The Impact of Lynx and Wolf on Roe Deer Hunting Value in Sweden 2002-2012

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ABSTRACT

Large carnivores provide ecosystem and cultural benefits but also impose costs on livestock owners, due to predation, and on hunters, due to the competition for game. The benefits as well as the costs that accrue to livestock owners have been studied, but this is not the case for the costs that accrue to hunters. The aim of this paper was to identify the impact of lynx (*Lynx lynx*) and wolf (*Canis lupus*) on roe deer (*Capreolus capreolus*) hunting value. We applied a production function approach, using a bioeconomic model where the number of roe deer harvested was assumed to be jointly determined by hunting effort, abundance of predators, availability of other game, and climatic conditions. The impact of the predators on the roe deer harvests was estimated econometrically, and carnivore impacts for a constant and adjusted, steady state hunting effort were derived. The results showed that the marginal cost in terms of hunting values foregone varied between the counties and ranged between 18,000 and 58,000 EUR for lynx and 79,000 and 336,000 EUR for wolf. Larger costs were found in counties where the hunting effort was high, mainly located in south Sweden. The regional variation in costs has implications for decisions on policies affecting the regional distribution of wolf and lynx.

KEY WORDS costs, hunting, lynx, moose, predation, production function approach, roe deer, wolves.

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INTRODUCTION

Hunting is an important leisure activity, which generates significant economic activity and tends to increase land values (Pinet 1995; Lecocq 2004; Mattson et al. 2008; U.S. Fish & Wildlife Service 2012; Hussain et al. 2013). Large wild carnivores can have a considerable impact on game species populations (Graham et al. 2005), and the resulting competition for game creates conflicts between the hunters and the predators. Historically, this has led to a reduced predator abundance. 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). Nevertheless, the larger carnivore populations are likely to affect hunting values. This affects the benefits experienced by hunters as well as the revenues obtained by landowners that sell or lease out hunting rights (Livengood 1983; Lundhede et al. 2016; Rhyne et al., 2009). The Swedish Hunters' Association estimates that the reduction in hunting value due to carnivores is about 50 million EUR per year (Svensk Jakt 2009), and the Norwegian forest owner organization claims that the wolf 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 mid Sweden (Vargfakta 2011), and when a genetically important wolf was moved from the reindeer herding areas in northern Sweden, where wolves are not permitted, to a county in mid Sweden (Lövbom 2013). In the absence of policies to overcome such conflicts carnivores are often poached by hunters opposing carnivore conservation (Liberg et al. 2012, 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).

Few studies have estimated of the costs that accrue to the hunters as a consequence of increased carnivore abundance. Boman et al. (2003) calculated a constant cost per carnivore, obtained by multiplication of moose kill rate and hunting value. In general, this approach could be questioned: if the hunting effort is zero, the impact on harvest and hunting value would also be zero, independently of the kill rate. Skonhoft (2006) calculated the costs of wolf depredation on moose (*Alces alces*) using a programming model. He carried out simulations under alternative assumptions about the predation rate, with the purpose of comparing economic outcomes under different stylized harvesting regimes. A similar approach is applied in Nilsen et al. (2005). Thus, none of the above mentioned studies attempted to empirically estimate the effect of increased carnivore abundance on game harvest values, while acknowledging the interaction between carnivore abundance and hunting effort with respect to harvest. In contrast, an applied fishery economics study, Knowler et al. (2001), evaluated the negative effect of a predator species, the invasive comb jelly, on an anchovy fishery in the Black Sea, assuming that the presence of the predator caused a discontinuous shift in the recruitment function.

The aim of this paper was to estimate the estimate the cost of two carnivores, lynx (*Lynx lynx*) and wolf (*Canis lupus*), in terms of their impact on roe deer (*Capreolus capreolus*) harvests in south and middle Sweden between 2002 and 2012. The choice of game species was motivated by the roe deer being the second most valuable hunted species in Sweden after the moose, accounting for one-fifth of the total hunting value (Mattson et al. 2008). Moreover, roe deer harvests in Sweden decreased by approximately 45% between 2002 and 2012, which is argued to be due to increased predator pressure from lynxes, wolves and red foxes (*Vulpes vulpes*) (Jarnemo and Liberg 2005). 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 climatic conditions. The harvest function, derived from this model was estimated empirically using data from 2002 to 2012. Based on the results from the estimations, we calculated the cost of the two carnivores for a constant as well as an adjusted, steady-state equilibrium effort. Further, costs for the two carnivores where compared across counties. This was motivated by the Swedish carnivore protection policies for wolves having a spatial component: a further dispersal southwards is explicitly aimed for (EPA 2014a).

HUNTING INSTITUTIONS IN SWEDEN

In Sweden, the right to hunt 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 leased out the hunting right on his land in whole or in part (Sandström et al. 2013). Both long-term leases, usually on an annual basis or for several years, and short-term leases on a daily or weekly basis can be found. The long term leases are more common and generally imply that the landowner grants a hunting team the right to hunt all species on the land. Hunting occurs to some extent on most land where it is legally permitted. For most species, including roe deer, fallow deer and different small game, the hunting team is free to decide on harvest rates, as long as crop and forest damages are held within reasonable limits[2] (Mensah and Elofsson, 2017). There are over 300,000 hunters in Sweden, and the annual gross hunting value is estimated to be more than EUR 360 million[3] (Mattson et al. 2008).

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[2] Exceptions apply to moose and red deer hunting, where hunting is required by law to be coordinated across larger areas, and agreed upon by affected stakeholders (Sandström et al., 2013).

