

# Roe deer population growth and lynx predation along a gradient of environmental productivity and climate in Norway<sup>1</sup>

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**Abstract:** The extent to which large carnivores compete with hunters for harvestable populations of wild ungulates is a topic of widespread controversy in many areas of the world where carnivore populations are recovering or are reintroduced. Theory predicts that predation impacts should vary with prey density and environmental conditions. To test this prediction, we analyzed trends in an index of population abundance of roe deer (*Capreolus capreolus*) over 9 y in 144 Norwegian municipalities. The municipalities span a wide range of landscapes and climatic conditions and were associated with a varying degree of Eurasian lynx (*Lynx lynx*) presence. There was a wide variation in trends of roe deer abundance (estimated long-term average  $\lambda$  ranging from 0.69 to 1.23) among municipalities. Roe deer population growth rates were lower in the municipalities with lynx and harsh climatic conditions than in municipalities with mild climatic conditions and/or without lynx. Thus, lynx presence appears to be having a negative impact on roe deer populations; this was especially evident in areas with unfavourable environmental conditions. Our finding that estimated long-term average values of  $\lambda$  were less than 1 in many municipalities indicates that roe deer populations in Norway may not be able to sustain current combined mortality from hunters and lynx, especially in marginal areas.

**Keywords:** population dynamics, predation, top-down control, ungulate, vegetation productivity, winter harshness.

**Résumé :** L'intensité de la compétition entre les grands carnivores et les chasseurs pour la récolte de populations d'ongulés sauvages est un sujet controversé dans plusieurs régions du monde où les populations de carnivores se rétablissent ou sont réintroduites. La théorie prédit que les impacts de la prédation devraient varier avec la densité des proies et les conditions environnementales. Pour tester cette prédiction, nous avons analysé les tendances d'un indice d'abondance de populations de chevreuils (*Capreolus capreolus*) durant 9 ans dans 144 municipalités norvégiennes. Les municipalités couvrent une vaste gamme de paysages et de conditions climatiques et sont associées à des niveaux variables de présence du lynx d'Eurasie (*Lynx lynx*). Il y avait une grande variation dans les tendances d'abondance du chevreuil entre les municipalités (moyenne à long terme estimée  $\lambda$  variant de 0.69 à 1.23). Les taux de croissance des populations de chevreuils dans les municipalités avec présence du lynx et ayant des conditions climatiques difficiles étaient inférieurs à celles ayant des conditions climatiques douces et/ou sans la présence du lynx. Ainsi, la présence du lynx semble avoir un impact négatif sur les populations de chevreuils, ce qui était particulièrement évident dans les zones ayant des conditions environnementales défavorables. Nos estimations des valeurs moyennes à long terme de  $\lambda$  qui étaient inférieures à 1 pour plusieurs municipalités indiquent que les populations de chevreuils en Norvège ne sont peut-être pas en mesure de supporter la mortalité combinée due aux chasseurs et au lynx en particulier dans les habitats marginaux.

**Mots-clés :** contrôle du haut vers le bas, dynamique de population, ongulé, prédation, productivité végétale, rudesse de l'hiver.

**Nomenclature:** MacDonald, 2001.

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## Introduction

Recovering populations of large carnivores are associated with a diverse range of conflicts with human interests. Attacks on people, depredation on livestock, and wider social conflicts have been the focus of considerable attention in both the popular and scientific literature (Skogen & Krangle, 2003; Løe & Røskaft, 2004; Breitenmoser *et al.*, 2005; Graham, Beckerman & Thirgood, 2005). In many situations there is also a widespread perception of a conflict between recreational hunters and large carnivores that pursue the same game species, especially wild ungulates. This conflict has not yet received as much focus as the other ones, however, and there is still considerable discussion about whether the conflict is really occurring or simply perceived (Mech & Nelson, 2000). Much of the problem lies in the complexity, and therefore the resulting uncertainty, in studying the impact of predation by large carnivores on wild ungulates (Fritts *et al.*, 2003).

For decades ecologists have debated the relative importance of top-down and bottom-up processes in structuring populations and ecosystems (Murdoch, 1966; Ehrlich & Birch, 1967; Hunter & Price, 1992; Meserve *et al.*, 2003). Recent empirical evidence shows that both top-down and bottom-up processes interplay in most systems and that the relative importance of these processes is context-specific. For instance, a recent comparative analysis at a European scale of roe deer (*Capreolus capreolus*) density and predation by lynx (*Lynx lynx*) and wolf (*Canis lupus*) showed that predation has stronger effects on populations in less productive areas (Melis *et al.*, 2009). However, this study was conducted on averaged roe deer densities across a wide range of climatic and productivity conditions, where roe deer experience different predator and ungulate communities and management situations.

