

# Climate, season, and social status modulate the functional response of an efficient stalking predator: the Eurasian lynx

Erlend B. Nilsen<sup>1\*†</sup>, John D. C. Linnell<sup>2</sup>, John Odden<sup>3</sup> and Reidar Andersen<sup>2‡</sup>

<sup>1</sup>Faculty of Forestry and Wildlife Management, Hedmark University College, Evenstad, NO-2480 Koppang, Norway;

<sup>2</sup>Norwegian Institute for Nature Research, NO-7485 Trondheim, Norway; <sup>3</sup>Norwegian Institute for Nature Research, NO-0349 Oslo, Norway

## Summary

1. Predation plays a major role in shaping the structure and dynamics of ecological communities, and the functional response of a predator is of crucial importance to the dynamics of any predator–prey system by linking the trophic levels. For large mammals, there is a dearth of field studies documenting functional responses, and observations at low prey density are particularly scarce. Furthermore, there is a lack of understanding about how variables such as season, social status and climate modulate the functional response curves.

2. We analysed kill rate data collected over a 10-year period based on radio-marked lynx (*Lynx lynx*) mainly preying on roe deer (*Capreolus capreolus*) along a steep prey density gradient in south-eastern Norway.

3. The asymptotic kill rate was reached at a very low prey density for both solitary individuals and family groups (i.e. females with their dependent kittens), indicative of an efficient predator. This highlights the importance of understanding the interplay between predator and prey at low prey densities.

4. A purely prey-dependent functional response was a poor descriptor of the data, as the curve was strongly modulated by season and differences between lynx of different social status. In addition, there was a clear effect of abiotic climatic factors (indexed by the North Atlantic Oscillation) on observed kill rates in the more snow-rich portion of our study area.

5. Our analysis suggests that simple functional response curves might be poor descriptors of predator consumption rates in complex natural system, and that auxiliary factors are likely to induce complexity into any predator–prey systems that would not be captured by simple deterministic approaches.

**Key-words:** *Capreolus capreolus*, consumption rates, kill rate, *Lynx lynx*, NAO, predator–prey

## Introduction

Describing the functional response of a consumer is one of the cornerstones in community ecology research and largely determines the effect of a predator population on the prey population (Abrams & Ginzburg 2000). Although functional responses have a long history in the ecological literature (Holling 1959), a central discussion during the last couple of

decades has concerned how the consumption rate is best modelled (see e.g. discussion in Abrams & Ginzburg 2000). Importantly, different forms give rise to widely differing predictions about the scaling of biomass across food webs (Ginzburg & Akçaya 1992; Vucetich, Peterson & Schaefer 2002) as well as the persistence of predator–prey systems with an efficient predator (Arditi & Berryman 1991). However, the outcome from purely deterministic approaches might have limited predictive value if per capita prey consumption is strongly modulated by auxiliary biotic and stochastic abiotic factors (e.g. Post *et al.* 1999). While the relative importance of deterministic and stochastic factors has been a central tenet in population ecology for at least five decades (see Coulson, Rohani & Pascual 2004 for a recent summary), the theoretical

\*Correspondence author. e-mail: erlend.nilsen@nina.no

†Present address: Norwegian Institute for Nature Research, NO-7485 Trondheim, Norway.

‡Present address: Section of Natural History, Museum of Natural History and Archaeology, Norwegian University of Technology and Science, NO-7491 Trondheim, Norway.

debate in predator–prey ecology seems so far to be dominated by deterministic models (but see van der Meer & Smallegange 2009). There is therefore still a clear need for empirical studies investigating the relationships in complex, natural systems (Abrams & Ginzburg 2000).

A number of factors in addition to prey density are likely to induce spatial and temporal variation in consumption rates within and between predator populations, including predator age class, spatial distribution of prey (Errington 1946), predator and prey grouping behaviour (Fryxell *et al.* 2007), predator density (Vucetich *et al.* 2002), surplus killing (Odden *et al.* 2002), and the presence of other predator and prey species (Miller *et al.* 2006). In addition, consumption rates often vary during the year, due to differences in prey susceptibility (Sand *et al.* 2008), energetic requirements of the predators and the age of the prey (Sand *et al.* 2008). The modulating effect of external abiotic factors (such as weather) has received considerable attention recently, and has been shown to affect consumption rates (Stenseth *et al.* 2004) and thereby the dynamics of predator–prey systems (Post *et al.* 1999; Stenseth *et al.* 1999; Hebblewhite 2005). In fact, a few recent studies have suggested that such abiotic factors might be just as important as top-down effects in shaping prey dynamics even in simple predator–prey systems (Vucetich & Peterson 2004). In effect, predation events ought to some extent to be seen as a stochastic process (Festa-Bianchet *et al.* 2006), and different age/sex classes within the predator population might behave very differently under similar conditions.

The mammalian functional response literature is dominated by studies from wolf *Canis lupus* L. ungulate systems (see e.g. Hayes & Harestad 2000; Vucetich *et al.* 2002; Jost *et al.* 2005), whereas there is a dearth of published functional responses for large solitary predators with other hunting techniques (but see O'Donoghue *et al.* 1998; Stenseth *et al.* 2004). To expand the existing knowledge about the factors that affect the rate at which prey is killed from such systems is in particular important because theoretical studies indicate that systems dominated by stalking predators will be affected by environmental factors such as climate variations in different ways than systems dominated by coursing predators (Wilmers, Post & Hastings 2007). We studied the functional response of the Eurasian lynx *Lynx lynx* L. preying on roe deer *Capreolus capreolus* L. in a northern boreal forest ecosystem. In areas of sympatry, predatory interactions between the Eurasian lynx and roe deer are common (Jedrzejewski *et al.* 1993). While the genus *Lynx* is generally specialized on lagomorphs (Werdelin 1981), the Eurasian lynx usually show preference for roe deer (Jedrzejewski *et al.* 1993; Odden, Linnell & Andersen 2006). Our study system thus represents a classical predator–prey system, but has some characteristics that make it particularly suitable for studying predator consumption rates. First, in the northern boreal forests, roe deer densities are generally low compared to more temperate regions (Holand *et al.* 1998) allowing us to also examine consumption rates below predator satiation thresholds. Second, there is a clear spatial and seasonal difference in climate and snow cover, potentially inducing variation in hunting success (Stenseth *et al.* 2004)

and prey spacing behaviour (Mysterud, Bjørnsen & Østbye 1997). Third, although different age and sex categories might often have different probabilities of being captured by a predator (Okarma 1984), earlier studies have shown that lynx in our study area show no selection with respect to size, age or body condition of roe deer (Andersen *et al.* 2007) under boreal conditions. Finally, lynx densities are maintained below saturation levels by recreational harvest (Herfindal *et al.* 2005a) – thus, although ratio-dependent predation has been documented in a few recent studies for e.g. wolf–moose systems (Vucetich *et al.* 2002; Jost *et al.* 2005), variation in predator density is unlikely to influence consumption rates in our study area.

Based on kill rate data from radiocollared lynx collected over a 10-year period in south-eastern Norway, we ask some fundamental questions relevant to understanding the relationship between consumers and their prey. We are particularly interested in the shape of the relationship between lynx kill rates and roe deer density at low prey densities. The interpretation of this is of crucial importance for our understanding of the shape of functional response curves, and therefore our understanding of the predator–prey dynamics. Then, we investigated to what extent additional factors modulate the functional response curves of the lynx in a complex, natural system. More precisely, we examined how social status of the lynx, season, and climatic variability influenced the observed kill rates.

