



The impact of lynx and wolf on roe deer hunting benefits in Sweden

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Abstract

Large carnivores provide ecosystem and cultural benefits but also impose costs on hunters due to the competition for game. The aim of this paper was to identify the marginal impact of lynx (*Lynx lynx*) and wolf (*Canis lupus*) on the harvest of roe deer (*Capreolus capreolus*) in Sweden and the value of this impact. We applied a production function approach, using a bioeconomic model where the annual number of roe deer harvested was assumed to be determined by hunting effort, abundance of predators, availability of other game, and winter severity. The impact of the predators on the roe deer harvests was estimated econometrically, and carnivore marginal impacts were derived. The results showed that if the roe deer resource was harvested under open access, the marginal cost in terms of hunting values foregone varied between different counties, and ranged between 18,000 and 58,000 EUR for an additional lynx family, and 79,000 and 336,000 EUR for an additional wolf individual. Larger marginal costs of the wolf, in terms of the impact on roe deer hunting, were found in counties where the hunting effort was high and the abundance of moose (*Alces alces*) was low. If instead, hunters could exert private property rights to the resource, the average marginal cost was about 20% lower than it would have been if there was open access, and the difference in wolf impact between counties with high and low moose density was smaller. Together, results suggest that the current plan for expanding the wolf population in south Sweden can be associated with a substantial cost.

Keywords Human-large carnivore conflict · Lynx · Predation · Production function approach · Wolves

JEL codes Q51 · Q57

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1 Introduction

Hunting is an important leisure activity, which generates significant economic activity and tends to increase land values (Pinet 1995; Lecocq 2004; Mattsson et al. 2008; US Fish and Wildlife Service 2018; Hussain et al. 2013). Large wild carnivores can have a considerable impact on game species populations, and the resulting competition for game creates conflicts between the hunters and the predators. Historically, this has led to a reduced predator abundance (Graham et al. 2005). More recently, efforts to protect threatened carnivores, e.g., through conservation programs, have increased (Graham et al. 2005; Chapron et al. 2014). The conservation efforts have considerable public support, reflected by the high willingness to pay for preservation (Bostedt et al. 2008; Broberg and Brännlund 2007; Ericsson et al. 2007, 2008; Johansson et al. 2012). The support for conservation can be related to the perceived ecosystem benefits, such as regulation of the community structure of natural ecosystems; cultural benefits, such as ecotourism; and preservationist values generated (Ericsson et al. 2004; Lute et al. 2018). Nevertheless, the growing carnivore populations are likely to affect hunting benefits experienced by hunters, and by reducing game abundance they can also affect the revenues obtained by landowners that sell or lease out hunting rights (Livengood 1983; Lundhede et al. 2015; Mensah and Elofsson 2017; Mensah et al. 2019; Rhyne et al. 2009). The Swedish Hunters' Association has estimated that the reduction in hunting value due to carnivores is about 50 million EUR per year¹ (Svensk Jakt 2009), and the Norwegian forest owner organization has claimed that the wolf (*Canis lupus*) causes a loss of property value equal to about 100 million EUR (Norskog 2018). Claims for compensation have been raised in connection with increased wolf population numbers and cancelled wolf license hunting in central Sweden (Vargfakta 2011), and when a genetically important wolf was translocated from the reindeer (*Rangifer tarandus*) herding areas in northern Sweden, where the national wolf management policy places strong restrictions on its abundance (EPA 2014a), to a county in central Sweden (Lövbom 2013). In the absence of policies to overcome conflicts between conservation and hunting interests, carnivores are poached by hunters opposing carnivore conservation (Gangaas et al. 2013; Rauset et al. 2016; von Essen and Allen 2017), thereby challenging conservation aims (Andrén et al. 2006; Persson et al. 2009; Liberg et al. 2011).

Few economic studies have estimated the costs that accrue to the hunters as a consequence of increased carnivore abundance. Boman et al. (2003) and Skonhoft (2006) apply bioeconomic analysis, where available estimates of predation rates were used in the modelling. Boman et al. (2003) calculated a constant cost per carnivore, obtained by multiplication of moose (*Alces alces*) kill rate and the unit hunting value. In general, this approach could be questioned: if there is no hunting, additional carnivores have no impact on harvests even if the number of killed prey increases. Skonhoft (2006) calculated the costs of wolf predation on moose using

¹ The estimate was based on hunting values in Mattsson et al. (2008) and carnivore predation rates.

a programming model where the socioeconomic outcome of different stylized harvesting regimes (threshold harvesting with a constant stock over time, proportional harvesting, and harvesting of a fixed number each year) were compared for alternative assumptions about the predation rate. Different to those, Mensah et al. (2019) and Lozano et al. (2020) estimated the impact of carnivore abundance on hunting lease prices, using the hedonic pricing method. Mensah et al. (2019) disentangled the effect due to reduced game harvest, and the effect of other factors, such as the fear for attacks on hunting dogs, while Lozano et al. (2020) compared the negative impact due to reduced game abundance to the positive impact of large carnivore license hunting. Also relevant to our analysis are a couple of ecological studies that have analyzed harvest adjustments in the presence of large carnivores. Using a sex-and-age-structured moose population model, Nilsen et al. (2005), compared optimal moose harvests with and without carnivore predation, when the purpose was to maximize the number of harvested animals or the quantity of meat. Using similar models, Jonzén et al. (2013) and Chapron (2015) suggested online decision-support tools for science-based harvest of moose in the presence of large carnivores. Results in Jonzén et al. (2013) suggested that the reduction in harvest due to large carnivores can be ameliorated by increasing moose density and redistributing the harvest towards more bulls, as hunters have a preference for shooting prime bulls.

The aim of this paper was to estimate the marginal economic cost of two carnivores, lynx (*Lynx lynx*) and wolf, in terms of their impact on roe deer (*Capreolus capreolus*) harvests in the south and central Sweden between 2002 and 2012. The roe deer was the second most valuable hunted species in Sweden after the moose, accounting for about one-fifth of the total hunting value (Mattsson et al. 2008). Moreover, the hunting bag statistics revealed that roe deer harvests in Sweden decreased by approximately 45% between 2002 and 2012.² Predation pressure from lynxes, wolves and red foxes (*Vulpes vulpes*) has been argued to be a major determinant of roe deer population size (Jarnemo and Liberg 2005; Melis et al. 2010; Gervasi et al. 2013), suggesting that carnivores could be of importance for the decline. To study this issue, we applied a production function approach, using a bioeconomic model where roe deer harvest was jointly determined by hunting effort, abundance of predators, availability of alternative prey, and winter severity. The harvest function derived from this model was estimated empirically using county-level data from 2002–2012 on hunting bags, carnivore numbers, the number of hunters, and meteorological data on snow depth. Based on the results from the estimations, we calculated the marginal cost of the two carnivores for a constant as well as an adjusted, steady-state equilibrium effort. Further, marginal costs for the two carnivores were compared across counties. This comparison was motivated by the Swedish carnivore management policy for wolves having a spatial component: the national management plan supports further dispersal and increase in population numbers in the southern part of the country (EPA 2014a). Our study contributes to the economic literature on wildlife-carnivore management by applying the production function approach and to our best knowledge, no earlier study has applied this method to

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the analysis of wildlife-carnivore management. Empirically, it provides knowledge about the costs that can be expected as a consequence of the targeted expansion of the wolf population to South Sweden, and knowledge about the relative costs of wolf and lynx, respectively.

2 Hunting institutions in Sweden

There are about 300,000 hunters in Sweden, corresponding to about three percent of the population. Based on hunters' expenditures the annual gross hunting value is estimated to be more than EUR 370 million (Mattsson et al. 2008). Hunting occurs to some extent on most land where it is legally permitted. Anyone who has completed a short course in hunting can acquire a personal hunting licence from the Environmental Protection Agency for about EUR 30. This license is required for all hunters. The right to hunt on a specific plot of land is tied to land ownership. Landowners have the exclusive right to hunt on their own land, including the right to the game meat and the trophies. The landowner can also lease out the hunting right on his land in whole or in part (Sandström et al. 2013). The landowner and the hunter are then free to decide on the contractual details regarding, e.g., the duration of the lease, and the game species included. Access to hunting land can thus be acquired through lease, and there is a considerable supply of hunting opportunities on the market (Mensah and Elofsson 2017). Both long-term leases where contracts are on an annual basis but are renewed and thus in practice extend over several years, and short-term leases on a daily or weekly basis, can be found. The long term leases are more common and typically imply that the landowner grants a hunter the right to hunt all mammals and birds on the land that are eligible for hunting. For most species, including roe deer, fallow deer (*Dama dama*) and different small game, the hunter is free to decide on the number of hunting days and on harvest rates, as long as crop and forest damages are held within reasonable limits (Mensah and Elofsson 2017).³ The hunter that leases the hunting rights is usually free to invite additional hunters as permanent paying members of the hunting team, or as temporary guests.

