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Swedish University of Agricultural Sciences

Department of Economics

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Estimating the Marginal Impact of Large Carnivores on the Hunting Value of Roe Deer

Tobias Häggmark Svensson and Katarina Elofsson
Economics

Abstract

Hunting is an important recreational activity for large numbers of people. The roe deer is one of the most popular types of game in Sweden; however, recently the roe deer population has decreased. It is argued that this decrease is due to an increase in predator populations. The aim of this paper is to identify and compare the impact of lynxes and wolves on the hunting values of roe deer, taking into account that the impact depends on the hunting effort. The impact of the predators on the roe deer harvests is estimated econometrically, using a production function approach that accounts for the abundance of predators and the alternative prey, as well as the climatic conditions. The results show that the marginal cost of wolves is larger than that of additional lynx families in terms of their impact on the roe deer harvest values. The marginal costs of the predators vary with the hunter effort and the presence of alternative prey, which can have implications for policies affecting the regional allocation of the wolves and the lynxes.

Keywords: Production function approach; Hunting; Costs; Roe deer; Lynx; Wolf.

1. Introduction

Hunting is an important leisure activity for large numbers of people. In Sweden and North America, 3%–4% of the populations are registered hunters (Mattson et al., 2008; U.S. Fish & Wildlife Service, 2012). In Europe, there are about 7 million hunters in total, spending approximately 12 billion EUR annually. In addition, the activity creates more than 100,000 jobs (Lecocq, 2004; Pinet, 1995), and hunting has a considerable impact on land values (e.g., through the markets for hunting leases) (Hussain et al., 2013).

Hunters share their preference for hunting with wild carnivores. Based on a survey, Graham et al. (2005) concluded that predators can take up to 9% of the game species populations. The competition for game creates conflicts between the hunters and the predators. Historically, this has led to a reduced predator abundance in population-dense areas. Recently, however, efforts to protect threatened carnivores (e.g., through conservation programs) have increased (Graham et al., 2005). The conservation efforts have considerable support, reflected through the high willingness to pay for preservation (Bostedt et al., 2008; Broberg and Brännlund, 2007; Ericsson et al., 2007, 2008; Johansson et al., 2012).

With larger conservation efforts and, hence, larger carnivore populations, the hunting values are likely to be affected. A considerable number of studies investigated the economic value of the impact of carnivores on livestock and semi-domesticated animals (e.g., Häggmark-Svensson et al. [2015]). In contrast, there are relatively few studies that try to quantify the value of the costs that accrue to the hunters as a consequence of carnivore preservation. Among those, Boman et al. (2003) assume a constant cost per carnivore, independent of populations and hunting effort, while Skonhoft (2006) accounts for the impact of prey population on wolves' kill rate, and hence on the associated impact on hunting values. While Bostedt and Grahn (2008) estimate the cost to reindeer owners due to carnivores, rather than the hunters' costs, they do this while taking into account the role of alternative wild prey for this cost. The major challenges in studies of this type are the difficulties to simultaneously account for carnivore, hunter, and game responses and the lack of game population data.

The aim of this paper is to estimate the value of the impact of the carnivores on the roe deer hunting values in Sweden. The roe deer is the second most valuable hunted species in Sweden, accounting for one-fifth of the total hunting value (Mattson et al., 2008). The roe deer harvests in Sweden have decreased by approximately 45% between 2002 and 2012. Available studies suggest that increased predator pressure

from lynxes, wolves and red foxes explains this development (Jarnemo and Liberg, 2005; Liberg and Andrén, 2011). We aim to identify and compare the marginal impact of the different carnivore species on the roe deer hunting values and to investigate how this impact varies regionally. The latter is motivated as the hunting effort varies across the country. If the impact of the carnivores varies across space, this can have implications for the policies that regulate the spatial distribution of the carnivores.

Several earlier studies use a production function approach for the valuation of the impact of the ecosystem changes on the value of the harvest of natural resources. Typically, it is assumed that the ecosystems serve as the inputs into the production of marketed goods or services, such as fisheries (Barbier, 2007). Examples include Barbier and Strand (1998), who estimated the impact of mangrove forests on a shrimp fishery, and Foley et al. (2010), who analysed the effect of cold water corals on a redfish fishery. Both of these studies built an analysis on a predator-prey model (Clark, 1990); however, different from a predator-prey model, they assume a positive, continuous impact of the habitat conditions on the fish harvests. In contrast to those studies, Knowler et al. (2001) evaluated the negative effect of a predator species, the comb jelly, on an anchovy fishery in the Black Sea, assuming that the predator causes a discontinuous shift in the recruitment function. Similarly, Kataria (2007) investigated the negative economic impact of an introduction of the invasive signal crayfish, which can cause a regime shift, leading to the eradication of the native noble crayfish. All of these studies are based on an analysis of steady-state conditions. A few past studies recognised the need for a more complex analysis, including harvesting decisions when the system is outside the steady state (Barbier, 2007) or when there is a reciprocal relationship between a predator and a prey species (Tschirhart, 2009). Empirical applications of such economic models are scarce and typically are confined to simulation models, where the magnitude of the mutual impact is assumed to be known.

Our modelling follows the approach by Barbier and Strand (1998) and Foley et al. (2010) through the use of an open-access, bioeconomic model where the ecosystem characteristics affect the growth of the harvested species. We contribute to the literature by applying such a model to wildlife hunting in the presence of multiple carnivores, as well as alternative prey species. The harvest equation is estimated econometrically using county-level panel data from south and middle Sweden from 2001 to 2011. The results from these estimations are used to calculate the marginal cost of additional lynx families and

wolves, in terms of their impact on the roe deer harvests. The results show that the marginal costs vary considerably across the country due to the differences in the hunting effort and the availability of the alternative prey.

The remainder of the paper is organised as follows: Section 2 describes the problem background. Section 3 presents the model, and chapter 4 describes the data used. In chapter 5, the results are presented, while chapter 6 provides the discussion and the conclusions.

2. Roe deer and its predators

The European roe deer has been a part of the Swedish fauna for centuries. The main predators of the roe deer are the lynx, the wolf and the red fox. In the following sections, we briefly describe all four species.

Roe Deer (Capreolus capreolus)

The roe deer is a relatively small ungulate species that has been long established in Sweden. The species was close to extinction in the beginning of the 19th century (Cederlund and Liberg, 1995), and only smaller patches of the deer remained in the southern part of the country. Through restricted hunting, the roe deer population recovered and spread to other parts of Sweden. The re-colonisation was facilitated by the small populations of wolves and lynxes at the time. In modern times, roe deer are found throughout the country, with lower population densities further north and only small patches of the deer in the northernmost parts of the country.

