

ARTICLE

Numerical response of predator to prey: Dynamic interactions and population cycles in Eurasian lynx and roe deer

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Abstract

The dynamic interactions between predators and their prey have two fundamental processes: numerical and functional responses. Numerical response is defined as predator growth rate as a function of prey density or both prey and predator densities [$dP/dt = f(N, P)$]. Functional response is defined as the kill rate by an individual predator being a function of prey density or prey and predator densities combined. Although there are relatively many studies on the functional response in mammalian predators, the numerical response remains poorly documented. We studied the numerical response of Eurasian lynx (*Lynx lynx*) to various densities of its primary prey species, roe deer (*Capreolus capreolus*), and to itself (lynx). We exploited an unusual natural situation, spanning three decades where lynx, after a period of absence in central and southern Sweden, during which roe deer populations had grown to high densities, subsequently recolonized region after region, from north to south. We divided the study area into seven regions, with increasing productivity from north to south. We found strong effects of both roe deer density and lynx density on lynx numerical response. Thus, both resources and intraspecific competition for these resources are important to understanding the lynx population dynamic. We built a series of deterministic lynx–roe deer models, and applied them to the seven regions. We found a very good fit between these Lotka–Volterra type models and the data. The deterministic models produced almost cyclic dynamics or dampened cycles in five of the seven regions. Thus, we documented population cycles in this large predator–large herbivore system, which is rarely done. The amplitudes in the dampened cycles decreased toward the south. Thus, the dynamics between lynx and roe deer became more stable with increasing carrying capacity for roe deer, which is related to higher productivity in the environment. This increased stability could be explained by variation in predation risk, where human presence can act as prey refugia, and by a more diverse prey guild that will weaken the direct interaction between lynx and roe deer.

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KEYWORDS

bottom-up, functional response, numerical response, population cycles, population dynamic, predator, prey, prey refugia, top-down

INTRODUCTION

The dynamic interaction between predators and their prey is a fundamental part of ecology and ecological theory. Lotka (1924) and Volterra (1926) developed the first predator–prey model. This model is very simple, where the predator growth rate is only a function of the prey density [$dP/dt = f(N)$], and the prey growth rate is only a function of the predator density [$dN/dt = f(P)$]. Rosenzweig and MacArthur (1963) introduced a carrying capacity for the prey, that is, the prey growth rate is a function of both the prey and predator densities [$dN/dt = f(N, P)$]. Still later, Arditi and Ginzburg (1989) introduced predator growth rate as a function of the ratio between prey and predator densities [$dP/dt = f(N/P)$]. Tanner (1975) explored a different kind of predator–prey models and found, for example, that the presence of intra-specific competition for prey among the predators increased the stability of the dynamics. Including two habitat types, one with good cover for the prey and one with poor cover, also increased the stability in the dynamics. He also found that similar growth rates in predator and prey may cause cyclic predator–prey dynamics.

There are two fundamental processes that shape the dynamics between predator and prey: the numerical response and the functional response. The numerical response is defined as the predator growth rate, either as a function of prey density alone [$dP/dt = f(N)$] or, to account for the competition among the predators for the prey, as a function of both prey density and predator density ($dP/dt = f(N, P)$, Bayliss & Choquenot, 2002; Oksanen et al., 2001; Solomon, 1949). Numerical response has sometimes been defined as the predator density per se as a function of prey density ($P = f(N)$, e.g., Grange & Duncan, 2006; Holling, 1959; Messier, 1994). However, this definition of numerical response assumes that the predator density responds instantaneously to changes in prey density, so that predator and prey densities are always in equilibrium (Eberhardt et al., 2003). This is rarely, if ever, the case in a temporal dynamic process between a mammalian predator and its prey.

Functional response is defined as the kill rate by an individual predator being a function of either prey density alone (Holling, 1959; Solomon, 1949), or a function of both prey and predator densities (Arditi & Ginzburg, 1989; Holling, 1959). The rationale for including predator density in the functional response is increasing interference

between predators when their density increases, and/or increasing competition between predators, especially during time periods when prey is not growing, that is, the time between birth pulses in seasonally breeding prey, such as northern herbivores (Arditi & Ginzburg, 1989).

Although there are relatively many studies on the functional response in mammalian predators (Chan et al., 2017; Dale et al., 1994; Nilsen, Linnell, et al., 2009; O'Donoghue et al., 1998; Vucetich et al., 2002; Zimmermann et al., 2015), numerical responses remain poorly documented. We believe the reason could be that functional response can be revealed in relatively short time studies, or by combining data from several different studies, while obtaining data on numerical response requires studies spanning very long time periods (e.g., Eberhardt et al., 2003; Hone et al., 2007; Vucetich & Peterson, 2004a), which rarely is possible, not least for financial reasons. Studies of numerical response also require large variation in the density of both prey and predator during the study period. In this study, we were able to overcome both these obstacles by exploiting an unusual event, similar to a natural experiment.

After a long absence from central and southern Sweden, while still remaining in the north, the Eurasian lynx (*Lynx lynx*, hereafter “lynx”), began a recolonization of this part of the country successively, from north to south, starting in the early 1990s. Roe deer (*Capreolus capreolus*) populations, the primary prey for lynx, had grown to high densities during this period of lynx absence (Cederlund & Liberg, 1995). Thus, we used this natural experiment where the lynx densities at the beginning of the study were low or zero, while the roe deer densities had grown high in the absence of lynx. Importantly, primary production, determining carrying capacity for roe deer, also showed an increasing gradient, from north to south. We divided the study area into seven regions, across this gradient to follow the successive lynx recolonization (Figure 1).

This study aimed to answer three specific questions. The first was whether we could demonstrate a numerical response in lynx, both to varying densities of its primary prey species, roe deer, and to its own density. If this is true, the numerical response of the predator (lynx) can be expressed as $dP/dt = f(N, P)$. Connected to this question, we also expected a large impact of lynx on roe deer dynamics, because lynx is an extremely efficient predator on roe deer (Gervasi et al., 2012).

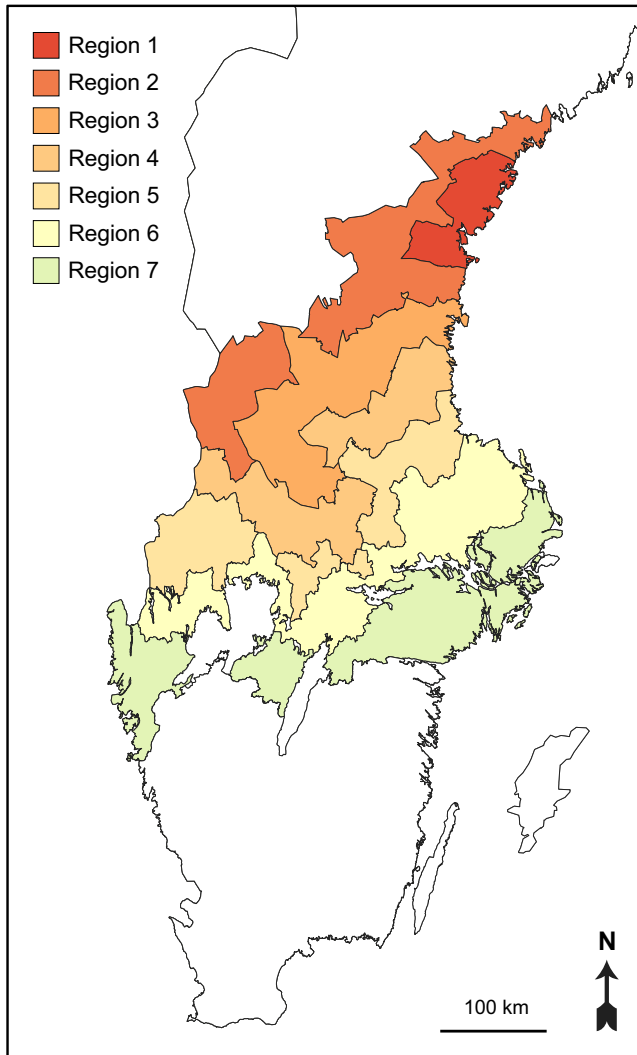


FIGURE 1 The study area in Sweden divided into seven regions.