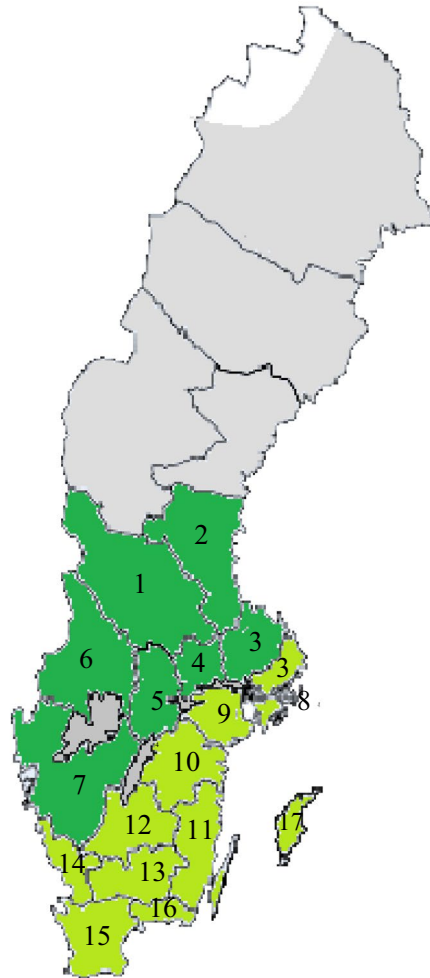
Our study area in the south and central Sweden includes 15 of the total of 21 counties in Sweden⁴, see Fig. 1. It covers 45 percent of the country's total area and is the main distribution range in Sweden for the European roe deer⁵. In our study area, 50–90% of the land is privately owned, and the average private owner has 35 hectares of forest. A female roe deer, together with the fawns, has a home range of about 25–150 hectares, while the home range of the males is 1.5 times greater (Kjellander et al. 2004). Hence, roe deer home ranges overlap several plots of land where

³ An exception is the moose, for which management plans are required by the so called Moose Management Areas (MMAs). Compared to the roe deer, the moose is larger, and is associated with both larger wildlife damages to forest crops, and larger hunting values.

⁴ The county level is the regional administrative level.

⁵ The reindeer herding areas in north Sweden were excluded due to the lower number of roe deer in combination with the different prey species available to the predators.

Fig. 1 Map over study area in Sweden. The Southern and Central Management Areas (MOEE 2013) are indicated in the figure by light and dark green color, respectively. The grey area shows the distribution of roe deer outside the Southern and Central Management Areas. Counties: 1. Dalarna, 2. Gävleborg, 3. Uppland, 4. Örebro, 5. Västmanland, 6. Värmland, 7. Västra Götaland, 8. Stockholm, 9. Södermanland, 10. Östergötland, 11. Kalmar, 12. Jönköping, 13. Kronoberg, 14. Halland, 15. Scania, 16. Blekinge, 17. Gotland. Note: we do not distinguish between the two management areas, thus Uppland (3) which is divided between the two areas is treated as one county. Gotland county (17) and Stockholm county (8) were excluded from the estimations due to the absence of large carnivores, and for statistical reasons, respectively



the hunting rights are owned by different people, implying that private property rights to the roe deer resource can be difficult to enforce. It is only permitted to hunt roe deer during the hunting season, which in most parts of the country occurs in the autumn and winter, and ranges between 4 and 5.5 months depending on age and sex of the animal. Regulation of the hunting season length has not yet been used as an instrument to control the size of ungulate populations, albeit recently the possibility to do so has been discussed (EPA 2017). Finally, the possibilities for monitoring and enforcement are limited; there is no monitoring of hunting or ungulate populations carried out by public agencies. Hunting teams sometimes have informal agreements about the number of roe deer to be harvested in a given season, but it cannot be ensured that individual hunters comply with such agreements because peer monitoring and enforcement is very expensive in terms of time and may not be seen as socially acceptable, respectively.

3 The roe deer and its predators

The main predators of the roe deer are lynx, wolf and red fox (Jarnemo and Liberg 2005; Andrén et al. 2010; Sand et al. 2016). In the following sections, we briefly describe all four species.

3.1 Roe deer (*Capreolus capreolus*)

The roe deer is a relatively small ungulate species with a shoulder height of 0.70–0.75 m, and adults weighing 20–30 kg. It is found throughout the country, with lower population densities further north and only small patches in the northernmost parts of the country. Roe deer hunting is a popular activity: in the season 2005/06 the average Swedish hunter spent 26 days per year hunting, and one-fifth of this time was allocated to roe deer (Mattsson et al. 2008). The main causes of mortality are predation, winter starvation and hunting (Cederlund and Liberg 1995; Hagen et al. 2017). A large snow depth is a major reason for winter starvation and has a negative impact on reproduction and survival (Gaillard et al. 1993; Lindström et al. 1994; Mysterud et al. 1997; Kjellander and Nordström 2003). Obviously, winter starvation is of greater importance in the central and northern parts of the country.

3.2 Lynx (*Lynx lynx*)

The lynx is the only large cat in Sweden, and it is present in all parts of the country except on the islands of Öland and Gotland. The highest population number was recorded during the 2008/2009 hunting season, indicating somewhere between 1500 and 2000 lynxes in total (EPA 2014a). After that, the lynx population has experienced a slight decline (Fig. 2). The current management goal suggests that the population should exceed 870 individuals, a target that was met during our study period (EPA 2014a). In recent decades, license hunting has sometimes been implemented to avoid livestock damage, taking into account population status in relation to conservation goals (EPA 2014b).

The lynx usually hunts as a lone stalker, and the main prey in the southern and central parts of Sweden is the roe deer in combination with small prey species (Liberg and Andrén 2006). The lynx population is shown to greatly affect the abundance of roe deer (Gervasi et al. 2012; Arbieu 2012). The effect can be even stronger for low densities of roe deer, for example in areas with a lower environmental productivity where other types of food sources are scarce (Odden et al. 2006; Melis et al. 2010). The lynx success rate in roe deer hunting can be positively affected by a larger snow depth, because roe deer mobility and escape success is reduced in deep snow, amplifying the negative effect of snow on the abundance of roe deer (Melis et al. 2009, 2010).

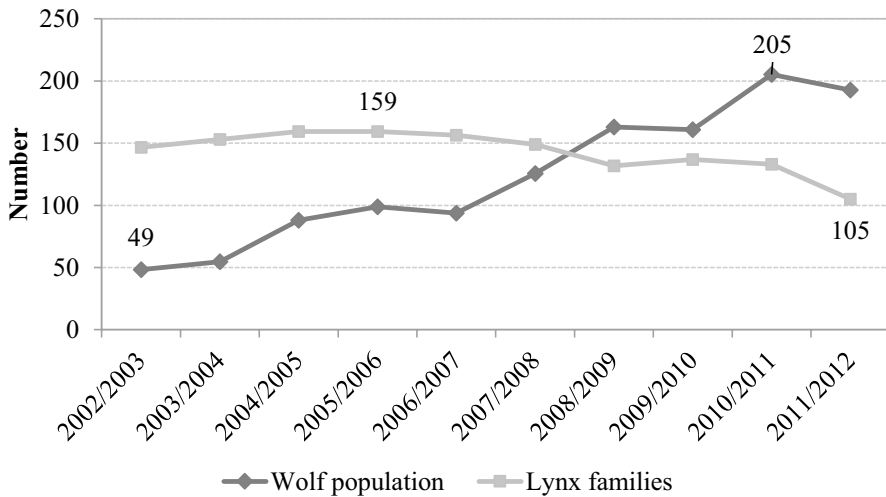


Fig. 2 Number of wolves (individuals) and lynxes (family groups) in south and central Sweden. A lynx family consists of a female with its dependent kittens. The number of wolf individuals includes both adult and young individuals. Sources: Andrén et al. (2010), Danell and Svensson (2011), Zetterberg (2014), and Wildlife Damage Center (2016)

3.3 Grey wolf (*Canis lupus*)

Due to human persecution, only about 10 wolves remained in Sweden in 1966, when the species was placed under protection (Franzén 1991). Since the early 1980's the population has grown, and from the 1990's the numbers have increased rapidly (Wabakken et al. 2001). Figure 2 shows the development of the wolf population in the study area since 2002. In 2013, the Swedish government decided that the minimum level of the wolf population should be 170–270 individual wolves to ensure favorable conservation status (MOEE 2013). Before 2010, derogations to harvest wolves were permitted only on culling wolves that were depredating on domestic animals or behaving boldly near human settlements. In 2010, the Swedish government launched quota harvest for wolves,⁶ and it was decided that license hunting should regulate the total population while targeting wolves according to the same criteria as for culling, considering also the genetic value of wolf individuals. Due to protests, quota hunting was then cancelled in the following years.

Wolves are effective hunters because of their ability to form and hunt in packs and to cover long distances (Bjärvall and Ullström 1995). Moose is the main prey (Sand et al. 2008), but roe deer become increasingly important in the diet with increased densities (Sand et al. 2016).

⁶ SVA, National Veterinary Institute, <https://www.sva.se/djurhalsa/vilda-djur/stora-rovdjur/licensjakt-pa-varg>, reports that 28 and 19 individuals were killed in 2010 and 2011, respectively.

3.4 Red fox (*Vulpes vulpes*)

The red fox is a generalist predator with lagomorphs, rodents and roe deer fawns as the main prey (Jarnemo and Liberg 2005). The predation rates on the roe deer fawns can be considerable, and the effect is larger in open habitats, such as pastureslands, compared to dense habitats, such as woodlands (Aanes and Andersen 1996; Linnell et al. 1995; Jarnemo and Liberg 2005; Panzacchi et al. 2008). Both lynx and wolves have been found to kill red foxes regularly. There are cases found with a negative correlation between lynx and fox abundance, argued to be the result of predation or of fox avoiding areas with higher lynx densities (Helldin et al. 2006). However, lynx and wolves could also provide food for the red foxes through leftovers from carcasses, thereby benefitting the fox (Helldin and Danielsson 2007; Wikenros et al. 2013). In particular, this can be of importance when the snow depth is large, resulting in a difficult hunt for rodents (Selås and Vik 2006). Comparing the relative impacts of red fox and lynx predation on roe deer growth rates in south-central Norway, Nilsen et al. (2009) concluded that the impact of lynx is substantially larger than that of red fox. The red fox is hunted during most of the year except late spring and summer, and the purpose of the hunt is mainly to reduce impacts on roe deer.

