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Faculty of Biosciences, Fisheries and Economics (BFE)

Predictive state-space modelling of lemming population outbreaks on the Fennoscandian tundra:

Are determinants of spatial variation in outbreak amplitude temporally consistent?

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Eivind Flittie Kleiven

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Innhold

Abstract

Lemmings are famous for their spectacular population cycles that causes waves of biomass through the arctic tundra. Both climate variability and the interaction with the sympatric grey-sided vole have been shown to effect lemming outbreaks. However little is known about the transferability of these effects between peaks. I analyzed the spatial variability using snap-trapping data from two consecutive lemming outbreaks, sampled at 98-109 sites on the Fennoscandian tundra in the period from 2004 to 2013. I estimated the interaction between lemming and grey-sided vole, and the sensitivity of lemmings to climate variability as well as the temporal consistency of these effects. Effects were estimated using hierarchical state-space models, where the observation error was modeled using a removal model. My results suggested a positive effect of altitude on lemming abundance in 3 out of 4 seasons. In line with an earlier study, a mutualistic interaction between lemmings and the sympatric grey-sided vole was indicated for the winter of 2006/07, an effect likely driven indirectly by shared predators. However, I found that this interaction was neither consistent between seasons (winter and summer) nor between the two consecutive peaks. Therefore, determinants of lemming peaks, especially the interaction with grey-sided vole, have poor temporal transferability. I propose this to be due to the large temporal variability in snow properties in addition to the temporally long spanning arctic winter where little is known about both the predator and the lemmings. I also discuss how monitoring data could be improved to provide better efficiency of statistical models aimed at estimating predictors of lemming population dynamics.

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Introduction

Sympatric species at the same trophic level are somehow bound to interact. However, how interspecific interactions effect abundance of species has been and engendered controversy among ecologists from decades (Connell 1983). Moreover, an interspecific interaction can take many forms, it can be either direct or indirect and it can take the form of competition or mutualism. The theoretical possibility of multiple prey species to interact through a shared guild of predators has been highlighted numerous times. These described interactions commonly follow the logic that an increase in one prey species has a negative impact on another through increasing the predator population size, i.e. apparent competition (Holt 1977). However, theoretical work has shown that mutualism between prey species may be an even more likely outcome (Abrams and Matsuda 1996, Abrams et al. 1998). Apparent mutualism happens if the functional response of a predator on one prey species decreases when the abundance of another prey species increases. This can be mediated either by predator switching, if the predator cannot hunt all prey species simultaneously, or through reduction in predators hunting effort, called saturation(Abrams and Matsuda 1996). Moreover, theoretical models have suggested that a decrease in prey population size has a larger negative effect on predator growth rate than the positive effect from an increase of equal magnitude(Abrams et al. 1998). This implies that cyclicity in prey population dynamics has a positive effect on mean prey population size(Abrams et al. 1998). Based on this, multiple prey species that experience strong population cycles might be more likely to have a mutualistic relationship through shared predators than more stable prey species. However, for this mutualism to occur the prey species need to differ in either growth rate or in the rate they are captured by the predator. In addition there must be a non-linearity in the predators functional or numerical response (Abrams et al. 1998).

One of the most famous population cycles in the science literature is the cycle of the Norwegian lemming (*Lemmus lemmus*). Since the English ecologist Charles Elton described it, with data from Robert Collett almost a century ago (Elton 1924), it has caught the attention of researchers worldwide. This is mainly due to the importance of herbivores with high-amplitude population cycles to the functioning of the tundra ecosystem, which has been highlighted numerous times (Batzli et al. 1980, Ims and

Fuglei 2005). The Norwegian lemming is considered a key species on the Fennoscandia tundra, influencing numerous other species, either as a prey or a predator (herbivory) (Ims and Fuglei 2005, Krebs 2011).

Attempts to explain the driver(s) of these population cycles have been numerous. Already back in the 1920s, Elton was convinced that climate fluctuations caused these regular cycles (Lindstrøm et al. 2001). In 1942, he and Nicholson summarized their current knowledge about the driving mechanisms of population cycles exemplified by the snowshoe hare and lynx cycle: "We have at present no clue at all to the nature of the factor controlling this enormous wild-life rhythm in the northern forest, except that is seems almost certain that climatic fluctuations must play a controlling part" (Elton and Nicholson 1942). Thousands of scientific papers have been published on this topic since then and quite a number of hypotheses has been proposed about the driving mechanisms including food limitation, predation, weather, stress, behavior, and genetics (Lindstrøm et al. 2001). The main hypotheses can be divided into three classes of mechanisms; trophic interactions either top-down controlled or bottom-up controlled or behavioral-mediated feedback mechanism within the rodent populations (Krebs 2011). There are even convincing evidence for some of them in given systems. Like Gilg et al. (2003), which found evidence that predation from the resident specialized predator, stoat (*Mustela erminea)*, causes the fluctuations in population size in collared lemmings (*Dicrostonyx groenlandicus*) at a location in Greenland through a top-down mechanism. On the other hand, Oksanen et al (2008) has claimed the Lemming cycle in Fennoscandia to be bottom-up driven through plant herbivore interactions.

An interesting property of the lemming population cycle is that it is often spatially synchronized over large geographical areas (Angerbjörn et al. 2001, Krebs 2011). In addition, in systems with more than one small rodent species with cyclic dynamics all species seems to show temporal synchrony in their population cycles (Stenseth and Ims 1993). This implies that at least one of the mechanisms that are involved in the generation of the cycles is shared among the sympatric small rodent species. However, the grey-sided vole *(Myodes rufocanus)* - the most abundant vole species on the Fennoscandia tundra - differ from lemmings in both diet and habitat preference (Andersson and Jonasson 1986, Heske and Steen 1993, Ims and Fuglei 2005, Soininen et

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al. 2013a, Soininen et al. 2013b). Thus, the dynamical link between them must lie elsewhere. Both nomadic predators and climate have been proposed as likely drivers of interspecific synchronous population cycles (Ims and Steen 1990, Huitu et al. 2003). However, Ims et al (2011) found interesting evidence of a mechanistic link through shared predators, mainly during winter. During the winter period, the small rodent community lives in the sub-nivean space at the bottom of the snowpack, where they find food and refuges from most predators (Korslund and Steen 2006). However, the most specialized small rodent predators in Fennoscandia, the stoat and the least weasel, are resident year round and are thought to have a large impact on the small rodents also during winter (Hanski and Henttonen 1996, Hansen et al. 1999). Lemmings are larger and have been said to appear "clumsier" than voles and thereby more exposed to predation (Ims et al. 2013). Moreover, lemmings are known to reproduce faster than grey-sided voles (larger litter and more rapid sexual maturation; (Semb-Johansson et al. 1993)) and have a longer reproductive season (Andersson and Jonasson 1986), which results in a higher population growth rate. The lemming is the only small rodent species that starts reproduction in midwinter under the snow (Ims and Fuglei 2005). The resulting higher maximum growth rate of lemmings may cause the different shape of the population peaks of grey-sided vole and lemming (Ims et al. 2011), with lemming peaks "sharper" compared to the more blunt peaks of grey-side vole. Alternatively, this has been explained by difference in drivers, where the lemming cycle is said to be bottom-up and controlled by food abundance while the grey-sided vole is proposed to be top-down driven by mustelid predation (Oksanen and Oksanen 2000, Turchin et al. 2000).

It is evident from time series data from the last 3-5 decades that the grey-sided vole in the sub-arctic tundra in northern Fennoscandia has exhibited a regular 4-5year cycle. In contrast, the same series has demonstrated a simultaneous irregularity of the lemming dynamics in the same region, with long periods with missing or very little distinct cyclic peak years (Ims et al. 2008). From the 70's to the mid 2000's the lemming population erupted only twice in the northern Fennoscandian tundra. It has been argued that the lemming-plant interactions are more prone to be impacted by climate change than the vole-predator interaction (Oksanen et al. 2008). Lemmings could also be more sensitive to climate change due to traits like winter reproduction and foraging on mosses that are likely encapsulated by ice in mild winters (Angerbjörn et al. 2001, Ims et al. 2008). A

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third possible explanation could be that lemmings are indirectly affected by voles through shared predators (Hanski and Henttonen 1996, Hansen et al. 1999, Ims et al. 2011), and that the sign and strength of this interaction may shift depending on the ecological context (Abrams et al 1998). Although there strong cases for the impact of winter climate on lemming dynamics exist (Kausrud et al. 2008, Gilg et al. 2009, Ims et al. 2011), only one previous study have assessed the importance of indirect interaction with voles (Ims et al. 2011).

One of the big challenges in lemming research is that lemmings are generally difficult to trap (Jensen et al. 1993). Most scientific trapping programs are only able to catch lemmings in the phases of late increase and at the peak of the population cycle (Krebs 1993). Even more, in ecology exact measurements of abundance are rare, and most observations contain errors (Clark and Bjørnstad 2004). However, the effects from observation errors on parameter estimates in empirical models are generally ignored (Calder et al. 2003), often due to the shortcoming or under-use of adequate statistical methods together with insufficient data (Stenseth et al. 2003). During recent years there has been an increased awareness of the importance of including observational errors in statistical models applied to ecological data to avoid biased parameter estimates (Calder et al. 2003, Stenseth et al. 2003, Yoccoz and Ims 2004, Kery 2010).