In Norway, abiotic factors such as snow have been shown to have dramatic effects on roe deer populations' dynamics (Grøtan *et al.*, 2005; Mysterud & Østbye, 2006). Very severe winters with deep snow cover can be a major cause of density-independent mortality in roe deer (Okarma *et al.*, 1995; Danilkin, 1996), whereas at European scale a marked effect of winter severity on roe deer abundance was found only in localities with large predators (Melis *et al.*, 2009).

To better understand the relationship between environmental conditions (*e.g.*, productivity, winter harshness) and predation, we quantified the impact of lynx predation on changes in roe deer abundance in a large number of populations distributed along an environmental gradient in Norway.

The European roe deer is a widespread small ungulate that successfully recolonized Norway during the 20<sup>th</sup> century (Andersen *et al.*, 2004). Predation by Eurasian lynx and red fox (*Vulpes vulpes*) and hunter harvest are the major sources of roe deer mortality in Norway. Climate (Danilkin, 1989; Grøtan *et al.*, 2005) and primary productivity (Pettorelli *et al.*, 2006) also shape roe deer distribution and dynamics.

Lynx in Norway have followed the general pattern of large carnivore abundance and distribution in Europe (Linnell *et al.*, 2010). After being almost exterminated by the mid 20<sup>th</sup> century as a consequence of a state-sponsored

bounty program that started in 1846, they persisted in 2 remnant populations in southeastern and central Norway. However, as a result of more restrictive hunting legislation, lynx expanded during the late 20<sup>th</sup> century and are now present throughout most of the country, with the exception of the southwest. As a consequence of conflicts with humans because of depredation on domestic sheep (Odden *et al.*, 2002) and semi-domestic reindeer (Pedersen *et al.*, 1999) and competition for game species (Odden, Linnell & Andersen, 2006), Norwegian lynx populations are managed as a game species with the aim of limiting their density and distribution (Ministry of the Environment, 2004). There has been a considerable debate about the impact of lynx on roe deer populations and the extent to which roe deer hunters should adjust their hunting quotas to take this predation into account. Determining the extent of this impact is thus important in order to improve both current management and our understanding of predator-prey interactions.

From monitoring data on lynx and roe deer, we aimed to assess how trends in roe deer population abundance are influenced by the presence of resident lynx while controlling for the effects of climate and environmental conditions. We thus tested the following predictions: 1) the trend in roe deer abundance would be negatively influenced by the presence of reproductive lynx; and 2) the effect of lynx presence on the trend in roe deer abundance would be greater in areas with unfavourable environmental conditions.

## Methods

### ROE DEER DATA

Roe deer are present in the whole southern and central part of Norway between 58° and 65° N, with the exception of western areas. The number of roe deer harvested annually in each municipality was divided by the area of suitable habitat (*i.e.*, excluding open water and alpine tundra areas), and the result was used as an index of roe deer abundance. This type of index has been previously used for roe deer in Norway (Herfindal *et al.*, 2005; Mysterud & Østbye, 2006), and it correlates well with other indices of population abundance (Grøtan *et al.*, 2005; Mysterud & Østbye, 2006). Hunting success for roe deer is low in Norway (Mysterud & Østbye, 2006). During the years 1995–2002, only  $33.0 \pm 17.6\%$  (mean  $\pm$  SD) of quotas were filled on average in Norway ( $n = 1883$ ); therefore, the number of roe deer harvested is likely to reflect changes in population abundance rather than being an artefact of quotas (Grøtan *et al.*, 2005; Mysterud & Østbye, 2006).

Hunting effort could potentially confound the use of this index. We could not obtain statistics on the number of roe deer hunters at the municipality level, and for the county level we obtained data only for the second half of the study period (2001–2005). During this period, the number of roe deer hunters in the study area only increased on average by 1.7%. However, there may have been regional differences in the changes in hunting effort. By investigating the data county-wise, we did in fact observe that in the northernmost areas (Nord-Trøndelag County) the number of hunters increased by *ca* 31%. To try to control for this, we reran the analyses after excluding this area.

We focused our analysis on the temporal variation in abundance (trends in the number of harvested roe deer per municipality) rather than spatial variation in abundance (average number of harvested roe deer per municipality) because we expected temporal variation to be more consistent throughout the country and independent of possible local differences in hunting effort and hunting success. Moreover, we sought to detect the impact of lynx after their re-establishment in many areas of southern Norway during the last decade independent of average roe deer abundance, which was likely to have been set long before lynx recolonization.

