Shared Predation and its Impact on two Sympatric Rodent Species

Adding to nature's complexity

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Anthine Moen
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To get lost is to learn the way

-African proverb

Acknowledgments

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Abstract

Specialist predators generally prey on the whole community of small mammal species, although they may have preferences for certain species. In that case, the phenomenon of shared predation can have a large impact on the dynamics of the system. Shared predation may mediate a relationship between two sympatric prey species without direct interaction. The grey-sided vole (*Myodes rufocanus*) and the Norwegian lemming (*Lemmus lemmus*) are known to coexist and have synchronized cyclic peaks in the arctic-alpine tundra of Fennoscandia. They are not known, however, to compete or have any interaction other than through shared predators. I used a theoretical model with different predatory preference relationships but with no direct competition. Simulated time series were statistically analysed to evaluate changes in rodent dynamics, with respect to periodicity, synchrony, amplitude and symmetry. The study found that shared predation could mediate a relationship between the two rodents to some extent. Periodicity increased on average for both species but decreased in the scenarios were the predator response was very rapid for the alternative prey. When this was applied to the main prey, extinction occurred. Synchrony was at its strongest when there was a slight preference for the lemming and amplitude showed very little variation but increased when the rodents were coupled in the more complex model. There was no consistent pattern concerning changes in symmetry but a tendency towards higher asymmetry when there was a very high preference for main prey.

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1. Introduction

Enemy-victim interactions are among the most dramatic interactions that can be witnessed in the natural world. Processes such as wolves chasing down ungulates in Yellowstone, a European sea eagle diving after fish, or even a copepod eating microscopic phytoplankton are all processes that can be described by the use of predator-prey theory (Stevens, 2009). Furthermore, the description of the relationship between a predator and its prey has been one of the most central themes throughout the history of ecological science. One of the simplest mathematical frameworks that describe this relationship would be the framework developed by Alfred J. Lotka and Vito Volterra around 1926 (Berryman, 1992). Its simplicity makes it well suited to explain trophic interactions. It also lays the foundation for models of other consumer-resource interactions (Stevens, 2009). Most predator-prey interactions are described by the use of stable point equilibrium or stable-limit cycles (May, 1973). In a stable-limit cycle the populations in question undergo well-defined cyclic alterations in time, and the amplitude (the minimum and maximum values the populations reach during the cycle) are dependent on parameters such as growth rates, predation rates and carrying capacities (May, 1973).

Predators are divided into two wide groups termed generalists and specialists (May, 1973). Anderson and Erlinge (1977) also made a distinction between two types of specialists; resident specialist and nomadic specialists. These groups of predators will show different functional responses depending on their dynamics and life history. The specialist predators will show a type II response, a response that shows where predators utilise prey even though their numbers are very small. This means the shape of the response will show a rapid acceleration towards an asymptote. A generalist predator will, in contrast, show a type III functional response, as learning and handling time will increase for this kind of predator, which again will result in the sigmoidal shape of the response (Berryman, 1992). The two responses do affect prey populations differently. For instance, the type III response incorporates switching behaviour. This means that at low prey numbers, predators can switch to an alternative prey type, allowing the main prey to recover. In contrast, the predators that show a type II response can very much utilise the low prey numbers and potentially drive the population closer to extinction (Klepac et al, 2007).

Although classical predator-prey models deal with the interaction between one prey species and one predator species, in a natural system, a more realistic scenario would be to have several prey species available and maybe a guild of predators, even in the case of quite specialized predators. For instance, specialist predators on small mammals generally prey on the whole community of small mammal species, although there may be preferences for certain species (Sundell & Ylönen, 2008). In that case, there is also the phenomenon of *shared predation* that can have a large impact on the dynamics of the system. In addition to the assumptions and factors affecting a one-prey-one-predator system, one would also need to incorporate factors that link several species together. The factors one needs to consider in such more complex system are the possible direct competitive interactions between the prey species, how vulnerable they are to predation, their relative density and last but not least the preference of the predator. In some cases, shared predation alone could act as a mechanism to synchronise the populations of coexisting prey species that show no other overlap in niche characteristics (Holt 1977; Holt and Lawton 1994, Abrams and Ginzburg, 2000).

Shared predation, when present, may to a large extent mediate a relationship between two sympatric species that intrinsically are very different. This relationship will be clear through the assignment of the roles as main and alternative prey (Hagen 1952, Lack 1954, Angelstam et al. 1984). The alternative prey species will be influenced by the dynamics of the primary prey through the predator's numerical and functional response. Predator numerical response can have an influence through movement and aggregation (Turchin and Hanski, 1997), but can also have an impact through changes in demographics, i.e. reproductive changes. Usually it is a combination of both. In contrast, an alteration in functional response following an increase in primary prey numbers will have opposite effects on the alternative prey. Individuals in the predator population will start eating less of the alternative prey. However, in the long run, this can result in an increase in the predator population that again can have a negative impact on the alternative prey. In other words, primary prey can have a positive or negative impact on alternative prey (Barraquand et al. 2015). According to classical theory, when the predator numerical response is strong the impact of the primary prey on the alternative prey will be negative. In contrast, when the numerical response is weak and the functional response saturates (as is

the case for a type III functional response), the impact on alternative prey by primary prey can be positive (Holt, 1977; Barraquand et al. 2015). Therefore, the relationship between the prey species can both be defined as apparent mutualism and apparent competition (Holt 1977). In a system with a primary prey species and an alternative prey species, dynamics of the community may very well be altered by a shared predator that show multiple functional responses for the different species, i.e. the predator can have one functional response for the preferred prey and another for the alternative. This is termed a multi-species functional response (Smout et al. 2010).

Population cyclicity and the role predation plays in creating cyclic dynamics have been discussed for many years and there are many examples of systems that have undergone serious investigation (Krebs, 1974). One example in particular is the cyclic population dynamics of small rodents and their specialist predators, more specifically the rodent community found in Fennoscandia (Turchin, 2003). This rodent community is very much a keystone community that sustains a large guild of both specialist and generalist predators (Warhol, 2007). The interaction between the predators and rodents had been modelled several times, but mostly as a one-prey species and one-predator interaction. Hanski and Henttonen (1996) created therefore a model that incorporated two prey species and a shared predator. Their study system comprised of field voles (*Microtus sp.*) and bank voles (*Clethrionomys sp.*). The model has an interaction (i.e. inter-specific competition) parameter for the two rodent prey species. The bank vole is said to be competitively inferior to the field vole, despite the field vole being more vulnerable to predation (Hanski & Henttonen, 1996). There are up to 8 rodent species in Fennoscandia that might coexist and more species coexist in the north rather than in the south. Some of the coexisting species are known to compete and while they are all predated on by the same predators. Hanski and Henttonen (1996) then deduced that the model created could describe many unanswered questions regarding population cycle patterns in the rodent community.

However, there are two other species of rodents in Fennoscandia that are known to coexist and have synchronized cyclic peaks, yet they are not known to directly compete or have any interaction other than through shared predators. The grey-sided vole (*Myodes rufocanus*) and the Norwegian lemming (*Lemmus lemmus*) are both

found in the arctic and alpine tundra in Fennoscandia. They reside in the same or adjacent habitats (Ims et. al., 2013), but do not overlap much in diets (Soininen et al. 2013). The two species also differ substantially in their demographics (Ims et al. 2011). Among the predator present, the two resident specialists the least weasel (*Mustela nivalis*) and the slightly larger stoat (*Mustela erminea*), is believed to be behind most of the predation of the two rodent species (Henttonen et al. 1987).

Due to the lack of interaction between the grey-sided vole and the lemming there has been some disagreement to what causes the synchrony that occurs (Tuchin et al. 2000 vs. Ims et al. 2011). The aim of my thesis is therefore to investigate how shared predation by specialist mustelids influence the dynamics the two species. A very typical way of evaluating change in cyclic rodent dynamics is to look at characteristics like inter-specific synchrony, periodicity, cycle amplitude and symmetry. By focusing on such characteristics, one can show how shared predation and the predatory preference affect the relative dynamics between the lemming and the grey-sided vole. Furthermore, my main focus will be on how preference switching in the predator can alter the relationship between two sympatric rodent populations. The base for this thesis is mostly inspired by the work done by Hanski and Henttonen and their colleagues, particularly their work published in 1993 and 1996, which provides a clear and empirically based representation of the focal predator-prey system.

2. Methods

2.1.The one-prey species model

The starting point for this thesis was to create a simple model that represented the system and depict the dynamics known from empirical studies (see Hanski et al. 1991, 1993, Hanski and Henttonen, 1996) and thus use this as a baseline to compare to when an interaction was added. Therefore, a general predator-prey model was used (eq. 1 and eq. 2) and the species were modelled separately (also see Hanski et. al. 1993).

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - \frac{cPN}{N+D} \qquad \text{(eq. 1)}$$

$$\frac{dP}{dt} = vP\left(1 - \frac{qP}{N}\right) \qquad \text{(eq. 2)}$$

The basal prey model has the assumptions of logistic growth and a predator type II functional response (see equation 1), where N is the prey population size, K is the carrying capacity, r is growth rate and c is the maximum per capita predation rate of the predator P. The assumption of a type II functional response for the predator is not unreasonable as the predator is assumed to be a specialist mustelid (e.g. stoat). Seasonality is incorporated by having two sets of parameters for carrying capacity and growth rate, with one value for summer and one for winter. For the predator (see equation 2), v is the predators' growth rate; q is the population size when the predator population, P, is in equilibrium in relation to prey numbers. In addition, the predator per capita rate of decline is dependent on the parameters d_{low} and d_{high}. Predator numbers will change according to equation 2 when N is above a critical threshold ($N_{crit} = 10$) and the death rate in the predator population will be low (d_{low}). If not, the decline will be exponential. This is expressed in the way of equation 3.

$$\frac{dP}{dt} = -d_{high}P \qquad \text{(eq. 3)}$$

Therefore, when no reproduction occurs, the rate of decline is assumed to be d_{high}. Also, during winter the decline in predators can be low (d_{low}) when $N > N_{crit}$ or high (d_{high}) when prey availability is low.

The predator growth rate is a function of the prey/predator ratio $(\frac{D}{N})$ at high densities (Eq. 2). Therefore it is taking into consideration the competitive interactions among the predators. However, at low densities the predator population decline, thus avoiding a problem occurring in the standard ratio-dependent theory (Hanski et al. 1991).

2.2.The two-prey species model

Following the construction of the simple one-prey-one-predator model, I wanted to show the effects of adding a sympatric species to the dynamics and construct a way to create a variation of predatory preference between the two prey species.

For this I used, as a starting point, Hanski and Henttonen's (1996) development of the Hanski et. al. (1991) model to include two prey species. However, I did add a few modifications, the main modification was that the interaction parameter α was removed due the assumption that there is no direct link (i.e. interspecific competition) between the two prey species I have chosen. Furthermore β, a vulnerability parameter used in Hanski and Henttonen (1996), expressed by the ratio of the two prey species half-saturation constants D_1 and D_2, was substituted with the actual ratio to see more clearly how the predatory preference can change the dynamics of the two prey species. This resulted in the two prey equations below:

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K_1}\right) - \frac{cPN_1}{D_1 + N_1 + (\frac{D_1}{D_2})N_2} \quad eq.\ 4$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2}{K_2}\right) - \frac{cPN_2}{D_2 + N_2 + (\frac{D_2}{D_1})N_1} \quad eq.\ 5$$

N_1 and N_2 here represent the two different species, N_1 denoting the lemming and N_2 the grey-sided vole. K_1 and K_2 are their respectively carrying capacities and r_1 and r_2 their intrinsic growth rates.