## Materials and methods

### STUDY AREA

The 32 000 km<sup>2</sup> study area encompasses an environmental gradient (roughly north-east–south-west) in the counties of Hedmark, Akershus and Østfold in south-eastern Norway (Figs S1 and S2). The 'northern' portion of the study area is characterized by several river valleys at around 200–300 m above sea level, separated by hills reaching to 700–800 m above sea level. The forest is mainly composed of Norwegian spruce *Picea abies* L. and Scots pine *Pinus sylvestris* L. and most of it has been logged and regenerated throughout the last 100 years. The roe deer density in this portion of the study area is generally lower than in the southern one (0.01–0.65 individuals harvested annually km<sup>-2</sup> of forested area). The 'southern' portion of the study area includes patches of deciduous forest, represented mainly by birch *Betula* spp. and the landscape is more human-modified, with the forest fragmented by cultivated land. The altitude is not higher than 300 m above sea level, and roe deer occur at higher densities (0.10–2.50 individuals harvested annually/km<sup>2</sup> of forested area). Throughout the study area, roe deer co-exist with moose *Alces alces* L., mountain hares *Lepus timidus* L. and forest birds such as black grouse *Tetrao tetrix* L. and capercaillie *Tetrao urugallus* L. A few red deer *Cervus elaphus* L. were available as prey in small pockets, wild mountain reindeer *Rangifer tarandus* L. were seasonally available at higher altitudes in the northern part of the study area, and in parts of the study area free-ranging domestic sheep *Ovis aries* L. were available during the summer season (Odden *et al.* 2006). The density of lynx, including dependent offspring, inside the study area has been estimated to be ca. 0.3 per 100 km<sup>2</sup> in the northern part of the study area and ca. 0.4 per 100 km<sup>2</sup> in the southern part (Odden *et al.*

2006). The lynx management goals for different regions are set by the Norwegian parliament in terms of the desired number of confirmed annual reproductions, above which the population is limited by an annual recreational harvest. Lynx populations are monitored annually in a coordinated programme using standardized methods (Andrén *et al.* 2002; Linnell *et al.* 2007).

#### ANIMAL CAPTURE

We captured 79 lynx in the study area between 1995 and 2007, of which we obtained kill rate data (see below) from 34 individuals (17 males: 17 females). Adult lynx and juveniles (> 5 months) were captured in walkthrough box traps, spring-loaded foot-snares and treed using trained dogs. We also immobilized lynx from cars and helicopters. In addition, neonatal kittens were captured by hand at natal lairs. We recaptured lynx every second year when possible. The walkthrough box traps were made of wood or metal, baited with lynx urine, and placed along known lynx trails. We checked radio-alarms on the box traps twice per day to minimize the time lynx spent in the box. The spring-loaded foot-snares were placed at lynx-killed roe deer. These snares were continually monitored using radio-alarms, and our reaction time upon capture was < 15 min. When recapturing lynx with trained dogs, the dogs were released as close to the radio-located lynx as possible, and the lynx was chased until it escaped, climbed a tree, or sought refuge under rocks. Once a lynx was in a tree, they were darted and caught in a net if they fell. Occasionally, we also immobilized lynx by darting from car, helicopter or by stalking on foot. All adult animals were immobilized using a mixture of ketamine (100 mg) and medetomidine (4 mg), reversed with atipamezole (5 mg); juveniles received a half dose. We administered drugs intramuscularly by hand, blow-pipe or gas-powered darting rifle. All procedures were approved by the Norwegian Experimental Animal Ethics Committee, and permits for wild animal capture were obtained from the Norwegian Directorate for Nature Management. We equipped 57 lynx with VHF radiocollars (Telonics MOD-335 transmitter with mortality sensor, Telonics Inc., Mesa, AZ, USA), 17 kittens received free-floating intraperitoneal implant transmitters (Telonics IMP/150/L and IMP/400/L implantable transmitter with mortality sensor, Telonics Inc., Mesa, AZ, USA), and 5 lynx received global positioning system (GPS) collars (four store-on-board Posrec 300 and one GPS/GSM Tellus 3H2A, TVP Positioning AB, Lindesberg, Sweden) (Arnemo *et al.* 1999, Arnemo *et al.* 2006). Collars weighed 150 g or less than 1% of an adult female's body weight.

#### Estimation of kill rates

Data on lynx kill rates on roe deer (defined as number of roe deer killed 100 days<sup>-1</sup> lynx<sup>-1</sup>) were sampled during summer (1 May–30 November) and winter (1 December–30 April) following three different sampling protocols:

1. Periods of at least 10 days where lynx were located every 15 min during either the night, or the entire 24-h period.
2. Periods of at least 10 days with 1 radiolocation a day.
3. Periods of at least 10 days with at least 1 radiolocation a day, and also allowing gaps in a radiotracking sequence based on the following rule:

- Female with kittens – winter: no gap allowed.
- Female with kittens – summer: no gap allowed
- Single lynx – winter: 2-day gap allowed.
- Single lynx – summer: 1-day gap allowed.

The rule for accepting 'gaps' in the data set were made from estimates of handling time of lynx with respect to sex, age and season (Øvrum 2000), and we used the lower 95% confidence interval of estimated mean handling time of ungulate prey. Although this rule is likely to underestimate the number of small prey items and to some extent domestic sheep, we are confident that it gives a good representation of the number of roe deer prey, which was the focus of this study. Under protocol 1, we searched all locations where the lynx stopped for at least 1 h during its travels at night in order to locate potential kills. Using these methods, we located carcasses from many domestic sheep, kills of small prey (capercaille, black grouse, mountain hares), and large kills that were mainly roe deer (Odden *et al.* 2006). It soon became apparent that large kills of wild ungulates were handled in a stereotyped manner – with the lynx returning to the kill each night soon after dusk to consume a meal, and then withdrawing to a daybed at some distance from the kill (Pedersen *et al.* 1999; Øvrum 2000). This usually continued for several days until the kill was more or less totally consumed and the lynx moved on. This resulted in an easily recognizable clustering of locations around a kill, separated by more widely distributed intermediate points. Therefore, when collecting data that was only intended to quantify predation on large wild ungulates like roe deer, we supplemented protocol 1 data with sequences that were based on a single daily location. In many cases when this single location was at dusk, or when snow conditions permitted backtracking, it was possible to locate the kill. However, we were not able to search for, or find, all possible kills. Therefore, we included 'virtual kills' where lynx behaviour conformed to the stereotyped behaviour observed when kills were confirmed, even in situations where the kill was not located (following Jobin, Molinari & Breitenmoser 2000). This conforms to the methods being developed for interpreting predation behaviour from predator movement data where GPS-telemetry technology is being utilized (Anderson & Lindzey 2003; Sand *et al.* 2005; Zimmermann *et al.* 2007). Based on the lower 95% boundary of estimated mean handling time and upper 95% boundary of mean distance between a kill and a daybed, we made the following rules for virtual kills.

1. Single animals – all year – three out of four consecutive daybeds within a radius of 2.6 km
2. Female with kittens – winter: two consecutive daybeds within a radius of 2.6 km
3. Female with kittens – neonatal lair period: three hunting trips to the same point
4. Female with kittens – summer after neonatal lair period: three out of four consecutive daybeds within a radius of 2.6 km.

Table 1 gives a summary of the number of lynx-killed roe deer included in the analysis, as well as the proportion of the kills that were 'virtual kills'.

Initial analysis suggested that the estimated kill rates were sensitive to the length of the tracking period, but that the estimates stabilized when periods longer than 7 days were used. Here, we use data from intensive radiolocation periods ranging from 10 to 125 days to estimate kill rate.