Roe deer hunting is a popular activity. The average hunter spends 26 days per year hunting, and one-fifth of this time is allocated to roe deer (Mattson et al., 2008). However, the number of bagged roe deer has fallen considerably over the last decades (Figure 1). Figure 1 shows the number of bagged animals for the three most hunted species in Sweden (i.e., roe deer, moose and wild boars) for the 2002/2003 to 2011/2012 hunting seasons.
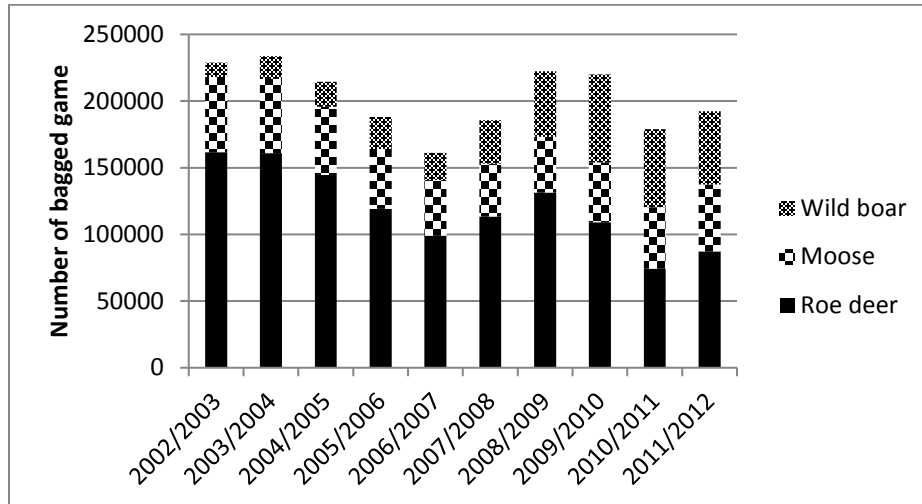
Fig. 1. Number of bagged animals in Sweden, 2002/2003 to 2011/2012 hunting seasons.
Source: The Swedish Hunting Association, www.viltdata.se.

The main causes of mortality for the roe deer are predation, winter starvation and hunting (Cederlund and Liberg, 1995). Obviously, winter starvation is of greater importance in the middle and northern parts of the country. A large snow depth is a major reason for winter starvation, and it has a negative impact on reproduction (Lindström et al., 1994). Moreover, the population dynamics of roe deer is sensitive to predation pressure (Melis et al., 2009, 2010; Wabakken et al. 2001).

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, suggesting it has a strong demographic effect on its prey (Gervasi et al. 2012). Throughout history, the lynx has been exposed to human persecution, and the development of the lynx population is characterised by a large variation over time (MOEE, 2013). It has been the subject of several governmental interventions that have alternatively encouraged and prohibited hunting, with associated effects on the abundance level of the lynx population (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, 2014a). After that, the lynx

population has experienced a slight decline (Figure 2). The current management goal for the lynx population suggests that the population should exceed 870 individuals. This target was met until 2014, when the population number fell below the goal of the favourable conservation status (EPA, 2014).

Historically, since roe deer were hardly present in the southern and middle parts of Sweden during the 19th century, the lynxes have preyed on small animals, such as rabbits (Franzén, 1991b). Recently, however, the main prey in these areas is the roe deer in combination with small prey species; in northern Sweden, the main prey is the reindeer (Bostedt and Grahn, 2008).

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 annual mortality rate of roe deer. Gervasi et al. (2012) reported that a 50% increase in lynx predation reduced the growth rate of roe deer by 8%. The effect can be even stronger for low densities of roe deer, which can occur in areas with a lower environmental productivity where other types of food sources are scarce (Melis et al., 2010; Odden et al., 2006). The lynx population's 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., 2010).

Grey Wolf (Canis lupus)

In the beginning of the 19th century, the wolf still existed in all of the Swedish counties except on the islands of Gotland and Öland. Thereafter, there was a rapid decline in the wolf population due to human persecution. In the 1960s, it was close to extinction. In 1966, when approximately 10 wolves remained, the species was placed under protection (Franzén, 1991a). Since the 1970s, the wolf population has grown rapidly. The growth rate was about 30% per year in the 1990s (MOEE, 2013), falling to about 15% per year after 2002 (EPA, 2014b). Figure 2 shows the development of the wolf population since the 2002/2003 hunting season for the counties included in the study. 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). This target was satisfied in 2014.

Wolves are effective hunters because of their ability to form and hunt in packs and to cover long distances (Boman et al., 2003; Bostedt and Grahn, 2008). The moose (*Alces alces*) are the main prey of the wolves (Skonhoft, 2006); the roe deer are secondary in the wolves' diet when the moose are present (Boman et al., 2003). The effect of the wolves on the roe deer populations and growth is smaller than that of the lynxes due to the difference in the favoured diets, combined with the fact that the wolves have a higher share of the juvenile roe deer in their diet (Gervasi et al., 2012).
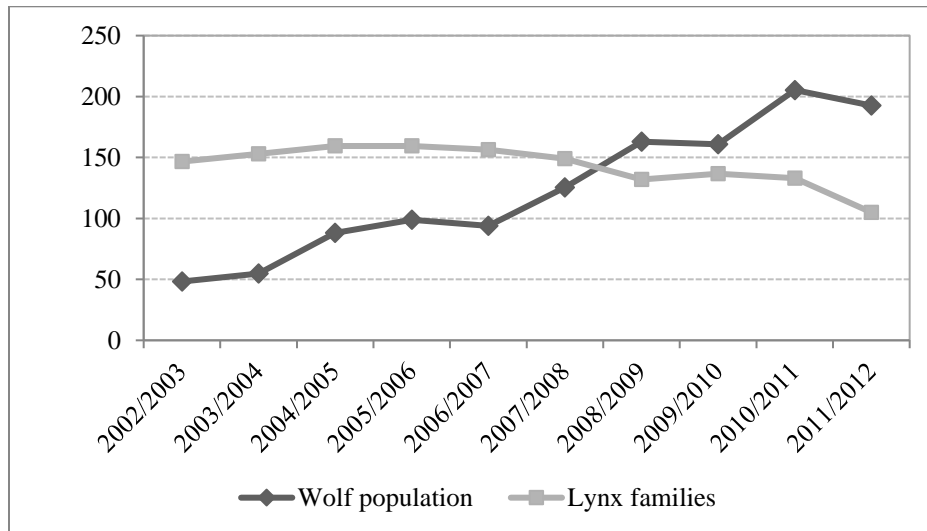

Fig. 2. Number of wolves (individuals) and lynxes (family groups) in south and middle Sweden.

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 pasturelands, compared to dense habitats, such as woodlands (Aanes and Andersen, 1996; Panzacchi et al., 2008). In some instances, a predation rate of 60%–85% on the fawns has been observed (Jarnemo and Liberg, 2005; Linell et al., 1995). There are no fox population

counts; however, Figure 3 shows the annual number of bagged red foxes since the 2002/2003 hunting season, which fluctuates approximately 50–60 thousand per year.

The lynxes have been found to kill the red foxes regularly, and a negative spatial correlation of the abundance of the red foxes and the lynxes has been observed, although it is not evident whether or not this correlation is the result of predation or of the foxes avoiding areas with higher lynx densities (Helldin et al., 2006). However, it has also been suggested that the lynx could provide food for the red foxes through leftovers from carcasses, thereby benefitting the lynx (Helldin, 2004). This could prove even truer when the winter conditions are hard and the snow depth is large, resulting in a difficult hunt for rodents (Selås and Vik, 2006).
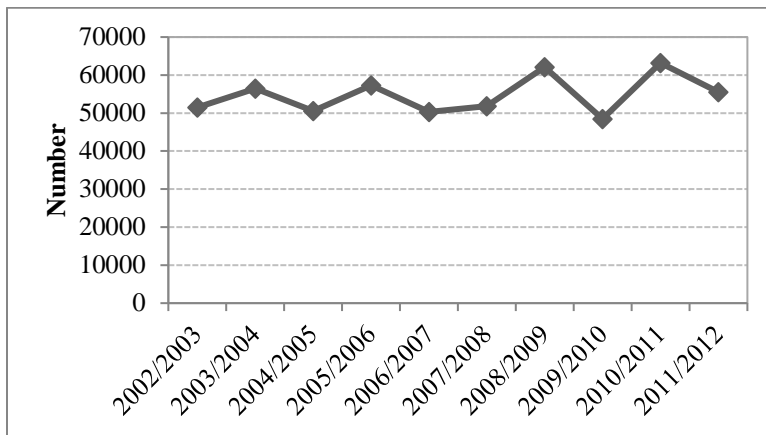

Fig. 3. Bagged red fox (individuals), 2002/2003 to 2011/2012 hunting seasons.