Since the predator preference is the key issue of this thesis, it is vital to know the dynamics of the functional response and how it changes in relation to the ratio

between D_1 and D_2, i.e. predator preference. The half-saturation constant tells us how fast the predator responds to the prey population. A fast response (low D) is here an indication of preference. When the response becomes slow (high D), the preference is reduced. As seen in equation 4 and 5, the ratio is represented differently according to which species is the focal prey. If one takes the example of equation 4, which in this case represents the lemming (N_1); if there is a main preference for the vole, it means that D_1 is larger than D_2. If one uses a larger numerator than the denominator one gets a larger number. This also means that the expression below the fraction bar becomes larger than the expression above it. The result is then that the entire functional response becomes smaller and therefore predation has a lesser effect on this prey species.

If one were to switch things around and increase the preference for the lemming one would get a different result. The ratio will become smaller and the expression below the fraction bar will be smaller. Therefore, will the functional response be larger and predation will have a larger effect on the population.

The same will happen if one considers equation 5. The only difference would be that the grey-sided vole would act as the main prey and the lemming as the alternative prey. It is therefore important to determine what species is the main prey and the alternative and if one wants to alter the preference for the main or alternative prey. This is because this distinction could create very different dynamics.

The dynamics for the predator population was again modelled separately as a continuous time model (see eq. 6 and 7):

$$\frac{dP}{dt} = vP\left(1 - \frac{qP}{N_1 + \beta N_2}\right) \quad if\ N_1 + \frac{D_1}{D_2}N_2 > N_{crit} \quad eq.\ 6$$

$$\frac{dP}{dt} = -d_{high}P,\ if\ N_1 + \frac{D_1}{D_2}N_2 \leq N_{crit}\ eq.\ 7$$

In the two-prey-species model, the critical values for the predator need to have both prey species within the critical values, i.e. a combined density of prey, meaning that

N_{crit} is a sum of both species abundances. Therefore, during winter the decline in predators can be low (d_{low}) when $N_1 + \frac{D_1}{D_2} N_2 > N_{crit}$ or high (d_{high}) when prey availability is low.

In Hanski and Henttonen (1996) the predator can start reproducing anytime during the summer as long as the combined density of prey is higher than N_{crit}. In my model, however, the predator is assumed to only be able to reproduce once a year. Therefore the structure of the predator reproduction and properties of N_{crit} resembles the structure used in the model by Gilg et al. (2003), which also assumed a stoat-type predator. One of the risks of modelling it this way was that the predator numbers could become too low. The risk of having a low predator population is the larger risk of extinction of the predators. Therefore another parameter was added to represent a number of stoat offspring added to the predator population each year. Stochasticity was added through using *(0.5+R)*, where R is a random variate with a uniform distribution between 0 and 1. This stochasticity was added to the predator population at the beginning of summer. This way, environmental stochasticity is added and the small number of predators is accounted for.

2.3. Simulations

All the equations listed above were coded as functions in Matlab and made ready for simulations of different scenarios. All simulations of the model were conducted in MATLAB R2015a (The MathWorks Inc., Natick, MA) and the model was run each time using the built-in ordinary differential equation (ODE) solver ode45. The values of the parameters used for the two rodent species in all three equations were chosen to reflect their demographic characteristics as described in the literature (see for instance Turchin, 2003 and Hanski et. al. 2001). For instance, lemmings have winter reproduction while the voles have not (Stenseth & Ims, 1993). The values of the parameters that were kept as constant in the simulations, i.e. they were not altered during the simulation, are displayed in table 1. The simulation was run for 150 years.

Table 1: The combination of parameter for vole, lemming and predator that were kept as constant in the simulations.

Prey	Grey-sided vole	Lemming	Predator	Stoat
K summer	100	100	v	2.8
K winter	25	50	c	600
r summer	5.4	5.0	q	100
r winter	2.5	4.7	dhigh	5.0
			dlow	0.1

The key issue of the present study was to investigate how the predator's preference for the two rodent species could influence their population dynamics, through changes in symmetry, periodicity of the peaks and amplitude as well as the interspecific synchrony of the two species. These are descriptors of the population dynamics that are widely used within studies surrounding small rodent dynamics and thus give good opportunity for comparison to other studies. Therefore, only the two half-saturation constants, D_1 and D_2, reflecting the predator preference, were varied during the simulations. These parameters were both given a range of 5 values (4, 6, 8, 10, 12) each and the simulations would run in a way that D_1 would only change every 6th simulation. The end result is therefore 25 scenarios in a 5x5 matrix.

The matrix creates an increasing preference for N_1, i.e. the lemming, horizontally. This means that if there is an increase in preference for the lemming (D_2 becomes larger), the ratio (D_1/D_2) will gradually (see eq. 4 and 5) decrease so the total functional response will become larger. This will result in a decrease in the lemming population, as the predation pressure becomes higher. This means that the vertical direction are the scenarios where there is a gradual increase in preference for the vole. What happens here then is that the ratio becomes larger, as it is D_1 that will increase, and the total functional response becomes smaller and the predation pressure for the lemming becomes smaller. It is also important to note that the diagonal represent the scenarios were the preference is equal, but also the value of the half-saturation constant increases along the diagonal. An increase in the half-saturation constant means an overall reduction of predator efficiency. This means

that down the diagonal there is a gradual decrease in predator efficiency which means that the predation overall becomes less, i.e. the total effect of the predator on both prey is smaller and less prey is eaten.

Since the model consist of two equations, one for the lemming (N_1) and one for the grey-sided vole (N_2), two sets of matrices for the statistical analyses (except the correlation) were constructed. For each analysis I wanted to compare the dynamics when the lemming is the main prey and the vole is the alternative prey and vice versa. Therefore, each species is analysed separately.

The resulting factorial design of the simulation means that this is the most appropriate way to present the results from both the simulation and the corresponding statistical analyses.

2.4. Statistical analysis of time-series

An annual (autumn) value for each species was extracted from the simulated time series for further analyses. Autumn values are the usual values used in studies, based on empirical time series. This resulted in 101 time steps for the one-prey-model and a 101 x 25 matrix for the two-prey-model due to only including the years 50-150 in the analysis. This is to avoid the "starting phase" of the model. Then in order to evaluate the nature of changes in prey population dynamics when predator preference varies, descriptors of periodicity, interspecific synchrony, cycle amplitude and symmetry were calculated for each of the simulations.

2.4.1. Periodicity

In order to evaluate changes in period length, a spectral analysis was performed, inspired by Henden et. al. (2009), only it was performed in Matlab instead of R. This is a frequently used method in order to determine the power of a signal. Since the system of interest is a cyclic one, a spectral analysis was needed to determine the periodicity, more specific the dominant periodicity of each simulated time-series. The frequency was calculated in Matlab and then converted to periods (1/frequency).

Following, the power of the signals were calculated and used to determine which part of the spectrum had the most power. These were extracted and used as the dominant period of the time-series.

2.4.2. Amplitude

In order to assess changes in the amplitude, i.e. the variability, for the two prey species, the S-index (e.g. Turchin & Hanski, 1997) was used. This index was calculated by taking the standard deviation of log-transformed densities. This resulted in one value per prey species for each simulation.

2.4.3. Peak symmetry

The peak symmetry was calculated by taking the difference in growth rates before ($r_{pre-peak}$) and after ($r_{post-peak}$) the cyclic peak densities in the simulated time series. I used the average for both $r_{pre-peak}$ and $r_{post-peak}$ from each time series. Finally, the difference was found by subtracting $r_{pre-peak}$ from $r_{post-peak}$. A small value would indicate a higher degree of symmetry than a larger one. A zero difference indicates complete symmetry.

2.4.4. Inter-specific synchrony

Cross-correlation analyses were performed to describe how inter-specific synchrony varied with of predatory preference. Correlations were calculated with log-transformed time series between corresponding scenarios for the two species, resulting in 25 correlations. The correlations were calculated by using the ccr function in R. Maximum time lags were set to 3 due to the cyclicity of the system as the periodicity is around 4-5 years and therefore isolates only one peak for analysis. Only the highest correlations for each simulation are presented in the result chapter. The correlation plots are presented in the appendix.

All statistical analyses were performed using RStudio Team (2015) wrapper with the exception of the spectral analysis, which was performed in MATLAB R2015a (The MathWorks Inc., Natick, MA).

3. Results

3.1. One-prey-one-predator model

Running the simulation with the parameter combination listed in table 1 and then extracting the autumn values resulted in close to 5-year population cycles for both rodent species when they were the sole prey species for the predator (Table 2, Figure 1). The amplitude of the cycle was larger for the lemming than the vole, while the peaks of the cycle was more symmetric for the lemming that for the vole (Table 2). The symmetry values were negative for both species meaning that the crash phase was steeper than the increase phase. Synchrony is not of consideration here since the two prey species was modelled independent of each other.

Table 2: Results from calculation of characteristics of population dynamics for the Norwegian lemming and the grey-sided vole.