The trend in roe deer abundance between the years 1997 and 2005 was calculated for each municipality by regressing the abundance index (on a log scale) against years (Figure 1). The exponent of the slope of that regression corresponded to the rate of increase of the population (denoted  $\lambda$  hereafter; Royama, 1992). We selected municipalities that had a biologically plausible  $\lambda$  (see Largo *et al.*, 2008 for similar approach) both from year to year and across the overall time series. Therefore, we only retained municipalities with an estimated  $\lambda \leq 1.35$ . The municipalities with higher  $\lambda$  were characterized by a very low number of roe deer harvested, which could lead to high stochasticity and overestimation of the  $\lambda$  (Grøtan *et al.*, 2005). The final dataset consisted of 144 municipalities (Figure 1, 5-y series,

$n = 7$ ; 6-y series,  $n = 5$ ; 7-year series,  $n = 4$ ; 8-y series,  $n = 5$ ; and 9-y series,  $n = 123$ ).

#### LYNX DATA

Data on the presence or absence of reproductive lynx in each municipality are available since 1996 based on non-replicated counts of family groups (*i.e.*, a female with dependent young of the year) and records of tracks in the snow collected by hunters, game wardens, and the public and checked by game wardens (Linnell *et al.*, 2007) within the framework of a national large carnivore monitoring program. We used these data to obtain an index of presence of a resident lynx population (when the municipality hosted a reproductive lynx in at least in 1 year during the period 1997–2005) versus absence (when no reproductive lynx were present during any of the 9 years of the study). Of the 144 municipalities included in the analysis, 62 were categorized with lynx absence and 82 with lynx presence.

#### ENVIRONMENTAL DATA

The climatic variables yearly mean temperature (*Temp*), heat (*Heat* = day-degree-sum for days when mean temperature was above 5 °C), and length of the growing season (*GrowTemp* = number of days with mean temperature above 5 °C) were obtained from the Norwegian Meteorological Institute on a municipality scale as a single normal value (for the period 1961–1991, which corresponds to the most recent “normal” value available) per municipality. The data on snow depth (*SnowMax* = maximum snow depth, *SnowDays* = number of days with more than 250 mm of snow depth) were obtained from the same source but were averaged for the 9 years 1997–2005.

Variables describing plant phenology were extracted from annual curves of the normalised difference vegetation index (NDVI), based on bimonthly values of NDVI from the Global Inventory Monitoring and Modelling System (GIMMS) data set (Karlsen *et al.*, 2006). The GIMMS data set consists of the maximum values of NDVI for 15-d periods with a spatial resolution of approximately  $8 \times 8$  km<sup>2</sup>, covering the world and available from 1982 until 2002 at the time of the calculation of the plant phenology variables (Karlsen *et al.*, 2006). The NDVI is based on the relationship between reflected red and near-infrared radiation from the ground. NDVI is closely related with photosynthetic activity, plant biomass, and net primary productivity (Myneni *et al.*, 1995). The GIMMS data set enables calculation of annual NDVI-curves and the extraction of variables that describe annual plant phenology (Pettorelli *et al.*, 2005; Garel *et al.*, 2006; Herfindal *et al.*, 2006a; Pettorelli *et al.*, 2006). Plant phenology variables (*GrowNDVI* = length of the growing season based on the NDVI-curve, *SumNDVI* = sum of NDVI-values during the growing season, *Spring* = onset of spring) were calculated for each pixel in the GIMMS data set, and a multi-year average was obtained for each municipality for the years 1997–2002, excluding pixels representing large areas of open water and alpine tundra areas (above the tree-line), which are not roe deer habitat.

Since plant phenology and climatic variables were highly intercorrelated (Table I), we chose to run separate models for each variable. We also performed a Principal

