number of lynx- and wolverine-killed reindeer with and without scavenging. We used the same model for simulations with and without scavenging. However, we set the proportion of wolverine-killed reindeer ($W_{minimum}$) to 1 (i.e. the wolverine only fed on self-killed reindeer) and the effect of wolverine on lynx kill rate (A) to 0 (i.e. no effect of wolverine on the lynx kill rate) in the simulations without scavenging. We then explored the effect of different variables using multiple linear regressions with the reduction in total number of predator-killed reindeer as the dependent variable.

To estimate the probability of obtaining a lower number of reindeer killed per predator at any lynx-wolverine ratio, we classified the outcome of a simulation as 1, if the total number of reindeer killed per predator first decreased and then increased as the lynx-wolverine ratio increased. This outcome means that the lowest number of reindeer killed per predator will be at some lynx-wolverine ratio. Other outcomes we classified as 0.

Results

The estimated wolverine kill rate in the absence of lynx was 1.5 reindeer/month (± 0.44 SD; Fig. 1 and Table 2), which was lower than the estimated lynx kill rate of 4.0 reindeer/month (± 0.58 SD, see Table 2). The wolverine kill rate decreased to 0.59 (± 0.44 SD) per month at a lynx-wolverine ratio of 1 and to 0.40 (± 0.31 SD) at a ratio of 2 (Fig. 2). The lynx kill rate also decreased as the lynx-wolverine ratio increased, because the impact of wolverine (variable A) on lynx kill rate decreased (see Fig. 2). The combined kill rate increased with increased lynx-wolverine ratio and approached the lynx kill rate (see Fig. 1).

The total kill rate (i.e. number of reindeer killed per predator individual and month) decreased on average by 7.9% (± 4.8 SD) when wolverine scavenging was included in the model (see Fig. 1). Total combined kill rate when wolverine scavenging was included was mainly influenced by lynx kill rate, and the total combined kill rate increased as lynx kill rate increased (Table 3). An increase in lynx kill rate by 1.0 reindeer/month will increase the total combined kill rate by approximately 0.46 reindeer/month. The second most important variable was the amount of available food on a reindeer and the kill rate deceased as the amount of available food on a reindeer increased (see Table 3).

Table 2. Lynx, wolverine and combined kill rate (number of reindeer kill per predator individual and month) for two management goals; lynx and wolverine occur together in the same area and lynx and wolverine occur separately.

Occurrence	Lynx	Wolverine	Combined
Together (i.e. including scavenging)	4.45 ± 0.71	0.59 ± 0.44	2.52 ± 0.33
Separately	4.00 ± 0.58	1.50 ± 0.44	2.75 ± 0.36

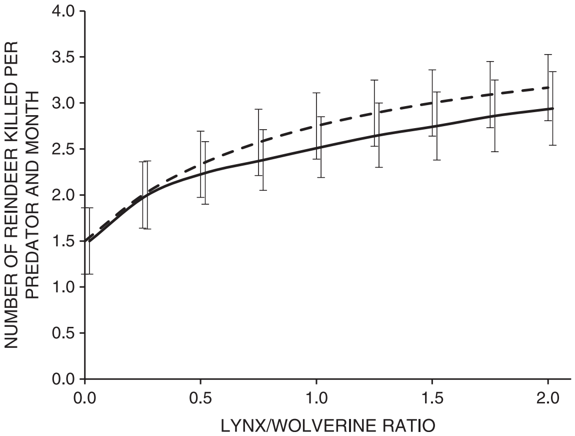

Figure 1. Mean number (± SD) of reindeer killed per predator individual per month using the range of values from Table 1 in relation to the lynx-wolverine ratio. The unbroken line shows the outcome of the model when wolverines scavenge on lynx-killed reindeer, and the dotted line shows the outcome when wolverines do not scavenge.