3. The theoretical model

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

3.1 Roe deer growth and harvest functions

As described above, the growth and, hence, the abundance of roe deer is affected by the presence of the predators, the winter conditions and the hunting efforts. 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, 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 snow cover (S). The change in the stock of the roe deer from time t to $t+1$ can be defined as follows:

$$X_{t+1} - X_t = F(X_t, Z_{it}) - h(X_t, E_t), F_x > 0, F_Z > 0 \tag{1}$$

The growth in the roe deer population, $F(X_t, Z_{it})$, 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 roe deer stock and the hunting effort. Following Clark (1990), we assume a logistic growth function, where the predators and the snow cover negatively affect both the intrinsic growth rate, r, and the carrying capacity, K, of the roe deer (Equation 2).

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

for $F_x > 0, F_{Z_i} < 0, F(X, 0) > 0$ for $X > 0$,

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.

Furthermore, we assume a simple Schaefer harvesting function:

$$h_t = qX_tE_t,$$ (3)

where q is the catchability coefficient, which is assumed to be constant. This assumption is a simplification, as the hunters' choice of technology could be affected by the presence of large carnivores, as well as the weather 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), or if the snow is too deep. This simplification is motivated by the lack of research studies and empirical data regarding hunter technology choices under different conditions.

3.2 Bioeconomic model

We assume that the roe deer are harvested under open-access conditions. The open-access assumption is motivated by the absence of the regulation of the roe deer harvesting in combination with the institutional structure of hunting. The hunting rights in Sweden follow the owner of the land and can be leased out, usually to a group of hunters. The roe deer migrates; therefore, it is not possible for a hunting group or a land owner to restrict access to the roe deer. Within a given hunting group, there can be informal agreements about the number of roe deer to be harvested in a given season, but the possibilities to monitor and ensure compliance with such agreements are small. Roe deer hunting is only permitted during the hunting season, which occurs in the autumn in most parts of the country; however, this does not affect the open-access assumption. Together, this suggests that an assumption about open access is a reasonable approximation of the prevailing conditions.

We will proceed to analyse the open-access equilibrium (i.e., the situation where the roe deer population and the level of hunting effort is constant over time). Following the standard approach in natural resource economics, it is assumed that the hunting effort over the next period will adjust in response to the real profits made in the current period (Clark, 1990; Conrad, 1995). Let p represent the constant unit value of the harvested roe deer, 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:

$$E_{t+1} - E_t = \theta[ph(X_t; E_t) - cE_t].$$ (4)

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:

$$X = \frac{c}{pq}, for \; E_{t+1} = E_t = E \tag{5}$$

$$E = \frac{r((K+\delta_i Z_i)-X)}{q}, \; for \; X_{t+1} = X_t = X \tag{6}$$

Equation (5) indicates a zero profit in the long run, while equation (6) 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 (6) we have:

$$\frac{\partial E}{\partial Z_i} = \frac{r\delta_i}{q} < 0. \tag{7}$$

Following Barbier and Strand (1998), the comparative static loss in the harvest, using equations (3) and (6) and the steady-state condition (5), will be:

$$\frac{\partial h}{\partial Z_i} = qX \left(\frac{rk+r\delta_i Z_i-rX}{q} \right) = \frac{r\delta_i c}{pq}. \tag{8}$$

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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:

$$p\partial h = \frac{r\delta_i c}{q}\partial Z_i < 0. \tag{9}$$

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 (7) and solving for h_t yield an equation that can be estimated:

$$h = qKE + q\delta_i Z_i E - \frac{q^2}{r}E^2 \;, \tag{10}$$

which can be expressed as:

$$h = \alpha E + \beta_i Z_i E + \gamma E^2 \;, \tag{11}$$

where α, β_i and γ are the coefficients to be estimated (see Table A.3, Appendix, for the identity of the coefficients).

3.3 Comparative statics

The marginal products of E and Z_i, derived using equation (11), are shown in equations (12) and (13):

$$MP_E = \frac{\partial h}{\partial E} = \alpha + \beta_i Z_i + 2\gamma E \tag{12}$$

and

$$MP_{Z_i} = \frac{\partial h}{\partial Z_i} = \beta_i E. \tag{13}$$

From equation (6), 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 (5), gives the change in the equilibrium harvest when Z_i changes:

$$\partial h = \frac{r\delta_i c}{pq} \partial Z_i = -\frac{c\beta_i}{p\gamma} \partial Z_i \tag{14}$$

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

$$p\partial h = \frac{r\delta_i c}{q} = -\frac{c\beta_i}{\gamma} \partial Z_i \tag{15}$$

Using equations (14) and (15), the comparative static effect on the harvests and the revenues can be evaluated when c and p are known.

3.4 Alternative specification of the regression function

The roe deer is not the main prey for the wolf. Therefore, it is relevant to consider how the availability of the moose, which is the wolf's primary prey, could affect the wolf impact on the roe deer harvests. Therefore, we specify an alternative version of equation (10), where we introduce a dummy variable for

the counties with a relatively high moose density compared to the roe deer density. The new regression equation (10´) is then specified as follows:

$$h = \alpha E + \theta_1 D Z_W E + \theta_2 (1 - D) Z_W E + \beta_j Z_j E + \gamma E^2, \qquad\qquad (10')$$

with $D = 1$ for the counties with a comparatively high moose density, $D = 0$ for the other counties and j = L, F, S. The corresponding static effect is calculated similarly for equation (10), except that equation (10') 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 wolves in the counties with a higher relative moose density for a given hunting effort, while θ_2 represents the corresponding impact in the other counties.

4. 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. Table 1 shows the descriptive statistics for our panel dataset, which includes 16 counties for the period of the 2002/2003 to 2011/2012 hunting seasons. 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[1] to for account for county size. For the descriptive statistics per square kilometre, see Table A.1, Appendix.

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[1] 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).

4.1 Hunting bag statistics

The dependent variable in the model is the number of bagged 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. Figure 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 boars, fallow deer and red deer. The roe deer share in the total hunting bag has decreased over the studied period for all of the counties (Figure 5). Figure 5 also shows the bagged number of roe deer in the first year and the last year of the study period for each county. As seen, the reduction varies substantially across the different counties. Over the studied time period, the relationship between the three major game species (i.e., roe deer, moose and wild boars) has changed. 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.

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 the approach by Beverton and Holt (1957), originally developed for fisheries. 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[2] can be seen as an equivalent to the number of vessels. Figure 4 shows the development over time of the number of hunting licences. We calculated the share of effort devoted to roe deer hunting as the share in the harvest of the three major game species (i.e., moose, roe deer and wild boars), fallow deer and red deer. Our measure of the hunting effort in a given year was then calculated as:

$$E = \frac{\left(\frac{bagged\ amount\ of\ roe\ deer}{total\ number\ of\ bagged\ game}\right) * number\ of\ hunting\ licenses}{area\ of\ county\ in\ km^2} \quad (4.1)$$

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 hunted due to its negative impact on the roe deer populations.

Evidently, this is a relatively simple measure of effort. The measure is more relevant if the number of hunting days per hunter can be assumed to be constant over time and across counties and if each species is hunted separately. We think it is reasonable to assume that the number of hunting days has been approximately constant 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 hunters or a few hunters, usually around sunset,

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[2] Every hunter must acquire a national hunting licence each year from the Environmental Protection Agency, at a cost of about 30 euros. Once in possession of such a licence, the hunter is allowed to hunt all non-protected species, provided access to the hunting land.