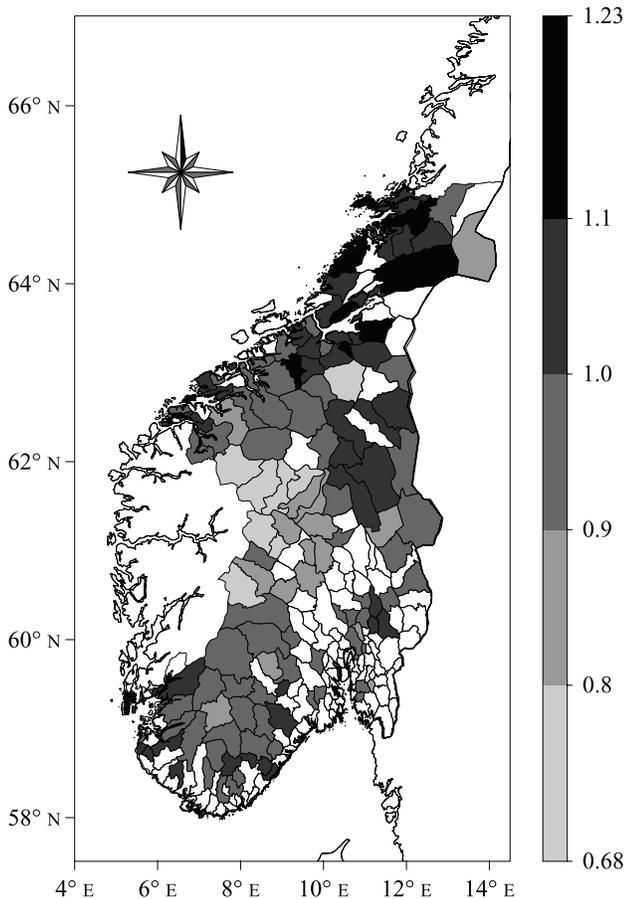


FIGURE 1. Map of roe deer  $\lambda$  in 1997–2005 in 144 municipalities in Norway. White = no data or excluded municipalities.

TABLE I. Pearson correlation coefficients between environmental variables, all  $P < 0.001$ ,  $df = 142$ .

	<i>GrowTemp</i>	<i>Heat</i>	<i>SnowDays</i>	<i>SnowMax</i>	<i>Spring</i>	<i>SumNDVI</i>	<i>Temp</i>	<i>PCAI</i>
<i>GrowNDVI</i>	0.74	0.71	-0.75	-0.77	-0.89	0.80	0.66	-0.87
<i>GrowTemp</i>		0.92	-0.93	-0.83	-0.84	0.54	0.97	-0.95
<i>Heat</i>			-0.91	-0.84	-0.87	0.56	0.86	-0.94
<i>SnowDays</i>				0.91	0.88	-0.54	-0.89	0.96
<i>SnowMax</i>					0.88	-0.62	-0.71	0.92
<i>Spring</i>						-0.66	-0.76	0.95
<i>SumNDVI</i>							0.44	-0.70
<i>Temp</i>								-0.88

Component Analysis (PCA) on all climatic drivers and used the first PCA component (*PCAI*) as an explanatory variable in order to reduce multicollinearity (Graham, 2003).

#### STATISTICAL ANALYSES

We first investigated the curvature in the relationship between the response variable ( $\lambda$ ) and each environmental driver (Crawley, 2005) for areas with and without lynx separately using Generalized Additive Models (GAM; Wood, 2006). Since several relationships were not linear we introduced a quadratic term in our models. Only one of the GAMs (*Heat*) provided support for a more complex relationship that would justify the additional inclusion of a cubic term; therefore, we did not include polynomial terms of order higher than 2. We used multiple linear regression to analyze the relationship between  $\lambda$ , the environmental driver, and the presence of reproductive lynx by performing a model selection starting from the full model:  $\lambda \sim \text{Driver} + (\text{Driver})^2 + \text{Lynx} + \text{Lynx} \times \text{Driver} + \text{Lynx} \times (\text{Driver})^2$ . We used  $AIC_c$  (Akaike Information Criterion corrected for small sample sizes; Burnham & Anderson, 2002) to select the minimum adequate model (MAM hereafter). We ranked candidate models separately for each environmental driver according to  $AIC_c$ . We provided  $R^2$  values to assess the contribution of environmental drivers to observed variation in roe deer abundance. We also plotted prediction lines for the MAM for the best performing model.

To investigate whether a lack of spatial independence could lead to a Type I error (Legendre, 1993) a Moran test was performed on the residuals of the MAM as selected by  $AIC_c$ . Since the test revealed a positive spatial correlation (Moran's  $I = 0.28$ ,  $P < 0.001$ ), a spatially simultaneous autoregressive model based on the generalized least squares method was run as suggested by Diniz-Filho, Bini, and Hawkins (2003) and the estimates were compared to the ones of the ordinary least squares model. The autoregressive model including the same variables as the ordinary least squares full model provided very similar results in terms of direction and significance of the effects. Since the estimates of the 2 models were highly correlated ( $r_p = 0.995$ ,  $df = 4$ ,  $t = 19.38$ ,  $P < 0.001$ ), we retained the ordinary least squares model to provide an estimate of explained variation (the  $R^2$ ). The analyses were conducted using R 2.7.2 Software (R Development Core Team, 2008). Spatial autocorrelation was investigated using the R package *spdep* (Bivand, 2007).

## Results

In the period 1997–2005 the long-term average  $\lambda$  was  $0.98 \pm 0.10$  (mean  $\pm$  SD) across all municipalities. It was

$1.01 \pm 0.08$  in the absence and  $0.96 \pm 0.11$  in the presence of lynx (Figure 2), indicating a weak negative impact of lynx on roe deer population dynamics. There was a positive correlation between long-term average  $\lambda$  and roe deer abundance ( $r_p = 0.29$ ,  $df = 142$ ,  $t = 3.60$ ,  $P < 0.001$ ), indicating an occurrence of inverse density-dependence.