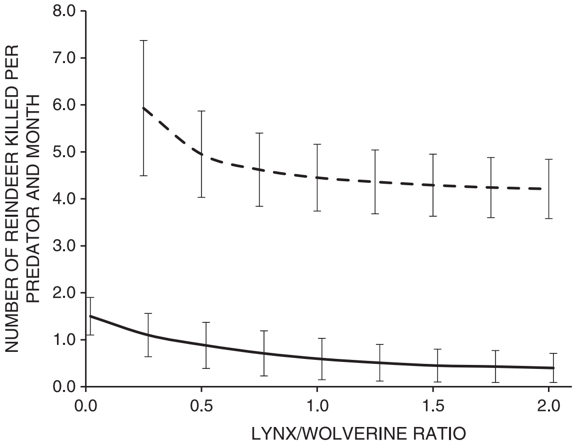

Figure 2. Mean number (± SD) of reindeer killed/lynx individual (-----) and wolverine individual/month (——) using the range of values from Table 1 in relation to lynx-wolverine ratio.

Table 3. Sensitivity analyses (multiple regression) of the four most important variables influence the total combined kill rate. Total $R^2 = 91.0\%$.

Variable	Partial R^2	Coefficient
$L_{kill\ rate}$ (lynx kill rate without wolverines, no. of reindeer/lynx and month)	55.0%	0.46
R_{mass} (food available on a reindeer, in kg)	19.6%	-0.03
A (effect of number of wolverine on lynx kill rate)	10.1%	1.57
$W_{carcass\ use}$ (proportion of a lynx-killed reindeer consumed by a wolverine after lynx consumption)	2.0%	-0.89

The lowest kill rate per predator individual occurred when only wolverines were present in an area. Actually, only two simulations out of 5,000 simulations (0.04%) resulted in a lowest number of reindeer killed per predator individual at a certain lynx-wolverine ratio. Consequently, we could not perform a sensitivity analysis.

The kill rate was lowest in 93% of the 5,000 simulations when lynx and wolverine existed together, and it was on average 9.2% (± 5.7 SD) lower than in a situation where lynx and wolverines exist separately (see Table 2). The most important variable affecting the reduction in total kill rate when wolverines scavenge on reindeer killed by lynx was how the number of wolverines in the area influences lynx kill rate (A in Table 1), and the differences between the models with and without wolverine scavenging decreased as the impact of wolverine on lynx kill rate increased (Table 4). Increasing the variable A by 0.1 will decrease the difference in total kill rate by approximately 0.16 reindeer/month between a model with and a model without scavenging. The second most important variable was wolverine use of lynx-killed reindeer and an increased use increased the differences (see Table 4).

Discussion

The combined predation of lynx and wolverine

In the absence of lynx, the estimated wolverine kill rate was much lower than the estimated lynx kill rate. Consequently, the lowest total predation occurred in areas with only wolverines (see Fig. 1). Incorporating wolverine scavenging on lynx-killed reindeer in the model reduced the total kill rate (i.e. number of reindeer killed per predator individual and month) by 7.9% (± 4.8 SD; see Fig. 1).

A lowest number of predator-killed reindeer at a certain lynx-wolverine ratio is unlikely, probably because wolverines are smaller than lynx and therefore have lower food requirements and likely a lower kill rate. Consequently, the total food requirement for wolverine and lynx together, as well as the kill rate, will increase as the lynx-wolverine ratio increases. Thus, if the management goal is a constant number of any of the predators in an area, our model suggests that the lowest predation will be with only wolverines. If the management goal instead is a constant number of lynx and wolverines, the lowest total predation will be in areas where the two predators coexist. In these areas the estimated total predation was lower (93% of the simulations) than when they existed separately. However, the sensitivity analysis showed that this result was mainly influenced by how the number of wolverines influences the lynx kill rate (A in Table 1). When the influence of wolverines on lynx kill rate increases, the differences in total predation between areas where lynx and wolverine coexist, and areas where lynx and wolverine exist separately, decreases. Thus, to better understand the total combined kill rate on reindeer, one has to improve the data on how wolverine affect the lynx kill rate (variable A), lynx kill rate, wolverine use of both lynx-kill reindeer and self-kill reindeer.