4 The theoretical model

In the following section, we develop a relatively simple bioeconomic model that aims to identify the relationship between the roe deer harvest, the hunting efforts, the predator abundance and the winter conditions.

4.1 Roe deer growth and harvest functions

We assume that the development of the roe deer population over time is determined by the roe deer population, X_t ; the hunting effort, E_t ; and a vector of variables, \mathbf{Z}_{it} , that increase roe deer mortality and where $i = W, L, F, S$ indicates the factors of concern: the populations of the wolves (W), the lynxes (L), the red foxes (F), and the number of days with thick snow cover (S). The change in the stock of the roe deer from time t to $t + 1$ can be defined as follows:

$$X_{t+1} - X_t = G(X_t, \mathbf{Z}_t) - h(X_t, E_t), G_x > 0, G_z < 0, \quad (1)$$

where $G(X_t, \mathbf{Z}_t)$ is the biological growth in the roe deer population, and $h(X_t, E_t)$ is the harvest level. We assume a logistic growth function, where the sensitivity of the roe deer growth to changes in \mathbf{Z} is determined by a vector of constant coefficient, δ , see Eq. (2). Although the assumption of linearity in \mathbf{Z} , i.e., constant δ , is a simplification, it is consistent with increases in predator populations increasing prey mortality through predation, and reducing prey population growth due to the impact on the prey's habitat selection, where the latter could reduce feed availability (Bongi

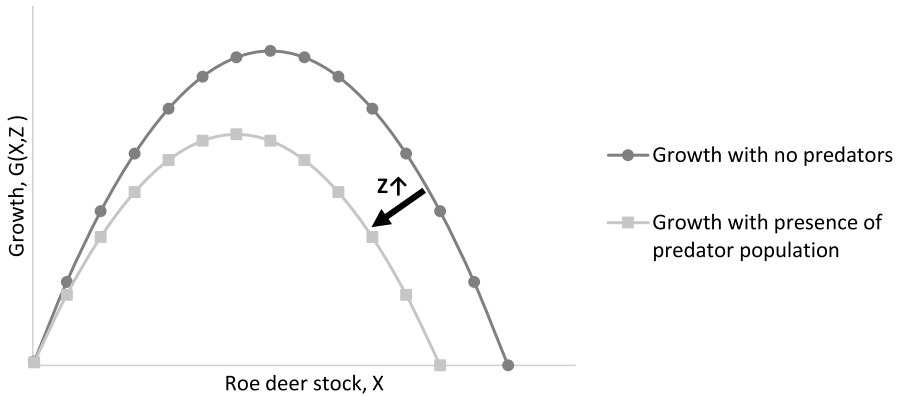


Fig. 3 The roe deer population growth function. An increase in the population of a predator, or a longer period with thick snow cover, shifts the growth function inwards

et al. 2008; Thaker et al. 2011) and, hence reproduction. Similarly, weather conditions could affect both mortality and reproduction.

$$G(X, Z) = rX \left(1 - \frac{X}{K} \right) - \delta Z X, \tag{2}$$

with $G >> 0$, $G_Z < 0$, and $G(X, 0) > 0$ for $0 > X > K$.

In Eq. (2), the term r expresses the intrinsic growth rate of the roe deer population, and K expresses the carrying capacity, i.e., the maximum number of roe deer in the absence of predators, both assumed to be constants. Given the roe deer growth function in Eq. (2), an increase in Z_i shifts the growth function inwards, see Fig. 3. Furthermore, we assume a simple Schaefer harvesting function:

$$h_t = qX_t E_t, \tag{3}$$

where q is the catchability coefficient, which is assumed to be constant. This assumption is a simplification, as the catchability could be affected by the presence of large carnivores or by climatic conditions. For example, the hunters could be reluctant to release their hunting dogs if there are wolves in the neighbourhood, given the potential risk of injuries (Kojola and Kuittinen 2002), which would reduce catchability. This simplification is motivated by the lack of data on catchability under different conditions, as well as on hunting dogs and their use.

In the general case, there can be a feedback effect as the size of the roe deer population could influence predator population growth. However, wolf and lynx populations in Sweden are subject to protection,⁷ and culling as well as licence hunting is permitted, respectively, when individuals of these species give rise to livestock damages and their numbers exceed governmental targets for favourable conservation

⁷ They are protected by the European Union Habitats Directive (Council Directive 92/43/EEC), which is guiding national legislation and management plans.

status (EPA 2014a, b). Hence, the feedback effect is less obvious, as predator populations may not respond numerically to variations in the roe deer population. We, therefore, do not include a numerical response of the predators but assume that predator population numbers are determined by policy makers.

4.2 Bioeconomic model

Real-world markets for hunting are unlikely to completely match the theoretical criteria for open access or private property resource management regimes. Open access resources are characterized by non-excludability, free entry and exit, lack of enforcement of property rights, and costly monitoring. As described in Sect. 2, the hunting market for roe deer in Sweden shares many of these features: there is no regulation of roe deer harvesting, and roe deer home ranges typically overlap several plots of privately owned land where different decision-makers possess the hunting rights and, therefore, the populations cannot be fully controlled by any single decision-maker. Together, the lack of regulations, monitoring and enforcement, in combination with free entry and exit for individual hunters, and roe deer mobility across the land with hunting rights owned by different people, suggests that open access could be a plausible approximation of the prevailing conditions. On the other hand, the relevance of the open-access assumption for this market depends on the extent of overlap between roe deer home ranges and hunting plots, and of peer monitoring and enforcement. If the spatial overlaps are small, and peer enforcement is strong in practice, e.g. due to concerns for the social relationships with neighbouring hunters, a private property regime could be a better approximation of the prevailing conditions. In addition, the fact that most contracts are long-term tends to increase incentives for hunters to account for impacts of their actions on future harvests, supporting private property management. In the following we, therefore, pursue analysis both for open access and private property regimes, acknowledging that our data could potentially fit with either of those.

Further, we assume that the system is in a steady-state biological or bioeconomic equilibrium.⁸ The assumption about a steady state is a simplification, and to be a reasonable approximation of reality it is necessary that the roe deer population and the hunting community respond relatively rapidly to changes in predator populations and winter weather conditions. The fact that roe deer harvesting is mostly done in the autumn supports this, as hunters have time to adopt to the impact of predators and winter conditions on roe deer populations earlier in the same year. The assumption that such adjustments occur rapidly is further supported by results in Wikenros et al. (2015), where it is shown that hunters respond quickly to reduced moose abundance caused by increased wolf numbers, then reducing their harvest of moose.

Given the above described Eqs. 1–3 and the assumption about a biological equilibrium, we can derive an equation that can be estimated (see the Appendix for details):

⁸ The choice to analyse equilibrium conditions is also motivated by the fact that our dataset is too small for a time dynamic model to be estimated.

$$h = \alpha E + \beta Z E + \gamma E^2, \quad (4)$$

where $\alpha > 0$, $\beta < 0$, and $\gamma < 0$ are the coefficients to be estimated. Using Eq. (4), the marginal products of E and Z_i , are obtained as:

$$MP_E = \frac{\partial h}{\partial E} = \alpha + \beta Z + 2\gamma E \quad (5)$$

and

$$MP_{Z_i} = \frac{\partial h}{\partial Z_i} = \beta_i E, \quad (6)$$

respectively. The marginal product of predators, MP_{Z_i} , expresses the change in harvest when the predator population increases by one unit, while effort is held constant, hence reflecting a biological equilibrium. The marginal product of predators is negative and decreasing in the effort level. The marginal product of effort, MP_E , expresses the harvest increase when the effort is increased by one unit, while predator numbers are held constant. It is decreasing in the level of effort and predator numbers.

In Eqs. (5), (6), the effects were calculated for a given hunting effort. However, with a constant hunting effort increases in the number of predators would eventually lead to the depletion of the roe deer stock. To avoid such outcomes, the effort level must be adjusted. To consider such an adjustment, we impose an additional assumption, namely that the effort level is adjusted such that a positive stock and effort can be maintained over time, implying that the system is in an economic equilibrium, see Appendix for details. Here below, we present the comparative static effect of changes in predator populations, on roe harvest, $\partial h / \partial Z_i$, and hunting revenues, $p \cdot \partial h / \partial Z_i$ in each of the two equilibria. The comparative static effect in the open-access equilibrium can then be obtained as:

$$\frac{\partial h}{\partial Z_i} = -\frac{r\delta_i c}{pq} = -\frac{c\beta_i}{p\gamma}, \quad (7)$$

and

$$p \frac{\partial h}{\partial Z_i} = -\frac{r\delta_i c}{q} = -\frac{c\beta_i}{\gamma},$$

where p and c are the unit revenue of roe deer harvest and unit cost of effort, respectively. The unit revenue and cost are both assumed to be constants, which is motivated by the convenience of modelling in this section as well as a scarcity of data for the empirical analysis.⁹ Equations (7), (8) show that the open-access equilibrium reduction in harvest and revenue is increasing in r and δ_i , and decreasing in q . The

⁹ There can also be additional values of hunting, not directly related to the bagged number, e.g., linked to the recreational value of the hunting trip and hunting experience. The parameter p should thus be interpreted as the partial value related to the bagged number of roe deer.

harvest reduction is further increasing in the ratio of unit harvesting cost and revenue. The open-access comparative static effect of predators on the harvests and the revenues can thus be evaluated when c and p are known. One can note that for a low-cost hunting industry where the open access stock is below maximum sustainable yield, $\partial h/\partial Z_i$ can be expected to be lower than MP_{Z_i} , whereas the opposite would hold for a high-cost hunting industry where the stock is above maximum sustainable yield (see Appendix Fig. 5).