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

THE ROE DEER AND ITS PREDATORS

Our study area includes the South and Middle Carnivore Management Areas, as defined in

MOEE (2013), see Fig. 1.This area is the main distribution range in Sweden for the European roe

deer. The main predators of the roe deer are lynx, wolf and red fox (Jarnemo and Liberg 2005,

Andrén et al. XXX, Sand et al. 2016). In the following sections, we briefly describe all four
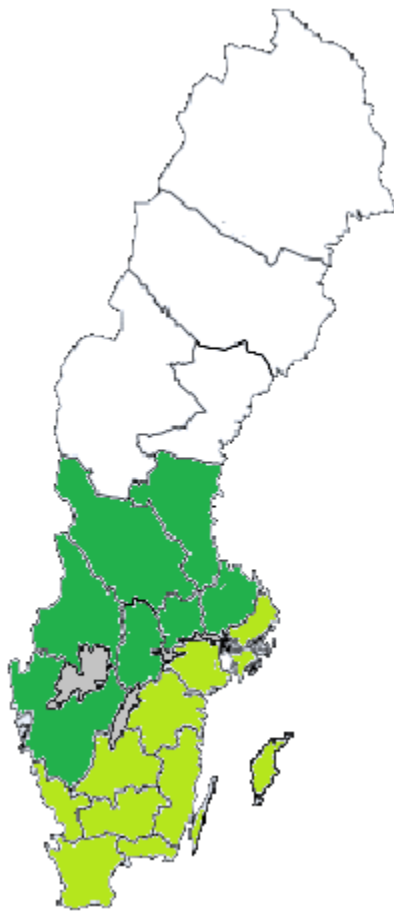
species.

Fig. 1. Map over study area in Sweden. The Southern and Middle Management Areas are

indicated in the figure by light and dark green color, respectively. The Middle Management Area

includes Dalarna, Gävleborg, Västra Götaland, Värmland, Örebro, Västmanland and Uppsala län county. The Southern Management Area includes all counties south of those.

Roe Deer (*Capreolus capreolus*)

The roe deer is a relatively small ungulate species. 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 (Mattson et al. 2008). The number of harvested roe deer has fallen considerably over the last decades. The main causes of mortality are predation, winter starvation and hunting (Cederlund and Liberg 1995, Kjellander XXX). 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 middle and northern parts of the country. Moreover, the population dynamics of roe deer is sensitive to predation (Melis et al. 2009, 2010, Refs???).

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 lynx usually hunts as a lone stalker, and can have a strong demographic effect on its prey (Gervasi et al. 2012). Throughout history, the lynx has been the subject of several governmental interventions that have alternatively encouraged and prohibited hunting, with associated effects on the abundance level (Bostedt and Grahn 2008). The highest count of lynxes was recorded during the 2008/2009 hunting season, indicating somewhere between 1500 and 2000 lynxes in total (EPA, 2014*a*). After that, the lynx population has

experienced a slight decline (Fig. 2). The current management goal suggests that the population

should exceed 870 individuals. This target was met until 2014, when the population number was

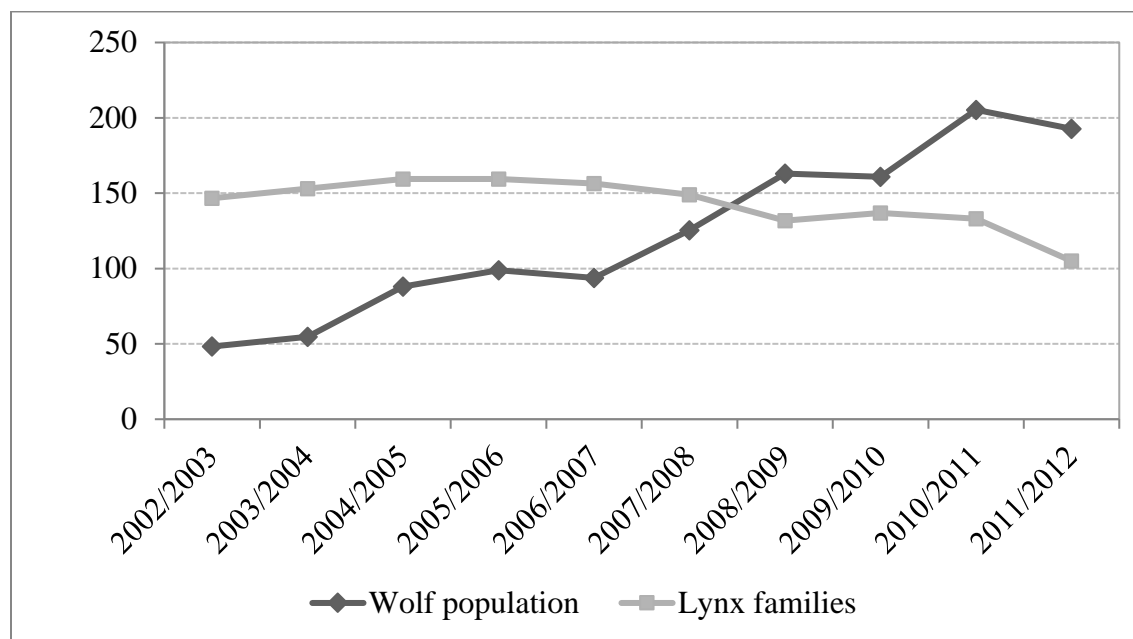slightly below the goal (EPA 2014*a*).

Fig. 2. Number of wolves (individuals) and lynxes (family groups) in south and middle Sweden.

The main prey in the southern and middle parts of Sweden is the roe deer in combination with

small prey species (Liberg and Andrén 2006). The lynx population can greatly affect the

abundance of roe deer (Liberg and Andrén 2006), given that 65% of a lynx's diet can consist of

adult roe deer (Gervasi et al. 2012). Based on a study in the Grimsö Research Area, Arbieu

(2012) estimated that the lynx population accounted for approximately 22.5% of the total ?

annual mortality rate of roe deer. Gervasi et al. (2012) estimated that a 50% increase in lynx

predation reduced the annual growth rate of roe deer by 8%. 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, amplifying the

negative effect of snow on the abundance of roe deer (Melis et al. 2009, 2010).