Second, we were particularly interested in exploring whether there would occur stable predator–prey cycles in any of the regions in this lynx–roe deer system, as population cycles never have been demonstrated in large predator–large herbivore systems (Post et al., 2002), and also explored under what conditions such population cycles would occur.

Finally, based on Tanner’s (1975) findings that including two habitats with different predation risks, that is, the existence of so-called prey refugia, increased the stability in the predator–prey dynamics, we predicted that the stability of lynx–roe deer dynamic in this system will increase from north to south, with an increasing proportion of agricultural land among the regions. Basille et al. (2009) found that the roe deer densities were higher in areas with a high proportion of agricultural land and human infrastructure, because lynx avoided these areas.

To answer these questions, we combined data on lynx numerical response from this study, with data on functional

response (Nilsen, Linnell, et al., 2009). Based on these data, we then built a number of deterministic predator–prey models, separate for each region, to explore the dynamics of lynx–roe deer interaction over this gradient of primary production. The models included established knowledge of roe deer population dynamics; that is, maximum growth rate (Andrén & Liberg, 2015; Kjellander et al., 2004; Nilsen, Gaillard, et al., 2009) and density dependence (Gaillard et al., 1998; Kjellander et al., 2004).

STUDY AREA

The study was performed over the period 1994–2022 (29 years) in south-central Sweden (57°45′–63°30′ N, 11°10′–19°15′ E). The study area (ca. 120,000 km²) is within the boreal vegetation zone (Esseen et al., 1997), where forests are dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) interspersed with birch (*Betula pubescens* and *B. verrucosa*) and aspen (*Populus tremula*). In the southernmost regions there is an increasing proportion of broad-leafed deciduous tree species, primarily oak (*Quercus robur*). The forests are intensively managed for pulp and timber, which creates a mosaic of even-aged forest stands of different ages. There is a general decrease in winter length and snow cover, increasing mean annual temperature and plant productivity within the study area from northwest to southeast (Appendix S1: Table S1). The proportion of agricultural land, densities of humans, roads and roe deer also increase along the same gradient. We divided the study area into seven regions with increasing carrying capacity for roe deer along this gradient, based on vegetation zones (Figure 1). The numbering of the regions followed this gradient, with one exception, region 1. Being coastal and with a milder climate and a higher proportion of agricultural land than regions 2 and 3, it had several characteristics more similar to region 4 than regions 2 and 3. Also, this was the region with the highest density of lynx at the start of the study, likely a result of its northern location in combination with a relatively high carrying capacity for roe deer. Also, during the winter there occurred semi-domestic reindeer (*Rangifer tarandus*), an alternative prey for lynx, in region 1 (Hobbs et al., 2012). The borders between the regions were determined on the smallest spatial unit (hunting district) for reporting roe deer harvest.

MATERIALS AND METHODS

Lynx monitoring

Lynx monitoring in Sweden is based on un-replicated counts of snow tracks from family groups (Gervasi et al., 2013;

Linnell, Fiske, et al., 2007; Linnell, Odden, et al., 2007). The monitoring is mainly conducted from late November to the end of February, and is largely based on snow-tracking and identifying lynx tracks from two or more individuals traveling together, which are assumed to be a family group consisting of an adult female and her accompanying kittens. The count is ended before the mating season in March, to avoid confusing tracks of family groups from those of males consorting a female in estrus (Linnell, Odden, et al., 2007). Criteria based on home-range sizes and movement patterns from radio-marked female lynx with kittens are used to separate observations of different family groups, to ensure that counts of family groups are distinct (Gervasi et al., 2013; Linnell, Odden, et al., 2007). Nilsen et al. (2011) found a good fit between the monitored number of lynx family groups and the reconstructed population size. Thus, the lynx monitoring provides a proxy of all lynx in an area. On average, the number of lynx family groups constitutes 0.184 ± 0.013 (mean \pm SD) of the total lynx population (recalculated from Andrén et al., 2002); that is, the ratio of the number of lynx family groups/total lynx population. Personnel from the County Administration Boards perform the lynx monitoring. Game wardens, hunters, and the public can report records of lynx tracks, but all observations of tracks from two or more individuals have to be verified by authorized personnel from the County Administration Boards. The lynx monitoring data came from several sources. We used the monitoring results from the carnivore database (Rovbase; rovbase30.miljodirektoratet.no) and lynx monitoring reports (Andrén et al., 2010; Liberg & Andrén, 2006). We also used data on shot lynx registered in the carnivore database (Rovbase; rovbase30.miljodirektoratet.no). See Appendix S1: Table S2 for descriptive statistics of lynx and roe deer abundances.

Roe deer density

We used annual roe deer harvest reports (estimated mean and standard deviation; Lindström & Bergqvist, 2020) at the hunting district level in Sweden (Swedish Association for Hunting and Wildlife Management, available at www.viltdata.se) as a proxy for roe deer density. In Sweden there is an open hunting season with no bag limits for roe deer. Local hunting bag records are collected annually using the same reporting system over time, ensuring consistency between years and areas. We assumed that roe deer hunting bag statistics is a good functional proxy for roe deer density, as it is related to other measurements of roe deer density (Bouyer et al., 2015, Spearman rank correlation, $r = 0.88$). For parts of the study area, we could confirm that roe deer harvest was strongly related ($r > 0.87$) to roe deer density (Appendix S1: Figures S2 and S3). Furthermore, Melis et al.

(2013) showed that roe deer harvest effort was not affected by roe deer density, which means that hunters did not adjust their harvest rate or effort to roe deer density, and thus roe deer harvest will be a good proxy for roe deer density.

In the model we used a harvest rate of 0.169 ± 0.028 (SD), which is the joint distribution estimated from two independent sources and methods (Appendix S1: Figure S5). First, we used the data from Melis et al. (2013) to estimate an average roe deer harvest rate for a roe deer population, by weighing the sex and age-specific harvest mortalities by the proportion of the specific sex and age class in the population. The estimated average harvest rate was 0.167 ± 0.022 (SD; Appendix S1: Figure S4). Second, we also estimated the roe deer harvest rate within parts of the study area (Appendix S1: Figure S1). The harvest rate (0.170 ± 0.032 SD; Appendix S1: Figure S5) was estimated by dividing the number of harvested roe deer, including a measure of uncertainty, with the roe deer population size, also including an uncertainty. The roe deer population was estimated using pellet group counts (Mitchell et al., 1985).

Lynx population model

We estimated lynx growth rate in relation to roe deer density and lynx density, that is, lynx numerical response [$dP/dt = f(N, P)$], using a model with additive effects of log(roe deer density) and lynx density, similar to Hone et al. (2007). We expect a positive, but exponential declining (concave curve) effect of roe deer density on lynx growth rate, as lynx have a Type II functional response (Nilsen, Linnell, et al., 2009). Therefore, we used log(roe deer density). We used a Bayesian hierarchical population model to estimate the posterior distribution of the unobserved lynx population size with process and observation equations.