Furthermore, the comparative static effect on harvest in the private property equilibrium can be obtained as:

$$\frac{\partial h}{\partial Z_i} = -\frac{\delta_i K}{2} + \frac{\delta_i^2 K}{2r} Z_i = -\frac{\alpha \beta_i}{2\gamma} - \frac{\alpha \beta_i}{2} Z_i, \tag{9}$$

see Appendix for details of the calculation. The corresponding impact on revenues is then obtained as:

$$p \frac{\partial h}{\partial Z_i} = p \left(-\frac{K \delta_i}{2} + \frac{\delta_i^2 K}{2r} Z_i \right) = p \left(-\frac{\alpha \beta_i}{2\gamma} - \frac{\alpha \beta_i}{2} Z_i \right). \tag{10}$$

In Eqs. (9), (10), the first term is negative and the second is positive. The equations show that the private property equilibrium reduction in harvest and revenue is decreasing in r , and increasing in δ_i if $r > \delta_i Z_i$, which holds in an equilibrium with a positive roe deer stock. The private property comparative static effect of predators on the revenues can then be evaluated when p is known.

4.3 Alternative specification of the regression function

Within our study area and during the studied time period the wolf’s main prey, moose, is more abundant in central Sweden compared to the south. This could potentially imply that the impact of a wolf on roe deer harvests differs, e.g., because of wolves’ preferences for different prey. In a study on wolves’ preferences for different prey in central Sweden, where moose and wolf are both relatively more abundant than in the south, Zimmermann et al. (2015) conclude that the kill rate of roe deer by wolf is related to roe deer density but independent of moose abundance. However, Zimmermann et al. (2015) does not include south Sweden where moose are relatively less abundant while at the same time the roe deer are more common. We, therefore, consider the possibility that the impact of a wolf on roe deer harvests could differ depending on moose abundance. This is done through an alternative version of Eq. (2), where the impact of a wolf on roe deer population growth depends on moose abundance, Y :

$$G(X, Z) = rX \left(1 - \frac{X}{K} \right) - \delta(Y)ZX, \tag{2'}$$

with $\delta'_i(Y) = 0 \forall i = L, F, S$, and $\delta'_i(Y) \leq 0 \forall i = W$. This would motivate a new regression, displayed in Eq. (4'), including a dummy variable for the counties with

Table 1 Descriptive statistics, per county and year

Variable	Mean	SD	Median	Min	Max
Wolf individuals (#)	7.7	14.7	0	0	72
Lynx families (#)	8.9	10.1	1.88	0	38
Days of snow cover > 30 cm	16.2	25.7	1.17	0	116.5
Hunting licences (#)	12,995.5	7423.5	10,764.5	4788	37,401
Bagged roe deer (#)	7506.2	5594.7	6189.5	1386	29,610
Bagged moose (#)	2952.1	2338.6	2109.5	189	9711
Bagged wild boar (#)	2200.9	2792.7	1233.5	0	14,645
Bagged red fox (#)	3419.9	2178.8	2828.5	715	12,439

Source Swedish Hunter's Association, Swedish Meteorological and Hydrological Institute (SMHI), Swedish Environmental Protection Agency

a high moose density compared to the roe deer density. The new regression is then specified as follows:

$$h = \alpha E + \theta_1 D Z_W E + \theta_2 (1 - D) Z_W E + \beta_j Z_j E + \gamma E^2, \quad (4')$$

where Z_W denotes the number of wolf, the dummy D indicates moose density, with $D = 1$ for the counties with a high moose density, $D = 0$ for the other counties, and the index j , with $j = L, F, S$, denotes lynx, red fox and snow cover. Thus for a given hunting effort, the coefficient θ_1 expresses the impact of the wolf on roe deer harvest in the counties with a high moose density, while θ_2 represents the corresponding impact in the other counties. The corresponding comparative static effect is calculated similarly as for Eq. (4), except that Eq. (4') permits us to identify the different impacts of the wolf in the moose-dense counties and the other counties.

5 The data

The primary data used in the analysis include the population estimates of the predators, the hunting bag statistics, the snow cover data and the number of hunting licences. Our panel dataset includes 15 counties for the period of 2002/2003–2011/2012 hunting seasons (for descriptive statistics see Table 1). In the regression analysis all of the data, except for the number of days with thick snow cover, are divided by the area of the county in square kilometres¹⁰ to account for county size, thereby obtaining the density of the variables (for the descriptive statistics per square kilometre, see Table S1 and S2 in the supporting material).

¹⁰ Excluding water, urban areas and national parks.

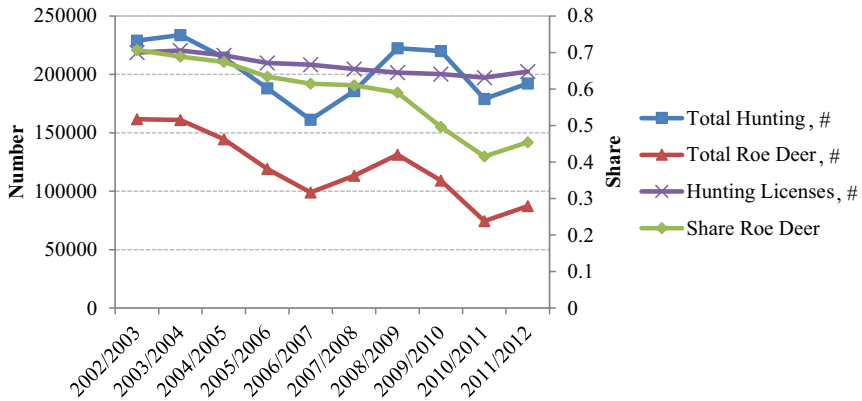


Fig. 4 Number of bagged animals and number of hunting licences (left y axis), and share of roe deer in total hunting bag (right y axis). Sources: the Swedish Hunter’s Association (www.viltdata.se) and the Swedish Environmental Protection Agency

5.1 Hunting bag and hunting effort

The dependent variable in the model is the number of harvested roe deer per square kilometre. The hunting bag statistics are based on the voluntary reports from the hunter groups and are managed by the Swedish Hunter’s Association. Figure 4 shows the development over time in total and in roe deer hunting and the resulting share of the roe deer in the total hunting bag, where the total hunting bag includes roe deer, moose, wild boar, fallow deer and red deer (*Cervus elaphus*). Over the studied time period, the number of bagged wild boars has increased in response to a rapid increase in the population, while the share of moose in the total hunting bag has been relatively constant. The roe deer share in the total hunting bag has decreased over the studied period, see Fig. 4. (The decline in different counties can be found in Figure S1 in the Supporting Material). The red fox was not included in the total number of bagged game, since it is not a primary game, but mainly hunted due to its negative impact on the roe deer populations.

Effort is a central variable in bioeconomic models, but the effort can be difficult to measure (McCluskey and Lewison 2008). Some studies, such as Fryxell (1991), use the number of hunting days per hunter for different types of game. For Sweden, however, there are no data on the number of hunting days per year. In addition, most hunters hunt several different species over the year. Instead, we followed an approach originally developed for fisheries (Beverton and Holt 1957; Foley et al. 2010). For fisheries, the approach involves converting all vessel types into a “standard vessel”. The effort devoted to one particular species in a multispecies fishery is then calculated based on the number of vessels, the number of fishing days and the target species’ share in the total catch. In our case, the number of hunting licences, see Fig. 4, can be seen as an equivalent to the number of vessels. We calculated the effort per square kilometre, devoted to roe deer hunting, as the number of licences, multiplied by the roe deer share in the total hunting bag:

$$E = \frac{\left(\frac{\text{bagged amount of roe deer}}{\text{total number of bagged game}} \right) \times \text{number of hunting licenses}}{\text{area of county in km}^2} \quad (11)$$

The effort measure in Eq. (11) is a relatively good proxy of actual effort if the number of hunting days per hunter is constant over time and across counties, if hunters hunt within the county where they live, and if different species are hunted on separate occasions¹¹. There is no evidence that suggests that the number of hunting days per hunter has changed over the studied time period. Hunters can be expected to mostly hunt within their county, except if the county area is small while simultaneously hosting a very large population, such as is the case for Stockholm county. Moreover, the three major game species are to a considerable extent hunted separately. The moose are typically hunted during the day over a relatively concentrated period in the autumn, and the hunts are organised jointly by several hunter groups that hunt simultaneously. Roe deer hunting is carried out by single or a few hunters, usually around sunset, and the hunting is spread over the entire autumn and winter seasons. Wild boar hunting is typically carried out by single hunters and requires hunting during the dark hours when the species is active. Hence, our proxy should be adequate for the purpose of the study.

5.2 Moose-dense counties

The counties are classified into those that have a higher moose density compared to the roe deer density and those that have not. This is done by first dividing the number of bagged moose in a county by the number of bagged roe deer. This exercise shows that for the counties of Dalarna, Gävleborg, Värmland, and Örebro, the ratio of moose to roe deer ranges between 1 and 2.6; while for the other counties, it ranges between 0.04 and 0.5. This difference is taken as an indicator of the moose density being higher in relation to the roe deer density in the four counties mentioned. Accordingly, the dummy D in Eq. (4) is set to one for these counties and zero otherwise.

5.3 Predator population and weather data

The data for lynx and wolf were based on census materials, while the data for red fox were based on hunting bag statistics. Weather data was obtained from the Swedish Meteorological and Hydrological Institute (SMHI).

¹¹ For example: if species are hunted on separate occasions, e.g. species A and B are each hunted for 5 days per year, then a reallocation of days from species A to species B would increase the share of species B in the hunting bag, *ceteris paribus*.