*PCAI* (i.e., the first component of the PCA performed on all climatic drivers) accounted for 81% of the observed variation in the environmental drivers and was negatively correlated with *Heat*, *Temp*, *GrowTemp*, *GrowNDVI*, and *SumNDVI* (Table I) and positively correlated with *SnowMax*, *SnowDays*, and *Spring* (Table I). The sets of models with  $\Delta AIC_c \leq 2$  obtained by model selection starting from the full model of variation in long-term average  $\lambda$  of roe deer are reported in Table III. The prediction lines obtained by the MAM for the best performing environmental driver for roe deer  $\lambda$  are shown in Figure 3.

The best performing MAM was the full model including the length of the growing season calculated using temperature as an environmental driver (Table II). This model accounted for 39% of the observed variation in  $\lambda$ . In the absence of lynx, the length of the growing season had only a minor effect on  $\lambda$ . Conversely, the lynx presence had a clear effect on  $\lambda$  since a negative main effect and both interaction terms were retained (Table II, Figure 3). Visual inspection of the effect of interaction between lynx and length of the growing season (Figure 3) suggested that the effect of predation was stronger when the growing season was

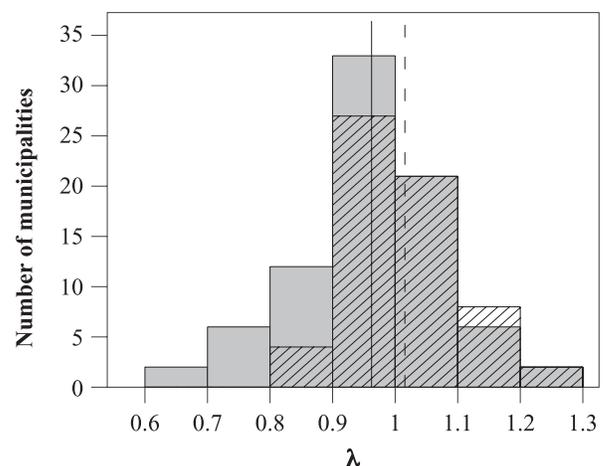


FIGURE 2. Frequency distribution of roe deer  $\lambda$  across the period 1997–2005 in 144 municipalities in Norway in the absence (shaded area, average = dashed line) and presence (grey area, average = solid line) of lynx.

short and that this variable had a relatively small influence on  $\lambda$  in the absence of lynx. When the length of the growing season was shorter than 140 d, the long-term average  $\lambda$  in absence of lynx (0.95 [0.85–1.05]) was higher than the long-term average  $\lambda$  in presence of lynx (0.89 [0.69–1.03]). When the length of the growing season was longer than 140 d, the long-term average  $\lambda$  was similar in the absence (1.02 [0.89–1.21]) and in the presence (1.03 [0.90–1.23]) of lynx.

The MAMs selected after testing for the effects of other environmental drivers accounted for a proportion of variance ranging between 13% and 35% and showed a consistent pattern. A harsh winter (*SnowMax*, *SnowDays*, *PCAI*), a low productivity, and a short growing season (*Heat*, *Temp*, *GrowTemp*, *GrowNDVI*, and *SumNDVI*, *Spring*, *PCAI*) all had negative effects on the long-term average  $\lambda$  (Table III). The models including the interaction between the effects of lynx presence and environment productivity indicated a stronger negative effect of lynx predation in harsh environments and were selected for all of the environmental drivers except *Spring*, which was the environmental driver receiving the weakest support.

TABLE II. Estimates of the selected model (using  $AIC_c$ ) of variation in yearly changes of roe deer abundance (long-term average  $\lambda$ ) in 1997–2005 in 144 municipalities in Norway.

$\lambda$	Beta	95% CI	
		Lower	Upper
Intercept	0.978	0.476	1.480
<i>Lynx</i>	-1.413	-2.260	-0.566
<i>GrowTemp</i>	-0.001	-0.007	0.005
<i>GrowTemp</i> <sup>2</sup>	0.066	-0.144	0.276
<i>Lynx</i> × <i>GrowTemp</i>	0.018	0.006	0.030
<i>Lynx</i> × <i>GrowTemp</i> <sup>2</sup>	-0.593	-1.003	-0.183

TABLE III. Sets of models with  $\Delta AIC_c \leq 2$  obtained by model selection starting from the full model:  $\lambda \sim Driver + (Driver)^2 + Lynx + Lynx \times Driver + Lynx \times (Driver)^2$ , explaining roe deer long-term average  $\lambda$  for 144 municipalities in Norway in 1997–2005. When the second ranked model had a  $\Delta AIC_c > 2$ , we show the first 2 ranked models. The models were ranked by the corrected Akaike Information Criterion ( $AIC_c$ ).  $k$  = number of parameters;  $\Delta AIC_c$  = difference in  $AIC_c$  between the best and the actual model;  $\omega_i$  = Akaike's weights, i.e., normalized likelihoods of the models. The model with the best explanatory power is shown in bold. Model 0 (including only intercept) had  $AIC_c = 246.3$  and  $R^2 = 0.00$ .