The deterministic process model is:

$$\mu_{i,t} = \log(\lambda_{i,t} \times P_{i,t-1} - H_{i,t-1}), \quad (1)$$

$$\log(\lambda_{i,t}) = b_{0,i} + b_1 \times \log[R_{i,t-1}/(\phi_i \times A_i)] + b_2 \times (P_{i,t-1}/A_i). \quad (2)$$

We include stochasticity in the process using:

$$P_{i,t} \sim \text{lognormal}(\mu_{i,t}, \sigma_{\text{proc}}), \quad (3)$$

$$R_{i,t} \sim \text{negative binomial}(E_{i,t}, \kappa_{i,t}), \quad (4)$$

$$\phi_i \sim \text{beta}(\alpha_{1,i}, \beta_{1,i}), \quad (5)$$

where $\mu_{i,t}$ is the prediction of the log(lynx population) at time t , $P_{i,t}$ is the unobserved lynx population size, $H_{i,t}$ is

the number of legally shot lynx, $R_{i,t}$ is unobserved the roe deer harvest and ϕ_i is the roe deer harvest rate in region i . A_i is the area (in 1000 km²) of region i and σ_{proc} is the process standard deviation on a log scale. To evaluate the effect of log(roe deer density) and lynx density on lynx log(growth rate) we use a regression where $b_{0,i}$ are region-specific intercepts (seven regions), b_1 is a regression coefficient describing the effect of log(roe deer density) and b_2 is a regression coefficient describing the effect of lynx density. The region specific intercepts ($b_{0,i}$) give the lynx log(growth rate) at zero log(roe deer density), and zero lynx density.

$E_{i,t}$ is the mean observed roe deer harvest, $\kappa_{i,t}$ is the dispersion parameter for the negative binomial distribution, which was computed using moment matching (Hobbs & Hooten, 2015; $E_{i,t}$; the mean, and $D_{i,t}$; the standard deviation of the observed roe deer harvest; Lindström & Bergqvist, 2020). The roe deer harvest rate (ϕ_i) in the geographical area i was drawn from a beta distribution with a mean and standard deviation of ϕ and σ_ϕ , which correspond to ϕ_i being a random factor from the hyperparameter ϕ and allows handling of some of the spatial variation. The parameters for the beta distribution ($\alpha_{1,i}$, $\beta_{1,i}$) were computed using moment matching.

The process equations were linked to data using the observation equations:

Observation equations:

$$y_{i,t} \sim \text{Poisson}(\delta_i \times P_{i,t}), \tag{6}$$

$$\delta_i \sim \text{beta}(\alpha_{2,i}, \beta_{2,i}). \tag{7}$$

where $y_{i,t}$ is the observed number of lynx family groups in region i at time t . The ratio number of lynx family groups/total lynx population (δ_i) in geographical area i , was drawn from a beta distribution with a mean and standard deviation of δ and σ_δ , which correspond to δ_i being a random factor from the hyperparameter δ and allows handling of some of the spatial variation. The parameters for the beta distribution ($\alpha_{2,i}$, $\beta_{2,i}$) were computed using moment matching.

Vague prior distributions were assigned to $b_{0,i}$, b_1 , b_2 , and σ_{proc} (Appendix S1: Table S5). The priors for the roe deer harvest rate (ϕ , σ_ϕ) were computed from the combined estimate based on Melis et al. (2013) and an estimate based on a roe deer survey in parts of the study area (Appendix S1: Figure S5), using moment matching (Appendix S1: Table S5). The priors for the ratio number of family groups/total lynx population (δ , σ_δ) were computed from Andrén et al. (2002), using moment matching (Appendix S1: Table S5).

Model fitting and evaluation

We approximated the marginal posterior distributions of parameters, fitting the models to data using the Markov chain Monte Carlo algorithm implemented in rjags and coda packages (Plummer, 2003) in R (R Core Team, 2021). We ran three chains of 100,000 iterations following a 50,000 burn-in. Convergence was checked by visual inspection of trace plots and by the diagnostics of Heidelberger (Heidelberger & Welch, 1983) and Gelman (Brooks & Gelman, 1997), implemented in the coda package (Plummer, 2003). We used posterior predictive checks to evaluate lack of fit between models and data, using Bayesian p -values (Hobbs & Hooten, 2015). We present posterior means and SD with associated 95% Bayesian credible intervals (BCI).

We chose to only use the full but relatively simple models with well established biological foundations, rather than choosing model selection. We chose to examine the main effects alone, without considering interactions.

Lynx-roe deer model

We used the estimated parameters b_0 , b_1 and b_2 to build a deterministic model for lynx:

$$P_{t+1} = (P_t - H_t) \times \exp [b_0 + b_1 \times \log(N_t) + b_2 \times P_t]. \tag{8}$$

To estimate the isocline for lynx, that is, when the growth rate $\lambda = 1$ or $\log(\lambda) = 0$, we assume no lynx harvest ($H_t = 0$) and the model is reduced to:

$$0 = b_0 + b_1 \times \log(N_t) + b_2 \times P_t. \tag{9}$$

By rearranging the model, one gets lynx density as a function of roe deer density when lynx growth rate $\log(\lambda) = 0$:

$$P_t = [b_0 + b_1 \times \log(N_t)] / (-b_2). \tag{10}$$

Unfortunately, we cannot fit a model directly to the roe deer data, as we only have roe deer harvest as a proxy for roe deer density, and the model has to include both population size and harvest. Instead, we built a deterministic model for roe deer population size (N_t), based on established knowledge of roe deer demography. The model includes a constant roe deer harvest rate (H_r), the maximum growth rate on a log scale (r_{max}) and carrying capacity (K), which results in a linear density dependence. The lynx influence the roe deer population, both by number of lynx (P_t) and by their kill rate. We used a

functional Type II response (Nilsen, Linnell, et al., 2009), where a is the asymptote and h is the half saturation:

$$N_{t+1} = (N_t - H_r \times N_t) \times \exp [r_{\max} \times (1 - N_t/K)] - P_t \times [(a \times N_t)/(h + N_t)]. \quad (11)$$

The roe deer isocline, when the growth rate $\lambda = 1$ or $\log(\lambda) = 0$, means that $N_{t+1} = N_t$. Rearranging the model by setting $N_{t+1} = N_t$, one can estimate the lynx density at which the roe deer growth rate $\log(\lambda) = 0$ is a function of roe deer density:

$$P_t = ([N_t - H_r \times N_t] \times \exp [r_{\max} \times (1 - N_t/K)] - N_t) / [(a \times N_t)/(h + N_t)]. \quad (12)$$

In the model we used a constant roe deer harvest rate (H_r) of 0.169 (Appendix S1: Figure S5). We set the maximum growth rate on a log scale; $r_{\max} = 0.42$, which is the mean from three independent estimates. Kjellander et al. (2004) found that a roe deer population increased from 9.9 to 36.1 roe deer/km² in 3 years, in an experimental population, which resulted in an annual increase of $\log(\lambda) = 0.43$. Nilsen, Gaillard, et al. (2009) estimated roe deer growth rate to $\log(\lambda) = 0.36$, using survival and reproduction from radio-marked individuals in a Leslie matrix. Finally, Andrén and Liberg (2015) used roe deer monitoring data and found that the roe deer growth rate at zero roe deer density (the intercept) was $\log(\lambda) = 0.46$.

The asymptotic kill rate (a) was set to 15 roe deer per lynx individual, per 100 days (Nilsen, Linnell, et al., 2009). However, we used a 1-year time step in our model. Thus, the asymptotic kill rate was set to $15 \times 365/100 = 55$ roe deer per lynx individual per year in our model. This asymptotic kill rate is similar to other studies (Andrén & Liberg, 2015; Krofel et al., 2014). The half saturation (h) was set at the density of 1 roe deer per km² (Nilsen, Linnell, et al., 2009). However, in the model we used the unit roe deer per 1000 km² which results in a half saturation (h) of 1000 roe deer per 1000 km².