**Table 1.** The number of lynx killed roe deer included in the functional response analysis, separated by social status and season. The number in parentheses represents the proportion of the total number of kills that are based on the 'virtual kill' method (see Methods)

	Summer	Winter	Total
Family groups	38 (50%)	61 (38%)	99 (42%)
Solitary	80 (46%)	75 (52%)	155 (49%)
Total	118 (47%)	136 (46%)	254 (46%)

#### ROE DEER DENSITY INDEX

As an index of local roe deer density, we used hunting bag statistics at the municipality level, available from Statistics Norway ([www.ssb.no](http://www.ssb.no)). Although hunting bag data might be expected to give only a coarse representation of roe deer densities, a previous comparison between hunting bag data and several independent indexes of roe deer abundance reported a very good concordance between them (Grøtan *et al.* 2005). First, within our study area (Akershus, Østfold and Hedmark) the hunting statistics are strongly correlated with road traffic kills (Table 1 in Grøtan *et al.* 2005). Second, in parts of the study area where supplemental feeding of roe deer was conducted, there was a strong correlation between annual variation in sightings on feeding stations and number of roe deer shot in the area (Grøtan *et al.* 2005). Third, although the roe deer harvest is regulated through a quota system, only a low fraction of the quotas were actually harvested (Grøtan *et al.* 2005). Consequently, we expect the temporal variation in our roe deer density index to largely reflect temporal variations in roe deer density fairly well. Finally, based on radiocollared roe deer in the study area (based on  $n = 229$  radio-marked roe deer; C. Melis, J. D. C. Linnell, J. Odden, & R. Andersen, unpublished data), we found only a weak relationship between harvest rate and the hunting bag data, indicating that variation in harvest rates across regions did not contribute substantially to the variation in our roe deer density index. For the ease of interpretation, we rescaled our roe deer density index (i.e. number of roe deer shot/km<sup>2</sup> forested area) based on the assumption that the harvesting rate was constant (~14%) across years and regions. Note however that since the spatial extension of our roe deer study area is much less than the lynx study area, we would not be able to calculate roe deer densities based on capture-mark-recapture analysis covering the study area.

In the analysis, the roe deer density index was calculated as the average across the municipalities in which the individual lynx travelled during the intensive tracking periods. Although this density index is crude, we believe that it is functional across such a massive variation in roe deer density (2–3 orders of magnitude).

#### CLIMATE DATA

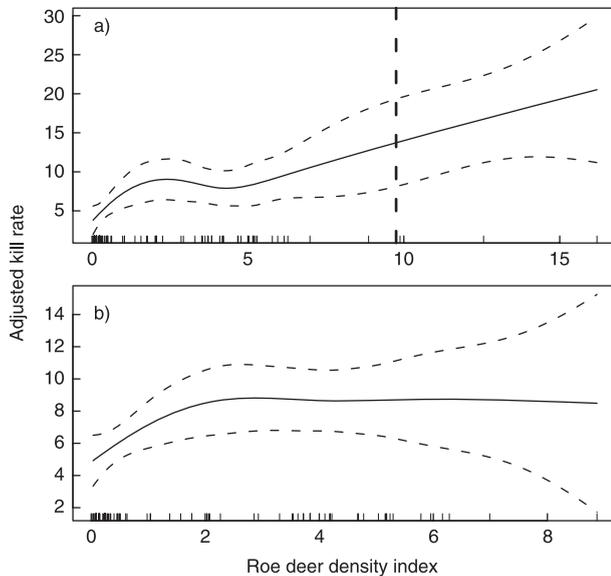
We used the winter index for the North Atlantic Oscillation (NAO) as an index of climate (Hurrell 1995). This index,

which measures the sea pressure difference between the Azores and Iceland, has become a popular large-scale index for climate variability in ecological research (see e.g. Post *et al.* 1999; Stenseth & Mysterud 2005). Although local conditions are what individual lynx experience when hunting roe deer, it has recently been shown that global-scale climate indices such as NAO are reasonable composites of several local climate variables (see Stenseth & Mysterud 2005 and references therein). Here, we used this index as a substitute for local weather conditions as it allows us to avoid arbitrary choice of time frame, spatial resolution and climatic variables to measure (Stenseth & Mysterud 2005).

In general, a high NAO index is correlated with mild winter temperature and much precipitation in the Scandinavian region (Stenseth & Mysterud 2005), and a low index with low temperatures and little precipitation. However, whether this precipitation comes as snow or rain varies with altitude and latitude. Based on meteorological data (downloaded from the Norwegian Meteorological Institute; <http://www.met.no>), we investigated the relationship between winter-NAO and snow cover (mean cover from January–March) for meteorological stations ( $n = 20$ ) located across the study area (Figs S1 and S2). Preferably, we used a meteorological station located central in the municipality, but not all municipalities have weather stations and not all of them covered the entire study period (1995–2005). We therefore selected weather stations spread around the study area, and searched for general patterns in the relationship between NAO and snow cover. In the northern part of the study area, snow cover (in January–March) was generally deep and NAO was positively correlated with snow cover [mean  $r = 0.39$  (range: 0.21–0.71), Figs S1 and S2], which might facilitate lynx hunting success (lynx have a smaller sinking depth than roe deer). In the southern part of the study area, however, snow cover is much less deep and not correlated with NAO [Figs S1 and S2; mean  $r = -0.08$  (range -0.28–0.11)]. In our statistical analysis, we used an indicator variable (I: see below) to investigate whether the correlation between NAO and kill rates differed between these regions.

#### STATISTICAL ANALYSIS OF THE FUNCTIONAL RESPONSE

Regardless of the class of functional response, predator satiation seems to be a common feature emerging from studies of mammalian (Jost *et al.* 2005) and other (Skalski & Gilliam 2001) predator–prey systems. To assess this assumption, we initially modelled the relationship between lynx kill rate and roe deer density using a generalized additive mixed effects model (Woods 2006), using the gamm procedure in the library *mgcv* in the R 2.6.2 software (R Development Core Team 2008). This nonparametric approach allows for full flexibility in the relationship between the response and explanatory variable and is thus well suited to investigate this assumption. In the models, season (summer vs. winter), social status (solitary individuals vs. females with dependent kittens) and their interaction were fitted as parametric fixed effects, and the relationship between roe deer density and kill rates were



**Fig. 1.** The relationship between lynx kill rates and roe deer density index, as revealed by generalized additive mixed models with the effect of season and social status fitted as fixed parametric effects, the relationship between roe deer density and kill rate modelled by a smoothing spline, and lynx individual fitted as random effect. In panel a) the relationship is plotted for the complete range of the roe deer density index. The dashed line represents the 97.5% percentile of the roe deer density distribution. In panel b) the model is fitted without the three observations outside the 97.5% percentile of the roe deer density distribution. The y-axis represents kill rates after the effect of season and social status are removed. See Methods section for a description of the approach.

modelled using cubic smoothing splines (Woods 2006). As we had more than one observation of kill rates for some lynx individuals, lynx individual identity was included as a random effect in the models. Visual inspection of the models (Fig. 1a) suggested that this assumption might not be completely supported, as there was some evidence that kill rates increased with roe deer density also above a threshold density. However, this pattern was entirely caused by three extreme observations at the highest roe deer density (outside the 97.5% percentile of the observed roe deer density distribution). When fitting the model only with observations within the 97.5% percentile of the roe deer density distribution, visual inspection of the model suggested no increase in kill rates above a threshold roe deer density (Fig. 1b). As we had few observations of lynx kill rates at the highest roe deer densities, our data did not allow us to conduct robust tests to investigate if this pattern is biologically significant or a result of sampling error or stochasticity.

In subsequent modelling, we therefore assumed that lynx kill rates could be described by a type II functional response. Also, as the lynx density was relatively constant throughout the study period, we would not be able to distinguish between a purely prey-dependent model and a ratio-dependent model. We used the disc equation to model the kill rates (note that this equation is equivalent to the one originally used by Holling, but the parameters are interpreted differently);  $\text{killrate} = (a \cdot P) /$

$(h + P)$ , where  $a$  is the asymptotic kill rate (i.e. kill rate when the prey density is high),  $P$  is the prey density and  $h$  is the half-saturation density (i.e. prey density when the kill rate is  $1/2 a$ ). As some individuals had several observed kill rates (over several years or seasons), we had to account for pseudo-replication (Hurlbert 1984); consequently, we fitted nonlinear mixed effects regression models (Pinheiro & Bates 2002) with lynx individual fitted as a random effect. The models were fitted using the *nlme*-procedure in the *nlme* library in R 2.6.2 (R Development Core Team 2008), under the assumption that the random variable is  $N(0, \sigma^2)$  (Skrondal & Rabe-Hesketh 2004).