	Intercept	<i>Lynx</i>	<i>Driver</i>	<i>Driver</i> <sup>2</sup>	<i>Lynx</i> × <i>Driver</i>	<i>Lynx</i> × <i>Driver</i> <sup>2</sup>	k	R <sup>2</sup>	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	ω <sub>i</sub>
<b><i>GrowTemp</i></b>	<b>0.9785</b>	<b>-1.4129</b>	<b>-0.0009</b>	<b>0.0662</b>	<b>0.0185</b>	<b>-0.5935</b>	<b>7</b>	<b>0.393</b>	<b>-307.3</b>	<b>0.000</b>	<b>0.802</b>
	0.8258	-0.2521	0.0011		0.0016		5	0.353	-302.6	4.694	0.077
	1.0238	0.0130	0.0004	-0.0452		-0.0354	6	0.320	-293.3	4.556	0.087
<i>Heat</i>	0.9324	-0.3863	0.0001	-0.0002	0.0010	-0.0065	7	0.343	-296.1	0.000	0.989
	0.7641	-0.0274	0.0005	-0.0025			5	0.271	-285.3	10.750	0.005
<i>Temp</i>	0.9523	-0.0533	0.0147		0.0198		5	0.332	-298.1	0.000	0.461
	0.9537	-0.0546	0.0129	0.0003	0.0205		6	0.332	-295.9	2.147	0.157
<i>PCAI</i>	1.0095	0.0030	-0.0123	-0.0009		-0.0065	6	0.317	-292.7	0.000	0.932
	1.0110	0.0010	-0.0102	-0.0008	-0.0051	-0.0060	5	0.277	-286.6	6.058	0.045
<i>SnowMax</i>	1.0440	0.0160	-0.0002		-0.0002		5	0.261	-283.6	0.000	0.381
	1.0448	-0.0084	-0.0002	0.0004		-0.0040	6	0.270	-283.0	0.593	0.283
	1.0380	0.0130	-0.0001	-0.0013	-0.0002		6	0.263	-281.7	1.874	0.149
<i>SumNDVI</i>	1.2111	-1.3532	-0.0780	0.0073	0.4332	-0.0350	7	0.199	-267.5	0.000	0.913
	1.0227	-0.2844	-0.0012		0.0399		5	0.138	-261.3	6.199	0.041
<i>GrowthNDVI</i>	1.6359	-2.9434	-0.0709	0.0020	0.2897	-0.0071	7	0.197	-267.1	0.000	0.463
	0.9083	-0.3843	0.0054		0.0179		5	0.164	-265.8	1.338	0.236
<i>Spring</i>	1.3412	-0.0367	-0.0162				4	0.136	-263.1	0.000	0.415
	0.6351	-0.0387	0.0525	-0.0017			5	0.139	-261.5	1.583	0.189
	1.2811	0.0940	-0.0132		-0.0063		5	0.139	-261.4	1.713	0.176

When we excluded Nord-Trøndelag County from the data set, the results did not differ in terms of direction and significance of the effects: the MAM explained 40% of variation in the long-term average  $\lambda$  and included interactive effects of the length of the growing season and of lynx presence ( $\Delta AIC_c$  between the first- and the second-ranked model = 2.17,  $AIC_c$  weight of the MAM = 0.500).

The fact that the negative effect of lynx was stronger in low productivity indicates that the increase in hunting effort

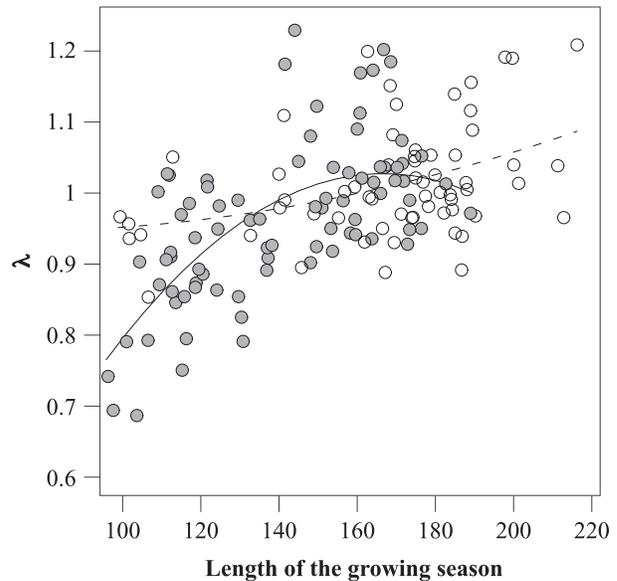


FIGURE 3. Prediction lines according to the most parsimonious model for roe deer  $\lambda$  in Norway ( $n = 144$  municipalities, years 1997–2005) with varying length of the growing season in the presence (black line, filled circles) and absence (dotted line, hollow circles) of reproductive lynx.

in the northernmost part of the study area was not a confounding factor in our results.