Characteristic	Lemming	Vole
Period	5,3	5,05
Amplitude (S)	1,1	0,67
Symmetry	-0,37	-0,63
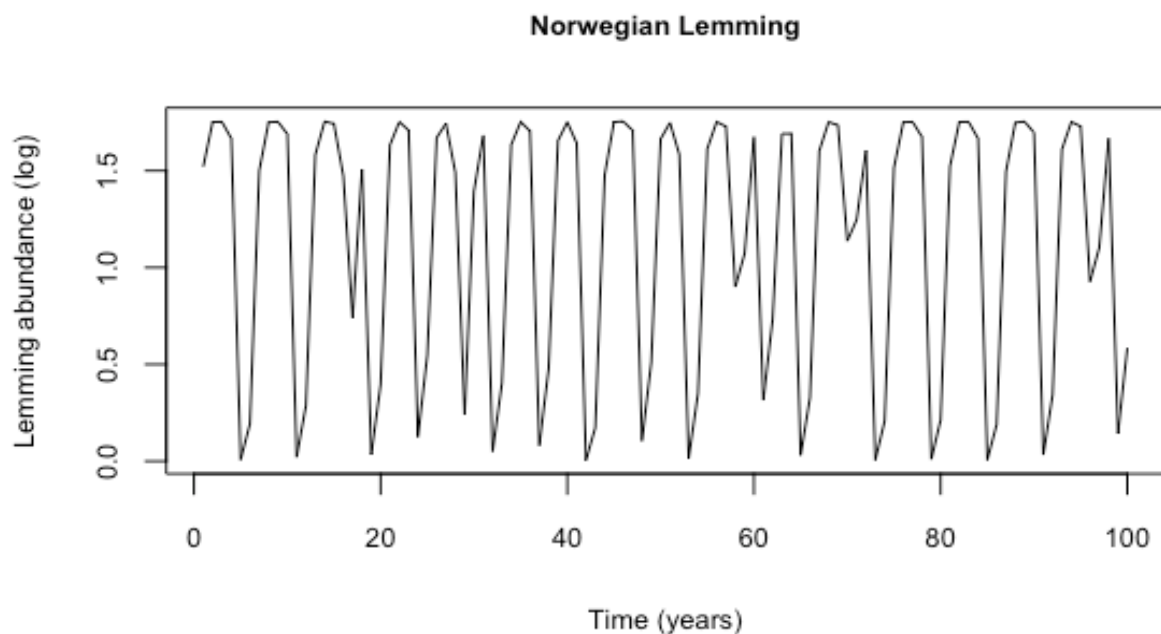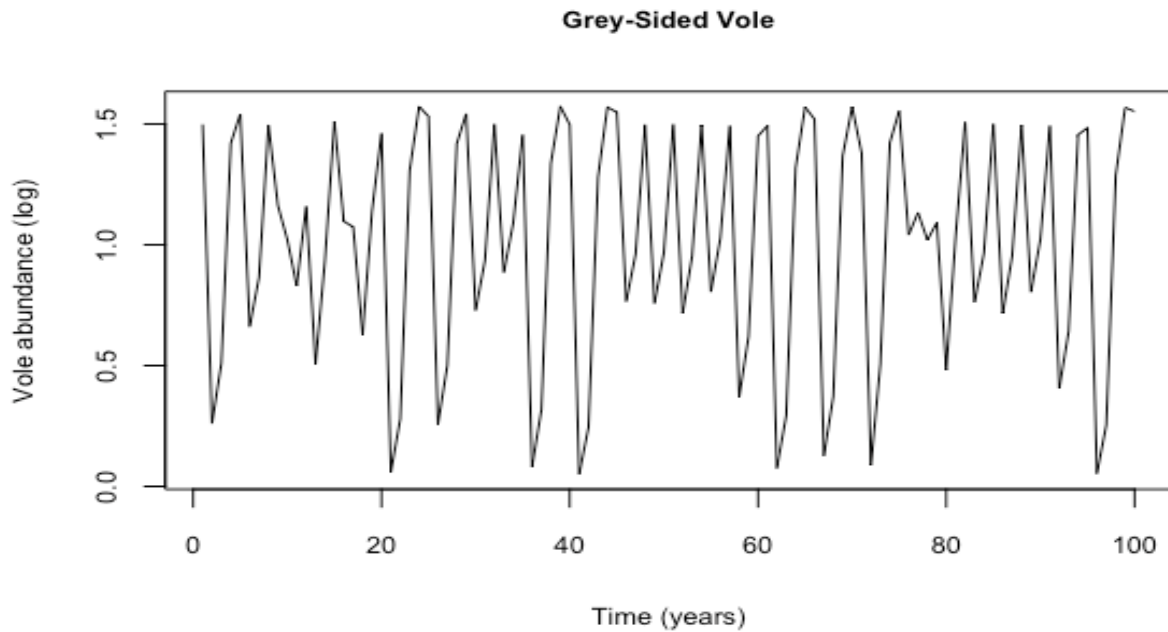
Grey-Sided Vole

Figure 1: Population trajectories of the Norwegian lemming (upper) and the grey-sided vole (lower) depicted on a log-scale.

3.2. Two-prey-one-predator model

The simulation with two prey species resulted in the dynamics displayed in figure 3. Here, only 5 of the scenarios are chosen to better present changes in dynamics in a clear way. The magnitude of these changes is presented in the statistical analysis chapter.

Fig 2: Simulated population dynamics of lemming (blue) and vole (red) resulting from 5 combinations of the in total 25 combinations of D_1/D_2 values (for an interpretation of the different scenarios see figure 3 below)

3.2.1 Cycle period

When the preference for one of the prey species is very high compared to the preference for the other, the population dynamics of the most preferred species collapses (i.e. crashes) yielding a nonsensical value (101 years) for the periodicity (Figure 3). The more sensible values for both species simultaneously are achieved when the predator has slower functional responses (D-values 10-12). Then however, periodicity is still often larger than the 5-year cycle that was obtained for the one-prey models (see Table 2). The most realistic period (3-5 years) for both lemmings and voles found in case of so high preference that the response is so rapid that it results in collapsed population dynamics in the other species.
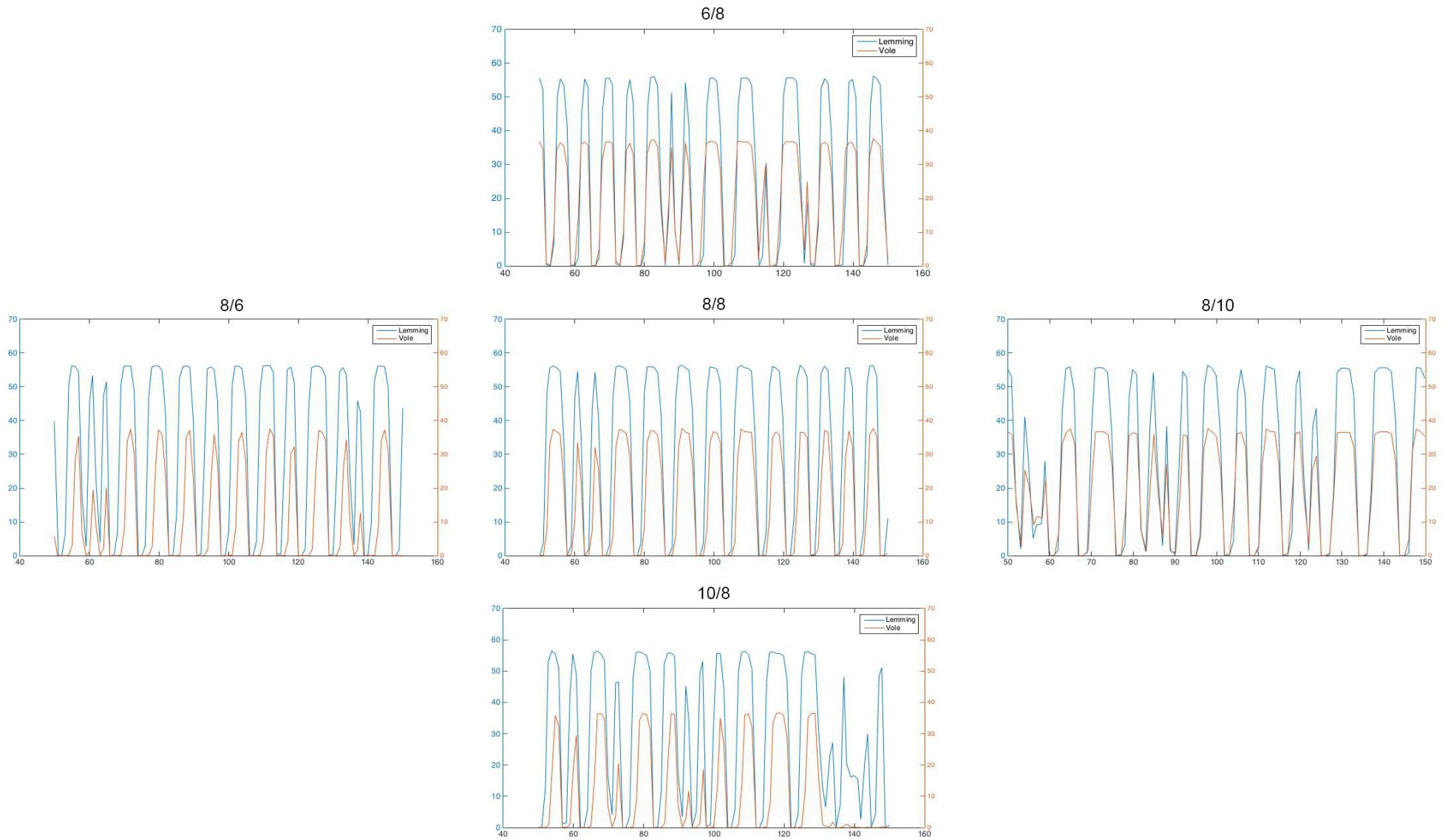
A) Lemming cycle period

LOW D	INCREASING PREFERENCE FOR LEMMING →					
INCREASING PREFERENCE FOR VOLE ↓	**9.2** **(4/4)**	7.8 (4/6)	~~101.0~~ (4/8)	~~101.0~~ (4/10)	~~101.0~~ (4/12)	
	8.4 (6/4)	**7.7** **(6/6)**	<u>6.7</u> <u>(6/8)</u>	~~101.0~~ 6/10	~~101.0~~ (6/12)	
	7.2 (8/4)	<u>7.2</u> <u>(8/6)</u>	**<u>7.2</u>** **<u>(8/8)</u>**	<u>8.4</u> <u>(8/10)</u>	8.4 (8/12)	
	5.9 (10/4)	5.9 (10/6)	<u>7.2</u> <u>(10/8)</u>	**7.2** **(10/10)**	6.7 (10/12)	
	5.3 (12/4)	4.8 (12/6)	4.8 (12/8)	6.3 (12/10)	**8.4** **(12/12)**	
						HIGH D

B) Vole cycle period

	INCREASING PREFERENCE FOR LEMMING →				
LOW D					
INCREASING PREFERENCE FOR VOLE ↓	**9.2** **(4/4)**	11.2 (4/6)	4.6 (4/8)	3.6 (4/10)	2.1 (4/12)
	8.4 (6/4)	**7.7** **(6/6)**	6.7 (6/8)	5.9 6/10	3.1 (6/12)
	~~101.0~~ (8/4)	7.2 (8/6)	**7.2** **(8/8)**	8.4 (8/10)	8.4 (8/12)
	~~101.0~~ (10/4)	~~101.0~~ (10/6)	7.2 (10/8)	**7.2** **(10/10)**	7.2 (10/12)
	~~101.0~~ (12/4)	~~101.0~~ (12/6)	~~101.0~~ (12/8)	6.3 (12/10)	**8.4** **(12/12)**
					HIGH D

Figure 3: Matrix showing the changes in lemming periodicity when prey preference and total predation rate changes based on D1/D2 ratios (the ratios are given in parameters for each of the 25 combinations). Red area shows the scenarios where there is a main preference for lemming, while the blue area shows when there is preference for the grey-sided vole. Grey areas along the diagonal of the matrix are the scenarios were preference is equal. Horizontal direction has an increasing value of D_2 and a constant value of D_1. Vertical direction has an increasing value of D_1 and a constant value of D_2. The constant values increase every 6 scenario. It increases vertical for the grey-sided vole and horizontal for the lemming.