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 1980s the population has grown,

and since the 1990's the numbers have increased rapidly (Wabakken et al. 2001). Fig. 2 shows

the development of the wolf population since the 2002/2003 hunting season for the counties

included in the study. Sweden is a member of the European Union (EU) where large carnivore

management and conservation is regulated by the European Union's Habitats Directive (Council

Directive 92/43/EEC) that lists the wolf among the strictly protected species. Before 2010,

derogations to harvest wolves were permitted only on shooting wolves that were depredating on

domestic animals or behaving boldly near human settlements. In 2010, the Swedish government

launched quota harvest for wolves, which has been repeated in multiple years since then. In

2013, the Swedish government decided that the minimum level of the wolf population should be

170–270 individual wolves to ensure the favourable conservation status (MOEE 2013). Wolves

are effective hunters because of their ability to form and hunt in packs and to cover long

distances (Bjärvall and Ullström 1995). Moose (*Alces alces*) is the main prey (Sand et al. 2005,

2008), but roe deer become increasingly important in diet with increased densities (Sand et al.,

2016).

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 was larger in open habitats, such as pasturelands, compared to dense habitats, such as woodlands (Aanes and Andersen 1996; Linell et al. 1995; Jarnemo and Liberg 2005; Panzacchi et al. 2008). Both lynx and wolves have been found to kill red foxes regularly, and both negative and positive spatial correlation of the abundance of the red foxes and the two predator species has been observed (Wikenros et al. 2017), although it is not evident whether these trends are the result of predation or of fox avoiding areas with higher lynx densities (Helldin et al. 2006). On the other hand, lynx and wolves could provide food for the red foxes through leftovers from carcasses, thereby benefitting the fox (Helldin and Danielsson, 2007, Wikenros et al. 2013). This could prove even more important during the winter when conditions are hard and 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 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.

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 the habitat conditions, $\mathbf{Z_{it}}$, where $i = W, L, F, S$

indicates the habitat conditions of concern: the populations of the wolves (W), the lynxes (L) and

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:

$$X_{t+1} - X_t = G(X_t, \mathbf{Z_{it}}) - h(X_t, E_t) , G_x >< 0, G_{\mathbf{Z}} < 0 \tag{1}$$

The growth in the roe deer population, $G(X_t, \mathbf{Z_{it}})$, thus depends on the presence of the predators,

the winter conditions, and the size of the roe deer population, while the harvest level, $h(X_t, E_t)$,

is a function of the size of the roe deer population and the hunting effort. We assume a logistic

growth function, where increases in the predator populations and in the length of the period with

thick snow cover reduces roe deer population growth (Equation 2). This property of the growth

function is obtained by introducing a factor $(K + \boldsymbol{\delta_i Z_i})$, where the δ_i:s with $\delta_i \leq 0 \ \forall i$ are

coefficients that express the sensitivity of the roe deer growth and the carrying capacity to the

different predators and to the winter conditions:

$$G(X, \mathbf{Z_i}) = rX(K + \boldsymbol{\delta_i Z_i})(1 - \frac{X}{(K+\boldsymbol{\delta_i Z_i})}) \tag{2}$$

with $G >< 0$, $G_{\mathbf{Z_i}} < 0$, $G(X, 0) > 0$ for $X > 0$. This formulation of the growth function,

originally suggested by Barbier and Strand (1998), is chosen because it possesses the desired and

empirically relevant property (a negative impact of predators and severe winters on growth),

while also being analytically convenient when the purpose is to analyse bioeconomic outcomes.

It can be noted in the absence of predators and severe winters, the carrying capacity equals K,

and the intrinsic growth rate equals rK. With this formulation increasing values of Z_i reduce both

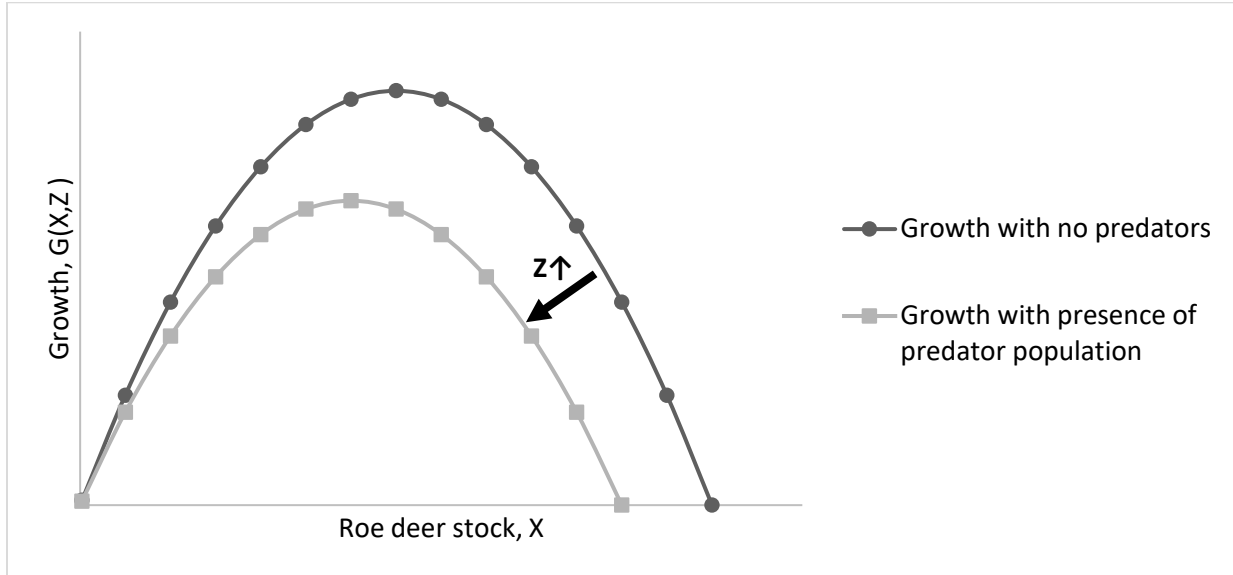the growth rate and carrying capacity, which is illustrated in Figure 3.