For region 4 we set roe deer carrying capacity to 7500 roe deer per 1000 km², based on Andrén and Liberg (2015), who found a linear density-dependent growth rate in roe deer and the density at $\log(\lambda) = 0$ was 7.5 roe deer per km² (Appendix S1: Figure S6). Roe deer carrying capacity was estimated for each region, based on a number of environmental variables that we judged are important for the roe deer survival and productivity. The characteristics chosen were forest productivity, duration of the growing season, mean annual temperature and number of days with snow cover, with region 4 as a baseline. We used forest site class productivity and duration

of the growing season as proxies for primary production. Roe deer are also influenced by the length of the snow period, which is related to the mean annual temperature (Grøtan et al., 2005). The roe deer carrying capacity for the different regions was set to be strongly correlated with the four environmental variables chosen (all $|r| > 0.98$; Appendix S1: Figure S7), and these four environmental variables were also highly correlated with one another (all $|r| > 0.97$; Appendix S1: Table S1).

We used a baseline scenario with the most likely values for the included parameters. To test the sensitivity of the input parameters in the deterministic lynx-roe deer model, we varied seven parameters and compared the results with the baseline scenario (Appendix S2: Table S1). The seven parameters were; effect of $\log(\text{roe deer density})$ on lynx growth rate (b_1), effect of lynx density on lynx growth rate (b_2), roe deer harvest rate (ϕ), the ratio lynx family groups/total lynx population (δ), roe deer maximum growth rate at log scale (r_{\max}), roe deer carrying capacity (K) and finally the functional response; half saturation (h) with a lower and upper value for one parameter at the time (Appendix S2: Table S1). This resulted in 14 different scenarios that were compared with the baseline scenario. The ecological consequences of these changes are:

1. A weaker positive effect of roe deer density on lynx growth rate (b_1) will lead to a slower recovery at a lynx low roe deer density.
2. A weaker negative effect of lynx density on lynx growth rate (b_2) will lead to a faster response of lynx to changes in roe deer density.
3. A lower roe deer harvest rate (ϕ) will give more roe deer available for lynx.
4. A lower ratio of lynx family groups/total lynx population (δ) will give more lynx in the area.
5. A lower roe deer maximum growth rate (r_{\max}) will give a lower roe deer growth rate at low roe deer density.
6. A lower roe deer carrying capacity (K) will bring a lower maximum roe deer density and a lower roe deer growth rate at high roe deer density.
7. A lower half saturation density (h) in the Type II function response will lead to a higher lynx kill rate at lower roe deer density.

RESULTS

Lynx population model

The lynx monitoring data demonstrated a gradual southward expansion of lynx in both distribution and abundance during the period (Figure 2). In the two

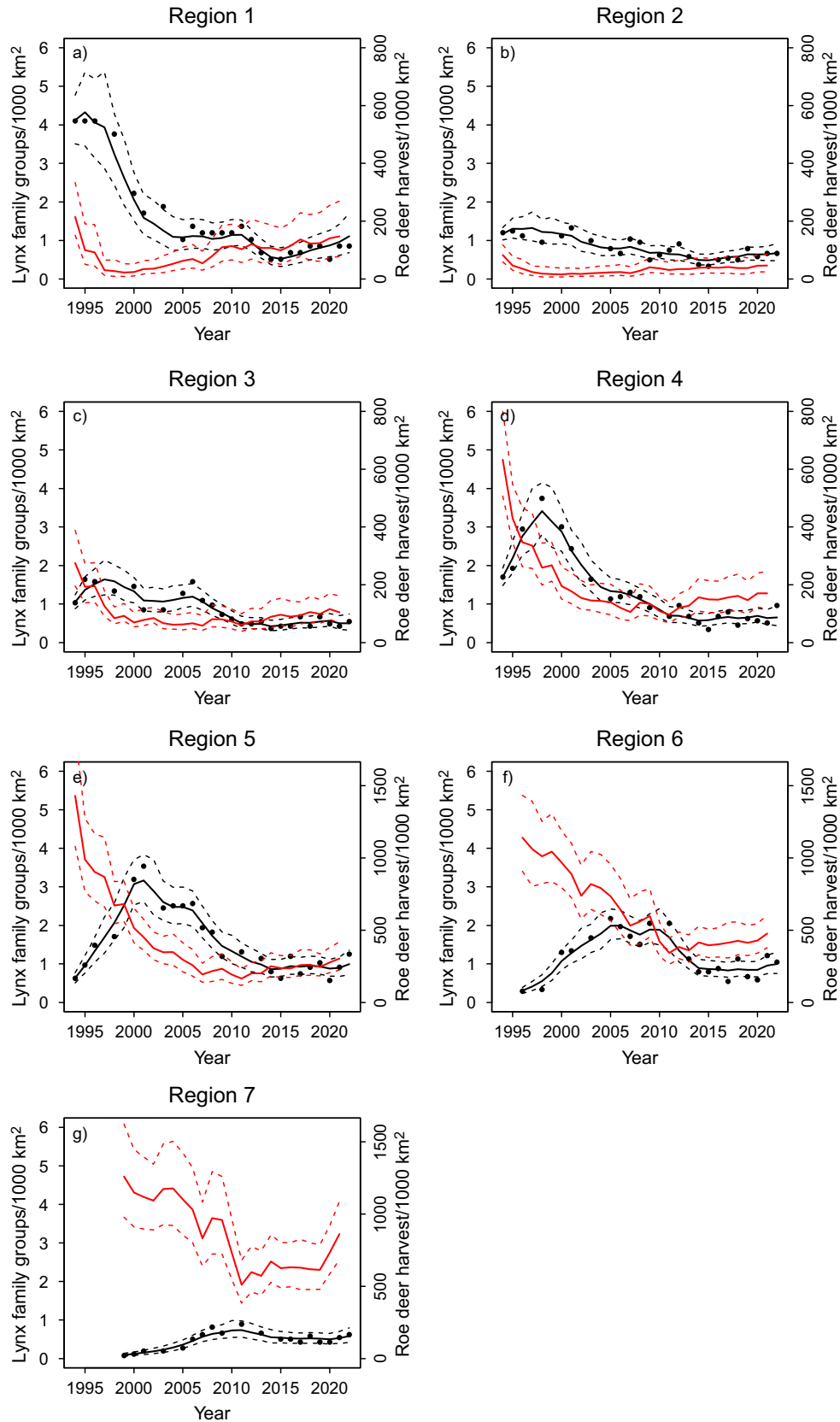


FIGURE 2 Lynx monitoring data (black dots) and model predictions (black line) with 95% Bayesian credible intervals (BCI) (dashed lines), as number of lynx family groups per 1000 km² (left Y-axis). Roe deer harvest data (red line) with 95% BCIs (dashed lines) per 1000 km² (right Y-axis). Note the difference in scale for the roe deer harvest data. The maximum on the Y-axis for regions 1–4 is 800 roe deer harvested per 1000 km² and for regions 5–7 it is 1500 roe deer harvested per 1000 km².

southernmost regions, that is, regions 6 and 7, there were no lynx at all during the first few years. The lynx densities in regions 2 and 3 were low at the start of the study period and decreased further during the whole period. In region 1 the lynx density was high at the beginning of the study period but then decreased. In regions 4 to 7 the lynx density first increased, then peaked and finally decreased. In region 4 lynx peaked in 1998; in region 5 the peak density was reached in 2000–2001, and in region 6 from 2005 to 2006. Finally, in region 7 there was no distinct lynx peak, but the density increased slowly to 2011, and then stabilized on a somewhat lower level. The roe deer harvest decreased during the first part of the study period in all regions, but with a varying degree of recovery in the latter part of the study period, except in region 2, the region with the lowest roe deer carrying capacity, where roe deer harvest appeared to stabilize at low levels (Figure 2).