To accommodate tests for the effects of season, social status and climatic conditions (indexed by NAO), we modified the equation such that the asymptote was written  $[a + (b_1 \times x_1) + (b_2 \times x_2) + (b_3 \times x_3)]P$ , where  $b_1$ ,  $b_2$  and  $b_3$  are the effects of covariate  $x_1$ – $x_3$  on the asymptotic value. Similarly, we modified the half saturation level by writing  $[h + (b_1 \times x_1) + (b_2 \times x_2) + (b_3 \times x_3)] + P$ , where again  $b_1$  is the effect of covariate  $x_1$  on the half saturation value. In our analysis, we first investigated the effects of social status and season as covariates in the functional response models, by running a total of 16 candidate models (Table 1). Then we investigated the effect of NAO on observed kill rates, by modifying the model with the lowest Akaike information criterion (AIC) value (see below) in the subsample described above. To investigate whether the effect of NAO differed between regions (as described in Climate data), we included an indicator variable for region (see also Vucetich *et al.* 2002 for the use of indicator variables); 0 for areas within the southern region (mean snow cover < 35 cm), and 1 for areas with > 35 cm snow cover through the winter (see Figs S1 and S2). Thus, the term becomes  $b_3 \times I \times \text{NAO}$ , implying that NAO will only have an effect in regions where snow cover is correlated with the NAO value (Figs S1 and S2). In effect, this means that the effect of NAO is  $b_3$  in region 1 and 0 in region 0. Finally, we investigated the potential for a different effect of NAO on summer and winter kill rates by modelling  $b_3 \times \text{season} \times I \times \text{NAO}$ .

The performance of the models was investigated based on their AIC values (Burnham & Anderson 2002), where the model with the lowest AIC value indicates the best model among the examined models, given the data. For each model, we also computed Akaike weights ( $w_i$ ) (Burnham & Anderson 2002). The Akaike weight is a measure of the relative support for each of the models in the subset, given the data and the model subset, and the sum of  $w_i$  is equal to 1. The relative importance of the covariates social status and season was calculated by summing up  $w_i$  across all models where the parameter of interest is present (Burnham & Anderson 2002). As model parameters do not only depend on the data but also on the model structure, we also computed model averaged model parameters (effect sizes and standard errors) by following the procedure described by Burnham & Anderson (2002). Note that while this is generally not recommended for nonlinear models if structural parameters are removed, we always used the same general model structure based on the type II functional response. Thus, model parameters were not

**Table 2.** Results from the model selection based on Akaike information criterion (AIC), comparing models with the effect of season and social status on observed kill rates. A total of 16 nonlinear type II functional response models were evaluated

Model	$a^a$		$h^a$		AIC	$\Delta$ AIC	$w_i$	$r^2$ (*)
	Season	Social	Season	Social				
$\Phi$ 1					582.37	22.03	< 0.0001	0.15
$\Phi$ 2	x				580.44	20.10	< 0.0001	0.19
$\Phi$ 3		x			565.56	5.22	0.0150	0.32
$\Phi$ 4			x		577.86	17.52	< 0.0001	0.24
$\Phi$ 5				x	613.84	53.50	< 0.0001	0.07
$\Phi$ 6	x	x			563.74	3.40	0.0374	0.35
$\Phi$ 7	x		x		576.58	16.23	0.0001	0.15
$\Phi$ 8	x			x	563.79	3.45	0.0363	0.35
$\Phi$ 9		x	x		560.34	0.00	0.2043	0.37
$\Phi$ 10		x		x	561.61	1.27	0.1081	0.37
$\Phi$ 11			x	x	566.05	5.71	0.0117	0.31
$\Phi$ 12	x	x	x		562.32	1.98	0.0760	0.37
$\Phi$ 13	x	x		x	560.37	0.03	0.2011	0.39
$\Phi$ 14	x		x	x	565.79	5.45	0.0134	0.35
$\Phi$ 15		x	x	x	560.41	0.07	0.1974	0.39
$\Phi$ 16	x	x	x	x	561.79	1.45	0.0992	0.40

<sup>a</sup> $a$  is the asymptotic value in the functional response, whereas  $h$  is the prey density at which the kill rate is 1/2 of  $a$ . In the models, we allowed these parameters to vary between season (summer and winter) or between groups of different social status (i.e. females with their kittens compared to solitary individuals). \*See methods for the computation of  $r^2$  values.

dependent on one model, but took into account model selection uncertainty. Assumptions of the models were investigated as described by Pinheiro & Bates (2002).

To investigate the amount of variation that could be attributed to the fixed and random parts of the models, we followed a two-step process. First, we evaluated the proportion of the total residual variation that could be attributed to individual identity, also known as the intraclass correlation  $\rho$  (Skrondal & Rabe-Hesketh 2004). Then we examined the correlation between the fitted and observed values, without the effect of the random factors. We here report the squared correlation coefficient ( $r^2$ ), and note that this gives very similar results to single-level models.

## Results

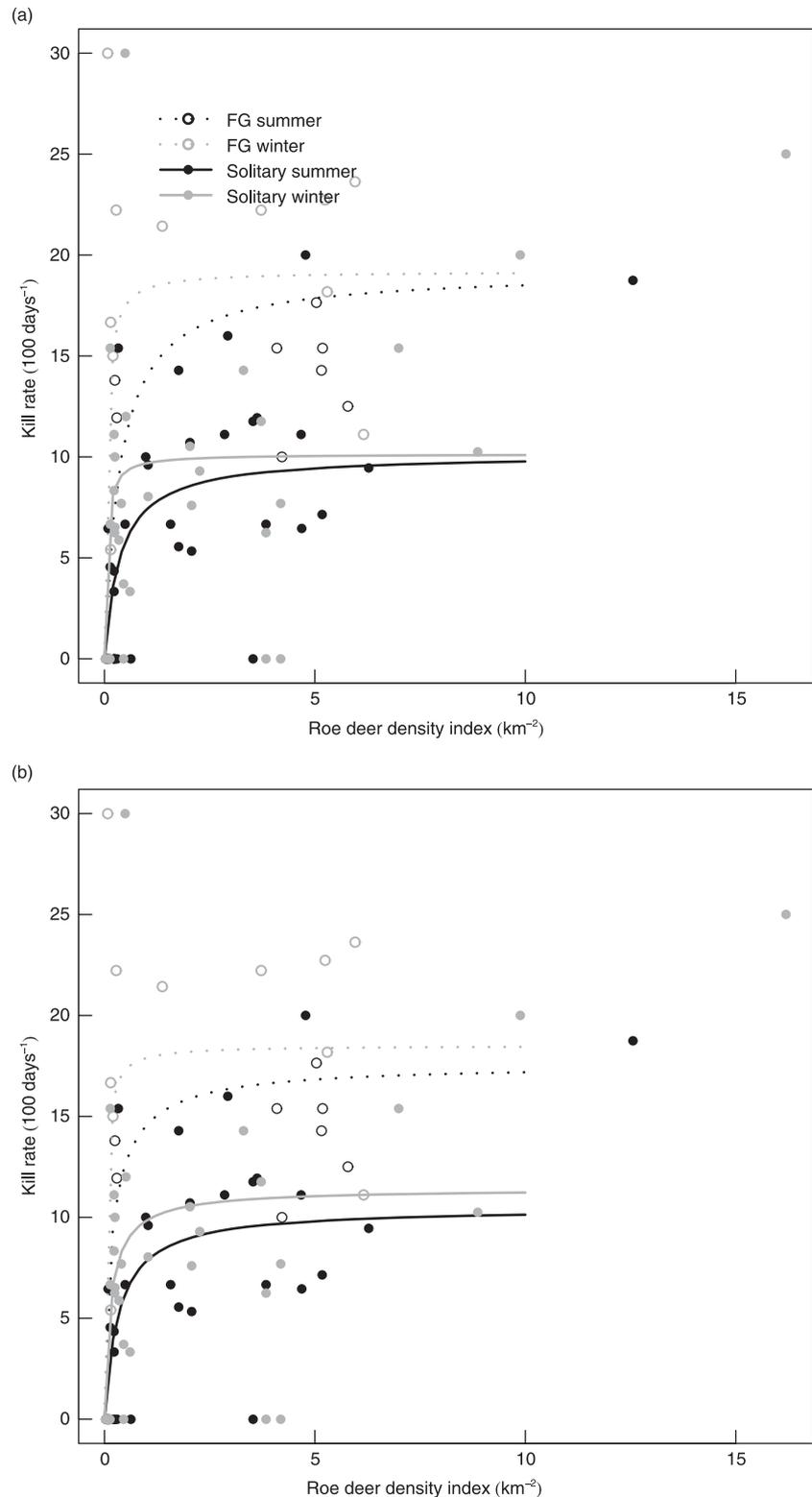
The results from fitting nonlinear type II functional response models with season and social status as covariates indicate that both covariates are needed to adequately describe the observed kill rates (Table 2; Fig. 2a and b). Although there was considerable uncertainty in the model selection (Table 2), a common feature for all models with a high rank is that family groups (i.e. females with dependent kittens) had a higher asymptotic kill rate than solitary individuals (Tables 3 and 4; Fig. 2a and b). Furthermore, there was a strong indication that both groups were more efficient during winter (i.e. a lower half saturation value; Tables 3 and 4), and that family groups were slightly more efficient than solitary individuals at low prey densities (Tables 3 and 4). The covariate having the least relative importance was the effect of season on the asymptotic kill rate (Table 4), although the model averaged parameter suggests slightly higher values during winter than during