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.

Furthermore, we assume a simple Schaefer harvesting function:

$$h_t = qX_tE_t, \tag{3}$$

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). This simplification is motivated by the lack of data regarding catchability under different

conditions.

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 controlled by policy makers, and protective as well as licence hunting is permitted, respectively, when individuals of these species give rise to livestock damages and numbers exceed governmental targets for favourable conservation 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 populations are exogenously determined.

Bioeconomic Model

We follow Knowler et al. (2001) by assuming that the prey, roe deer, is harvested under open access conditions, and that the system is in a steady state equilibrium. Open access resources are typically characterized by non-excludability, free entry, lack of enforcement of property rights, and costly monitoring. In this case, the open access assumption is motivated by the absence of the regulation of the roe deer harvesting in combination with roe deer home ranges typically overlapping several plots of privately owned land, where different decision makers possess the hunting rights. 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 to 150 hectares size, while the home range of the males is 1.5 times greater (Kjellander et al. 2004). Hence, private property rights to roe deer cannot be enforced. Moreover, there are no restrictions to entry: anyone who has completed a short course in hunting can acquire a hunting licence from the Environmental Protection Agency at low cost, and access to hunting land can be acquired through lease. Hunters that lease hunting rights are free to not only decide on roe deer harvests, but are also typically free to invite additional hunters as guests or

permanent paying members of the hunting team, and here is a considerable supply of short and

long term hunting opportunities on the market. Finally, the possibilities for monitoring of

population size and enforcement are limited; there is no monitoring carried out by public

agencies, and it would be extremely costly for land owners and hunting teams to carry out such

monitoring. 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. Together, lack of regulations, monitoring and enforcement, free entry for individual

hunters, and roe deer home ranges overlapping land with hunting rights owned by different

people, suggests that open access is a good approximation of the prevailing conditions[4].

The assumption about a steady state implies that the hunting community and the roe deer

population respond relatively rapidly to changes in predator populations. This assumption is

supported by results in Wikenros et al. (2015), where it is shown that hunters may respond

quickly to increased wolf numbers by reducing harvest of moose.

Given the above described Equations (1)-(3) and the assumption about a biological equilibrium,

we can derive an equation that can be estimated (see the Appendix for details):

$$h = \alpha E + \boldsymbol{\beta_i}\boldsymbol{Z_i}E + \gamma E^2 \qquad , \qquad\qquad\qquad\qquad (4)$$

where $\alpha > 0$, $\beta_i < 0$, and $\gamma < 0$ are the coefficients to be estimated. Using (4), the marginal products of

E and $\boldsymbol{Z_i}$, are obtained as:

$$MP_E = \frac{\partial h}{\partial E} = \alpha + \beta_i Z_i + 2\gamma E \qquad\qquad\qquad\qquad (5)$$

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[4] Notably, the disadvantages with the open access practice has been observed by the EPA, which has investigated possibilities to control large ungulate populations through hunting season lengths, albeit at this point in time this is not yet applied (EPA, 2017).

and

$$MP_{Z_i} = \frac{\partial h}{\partial Z_i} = \beta_i E, \tag{6}$$

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. It is negative and

decreasing in the effort level. The marginal product of effort, MP_E, expresses the harvest increase

when effort is increased by one unit, while predator numbers are held constant. It is decreasing in

the level of effort and predator numbers.

In Equations (5) and (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. The assumption about an economic, open access equilibrium

imposes a requirement that the effort level is adjusted such that a positive stock and effort can be

maintained over time. Derivations of the open access steady equilibrium can be found in the

Appendix. Here, we present the comparative static effect of changes in Z_i on roe harvest, ∂h, and

hunting net revenues, $p\partial h$, in the open access equilibrium, i.e. when the effort has adjusted in

response to the change in Z_i, which can be obtained as:

$$\partial h = \frac{r\delta_i c}{pq} \partial Z_i = -\frac{c\beta_i}{p\gamma} \partial Z_i \tag{7}$$

and

$$p\partial h = \frac{r\delta_i c}{q} \partial Z_i = -\frac{c\beta_i}{\gamma} \partial Z_i, \tag{8}$$

where p and c are the unit revenue and unit cost of roe deer harvests, respectively (see Appendix

for the derivations). Equations (7) and (8) show that the equilibrium reduction in harvest and

revenue is increasing in r and δ, decreasing in q, and increasing in the ratio of unit harvesting

cost and revenue. The comparative static effect on the harvests and the revenues can thus be

evaluated when c and p are known. One can note that for a low-cost industry, where the open

access stock is below maximum sustainable yield, ∂h can be expected to be lower than MP_{Z_i},

whereas the opposite would hold for a high cost industry where the stock is above maximum

sustainable yield (see Fig. A.1 in the Appendix).

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 mid Sweden compared to the south. This could potentially imply that the impact of

wolf on roe deer harvests differs, e.g., because of wolves' preferences for different prey. In a

study in mid Sweden, where moose and wolf are relatively more abundant, Zimmermann et al.

(2015) conclude that the kill rate of roe deer by wolf is independent of moose abundance.

However, the study does not include south Sweden where roe deer are relatively more abundant,

and conditions are potentially different. We therefore account for a possible effect of moose

abundance on the impact of wolf on roe deer harvests. This is done through an alternative version

of equation (4), where we introduce a dummy variable for the counties with a high moose

density compared to the roe deer density. The new regression equation (4') is then specified as

follows:

$$h = \alpha E + \theta_1 D Z_W E + \theta_2 (1 - D) Z_W E + \boldsymbol{\beta_j} \mathbf{Z_j} E + \gamma E^2, \tag{4'}$$

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,

denote lynx, red fox and snow cover. The corresponding comparative static effect is calculated

similarly as for equation (4), except that equation (4') permits us to identify the different impacts of the wolf in the moose-dense counties and the other counties. Thus, the coefficient θ_1 expresses the impact of the wolf on roe deer harvest in the counties with a high moose density for a given hunting effort, while θ_2 represents the corresponding impact in the other counties.