5.3.1 The lynx population

The lynx dataset was obtained from Andrén et al. (2010), except for the observations for 2010 and 2011, which were obtained from Danell and Svensson (2011) and Zetterberg (2014), respectively. The number of lynx families were estimated using the accumulated records of tracks and observations during the snow tracking period, compiled at the end of the season. The censuses were adjusted for the number of nights of tracking, and the extrapolations to obtain full spatial coverage were made accounting for landscape heterogeneity (Liberg and Andrén 2006; Andrén et al. 2010). Here, the census estimates for the nine different biogeographical regions in South and Central Sweden were transferred to the counties in proportion to the area of different biogeographical regions within the county, thereby following the approach of Andrén et al. (2010). Lynx were present in all counties during the study period but were missing for single years in some of the counties. About 6% of our observations on the lynx population are zeros.

5.3.2 The wolf population

The wolf censuses were conducted by the Wildlife Damage Center at the Grimsö Research Station, together with the respective counterparts in Norway and Finland, and were published annually. The estimates were based on snow tracking, radio telemetry, and DNA analysis. In the census reports, the wolf presence was recorded as family groups (packs), scent-marking pairs, other resident wolves and other wolves and the number of wolves belonging to each classification. The wolf population was partly shared with Norway, and the home range of the wolves and the wolf packs could cover more than one county. To correct for this, the number of wolves in the border areas were equally divided over the relevant countries or counties. In five counties, there were no wolves during the study period, and in some counties wolf occurred only occasionally. For 56% of the observations, the wolf population number, therefore, equalled zero.

The wolf census reports minimum and maximum values, where the minimum values are based on the estimates and the reports from experienced trackers, while the maximum values include the reports from the public and are more uncertain. Here, we used the minimum values to reduce the uncertainty and because in some instances, no maximum numbers were reported. One can note that using the minimum values, a higher estimated effect per wolf can be expected than when using the maximum values. The average rate of the minimum number to the maximum number over the study period was 1:1.18 (Wildlife Damage Center 2016).

We used two alternative measures of the wolf population number: the total number of wolf individuals and the number of wolf territories in a county. The latter was calculated as the sum of the numbers of the family groups and the territory-marking couples. The use of the territories was motivated by the observation by Zimmermann et al. (2015) that the number of moose killed was determined by the number of territories, rather than the number of individuals because the territories with a few individuals leave more meat on a carcass. This could potentially apply also for roe deer predation; however, the effect is likely to be smaller given the smaller size

of the prey and, hence, the larger probability that more of a carcass is consumed immediately. The average rate of the minimum number of individual wolves to the number of territories over the study period was 1:4.71 (Wildlife Damage Center 2016).

5.3.3 The red fox population

There are no population data on the red fox. Noting that the hunting bag statistics are frequently used as an indicator of the size of wildlife populations in the ecological literature (Forchhammer and Asferg 2000; Liberg and Andrén 2006; Elmhagen et al. 2011), we used the red fox hunting bag statistics as a proxy for its population. Admittedly, this is not ideal as the fox is mainly hunted for its negative impact on game, in particular roe deer. In addition, the coverage of the fox hunting in the hunting bag statistics is more uncertain than for ungulates.

5.3.4 Snow data

As a measure of winter severity, we use the number of days with a snow cover deeper than 30 cm. Snow data have been collected from the SMHI measuring stations. For all of the counties (except for Halland and Västmanland, which have only one station), at least two stations were used to calculate the average value of the number of days with a snow cover greater than 30 cm per year and county. The choice of stations was determined by the availability of the data while aiming at a good spatial coverage. For stations where the snow depth data are missing, data were interpolated, assuming that the snow depth changes linearly over days.¹² The average number of days with a snow cover greater than 30 cm varies considerably between years. Data for years and counties are found in Figure S2 and Table S3 in the Supporting Material.

5.3.5 The unit value of bagged roe deer

The unit value of a bagged roe deer consists of both the recreational value and the meat value; there are a few estimates in the literature. Based on interviews with experienced hunters, Karlsson (2010) reported that the value of one harvested roe deer is 239 EUR.¹³ Elofsson et al. (2017) and Lundhede et al. (2015) reported values around 525 and 440 EUR, respectively. However, the two latter studies seem less representative for our case, as the first study reports values that are based on organized hunts at a large estate, a submarket where prices are comparatively high; the latter study investigates conditions in Denmark, where hunting opportunities are scarcer, hence prices are higher.

¹² Snow depth should, in principle, be measured every day, so the distance of the interpolated data is small.

¹³ In 2014 year value, using the average exchange rate from the Swedish Riksbank, 1 EUR=9,0968 SEK (Swedish crowns).

Table 2 Overview of regression models

	Model 1	Model 2	Model 3	Model 4
Wolf population proxy	Number of individuals	Number of individuals	Number of territories	Number of territories
Spatial differentiation of wolf impact	None	Different impact in moose-dense and other counties	None	Different impact in moose-dense and other counties

6 Econometric approach

Equations (4) and (4') are estimated using a regression analysis in a panel data setting. Fixed effects are not included because they would imply that harvests could be different from zero when the hunting effort is zero, which is inconsistent.

In total, we estimate four models, using either the number of wolves or the number of wolf territories, and using either Eq. (4) or (4'), see Table 2. In models 1 and 2 the wolf population is measured as the total number of wolf individuals in a county, and in models 3 and 4 it is measured as the number of wolf territories in a county. Models 1 and 3 are based on Eq. (4) and, hence, do not distinguish between moose-dense and other counties, while models 2 and 4 are based on Eq. (4') and make such a distinction.

The statistical properties were examined in the following manner. We used the Breusch-Pagan/Cook-Weisberg test for homoscedasticity to check the null hypothesis that the error variances are all equal versus the alternative that the error variances are a multiplicative function of one or more variables. A large Chi-square then indicates that there is heteroscedasticity present and that the null-hypothesis should be rejected. Following Hoechle (2007) and Hoyos and Sarafidis (2006), we tested for cross-sectional dependence among the residuals using the Pesaran's cross-sectional dependence test, and the null-hypothesis of no dependence was rejected at a 10% significance level. Autocorrelation was rejected according to the Wooldridge test for autocorrelation in the panel data (Appendix Table 8). Further, the variable for the bagged number of red foxes was dropped due to multicollinearity according to a high variance inflation factor (VIF).

Given that heteroscedasticity and cross-sectional dependence are present in the dataset the regressions were done using Driscoll-Kraay robust standard errors for panel regression with cross-sectional dependence (Driscoll and Kraay 1998; Hoechle 2007), which will give consistent estimates when cross-sectional dependence and heteroscedasticity are present. The results are based on a pooled-regression analysis, estimated in levels, where the intercept has been suppressed according to the theoretically specified regression equation. Pooled regression provides the possibility to analyse the panel dataset while remedying the problems concerning the statistical properties. Note that due to running the regression without an intercept, the coefficient of determination, R^2 , cannot be interpreted as usual.

Table 3 Pooled regression results with Driscoll-Kraay standard errors

Variable	Model 1	Model 2	Model 3	Model 4
Effort (E)	1.7757***	1.7601**	1.7697***	1.7636***
Effort Squared (E^2)	- 0.5327***	- 0.5169**	- 0.5269***	- 0.5210***
$E \times \text{Wolf}$	- 339.448***	-	-	-
$E \times \text{Wolf}_{\text{territory}}$	-	-	- 959.5499***	-
$E \times \text{Lynx}$	- 76.4479**	- 70.7912*	- 61.6062**	- 60.2480*
$E \times \text{Snow Cover}$	- 0.0022	- 0.0021	- 0.0024*	- 0.0024*
$D \times E \times \text{Wolf}$	-	- 301.5968***	-	-
$(1 - D) \times E \times \text{Wolf}$	-	- 407.3479***	-	-
$D \times E \times \text{Wolf}_{\text{territory}}$	-	-	-	- 918.9866***
$(1 - D) \times E \times \text{Wolf}_{\text{territory}}$	-	-	-	- 1002.22***
Prob > F	0.000	0.000	0.000	0.000
Number of observations	150	-	-	-

Dependent variable harvest of roe deer per km²

*significant at $p < 0.1$, **significant at $p < 0.0$ and ***significant at $p < 0.001$

Additionally, we studied the effect of individual observations on the outcome with leverage versus residual (LVR) plots and Cook's distance. The LVR plot indicated that Stockholm has high leverage and large squared residuals, which is an undesirable combination. The county Södermanland had a large residual in one year but below average leverage, indicating that the effect of the residual is low and can be left in the dataset. However, the county Stockholm was removed from the dataset following the LVR plot. It can be expected that Stockholm has an inflated number of hunters, while a large share of those hunt outside the county's borders. Hence, the hunting effort variable is not a good measure of the effort in Stockholm. The estimated parameters all have the expected signs and are significant at least at a 10% level, except for the snow cover in models 1 and 2 (Table 3).

7 Results

In the following, we present the results on the marginal product of carnivores and effort, output elasticities, and comparative statics. Finally, we calculate and compare the county level impacts for the open-access case.