3.2.2 Amplitude

The amplitude of the population dynamics for the 25 scenarios is on average higher for the lemming than for the vole. However, within each of the two species there is very little variation between the different preference and predation rate scenarios (see figure 4)

A) Lemming amplitude

LOW D	INCREASING PREFERENCE FOR LEMMING ➡					
INCREASING PREFERENCE FOR VOLE ⬇	**0.75** **(4/4)**	0.77 (4/6)	0.77 (4/8)	0.75 (4/10)	0.78 (4/12)	
	0.79 (6/4)	**0.75** **(6/6)**	<u>0.76</u> <u>(6/8)</u>	0.75 6/10	0.78 (6/12)	
	0.75 (8/4)	<u>0.77</u> <u>(8/6)</u>	**<u>0.78</u>** **<u>(8/8)</u>**	<u>0.77</u> <u>(8/10)</u>	0.79 (8/12)	
	0.78 (10/4)	0.77 (10/6)	<u>0.79</u> <u>(10/8)</u>	**0.78** **(10/10)**	0.78 (10/12)	
	0.76 (12/4)	0.76 (12/6)	0.77 (12/8)	0.77 (12/10)	**0.75** **(12/12)**	
						HIGH D

B) Vole amplitude

LOW D	INCREASING PREFERENCE FOR LEMMING ➡					
INCREASING PREFERENCE FOR VOLE ⬇	**0.68** **(4/4)**	0.65 (4/6)	0.68 (4/8)	0.65 (4/10)	0.68 (4/12)	
	0.69 (6/4)	**0.69** **(6/6)**	<u>0.67</u> <u>(6/8)</u>	0.65 6/10	0.67 (6/12)	
	0.67 (8/4)	<u>0.69</u> <u>(8/6)</u>	**<u>0.68</u>** **<u>(8/8)</u>**	<u>0.68</u> <u>(8/10)</u>	0.68 (8/12)	
	0.69 (10/4)	0.67 (10/6)	<u>0.68</u> <u>(10/8)</u>	**0.71** **(10/10)**	0.68 (10/12)	
	0.68 (12/4)	0.68 (12/6)	0.67 (12/8)	0.71 (12/10)	**0.69** **(12/12)**	
						HIGH D

Figure 4: Matrix showing the changes in amplitude for lemming (upper) and vole (lower) when preference and predation rate changes. See Figure 3 for explanation of the different scenarios.

3.2.3 Peak symmetry

The peak symmetry was calculated to be negative for both species (see fig 5), i.e. the peaks are negatively skewed meaning the decline is more rapid than the increase. There does not seem to be any clear pattern concerning predatory preference and its effect on symmetry. For the lemming there seems to be a greater tendency to asymmetry when the preference for lemming is very high and the response works rapidly (at low saturation constant). The highest degree of symmetry for the lemming occurs when the predator responds twice as fast to the vole than for the lemming (8/4), meaning that the preference for the vole is twice as high as for the lemming. For the vole, the highest degree of asymmetry is found when the difference is preference is large, more specifically when the preference for the lemming is low and the preference for the vole is large. However, there is also a scenario that is very much symmetric when there is hardly any preference for the lemming and a very rapid response towards the vole (12/4). In addition, there is another scenario that is very symmetrical but here it is the lemming that is the preferred prey (10/12) and the total response is relatively slow for both species.

A) Lemming peak symmetry

LOW D	INCREASING PREFERENCE FOR LEMMING →				
INCREASING PREFERENCE FOR VOLE ↓	**-0.32** **(4/4)**	-0.31 (4/6)	-1.37 (4/8)	-0.99 (4/10)	-0.99 (4/12)
	-0.47 (6/4)	**-0.69** **(6/6)**	-0.52 (6/8)	-0.74 6/10	-1.17 (6/12)
	-0.02 (8/4)	-0.47 (8/6)	**-0.32** **(8/8)**	-0.56 (8/10)	-0.12 (8/12)
	-0.26 (10/4)	-0.43 (10/6)	-0.21 (10/8)	**-0.37** **(10/10)**	-0.42 (10/12)
	-0.63 (12/4)	-0.26 (12/6)	-0.35 (12/8)	-0.81 (12/10)	**-0.18** **(12/12)**
					HIGH D

B) Vole peak symmetry

LOW D	INCREASING PREFERENCE FOR LEMMING →					
INCREASING PREFERENCE FOR VOLE ↓	**-0.13** (4/4)	-0.48 (4/6)	-0.45 (4/8)	-0.31 (4/10)	-0.23 (4/12)	
	-0.28 (6/4)	**-0.25** (6/6)	<u>-0.33</u> (6/8)	-0.53 6/10	-0.71 (6/12)	
	-0.29 (8/4)	<u>-0.69</u> (8/6)	**<u>-0.34</u>** (8/8)	<u>-0.25</u> (8/10)	-0.18 (8/12)	
	-0.83 (10/4)	-0.48 (10/6)	<u>-0.24</u> (10/8)	**-0.17** (10/10)	-0.04 (10/12)	
	-0.02 (12/4)	-0.98 (12/6)	-1.11 (12/8)	-0.34 (12/10)	**-0.29** (12/12)	
						HIGH D

Figure 5: Matrix showing the changes in symmetry for lemming (upper) and vole (lower) when preference and predation rate changes. See Figure 3 for explanation of the different scenarios.

3.2.4 Inter-specific synchrony

From the cross-correlation analyses it was found that the highest correlations for each scenario are at a zero time lag (see appendix X). The highest degree of synchrony occurs for combinations of D-values one-step off diagonal in the bottom corner of the matrices, i.e. the scenarios with a lower total predation pressure (high D) and also a slight preference for either of the two species.

LOW D	INCREASING PREFERENCE FOR LEMMING →					
INCREASING PREFERENCE FOR VOLE ↓	**0.17** **(4/4)**	0.19 (4/6)	0.20 (4/8)	0.12 (4/10)	0.19 (4/12)	
	0.26 (6/4)	**0.19** **(6/6)**	0.21 (6/8)	0.13 6/10	0.17 (6/12)	
	0.28 (8/4)	0.25 (8/6)	**0.24** **(8/8)**	0.27 (8/10)	0.16 (8/12)	
	0.21 (10/4)	0.29 (10/6)	0.13 (10/8)	**0.27** **(10/10)**	0.34 (10/12)	
	0.17 (12/4)	0.08 (12/6)	0.28 (12/8)	0.34 (12/10)	**0.21** **(12/12)**	
						HIGH D

Figure 6: Matrix showing the changes in synchrony for lemming (upper) and vole (lower) when preference and predation rate changes. See Figure 3 for explanation of the different scenarios.

5. Discussion

The fundamental understanding of a predator and its prey is rooted in the knowledge obtained around the way predation varies with prey and predator densities. The understanding of numerical and functional responses is pivotal in order to determine the effect predation can have on a prey population and how the prey population will respond dynamically to the changes in predation rate (Van Leeuwen et. al. 2007). In result, this mutual kind of regulation of populations becomes a vital component in ecosystem structure and therefore vital to understand in relation to how the ecosystem functions.

Shared predation and its distribution of preference showed in this thesis to have an impact on periodicity, some impact on synchronicity and symmetry and very little impact on amplitude.

The simple one-prey-one-predator model created a periodicity for both rodents at ~5 years. However, the transition to a more complex model created an increase in periodicity for most of the scenarios. The scenarios that showed periods within the range observed for Fennoscandia (3-5 years) were the scenarios where the alternative species went extinct due to high predation pressure. However, the vole seems to be more sensitive to predation pressure than the lemming due to the fact that the vole population went extinct one more time than the lemming population. The reason for this can be differences in life-history traits for the two rodents, more specifically their reproductive strategy. As mentioned, the grey-sided vole only reproduces during the summer while the lemming can reproduce all year (Ims et al. 2011). Lemmings rely on snow cover to provide shelter and access to fodder during winter and the burrowing behaviour also provide shelter from predators and the cold. This again results in the lemmings having a prolonged breeding season (Crawford, 2014). This also results in the lemming having a stronger numerical response and can probably therefore withstand higher predation pressure.

It did not seem that any combination of preference had much to say for the amplitude, due to the fact that there was little variance between the scenarios for both species. The lemming had slightly higher amplitude on average than the vole.

Norwegian lemmings are known for having large amplitudes in their cycles and the lemmings have been known to exhibit larger variations in amplitude than voles due to them being more sensitive to snow conditions (Kausrud et. al. 2008). Therefore it seems to be reasonable that the change in amplitude is larger for the lemming than for the grey-sided vole. However, if one considers the average amplitude for both lemming and vole and compare this to findings based on results from other studies (s≈0.3, Turchin & Hanski, 1997) the amplitudes that resulted from my models were larger for both rodents. It is very important to notice that there are many factors within the arctic system that can affect both lemming and the grey-sided vole amplitudes. As the type of predator used in the model is based on a single resident specialist (mustelid), this theoretical view of the system is very simplistic. In contrast, most natural ecosystems have several predator groups present. In Fennoscandia there have been many studies concerning how specialist and generalists can affect prey-populations differently. One of these differences is how they affect cycle amplitude. It is said that it exists a gradient of amplitude from high in the north to low in the south of Fennoscandia (Turchin and Hanski, 1997). The systems in the arctic have a lesser presence of the generalists who promotes dampening of amplitude, while in the south there is a larger presence of generalists. The generalists have a stabilising effect on the cycles, thus dampening the amplitude (Erlinge et al. 1984).

Peak symmetry has also been used as an indicator on how rodent dynamics can be affected by different factors (Turchin & Hanski, 1997). Furthermore, according to predictions made by resource-consumer interactions, voles and lemmings will show distinctive differences in peak characteristics. According to a study done by Turchin et al. (2000), voles are considered resources (i.e. prey) and will therefore show blunted rounded peaks, while the lemming is considered a consumer and will therefore show sharp angular peaks. Therefore one would expect a rapid crash phase alongside the sharp peaks as one would expect density-dependence to have a negative effect on the lemming population (Framstad et. al. 1997). This is also indicated in the results found in this thesis, which is that the lemming populations simulated are negatively skewed. However, the vole populations are also negatively skewed which means that the crash phase for this species as well is larger than the pre-peak growth rate.

How predators can synchronise fluctuating prey populations has been described through two main hypotheses: the alternative prey hypothesis (APH), where prey is killed selectively (Angelstam et al. 1984; Korpimäki et al., 2005) or the shared predation hypothesis (SPH), where prey are killed unselectively (Norrdahl & Korpimäki, 2000; Korpimäki et al. 2005). The difference between these two is the presence of switching behaviour. APH divides prey into main and alternative prey and that the predator utilise the main prey population until densities are significantly decreased, then they switch to an alternative prey group. In contrast, the SPH states that the prey groups suffer proportional equal losses to the predator population during every phase of the population cycle. So even though the proportion of alternative prey in the diet is lower within years with high densities of main prey, alternative prey will be a part of the predator's diet throughout the cycle (Korpimäki et al. 1990). Furthermore, the presence of a rapid numerical response to main prey and its densities, the proportion of alternative prey in diet might be higher in years with high abundances of main prey rather than low densities (Korpimäki et al. 2005). In contrast, the alternative prey hypothesis concerns how predators' effect on the alternative prey depends less on the ratio of predators to alternative prey, but more on the density of main prey. The result of this is that the mechanisms behind APH will have a shorter time span regulating the impact on alternative prey than under the SPH. Subsequently, what is common for both hypotheses is that in order for synchrony to occur the predator population needs to be a strong enough force behind the decrease of the alternative prey population, at least periodically (Barraquand et. al. 2014; Korpimäki et al. 2005).

Interspecific synchrony has also been observed in rodent communities with cyclic population dynamics in Fennoscandia. For instance, a study in western Finland showed that several small rodent populations showed synchronised fluctuations with a 3-year period (Korpimäki et al. 2005). These studies concerns different species than used here, but there are many similarities between them. A study done by Korpimäki et al (2005) found that effects of predation resulted in a synchronisation of the low phases of the rodent community. As the community modelled here only has shared predation as a link between the two rodents one can easily assume that the same mechanisms are at work here.