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, which includes 16 counties for the period of the 2002/2003 to 2011/2012 hunting seasons (for descriptive statistics see Table 1). The area covered in the study refers to the Southern and Middle Management Areas. The reindeer herding areas in northern Sweden were excluded due to the lower number of roe deer in combination with the different prey available to the predators. In the regression analysis, all of the data, except for the number of days with snow cover, are divided by the area of the county in square kilometres[5] to for account for county size (for the descriptive statistics per square kilometre, see Table S1 in the Supporting Material).

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[5] Excluding water, urban areas and national parks.

Table 1

Descriptive statistics, totals.

Variable	Mean	SD	Min	Max
Wolf Numbers	7.7	14.7	0	72
Lynx Families	8.9	10.1	0	38
Days of Snow Cover	16.2	25.7	0	116.5
Hunting Licences	12995.5	7423.5	4788	37401
Roe Deer	7506.2	5594.7	1386	29610
Moose	2952.1	2338.6	189	9711
Wild Boar	2200.9	2792.7	0	14645
Red Fox	3419.9	2178.8	715	12439

Source: Swedish Hunting Association, Swedish Meteorological and Hydrological Institute
(SMHI), Swedish Environmental Protection Agency.

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 Hunting Association. Fig. 4 shows the development over time in total
and in roe deer hunting and the resulting share of the roe deer of the total hunting bag, where the
total hunting bag includes roe deer, moose, wild boar, fallow deer and red deer. 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 countries can be found in Fig. S1 in the Supporting Material.)

Effort is a central variable in bioeconomic models, but 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 of the 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 devoted to roe deer hunting as the number of licenses, multiplied by the roe deer share in the total hunting bag:

$$E = \frac{\left(\frac{bagged\ amount\ of\ roe\ deer}{total\ number\ of\ bagged\ game}\right)*number\ of\ hunting\ licenses}{area\ of\ county\ in\ km^2} \tag{9}$$

where E is the effort per square kilometre. Notably, the red fox was not included in the total number of bagged game, since it is not a primary game. The red fox is mainly hunted due to its negative impact on the roe deer populations.

The effort measure in Equation (9) is a relatively good proxy of actual effort if the number of hunting days per hunter are constant over time and across counties and if different species are hunted on separate occasions. There is no evidence that suggests that the number of hunting days per hunter has changed over the studied time period. 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.
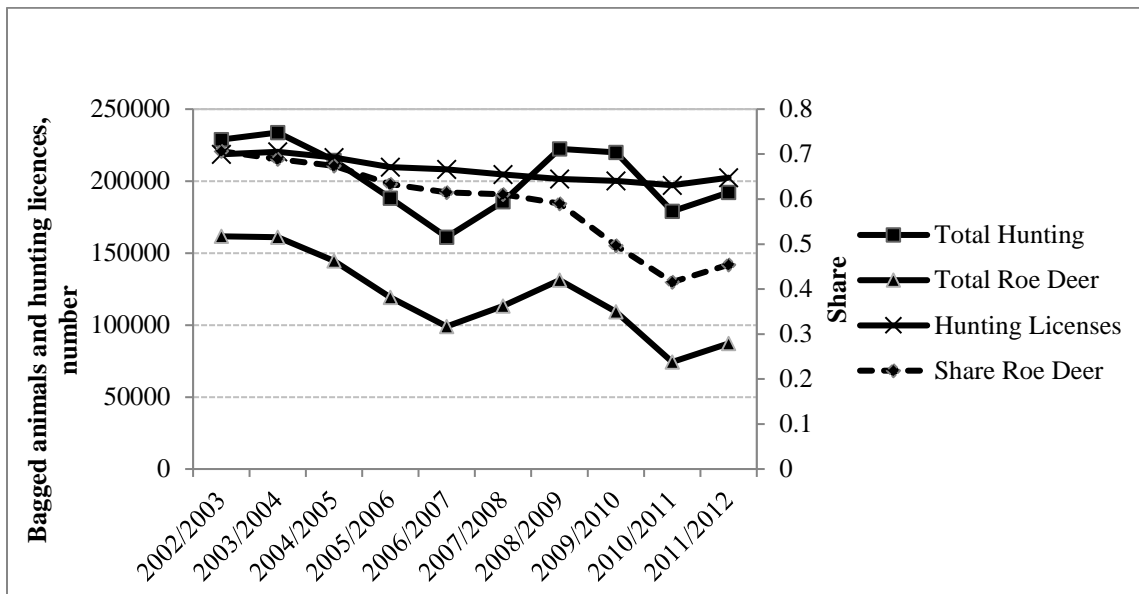

Fig. 4. Hunting bag statistics and hunting licences. Source: The Swedish Hunting Association (**www.viltdata.se)** and the Swedish Environmental Protection Agency.

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; however, 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 equation (4') is set to one for these counties and zero otherwise.

Predator Population and Weather Data

The data for lynx and wolf were based on census materials. Notably, some counties have had zero presence of lynxes or wolves in certain years, but over the full time period, all of the counties hosted either lynxes or wolves. Weather data were obtained from the Swedish Meteorological and Hydrological Institute (SMHI).

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 are made accounting for landscape heterogeneity (Liberg and Andrén 2006; Andrén et al. 2010). The census estimates for the different ecological regions are transferred to the counties, following the approach of Andrén et al. (2010).

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. In order to correct for this, the number of wolves in the border areas were equally divided over the relevant counties. In some of the counties, wolf occurred only occasionally.

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 by using the minimum values, a higher estimated effect per wolf can be expected than when using the maximum values. The average rate of minimum number to maximum number over the study period was 1:1.18 (Wildlife Damage Center, 2016).