## Discussion

The results of these analyses provide clear support of our 2 predictions. The top-down effect of lynx predation negatively influenced the long-term average  $\lambda$  of roe deer populations; however, the strength of this top-down effect was not the same along the whole range of environmental variation, being greater in harsher environmental condition.

### INFLUENCE OF LARGE-SCALE PATTERNS

In our study area, variation in climate and plant phenology follows not only a north–south gradient, but also a gradient from continental to coastal areas and from high altitudes to lowlands, which explains why high values of the long-term average  $\lambda$  of roe deer populations did not occur only at low latitudes.

Among the variables describing environmental conditions, length of the growing season accounted for the largest proportion of variation in long-term average  $\lambda$  of roe deer populations once the presence/absence of lynx was taken into account. This might be a consequence of a longer period with access to high-quality forage, which is likely to affect positively body condition, recruitment, and winter survival of roe deer. Alternatively, the longer snow cover period might negatively influence roe deer population through higher winter mortality. In roe deer populations, climate has been considered one of the major causes of mortality at both broad (Danilkin, 1989; 1996) and fine (Gaillard *et al.*, 1998) spatial scales. Deep snow restricts mobility and increases the energetic cost of movement, as well as reducing access to forage and increasing the hunting success of predators (Holand *et al.*, 1998). Mysterud and Østbye (2006) found that population growth rate was negatively affected by increasing snow depth in a population in southern Norway. The length of the snow period was indeed the second best environmental driver, accounting for 35% of variation in the long-term average  $\lambda$ , with the lowest values occurring when the snow period was longest and in presence of lynx.

NDVI-related indices have been successfully related to herbivore performance (Pettorelli *et al.*, 2005; Garel *et al.*, 2006; Herfindal *et al.*, 2006a,b; Pettorelli *et al.*, 2006). On a small spatial scale, in the predator-free roe deer population at Chizé (western France), density-dependence has also been shown to rely on the interaction between population density and habitat quality (Pettorelli *et al.*, 2003). Roe deer are selective browsers (Tixier & Duncan, 1996), and they are small compared to other deer species; thus, they are less dependent on the quantity and more on the quality of vegetation. Moreover, roe deer prefer early successional stage forests to mature ones (Gill *et al.*, 1996) and avoid habitats like mountain tundra (Danilkin, 1996). NDVI, which primarily measures the quantity of radiation adsorbed by plants, including coniferous and old stages of forests, and focuses heavily on the canopy, might therefore not be the most suitable measure of food availability for roe deer in Norway. Pettorelli *et al.* (2006) found a strong relationship

between NDVI and body mass of roe deer fawns in France in an area (Chizé) where the summer often is unfavourable because of drought. However, in Norway summer droughts do not occur and therefore cannot be the factor limiting food availability for roe deer.

### INFLUENCE OF PREDATORS

The presence of lynx was negatively correlated with the roe deer long-term average population growth rate across southern Norway. In accordance with the predictions of Jędrzejewska and Jędrzejewski (2005), the impact of predation was greatest in areas with harsher environmental conditions (*i.e.*, low primary productivity and harsh winter). Therefore, our results suggest a top-down limitation of lynx on roe deer, but this limitation went further than expected, since many roe deer populations actually appeared to be decreasing in the presence of the predator. Our results indicate that lynx have a stronger impact on roe deer growth rate in areas of low productivity. Field data indicate that Eurasian lynx vary their kill rates only by a factor of 2 to 3 across a range of prey densities spanning 2 orders of magnitude (Breitenmoser & Haller, 1993; Okarma *et al.*, 1997; Molinari-Jobin *et al.*, 2002; Nilsen *et al.*, 2009a). These relatively stable kill rates, even in the absence of numerical responses on the part of the predator, will automatically lead to an increase in the impact of lynx at low-density prey populations, pushing roe deer populations into an extinction vortex at low density (occurrence of a “predator pit” *sensu* Messier, 1994). The substrate properties of snow, which facilitate greater hunting success for lynx (Haglund, 1966), might also contribute to the higher impact of lynx predation in environments with deep snow.