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.
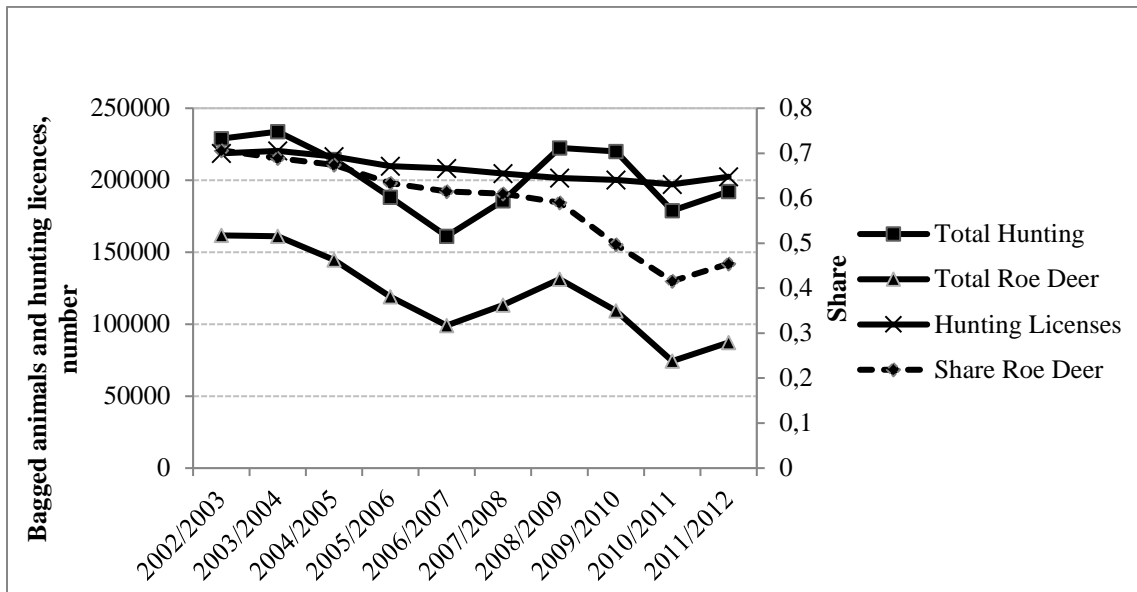

Fig. 4. Hunting bag statistics and hunting licences.

Source: The Swedish Hunting Association (www.viltdata.se) and the Swedish Environmental Protection Agency.
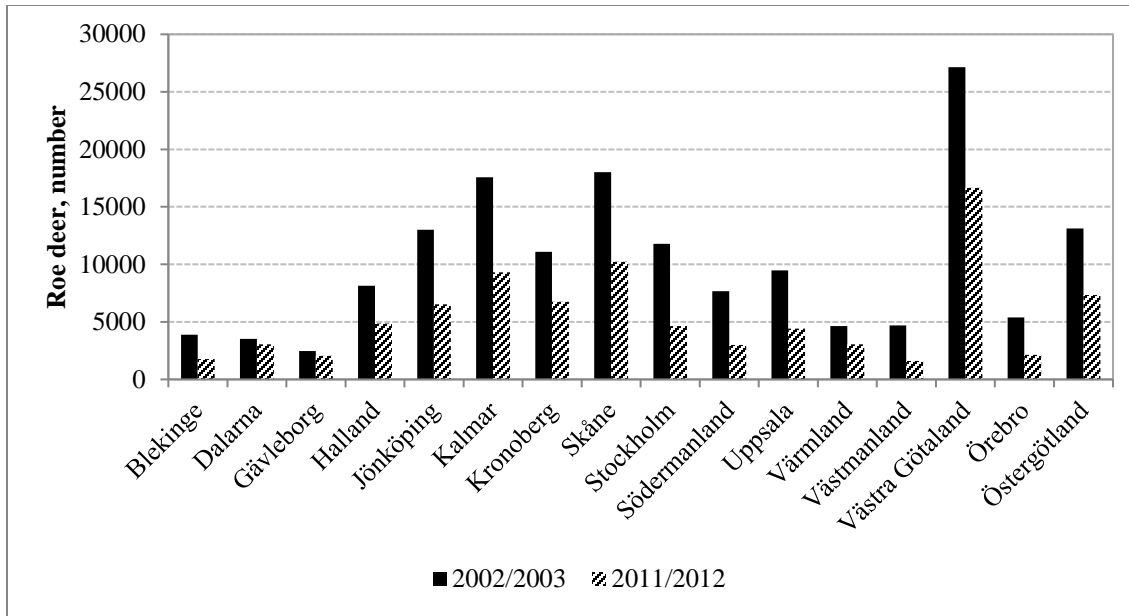
Fig. 5. Roe deer hunting bag in different counties, 2002/2003 to 2011/2012 hunting seasons.

Source: The Swedish Hunting Association (www.viltdata.se).

4.1.1 Moose-dense counties

The counties are classified into those that have a higher moose density compared to the roe deer density. 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 (10') is set to one for these counties and zero otherwise.

4.2   Predator population and weather data

The data for the lynxes and the wolves were based on census materials published by the Wildlife Damage Center. Notably, some counties have had zero presence of lynxes or wolves in certain years, but over the

full time period, all of the counties host either lynxes or wolves. Weather data have been obtained from the Swedish Meteorological and Hydrological Institute (SMHI).

4.2.1 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[3]. The number of lynx families is estimated using the accumulated records of tracks and observations during the snow tracking period, compiled at the end of the season. The censuses are adjusted for the number of nights of tracking, and the extrapolations to obtain full spatial coverage are made accounting for landscape heterogeneity (Andrén et al., 2010; Liberg and Andrén, 2006). The census estimates for the different ecological regions are transferred to the counties, following the approach of Andrén et al. (2010).

4.2.2 The wolf population

The wolf censuses are conducted by the Wildlife Damage Center at the Grimsö Research Station, together with the respective counterparts in Norway and Finland, and are published annually. The estimates are based on snow tracking, radio telemetry and DNA analysis. In the census reports, the wolf presence is 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 is partly shared with Norway, and the home range of the wolves and the wolf packs can cover more than one county. In order to correct for this, the number of wolves in the border areas have been equally divided over the relevant counties. In some of the counties, the wolves occur 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. In some instances, the values coincide. The census data used in this

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[3] The size of a lynx family can vary to some extent. To approximate the number of individuals, one can use a scaling factor of 5.48–6.24, where the lower (higher) number applies in the ecological areas with a lower (higher) prey density (Andrén et al., 2002). The ecological areas do not correspond to the counties, implying that for our data, the appropriate scaling factor lies within the range of these numbers.

paper were based on the minimum values to reduce the uncertainty and because, in some instances, no maximum numbers were reported.

When doing the regression analysis, we will consider two alternatives: one where we use the total number of wolf individuals in a county and one where we use 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 Sand et al. (2011) 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.

4.2.3 *The red fox population*

There are no population data on the red fox. Noting that the hunting bag statistics are frequently used as a proxy for the wildlife populations in the ecological literature (Elmhagen et al., 2011; Forchhammer and Asferg, 2000; Liberg and Andrén, 2006), 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 the roe deer. Therefore, the fox hunting bag is not an ideal proxy for the population in this case. In addition, the coverage of the fox hunting in the statistics could be more uncertain than for the other species.