Table 4. Sensitivity analyses (multiple regression) of how the four most important variables influence the differences in total combined kill rate between the models with and without scavenging. Positive coefficients mean that the differences in total combined kill rate increased between the models with and without scavenging. Total $R^2 = 75.2\%$.

Variable	Partial R^2	Coefficient
A (effect of number wolverine on lynx kill rate)	49.1%	-1.62
$W_{carcass\ use}$ (proportion of a lynx-killed reindeer consumed by a wolverine after lynx consumption)	9.3%	0.91
$W_{reindeer\ use}$ (proportion of a self-killed reindeer consumed by a wolverine)	7.1%	-0.76
$L_{kill\ rate}$ (lynx kill rate without wolverines, no. of reindeer/lynx and month)	3.4%	0.05

The outcome of a model depends on the model structure and the input into the model. An important question is whether our model is realistic. Pedersen et al. (1999) found that a lynx family group (i.e. adult female with one or two kittens) consumed on average 61% (± 24 SD) of a killed reindeer in winter. According to our model, an average lynx will consume 41% (± 12 SD) of a killed reindeer (see section Methods). However, lynx males consume less of a large prey than family groups (Breitenmoser & Haller 1993, Okarma et al. 1997, Odden et al. 2002). The estimated consumption of a lynx-killed reindeer by a family group (i.e. an adult female with one or two kittens) is between 56 and 83% according to our model. This estimated consumption is based on a kill rate of 5.9 reindeer/month (Pedersen et al. 1999), a daily food requirement between 3.4 and 5.1 kg for a family group, a reindeer body mass of 28 kg and reindeer comprising 90% of the lynx diet, (two or three individuals; (2 or 3 × 1.7 kg/day × 30 days × 90% reindeer in the diet)/(28 kg reindeer × 5.9 reindeer/month)). Consequently, we suggest that the model provides a realistic illustration of the lynx-reindeer interaction.

The effect of wolverine on lynx kill rate (variable A) was an important factor for the kill rate on reindeer, but this variable is unknown in the system. From other systems, dominant predators regularly steal food from subordinates species. For example, lions and hyenas steal from cheetahs *Acinonyx jubatus* and African wild dogs (Creel et al. 2001), which causes an increased hunting time for the subordinate species (Gorman et al. 1998). It is also common that facultative scavengers visit kills from other predators; e.g. grizzly bears regularly visit cougar kills (Koehler & Hornocker 1991, Creel et al. 2001). Mattisson (2011) found that the time to next lynx kill was only weakly affected by wolverine presence at the reindeer carcass. Mattisson (2011) concluded that other scavengers, like ravens, may have a larger impact on the available amount of food for the lynx than wolverines. Vucetich et al. (2004) estimated that groups of ravens have the potential to scavenge 2-20 kg of food /day. The range of A (0-0.25) includes a quite strong effect on lynx kill rate by wolverine and an increased kill rate by 50% at a wolverine-lynx ratio of two, which most likely includes the possible effect of wolverine on lynx predation on reindeer.

Mattisson (2011) found that wolverine scavenged on 68% of all lynx-killed reindeer, but wolverines continued to kill reindeer even if there were lynx-killed reindeer available in the area. Furthermore, the wolverines used the wolverine-killed reindeer about twice as much as compared with lynx-killed reindeer (Mattisson 2011). Thus, we suggest that model capture the lynx/wolverine*reindeer interaction qualitatively; i.e. wolverine use of self-killed reindeer should be higher than wolverine use of lynx-killed reindeer and there should also be a minimum level in wolverine kill rate, although the values for these variables are not exactly known.

Ongoing research in northern Sweden with radio-marked lynx and wolverines, has estimated lynx density to be between 0.2 and 0.7 lynx/100 km^2 (Danell et al. 2006) and wolverine density to be 1.4 wolverine/100 km^2 (Persson et al. 2006), which corresponds to lynx-wolverine ratios between 0.14 and 0.5. In our study area, the home ranges of lynx are about twice as large as the home ranges of wolverines (Linnell et al. 2001, Persson et al. 2010, Mattisson et al. 2011). In other parts of northern Sweden, the lynx densities are higher and the wolverine densities lower (survey data from Swedish Environmental Protection Agency and county administrative board). Consequently, we have modelled realistic relative abundances of lynx and wolverine.