To what degree stoat show any selectivity (i.e. preference) for lemming or grey-sided voles is unknown, but there are some theories ranging from level of boldness to anti-predator defence mechanisms such as aposematism and crypsis. For instance, the Norwegian lemming was found to utilise more warning calls against predators. In addition, they are very brightly coloured compared to other rodents that may be more cryptic in colouration (Andersson, 2014). However, this is a subject still under a lot of discussion, so to draw any conclusions now will be premature. However, if one considers the findings in this thesis, especially concerning the synchrony, one could wonder if there is a preference towards the lemming by the stoat as the combination of making noise and being brightly coloured could attract predators more easily. However, again, this theory is still very uncertain. Furthermore, if indeed the numerical response of the lemming is larger than that of the vole, the predator might show a preference towards the lemming due to its capacity to withstand higher predation pressure.

The Arctic tundra ecosystems are one of the more simple ecosystems found on Earth, yet it is still complex. Any attempt of modelling a complete system with every species guild, community links both indirect and direct and many other contributing factors such as climate and human impacts will result in an extremely large model, which will be hard to make any sense of. Many of the findings in this thesis deviate somewhat from what is seen in nature. However, the scenarios are modelled with only shared predation from a specialist as a factor affecting the prey populations, besides self-limitation that is incorporated in the logistic part of the prey equations. Many studies have been made concerning the relationship between rodents and their food plants and vegetation (Turchin & Batzli, 2001) and this could also have an effect on the cyclic topography and indicators. Furthermore, predation pressure and preference is also more complex in nature than it is displayed here. This is due to the fact that there is a presence of other predator types such as generalist and nomadic specialists in addition to the resident specialists. Avian nomadic specialist have been shown to have a dampening effect on amplitude on a regional scale due to a large range and a rapid numerical and aggregative response (Ims & Steen, 1990). Furthermore, effects of climate create a foundation for theorems such as the Moran effect that has been known and theorised to create synchrony of populations on a larger geographical scale (Ranta et al. 1995).

The development of the framework of Hanski et al. (1991, 1993) and Hanski & Henttonen (1996) used in this thesis has proven to be extremely useful in identifying mechanisms that can alter a relationship between prey species and their predator. This development has been enlightening due to the fact that I have been able to follow the development from a simple one-prey-one-predator framework to a framework that consists of two prey species that can be connected by a direct link (competition), an indirect link (shared predation) or both. This has allowed me to isolate predation as a single mechanism and determine its effect on prey populations. The alteration made to equation 4 and 5 has made it possible to also investigate how preference alters dynamics along a gradient. When the basic Lotka-Volterra framework failed to describe the unique characteristics of small rodent dynamics in Fennoscandia, the gaps were filled by Hansson and Henttonen's observations during the 1980's (Henttonen et al. 2017). These observations included the importance of seasonality particularly considering snow cover, the patterns of amplitude and periodicity on a large geographical scale and lastly community composition and dynamics for both prey and predator. These observations inspired Ilkka Hanski to create the succession of models that have resulted in the framework that inspired this thesis (Henttonen et al. 2017). Therefore one can say that the Finns have been pioneering and driving the development of modelling small rodent dynamics, resulting in a legacy that should be maintained in the future.

6. Conclusion

To conclude, this study found that shared predation could have some effect on the mediation of a relationship between two rodents that there is large insecurity around the magnitude of their relationship. This is especially clear when one looks at the transition from a one-prey-one-predator model to the larger model with two coexisting prey species. The effect of the preference seem to affect trajectory characteristics in some ways, most clearly in synchrony as it seems that the synchrony is at its strongest when there is a slight preference for the lemming. Also, the amplitude was dampened for the lemming in the model transition, however there was little variation between scenarios for both species. The amplitude found here was greater than what was found in earlier studies (Turchin & Hanski, 1997), but this could be due to the lack of generalists and other dampening effects. Periodicity increased on average for both species but decreased in the scenarios were the predator response was very rapid for the alternative prey. When this was applied to the main prey, extinction occurred. There was no consistent pattern concerning changes in symmetry but a tendency towards higher asymmetry when there was a high preference for main prey heading for extinction.

The further development of this study could comprise of a distinction of habitat, reflected through a difference in abundances, as lemmings and voles ideal habitats are different. This could be reflected in a difference in carrying capacities as in this study they are equal and represent equal abundance. Furthermore, one could include a generalist predator represented by a type III response. This could result in creating dynamics that are approaching the dynamics observed in nature and provide a stepping-stone onto a deeper understanding of the life on the harsh Arctic tundra.

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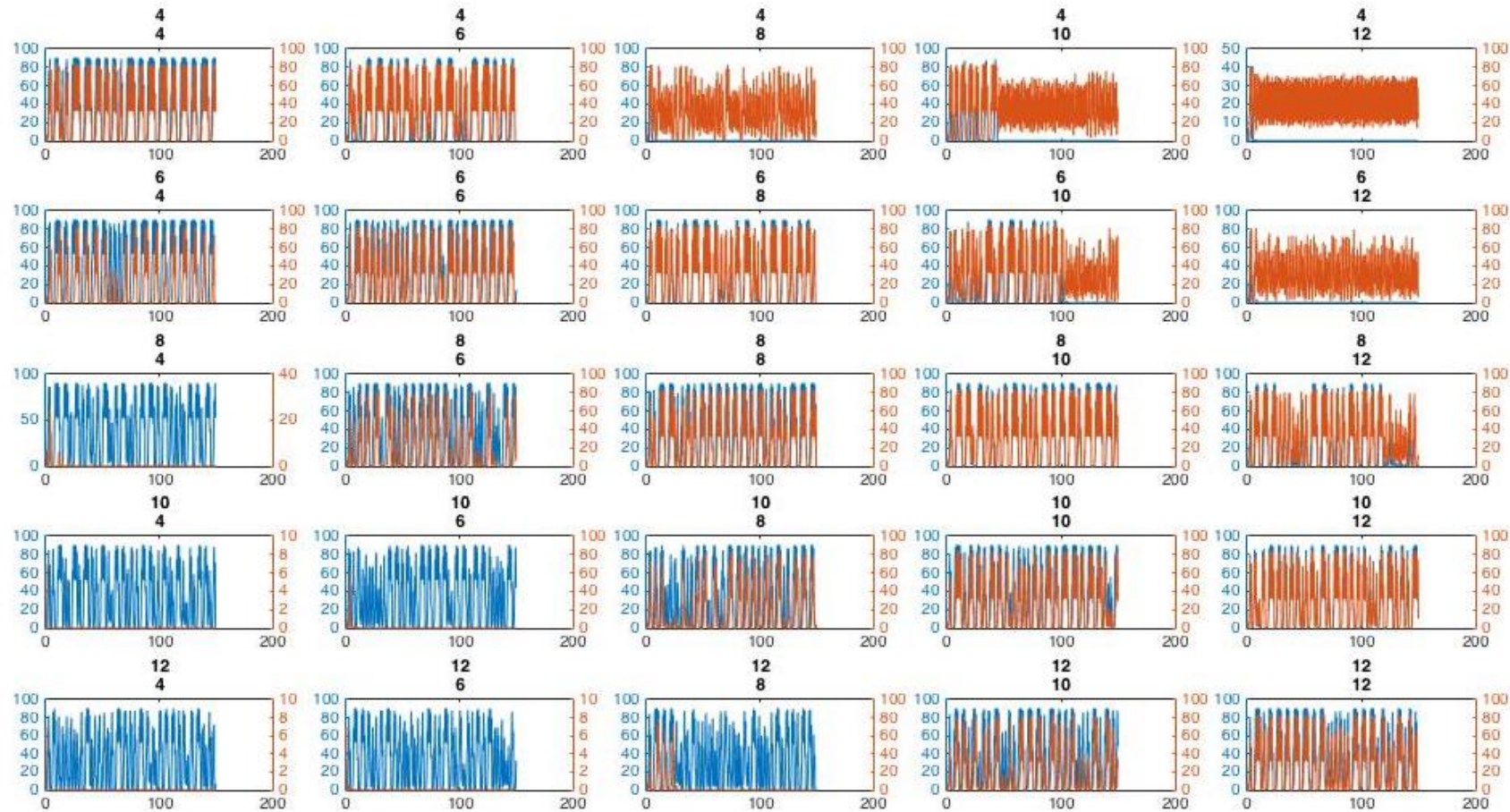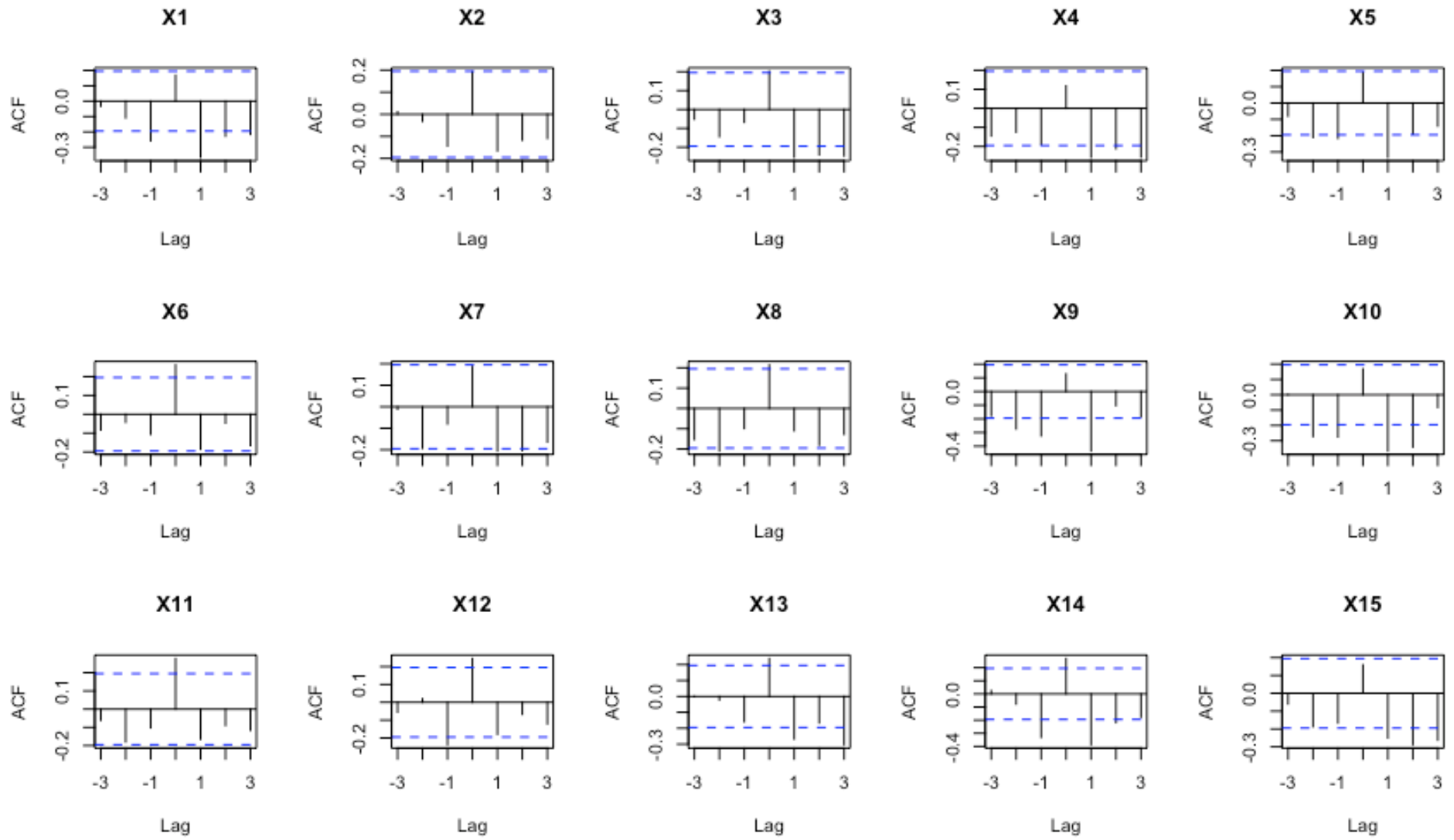
Appendix

X1.