4.2.4 Snow data

Severe winters lead to starvation and reduced survival and reproduction of the roe deer (Gaillard et al., 1993; Kjellander and Nordström, 2003; Mysterud et al., 1997). Snow depth is an important factor in this context. 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 (Table A.2, Appendix). 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[4]. As shown in Figure 6, the average number of days with a snow cover greater than 30 cm varies considerably between years. Table A.2 illustrates the fact that the average snow cover decreases from north to south.
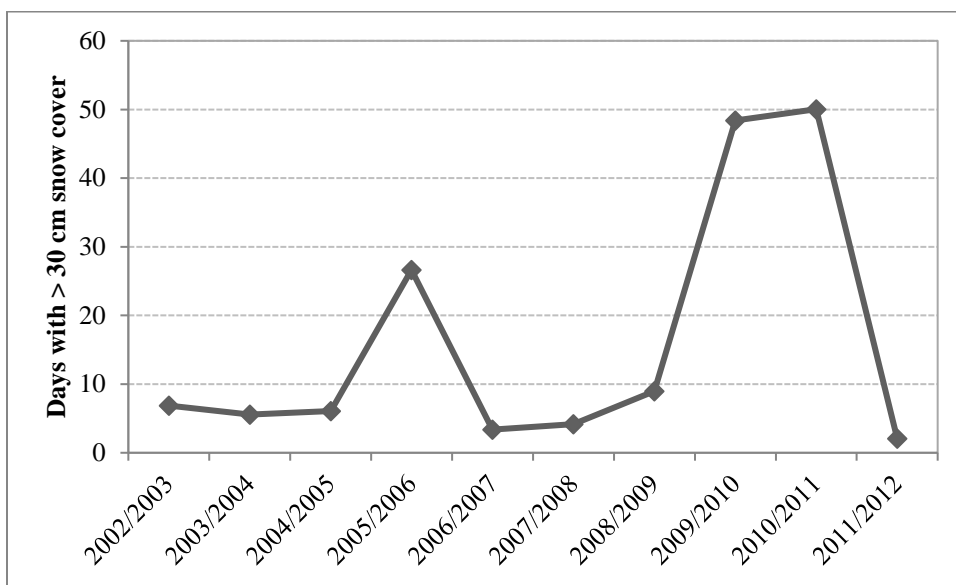
Fig. 6. Average over counties, number of days with snow cover > 30 cm.
Source: Swedish Meteorological and Hydrological Institute (SMHI).

5. Estimation and results

In the following section, the estimation procedure is explained, and the relevant statistical properties are evaluated. This is followed by a presentation of the results. Equations (10) and (10') are estimated using a regression analysis in a panel data setting. In total, we estimate four models, using either the number of wolves or the number of wolf territories.

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

The statistical properties were examined in the following manner: the Breusch-Pagan/Cooks-Weisberg test for homoskedasticity rejected the null-hypothesis, implying that there is heteroskedasticity 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.4, 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, heteroskedasticity 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 heteroskedasticity 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 (Figure A.1, Appendix) and Cook's distance. The LVR plot indicated that Stockholm has high leverage and large squared residuals, which is an undesirable combination. Södermanland had a large residual in 1 year but below average leverage, indicating that the effect of the residual is low and can be left in the dataset. However, Stockholm was removed from the dataset following the LVR plot. It can be expected that Stockholm has an inflated number of hunters in the county, while a large share of hunters hunt outside of Stockholm. Hence, the hunting effort variable is not a good measure of the effort in Stockholm.

The results from the pooled regression can be found in Table 2 for all four of the models. 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

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 $p < 0.001$.

5.1 Results

Using the estimated coefficients in combination with equations (12)–(15), 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 lynxes, 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 would decrease the roe deer harvest by 44–55 units. To obtain comparable results for the wolf, we divided MP_W in models 3 and 4 by 2.83, which is the average number of wolves per territory. Accordingly, the marginal productivity of one additional wolf is 86–93 in moose-dense counties and 308–355 in other counties. When not controlling for moose density, the use of the wolf numbers and territories (models 1 and 3) yielded approximately the same reduction in the roe deer harvest (243).

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 can to some extent be 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 can be 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 percentage 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.

5.2 Bioeconomic steady-state adjustments

In the previous section, the effects were calculated for a given, average hunting effort. However, with a constant hunting effort, increases in the number of predators will eventually lead to the depletion of the roe deer stock. Therefore, in this section, we will analyse the effect of the lynxes and the wolves in a steady-state bioeconomic equilibrium in which the hunters instantaneously adjust the effort level when the predator levels increase, hence moving to a new equilibrium.

The equilibrium results were calculated using equations (13) and (14), satisfying both the biological and the open-access steady-state conditions. Following Barbier and Strand (1998), we utilised the 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 2,170 SEK[5]. Mensah et al. (2015) and Lundhede et al. (2015) reported values around 4,000 SEK. However, these 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 more scarce. Therefore, we used the estimate in Karlsson (2010), which is a more representative value for Swedish hunting in general. This estimation also gives a conservative value for the costs of predation. The cost c is computed for each county and year, yielding a corresponding change in harvest. From Table 4, we can see that an

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[5] Swedish crowns, in 2014 year value.

increase in the predator levels will decrease the steady-state harvest level of roe deer, thus reducing the revenues from hunting activities. The results indicated that 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 of the roe deer harvest by 697–703 units[6]. When distinguishing between the moose-dense counties and the other counties, an increase in the number of individual wolves in the moose-dense counties would have a smaller impact on the roe deer harvests (411–439 units) compared to that in the other counties (728–943 units).

Table 4

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

	Wolf, Harvest Impact	Lynx, Harvest Impact	Wolf, Revenue Impact (SEK)	Lynx, Revenue Impact (SEK)
Model 1	-697	-157	-1,511,438	-340,395
Model 2	-943[a]	-150	-2,110,826[a]	-366,831[a]
	-411[b]		-892,414[b]	-209,468[b]
Model 3[c]	-1991	-128	-4,319,834	-277,347
Model 4[c]	-2062[a]	-126	-5,151,694[a]	-309,692[a]
	-1243[b]		-2,697,421[b]	-176,841[b]

[a] Other counties.

[b] Moose dense counties.

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

5.3 County-level impacts

Table 5 shows the county-level impact of the predators based on model 2, which makes use of the wolf numbers and distinguishes between the moose-dense counties and the other counties. We calculated the

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[6] Note that for models 3 and 4, the wolf figures have to be divided by 2.83.

effects assuming that there was a bioeconomic equilibrium in each year and county. Table 5 presents the average values for each county.

The impact of the predators on the roe deer harvests is determined by the marginal product of effort, which varies across the counties (Table A.5, 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. Given the monetary value of the roe deer harvests, the marginal cost in terms of hunting values foregone varies between the counties and ranges between 169,000 and 531,000 SEK for the lynxes and 718,000 and 3,058,000 SEK 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 (SEK)	Wolf, revenue impact (SEK)
Blekinge	-126	-723	-272,611	-1,568,666
Dalarna	-90	-382	-194,552	-828,866
Gävleborg	-78	-331	-168,579	-718,210
Halland	-148	-852	-321,277	-1,848,696
Jönköping	-159	-914	-344,551	-1,982,624
Kalmar	-241	-1,389	-523,483	-3,012,236
Kronoberg	-206	-1,184	-446,501	-2,569,267
Skåne	-155	-890	-335,590	-1,931,059
Södermanland	-245	-1,410	-531,366	-3,057,598
Uppsala	-160	-923	-347,803	-2,001,335
Värmland	-103	-438	-223,097	-950,477
Västmanland	-104	-599	-225,771	-1,299,134
V. Götal.	-112	-645	-243,330	-1,400,175
Örebro	-116	-494	-251,645	-1,072,103
Östergötland	-204	-1,175	-442,857	-2,548,298
Average moose counties	*-97*	*-411*	*-209,468*	*-892,414*
Average other counties	*-170*	*-973*	*-366,831*	*-2,110,826*
Average total	*-150*	*-823*	*-324,868*	*-1,785,916*

6. Discussion and conclusions

Our results regarding the harvest impact of carnivores, MP_W and MP_L, can be compared to the results in the ecological studies where the kill rates are estimated. These productivities can be interpreted as the reduction in harvest required if the roe deer population is kept constant at a given level of effort.