Reindeer herding and large predators

Reindeer husbandry is deeply tied to the Sámi culture in Fennoscandia. Reindeer husbandry suffers, at least locally, from heavy predation by large predators (lynx, wolverine, wolf, bear and golden eagle). As a consequence, managers in Fennoscandia face a unique problem of compromising between the sustainability of Sámi culture and conservation of predators with their main prey being semi-domesticated reindeer. In Sweden, the government compensates reindeer herders for damage caused by predators, where the yearly cost for all predators altogether amounted 60 million SEK (~ 6 million €) in 2008 (Swedish Environmental Protection Agency). Lynx and wolverines are the most important predators, and 29 million SEK (~ 2.9 million €) and 20 million SEK (~ 2.0 million €) were paid, respectively, in compensation in 2008. The Swedish compensation scheme is based on the number of predators present within a reindeer-grazing district. In 2008 ,the compensation was 200,000 SEK (~ 20,000 €) for each lynx family group (i.e. an adult female with her kittens of the year), and for each wolverine reproduction (i.e. natal den or observations of cubs) found within a reindeer-grazing district during yearly surveys. Under this compensation scheme, the reindeer owners accept some losses to predators, and the Swedish government should give full compensation, both for the financial losses due to reduced slaughter and other costs caused by the predators; e.g. increased herding costs caused by disturbance of the herds.

Under the current compensation scheme, it will be profitable for reindeer owners to increase the protection of reindeer from predators. If the true losses decrease due to better protection, then reindeer owners will increase the income from the reindeer harvest. However, the compensation for damage caused by predators will still be the same if the same number of predators remains. Nevertheless, it is important to remember that both lynx and wolverines are dependent on reindeer for their survival and there will always be predation on reindeer from both these predators. Therefore, the acceptance of predators by reindeer herders is crucial for the conservation of both species.

The compensation system adds the number of predators of different species in an area independent of one another (Swenson & Andrén 2005, Zabel & Holm-Müller 2008). This system assumes that the loss of reindeer to predators is not influenced by the species composition of the predators. If the predation by one predator species decreases when coexisting with another species, then the reindeer owners will benefit from having different predator species together. The model in our paper suggests that the combined predation from wolverine and lynx will be lower, if they are coexisting as compared to existing in separate areas. If the management goal is a constant number of predators, our model suggests that it is unlikely there will be a lower number of killed reindeer at a certain lynx-wolverine ratio. Our model actually suggests that the kill rate is lowest when only wolverines are present. As the compensation is the same for wolverine and lynx, it should be financially most beneficial for a reindeer-grazing district to have only wolverines at a given number of predators. On the other hand, if the management goal is a constant number of lynx and wolverines, then our model suggests that the two predators should coexist in the same area. Furthermore, the wolverine is not as efficient as a predator as the lynx, and wolverine predation events cause more disturbances to reindeer herds than lynx do (Haglund 1966). The extra work caused by wolverine disturbance might be lower when wolverines and lynx coexist. Consequently, reindeer management may benefit from having all lynx and wolverines together, both because the total combined kill rate might be lower and because the disturbance from wolverines on the reindeer herd might be lower when wolverines use more lynx killed reindeer.

In conclusion, our model shows that the kill rate is lowest where only wolverines are present, and that it is unlikely that there is a lowest number of killed reindeer at a certain lynx-wolverine ratio. On the other hand, if the management goal is a constant number of lynx and wolverines, then our model suggests that the two predators should coexist in the same area. Wolverines will probably also benefit from coexisting with lynx, as lynx predation increases the carcass availability, which in turn can result in increased wolverine reproduction (Persson 2005). From a conservation point of view, wolverine populations may be more viable, when lynx are present. Thus, coexistence of wolverines and lynx should be desirable from a conservation perspective and probably also from a reindeer husbandry perspective.

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