Fig X1: Initial output from two-prey-one-predator model Figure includes all years from 0-200 and all seasons. Lemmings are depicted in blue, vole in red.
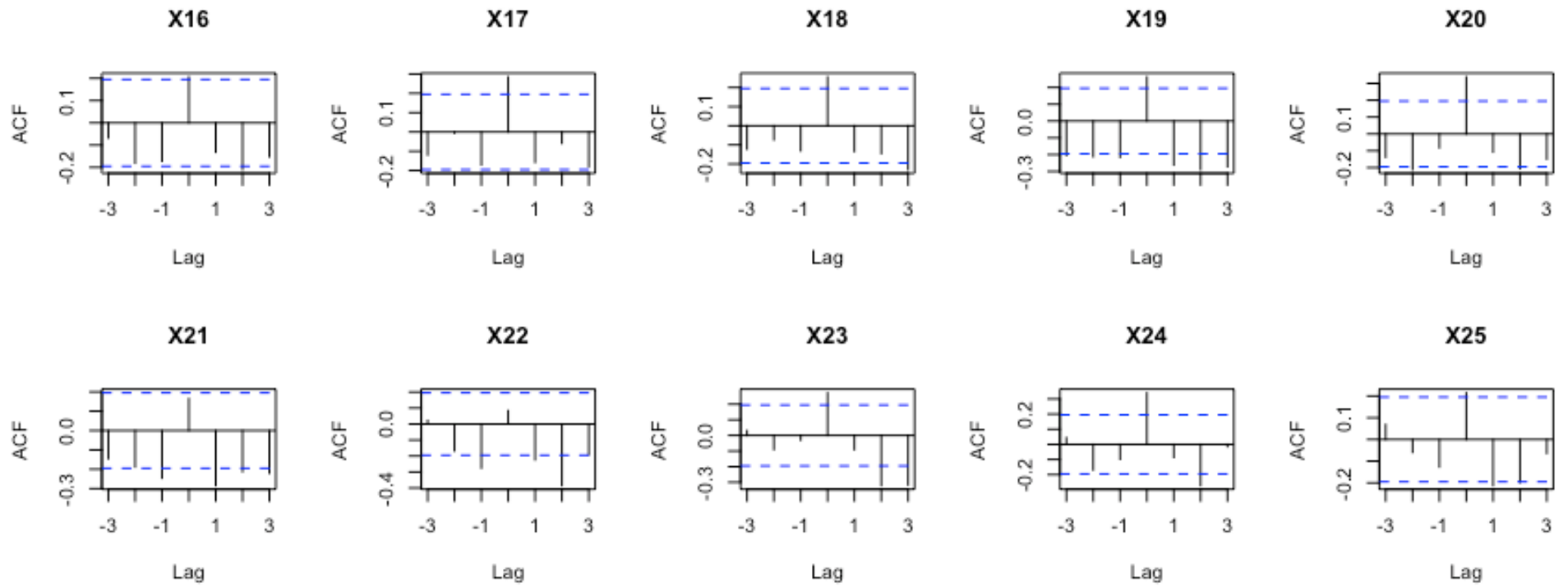
X2.

Fig X2: Correlation plots for the cross-correlation analysis for each of the 25 combination of D_1 and D_2.
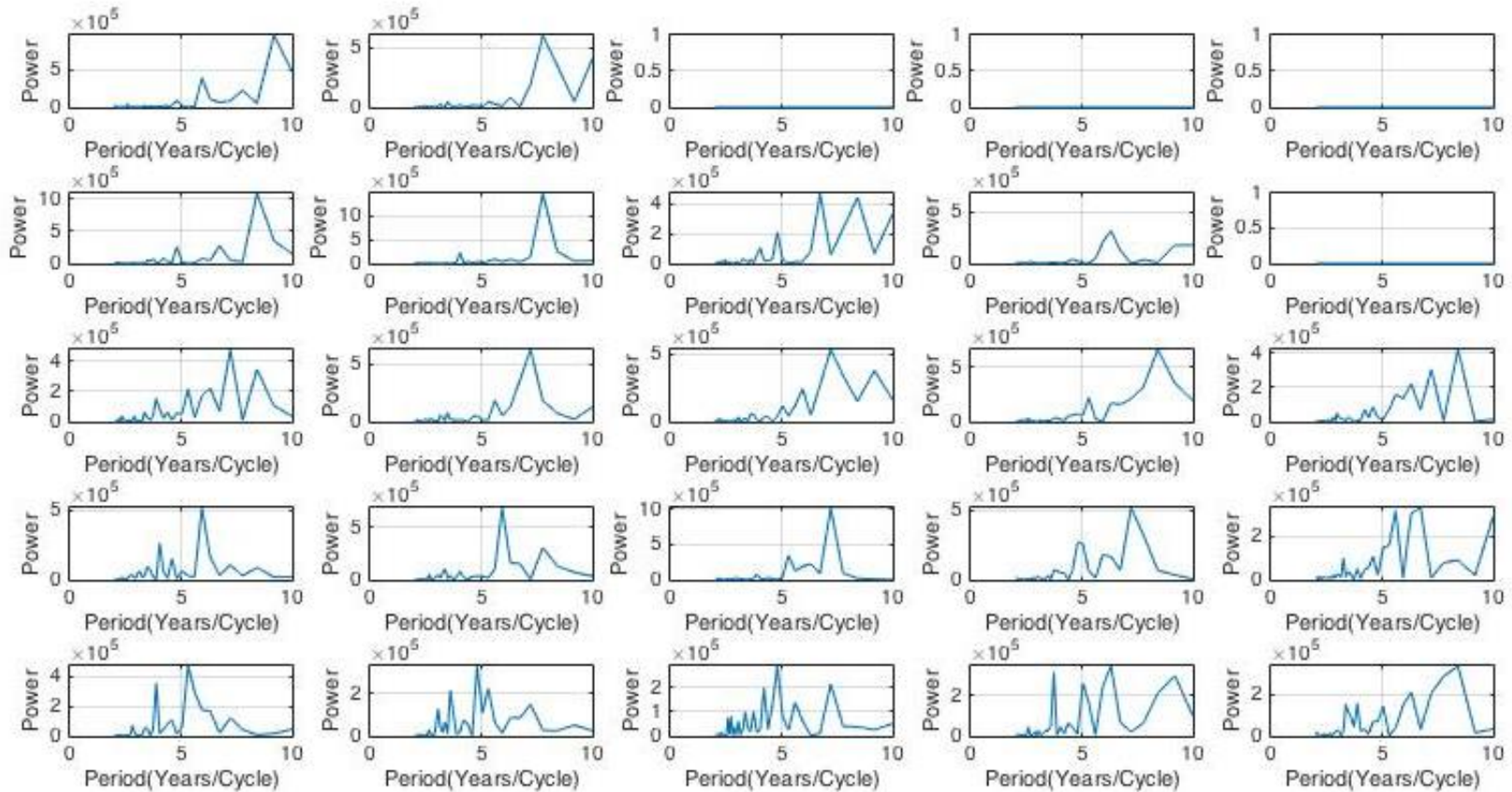
X3.

Fig X3: Calculation of period with highest power for each of the 25 combinations of D_1 and D_2 for the lemming.
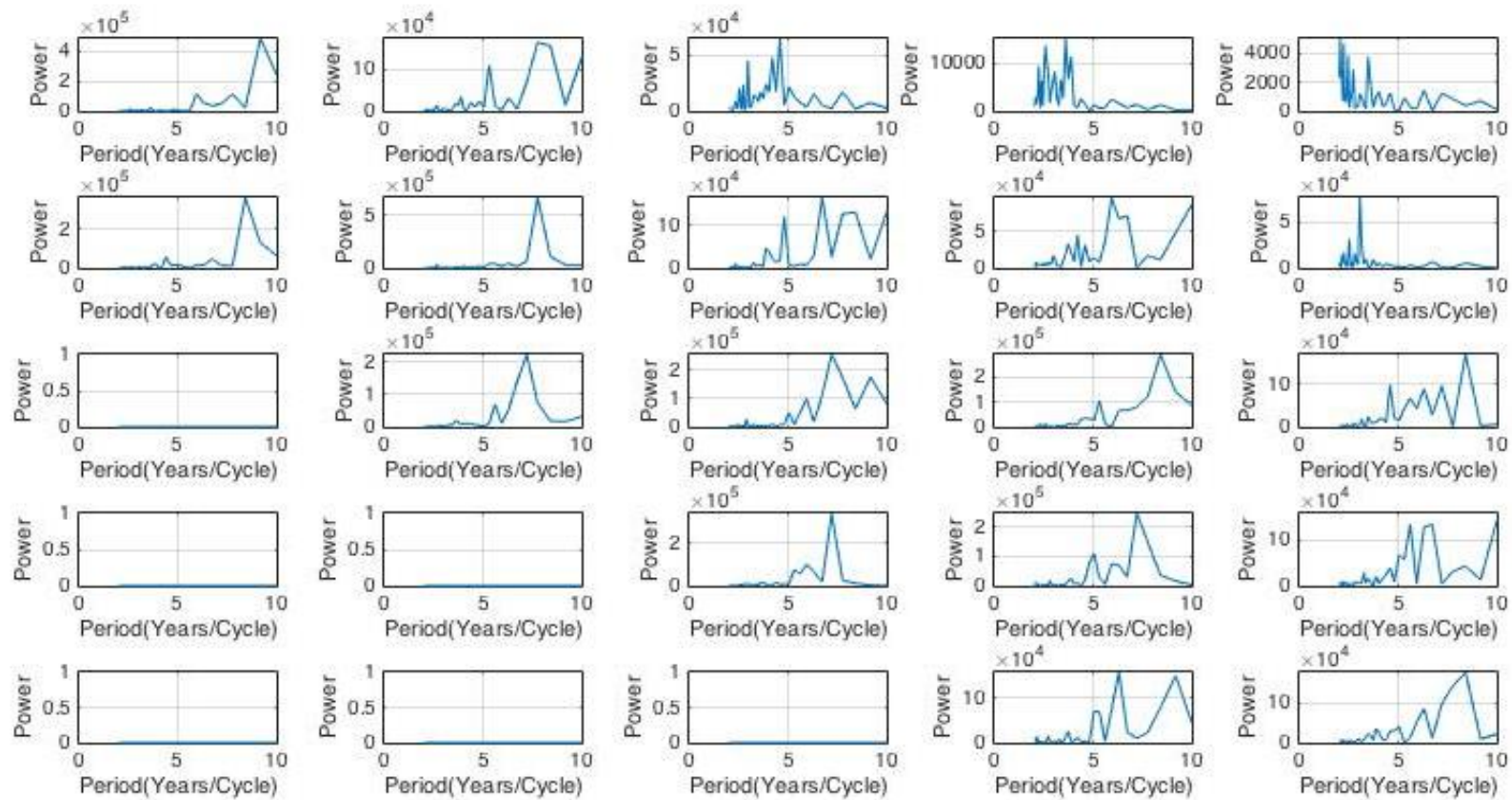
Fig X3: Calculation of period with highest power for each of the 25 combinations of D_1 and D_2 for the vole.