Lynx are not the only predator of roe deer in the study area: foxes also prey upon roe deer fawns (Cederlund & Lindström, 1983; Aanes & Andersen, 1996; Elmhagen & Rushton, 2007; Panzacchi *et al.*, 2008). However, foxes rarely act as roe deer specialists, instead opportunistically killing fawns if encountered when hunting for alternative prey (Panzacchi *et al.*, 2008). Moreover, foxes are present throughout the whole study area, although occurring at varying densities, and their effect on fawns is mainly restricted to the few weeks following the highly synchronized fawning times in May–June, whereas lynx prey upon roe deer typically older than fawns throughout the whole year irrespective of roe deer density (Odden, Linnell & Andersen, 2006; Nilsen *et al.*, 2009a). As the growth rate of ungulate populations, including roe deer, is much more sensitive to a given change in adult survival than to the same change in juvenile survival (Gaillard *et al.*, 2000), lynx predation rather than fox predation should account for most of the observed variation in the long-term average growth rates observed among roe deer populations. In a recent comparative demographic analysis of roe deer populations, Nilsen *et al.* (2009b) found that changes in adult survival accounted for most of observed changes in population growth in declining populations. In areas in Fennoscandia where lynx and roe deer co-exist, roe deer are the main prey of lynx and constitute up to 83% of their winter diet and 34% of their summer diet even in low-abundance roe deer areas (Odden, Linnell & Andersen, 2006). Overall, the

available information strongly indicates that lynx have far a greater impact on roe deer populations than foxes in our study area.

We did not include roe deer abundance as an explanatory variable in the model selection to avoid redundancy, since this index was also used to calculate  $\lambda$ . The source of the positive spatial correlation that was found in the residuals might be the presence in our data set of small, clustered municipalities that are not associated with distinct roe deer populations. Also, lynx home ranges are so large that they are rarely, if ever, embraced by a single municipality (Herfindal *et al.*, 2005). Grouping the municipalities by county would have been rather artificial, however, since there is no biological or human-related justification, such as hunting traditions or management administration, for using county as a grouping variable. In addition, the size of counties is so large that they would embrace too wide a range of environmental conditions. Dispersal of yearlings between neighbouring populations (*e.g.*, Linnell, Wahlström & Gaillard, 1998 for a review) might also explain the occurrence of spatial autocorrelation in our data. Finally, we could not account for red fox predation that exerts a strong impact on roe deer fawns (Cederlund & Lindström, 1983; Aanes & Andersen, 1996; Elmhagen & Rushton, 2007; Panzacchi *et al.*, 2008). Lynx harvesting might also be a confounding factor in our results; however, the objective of the harvest is to maintain a stable lynx population within its current distribution. Annual quotas are set based on the annual census, so in many ways harvest has served to stabilize the lynx population. There have been no dramatic changes in lynx distribution in our study area during the study period. Accordingly, we consider lynx presence as a valid measure of depredation on roe deer populations irrespective of lynx harvesting.

These uncertainties underline the limitations intrinsic to this type of broad-scale study. There was a great deal of variation that we were not able to explain. A wide range of human and non-human factors clearly influence roe deer populations across Norway, and it is unlikely that any model will be able to account for more than a fraction of them. As reviewed by Møller and Jennions (2002), most selected models in ecology only account for a small part of observation (about 7% on average). Our model had a much higher explanatory power, accounting for about 40% of the variation observed in trends in roe deer abundance in terms of climate, habitat productivity, and lynx presence. Furthermore, our results are consistent both with recent results on lynx kill rates, which are consistently high even at low prey densities (Nilsen *et al.*, 2009a), and with observed variation in roe deer hunting success, which is higher on roe deer with increasing snow depth (J. Odden & J. D. C. Linnell, unpubl. data). Our results therefore support the pattern of environmentally conditional predation impacts previously reported by Jędrzejewska and Jędrzejewski (2005) and Melis *et al.* (2009) at a much broader spatial scale.

The additional presence of lynx on top of other mortality factors is lowering roe deer population growth, and in many cases is inducing a negative population trend. This result, recently supported by a comparative demographic analysis from individually marked roe deer in Norway and France (Nilsen *et al.*, 2009b), has obvious conservation

implications. Overall, it appears that in some areas of lower productivity (in some of the Norwegian populations) the present roe deer management regime is not sustainable unless it is being supported by large-scale immigration. In such areas it would appear that hunters are facing real competition for roe deer. However, in areas of higher productivity it would appear that lynx presence has much less obvious impacts on the sustainability of roe deer populations.

These results indicate that roe deer managers have a real need to adjust hunting quotas in low productivity areas where lynx are present. This requirement might be extended to other systems including species experiencing similar conflicts between hunters and predators.

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