Andrén and Liberg (2015) estimated that a lynx family kills 6.2 ± 0.83 roe deer per month, corresponding to a kill rate of 64–85 roe deer per year. Our model 2 (Table 3) implies a 50-unit reduction in the roe deer harvest due to an additional lynx family. Although our finding is slightly below that in the study of Andrén and Liberg (2015), the calculated impact in several of the counties falls within their estimated interval, suggesting that our findings are plausible.

There are no corresponding data on the kill rate of the roe deer by the wolves; however, it is estimated that in the summer, the wolf kill rate on moose corresponds to approximately 6.6 kg of prey biomass per day in areas with a higher moose density (Sand et al., 2008). Assuming constant kill rates over the year, a wolf would kill approximately 2,400 kg biomass annually[7]. 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). To obtain a crude measure of the number of roe deer that would give the same total biomass per year, we calculated this number for different assumptions about the distribution of the adults and juveniles in the population. The corresponding number of killed roe deer then ranges from 128 to 321 units per year, when the share of the juveniles in the wolf diet is changed from 0% to 100%. This can be compared to the results from model 2 (Table 3). These results suggest that in non-moose counties, an additional wolf reduces the roe deer harvests by approximately 355 units. In moose counties, the corresponding reduction is 86 units. Thus, we obtained the numbers that are reasonable in comparison to the estimates from Sand et al. (2008); however, there is some uncertainty involved because the wolves do not solely consume moose in moose-dense areas or solely roe deer in other areas.

Our cost estimates can be compared to the results in the economic studies where other types of carnivore-related costs are investigated. We found that in a bioeconomic equilibrium, the cost of an additional lynx

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[7] This is a high-end estimate since winter kill rates are typically lower (Sand et al. 2008).

family is 180–370 kSEK, and the cost of an additional wolf is 950–2100 kSEK. This can be compared to the total value of hunting in Sweden, which is estimated to be 3.4 billion SEK in the 2015 year value (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, but they can have a considerable effect on the local level. Further, Widman and Elofsson (2016) estimated that the marginal cost of wolves and lynxes, in terms of depredation on sheep, is on average 4250 and 150 SEK, respectively, suggesting that the economic impact on the roe deer hunters substantially exceeds that of the sheep farmers. Based on the average hunting values, Boman et al. (2003) calculated that the cost of wolves in Sweden, in terms of the impact on moose and roe deer hunting, amounts to 30–70 kSEK per wolf, while in the areas with reindeer herding, reindeer depredation costs are approximately 115 kSEK per wolf. These values are far below our estimates, which is explained partly by the use of averages in the calculations. Finally, although the willingness to pay for the preservation of large carnivores is estimated to be large (e.g., Bostedt et al., 2007; Broberg and Brännlund, 2007; and Ericsson et al., 2008), marginal values cannot be inferred from the studies; therefore, comparisons are difficult to make.

6.1 Conclusions

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 negative effect of the marginal increase in the predators is stronger 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, for example increased wolf numbers in Dalarna and Värmland. However, this can have considerable distributional implications, as the wolf numbers are already the largest in these counties, implying that that the people in these counties already carry a large share of the costs for wolf preservation. Our conclusions in this regard are similar to those in Boman et al. (2003).

Furthermore, our results showed that the relative availability of different prey has a large importance for the cost of harvest reductions of the studied species. This has policy implications as well. 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 and will depend on the degree of flexibility in

the dietary choice of the carnivore species in question. This finding also raises the question of possibilities to undertake actions that benefit low-valued alternative prey, which could reduce the pressure on the more high-value game species.

Finally, the results showed that a larger number of days with deep snow reduces the roe deer harvests. Climate change is expected to reduce the number of days with deep snow cover. However, climate change may also lead to other changes in the ecosystem, which we did not account for in this study. Therefore, we cannot draw any conclusions about the impact of climate change on the roe dear harvest values.

Our study has several limitations, which should be considered when interpreting the results. For example, we did not account for the possible feedback effects from game abundance on the carnivore populations, and our analysis is limited to that of a static equilibrium. This is a simplification, as the predator-prey relationship between the roe deer and the lynx is relatively intricate, and it is possible that both the roe deer and the lynx will eventually be stuck at low population levels (Liberg and Andrén, 2011). In addition, we did not account for the possibility that the hunters change their use of hunting dogs or their choice of hunting dog type in response to an increased wolf abundance because of the risk of the wolves causing injuries to the hunting dogs (Franzén, 1991a). Further research on these subjects would be valuable.

References

Aanes, R., Andersen, R., 1996. The effects of sex, time of birth, and habitat on the vulnerability of roe deer fawns to red fox predation. Canadian Journal of Zoology 74, 1857-1865.

Andrén H., Svensson, L., Liberg, O., Hensel, H., Thompson H., Chapron, G., 2010. Den svenska lodjurspopulationen 2009-2010 samt prognoser för 2011-2012. [The Swedish lynx population 2009-2010 and forecasts for 2011-2012]. Census report 2010-4, Wildlife Damage Center, Department of Ecology, Swedish University of Agricultural Sciences, Riddarhyttan.

Andrén, H., Linnell, J. D. C., Liberg, O., Ahlqvist, P., Andersen, R., Danell, A., Franzen, R., Kvam, T., Odden, J., Segerstrom, P., 2002. Estimating total lynx (*Lynx lynx*) population size from censuses of family groups. Wildlife Biology 8, 299-306.

Andrén, H., Liberg, O., 2015. Large impact of Eurasian lynx predation on roe deer population dynamics. PLoS ONE, 10(3), e0120570. http://doi.org/10.1371/journal.pone.0120570.

Arbieu, U. 2012. Predator Community and Prey Dynamics – A Case Study of Roe Deer and Re-colonizing Fox, Lynx and Wolf. Master thesis 2012:14, Department of Ecology, Swedish University of Agricultural Sciences, Uppsala.

Barbier, E., Strand, I., 1998. Valuing Mangrove-Fishery Linkages. Environmental and Resource Economics 12, 151-166.

Barbier, E.B., 2007. Valuing ecosystem services as productive inputs. Economic Policy 22(49), 177–229.

Beverton, R.J.H., Holt, S.J., 1957. On the dynamics of exploited fish populations. Fisheries Investigations Series 2(19). Ministry of Agriculture, Fisheries, and Food, London, UK.

Boman, M., Bostedt, G., Persson, J., 2003. The bioeconomics of the spatial distribution of endangered species: The case of the Swedish wolf population. Journal of Bioeconomics 5, 55-74.

Bostedt, G., Grahn, P., 2008. Estimating cost functions for the four large carnivores in Sweden. Ecological Economics 68, 517-524.

Bostedt G., Ericsson G., Kindberg J., 2008. Contingent values as implicit contracts: estimating minimum legal willingness to pay for conservation of large carnivores in Sweden. Environmental and Resource Economics 39, 189–198.

Broberg, T., Brännlund, R., 2007. On the value of preserving the four large predators in Sweden: a regional stratified contingent valuation analysis. Journal of Environmental Management 88, 1066–1077.