When doing the regression analysis, we considered two alternative measures of the wolf population: the total number of wolf individuals in a county and the number of wolf territories in a county, where the latter is calculated as the sum of the numbers of the family groups and the territory-marking couples. The use of the territories is motivated by the observation by Zimmermann et al. (2015) that the number of moose killed is 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).

   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 statistics is more uncertain than for the other

species.

   Snow data.— As a measure of winter severity, we use the number of days with a snow

cover deeper than 30 centimetres. 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 have been used to calculate the average value of the number of days

with a snow cover greater than 30 centimetres per year and county. The choice of stations is

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[6]. 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 Fig. S2 and Table

S2 in the Supporting Material.)

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

ESTIMATION AND RESULTS

Equations (4) and (4') were 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.

The statistical properties were examined in the following manner: the Breusch-Pagan/Cooks-Weisberg test for homoscedasticity rejected the null-hypothesis, implying that there is heteroscedasticity present. 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 (Table A.2, Appendix). Further, the variable for the bagged number of red foxes was dropped due to multicollinearity according to a high variance inflation factor (VIF).

Following the prior discussion, heteroscedasticity and cross-sectional dependence are present in the dataset. Therefore, the regression was 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 regression without intercept, the coefficient of determination, R^2, cannot be interpreted as usual.

Additionally, we studied the effect of individual observations on the outcome with leverage versus residual (LVR) plots (Fig. A2 in the Appendix) 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 2).

Table 2. Pooled regression results with Driscoll-Kraay standard errors. Dependent variable:

Harvest of roe deer per km^2.

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 × Wolf	−339.448***	−	−	−
E × Wolf$_{territory}$	−	−	−959.5499***	−
E × Lynx	−76.4479**	−70.7912*	−61.6062**	−60.2480*
E × Snow Cover	−0.0022	−0.0021	−0.0024*	−0.0024*
D × E × Wolf	−	−301.5968***	−	−
(1 − D) × E × Wolf	−	−407.3479***	−	−
D × E × Wolf$_{territory}$	−	−	−	−918.9866***
(1 − D) × E × Wolf$_{territory}$	−	−	−	−1002.22***
Prob > F	0.000	0.000	0.000	0.000
Number of observations	150			

Note: *significant at $p < 0.1$, **significant at $p < 0.0$ and ***significant at $p < 0.001$.

Using the estimated coefficients in Table 2 and equations (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 3). The marginal product of effort, MP_E, shows the change in harvest for a one-unit

increase in effort. For the lynxes and the wolves, we have MP_L and MP_W, which are the change

in harvest for a one-unit increase in the lynx population, the wolf population or the wolf

territories, evaluated at the mean effort.

Table 3

Average marginal products and elasticities.

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]	−50	−355[a]	0.5859[a]	−0.0679	−0.0643[a]
	0.8142[b]		−86[b]	1.2238[b]		−0.6644[b]
Model 3[c]	0.8540	−44	−687	0.887	−0.0590	−0.093
Model 4[c]	0.7513[a]	−53	−874[a]	0.5456[a]	−0.0579	−0.0536[a]
	1.1516[b]		−264[b]	1.6987[b]		−0.2007[b]

[a] Other counties.

[b] Moose-dense counties.

[c] Wolf territory data are used instead of wolf numbers.

For a mean level of effort, 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 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 counties, which was explained by the comparatively lower effort levels in these counties.

The output elasticity of effort, computed as $\varepsilon_e = MP_e\left(\frac{\bar{E}}{\bar{h}}\right)$, 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 $\varepsilon_L = MP_L\left(\frac{\bar{L}}{\bar{h}}\right)$ and $\varepsilon_W = MP_w\left(\frac{\bar{W}}{\bar{h}}\right)$, 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.

Bioeconomic steady-state adjustments — The bioeconomic equilibrium results were calculated using equations (7) and (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. 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[7]. Elofsson et al. (2017) and Lundhede et al. (2015) reported values around 525 and 440 EUR, respectively. However, these two studies seem less representative for our case, as the first study reports values that are based on organised hunts at a large estate, a submarket where prices are comparatively high; the latter study reports on the results from Denmark, where hunting opportunities are scarcer, hence prices are higher. Therefore, we used the estimate in Karlsson (2010), which was a more representative value for Swedish hunting in general and gives a conservative value for the costs of predation. The cost c is computed for each county and year.

Results show that an increase in the predator levels will decrease the steady-state harvest level of roe deer, thus reducing the revenues from hunting activities (Table 4). An additional lynx family would reduce 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 would, on average, reduce the equilibrium roe deer harvest by 422–697 units[8], with the lower figure pertaining to the estimation with territories. 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 would have a smaller impact on the roe deer harvests (264–411 units) compared to that in the other counties (438–943 units), where the lower figures are obtained from regressions with territories. Results from the different models suggest that the average cost of an additional lynx family was between 19 and 40 thousand EUR, while the average 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 cost for moose dense counties

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[7] In 2014 year value, using the average exchange rate from the Swedish Riksbank, 1 EUR = 9,0968 SEK (Swedish crowns).
[8] Note that for models 3 and 4, the wolf figures have to be divided by 4.71.

was 63 to 98 thousand EUR per wolf, while the average cost for other counties was 120 to 232

thousand EUR.

Table 4

Average change in harvests and revenues for a marginal increase in predator populations.

	Wolf, Harvest Impact	Lynx, Harvest Impact	Wolf, Revenue Impact (EUR)	Lynx, Revenue Impact (EUR)
Model 1	−697	−157	−166,151	−37,419
Model 2	−943[a]	−150	−232,040[a]	−40,325[a]
	−411[b]		−98,102[b]	−23,027[b]
Model 3[c]	−1991	−128	−474,874	−30,488
Model 4[c]	−2062[a]	−126	−566,319[a]	−34,044[a]
	−1243[b]		−296,524[b]	−19,440[b]

[a] Other counties.

[b] Moose dense counties.

[c] Wolf territory data are used instead of wolf numbers.