**Table 3.** Parameter estimates for the three best models (i.e. lowest AIC values) in the global set of models presented in Table 1. Parameters are estimated based on maximum likelihood

Model/term	Parameter	Parameter value (SE)
$\Phi$ 9		
Asymptote	$a$	10.14 (1.22)
	social status <sup>a</sup>	9.05 (2.28)
Half saturation	$h$	0.37 (0.20)
	season <sup>b</sup>	-0.33 (0.19)
$\Phi$ 13		
Asymptote	$a$	10.06 (1.53)
	social status <sup>a</sup>	5.46 (2.22)
	season <sup>b</sup>	2.99 (1.72)
Half saturation	$h$	0.27 (0.14)
	social status <sup>a</sup>	-0.24 (0.14)
$\Phi$ 15		
Asymptote	$a$	11.03 (1.47)
	social status <sup>a</sup>	7.22 (2.58)
Half saturation	$h$	0.41 (0.21)
	social status <sup>a</sup>	-0.10 (0.10)
	season <sup>b</sup>	-0.29 (0.19)

<sup>a</sup>Solitary coded as 0, family group as 1. <sup>b</sup>Summer coded as 0, winter as 1.

summer. The fixed effects part model with the lowest AIC value ( $\Phi$  9) explained ~37% of the variation in kill rates, whereas ~20% of the residual variation could be attributed to differences between individual lynx (i.e.  $\rho$  – see Methods).



**Fig 2.** Estimated type II functional responses for lynx in south-eastern Norway, based on 10 years of field data. In a), the model with the lowest AIC value is plotted ( $\Phi 9$ ), whereas in b) the model is plotted based on model-averaged predictions.

In the subsequent models, we used the model with the lowest AIC value in the subset described above ( $\Phi 9$ ) as our base model. When including the effect of NAO as a covariable in the asymptote (i.e.  $b_3 \times \text{NAO}$ ), we found no clear effect (AIC; 559.52,  $\Delta\text{AIC}$ ;  $-0.84$  compared to  $\Phi 9$ ). However, when differentiating between the effect of NAO in the northern

region and southern region of the study area (see Figs S1 and S2) by including region as an indicator variable ( $b_3 \times \text{I} \times \text{NAO}$ ), model selection guided by AIC suggested that kill rates varied according to the climate in the northern region (AIC; 558.49,  $\Delta\text{AIC}$ ;  $-1.85$  compared to  $\Phi 9$ ). The parameter estimate ( $b_3 = 1.08 \pm 0.59$ ) indicates that kill rates in the northern area

**Table 4.** The relative importance of parameters based on the sum of Akaike's weights across all models where the parameter is present (Burnham & Anderson 2002), and model averaged parameter estimates. The structural parameters ( $a$  and  $h$ , respectively) are present in all models

Parameter	Relative importance	Model averaged parameter (SE)
$a$		10.48 (1.67)
season <sup>a</sup>	0.46	1.10 (1.72)
social status <sup>b</sup>	0.94	6.74 (3.04)
$h$		0.33 (0.20)
season <sup>a</sup>	0.60	-0.16 (0.20)
social status <sup>b</sup>	0.67	-0.14 (0.16)

<sup>a</sup>Summer coded as 0, winter as 1. <sup>b</sup>Solitary coded as 0, family group as 1.

were higher in years with a high NAO index, i.e. in years with deep snow cover. Surprisingly, when testing for a differential effect of winter NAO in summer and winter on observed kill rates (i.e.  $b_3 \times I \times \text{season} \times \text{NAO}$ ), this model performed less well than the model without any distinction between summer and winter (AIC; 560.10,  $\Delta\text{AIC}$ ; -0.24 compared to  $\Phi$  9). The model with the lowest AIC value explained ~40% of the variation, and 8% of the residual variation could be attributed to differences between individual lynx (i.e.  $\rho$  – see methods). All models in which NAO affected half-saturation value performed less well than the selected model (i.e.  $\Delta\text{AIC} > 2.0$  compared to  $\Phi$  9).

## Discussion

This study demonstrates how a suite of social, ecological and abiotic factors interact to influence predator consumption rates, clearly revealing that predator consumption rate is not just a simple function of prey abundance. In summary, (i) saturation levels varied between social categories of lynx, in this case between family groups and solitary individuals; (ii) there was a seasonal difference in the half-saturation constant but not in the asymptotic level; (iii) climatic variables, indexed by the NAO, affected the consumption rate of the predator in areas where NAO was associated with increased snow depth. These findings introduce both complex and stochastic aspects into the predator-prey dynamics (see also Post *et al.* 1999, Wilmers *et al.* 2007) illustrating the importance of achieving a mechanistic understanding of predator-prey dynamics in a world under the influence of climate change.

### THE POTENTIAL FOR PREDATOR DEPENDENCE IN THE FUNCTIONAL RESPONSE

We modelled the functional response as a type II prey-dependent response, despite a growing body of studies indicating that predator presence might affect prey behaviour and habitat selection (e.g. Caro 2005). If variation in lynx density

leads to modifications in prey behaviour, this could result in interference competition as prey might become temporarily immune to predation through increased vigilance after having been challenged by a predator (Caro 2005). In turn, this could potentially result in predator dependence on the functional response (see e.g. Abrams & Ginzburg 2000 for a discussion). However, the density of lynx remained relatively stable at around three to four lynx 1000 km<sup>-2</sup> throughout the study period because of the annual recreational harvest which seeks to maintain the regional lynx population within predetermined limits (Odden *et al.* 2006). Also, male and female lynx maintained home ranges (ranging between 200–1500 km) with low intrasexual overlap (Linnell *et al.* 2001; Herfindal *et al.* 2005b). We are thus confident that variation in predator density should not have affected our results, but urge further studies on this aspect for solitary stalking predators such as the lynx. Such studies should preferably come from areas where predator density is more variable than in our study and where predators also occur at higher densities (e.g. in unmanaged populations).