X4: One-prey-one-predator model (Matlab and R code)

```
%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
%%%%%%%%%%%%%%%%%%%%%%%%%
%%% Two-prey and one predator(based on Hanski and Henttonen, 1996 %%%%%
%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
%%%%%%%%%%%%%%%%%%%%%%%%%
clear all

global r1 r1w r2 r2w K1 K1w K2 K2w c a D1 D2 b v q dhigh dlow Ncrit beta Sr


%%Parameter values%%
% Lemming:
K1=350; % Carrying Capacity of prey in summer
K1w=100; % Carrying Capacity of prey in winter
r1=5.5; % prey intrinsic growth rate in summer
r1w=0.8; % prey intrinsic growth rate in winter
% Vole:
K2=450; % Carrying Capacity of prey in summer
K2w=5; % Carrying Capacity of prey in winter
r2=6.6; % prey intrinsic growth rate in summer
r2w=0.01; % prey intrinsic growth rate in winter
% Predator:
v=7.0;     %Predator intrinsic growth rate
c=1500; % maximum per capita predation rate
D1=8; % Predation half saturation constant
D2=8; % Predation half saturation constant
q=90; % equilibrioum prey/predator ratio
Ncrit=5; % critical prey density for predatior reproduction
dhigh=4.0; % predator mortality rate when prey is scarce
dlow=0.1; % predator mortality rate when prey is abundant
Sr = 4;
a=0.2;      % shape parameter or smooth season function omega
b=1;        % shape parameter for predator reproduction function delta
beta = D1/D2;  % different vulnerability to predation

%Using ode45
options= odeset('Events',@eventsFn,'Reltol',1e-5,'NonNegative',[1 2]);  % setting the options-structure
for sertain events happening: Stochasticity in predator

y0=[10,10,1.1,0];
y1=y0(1);                    % for prey1
y2=y0(2);                    % for prey 2
y3=y0(3);                    % for predator
y4=y0(4);                    % for time
yout = y0.'; tout=0; teout=[]; yeout=[]; ieout=[];   % output of events, teout=time when events occur,
yeout=values of species abundance at events, ieout=
tstart=0;                    % start-time
tstop=100;                    % end of timespan


R=unifrnd(0,1,1,round(tstop-tstart)+10); % The random values of unifrnd(0,1) added at beginning of
summer for predator (10 values to draw upon)
while tout(length(tout))<tstop
   [t,y,TE,YE,IE] = ode45(@hanski19962 ,[tstart tstop], y0,options);  % ode solver for function =
hanski1995 with stochasticity
   laenge=length(t);                % length of time (t)
   Rin=R(t(laenge)+0.5-mod(t(laenge)+0.5,1)+1); %To get stochasticity at end of winter
```

```matlab
    tout=[tout;t(2:laenge)];
    teout=[teout;TE]; yeout=[yeout;YE]; ieout=[ieout;IE];
    y1=[y1;y(2:laenge,1)];
    y2=[y2;y(2:laenge,2)];
    y3=[y3;y(2:laenge,3)];
    y4=[y4;y(2:laenge,4)];
%    y0=[y(laenge,1);y(laenge,2);y(laenge,3)*(0.5+Rin);y(laenge,4)];    % values of prey, pred and
time at the end (tstop)
    y0=[y(laenge,1);y(laenge,2);y(laenge,3)*Sr;y(laenge,4)];    % values of prey, pred and time at the
end (tstop)
    test=[y(laenge,3);0.5+Rin;y0(3)];                    % test for showing value befor stoch value, the stoch
value and value after adding stoch value
    tstart=t(laenge);                        % length of time-steps (tstop)
end;




function dy = hanski19962(t,y)

global r1 r1w r2 r2w K1 K1w K2 K2w c D1 D2 a b v q dhigh dlow Ncrit beta Sr

dy = zeros(4,1);
%Ncrit=(dlow+dhigh)/2;
beta= D1/D2;

psi=sin(2*pi*y(4));                        % sin function of time y(4)
omega=(sign(psi)/2)*abs(psi)^a+0.5;            % smooth-season function omega
delta=0.5+atan(b*((y(1)+beta*y(2))-Ncrit))/pi;    % Predator reproduction function delta
% delta=0.5+atan(b*(y(1)-Ncrit))/pi;            % Predator reproduction function delta

R=unifrnd(0,1);

% N1=r1*y(1)*(1-y(1)/K1) - c*y(3)*y(1)/(y(1)+beta*y(2)+D1);        % N1 Prey 1 equation_summer
% N2=r1w*y(1)*(1-y(1)/K1w) - c*y(3)*y(1)/(y(1)+beta*y(2)+D1);    % N2 Prey 1 equation_winter
N1=r1*y(1)*(1-y(1)./K1)-c*y(3)*y(1)./(y(1)+fix(D1./D2)*y(2)+D1);        % N1 Prey 1 equation_summer,
based only on D's
N2=r1w*y(1)*(1-y(1)./K1w)-c*y(3)*y(1)./(y(1)+(D1./D2)*y(2)+D1);    % N2 Prey 1 equation_winter,
based only on D's


% N12=r2*y(2)*(1-y(2)/K2) - c*y(3)*beta*y(2)/(y(1)+beta*y(2)+D1);        % N1 Prey 2 equation_summer
% N22=r2w*y(2)*(1-y(2)/K2w) - c*y(3)*beta*y(2)/(y(1)+beta*y(2)+D1);    % N2 Prey 2 equation_winter
N12=r2*y(2)*(1-y(2)/K2)-c*y(3)*y(2)/(y(2)+(D2/D1)*y(1)+D2);        % N12 Prey 2 equation_summer,
based only on D's
N22=r2w*y(2)*(1-y(2)/K2w)-c*y(3)*y(2)/(y(2)+(D2/D1)*y(1)+D2);    % N22 Prey 2 equation_winter,
based only on D's

% P1 Predator equation_summer if N > Ncrit
P1=v*y(3)*(1- (q*y(3))/ (y(1) + beta*y(2)));
% P1=v*y(3)*(1- (q*y(3))/ (y(1) + (D1/D2)*y(2)));

% P2 Predator equation_summer if N <= Ncrit & _winter if N < Ncrit, stochasticity added with event-
function
P2=-dhigh*y(3); %*(0.5+R));

% P3 Predator equation_winter if N >= Ncrit
P3=-dlow*y(3);%*(0.5+R));

% setting up a column vectors for the pop timeseries and TIME (y(4))
```

```matlab
dy = zeros(4,1);


%- END State event finder -%

dy(1) = omega*N1+(1-omega)*N2;                          % Prey equation
dy(2) = omega*N12+(1-omega)*N22;                        % Prey equation
dy(3) = omega*(P2+delta*(P1-P2))+(1-omega)*(P2+delta*(P3-P2));     % Predator equation
dy(4) = 1;                                      % Tidsderiverte av 1
end



%- State event finder -%
function [value,isterminal,direction]=events(t,y)
value= sin(2*pi*y(4));       % value declines through zero at onset of spring,
isterminal= [1];             % stop computation at event
direction=[-1];              % -1 means that event only occur when value is declining when passing zero
%- END State event finder -%



###########################################################################
########  Thesis: Shared Predation: One-prey-one-predator model  #######
###########################################################################

install.packages("R.matlab")
install.packages("e1071")
install.packages("xlsx")
install.packages("WriteXLS")
library("WriteXLS")
library("xlsx")
library("R.matlab")
library("e1071")
setwd("~/Desktop/Thesis-2017/R")


##### Importing time series from matlab with autumn values for all three species #####

lemming1 <- readMat('lem1series.mat')    # Autumn values for Norwegian Lemming
lemming1<-unlist(lemming1)
vole1 <- readMat('vole1series.mat')    # Autumn values for Grey-Sided Vole
vole1<-unlist(vole1)



plot(lemminglog1,type="l", ylab="Lemming abundance (log)", xlab="Time (years)", main="Norwegian
Lemming",
    cex.lab=0.8, cex.axis=0.8, cex.main=0.8, cex.sub=0.8)
plot(volelog1, type="l",ylab="Vole abundance (log)", xlab="Time (years)", main="Grey-Sided Vole",
    cex.lab=0.8, cex.axis=0.8, cex.main=0.8, cex.sub=0.8)

plot(lemminglog1,type="l",col="red")
lines(volelog1,type="l")


###########################################################################
########              ~STATISTICAL ANALYSIS~              ########
###########################################################################
```

```
lemminglog1<-log10(lemming1+1)
volelog1<-log10(vole1+1)

######### Cross-correlation analysis #########

par(mfrow=c(1,1))
ccf1<-ccf(lemminglog1,volelog1, lag.max=3)
ccfvalues1<-ccf1
signlevel<-2/sqrt(101)

######### Calculation of S-index (Standard deviation of logged time series) ##########

lemminga1<-sd(lemminglog1)
lemminga1


volea1<-sd(volelog1)
volea1


######### Calculating growth rates post- and pre-peak: symmetry #########


#### Lemming ####

localMaximalem <- function(lemming1) {
  # Use -Inf instead if x is numeric (non-integer)
  y <- diff(c(-.Machine$integer.max, lemming1)) > 0L
  rle(y)$lengths
  y <- cumsum(rle(y)$lengths)
  y <- y[seq.int(1L, length(y), 2L)]
  if (lemming1[[1]] == lemming1[[2]]) {
    y <- y[-1]
  }
  y
}

localMaximalem(lemming1)
lemminggrowth1<-diff(lemminglog1)/(lemminglog1)[-length(lemminglog1)]
lemmingdiff1<-(lemminggrowth1[4]-lemminggrowth1[5])
lemmingdiff2<-(lemminggrowth1[10]-lemminggrowth1[11])
lemmingdiff3<-(lemminggrowth1[15]-lemminggrowth1[16])
lemmingdiff4<-(lemminggrowth1[19]-lemminggrowth1[20])
lemmingdiff5<-(lemminggrowth1[23]-lemminggrowth1[24])
lemmingdiff6<-(lemminggrowth1[28]-lemminggrowth1[29])
lemmingdiff7<-(lemminggrowth1[32]-lemminggrowth1[33])
lemmingdiff8<-(lemminggrowth1[36]-lemminggrowth1[37])
lemmingdiff9<-(lemminggrowth1[41]-lemminggrowth1[42])
lemmingdiff10<-(lemminggrowth1[47]-lemminggrowth1[48])
lemmingdiff11<-(lemminggrowth1[52]-lemminggrowth1[53])
lemmingdiff12<-(lemminggrowth1[57]-lemminggrowth1[58])
lemmingdiff13<-(lemminggrowth1[61]-lemminggrowth1[62])
lemmingdiff14<-(lemminggrowth1[64]-lemminggrowth1[65])
lemmingdiff15<-(lemminggrowth1[69]-lemminggrowth1[70])
lemmingdiff16<-(lemminggrowth1[73]-lemminggrowth1[78])
lemmingdiff17<-(lemminggrowth1[84]-lemminggrowth1[85])
lemmingdiff18<-(lemminggrowth1[90]-lemminggrowth1[91])
lemmingdiff19<-(lemminggrowth1[95]-lemminggrowth1[96])
```

```r
lemgrowthrates1<-c(lemmingdiff1,lemmingdiff2,lemmingdiff3,lemmingdiff4,lemmingdiff5,lemmingdiff6,
           lemmingdiff7,lemmingdiff8,lemmingdiff9,lemmingdiff10,lemmingdiff11,lemmingdiff12,
           lemmingdiff13,lemmingdiff14,lemmingdiff15,lemmingdiff16,lemmingdiff17,lemmingdiff18,
           lemmingdiff19)

meangrowthlem<-mean(lemgrowthrates1)


#### Grey-Sided Vole ####

localMaximavole <- function(vole1) {
  # Use -Inf instead if x is numeric (non-integer)
  y <- diff(c(-Inf, vole1)) > 0L
  rle(y)$lengths
  y <- cumsum(rle(y)$lengths)
  y <- y[seq.int(1L, length(y), 2L)]
  if (vole1[[1]] == vole1[[2]]) {
    y <- y[-1]
  }
  y
}

localMaximalem(vole1)


volegrowth1<-diff(volelog1)/(volelog1)[-length(volelog1)]
volediff1<-(volegrowth1[2]-volegrowth1[3])
volediff2<-(volegrowth1[6]-volegrowth1[7])
volediff3<-(volegrowth1[9]-volegrowth1[10])
volediff4<-(volegrowth1[13]-volegrowth1[14])
volediff5<-(volegrowth1[16]-volegrowth1[17])
volediff6<-(volegrowth1[21]-volegrowth1[22])
volediff7<-(volegrowth1[25]-volegrowth1[26])
volediff8<-(volegrowth1[30]-volegrowth1[31])
volediff9<-(volegrowth1[33]-volegrowth1[34])
volediff10<-(volegrowth1[36]-volegrowth1[37])
volediff11<-(volegrowth1[40]-volegrowth1[41])
volediff12<-(volegrowth1[45]-volegrowth1[46])
volediff13<-(volegrowth1[49]-volegrowth1[50])
volediff14<-(volegrowth1[52]-volegrowth1[53])
volediff15<-(volegrowth1[55]-volegrowth1[56])
volediff16<-(volegrowth1[58]-volegrowth1[59])
volediff17<-(volegrowth1[71]-volegrowth1[72])
volediff18<-(volegrowth1[76]-volegrowth1[77])
volediff19<-(volegrowth1[78]-volegrowth1[79])
volediff20<-(volegrowth1[80]-volegrowth1[81])
volediff21<-(volegrowth1[83]-volegrowth1[94])
volediff22<-(volegrowth1[86]-volegrowth1[87])
volediff23<-(volegrowth1[89]-volegrowth1[90])
volediff24<-(volegrowth1[92]-volegrowth1[93])
volediff25<-(volegrowth1[96]-volegrowth1[97])

volegrowthrates<-c(volediff1,volediff2,volediff3,volediff4,volediff5,volediff6,
           volediff7,volediff8,volediff9,volediff10,volediff11,volediff12,
           volediff13,volediff14,volediff15,volediff16,volediff17,volediff18,
           volediff19,volediff20,volediff21,volediff22,volediff23,volediff24,
           volediff25)

meangrowthvole<-mean(volegrowthrates)
```