Recently, observation error has been included in abundance estimation in state-space models where the observational process is separated from the latent ecological process that drives the dynamics in the true population size (De Valpine and Hastings 2002). Frequently in these models, the distribution of the observational process has been chosen explicitly (Stenseth et al. 2003, Ims et al. 2011). However, in recent years these ad-hoc assumptions about observation error distributions have been criticized for being poor at incorporating observational error where estimates might be sensitive to the distribution chosen (Knape et al. 2011). In addition, critics have shown that such models may produce biased estimates if the false negative and false positive count do not cancel each other out on average or if the detection probability has a temporal trend (Kéry and Schaub 2012). Therefore, if replicated measurements are available, the detection error should be estimated explicitly, which allow us to use more of the information in the data (Dennis et al. 2010).

In this study, I used a temporally extended data set from the same trapping program as the study of Ims et al. (2011) with a spatial structure that allowed me to:

1) Investigate whether determinants of spatial variation in lemming population abundance during two consecutive cyclic peaks were temporally consistent (i.e. temporally transferable) by considering in particular the nature of the interaction between lemmings and grey-sided vole and the role of spatial climatic variation.

2) Investigate whether the assumptions regarding the distribution of observation error made in Ims et al (2011) were robust by explicitly estimating the detection probability through multinomial mixture models in a Bayesian framework.

Methods

Study area

The study area consists of the Nordkynn peninsula, Ifjordfjellet and Varanger peninsula located in the north-easternmost parts of Finnmark, northern Norway (70°N to 71°N) (Figure 1). Bio-climatically, the most northern part of the peninsulas is classified as low-arctic tundra; i.e. the tundra extends to the sea level (Walker et al. 2005). The tundra of fjord districts and inland areas are classified as sub-arctic (Virtanen and Oksanen 1995) and extend above the altitudinal tree line at 50-200 meters above sea level.
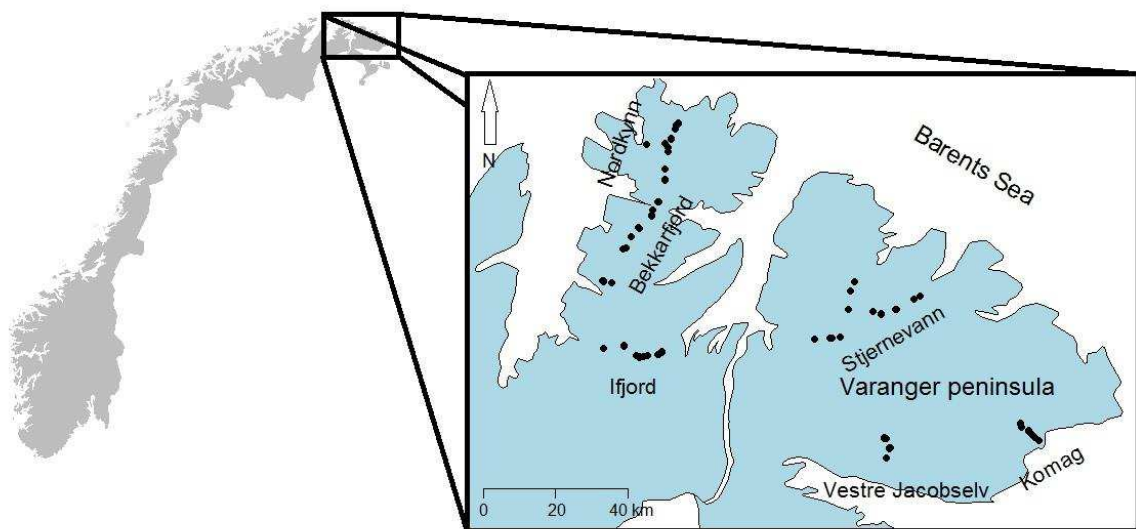

Figure 1: Map of the study area – mainland Norway (left) with the north-eastern part of Finnmark expanded in the right frame. Dots denote the trapping sites included in this study.

In both of these bio-climatic zones the vegetation is most typically dwarf-shrub tundra (Ravolainen et al. 2014) dominated by the non-palatable *Empetrum nigrum, Betula nana* and *Vaccinium* ssp. interspersed with more wet and mesic areas with palatable gramnoids and dicotyledons (Brathen et al. 2007). Common herbivores are reindeer (*Rangifer tarandus)*, hare (*Lepus timidus)* and ptarmigan (*Lagopus* spp.) alongside small rodents. The dominating small-rodent species are the Norwegian lemming, the grey-sided vole and the tundra vole (*Microtus oeconomus*).

The mammalian predator guild consists of two mustelid species, the stoat and the least weasel (*Mustela nivalis)*, which are considered resident specialists that feed on small rodents both during summer and when the ground is snow covered in the winter

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(Hanski and Henttonen 2002). In addition to the mustelids, red fox (*Vulpes vulpes)* and arctic fox (*Vulpes lagopus*) are present in the study area, both with small rodents as important prey, especially at peak small rodent densities (Angerbjörn et al. 1999). Small rodents also constitute the main prey base for a guild of avian predators. Most common are rough-legged buzzard (*Buteo lagopus)*, long-tailed skua (*Stercorarius longicaudus)* and parasitic skua (*Stercorarius parasiticus)* while snowy owl (*Bubo scandiacus)* are only occasionally present during peak lemming years (Killengreen et al. 2007). Even though these avian predators are highly specialized on small rodents, they are nomadic and all, except the snowy owl, are only present during the summer season.

Sampling design

Since spring 2004, extensive snap trapping has been performed on 109 permanent sites in the study area (Figure 1), all easily accessible from roads. The trapping sites are allocated within six geographic sub-regions within the overall study area that contained altitudinal gradients of varying ranges; Nordkynn (n=24 trapping sites, altitudes: 72-288m.a.s.l.), Bekkarfjord (n=18 sites, altitudes: 160-323 m.a.s.l.), Ifjord (n=18 sites, altitudes: 225-346 m.a.s.l.), Stjernevann (n=24 sites, altitudes: 125-341 m.a.s.l.), Vestre Jacobselv (n=11 sites, altitudes: 220-240 m.a.s.l.), and Komagdalen (n=14 sites, altitudes: 30-80 m.a.s.l.) The total altitude gradient span from 30 to 346 m.a.s.l., with a orographic effect of a decrease of approximately 0.6 °C per 100m, which makes altitude a proxy for climate (Karlsen et al. 2008). However, between spring 2009 and spring 2010, 9 sites at Ifjord, 2 sites at Bekkarfjord and 2 sites at Nordkynn were removed and 2 not previously sampled sites where added at Ifjordfjellet due to logistic reasons. Hence, the new total of sampled sites from spring 2010 is 98 sites, but with the same total altitudinal span. I assume that this rather small change of the sampling design will not affect the estimates of the altitude effect noteworthy.

As the two species of main interest are the grey-sided voles and lemmings, samples were therefore conducted in two vegetation strata; grey-sided voles were sampled in heath vegetation and lemmings in more moist tundra areas, rich with graminoids and mosses that are preferred by lemmings, but also to some extent by tundra vole (Andersson and Jonasson 1986, Killengreen et al. 2007).

Small rodent trapping

At each trapping site there was a small-quadrat snap trapping plot (Myllymäki et al. 1971); i.e. a 15m by 15m quadrat with three traps in each corner (i.e.12 traps per quadrat), baited with rolled oat and raisins. The traps were activated for 2 days in late June ("spring"), soon after snowmelt and in early September ("autumn") before the onset of winter. All sites where trapped within a time period of 10 days each season. The difference between individuals trapped in spring and autumn reflect the population changes through summer, while the difference between autumn and spring the consecutive year reflect the change through the winter period.

The years 2004-2013 of this trapping program, that encompassed two cyclic peaks (2007 and 2011) of both the focal rodent species, will be considered for the present analysis (Figure 2). Before 2007, the last high amplitude peak in eastern Finnmark was 1978 (Ims et al. 2011). This is contrary to grey-sided vole that at the same time has experienced regular peak with a 4-5-year periodicity (Ims et al. 2008).

Data analysis

Following Ims et al. (2011), the trapping data were analyzed at the site level over the two cyclic peaks contained in the time series (n=109 sites during first peak in 2006-2007 and n=98 sites during the second peak in 2010-2011). Trapping site was judged to be an adequate spatial scale for the analysis, as Ims et al (2011) found no residual spatial autocorrelation in lemming growth rates of the fitted models. The two peaks were analyzed separately. For each peak, the data from the pre-peak autumn (t-1) together with spring (t) and autumn (t) in the lemming peak year (t=year 2007 and year 2011) were included. The other years and seasons of the overall time-series had too few lemming captures to be analyzed. Thus the present analysis focused on the determinants of spatial variation in lemming abundance in the peak phase of the cycle, (i.e. outbreak amplitude) and how consistent such spatially structuring factors underlying outbreak amplitude are between different peaks.

To be able to explicitly include measurement error in the estimation of abundance, I used the two trapping days within a trapping season as temporal removal occasions,

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assuming the population to be closed (no immigration) over the two days (Leslie and Davis 1939). This assumption was supported by the fact that the observed counts (i.e. the number of trapped lemmings) were lower the second trapping day than on the first and that the composition relative to sex and weight seemed unchanged (Table 1).