Cederlund, G., Liberg, O., 1995. Rådjuret, viltet, ekologin och jakten. [The roe deer, wildlife, ecology and hunting]. The Swedish Hunters' Association, Spånga.

Clark, C.W., 1990. Mathematical bioeconomics. Second edition. Wiley, New York, New York, USA.

Conrad, J.M., 1995. Bioeconomic models of the fishery. In: Bromley, D.W. (Ed.), The Handbook of Environmental Economics. Blackwell, Oxford, pp. 405–432.

Danell, A., Svensson, L., 2011. Resultat från inventering av lodjur i Sverige vintern 2010/2011. [Results from the inventory of the lynx in Sweden winter 2010/2011.]. Census report 2011-11, Wildlife Damage Center, Department of Ecology, Swedish University of Agricultural Sciences, Riddarhyttan.

Driscoll, J.C., Kraay, C.A., 1998. Consistent Covariance Matrix Estimation with Spatially Dependent Panel Data. Review of Economics and Statistics 80, 549-560.

Elmhagen, B., Hellström, P., Angerbjörn, A., Kindberg, J., 2011. Changes in vole and lemming fluctuations in northern Sweden 1960-2008 revealed by fox dynamics. Annales Zoologici Fennici 48, 167-179.

EPA, 2014a. Nationell förvaltningsplan för lodjur – Förvaltningsperioden 2014-2019. [National management plan for lynx - Management period 2014-2019]. The Swedish Environmental Protection Agency, Stockholm.

EPA, 2014b. Nationell förvaltningsplan för varg – Förvaltningsperioden 2014-2019. [National management plan for wolf - Management period 2014-2019]. The Swedish Environmental Protection Agency, Stockholm.

Ericsson, G., Bostedt, G., Kindberg, J., 2007 Willingness to pay (WTP) for wolverine *Gulo gulo* conservation. Wildlife Biology 13(2), 2-12.

Ericsson, G., Bostedt, G., Kindberg, J., 2008. Wolves as a symbol for people's willingness to pay for large carnivore conservation. Society and Natural Resources 21, 1-16.

Foley, S.W., Armstrong, T., van Rensburg, M., 2010. Estimating Linkages between redfish and cold water coral on the Norwegian coast. Marine Resource Economics 25(1), 105-120.

Forchhammer, M.C., Asferg, T., 2000. Invading parasites cause a structural shift in red fox dynamics. Proceedings of the Royal Society B: Biological Sciences 267, 779-786.

Franzén, R., 1991a. Artfaktablad – *Canis Lupus Lupus* – Varg. [Fact sheet - *Canis Lupus Lupus* – Wolf]. The Swedish Species Information Center, Swedish University of Agricultural Sciences, Uppsala.

Franzén, R. 1991b. Artfaktablad – *Lynx Lynx* – Lodjur. [Fact sheet - *Lynx Lynx* – Lynx]. The Swedish Species Information Center, Swedish University of Agricultural Sciences, Uppsala.

Fryxell, J.M., Hussell, D.J.T., Lambert, A.B., Smith, P.C., 1991. Time lags and population fluctuations in white-tailed deer. Journal of Wildlife Management 55, 377-385.

Gaillard, J.M., Delorme, D., Boutin, J.M., Laere, G.V., Boisaubert, B., Pradel, R., 1993. Roe deer survival patterns: a comparative analysis of contrasting populations. Journal of Animal Ecology 62, 778-91.

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

Gervasi, V., Nilsen, E., Sand, H., Panacchi, M., Rauset, G., Pedersen, H., Kindberg, J., Wabakken, P., Zimmerman, B., Odden, J., Liberg, O., Swenson, J., Linell, J., 2012. Predicting the potential demographic impact of predators on their prey: A comparative analysis of two carnivore-ungulate systems in Scandinavia. Journal of Animal Ecology 81, 443-454.

Helldin, J.O., Liberg, O., Glöersen, G., 2006. Lynx (*Lynx lynx*) killing red foxes (*Vulpes vulpes*) in boreal Sweden – frequency and population effects. Journal of Zoology 270, 657–663.

Hoechle, D., 2007. Robust standard errors for panel regression with cross-sectional dependence. The Stata Journal 7(3), 281-312.

Hussain, A., Munn, I.A., Brashier, J., Jones, W.D., Henderson, J.E., 2013. Capitalization of hunting lease income into northern Mississippi forestland values. Land Economics 89(1), 137-153.

Häggmark-Svensson T., Elofsson K., Engelmann M., Gren I-M. 2015. A review of the literature on benefits, costs, and policies for wildlife management. Working Paper 2015:01, Department of Economics, Swedish University of Agricultural Sciences, Uppsala.

Jarnemo, A., Liberg, O., 2005. Red fox removal and roe deer fawn survival – A 14-year study. Journal of Wildlife Management 63(3), 1090-1098.

Johansson, M., Sjöström, M., Karlsson, J., Brännlund, R., 2012. Is human fear affecting public willingness to pay for the management and conservation of large carnivores? Society & Natural Resources: An International Journal 25, 610–620.

Karlsson, P., 2010. Externa kostnader för viltolyckor. [External costs of wildlife accidents]. Master's thesis 2010:21, Department of Ecology, Swedish University of Agricultural Sciences, Uppsala.

Kataria, M., 2007. A cost-benefit analysis of introducing nonnative species: the case of signal crayfish in Sweden. Marine Resource Economics 22, 15–28.

Kjellander, P., Nordström, J., 2003. Cyclic voles, prey switching in red fox, and roe deer dynamics - a test of the alternative prey hypothesis. Oikos 101, 338-44.

Knowler, D., Barbier, E.B., Strand, I., 2001. An open-access model of fisheries and nutrient enrichment in the Black Sea. Marine Resource Economics 16, 195–217.

Kojola, I., Kuittinen, J. 2002. Wolf attacks on dogs in Finland. Wildlife Society Bulletin 30:498-501

Lecocq, Y. 2004. Game management and hunting in an enlarged European Union. Game & Wildlife Science 21: 267-273.

Liberg, O., Andrén, H., 2006. The lynx population in Sweden 1994-2004. An evaluation of census data and methods. Wildlife Damage Center and Grimsö Wildlife Research Station, Swedish University of Agricultural Sciences.

Liberg, O., Andrén H. 2011. Rådjur styr lodjursstammen. [Roe deer control the lynx population]. Svensk Jakt 4.

Lindström, E.R., Andrén, H., Angelstam, P., Cederlund, G., Hörnfeldt, B., Jäderberg, L., Lemnell, P.-A., Martinsson, B., Sköld, K. & Swenson, J.E., 1994. Disease reveals the predator: sarcoptic mange, red fox predation, and prey populations. Ecology 75, 1042–1049.

Linnell, J.D.C., Aanes, R., Andersen, R., 1995. Who killed bambi? The role of predation in the neonatal mortality of temperate ungulates. Wildlife Biology 1, 209–223.

Lundhede, T.H., Jacobsen, J.B., Thorsen, B.J., 2015. A hedonic analysis of the complex hunting experience. Journal of Forest Economics 21, 51-66.

Mattson L., Boman M., Ericsson, G., 2008. Jakten i Sverige – ekonomiska värden och attityder jaktåret 2005/06 [Hunting i Sweden – economic values and attitudes hunting year 2005/06]. Report 1, Adaptive Management of Wildlife and Fish. Umeå, Sweden.

McCluskey, S.M., Lewison, R.L., 2008. Quantifying fishing effort: a synthesis of current methods and their applications. Fish and Fisheries 9, 188–200.