### THE RELATIONSHIP BETWEEN PREY DENSITY AND KILL RATES; SEASONAL DIFFERENCES AND THE EFFECT OF SOCIAL STATUS

Kill rates are determined by searching time and handling time (Holling 1959), and increasing densities of prey are likely to result in increased encounter rates and thus reduced searching time. Higher kill rates at higher prey densities could also emerge from density-dependent changes in prey habitat use (Errington 1946). However, the densities that our roe deer occurred at were generally very low (see e.g. Nilsen *et al.* 2009) even in the relatively higher density parts of our study area (Bunnefeld *et al.* 2006; Ratikainen *et al.* 2007), implying that it is unlikely that density-dependent effects in habitat use is causing increased kill rates under our study conditions.

Our analysis revealed a slight difference in the relationship between prey density and kill rates between summer and winter. More importantly, the half-saturation level was lower in winter than in summer, while there was only a trend towards an elevation in the asymptotic level during winter. In a recent study from a wolf-moose system in the same ecosystem, it was reported that kill rates are generally of higher in summer than in winter, due to the body development of juvenile prey (Sand *et al.* 2008). However, in our study area roe deer fawns are generally immune to lynx predation during their first months of life because of their hiding strategy (Panzacchi *et al.* 2008). Thus, there might not be a reason to expect higher kill rates in summer. In contrast, a lower half-saturation level during winter is probably related to higher encounter rates at low roe deer density in winter, caused by snow covering the ground that change prey spacing behaviour (Myrsterud *et al.* 1997). In winter, roe deer were clumped around human settlements (either around artificial feeding sites or close to agricultural land; see Bunnefeld *et al.* 2006) in much of our study area. A change from more uniform prey distribution in summer to a clumped and predictable

prey distribution in winter may facilitate a reduction in search time, since lynx maintain their territories, and the associated knowledge of prey distribution, for years (Breitenmoser-Würsten *et al.* 2007). Another potential explanation is that domestic sheep were available as an alternative lynx prey during summer in the parts of our study area with low roe deer densities (Odden *et al.* 2006). As domestic sheep might contribute substantially to the lynx diet, this might have suppressed lynx consumption of roe deer in summer in some areas. However, separate analyses have indicated that lynx select habitats associated with higher roe deer density rather than areas with free-grazing sheep (Moa *et al.* 2006; Odden *et al.* 2008), supporting the notion that lynx prefer roe deer prey when available.

Overriding the seasonal differences in kill rates was the difference between lynx of different social status; the consumption rate of females with their dependent kittens was much higher than those of solitary individuals. Such differences between different categories of individuals have been reported previously for puma preying on mule deer (Laundré 2008) and lynx preying on roe deer (Jobin *et al.* 2000), and is most likely related to different energetic demands (Laundré 2008).

#### CLIMATE VARIABILITY AND IMPLICATIONS FOR PREDATOR–PREY DYNAMICS

The mechanistic relationship between climate and kill rates is most likely linked to differing hunting success. A small reduction in speed of an escaping roe deer due to snow cover may affect the hunting success in winter. Surprisingly, however, our modelling also suggested that winter NAO had a carry-over effect through to the summer. At this stage, we feel that it is premature to suggest that this is a general pattern. However, previous studies have shown how roe deer are sensitive to winter climate, and that body weight in autumn might be related to conditions experienced during the previous winter (Herfindal 2006; Mysterud & Østbye 2006).

Relationships between climatic conditions such as snow cover and the dynamics of wolf-ungulate systems have been described several times (Post *et al.* 1999; Hebblewhite 2005), and in a recent analysis from Isle Royale climatic variation was reported to explain more of the variation in moose population growth rates than did wolf density (Vucetich & Peterson 2004). However, lynx and wolves have different social structures and hunting strategies, and for stalking predators (such as the lynx), similar studies are generally lacking (but see Stenseth *et al.* 2004). Simulation studies suggest that ambush or stalking predators should stabilize the dynamics of predator–prey systems, by inducing elevated mortality for prime-aged prey, and thus prolonging the predator pit and reducing the chance of prey irruption (Wilmers *et al.* 2007). We have previously shown that lynx frequently include adult roe deer in their diet in a proportion representing the standing age distribution (Andersen *et al.* 2007), thus one could expect lynx predation to stabilize the system (Wilmers *et al.* 2007). However, if climatic conditions affect the functional response

of the lynx, as we report here, one would expect climatic variation to destabilize these systems as well. This is also supported by demographic perturbation analysis of radiocollared roe deer in the study area; interannual fluctuation in roe deer growth rate is strongly affected by lynx predation and more so in the northern part of the study area (Nilsen *et al.* 2009). Our results further suggest that lynx impact on roe deer prey might increase in areas where climate change results in more snow (see also Post *et al.* 1999; Hebblewhite 2005), although the nonlinear relationships that are frequently observed in biological systems (e.g. Mysterud *et al.* 2001) require a cautious interpretation.

The fact that lynx were able to exhibit high kill rates at a very low roe deer density is indicative for a potentially strong top-down limitation of the prey population. This is in particular true in the northern parts of the study area, where roe deer densities are at the lowest, predation rates highest (C. Melis, J. Odden, R. Andersen, & J. D. C. Linnell, unpublished data), and lynx consumption rates are most closely linked to climatic factors. Indeed, a steep type II functional response coupled with a stable predator population (e.g. due to management) will result in a negative relationship between prey density and predation rates (see also Nilsen *et al.* 2005). If allowed to respond numerically however, an effective predator such as the lynx should result in a predator zero isocline intersecting the prey isoclines to the left of the hump (see Deng *et al.* 2007 and references therein). Theoretically, a vertical predator isocline should then result in increasing cycles ending up with prey and predator extinction (see also classical studies by Gauss 1934), whereas a sloped predator isocline (arising from predator dependence in kill rates or more generally in predator growth rate; Abrams & Ginzburg 2000; Deng *et al.* 2007) should lead to equilibrium points that are both low and stable (i.e. biological control; Deng *et al.* 2007). However, regardless of theoretical considerations based on deterministic models, the stochasticity induced by variation in the spatial distribution of lynx family groups and varying climatic conditions combined with the low half-saturation density, is likely to lead to high variability on a local scale.

Our analyses have highlighted that prey consumption rates by predators are more complex than being purely a function of prey density (see also Abrams & Ginzburg 2000; Miller *et al.* 2006). Indeed, we have shown that a purely prey-dependent functional response model might give a poor description of the data, and that additional factors are needed to obtain a reliable understanding of predator consumption rate. Such detailed knowledge is important if we are to make predictions about the nature of predator–prey relationships.

#### Acknowledgement

The study was supported by the Research Council of Norway, the Norwegian Directorate for Nature Management (DN), the Norwegian Institute for Nature Research (NINA), Hedmark University College, and the Nature Protection Divisions of the County Governor's Office for Oslo & Akershus, Østfold, Hedmark, Oppland, Buskerud and Telemark counties. We also want to thank the many people who have helped us in the field during the years of this study. Jos M. Milner, Harry P. Andreassen, Jean-Michel Gaillard and Fridolin Zimmermann provided valuable comments on the manuscript.