Table 1: The number of trapped animals of both species and sexes as well as their mean weights relative to the two trapping days.

Peak	Day	Sex	Lemming		Grey-sided vole	
			Number	Mean weight	Number	Mean weight
2006/07	1	Female	73	48.2	189	30.8
	2	Female	63	45.8	107	26.6
	1	Male	85	48.0	246	27.0
	2	Male	69	51.5	184	26.2
2006/07	1	Total	158		435	
	2	Total	132		291	
2010/11	1	Female	55	52.3	236	33.5
	2	Female	43	49.9	172	28.3
	1	Male	68	47.6	251	29.8
	2	Male	47	48.1	217	28.2
2010/11	1	Total	145		487	
	2	Total	90		389	

I further assumed that the observed counts in consecutive days followed a multinomial distribution with π as the probability for each individual present to be trapped on a specific day (Zippin 1956, Dorazio et al. 2005). Then an animal present could either be trapped the first day, with probability p, the second day with probability p(1-p) or not be trapped on any of the days with probability 1-(p+p(1-p)). I assumed the probability p to be equal for all individuals through both trapping days within a site within a season (Moran 1951).

Let $y_{i,j,k}$ be the observed data and $N_{i,k}$ the latent abundance at site *i*, in removal occasion *j* and in season *k*, then $y_{i,j,k}$ could be specified as:

$$y_{i,j,k}|N_{i,k} \sim dmultinom(N_{i,k}, \pi(p)) \qquad (1)$$

$$N_{i,k} \sim dpois(\lambda_{i,k})$$

However due to properties in the BUGS language used to implement the model (does not allow a random sample size argument in the multinomial distribution), I chose to formulate the model under a Poisson abundance model. Since $N_{i,k} \sim dpois(\lambda_{i,k})$ and $y_{i,j,k} | N_{i,k} \sim Multinom(\pi)$ where π is the cell probability, each element of the multinomial count vector can be regarded as an independent Poisson count with expected value(Π) = λπ.

$$y_{i,j,k} \sim dpois(\Pi_{i,j,k}) \qquad (2)$$
$$\Pi_{i,1,k} = p_{i,k} * \lambda_{i,k}$$
$$\Pi_{1,2,k} = p_{i,k} * (1 - p_{i,k}) * \lambda_{i,k}$$
$$N_{i,k} \sim dpois(\lambda_{i,k})$$

The model was fitted to calculate latent abundance for the two focal rodent species (grey-sided vole and lemmings) for each site (i) per season (k). This model decomposed the total variation in the count data into two components, a process and an observation equation. This allowed us to separate the factors affecting the observational process from those affecting the systematic process (Royle et al. 2008). Moreover, the model can deal with hidden states and missing values (Clark and Bjørnstad 2004).

Multinomial mixture sub-model were specified for each species for each peak. Assessment of model-fit is complicated in the Bayesian framework, especially for hierarchical models with different levels. Hence, I graphically checked potential predictor variables on lemming abundance with correlation plots of the raw data. Altitude, grey-sided vole abundance the previous season and previous season abundance seemed to correlate with lemming catches, in at least one of the peaks (see Appendix A). Moreover, I wanted to include similar predictor variables as Ims et al. (2011) to assess transferability between methods. Therefore, in the models for lemming abundance (λlem), I specified three parameters; β_{vole_k} for the effect of grey-sided vole abundance ($\lambda vole$) the previous season, β_{alti_k} for the effect of altitude and β_{dd_k} for the effect of lemming abundance the previous season (i.e. density dependence). To ease convergence, I rescaled the vector of altitudes of all sites ($alti_i$) to a mean of 0 and a variance of 1.

$$log(\lambda lem_{i,k}) = \alpha_{lem_k} + \beta_{vole_k} * log\left(\lambda_{vole_{i,k-1}}\right) + \beta_{alti_k} * alti_i + \beta_{dd_k} *$$
$$log\left(\lambda_{wplem_{i,k-1}}\right) \qquad\qquad (3)$$

$$log\left(\lambda_{vole_{i,k-1}}\right) = \alpha_{vole_{i,k-1}}$$
$$log\left(\lambda_{wplem_{i,k-1}}\right) = \alpha_{wplem_{i,k-1}}$$

I investigated the effect of these predictor variables on abundance, however because the model contained $\lambda_{wplem_{i,k-1}}$ (lemming abundance the previous season) the growth rate was given by:

$$\log(N_t) = \alpha_0 + \beta_{dd} * \log(N_{t-1}) \quad \rightarrow \quad R = \log\left(\frac{N_t}{N_{t-1}}\right) = \alpha_0 + (\beta_{dd} - 1) * \log(N_{t-1}) \quad (4)$$

Grey-sided vole abundance ($\lambda vole$) was estimated without predictors. I also estimated lemming abundance without predictor variables (i.e. λ_{wplem} in equation 3) for the density dependence predictor to avoid effects of the same predictor variables in different additive terms of the model. Given that density independence occurs when $\beta_{dd} = 1$, the effect of density dependence was estimated as $\beta_{dd} - 1$ (Knape 2008). In the equation for lemming abundance, the intercept included a random season effect, while for grey-sided vole and the lemming abundance without predictors (λ_{wplem}) the intercept included both a random season and a random site effect as to allow these (which was estimated without predictor variables) to vary both in space and time according to the other variable in the model. For the detection process, the logit link function contained no predictor variables and was allowed to vary between both sites and seasons (equation 5).

$$logit(p_{i,k}) = \alpha_{p_{i,k}} \qquad\qquad (5)$$

I used R-squared values to address how much of the variability in the data my model explained. However, such statistics should be interpreted with caution in a Poisson GLM (Cox and Wermuth 1992, Zheng and Agresti 2000). In addition, I plotted the estimated

counts against the sum of the observed counts over both trapping days, to investigate whether there were systematic differences between raw counts and estimated abundance.

To predict the lemming abundance in the next peak (i.e. 2010/11), I specified an equation using the parameter estimates for β_{vole_k}, β_{alti_k} and β_{dd_k} from the 2006/07 model, but using the values of the covariates from the second peak. I described the average model performance through mean absolute prediction error (MAPE), as have been proposed to be an intuitive and unambiguous measure of predictive ability of models (Willmott and Matsuura 2005), through the equation:

$$MAPE = [\, n^{-1} \textstyle\sum_{i=1}^{n} |e_i| \,]$$

Where $e_i = P_i - O_i$, with P being the predicted value and O the observed value. I used the multinomial model of lemming abundance estimates as the observed values in this performance check. This would make me able to investigate the temporal transferability of these interactions (i.e. from the first to the second peak).

Because my main interest is the spatially structuring factors underlying lemming peak abundances, I scaled e_i to remove a potential systematic effect from the mean abundance, which could be due to other factors affecting lemming abundance. In addition, with MAPE all individual differences are weighted equally.

The model was run in a Bayesian framework and priors were kept uninformative (Kéry and Schaub 2012). The Posterior distribution was obtained using Markov Chain Monte Carlo (MCMC) techniques computed through the package Rjags in software R (R Core Team 2015). I used 3 chains each of 500 000 iterations, with a burn-in of 200 000 (i.e. discarded the first 200 000 iterations of each chain, see Appendix for more detailed model descriptions). To assess convergence of the chains, trace plots for all parameters where investigated graphically as well as from the Gelman-Rubin diagnostic test (a parameter is said to converge if $\hat{R}<1.1$) (Gelman and Rubin 1992).

From the convergence checks most $\hat{R}$ values were less than 1.1, though a few were in the interval between 1.1 and 1.3. However, from the graphical interpretation of the trace plots, I was confident that all chains reached had converged to the posterior distribution. The R square statistics suggested that the predictive ability of the models were fairly good for both cyclic peaks (Spring model 2007: R^2=0.77, Autumn model 2007: R^2= 0.82, Spring model 2011: R^2=0.58, Autumn model 2011: R^2=0.81). Moreover, plots of estimated site-specific abundance relative to the observed abundance did not suggest any large discrepancies (Appendix B).

Results
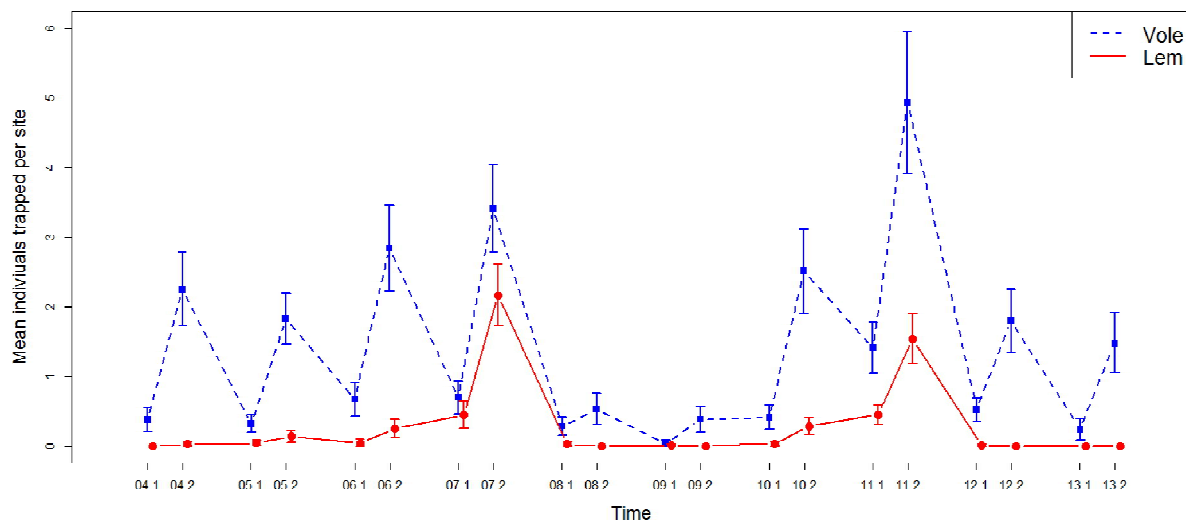
Figure 2: Mean catches with error bars (mean ± 2 x SE) of grey-sided vole (Vole) and Norwegian lemming (Lem) per site over the entire time series. The two trapping days are aggregated in each season from spring (.1) 2004 to autumn (.2) 2013.