7.1 Marginal products of carnivores and effort

Using the estimated coefficients in Table 3 and Eqs. (5)–(8), we computed the marginal products, as well as the elasticities of the hunting effort and the two predators, evaluated at the mean (Table 4). The marginal product of effort, MP_E , shows the change in harvest for a unit increase in effort. For the lynxes and the wolves, we have MP_L and MP_W , which are the change in harvest number for a

Table 4 Average marginal products and elasticity

Model	MP_E	MP_L	MP_W	ε_{hE}	ε_{hL}	ε_{hW}
Model 1	0.7394	– 55	– 243	0.729	– 0.0733	– 0.239
Model 2	0.7425 ^a 0.8142 ^b	– 50	– 355 ^a – 86 ^b	0.5859 ^a 1.2238 ^b	– 0.0679	– 0.0643 ^a – 0.6644 ^b
Model 3 ^c	0.8540	– 44	– 687	0.887	– 0.0590	– 0.093
Model 4 ^c	0.7513 ^a 1.1516 ^b	– 53	– 874 ^a – 264 ^b	0.5456 ^a 1.6987 ^b	– 0.0579	– 0.0536 ^a – 0.2007 ^b

Models 1 and 2 make use of the number of individual wolves, and model 3 and 4 use the number of wolf territories. Models 1 and 3 make no distinction between moose-dense and other counties, while models 2 and 4 distinguish between moose-dense and other counties. To obtain comparable results for the wolf numbers and wolf territories, MP_W in models 3 and 4 was divided by 4.71, which was the ratio of the average number of wolves per territory to the number of individual wolves

^aOther counties

^bMoose-dense counties

^cWolf territory data are used instead of wolf numbers

unit increase in the lynx population, the wolf population, or the wolf territories, evaluated at the mean effort.

Results show that a unit increase in the number of lynx families in an average county would decrease the roe deer harvest by 44–55 units. To obtain comparable results for the wolf numbers and wolf territories, we divided MP_W in models 3 and 4 by 4.71, i.e., ratio of the average number of wolves per territory to the minimum number of individual wolves. Accordingly, the marginal product of one additional wolf is 56–86 in moose-dense counties and 185–355 in other counties, with the lower numbers obtained from the regressions with territories. When not controlling for moose density, the use of the wolf numbers and territories yielded a reduction in the roe deer harvest by 146 and 243 in models with the territory and total numbers, respectively.

The marginal productivity of effort, MP_E , varied from 0.74 to 1.15, depending on the model specifications. The productivity was higher in the counties that are classified as moose-dense, which was explained by the comparatively lower effort levels in these counties.

The output elasticity of effort computed as $\varepsilon_E = MP_e \left(\frac{\bar{E}}{h} \right)$, ranged from 0.7 to 0.9 in the nationally aggregated models. Models 2 and 4 showed a comparatively lower elasticity in the counties with a lower moose density and an elasticity greater than one in the moose-dense counties, which was explained by the considerable difference in the effort levels between the county groups. The positive output elasticity for effort indicates that the reduction in the roe deer hunting effort over the studied time period has counteracted the decline in the roe deer harvests.

The output elasticities of lynxes and wolves computed as $\varepsilon_L = MP_L \left(\frac{\bar{L}}{h} \right)$ and $\varepsilon_W = MP_W \left(\frac{\bar{W}}{h} \right)$, respectively, show how a one percent increase in the number of predators affects the roe deer harvests in terms of percentage. The output elasticity of the lynx ranges from -0.058 to -0.073 . The output elasticity of the wolf is larger in the moose-dense counties.

7.2 Open access and private property equilibrium adjustments

The bioeconomic open access equilibrium results were calculated using Eqs. (7), (8), satisfying both the biological and the open-access steady-state conditions. We utilised the open access zero profit condition, $cE = ph$, to solve for the unit cost of effort. We used the unit value of bagged roe deer in Karlsson (2010), which is more representative for Swedish hunting in general and gives a conservative value for the costs of predation. Using the zero profit condition, the cost c , which is compatible with the open access equilibrium assumption, was then computed for each county and year.¹⁴ The private property equilibrium results were calculated using Eqs. (9), (10).

Results showed that an increase in the predator levels decreased the steady-state harvest level of roe deer, thus reducing the revenues from hunting activities (Table 5). If the system was managed under open access, an additional lynx family reduced the harvest of roe deer by 126–157 units on average. The national aggregate models 1 and 3 suggest that increasing the number of wolves by one individual reduced the open access equilibrium roe deer harvest by 423–697 units on average, with the lower figure pertaining to the estimation with territories. One can note that for models 3 and 4, the wolf figures in Table 5 had to be divided by 4.71 to obtain the effect per individual. When distinguishing between the moose-dense counties and the other counties (model 2 and 4), an increase in the number of wolves in the moose-dense counties had a smaller impact on the roe deer harvests (264–411 units) compared to that in the other counties (504–943 units), where the lower figures were obtained from regressions using territories as a measure of the wolf population. Results from the different models suggest that under open access, the average marginal cost of an additional lynx family was between 30 and 37 thousand EUR, while the average marginal cost for an additional wolf was between 101 and 166 thousand EUR when estimated on national data. When separating between moose dense and other counties, the average marginal cost for moose dense counties was 63–98 thousand EUR per wolf, while the average marginal cost for other counties was 120–232 thousand EUR.

When national data were used (models 1 and 3) to calculate comparative statics for the private property equilibrium, the impact of lynx and wolf on roe deer harvest

¹⁴ Hence, for the open access regime, we assume that data for each year and county reflect equilibrium conditions.

Table 5 Average reduction in the harvested number of roe deer, and an average reduction in roe deer hunting revenues, respectively, for a marginal increase in predator populations under open access and private property management

	Open access						Private property					
	Wolf individual/ territory		Lynx family		Wolf individual/ territory		Lynx family		Wolf individual/ territory		Lynx family	
	Harvest impact (# of roe deer)	Revenue impact (EUR)	Harvest impact (# of roe deer)	Revenue impact (EUR)	Harvest impact (# of roe deer)	Revenue impact (EUR)	Harvest impact (# of roe deer)	Revenue impact (EUR)	Harvest impact (# of roe deer)	Revenue impact (EUR)	Harvest impact (# of roe deer)	Revenue impact (EUR)
Model 1	-697	-166,151	-157	-37,419	-566	-135,274	-127	-30,439	-693 ^a	-165,661 ^a	-120	-28,797
Model 2	-973 ^a	-232,040 ^a	-150	-35,794	-513 ^b	-122,607 ^b	-103	-24,617	-1611	-385,029	-102	-24,357
Model 3 ^c	-1991	-474,874	-128	-30,488	-1696 ^a	-405,344 ^a	-102	-24,357	-1554 ^b	-317,406 ^b		
Model 4 ^c	-2374 ^a	-566,319 ^a	-126	-30,218								
	-1244 ^b	-296,524 ^b										

^aOther counties

^bMoose dense counties

^cWolf territory data are used instead of wolf numbers

Table 6 Average change in harvest and revenues in different counties under an open access assumption, over the 2002/2003 to 2011/2012 hunting seasons, based on model 2, which makes use of the number of wolf individuals, and distinguishes between moose-dense and other counties

County	Lynx family, harvest change	Wolf individual, harvest change	Lynx family, revenue impact (EUR)	Wolf individual, revenue impact (EUR)
Blekinge	– 126	– 723	– 29,968	– 172,442
Dalarna	– 90	– 382	– 21,387	– 91,116
Gävleborg	– 78	– 331	– 18,532	– 78,952
Halland	– 148	– 852	– 35,318	– 203,225
Jönköping	– 159	– 914	– 37,876	– 217,947
Kalmar	– 241	– 1,389	– 57,546	– 331,131
Kronoberg	– 206	– 1,184	– 49,083	– 282,436
Skåne	– 155	– 890	– 36,891	– 212,279
Södermanland	– 245	– 1,410	– 58,412	– 336,118
Uppsala	– 160	– 923	– 38,234	– 220,004
Värmland	– 103	– 438	– 24,525	– 104,485
Västmanland	– 04	– 599	– 24,819	– 142,812
V. Götaland	– 112	– 645	– 26,749	– 153,920
Örebro	– 116	– 494	– 27,663	– 117,855
Östergötland	– 204	– 1175	– 48,683	– 280,131
<i>Average, moose counties</i>	–	– 411	–	– 98,102
<i>Average, other counties</i>	–	– 973	–	– 232,040
<i>Average, total</i>	– 150	– 823	– 35,794	– 196,324

and revenues was about 20 percent lower than under open access. Also, comparing results from models 2 and 4 between the open access and private property equilibrium, results show that under open access the harvest impact in counties with lower moose density was 1.9–2.4 times larger than in that in counties with higher moose density, while under a private property regime the difference in harvest impact is smaller: the impact in the less moose dense counties is 1.3–1.4 times larger than that in counties with higher moose density.¹⁵

7.3 Open access county-level impacts

In the following we calculate the county-level effects under open access, using estimates from model 2, which makes use of the wolf numbers and distinguishes between moose-dense and other counties.¹⁶ The harvest effects are calculated using variable levels for each year and county, and averaging over years (Table 6).

¹⁵ In both cases, the lower figure is based on model 4 which uses wolf territories.

¹⁶ For the private property regime, there is very minor variation in harvest across counties (less than one roe deer per year and carnivore) other than obtained from the separation into moose dense and other counties. This is due to the second term in Eqs. (9), (10) being very small.

Results show that the impact of the predators on the harvest is closely related to the marginal product of effort, which varies across the counties (Appendix Table 9). For example, Västra Götaland and Blekinge, where the level of effort per square kilometre is similar, have quite different MP_E . The lower MP_E in Västra Götaland is explained by the considerable number of lynxes and wolves and is augmented by the larger number of days with a thick snow cover, compared to Blekinge. Kalmar and Örebro both have low effort levels, which should imply a high MP_E , *ceteris paribus*. However, the MP_E in Örebro is far smaller than that in Kalmar due to the high numbers of lynxes and wolves.

The largest marginal impacts on the harvest are found in Södermanland and Kalmar. These two counties have the highest harvest per effort levels, implying a stronger negative effect of increased predator pressure on the roe deer harvests. The opposite is true for Gävleborg, which has the lowest harvest per effort and, hence, the smallest impact on harvest by both lynxes and wolves. Moreover, Gävleborg is a moose-dense county, which implies a comparatively smaller effect of wolf predation on the roe deer harvests. The marginal cost in terms of hunting values foregone varies between the counties and ranges between 18,000 and 58,000 EUR for the lynxes and 79,000 and 336,000 EUR for the wolves.