County-level Impacts

In the following we calculate the county-level effects, using estimates from model 2, which

makes use of the wolf numbers and distinguishes between moose-dense and other counties. The

harvest effects are calculated using variable levels for each year and county, and averaging over

years (Table 5).

The impact of the predators on the roe deer harvests is closely related to the marginal product of effort, which varies across the counties (Table A.3, Appendix). 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 roe deer 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.

Table 5

Average change in harvest and revenues in different counties, 2002/2003 to 2011/2012 hunting

seasons, based on model 2.

County	Lynx, harvest change	Wolf, harvest Change	Lynx, revenue impact (EUR)	Wolf, 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	−104	−599	−24,819	−142,812
V. Götal.	−112	−645	−26,749	−153,920
Örebro	−116	−494	−27,663	−117,855
Östergötland	−204	−1,175	−48,683	−280,131
Average moose counties	*−97*	*−411*	*−23,027*	*−98,102*
Average other counties	*−170*	*−973*	*−40,325*	*−232,040*
Average total	*−150*	*−823*	*−35,712*	*−196,324*

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 hunting efforts or the existence

of equilibria. In spite of these conceptual differences, it could be noted that Andrén and Liberg

(2015) estimated that a lynx family kills 64–85 roe deer per year. Our results suggest a 44–55

unit reduction in the roe deer harvest due to an additional lynx family given a mean effort.

Although our finding is slightly below that in Andrén and Liberg (2015), the calculated effect in

several of the counties falls within their estimated interval. There are no corresponding data on

the annual kill rate of the roe deer by the wolf. Instead, most wolf studies focus on moose and are

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 constant kill rates over the year, a wolf would then

kill approximately 2,400 kg biomass annually[9]. 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 to 321 roe deer per

year[10]. Bearing in mind the conceptual differences, one can note that this number is in the same

order of magnitude as our estimated average harvest impact for a constant effort in counties with

low moose density, 185–355 roe deer.

Our 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 cost of an additional lynx family is 18–58 thousand EUR, and the cost of an

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[9] This is a high-end estimate since winter kill rates are typically lower (Sand et al. 2008).
[10] The lower number applies a 0% share of the juveniles in the wolf diet, and the upper to a 100% share.

additional wolf is 79–336 thousand EUR. This can be compared to the total value of hunting in Sweden, which is estimated to be over 370 million EUR (Boman and Mattsson 2012). Hence, small increases in the wolf and lynx populations have a minor impact on the hunting value on a national level, even though they can have a considerable effect on the local level. 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 46 and 1,450 EUR (for wolves) and 2 to 19 EUR (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 outcome and not the approach path, and not including changes in the use of hunting dogs in response to an increased carnivore abundance. Further research including these aspects would be valuable.

MANAGEMENT IMPLICATIONS

A county-specific analysis showed that the costs of increased carnivore populations depend on the relationship between harvest and effort. In counties with a high harvest per square kilometre, the cost of an increase in the number of predators is higher than in countries with low harvests. This has implications for policy, and suggests that from a national perspective, it is preferable if carnivore increases occur in areas with a lower harvest per effort. However, this can have considerable distributional implications, as the predator numbers are already the largest in these counties, implying that the hunters in these counties already carry a large share of the costs for preservation. Also, it contrasts with current aims to for increased establishment of wolves in the southern parts of the country (EPA 2014*b*). Our conclusions in this regard are consistent with

those in Boman et al. (2003) and Widman and Elofsson (2018). Furthermore, our results showed that the availability of other game has a large importance for the cost of carnivores in terms of game harvests. Hence, if a carnivore species is flexible in its choice of prey, the cost of the increased numbers of the carnivore species will vary spatially with the availability of different prey species.

ACKNOWLEDGEMENTS

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Appendix

Bioeconomic model

In the open−access equilibrium the roe deer population and the hunting effort is constant over time. Following the standard approach, 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 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:

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

In equilibrium, all of the variables are constant over time, implying that $X_{t+1} = X_t = X$ and $E_{t+1} = E_t = E$. It is also assumed that the populations of the predators and the winter conditions are initially in equilibrium (i.e., $Z_{it} = Z_{it+1} = Z_i$). Using equations (2)–(4), the steady−state level of the roe deer and the effort will then be:

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

$$E = \frac{r((K + \delta_i Z_i) - X)}{q},\ for\ X_{t+1} = X_t = X$$ (A3)

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

An increase in the predator levels will induce a comparative static effect on the optimal level of

harvesting. Using equation (A3) we have:

$$\frac{\partial E}{\partial Z_i} = \frac{r\delta_i}{q} < 0. \tag{A4}$$

Using equations (3) and (A3) and the steady−state condition (A2), the comparative static loss in

the harvest is:

$$\frac{\partial h}{\partial Z_i} = qX \left(\frac{rk + r\delta_i Z_i - rX}{q} \right) = \frac{r\delta_i c}{pq}. \tag{A5}$$

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:

$$p\partial h = \frac{r\delta_i c}{q} \partial Z_i < 0. \tag{A6}$$

Here, the left−hand side value of the impact on the revenues will be negative, since $\delta_i < 0 \ \forall i$.

Solving equation (3) for X_t, substituting it into equation (A5) and solving for h_t yield an

equation that can be estimated:

$$h = qKE + q\boldsymbol{\delta_i Z_i} E - \frac{q^2}{r} E^2 , \tag{A7}$$

which can be expressed as:

$$h = \alpha E + \boldsymbol{\beta_i Z_i} E + \gamma E^2 \qquad , \tag{A8}$$

where α, β_i and γ are the coefficients to be estimated (see Table A.1, Appendix, for the identity of

the coefficients).

Comparative statics

The marginal products of E and $\mathbf{Z_i}$, derived using equation (A8), are shown in equations (A9) and (A10):

$$MP_E = \frac{\partial h}{\partial E} = \alpha + \beta_i Z_i + 2\gamma E \tag{A9}$$

and

$$MP_{Z_i} = \frac{\partial h}{\partial Z_i} = \beta_i E. \tag{A10}$$

From equation (A3), the comparative static effect of a change in Z_i on the equilibrium level of the hunting effort can be calculated. Using this, together with equation (A2), gives the change in the equilibrium harvest when Z_i changes:

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

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

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

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

Table A.1

Identity of estimated coefficients.