Overall characteristics of the abundance dynamics

The overall characteristics of the abundance dynamics across the two cyclic peaks contained by the entire time series are shown in figure 2. The cyclic peaks of the two rodent species were synchronized (i.e. in the autumns of 2007 and 2011). As have been noted in several previous studies, the shape of the peaks is different for the two species. The peaks of the grey-sided vole have a longer build-up period and slower crash than the lemming peaks. The lemming dynamics also contain the very characteristic increase over the pre-peak winters, which is not present in the vole.

Considering the two consecutive peaks, there were some differences within each of the two species. This is also clear from the abundance estimates obtained from the fitted models (Table 1). For the lemming, the build-up towards the two peaks was similar (Figure 2), with similar estimated abundances in the two peak springs (Table 1). It should however be noted that the spatial variance in spring densities (i.e. the CV values in Table 1) was substantially larger in 2007 than in 2011. The growth of the lemming population over the peak summer was higher in 2007 than in 2011, leading to a 50 % higher estimated abundance in the autumn of the first peak. The grey-sided vole had a more gradual build-up to the first peak than the second peak, while the crash phase in the winter after the peak appeared to be slower in the second peak. Moreover, the

amplitude of the second grey-sided vole peak was also somewhat higher than in the first peak in terms of both spring and autumn abundances (Table 2).

Table 2: Estimates of grey-side vole and lemming abundance (estimated with predictor variables) for the different seasons and years. These abundances estimates are given as means of the posterior distribution from the multinomial mixture model for all seasons modelled. Coefficient of variation (CV) indicates the amount of spatial variance in abundances.

		Grey-sided vole		Lemming	
Year	Season	N*vole*	CV	N*lem*	CV
2006	Autumn	4.06	1.01	-	-
2007	Spring	1.56	0.91	0.78	1.46
2007	Autumn	-	-	3.72	0.65
2010	Autumn	4.58	1.12	-	-
2011	Spring	2.43	0.9	0.71	0.31
2011	Autumn	-	-	2.44	0.46

Table 3. Parameter estimates from the multinomial mixture models (Equations 3) of season- and cyclic peak-specific lemming abundances, given as mean of the posterior distribution and 95% Bayesian credible intervals (CI). One unit on the scaled altitude variable is equivalent to 86 meter.

Peak	Season	Vole density $\beta vole_k$	CI	Altitude $\beta alti_k$	CI	Density dependence $(\beta_{dd} - 1)$	CI
2006/2007	Spring	0.400	[-0.062 : 0.917]	0.948	[0.389 : 1.619]	-2.538	[-7.678 : 5.102]
	Autumn	0.091	[-0.222 : 0.447]	0.551	[0.326 : 0.787]	0.324	[-1.333 : 2.304]
2010/2011	Spring	-0.221	[-0.491 : 0.029]	-0.132	[-0.470 : 0.198]	-1.105	[-6.629 : 4.470]
	Autumn	-0.129	[-0.341 : 0.132]	0.366	[0.141 : 0.590]	-0.711	[-7.380 : 5.518]

Determinants of lemming peak abundances

The estimated coefficients of the fitted effect models (Equations 3) are given in Table 3. Several of the effects had wide 95 % Bayesian credible intervals that precluded any inferences about how they varied among seasons and cyclic peaks. In particular, this regarded the estimates of seasonal density dependence in lemming abundance. The most reliable estimates concerned the effect of altitude, which was consistently positive for the autumn abundances (i.e. lemming population growth in summer increased with increasing altitude; Figure 4). A positive effect of altitude was also found in the spring of the first peak, whereas no such effect related to winter growth was present for the second peak. Considering the interaction between the rodent species, there was some

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evidence for a positive effect of grey-sided vole autumn abundance on lemming abundance the next spring in the first peak (Figure 3). The estimates for the other seasons and the other cyclic peak were smaller and less certain (credible intervals encompassed 0 with good margins in addition to estimated effect sizes was close to 0; Table 3). It could however, be suggested that the sign of the impact of vole abundance on the spatial variation in lemming peak amplitude may change over time (Figure 3).
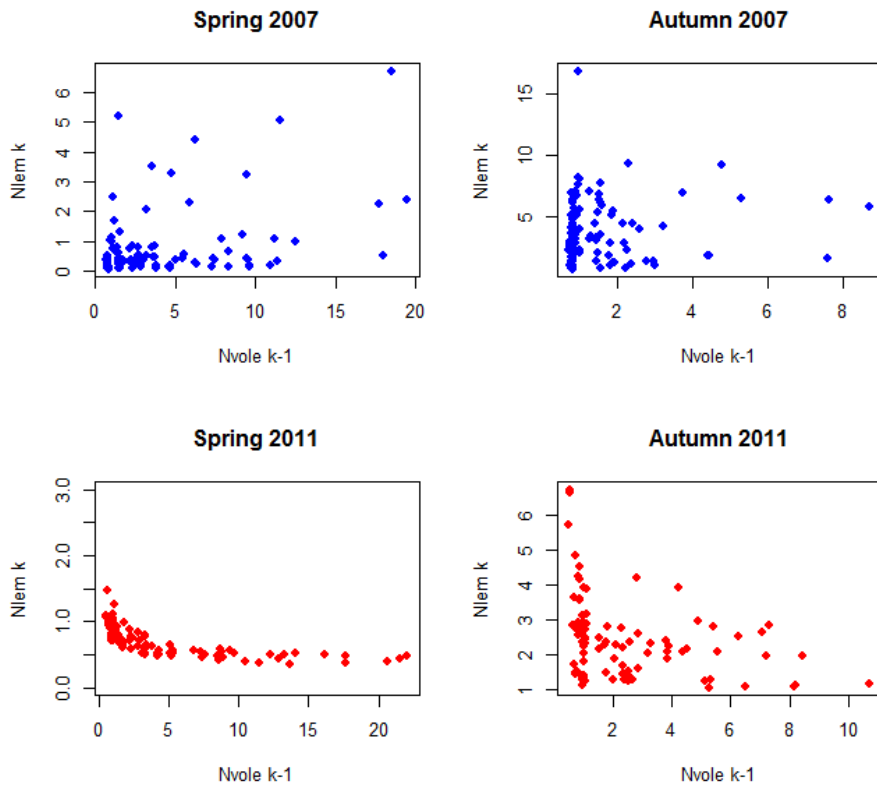

Figure 3: Estimated lemming abundance ($Nlem_{i,k}$, estimated with $\lambda lem_{i,k}$ (Equation 3)) plotted against estimated grey-sided vole abundance($Nvole_{i,k-1}$) the previous season estimated from the multinomial mixture model for each site each season.