8 Discussion

We calculated the harvest impact of carnivores for a given effort level and so obtained the reduction in harvest necessary to reach a new biological equilibrium. This measure is different from estimations of kill rates because the latter do not consider either hunting effort adjustments or equilibrium conditions. In spite of these strong conceptual and methodological differences, it could be noted that Andrén and Liberg (2015) estimated that a lynx family kills 64–85 roe deer per year. Our results suggested a 44–55 unit reduction in the roe deer harvest due to an additional lynx family given a mean effort. Although our finding was slightly below that in Andrén and Liberg (2015), the calculated open access effect in several of the counties falls within their estimated interval. There were no corresponding data on the annual kill rate of the roe deer by the wolf. Instead, most wolf studies focus on moose and were made in areas with high moose density. Sand et al. (2008) estimated that in the summer, the per capita wolf kill rate on moose corresponded to approximately 6.6 kg of prey biomass per day in areas with a higher moose density. Assuming a constant kill rate over the year, a wolf would then kill ~ 2400 kg biomass annually.¹⁷ The adult and juvenile roe deer weigh about 25 and 10 kg, respectively, and approximately 75% of the total weight is edible biomass (Sand et al. 2008). The same total biomass would then be obtained by killing 128–321 roe deer per year.¹⁸ Bearing in mind the conceptual differences between kill rates and our estimated harvest impacts, one can

¹⁷ This is a low-end estimate since winter kill rates in terms of biomass are typically higher (Sand et al. 2008).

¹⁸ The lower number applies a 0% share of the juveniles in the wolf diet, and the upper a 100% share.

note that these numbers are in the same order of magnitude as our estimated average marginal impact on harvest in counties with low moose density, 186–355 roe deer. This indicates that wolf might substitute roe deer for moose in areas with lower moose density, but further ecological research is necessary to understand the mechanisms at work.

Our marginal cost estimates can be compared to the results in the economic studies where other types of carnivore-related costs and benefits are investigated. We found that in a bioeconomic equilibrium, the nationwide average marginal cost of an additional lynx family is 24–37 thousand EUR per year, and the cost of an additional wolf is 82–166 thousand EUR per year. The cost for lynx could be compared to the reported implicit cost of an additional lynx family in terms of the impact of hunting lease prices in Mensah et al. (2019) and Lozano et al. (2020), which reported 162 and 141 thousand EUR per year, respectively, while Lozano et al. (2020) also provides an estimate of the corresponding cost of the wolf, 160 thousand EUR per year. The overall lower cost in the present study is likely to be explained by the fact that it only accounts for impacts on roe deer, but differences in the spatial scale of studies could also matter. Our results could further be compared to the total value of hunting in Sweden, which is estimated to be over 370 million EUR (Mattsson et al. 2008). Hence, small increases in the wolf and lynx populations have a minor impact on the hunting value on a national level, even though the local effect could be considerable. Further, Widman and Elofsson (2018) estimated that the marginal cost of wolves and lynxes in different counties, in terms of depredation on sheep, varies between 52 and 1067 EUR per year for wolves and 1–82 EUR per year for lynx, suggesting that the economic impact on the roe deer hunters substantially exceeds that on the sheep farmers.

Our study has limitations which should be considered when interpreting the results including, e.g., only considering equilibrium outcomes and not the approach path, and abstracting from spatial effects. Also, we do not account for changes in the use of hunting dogs in response to an increased carnivore abundance, or the potential of supplementary feeding to reduce winter mortality. In addition, our model did not account for age- and sex-specific ecological and economic effects, which could matter to both predation and hunters' preferences for the game (Jonzén et al. 2013; Chapron 2015; Elofsson et al. 2017; Elbroch et al. 2018). Moreover, it is argued by Cromsigt et al. (2013), that hunting efforts could be motivated also by an aim to scare ungulates away from valuable crops. Here, we did not consider browsing damage as a motivation for roe deer hunting effort, but one can note that the damages on agricultural crops from roe deer are small, amounting to, e.g., a loss of about 1.7% of the harvest of winter wheat (SCB 2016). Damage to forests includes sweeping damage on main stems bark and browsing on young forest plantations, albeit the magnitude of these damages is uncertain (Swedish Forest Agency 2019). We do not account for species interactions other than the predator–prey relationship in focus. We only account for one alternative prey, the moose, whereas other alternative prey might also affect the carnivore's predation rate on roe deer: even if there are very few known occurrences in Sweden, wolf could potentially prey on wild boar, and both wolf and lynx can prey on red and fallow deer (Gervasi et al. 2014; Jędrzejewski et al. 1992; Meriggi and Lovari 1996). In addition, concurrence among

ungulate species can influence the abundance of roe deer, and hence harvests (Ferretti et al. 2011; Torres et al. 2012; Elofsson et al. 2017). In addition, brown bears have been found to scavenge on roe deer carcasses, and lynx and wolf could respond to this by increasing their predation rate (Krofel et al. 2012; Tallian et al. 2017). With respect to habitat conditions, we account for snow depth, which is an indicator of the role of climate, but additional habitat quality factors can matter for roe deer density and harvests. In addition, predator–prey dynamics can be affected by human modifications of landscapes, and the provision of supplementary feeding for wildlife (Skuban et al. 2016). Due to limitations of our dataset, we cannot control for these factors, but further research applying bioeconomic modelling could potentially include these aspects.

8.1 Management implications

Similar to many other countries, the Swedish management of large predators includes policies for their spatial distribution. It is, therefore, of interest to identify how the costs of additional carnivores vary across space. With such knowledge, the policy-maker could aim for a spatial distribution which minimizes the costs of maintaining a given population of a large carnivore. The identification of such spatial variation in costs was, therefore, one of the aims of this study. Our analysis showed that conclusions on the spatial variation in costs differed depending on whether it was assumed that the roe deer was managed under an open access or private property regime during the study period. In both cases, we found a spatial cost differential for wolf between moose-dense and less moose dense countries, with higher costs in the latter category. Thus, we conclude wolves give rise to higher costs in the southern parts of the country, contrasting with current aims to for expansion of the wolf population further south (EPA 2014b), which is supported by results in Boman et al. (2003) and Widman and Elofsson (2018). The same result could indicate that the availability of alternative prey is important for the cost of additional carnivores. If a carnivore species is flexible in its choice of prey, the cost of increasing the numbers of that carnivore species will vary spatially with the availability of differently valuable prey species. For open access our results suggested additional spatial variation in costs: a county-specific analysis then showed that the costs of increased carnivore populations is higher in counties with a high harvest per unit of effort. Thus, if policymakers consider open access to be a more plausible approximation of the prevailing conditions, they could prefer to allocate carnivore increases to areas with a relatively lower harvest per effort. However, allocating large carnivores to moose dense areas and areas with a low harvest per effort can have unwanted distributional effects, as the predator numbers are already the largest in these counties, implying that the hunters and farmers in these counties already carry a large share of the costs for preservation.

Finally, compensation for carnivore predation is widely applied in the case of domestic animals (Widman and Elofsson 2018). Such compensation is argued to reduce conflicts on carnivore conservation. However, hunters and landowners are not entitled to any similar compensation. The cost estimates in this study could inform policymakers

about the magnitude of compensation that would be necessary to make hunters and landowners indifferent to having additional large carnivores on their land. The compensation could then be based on the number of additional carnivores. This would be partly similar to the performance payments to the reindeer communities where compensations are made based on carnivore abundance and rejuvenation (Zabel et al. 2014). A potential caveat is that compensation might affect hunter's and landowner's attitudes to carnivores, and given the lack of studies on the topic it is not possible to say beforehand whether the impact would be positive or negative. Finally, the observation that there has been a large decline in roe deer harvests, while there is no management plan, and no population counts available to evaluate the development, as well as highly limited possibilities to control harvests, is in itself a source of concern. There are, therefore, good reasons for policymakers to consider the need for policies that enhance the management of the roe deer resource.

Appendix

Bioeconomic model

Open access equilibrium

Following the standard approach in the bioeconomic literature, we assume that the hunting effort over the next period will adjust in response to the real net gains to hunters made in the current period (Clark 1990; Conrad 1995). Hence, if the hunting effort is relatively low in one time period, harvests are small, and the game will be relatively more abundant in the following time period, implying that the effort will be increased in the following time period, and vice versa. Let p represent the constant unit value of the harvested roe deer, which includes both meat and recreational value of deer hunting. Let c represent the unit cost of the hunting effort and $\theta > 0$ represent the adjustment coefficient. The hunting effort adjustment equation is then defined by:

$$E_{t+1} - E_t = \theta [ph(X_t, E_t) - cE_t]. \quad (\text{A1})$$

In equilibrium, all of the variables are constant over time, implying that $X_{t+1} = X_t = X$ and $E_{t+1} = E_t = E$. Using Eqs. (3), (A1) to calculate (A2), and Eqs. (1), (2), (3) to calculate Eq. (A3), the steady-state level of the roe deer and the effort will then be:

$$X = \frac{c}{pq}, \text{ for } E_{t+1} = E_t = E \quad (\text{A2})$$

$$E = \frac{r}{q} \left(1 - \frac{X}{K} \right) - \frac{1}{q} \delta Z \text{ for } X_{t+1} = X_t = X \quad (\text{A3})$$

Eq. (A2) indicates a zero profit in the long run, while Eq. (A3) shows the combination of the effort and predator predation that will lead to a constant level of the roe deer population.