## References

- Abrams, P.A. & Ginzburg, L.R. (2000) The nature of predation: prey dependent, ratio dependent or neither? *Trends in Ecology & Evolution*, **15**, 337–341.
- Andersen, R., Karlsen, J., Austmo, L.B., Odden, J., Linnell, J. & Gaillard, J.M. (2007) Selectivity of Eurasian lynx *Lynx lynx* and recreational hunters for age, sex and body condition in roe deer *Capreolus capreolus*. *Wildlife Biology*, **13**, 467–474.
- Anderson, C.R. & Lindzey, F.G. (2003) Estimating cougar predation rates from GPS location clusters. *Journal of Wildlife Management*, **67**, 307–316.
- Andrén, H., Linnell, J.D.C., Liberg, O., Ahlqvist, P., Andersen, R., Danell, A., Franzén, 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.
- Arditi, R. & Berryman, A.A. (1991) The biological-control paradox. *Trends in Ecology & Evolution*, **6**, 32–32.
- Arnemo, J.M., Linnell, J.D.C., Wedul, S.J., Ranheim, B., Odden, J. & Andersen, R. (1999) Use of intraperitoneal radio-transmitters in lynx *Lynx lynx* kittens: anaesthesia, surgery and behaviour. *Wildlife Biology*, **5**, 245–250.
- Arnemo, J.M., Ahlqvist, P., Andersen, R., Berntsen, F., Ericsson, G., Odden, J., Brunberg, S., Segerstrom, P. & Swenson, J.E. (2006) Risk of capture-related mortality in large free-ranging mammals: experiences from Scandinavia. *Wildlife Biology*, **12**, 109–113.
- Breitenmoser-Würsten, C., Zimmermann, F., Stahl, P., Vandel, J.M., Molinari-Jobin, A., Molinari, P., Capt, S. & Breitenmoser, U. (2007) Spatial and social stability of a Eurasian lynx *Lynx lynx* population: an assessment of 10 years of observation in the Jura Mountains. *Wildlife Biology*, **13**, 365–380.
- Bunnfeld, N., Linnell, J.D.C., Odden, J., van Duijn, M.A.J. & Andersen, R. (2006) Risk taking by Eurasian lynx (*Lynx lynx*) in a human-dominated landscape: effects of sex and reproductive status. *Journal of Zoology*, **270**, 31–39.
- Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, Springer-Verlag, New York.
- Caro, T.M. (2005) *Antipredator Defenses in Birds and Mammals* The University of Chicago Press, Chicago, Illinois.
- Coulson, T., Rohani, P. & Pascual, M. (2004) Skeletons, noise and population growth: the end of an old debate? *Trends in Ecology & Evolution*, **19**, 359–364.
- DelGiudice, G.D., Fieberg, J., Riggs, M.R., Powell, M.C. & Pan, W. (2006) A long-term age-specific survival analysis of female white-tailed deer. *Journal of Wildlife Management*, **70**, 1556–1568.
- Deng, B., Jessie, S., Ledder, G., Rand, A. & Srodulski, S. (2007) Biological control does not imply paradox. *Mathematical Biosciences*, **208**, 26–32.
- Errington, P.L. (1946) Predation and vertebrate populations. *Quarterly Review of Biology*, **21**, 144–177.
- Festa-Bianchet, M., Coulson, T., Gaillard, J.M., Hogg, J.T. & Pelletier, F. (2006) Stochastic predation events and population persistence in bighorn sheep. *Proceedings of the Royal Society B: Biological Sciences*, **273**, 1537–1543.
- Fryxell, J.M., Mosser, A., Sinclair, A.R.E. & Packer, C. (2007) Group formation stabilizes predator-prey dynamics. *Nature*, **449**, 1041–1044.
- Gause, G.F. (1934) *The Struggle for Existence*, Dover Publications.
- Ginzburg, L.R. & Akçakaya, H.R. (1992) Consequences of ratio-dependent predation for steady-state properties of ecosystems. *Ecology*, **73**, 1536–1543.
- Grotan, V., Saether, B.E., Engen, S., Solberg, E.J., Linnell, J.D.C., Andersen, R., Broseth, H. & Lund, E. (2005) Climate causes large-scale spatial synchrony in population fluctuations of a temperate herbivore. *Ecology*, **86**, 1472–1482.
- Hayes, R.D. & Harestad, A.A. (2000) Wolf functional response and regulation of moose in the Yukon. *Canadian Journal of Zoology*, **78**, 60–66.
- Hebblewhite, M. (2005) Predation by wolves interacts with the North Pacific Oscillation (NPO) on a western North American elk population. *Journal of Animal Ecology*, **74**, 226–233.
- Herfindal, I. (2006) Life history consequences of environmental variation along ecological gradients in northern ungulates. PhD thesis, Department of Biology, Norwegian University of Science and Technology, Trondheim, Norway.
- Herfindal, I., Linnell, J.D.C., Moa, P.F., Odden, J., Austmo, L.B., & Andersen, R. (2005a) Does recreational hunting of lynx reduce depredation losses of domestic sheep. *Journal of Wildlife Management*, **69**, 1034–1042.
- Herfindal, I., Linnell, J.D.C., Odden, J., Nilsen, E.B. & Andersen, R. (2005b) Prey density, environmental productivity and home-range size in the Eurasian lynx (*Lynx lynx*). *Journal of Zoology*, **265**, 63–71.
- Holand, Ø., Myrsterud, A., Wannag, A. & Linnell, J.D.C. (1998) Roe deer in northern environments: Physiology and behaviour. *European Roe Deer: The Biology of Success* (eds R. Andersen, P. Duncan & J.D.C. Linnell), pp. 117–139. Scandinavian University Press, Oslo, Norway.
- Holling, C.S. (1959) The components of predation as revealed by a study of small mammal predation of the European pine sawfly. *The Canadian Entomologist*, **91**, 293–320.
- Hurlbert, S.H. (1984) Pseudoreplication and the design of ecological field experiments. *Ecological Monographs*, **54**: 187–211.
- Hurrell, J.W. (1995) Decadal trends in the North Atlantic Oscillation – regional temperatures and precipitation. *Science*, **269**, 676–679.
- Jedrzejewski, W., Schmidt, K., Milkowski, L., Jedrzejewska, B. & Okarma, H. (1993) Foraging by lynx and its role in ungulate mortality: the local (Bialowieza Forest) and the Palaearctic viewpoint. *Acta Theriologica*, **38**, 385–403.
- Jobin, A., Molinari, P. & Breitenmoser, U. (2000) Prey spectrum, prey preference and consumption rates of Eurasian lynx in the Swiss Jura Mountains. *Acta Theriologica*, **45**, 243–252.
- Jost, C., Devulder, G., Vucetich, J.A., Peterson, R.O. & Arditi, R. (2005) The wolves of Isle Royale display scale-invariant satiation and ratio-dependent predation on moose. *Journal of Animal Ecology*, **74**, 809–816.
- Laundré, J.W. (2008) Summer predation rates on ungulate prey by a large keystone predator: how many ungulates does a large predator kill? *Journal of Zoology, London*, **275**, 41–348.
- Linnell, J.D.C., Andersen, R., Kvam, T., Andrén, H., Liberg, O., Odden, J. & Moa, P.F. (2001) Home range size and choice of management strategy for lynx in Scandinavia. *Environmental Management*, **27**, 869–879.
- Linnell, J.D.C., Odden, J., Andrén, H., Liberg, O., Andersen, R., Moa, P.F., Kvam, T., Segerström, P., Schmidt, K., Jedrzejewski, W. & Okarma, H. (2007) Distance rules for minimum counts of Eurasian lynx *Lynx lynx* family groups under different ecological conditions. *Wildlife Biology*, **13**, 447–455.
- Miller, D.A., Grand, J.B., Fondell, T.F. & Anthony, M. (2006) Predator functional response and prey survival: direct and indirect interactions affecting a marked prey population. *Journal of Animal Ecology*, **75**, 101–110.
- Moa, P.F., Herfindal, I., Linnell, J.D.C., Overskaug, K., Kvam, T., & Andersen, R. (2006) Does the spatiotemporal distribution of livestock influence forage patch selection in Eurasian lynx? *Wildlife Biology*, **12**, 63–70.
- Myrsterud, A. & Østbye, E. (2006) Effect of climate and density on individual and population growth of roe deer *Capreolus capreolus* at northern latitudes: the Lier valley, Norway. *Wildlife Biology*, **12**, 321–329.
- Myrsterud, A., Bjørnsen, B.H. & Østbye, 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*, **1**, 27–33.
- Myrsterud, A., Stenseth, N.C., Yoccoz, N.G., Langvatn, R. & Steinheim, G. (2001) Nonlinear effects of large-scale climatic variability on wild and domestic herbivores. *Nature*, **410**, 1096–1099.
- Nilsen, E.B., Pettersen, T., Gundersen, H., Milner, J.M., Myrsterud, A., Solberg, E.J., Andreassen, H.P. & Stenseth, N.C. (2005) Moose harvesting strategies in the presence of wolves. *Journal of Applied Ecology*, **42**, 389–399.
- Nilsen, E.B., Gaillard, J.-M., Andersen, R., Odden, J., Delorme, D., van Laere, G. & Linnell, J.D.C. (2009) A slow life in hell or a fast life in heaven: demographic analyses of contrasting roe deer populations. *Journal of Animal Ecology*, printed online (DOI: 10.1111/j.1365-2656.2009.01523.x)
- O'Donoghue, M., Boutin, S., Krebs, C.J., Zuleta, G., Murray, D.L. & Hofer, E.J. (1998) Functional responses of coyotes and lynx to the snowshoe hare cycle. *Ecology*, **79**, 1193–1208.
- Odden, J., Linnell, J.D.C., Moa, P.F., Herfindal, I., Kvam, T. & Andersen, R. (2002) Lynx depredation on domestic sheep in Norway. *Journal of Wildlife Management*, **66**, 98.
- Odden, J., Linnell, J.D.C. & 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*, **52**, 237–244.
- Odden, J., Herfindal, I., Linnell, J.D.C. & Andersen, R. (2008) Vulnerability of domestic sheep to lynx depredation in relation to roe deer density. *Journal of Wildlife Management*, **72**, 276–282.
- Okarma, H. (1984) The physical condition of red deer falling prey to the wolf and lynx and harvested in the Carpathian Mountains. *Acta Theriologica*, **29**, 283–290.
- Øvrum, L. (2000) *At the scene of the crime; lynx handling of prey in Hedmark*. MSc Thesis, Norwegian University for Science and Technology, Trondheim, Norway.
- 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.
- Pedersen, V., Linnell, J.D.C., Andersen, R., Andrén, H., Segerström, P. & Lindén, M. (1999) Winter lynx predation on semi-domestic reindeer in northern Sweden. *Wildlife Biology*, **5**, 203–212.