Posterior predictive checks showed that the model was able to simulate data that were consistent with the observations. Bayesian p -values for discrepancy statistics fell between 0.23 and 0.49 for all regions except region 1 (Bayesian p -value = 0.12), suggesting some lack of fit in region 1. The parameters ϕ , δ , σ_{proc} , $b_{0[1-7]}$, b_1 and b_2 all passed Heidelberger diagnostics. The upper confidence limits for all parameters were <1.01 in Gelman diagnostics, indicating very low variation between the three chains.

There was a strong positive effect of $\log(\text{roe deer density})$ on lynx growth rate (probability >0.999 that b_1 was positive, Table 1). There was also a strong negative effect of lynx density on lynx growth rate (probability >0.999 that b_2 was negative, Table 1). The intercepts ($b_{0[1-7]}$)

varied between the seven regions and decreased from the northernmost to the southernmost region (Table 1, Appendix S3: Figure S2).

Thus, the predicted lynx growth rate in the different regions depends on three factors: region, roe deer density and lynx density (Figure 3). The growth rate increases with $\log(\text{roe deer density})$, but decreases with lynx density. These two effects were additive. The region effect (the regional intercept ($b_{0[1-7]}$)) decreases from regions 1 and 7), meaning that for a given lynx density the roe deer density has to be higher from regions 1–7 to result in an increased lynx population (Figure 3, Appendix S3: Figure S3). The regional intercept ($b_{0[1-7]}$) was highly correlated with mean annual temperature, number of days with snow cover, duration of the growing season and forest productivity (all $|r| > 0.97$, Appendix S3: Figure S1). The predicted lynx growth rate, within the range of roe deer and lynx densities for a region (Appendix S3: Figure S3), did not exceed an earlier estimated maximum growth rate of $\lambda = 1.33$ (Andrén et al., 2006).

Deterministic lynx–roe deer model

We simulated the lynx and roe deer densities, based on the deterministic lynx–roe deer model, for 100 years. The deterministic models forecasted a dampened cycle for the lynx–roe deer interaction (Figure 4) for all regions, but the dynamic was almost cyclic in regions 2, 3 and 4. The forecasted amplitudes in a dampened cycles decreased toward the south. Thus, the dynamics between lynx and roe deer became more stable with increasing carrying capacity for roe deer, which is related to higher

TABLE 1 Statistics summarizing posterior distributions of parameters in the lynx population model, with 95% Bayesian credible interval (BCI).

Parameter	Mean (\pm SD)	95% BCI	Description
ϕ	0.169 \pm 0.028	0.118 to 0.227	Roe deer harvest rate
δ	0.182 \pm 0.013	0.157 to 0.209	Ratio lynx family groups/total lynx population
$b_{0(1)}$	−1.032 \pm 0.187	−1.382 to −0.657	Intercept region 1
$b_{0(2)}$	−0.897 \pm 0.162	−1.204 to −0.573	Intercept region 2
$b_{0(3)}$	−1.095 \pm 0.193	−1.457 to −0.710	Intercept region 3
$b_{0(4)}$	−1.185 \pm 0.212	−1.577 to −0.760	Intercept region 4
$b_{0(5)}$	−1.262 \pm 0.230	−1.688 to −0.798	Intercept region 5
$b_{0(6)}$	−1.368 \pm 0.247	−1.822 to −0.870	Intercept region 6
$b_{0(7)}$	−1.479 \pm 0.257	−1.952 to −0.960	Intercept region 7
b_1	0.189 \pm 0.030	0.129 to 0.243	Effect of $\log(\text{roe deer density})$
b_2	−0.0132 \pm 0.0034	−0.0203 to −0.0070	Effect of lynx density
σ_{proc}	0.123 \pm 0.0229	0.079 to 0.169	Process standard deviation on log scale

Note: See Appendix S3: Figure S2 for prior and posterior distributions of the parameters.

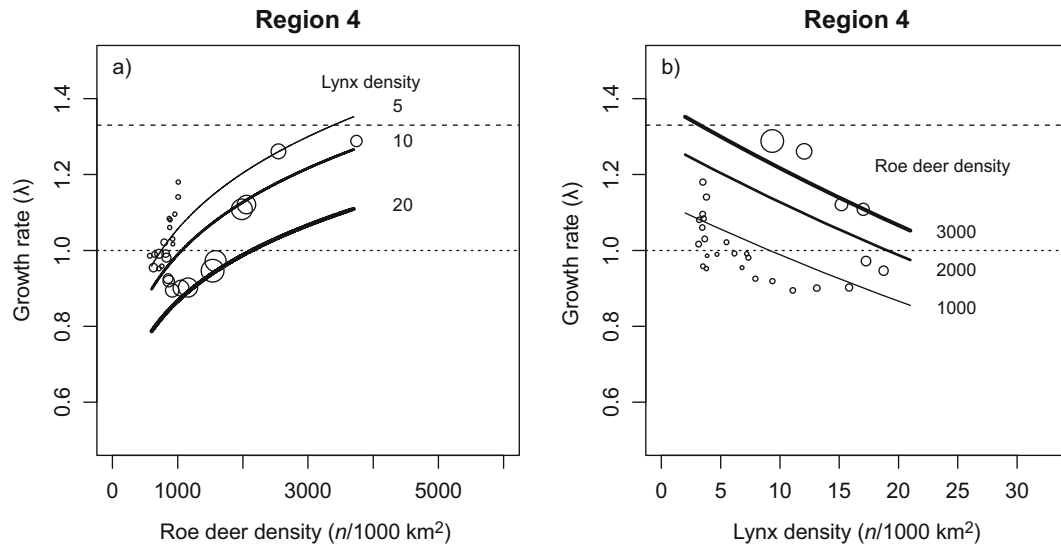


FIGURE 3 Predicted (lines) and observed (dots) lynx growth rate (λ) in relation to roe deer density panel (a) and lynx density panel (b) in region 4. The dot sizes are related to lynx density panel (a) and roe deer density panel (b). The growth rates were estimated within the range of roe deer and lynx densities within the region 4 and at three levels of roe deer and lynx densities. Left: The lynx densities were 5 (thin black line), 10 (black line) and 20 (thick black line) lynx per 1000 km². Right: The roe deer densities were 1000 (thin black line), 2000 (black line) and 3000 (thick black line) roe deer per 1000 km². The dotted horizontal lines indicate a $\lambda = 1$ and the dashed horizontal lines indicate a $\lambda = 1.33$, which is an approximate maximum growth rate for lynx (Andr n et al., 2006). See Appendix S3: Figure S3 for all regions.

plant productivity, longer growing season and shorter winter (Appendix S1: Table S1).

The correlations between the data (observed lynx and roe deer densities) from the 29-year study period and deterministic lynx and roe deer densities, varied between regions (Figure 4). In regions 4 and 5, the correlations were high and the slopes were close to 1 ($r > 0.89$; Appendix S3: Figure S4). The correlations were lower in regions 1, 2 and 3 ($0.78 > r > 0.60$; Appendix S3: Figure S4). In region 6 there was a high correlation for roe deer ($r = 0.89$), but it was lower for lynx ($r = 0.40$). In region 7, there was a lack of fit (Figure 4; Appendix S3: Figure S4).