The temporally consistent effect of altitude on lemming abundance in the autumn contributed to a relatively good ability of the autumn 2007 model to predict the site-specific autumn abundances for 2011 (Figure 5). The mean absolute predictive error (MAPE) was 0.46 individuals per site for this model. The error of the predictions was generally somewhat upward biased compared to the observations and increased with increasing abundance (Figure 5). In contrast, the 2006/2007-spring model performed poorly in terms of its temporal transferability to the spring of the next peak (2011), as expected from the inconsistent altitude and vole effects (Table 3). The MAPE of this model was 1.31 individual per site and a strong bias was evident (Figure 5).
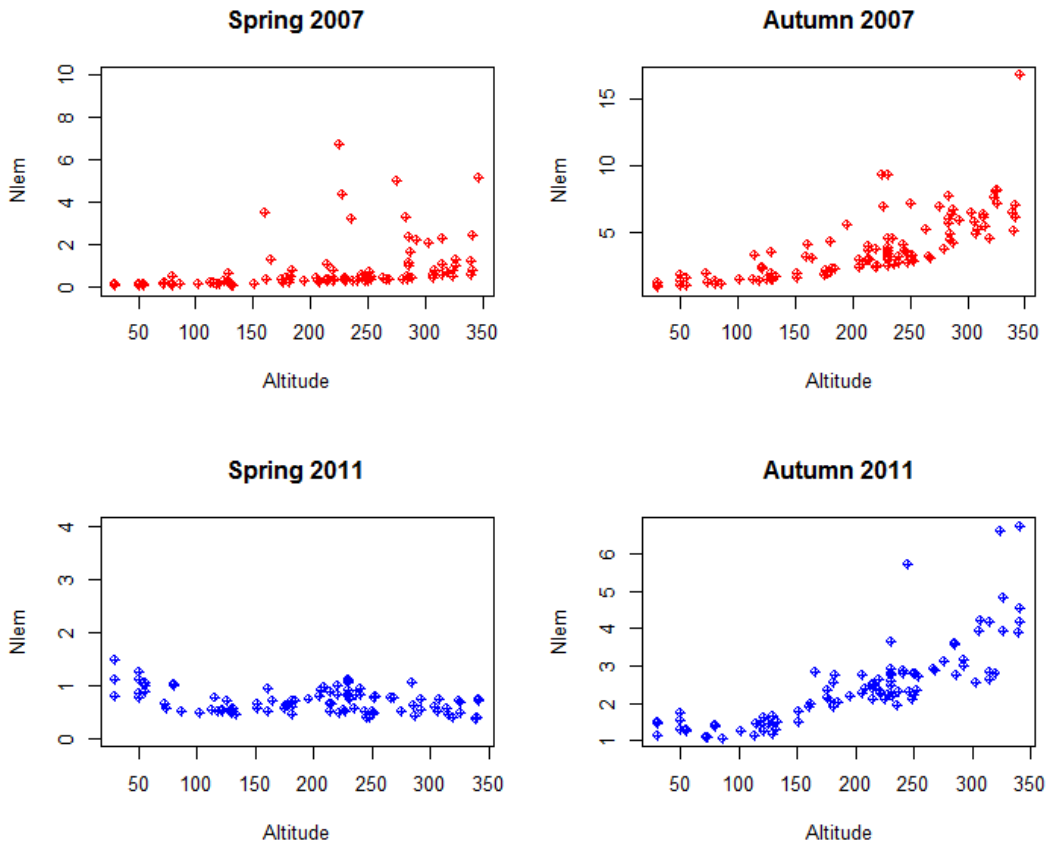
17

Figure 4: Effect of altitude on lemming abundance. Altitude plotted against estimated lemming abundance ($Nlem_{i,k}$, estimated with $\lambda lem_{i,k}$ (Equation 3)) from the multinomial mixture model for each site each season.
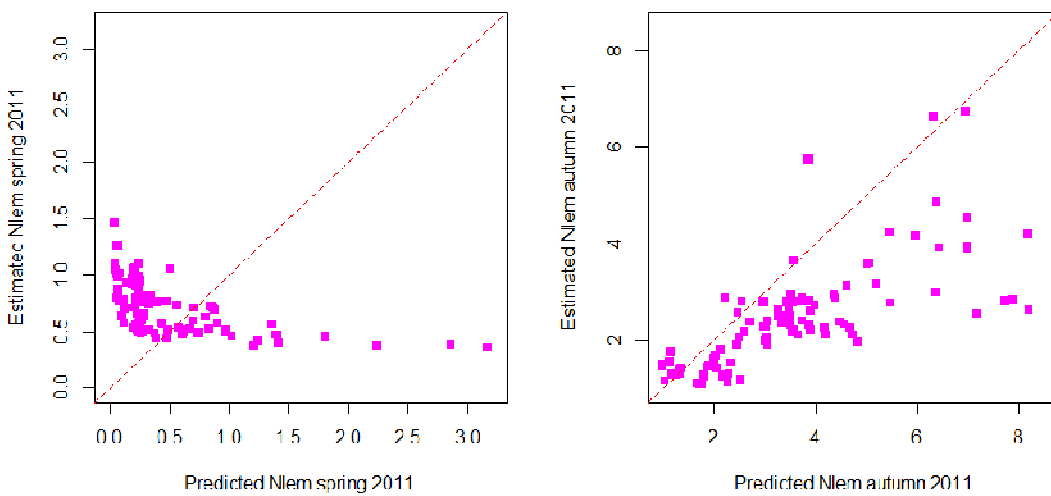

Figure 5: Graphical interpretation of the predictive ability of the 2006/07 model. Predicted lemming abundance per site in 2011 from covariate estimates from 2006/07 plotted against estimated lemming abundance for 2011 through a multinomial mixture model based entirely on data from 2010/11. The red dotted line illustrate y=x.

Discussion

My results suggest a positive effect of altitude on Norwegian lemming abundance in 3 out of 4 seasons analyzed. Furthermore, in line with the study by Ims et al. (2011) I found a positive effect of local grey-sided vole autumn abundances on the abundance of the sympatric Norwegian lemming in the consecutive spring of 2007. However, the present study shows that when including a new cyclic peak in the analysis this effect is not temporarily consistent. The modeling framework employed in the present study yielded, in contrast to Ims et al. (2011), no evidence of density-dependence in lemming abundance dynamics in any of the seasons due to very wide credible intervals of the estimated coefficients.

Effect of altitude

In the 2007 peak there is a significant positive effect of altitude on both the lemming summer and winter growth. While the summer effect stays consistently positive also for the consecutive peak (i.e. 2011), I find no such effect over the winter in the same peak (i.e. 2011). Given that altitude is likely a good proxy for climate variability, at least in some years, and that the effect being the strongest during winter of 2006/07, my results suggest a strong link between winter growth in lemmings and winter climatic conditions, such as snow properties. This is in line with other studies arguing that lemmings depend on long and cold winters to reach high densities (Kausrud et al. 2008, Ims et al. 2011). This is reasonable given their winter reproduction, a trait that is likely an adaptation to the long arctic winters. This together with the predator protection provided by a snow-covered ground could explain the observed positive effect of altitude on lemming growth during winter. Moreover mosses, the most important food resource for lemmings, have a higher lipid content during low temperatures, making its quality temperature dependent, an effect that might explain the consistent, positive altitude effect on lemming abundance during summer (Tast 1991).

More unexpected is the decoupling of lemming abundance and altitude in the spring of 2011. This could be due to underlying biological processes not measured in this study or it could be due to the applicability of altitude as a proxy for climate. Specifically, this poses the question how an altitudinal climate gradient relates to the actual biophysical

factors lemmings are sensitive too. For example, variation in the qualitative characteristics of the snow pack depend on whether the weather in a given winter vary according to altitude or not (Aars and Ims 2002, Korslund and Steen 2006, Kausrud et al. 2008). In some winters we might experience particular climatic events that disconnect the altitudinal gradient from snow properties. Such events have been reported from high arctic Svalbard where extreme rain-on-snow (ROS) events have been shown to lead to a continuous cover of ground ice, and poor foraging conditions for herbivores over all altitudes (Hansen et al. 2014). If such events appear in early winter with above 0°C temperatures and snow-free ground in low altitude areas and below 0°C temperatures and snow-covered ground in high altitude areas, it could create ground ice blocked pastures and the formation of bad foraging conditions for lemmings in high altitudes. In such a case, the local abundance of lemmings could in fact become negatively related to altitude. However, it is also likely that especially cold and stable winters with thick and extensive snow cover throughout the altitudinal range may decouple snow properties from altitude. The lemming peak in 2011 was, in contrary to the peak in 2007, spatially extensive in the sense that it encompassed almost the entire alpine and tundra range in Fennoscandia (Flagstad et al. 2011). It is also interesting to note that spatial variation in lemming spring abundances was substantially lower in 2011 than in 2007, thus reinforcing the impression that the conditions for lemmings were more spatially homogeneous during the winter of 2010/2011. Nonetheless, because I have no available local weather data or measurements of snow properties from the replicated altitudinal gradients in my study area, it is only possible to speculate about why the spatial variation in lemming abundance is not always consistently related to altitude.

Effect of grey-sided vole

Consistent with Ims et al. (2011) the estimated effect of grey-sided voles was positive in 2007. They reported a similar facilitating effect of grey-sided vole on winter growth in lemmings. The possibility of indirect mutualism between prey species through shared predators has been highlighted in theoretical work (Holt 1977, Abrams and Matsuda 1996). Indirect mutualism has even been proposed to be more likely in cyclic systems driven by predator-prey interactions than in more stable or erratic systems (Abrams et al. 1998). Mutualism due to shared predation has most convincingly been documented between birds and small-rodents in the northern areas (Gilg and Yoccoz 2010). Given

that the positive effect of grey-sided vole was only present during winter, when mustelids are the only significant predators present, coupled with the issue that attempts to find direct competition between the two species has not provided any clear evidence (Heske and Steen 1993), the interaction between the two rodent species is likely to be indirect through shared predation from these highly specialized predators. Even though indirect interspecific mutualism is not likely to be the reason for the cyclic behavior in lemming abundance (Hansen et al. 1999), it could potentially release lemmings from being trapped in a predator pit where they are constantly depressed at low density (Krebs 1996, Ims et al. 2011). This could explain the sharp and angular shape of lemming peaks, where they, after being released from the predator pit, increase rapidly due to their high population growth rate, especially during the winter.

Maybe more important is that my result suggests a lack of an effect of grey-sided vole on lemmings during the winter leading to the peak in 2011, therefore the effect of grey-sided vole on lemming growth can be said to be different between the two peaks. This finding can be expected given that the interaction might change due to changes in predator's functional as well as numerical response, factors that are unknown in this study system (see more detailed discussion below).