- Pinheiro, J. & Bates, D. (2002) *Mixed-Effects Modelling in S and S-Plus. Statistics and Computing Series*. Springer Verlag, New York.
- Post, E., Peterson, R.O., Stenseth, N.C. & McLaren, B.E. (1999) Ecosystem consequences of wolf behavioural response to climate. *Nature*, **401**, 905–907.
- R Development Core Team (2008) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Ratikainen, I.I., Panzacchi, M., Mysterud, A., Odden, J., Linnell, J. & Andersen, R. (2007) Use of winter habitat by roe deer at a northern latitude where Eurasian lynx are present. *Journal of Zoology*, **273**, 192–199.
- Sand, H., Zimmermann, B., Wabakken, P., Andren, H. & Pedersen, H.C. (2005) Using GPS technology and GIS cluster analyses to estimate kill rates in wolf-ungulate ecosystems. *Wildlife Society Bulletin*, **33**, 914–925.
- Sand, H., Wabakken P., Zimmermann, B., Johansson, Ø., Pedersen, H.C. & Liberg, O. (2008) Summer kill rates and predation pattern in a wolf-moose system: can we rely on winter estimates? *Oecologia*, printed online (DOI: 10.1007/s00442-008-0969-2).
- Skalski, G.T. & Gilliam, J.F. (2001) Functional responses with predator interference: viable alternatives to the Holling Type II model. *Ecology*, **82**, 3083–3092.
- Skrondal, A. & Rabe-Hesketh, S. (2004) *Generalized Latent Variable Modeling: Multilevel, Longitudinal and Structural Equation Models*, Chapman & Hall/CRC, Washington, DC.
- Stenseth, N.C. & Mysterud, A. (2005) Weather packages: finding the right scale and composition of climate in ecology. *Journal of Animal Ecology*, **74**, 1195–1198.
- Stenseth, N.C., Chan, K-S., Howell, T., Boonstra, R., Boutin, S., Krebs, C.J., Post, E., O'Donoghue, M., Yoccoz, N.G., Forckhammer, M.C. & Hurrell, J.W. (1999) Common dynamic structure of Canadian lynx within three climatic regions. *Science*, **285**, 1071–1073.
- Stenseth, N.C., Shabbar, A., Chan, K-S., Boutin, S., Rueness, E.K., Ehrlich, D., Hurrell, J.W., Lingjærde, O.C. & Jakobsen, K.S. (2004) Snow conditions may create an invisible barrier for lynx. *Proceedings of the National Academy of Sciences, USA*, **101**, 10632–10634.
- van der Meer, J. & Smallegange, I.M. (2009) A stochastic version of the Beddington-DeAngelis functional response: modelling interference for a finite number of predators. *Journal of Animal Ecology*, **78**, 134–142.
- Vucetich, J.A. & Peterson, R.O. (2004) The influence of top-down, bottom-up and abiotic factors on the moose (*Alces alces*) population of Isle Royale. *Proceedings of the Royal Society B: Biological Sciences*, **271**, 183–189.
- Vucetich, J.A., Peterson, R.O. & Schaefer, C.L. (2002) The effect of prey and predator densities on wolf predation. *Ecology*, **83**, 3003–3013.
- Werdelin, L. (1981) The evolution of lynxes. *Annales Zoologici Fennici*, **18**, 37–71.
- Wilmers, C.C., Post, E. & Hastings, A. (2007) The anatomy of predator-prey dynamics in a changing climate. *Journal of Animal Ecology*, **76**, 1037–1044.
- Woods, S. (2006) *Generalized Additive Models: An Introduction with R*. Chapman & Hall, Boca Raton, Florida.
- Zimmermann, B., Wabakken, P., Sand, H., Pedersen, H.C. & Liberg, O. (2007) Wolf movement patterns: a key to estimation of kill rate? *Journal of Wildlife Management*, **71**, 1177–1182.

Received 28 May 2008; accepted 3 March 2009

Handling Editor: Andre Gilburn

## Supporting Information

Additional supporting information may be found in the online version of this article:

**Fig. S1.** Map showing the study area in south-eastern Norway, and the demarcation of the regions (see Methods). In the northern region (dark grey shading indicates municipalities with kill rate data), snow cover is generally deep during winter and interannual variation is positively correlated with the NAO index. In the southern region (light grey shading indicates municipalities with kill rate data), snow cover is more shallow and not related with the NAO index (see Methods section of main document and Fig. S2).

**Fig. S2.** Correlation ( $r$ ) between annual variation in mean snow cover (January–March) measured at climate stations across the study area and winter NAO value, plotted against mean snow cover at the same stations. In general, there is a positive correlation between NAO value and snow cover in the snow-rich northern areas (black circles), whereas there is no, or only a weak, correlation in snow poor areas in south (open circles). In the analysis of the effect of NAO on observed kill rates, we differentiated between these regions (see Methods section in the main document and Fig. S1).

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting information supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.