The sensitivity analyses showed that the most important factor influencing the lynx–roe deer dynamic was the lynx numerical response (Appendix S2, Scenarios 1, 2, 3 and 4). The functional response (Appendix S2, Scenarios 13 and 14) also had a strong impact on the lynx–roe deer dynamic. The overall pattern, that the lynx–roe deer dynamic became more stable with increasing roe deer carrying capacity, remained in the sensitivity analyses (Appendix S2: Figure S1). The sensitivity analyses revealed two major expected patterns in the lynx–roe deer dynamic (Gotelli, 1998; Tanner, 1975). Scenarios that increased the impact of lynx on roe deer at low roe deer densities also increased the amplitude of the population fluctuations (Appendix S2: Figure S1, Scenarios 2, 3, 6, 7, 9 and 13). Conversely, in scenarios where lynx had a lower impact on roe deer at low roe deer densities, the amplitude in the fluctuations decreased, the dampened cycle

disappeared faster and the dynamic moved toward stability (Appendix S2: Figure S1, Scenarios 1, 4, 5, 8, 10, and 14).

DISCUSSION

First, we demonstrated a numerical response in lynx, affected by both the density of its primary prey, roe deer, and its own density. Second, we have demonstrated that stable population cycles can occur under certain conditions in the predator–prey system we studied. And third, we could demonstrate that the existence of refugia for the prey in this study indeed did increase the stability in the predator–prey system we studied.

Numerical response

We found strong evidence that the lynx numerical response, that is, the growth rate, was influenced by both roe deer and lynx densities [$dP/dt = f(N, P)$]. Thus, both the density of prey and intraspecific competition were important determinants of the lynx population dynamic. This might be expected, as the lynx is an unusually specialized and efficient predator of roe deer in areas when there are no other ungulates of similar size available (Gervasi et al., 2012). Lynx have a Type II functional response with a very step increase in kill rate at low roe deer density (Nilsen, Linnell, et al., 2009) and more than

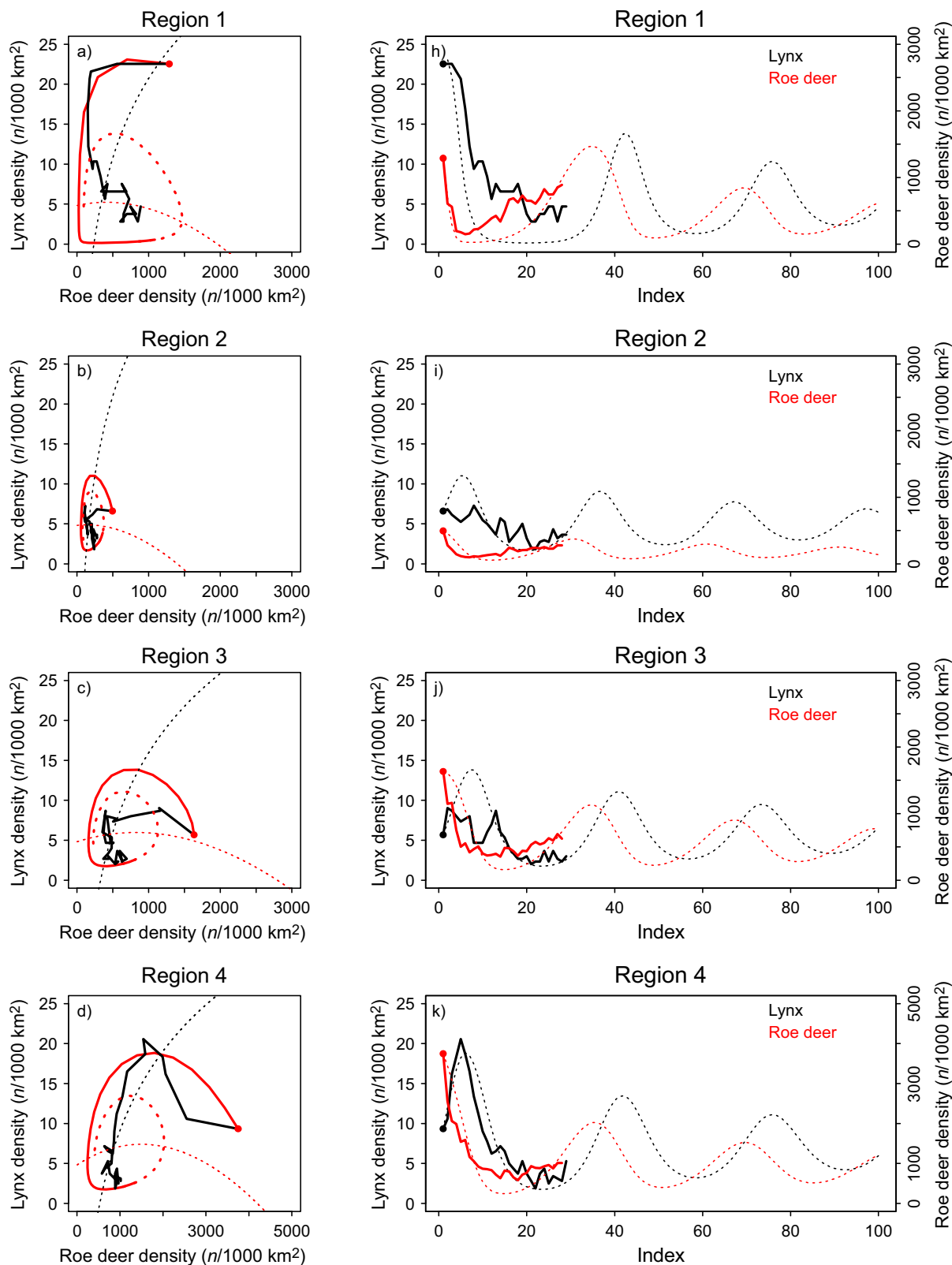


FIGURE 4 Phase diagram panels (a–g) of observed lynx and roe deer densities in the seven regions (black line). The dotted black line shows the predicted isocline for lynx, that is, lynx growth rate ($\lambda = 1$). The dotted red line shows the predicted isocline for roe deer, that is, roe deer growth rate ($\lambda = 1$). The deterministic phase diagram of lynx density and roe deer density (red line), with starting points based on observed lynx and roe deer densities in the regions (red dots). The thick dotted red line shows the deterministic for another 25 years. Time series panels (h–n) for lynx (black) and roe deer (red) densities in the seven regions (filled lines) and the deterministic time series (dotted lines), with common starting points (dots). The time series are extended to 100 years. Note that the scale for roe deer density varies between figures.