Temporal transferability

A rather novel aspect of my study is that I investigated the temporal consistency (i.e. transferability) of processes that may generate variation in spatial cycle amplitude. Specifically, I found the transferability of the processes during summer that generated the peak autumn abundances to be good between consecutive peaks. This suggests that the model contains most effects with a considerable impact on the summer processes and that they are consistent through time. In the arctic region, the summer season is generally short, in contrast to the long winters. Summer processes may also be expected to be more consistent between years than winter processes both because of the absence of snow as a highly variable factor and because arctic winter climates exhibit more temporal variation than summer climate (Yoccoz and Ims 1999).

The poor transferability of the winter processes found in this study is interesting in the light of the recent awareness of the difficulties connected to predicting ecological dynamics in space and time, often explained by the intermixing of systematical ecological processes with a fair degree of stochasticity (Bjørnstad and Grenfell 2001). Ecological models have also been criticized for focusing too much on the eventual long-term dynamics, while experimental and observation studies are done on a much shorter time scale (Hastings 2004). The transient state, which is defined as the state before a system reach its final behavior, can be long and might often be what we observe in short-term ecological studies (Hastings 2004). If we are truly observing a transient state in this system, a transition in the predator's functional response or initial abundance might change the interaction between the two preys completely. As I have no direct data on predators and their effect on the lemming-vole interaction I am not able to consider influential factors such as predator abundance or their functional or numerical response. However, the theoretical work of Abrams et al. (1998) suggests that the interaction between sympatric species that share predators is highly dependent on the numerical and the functional response of the predators. The mustelids, that are likely to cause this interaction, consists of the two species stoat and least weasel. However, little is known about their relative functional and numerical response to lemming or grey-sided vole. The stoats is larger than the least weasel, and has therefor been proposed to result in having a broader diet and greater food requirement than the least weasel (Erlinge 1975, Hanski et al. 2001). Moreover, the least weasel is known to have a higher reproductive potential than stoat (Korpimäki et al. 1991). Furthermore, the two mustelid species have been shown to differ both in functional and numerical response in another small rodents community in western Finland (Korpimäki et al. 1991). Therefore, I will argue that such differentiation is also likely to occur in the Fennoscandian tundra. This adds complexity to the system and makes the interaction between the two prey species even harder to predict.

Modeling approach

The fact that I find the same positive effect of abundance of grey-sided vole and altitude on the abundance of lemmings on a plot scale as Ims et al. (2011) is interesting, given the recent critique of state-space models which make implicit assumptions about the

distribution of the measurement error. The model used in this thesis makes use of more information in the data to explicitly calculate detectability, instead of making such ad-hoc assumptions of the distribution of the measurement error. Hence, the fact that I find the same effect as detected in an earlier study with another modeling approach suggests that the effect of grey-sided vole and altitude on lemming abundance is rather robust with regard to different implementations of measurement error.

The estimation of detection probabilities relies on only two trapping days at each site for each season. It has been argued that for animals with a low detection probability, two trapping days might not be enough and it could potentially lead to biased estimates (MacKenzie et al. 2002). However an advantage of the Bayesian approach is that by specifying hyper-priors estimated detectability on one site can "borrow strength" from other sites (Dorazio et al. 2005). Therefore, the sheer number of sites (i.e. 99-109) should contribute to more precise estimates of detectability even with only two temporal replicates. While there is no doubt that lemmings might be hard to detect (i.e. are little trappable), they also reproduce quickly and migrate into free habitats as soon as individuals are removed. Hence, two trapping days has been proposed as an optimal time scale for trapping most of the individuals present while simultaneously minimizing the effect of animals migrating into habitats opened by removal of individuals (Myllymäki et al. 1971). Also, even though we conduct trapping in 15m x 15m squares we cannot be sure of how large area this trapping really represents. It is possible that due to immigration into free habitats this area expands over consecutive removal occasions. Therefore, more than two consecutive trapping days might violate the assumption of closure within the trapping period. Two trapping days might therefore be a reasonable tradeoff between the number of sampling occasions and the assumption of closure to achieve more unbiased estimates.

Saturation of the traps, where all traps can be filled with lemmings, has been proposed to lead to an underestimation of the abundance, making the number of traps an upper bound of total abundance estimates. Other species trapped, like grey-sided vole and tundra vole, could cause a similar saturation of the traps (Leslie and Davis 1939), in particular, since voles are likely to be more attracted to the bait than lemmings (Jensen et al. 1993). This could potentially lead to underestimation of lemming abundance when

grey-sided vole and/or tundra voles are present in high abundances. This could then potentially affect our estimates of the grey-sided vole-lemming interaction towards a negative effect of grey-sided vole on lemmings. Hanski et al (1994) did however, not find any evidence for trap saturation when employing the small quadrat method for estimate population densities in the bank vole (*Myodes glareolus)*, which is a easily trappable species.

Another assumption made in this multinomial mixture model is that the detection probability *p* is equal between individuals and trapping days per site and season. This assumption has been discussed in the small rodent literature for more than 60 years (Moran 1951). There might be heterogeneity in trappability between weight and sex classes. Even though we see a slight weight reduction from the first trapping day to the next, both weight and sex ratio seems to be quite similar between the two trapping days (Table 1). Therefore I argue that if such differences exists, it must be between less conspicuous groups in the population that are more or less trap-shy. However, this is difficult to account for (but see Mantyniemi et al. (2005)).

In summary, I suggest that the use of temporally replicated measurements to explicitly estimate the detectability might be a step in the right direction on the way towards precise and unbiased abundance estimates that account for the detection process, even with the weaknesses discussed above.

Conclusion

Given the long arctic winter (defined as the period from early September to late June in this study) for which we have little knowledge about processes affecting the small rodent community and their predators under the snow. It is likely that trophic interactions and abiotic effects are heterogeneous both in time and space through such a long period without measurements. Moreover, winter processes in the arctic are known to be difficult to predict due to the complex winter dynamics in this arctic system (Yoccoz and Ims 1999).

I argue that determinants of lemming outbreaks in fact should be expected to be temporarily and spatially inconsistent and likely to cause considerable cycle amplitude variation.

To shed more light on this black box of winter processes I propose that increased efforts be put on more continuous sampling during winter. The Ten-month period between samples in autumn and spring, which at the present is the standard temporal sampling schedule for all lemming studies, seems too long to illuminate the complex winter processes. There is also a great need for studies giving deeper knowledge about mustelids functional and numeric response, to more explicitly investigate their true effect on the small-rodent community. Recent developments of camera traps that are continuously operative during the winter may help to fill these important knowledge gaps (Soininen et al. 2015).

Acknowledgement

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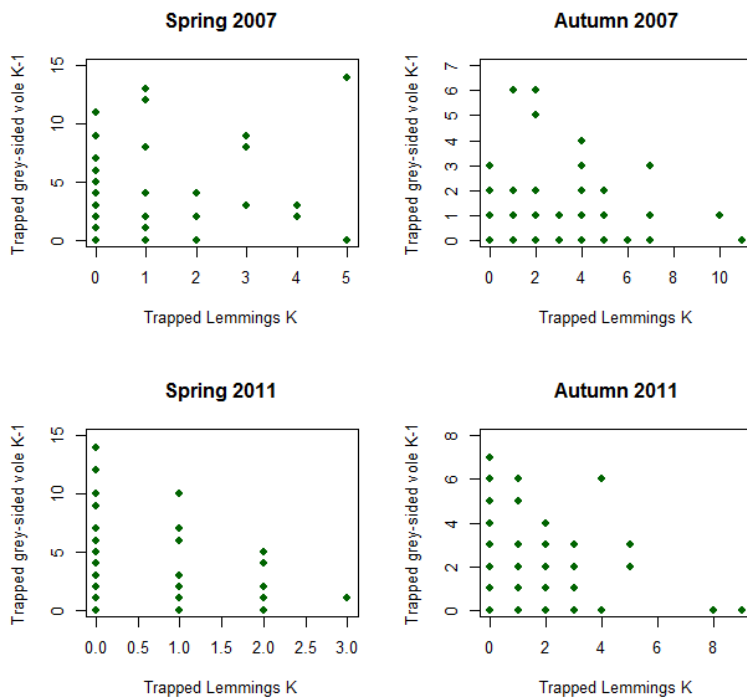
Appendix A

Plots from raw data:

Figure A-I: Plot showing the signal of grey sided vole abundance the previous season (k-1) on lemming abundance (k), from the raw-data.
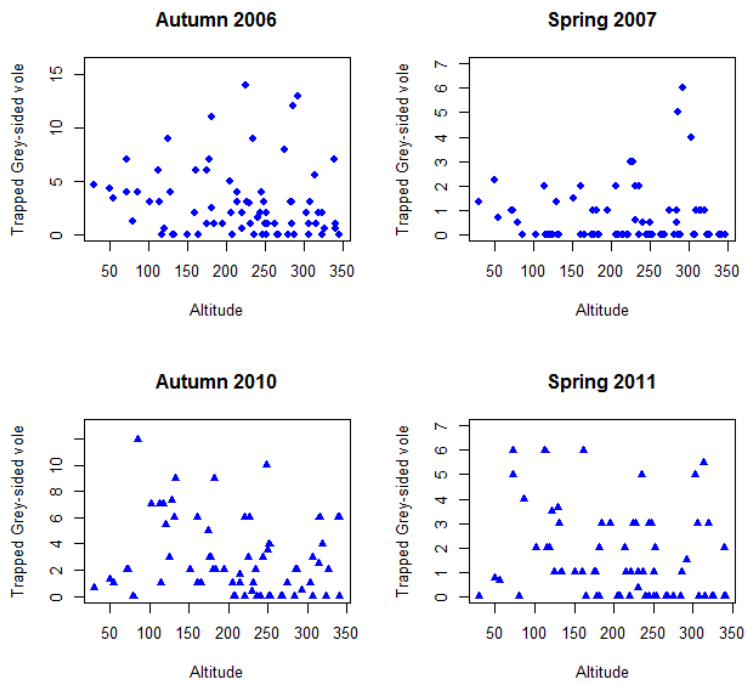