Melis, C., Basille, M., Herfindal, I., Linnell, J., Odden, J., Galliard, JM., Högda, KA., Andersen R., 2010. Roe deer population growth and lynx predation along a gradient of environmental productivity and climate in Norway. Ecoscience 17(2), 166-174.

Melis. C., Jędrzejewsk, B., Apollonio, M., Bartoń, K.A., Jędrzejewski, W., Linnell, J.D.C., Kojola, I., Kusak, J., Adamic, M., Ciuti, S., Delehan, I., Dykyy, I., Krapinec, K., Mattioli, L., Sagaydak, A., Samchuk, N., Schmidt, K., Shkvyrya, M., Sidorovich, V.E., Zawadzka, B., Zhyla, S., 2009. Predation has a greater impact in less productive environments: variation in roe deer, *Capreolus capreolus*, population density across Europe. Global Ecology and Biogeography 18, 724–734.

Mensah, J.T., Elofsson, K. & Kjellander, P., 2015. Economically optimal management of two deer species competing for food. Department of Economics Working Paper 2015:2, Swedish University of Agricultural Sciences, Uppsala, Sweden.

MOEE (Ministry of the Environment and Energy). 2013. En hållbar rovdjurspolitik. [A sustainable carnivore policy]. Prop. 2012/13:191. Ministry of the Environment and Energy, Stockholm.

Mysterud, A., Bjornsen, B.H., Ostbye, E., 1997. Effects of snow depth on food and habitat selection by roe deer *Capreolus capreolus* along an altitudinal gradient in south-central Norway. Wildlife Biology 3(1), 27-33.

Odden, J., Linnell, J., Andersen, R., 2006. Diet of Eurasian lynx, *Lynx lynx,* in the boreal forest of southeastern Norway: the relative importance of livestock and hares at low roe deer density. European Journal of Wildlife Research 53, 237-244.

Panzacchi, M., Linnell., J.D.C., Odden, J., Odden, M., Andersen, R., 2008. When a generalist becomes a specialist: patterns of red fox predation on roe deer fawns under contrasting conditions. Canadian Journal of Zoology 86, 116-126.

Pinet, J.M., 1995. The hunter in Europe. Federation of Associations for Hunting and Conservation of the EU. Available October 14, 2015 at http://www.kora.ch/malme/05_library/5_1_publications/P_and_Q/Pinet_1995_The_hunters_in_Europe.pdf 2006-11-25

Sand, H., Wabakken, P., Zimmermann, B., Johansson, Ö., Pedersen, H.C., Liberg, O., 2008. Summer kill rates and predation pattern in a wolf-moose system: can we rely on winter estimates? Oecologia 156, 53-64.

Sand, H., Andrén, H., Swenson, E. J., Kindberg, J., 2011. Fler jägare på älgpopulationen – predationsmönster hos varg och björn. [More hunters on the moose population - predation patterns of wolves and bears]. Fakta Skog 25, Swedish University of Agricultural Sciences, Uppsala.

Selås, V., Vik, J.O., 2006. Possible impact of snow depth and ungulate carcasses on red fox (*Vulpes vulpes*) populations in Norway. Journal of Zoology 269, 299–308.

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

Tschirhart, J., 2009. Integrated ecological-economic models. Annual Review of Resource Economics 1(1), 381–407.

U.S. Fish & Wildlife Service. 2012. 2011 National survey of fishing, hunting, and wildlife-associated recreation: National overview. As available October 14, 2015 at https://www.doi.gov/sites/doi.gov/files/migrated/news/pressreleases/upload/FWS-National-Preliminary-Report-2011.pdf

Wabakken, P., Sand, H., Liberg, O., Bjärvall, A., 2001. The recovery, distribution and population dynamics of wolves on the Scandinavian Peninsula,1978-1998. Canadian Journal of Zoology 79, 1-16.

Zetterberg, A., 2014. Resultat från inventering av lodjur i Sverige vintern 2012/2013. [Results from the inventory of the lynx in Sweden winter 2012/2013]. Census report 2013-05, The Wildlife Damage Center, Department of Ecology, Swedish University of Agricultural Sciences, Riddarhyttan.

Appendix

Table A.1

Descriptive statistics per km^2.

Variable	Mean	SD	Min	Max
Number of wolves	0.0005	0.00009	0	0.004
Lynx Families	0.0008	0.0009	0	0.004
Effort	0.7160	0.3792	0.1471	1.7276
Bagged Animals				
Roe Deer	0.8022	0.4735	0.0849	2.2705
Moose	0.2578	0.1028	0.0336	0.5223
Wild Boar	0.2852	0.3463	0	1.4647
Red Fox	0.3601	0.1858	0.0958	1.2460

Table A.2

Snow cover data.

County	Average Days of Snow Cover > 30 cm	Number of Stations
Blekinge	5.4	2
Dalarna	66.1	4
Gävleborg	27.3	2
Halland	14.9	1
Jönköping	12.9	2
Kalmar	9.4	3
Kronoberg	7.1	3
Skåne	0.8	3
Stockholm	13.5	2
Södermanland	14.6	2
Uppsala	25.3	2
Värmland	14.3	3
Västmanland	11.9	1
Västra Götaland	9.6	8
Örebro	16.1	3
Östergötland	9.9	2

Source: Swedish Meteorological and Hydrological Institute (SMHI).

Table A.3

Identity of estimated coefficients.

Coefficient	Identity
A	qK
β_i	$q\delta_i$
Γ	$-q^2/r$

Table A.5

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

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]*

[a] Moose-dense counties.

[b] Other counties

Table A.4

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

Note: *significant at $p < 0.1$, **significant at $p < 0.05$ and ***significant at $p < 0.001$.
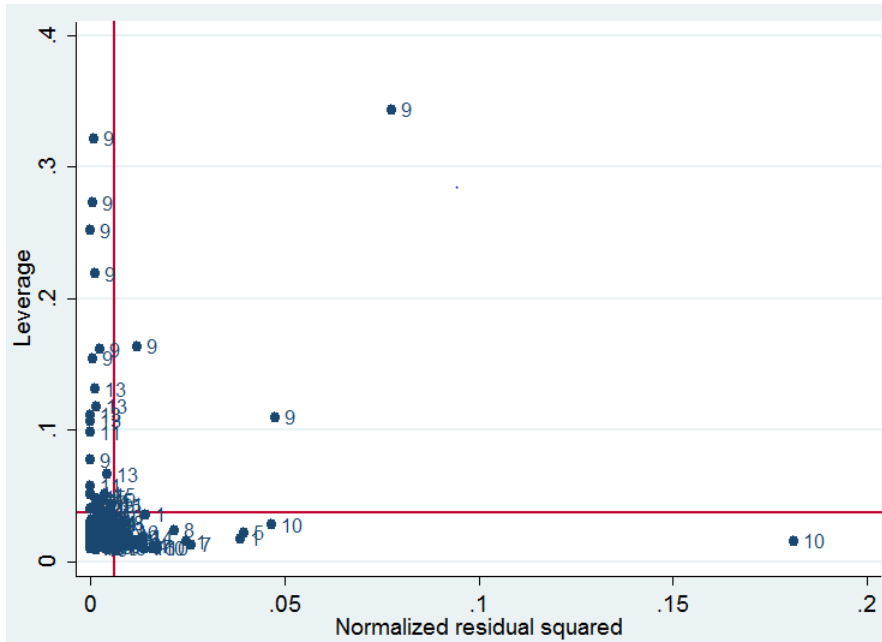
Fig. A.1. Leverage versus squared residual plot.

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.