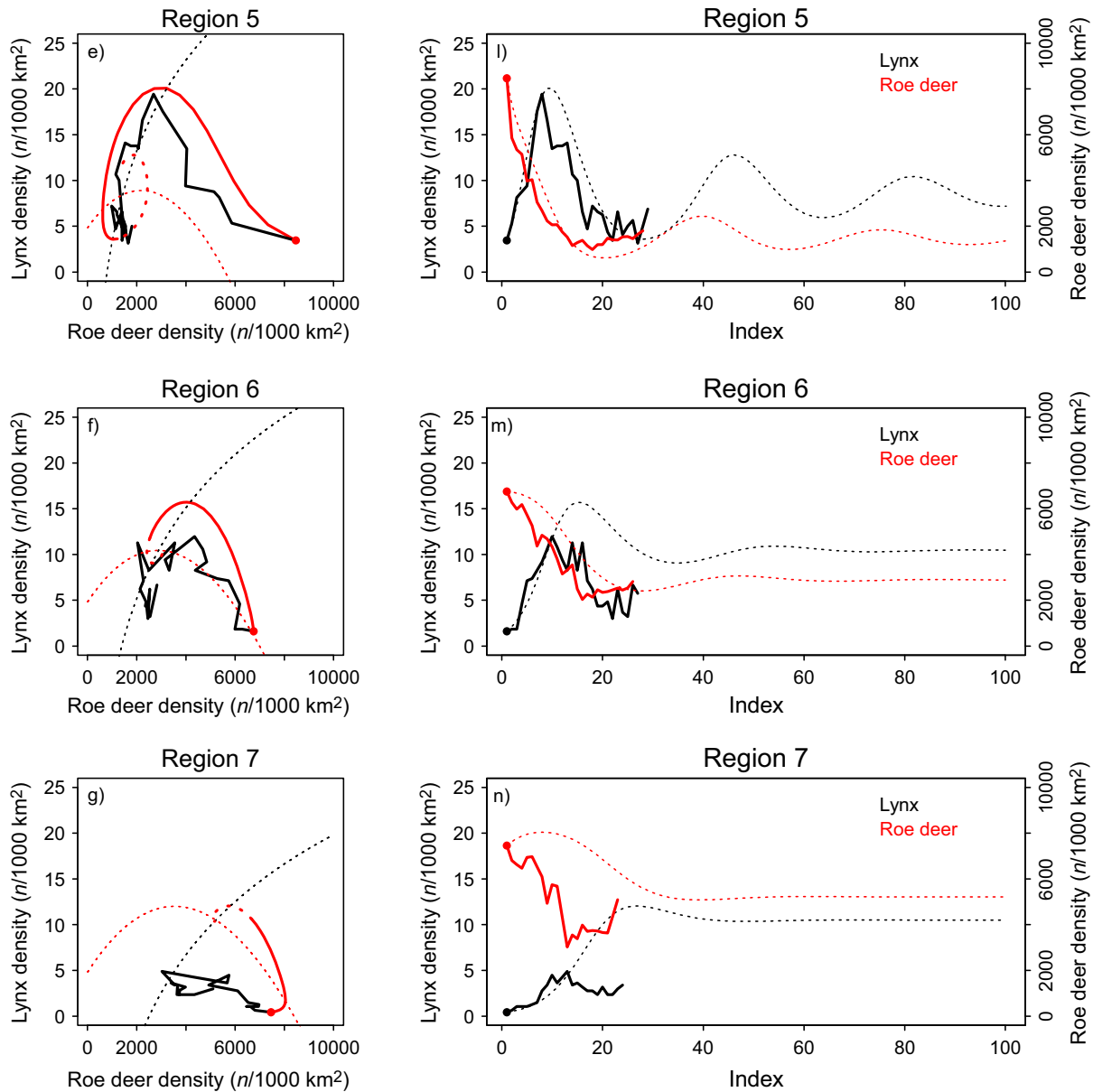


FIGURE 4 (Continued)

80% of the prey biomass consists of roe deer (Odden et al., 2006). Other predators that also show numerical responses related to both prey and predator densities are also prey specialists. For example, Hone et al. (2007) found that both snowshoe hare (*Lepus americanus*) and Canada lynx (*Lynx canadensis*) densities affected the growth rate in Canada lynx. The absolutely most important prey for Canada lynx is a snowshoe hare (O'Donoghue et al., 1998). Vucetich and Peterson (2004a) also found that growth rate in wolf (*Canis lupus*) was affected by both moose (*Alces alces*) and wolf densities on Isle Royale, in an almost single predator–single prey system (Peterson & Page, 1988).

The three studies, Vucetich and Peterson (2004a), Hone et al. (2007) and this study, are also similar in that they are based on extensive time series that include low and high densities of both prey and predator. Importantly, they also include all four combinations of low and high densities in both prey and predator, that is, periods where one is high and the other is low, and vice versa, as well as periods where both are high or both low. Vucetich and Peterson's (2004a) study was based on 45 years with about 4–5 times differences between low and high densities in both wolf and moose. Hone et al. (2007) used a 10-year time series, with a 10 times

differences between low and high densities in both Canada lynx and snowshoe hare. Our study covered a 29-year period with about 7–10 times differences between low and high densities in both lynx and roe deer (Appendix S1: Table S2). Our study differs somewhat from the other two, as it is based on a lynx recolonization after a long period of lynx absence or very low densities. This natural experiment has resulted in an exaggerated variation in both lynx and roe deer densities. With the exception of region 1, lynx densities were zero or very low, while roe deer densities were high or very high, in most of the regions at the beginning of the study period (Figure 2), which probably increased the statistical power to detect effects of both lynx and roe deer densities on lynx growth rate.

There are some studies describing the numerical response as the relationship between prey and predator densities (e.g., Grange & Duncan, 2006; Messier, 1994). This definition assumes that predator density should respond instantaneously to changes in prey density, and that predator and prey densities are always at equilibrium (Eberhardt et al., 2003). However, this is impossible in long-lived organisms like mammals (see also Figure 4a–g). Population dynamics in predator–prey systems also correspond to changes in population growth rate, which in turn is an emerging property of changes in survival, reproduction and dispersal (Caswell, 2001; Krebs, 2002; Legendre, 2020). Reproduction and survival can in turn be related to both the amount of resources and the intraspecific competition for these resources (Bayliss & Choquenot, 2002; Sinclair, 1989). To fully understand the numerical response and predator population dynamic and interaction between predator and prey, it is necessary to study the same population over time, as it is a temporal process (Damgaard, 2019).

Predator–prey cycles

The occurrence of classical predator–prey cycles in mammals, and the conditions for them to appear, have always been of great interest to ecologists, but to our knowledge population cycles have been demonstrated only in small mammals (e.g., Cornulier et al., 2013; Krebs et al., 1995), while, so far, there is no unequivocal demonstration of cycles in large mammals. The nearest is the wolf–moose system on Isle Royale. Post et al. (2002) claimed that the wolf–moose dynamic on Isle Royale was the first documentation of population cycles in large mammals (see also McLaren & Peterson, 1994; Peterson et al., 1984), with a cycle period of about 23 years. However, this claim has later been disputed by the same research team, who discuss whether the wolf–moose dynamic on Isle Royale

is really cyclic or if it just demonstrates aperiodic multiannual fluctuations, influenced more by other factors than predation, like weather stochasticity, variation in moose population age structure or parasites (Peterson et al., 2014; Vucetich & Peterson, 2003, 2004b).

The lynx–roe deer system can be described as both dynamic, the system varies over time, and interactive; lynx affect roe deer and vice versa. The strong dynamic interaction between lynx and roe deer, might be explained by lynx and roe deer having similar maximum growth rates; r_{\max} is around 0.29 for lynx (Andrén et al., 2006) and around 0.42 for roe deer (Andrén & Liberg, 2015; Kjellander et al., 2004; Nilsen, Gaillard, et al., 2009). A predator–prey system with similar growth rates for the predator and the prey is more likely to be cyclic and dynamic, than a system with a higher growth rate in the prey than in the predator (Tanner, 1975). Gervasi et al. (2012) also showed that the relative impact of lynx on roe deer demography was much higher than the impact of red fox (*Vulpes vulpes*) on roe deer or wolf and brown bear (*Ursus arctos*) on moose. Lynx differ from these other predators as they kill roe deer of all age classes and both sexes, that is, also prime-age females (Gervasi et al., 2012), probably because the body mass of an adult roe deer is only between 10% and 55% more than an adult lynx (Andrén & Liberg, 2015). This predator–prey size ratio is similar to mountain lion (*Puma concolor*) preying on mule deer (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*) and consequently no or little selection on age class or condition of the prey has been seen in that system (Hussemann et al., 2003; O’Gara & Harris, 1988). Therefore, we expect a strong predation effect in those system (Pierce et al., 2012).