Coefficient	Identity
α	qK
β_i	$q\delta_i$
γ	$-q^2/r$

Table A.2

Woolridge test for autocorrelation.

	Coefficient Estimates			
Variable	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

Note: *significant at $p < 0.1$, **significant at $p < 0.05$ and ***significant at $p < 0.001$.

Table A.3

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
Mean	*0.7425[a]*	*−51*	*−355[a]*	*0.5859[a]*	*−0.0679*	*−0.0536[a]*
	0.8143[b]		*−86[b]*	*1.2238[b]*		*−0.2007[b]*

Marginal products and elasticities, evaluated at the mean for model 2.

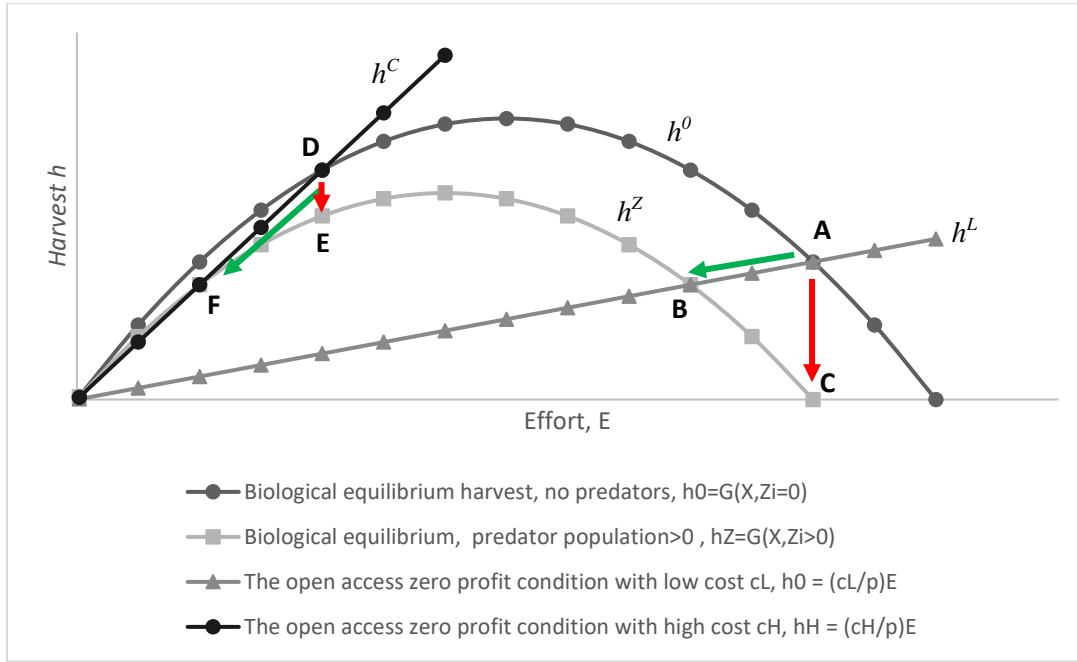[a] Moose−dense counties. [b] Other counties

Fig. A.1. The marginal product of carnivores, MP_{Zi}, and the bioeconomic steady state harvest effect, ∂h. The red arrows shows MP_{Zi} in the case of low harvesting cost (A to C) and high harvesting cost (D to E). The green arrows shows ∂h in the case of low harvesting cost (A to B) and high harvesting cost (D to F).
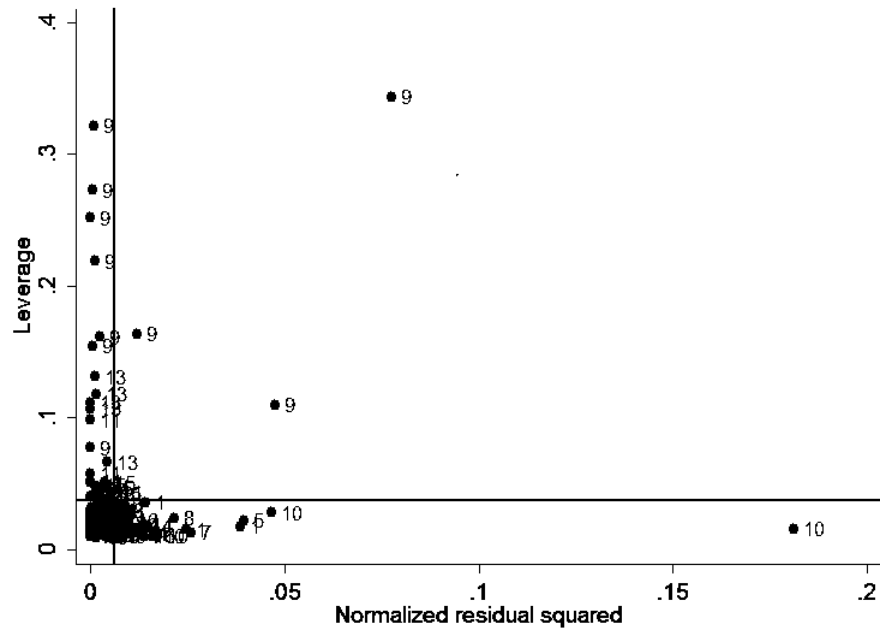
Fig. A.2. Leverage versus squared residual plot.

Note: (1) Blekinge, (2) Dalarna, (3) Gävleborg, (4) Halland, (5) Jönköping, (6) Kalmar, (7) Kronoberg, (8) Skåne, (9) Stockholm, (10) Södermanland, (11) Uppsala, (12) Värmland, (13) Västmanland, (14) Västra Götaland, (15) Örebro and (16) Östergötland.