Figure A-II: Plot showing the signal from altitude on grey-sided vole abundance in the raw data for all seasons analyzed.
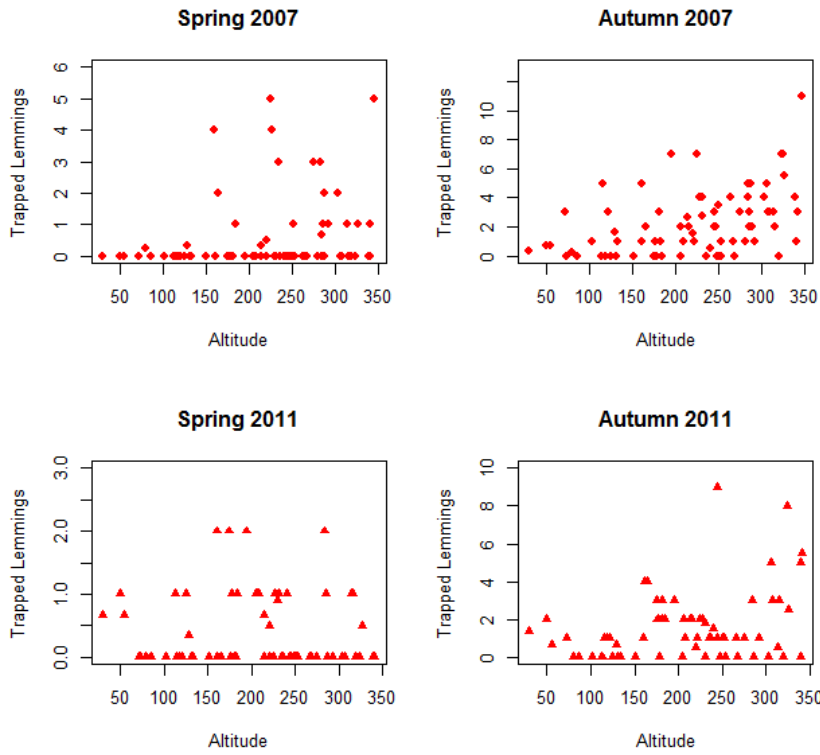
Figure A-III: Plot showing the signal from altitude on lemming abundance in the raw data for all seasons analyzed.
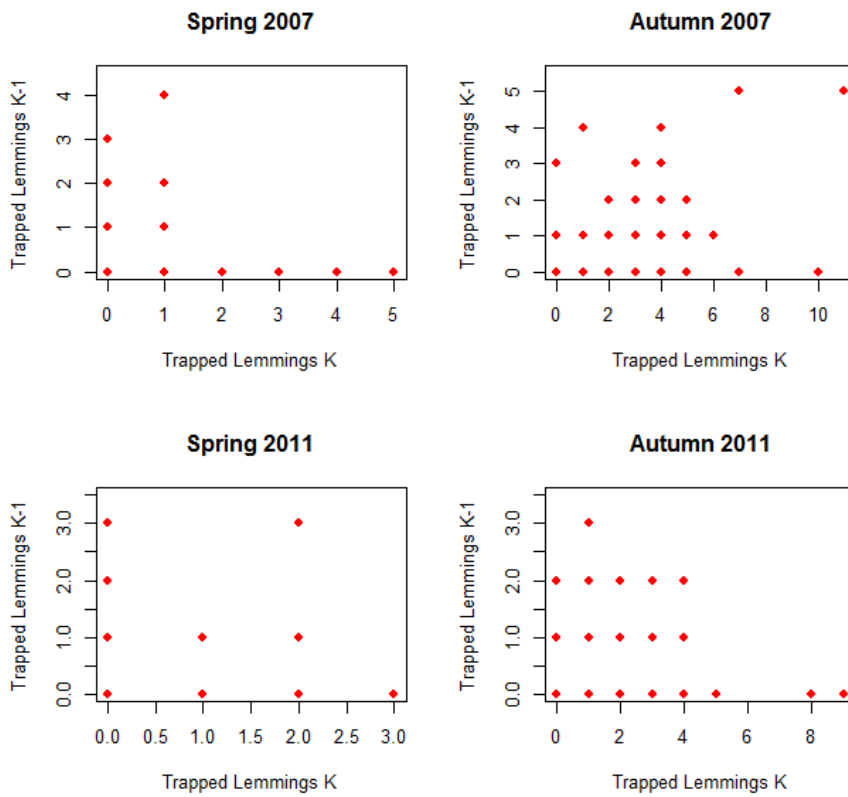

Figure A-IV: Plots showing the effect of number of trapped lemmings the previous season(k-1) on number of trapped lemmings this season(k), for all seasons analyzed.
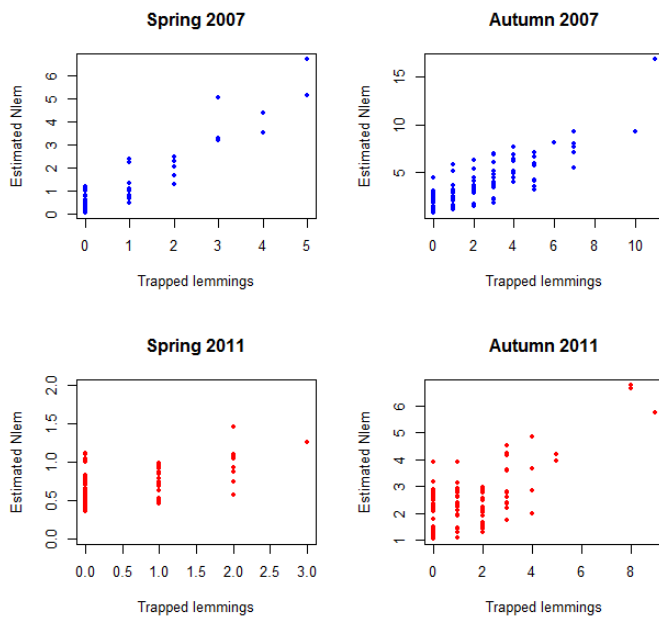
Appendix B

Figure B-I: Test of model fit. Estimated lemming abundance from the multinomial mixture model plotted against counted lemmings, as a total of both trapping days for each site. Plots for all seasons modelled.
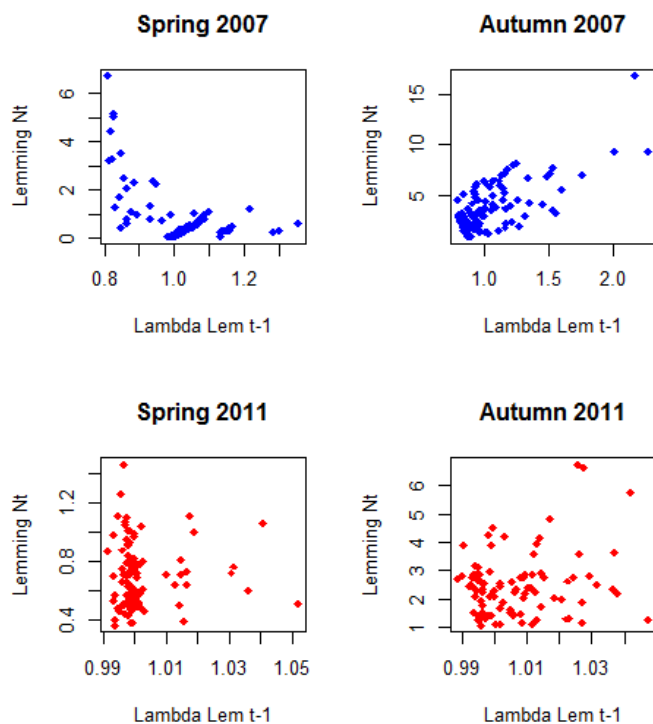

Figure B-II: Lemming abundance as a function of lemming abundance previous season. The naiv lemming abundance estimated for season k-1 plotted against estimated lemming abundance in season k.