We could forecast the lynx and roe deer densities 28 years beyond the data in most regions (Figure 4), by combining the lynx model (Equation 8) and the roe deer model (Equation 11), that is, using a Lotka–Volterra-like predator–prey model. The dynamic was almost cyclic or dampened cycles in five of the seven regions (Figure 4). The periods of the cycles or dampened cycles were around 30 years. Thus, given the ecological condition for lynx and roe deer; that is, lynx numerical and functional responses, roe deer growth rate and carrying capacity, it is possible to have population cycles in this system of large mammals. The cycle period in this system was similar to what Post et al. (2002) predicted for wolf–moose on Isle Royale (23 years). Their study spanned 42 years and the time series covered almost two cycles, which they found too short to demonstrate the occurrence of a cyclic system. This study spanned 29 years, which means that we observed less than one cycle. However, there are two important differences. First, we found a cyclic pattern in several different regions (2, 3 and 4), and second, as the

dynamics in these different regions were not in phase with each other, that is, the peak in lynx density in region 6 was about 10 years later than the peak in region 1, this simulates a longer period, than the time of this study lasted.

The different ecological conditions in the regions in this study, made it also possible to explore ecological conditions where population cycles are more likely. The lynx–roe deer dynamics were close to cyclic in regions 2, 3 and 4 (Figure 2). The system in these regions was also close to a single predator–single prey system. Furthermore, the system in these regions was even closer to cyclicity if the predator numerical response was even stronger related to prey density (Appendix S2: Figure S1, Scenario 2). Importantly, lynx and roe deer have similar maximum growth rates, which also makes the system more likely to be cyclic (Tanner, 1975). Still, we cannot beyond doubt conclude that this study has demonstrated cyclicity in a system with an ungulate and a large mammalian predator or if it is aperiodic multiannual fluctuations.

Even, if we have a 29-year time series, we have only studied one population cycle. Furthermore, the start of the period had exaggerated high roe deer density and low lynx density, as the lynx recolonized the area after a long period of absence. Unfortunately, the prospects of solving this dilemma by continued data collection from these regions are no longer possible, since the responsible authorities have drastically increased hunting quotas on lynx to favor the local hunter's demand for a more profitable roe deer harvest (Andrén, 2022). Furthermore, the system is also getting more complex as the wolf population is increasing in the area (Svensson et al., 2023), which also prey on roe deer (Sand et al., 2016).

The lynx–roe deer dynamic was most sensitive to changes in the numerical response and also to some extent to changes in the functional response (Appendix S2: Figure S1). Kill rate and predator growth rate at low prey density are usually hard to study and are therefore often extrapolated in predator–prey models used in management or conservation (Vucetich & Peterson, 2004a). However, the shape of both numerical and functional responses at low prey density, for example, only prey dependent, only predator dependent or both prey and predator dependent, have very large effects on the outcome of the predator–prey dynamics (Arditi & Ginzburg, 2012; Gotelli, 1998; Tanner, 1975; Vucetich & Peterson, 2004a).

Spatial effects on predator–prey interactions

We have studied lynx–roe deer interaction over a gradient with covariation in several environmental factors,

that all are expected to influence this dynamic, for example, snow cover, plant productivity, growing season and landscape composition (proportion of agricultural land). The ecological conditions are more favorable for roe deer in the southern part of the study area; for example, increased plant productivity will increase the carrying capacity for roe deer (Gaillard et al., 1998), and winter harshness, especially snow depth, influence roe deer winter mortality (Cederlund & Lindström, 1983; Grøtan et al., 2005). Landscape composition, like the proportion of agricultural land, will also influence the predation pattern (Gorini et al., 2012).

Tanner (1975) showed that including two habitats, one with high predation risk and one with low (“prey refugia,” sensu Tanner, 1975), increased the stability of the predator–prey system. In line with this prediction, we found that the dynamic between lynx and roe deer became more stable in the southernmost regions (6 and 7), with higher human density, higher proportion of agricultural land and higher road density, providing such refugia for roe deer (Figure 4; Appendix S1: Table S1). This was supported by Basille et al. (2009), who showed that roe deer densities were higher in areas with higher human density and road density. Lynx avoided using these areas, although the roe deer density was higher in these areas. The habitat use of lynx in this kind of landscape can be seen as a trade-off between roe deer density and avoidance of exposure to humans (Basille et al., 2009). Therefore, we think that this trade-off for lynx can explain the decreasing intercept toward the south, and as a result a higher density of roe deer was needed to get the same growth rate for a given lynx density (Appendix S3: Figure S3).

In addition, the prey guild is more diverse in the southernmost parts of the study area, including fallow deer (*Dama dama*), red deer (*Cervus elaphus*) and European hare (*Lepus europaeus*), which can serve as alternative prey for lynx at low roe deer densities (Gervasi et al., 2014; Heurich et al., 2016). Furthermore, Jarnemo and Liberg (2005) found high red fox predation on roe deer fawns in this agricultural landscape, which might affect roe deer density more than lynx do. All together this will weaken the direct interaction between lynx and roe deer.

These patterns suggest that the lynx–roe deer dynamics became more stable with increasing carrying capacity for roe deer, which was related to higher plant productivity, more agricultural land, less snow cover and longer growing seasons (Appendix S3: Figure S1). This is opposite to many predator–prey models where an increased carrying capacity for the prey leads to increased instability, the so-called “paradox of enrichment” (Rosenzweig, 1971). However, if not only the prey carrying capacity

increase with primary production, but there is also, for example, a change in the predator numerical response, then the predator–prey dynamic can be more stable as primary production increases.

The effect of an alternative prey might also explain the dynamic in the northernmost part (region 1). This region is partly a wintering area for semi-domestic reindeer (Hobbs et al., 2012) and within the reindeer husbandry area reindeer is an important prey for lynx (Mattisson et al., 2011; Sunde et al., 2000). The model fit improved when half saturation in the functional response increased (Appendix S2: Figure S1, Scenario 14). This means that there will be a lower impact of lynx on roe deer at low roe deer density, which can be a result of reindeer being an important alternative prey at low roe deer density (Sunde et al., 2000).

CONCLUSIONS

We found strong effects of both roe deer and lynx densities on lynx numerical response, that is, lynx growth rate [$dP/dt = f(N, P)$]. Importantly, this study was based both on extensive time series of both predator and prey, and on periods where one is high and the other is low, and vice versa, as well as periods where both are high or both low. We agree with Oksanen et al. (2001) and Eberhardt et al. (2003) that one should use the mechanistic definition of numerical response in predator–prey interactions, that is, the predator growth rate in relation to prey and predator densities, to fully understand predator–prey interactions.

We also found that a Lotka–Volterra type predator–prey model could explain the dynamic relationship between lynx and roe deer. The outcome of lynx–roe deer dynamic was most sensitive to lynx numerical response. The dynamic was almost cyclic or dampened cycles and the periods of the cycles or dampened cycles was around 30 years. Thus, we have documented that there could occur population cycles in this large predator–large herbivore system, and that population cycles were more likely to occur in single predator–single prey systems, especially if the predator numerical response was strongly related to prey density and the predator and prey have similar maximum growth rates.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Andrén & Liberg, 2023a) are available from Dryad at <https://doi.org/10.5061/dryad.9zw3r22mq>. Code (Andrén & Liberg, 2023b) is available from Zenodo at <https://doi.org/10.5281/zenodo.8363754>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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