Table 7 Identity of estimated coefficients in terms of the parameters in the bioeconomic model

Coefficient	Identity
α	qK
β_i	$-\frac{qK\delta_i}{r}$
γ	$-\frac{q^2K}{r}$

Solving Eq. (3) for X_t , substituting it into Eq. (A3) and solving for h_t yield an equation for the harvest that can be estimated:

$$h = qKE - \frac{qK\delta}{r}EZ - \frac{q^2}{r}KE^2, \quad (\text{A4})$$

which can be expressed as:

$$h = \alpha E + \beta ZE + \gamma E^2, \quad (\text{A5})$$

where α , β and γ are the coefficients to be estimated (see Appendix Table 7, for the identity of the coefficients). Eqs. (A4), (A5) describe the relationship between harvest, effort, predators, and climate in the biological equilibrium. The marginal products of E and Z_i , derived using Eq. (A5), are shown in Eqs. (A6), (A7):

$$MP_E = \frac{\partial h}{\partial E} = \alpha + \beta Z + 2\gamma E, \quad (\text{A6})$$

and

$$MP_{Z_i} = \frac{\partial h}{\partial Z_i} = \beta_i E. \quad (\text{A7})$$

An increase in the predator levels will induce a comparative static effect on the optimal level of harvesting. Using Eq. (A3) we have:

$$\frac{\partial E}{\partial Z_i} = -\frac{\delta_i}{q} < 0. \quad (\text{A8})$$

Using Eqs. (3), (A3) and the steady-state condition (A2), the comparative static loss in the harvest is:

$$\frac{\partial h}{\partial Z_i} = -\frac{c\delta_i}{pq} \tag{A9}$$

Calculating the marginal change in the revenues as the price multiplied by the marginal changes in the harvests, the change in the gross revenue will be:

$$p \frac{\partial h}{\partial Z_i} = -\frac{c\delta_i}{q} < 0. \tag{A10}$$

Here, the left-hand side value of the impact on the revenues will be negative, since $\delta_i > 0 \forall i$. The comparative static effect of a change in Z_i on the equilibrium level of the hunting effort can be calculated using the estimated coefficients α , β and γ . Using Eq. (A9) and coefficient identities associated with Eq. (A5), see Table A1, gives the change in the open-access equilibrium harvest when Z_i changes:

$$\frac{\partial h}{\partial Z_i} = -\frac{c\delta_i}{pq} = -\frac{c\beta_i}{p\gamma} \tag{A11}$$

Multiplying through by p gives the change in the roe deer hunting revenues, due to a change in Z_i :

$$p \frac{\partial h}{\partial Z_i} = -\frac{c\beta_i}{\gamma} \tag{A12}$$

Using Eqs. (A11), (A12), the comparative static effect on the open-access harvests and the revenues can be evaluated when c and p are known.

Comparative statics under private property: Whereas the open access case uses the law of motion [Eq. (A1)], the private property case is characterized by net profit maximization. Under a static private property regime, where the discount rate is implicitly assumed to be zero, the sole manager chooses effort E to maximizes profit, $\pi = ph - cE$, at steady state. The first order condition requires that marginal revenue equal marginal cost, i.e., $ph'_E - c$. With the zero discounting assumption, the golden rule holds at a steady state, i.e., the owner obtains the maximum net profit at the steady state. The reduced form of the net profit is given by Eq. as a function of the effort. Using the first-order condition, we can then solve for the private property bioeconomic equilibrium effort E as a function of Z , which gives Eq. (A13).

$$E = \left[\frac{r}{2q} - \frac{\delta}{2q}Z - \frac{rc}{2pq^2K} \right]. \tag{A13}$$

Inserting Eq. (A13) into Eq. (A4) and rearranging we obtain:

$$h = qK \left[\frac{r}{2q} - \frac{\delta}{2q}Z - \frac{rc}{2pq^2K} \right] \left\{ \frac{1}{2} - \frac{\delta}{2r}Z + \frac{c}{2pqK} \right\}. \tag{A14}$$

Table 8 Woolridge test for autocorrelation

Variable	Coefficient Estimates			
	Model 1	Model 2	Model 3	Model 4
Effort	1.8345**	1.8895**	1.8119**	1.9030**
Effort Squared	-0.1507	-0.1790	-0.1424	-0.1844
Effort×Wolf	-59.8887	–	–	–
Effort×Lynx	70.4113	87.57	79.8200	81.0538
Effort×Snow	0.0004	0.0004	0.0003	0.0003
D×Effort×Wolf	–	-155.4918**	–	–
(1-D) ×Effort×Wolf	–	46.8806	–	–
D×Effort×Wolf _{TERR}	–	–	-322.1221*	-855.9077**
(1-D) ×Effort×Wolf _{TERR}	–	–	–	-165.4405
H ₀ : No first order correlation	Prob > F = 0.31	Prob > F = 0.31	Prob > F = 0.30	Prob > F = 0.30

Differentiation of Eq. (A14) provides the comparative static effect of Z_i on harvest which can be rewritten in terms of the estimated coefficients α , β and γ , see Table A1:

$$\frac{\partial h}{\partial Z_i} = -\frac{K\delta_i}{2} + \frac{\delta_i^2 K}{2r} Z_i = -\frac{\alpha\beta_i}{2\gamma} - \frac{\alpha\beta_i}{2} Z_i. \quad (\text{A15})$$

The value of the comparative static harvest impact under private property management is then obtained as:

$$p \frac{\partial h}{\partial Z_i} = p \left(-\frac{K\delta_i}{2} + \frac{\delta_i^2 K}{2r} Z_i \right) = p \left(-\frac{\alpha\beta_i}{2\gamma} - \frac{\alpha\beta_i}{2} Z_i \right). \quad (\text{A16})$$

For the empirical calculations, $\frac{\partial h}{\partial Z_i}$ is evaluated at the mean Z_i .

Appendix

See Tables 7, 8 and 9 and Fig. 5.

Table 9 Marginal products and elasticities, evaluated at the mean for model 2, which makes use of the number of wolf individuals and distinguishes between moose-dense and other counties.

County	MP–Effort	MP–Lynx	MP–Wolf	ε_{hE}	ε_{hL}	ε_{hW}
Blekinge	0.5420	–82	–473	0.5931	–0.008	0
Dalarna	0.8998	–13	–53	1.3724	–0.106	–0.1264
Gävleborg	1.1480	–15	–63	2.0196	–0.151	–0.1029
Halland	0.6049	–76	–439	0.5658	–0.008	0
Jönköping	0.7266	–68	–393	0.6167	–0.007	0
Kalmar	1.1932	–37	–213	0.6995	–0.004	0
Kronoberg	1.0309	–48	–277	0.7069	–0.005	0
Skåne	0.5458	–83	–477	0.4912	–0.001	0
Södermanland	1.0183	–45	–261	0.5579	–0.022	0
Uppsala	0.7585	–55	–317	0.6383	–0.115	0
Värmland	0.6607	–20	–87	0.8701	–0.151	–0.2577
Västmanland	0.3802	–55	–318	0.4837	–0.218	–0.3551
Västra Götaland	0.3184	–83	–476	0.3841	–0.049	–0.2340
Örebro	0.5485	–34	–144	0.6331	–0.162	–0.3158
Östergötland	1.0484	–46	–263	0.7082	–0.011	0
<i>Mean</i>	<i>0.7425^a</i>	<i>–51</i>	<i>–355^a</i>	<i>0.5859^a</i>	<i>–0.0679</i>	<i>–0.0536^a</i>
	<i>0.8143^b</i>		<i>–86^b</i>	<i>1.2238^b</i>		<i>–0.2007^b</i>

^a Moose–dense counties. ^b Other counties.

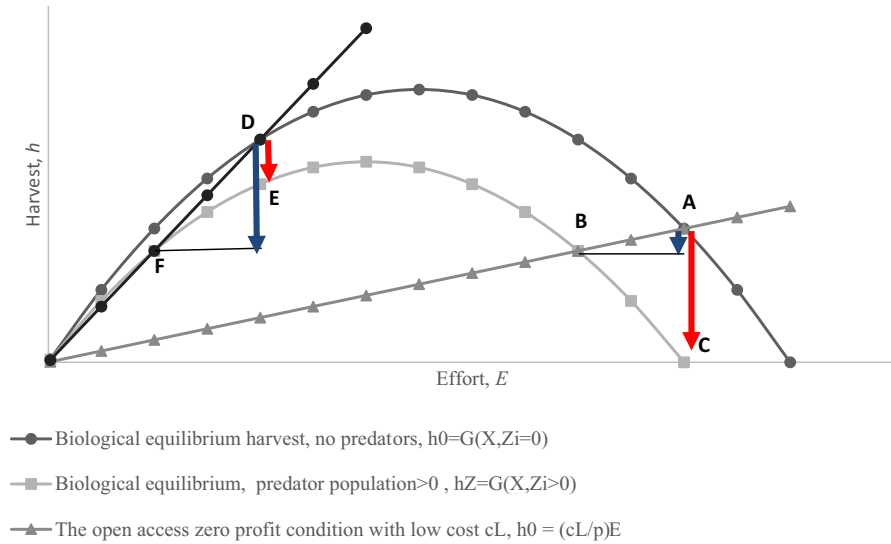


Fig. 5 The marginal product of carnivores, MPZ_i , and the open access bioeconomic steady state harvest effect, dh/dZ_i , depicted in harvest-effort space. The red arrows shows MPZ_i in the case of low harvesting cost (a – c) and high harvesting cost (d – e). The blue arrows shows the steady state harvest impact in the case of low harvesting cost (a – b) and high harvesting cost (d – f), respectively

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Compliance with ethical standards

Conflict of interest The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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