Appendix C

This appendix contains the JAGS code needed to run the model used in this thesis. Note that all text after the character #, but still on the same line is comments. I also changed the notation of the parameters describing effects of predictor variables to make there understanding more intuitive for the reader (beta1= $\beta vole$, beta2= $\beta alti$, beta3= βdd).

```
model{
########################
### MYO07 ###########
### Priors myo ###

for(k in 1:2){
for(i in 1:R){

alpha.am07[i,k] ~ dnorm(0,tau.am)
alpha.pm07[i,k] <- logit(pmyo0.07[i,k])
pmyo0.07[i,k] ~ dunif(0,1)
}
}

## Hyperpriorer ##
tau.am ~ dgamma(0.001,0.001)

### Conditional multinomial cell probablity ####

for(k in 1:2){
for(i in 1:R){

## logit-link for detection ##
logit(pmyo07[i,k]) <- alpha.pm07[i,k]

## log-link for Abundance ##
log(lambdamyo07[i,k]) <- alpha.am07[i,k]

### Conditional multinomial cell probablity ####
pimyo07[i,1,k] <- pmyo07[i,k]*lambdamyo07[i,k]
pimyo07[i,2,k] <- pmyo07[i,k]*(1-pmyo07[i,k])*lambdamyo07[i,k]

for(j in 1:2){
y[i,j,k] ~ dpois(pimyo07[i,j,k])
}

## Generate predictions for Nlem[i] ##
Nmyo07[i,k] ~ dpois(lambdamyo07[i,k])
}
}
```

```
###############################
### Naivlem07 ###########
### Priors Naiv lem 1 ###
for(k in 1:2){
for(i in 1:R){
alpha.nl1[i,k] ~ dnorm(0,tau.nl1)
alpha.pnl1[i,k] <- logit(p0.naiv.l1[i,k])
p0.naiv.l1[i,k] ~ dunif(0,1)
}
}

## Hyperpriorer ##
tau.nl1 ~ dgamma(0.001,0.001)

### Conditional multinomial cell probablity ####
for(k in 1:2){
for(i in 1:R){
## logit-link for detection ##
logit(p.naiv.l1[i,k]) <- alpha.pnl1[i,k]

## log-link for Abundance ##
log(lambda.naivlem.1[i,k]) <- alpha.nl1[i,k]

### Conditional multinomial cell probablity ####
pi.naivlem.1[i,1,k] <- p.naiv.l1[i,k]*lambda.naivlem.1[i,k]
pi.naivlem.1[i,2,k] <- p.naiv.l1[i,k]*(1-p.naiv.l1[i,k])*lambda.naivlem.1[i,k]

for(j in 1:2){
c.naivlem.1[i,j,k] ~ dpois(pi.naivlem.1[i,j,k])
}

## Generate predictions for Nlem[i] ##
N.naivlem.1[i,k] ~ dpois(lambda.naivlem.1[i,k])
}
}

###############################
### LEM07 ###########
### Priors lem ###

for(k in 1:2){
for(i in 1:R){
alpha.pl07[i,k] <- logit(plem0.07[i,k])
plem0.07[i,k] ~ dunif(0,1)
}

alpha.al07[k] ~ dnorm(0, tau.al)
beta1[k] ~ dnorm(0,0.1)
beta2[k] ~ dnorm(0,0.1)
```

```
beta3[k] ~ dnorm(0,0.1)
}

## Hyperpriorer ##
tau.al ~ dgamma(0.001,0.001)

for(k in 1:2){
for(i in 1:R){
## Logit-link for detection ##
logit(plem07[i,k]) <- alpha.pl07[i,k]

## Log-link for abundance##
log(lambdalem07[i,k]) <- alpha.al07[k] + beta1[k]*log(lambdamyo07[i,k]) +
beta2[k]*alti07[i,k] + beta3[k]*log(lambda.naivlem.1[i,k])

### Conditional multinomial cell probablity ####
pilem07[i,1,k] <- plem07[i,k]*lambdalem07[i,k]
pilem07[i,2,k] <- plem07[i,k]*(1-plem07[i,k])*lambdalem07[i,k]

for(j in 1:2){
y2[i,j,k] ~ dpois(pilem07[i,j,k])
}

## Generate predictions for Nlem[i] ##
Nlem07[i,k] ~ dpois(lambdalem07[i,k])
}
}

#######################
### MYO11 ###########
### Priors myo ###

for(k in 1:2){
for(i in 1:R2){
alpha.am.p2[i,k] ~ dnorm(0,tau.am.p2)
alpha.pm.p2[i,k] <- logit(pmyo0.p2[i,k])
pmyo0.p2[i,k] ~ dunif(0,1)
}
}

## Hyperpriorer ##
tau.am.p2 ~ dgamma(0.001,0.001)

### Conditional multinomial cell probablity ####
for(k in 1:2){
for(i in 1:R2){

## logit-link for detection ##
logit(pmyo.p2[i,k]) <- alpha.pm.p2[i,k]
```

X

```
## log-link for Abundance ##
log(lambdamyo.p2[i,k]) <- alpha.am.p2[i,k]

### Conditional multinomial cell probablity ####
pimyo.p2[i,1,k] <- pmyo.p2[i,k]*lambdamyo.p2[i,k]
pimyo.p2[i,2,k] <- pmyo.p2[i,k]*(1-pmyo.p2[i,k])*lambdamyo.p2[i,k]

for(j in 1:2){
ymyo.p2[i,j,k] ~ dpois(pimyo.p2[i,j,k])
}

## Generate predictions for Nmyo.p2[i] ##
Nmyo.p2[i,k] ~ dpois(lambdamyo.p2[i,k])
}
}

########################
### Naivlem11 ###########
### Priors Naiv lem 2 ###
for(k in 1:2){
for(i in 1:R2){
alpha.nl2[i,k] ~ dnorm(0,tau.nl2)
alpha.pnl2[i,k] <- logit(p0.naiv.l2[i,k])
p0.naiv.l2[i,k] ~ dunif(0,1)
}
}

## Hyperpriorer ##
tau.nl2 ~ dgamma(0.001,0.001)

for(k in 1:2){
for(i in 1:R2){
## logit-link for detection ##
logit(p.naiv.l2[i,k]) <- alpha.pnl2[i,k]

## log-link for Abundance ##
log(lambda.naivlem.2[i,k]) <- alpha.nl2[i,k]

### Conditional multinomial cell probablity ####
pi.naivlem.2[i,1,k] <- p.naiv.l2[i,k]*lambda.naivlem.2[i,k]
pi.naivlem.2[i,2,k] <- p.naiv.l2[i,k]*(1-p.naiv.l2[i,k])*lambda.naivlem.2[i,k]

for(j in 1:2){
c.naivlem.2[i,j,k] ~ dpois(pi.naivlem.2[i,j,k])
}

## Generate predictions for N.naivlem.2 ##
N.naivlem.2[i,k] ~ dpois(lambdalem.11[i,k])
```

```
}
}

####################
### LEM11 ###########
### Priors lem ###
for(k in 1:2){
for(i in 1:R2){
alpha.pl.11[i,k] <- logit(plem0.11[i,k])
plem0.11[i,k] ~ dunif(0,1)
}
alpha.al.11[k] ~ dnorm(0, tau.al.11)
beta4[k] ~ dnorm(0,0.1)
beta5[k] ~ dnorm(0,0.1)
beta6[k] ~ dnorm(0,0.1)
}

## Hyperpriorer ##
tau.al.11 ~ dgamma(0.001,0.001)

for(k in 1:2){
for(i in 1:R2){
## Logit-link for detection ##
logit(plem.11[i,k]) <- alpha.pl.11[i,k]

## Log-link for abundance##
log(lambdalem.11[i,k]) <- alpha.al.11[k] + beta4[k]*log(lambdamyo.p2[i,k]) +
beta5[k]*alti11[i,k] + beta6[k]*log(lambda.naivlem.2[i,k])

### Conditional multinomial cell probablity ####
pilem.11[i,1,k] <- plem.11[i,k]*lambdalem.11[i,k]
pilem.11[i,2,k] <- plem.11[i,k]*(1-plem.11[i,k])*lambdalem.11[i,k]

for(j in 1:2){
ylem.11[i,j,k] ~ dpois(pilem.11[i,j,k])
}

## Generate predictions for Nlem11[i] ##
Nlem.11[i,k] ~ dpois(lambdalem.11[i,k])
}
}
#### Predict next peak #####
for(i in 1:R2){
for(k in 1:2){
log(lambdalem.p2[i,k]) <- alpha.al07[k] + beta1[k]*log(lambdamyo.p2[i,k])+
beta2[k]*alti11[i,k] + beta3[k]*log(lambda.naivlem.2[i,k])

predNlem.p2[i,k] ~ dpois(lambdalem.p2[i,k])
}
```

```
}
###############################################################
############ Derived quantities #####################
for(k in 1:2){
mean.plem11[k] <- mean(plem.11[,k])
mean.plem07[k] <- mean(plem07[,k])
mean.pmyo07[k] <- mean(pmyo07[,k])
mean.pmyo11[k] <- mean(pmyo.p2[,k])
mean.Nmyo07[k] <- mean(Nmyo07[,k])
mean.Nmyo11[k] <- mean(Nmyo.p2[,k])
}
}
```

Appendix D

Table D I: Estimated detection probability (p) of one individual on a given trapping day, for grey-sided vole and Norwegian lemming in all seasons modeled given as mean from all sites with Bayesian credible intervals.

		Grey-sided vole		Lemming	
Year	Season	p	CI	p	CI
2006	Autumn	0,501	[0,453 : 0,550]	-	-
2007	Spring	0,471	[0,420 : 0,524]	0,487	[0,434 : 0,541]
2007	Autumn	-	-	0,436	[0,387 : 0,486]
2010	Autumn	0,470	[0,423 : 0,524]	-	-
2011	Spring	0,482	[0,430 : 0,534]	0,481	[0,427 : 0,537]
2011	Autumn	-	-	0,464	[0,410 : 0,517]