X5: Two-prey-one-predator model (Matlab and R code)

```
%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
%%%%%%%%%%%%%%%%%%%%%%%%%%%
%%%% Two-prey and one predator(based on Hanski and Henttonen, 1996) %%%%
%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
%%%%%%%%%%%%%%%%%%%%%%%%%%%
clear all

global r1 r1w r2 r2w K1 K1w K2 K2w c a D1 D2 b v q dhigh dlow Ncrit beta Sr


%%Parameter values%%
% Lemming
K1=100;       % Carrying Capacity of prey in summer
K1w=50;       % Carrying Capacity of prey in winter
r1=5.0;       % prey intrinsic growth rate in summer
r1w=4.7;      % prey intrinsic growth rate in winter
%Vole
K2=100;       % Carrying Capacity of prey in summer
K2w=25;       % Carrying Capacity of prey in winter
r2=5.4;       % prey intrinsic growth rate in summer
r2w=2.5;      % prey intrinsic growth rate in winter
% Stoat
v=2.8;        %Predator intrinsic growth rate
c=600;        % maximum per capita predation rate
D1=10;        % Predation half saturation constant
D2=10;
beta=D1/D2;
q=100;        % equilibrioum prey/predator ratio
Ncrit=10;     % critical prey density for predatior reproduction
dhigh=5;  % predator mortality rate when prey is scarce
dlow=0.1;     % predator mortality rate when prey is abundant
Sr = 4;
a=0.1;        % shape parameter or smooth season function omega
b=1;          % shape parameter for predator reproduction function delta




D1val = [4 6 8 10 12];
D2val = [4 6 8 10 12];
%K1val = [ ];
%K1wval = [];
%K2val = [];
%K2wval = [];

for i = 1:1:5             % first for-loop for variable 1
    figure(1)
    hold on
    for j = 1:1:5
    D1=D1val(i);
%   K1=K1val(i);
%   K1w=K1wval(i);
    D2=D2val(j);
```

```
    s=5*(i-1)+j;

%Using ode45
options= odeset('Events',@eventsFn,'Reltol',1e-4,'NonNegative',[1 2]);  % setting the options-structure
for sertain events happening: Stochasticity in predator

y0=[7,7,1,0];
y1(1,s) = y0(1);
y2(1,s) = y0(2);
y3(1,s) = y0(3);
y4(1,s) = y0(4);

yout = y0.'; tout=0; teout=[]; yeout=[]; ieout=[];  % output of events, teout=time when events occur,
yeout=values of species abundance at events, ieout=
tstart=0;                                % start-time
tstop=150;                               % end of timespan
lold(1,s) = 2;

R=unifrnd(0,1,1,round(tstop-tstart)+10);         % The random values of unifrnd(0,1) added at
beginning of summer for predator (10 values to draw upon)
while tout(length(tout))<tstop
    [t,y,TE,YE,IE] = ode45(@hanski19962 ,[tstart tstop], y0,options);  % ode solver for function =
hanski1996 with stochasticity
    laenge=length(t);                            % length of time (t)
    Rin=R(t(laenge)+0.5-mod(t(laenge)+0.5,1)+1);              %To get stochasticity at end of winter
        tout = [tout;t(2:laenge)];                   % time-output, number of time-steps
        yout = [yout;t(2:laenge)];                   % output of y follows the time-steps
        teout=[teout;TE]; yeout=[yeout;YE]; ieout=[ieout;IE];     % when events happen and values
        y1((lold(1,s)):(laenge+lold(1,s)-2), s) = y(2:laenge,1);
        y2((lold(1,s)):(laenge+lold(1,s)-2), s) = y(2:laenge,2);
        y3((lold(1,s)):(laenge+lold(1,s)-2), s) = y(2:laenge,3);
        y4((lold(1,s)):(laenge+lold(1,s)-2), s) = y(2:laenge,4);
%      y0=[y(laenge,1);y(laenge,2);y(laenge,3)*(0.5+Rin);y(laenge,4)];      % values of prey, pred and
time at the end (tstop)
    y0=[y(laenge,1);y(laenge,2);y(laenge,3)*(Sr*(0.5+Rin));y(laenge,4)];      % values of prey, pred and
time at the end (tstop)
    %test=[y(laenge,3);0.5+Rin;y0(3)];                % test for showing value befor stoch value, the
stoch value and value after adding stoch value
    test=[y(laenge,3);Sr;y0(3)];                 % test for showing value befor stoch value, the stoch
value and value after adding stoch value
    tstart=t(laenge);                            % length of time-steps (tstop)

lold(1,s) = laenge+lold(1,s)-2;


%          Time = y4(:,1:s); % matrix of tout of each sim.
%          Y = y1(:,1:s);   % matrix of grey-sided vole density for each sim.
%          X = y2(:,1:s);   % matrix of lemming density for each sim
%          Z = y3(:,1:s);   % matrix of mustelid density for each sim.


figure(1)
subplot(5,5,s);                                 % setting up grid of subplots
plotyy(y4(1:lold(:, s), s),y1(1:lold(:, s), s),...
    y4(1:lold(:, s), s),y2(1:lold(:, s), s))          % plotting prey & pred vs time for each
iteration/loop
title({D1 D2});
```

```matlab
    end;
end;
end;

%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%

%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
%%%%%%%%%%%%%%%%%%%%%%%%%%%
kA=1:length(y4);
%k2A=1:length(y4);
%k3=1:length(y4);


y1maxA=zeros(max(tstop),1);      %Autumn values lemming max


y2maxA=zeros(max(tstop),1);      %Autumn values vole max


y3maxA=zeros(max(tstop),1);      %Autumn values stoat max


y4maxy1A=zeros(max(tstop),1);     %Time
y4maxy2A=zeros(max(tstop),1);
y4maxy3A=zeros(max(tstop),1);


yearmaxA=zeros(max(tstop),1);



y1minA=zeros(max(tstop),1);      %Autumn values lemming min


y2minA=zeros(max(tstop),1);      %Autumn values vole min


y3minA=zeros(max(tstop),1);      %Autumn values stoat min


y4miny1A=zeros(max(tstop),1);   %Time
y4miny2A=zeros(max(tstop),1);
y4miny3A=zeros(max(tstop),1);




%%%%%%  For max and min values at parts of the year %%%%%%%
ts=25
for j=1:ts

   y1s = y1(:,j);
   y2s = y2(:,j);
   y3s = y3(:,j);
   y4s = y4(:,j);

for i=0:(tstop-1)
   y1maxA(i+1) =  y1s(kA(max(kA(y1s==max(y1s(y4s<(i+1) & y4s>(i+0.8)))))));
   y2maxA(i+1) =  y2s(kA(max(kA(y2s==max(y2s(y4s<(i+1) & y4s>(i+0.8)))))));
   y3maxA(i+1) =  y3s(kA(max(kA(y3s==max(y3s(y4s<(i+1) & y4s>(i+0.8)))))));
   y4maxy1A(i+1) = y4s(kA(max(kA(y1s==max(y1s(y4s<(i+1) & y4s>(i+0.8)))))));
   y4maxy2A(i+1) = y4s(kA(max(kA(y2s==max(y2s(y4s<(i+1) & y4s>(i+0.8)))))));
   y4maxy3A(i+1) = y4s(kA(max(kA(y3s==max(y3s(y4s<(i+1) & y4s>(i+0.8)))))));
   end;
```

```matlab
    y1matmA (:,j) = y1maxA;
    y2matmA (:,j) = y2maxA;
    y3matmA (:,j) = y3maxA;
    y4matmA1 (:,j) = y4maxy1A;
    y4matmA2 (:,j) = y4maxy2A;
    y4matmA3 (:,j) = y4maxy3A;


end;

    Ymax = [y1matmA y2matmA y3matmA y4matmA1 y4matmA2 y4matmA3];


%%Removing the "start-phase" of the model from the analysis
%%Removing the first 50 years of simulation


y1matmAred = y1matmA( [50:end] , : );
y2matmAred = y2matmA( [50:end] , : );
y3matmAred = y3matmA( [50:end] , : );
y4matmA1red = y4matmA1( [50:end] , : );
y4matmA2red = y4matmA2( [50:end] , : );
y4matmA3red = y4matmA3( [50:end] , : );
```

```r
##############################################
######### Thesis: Shared Predation  #######
##############################################
install.packages("R.matlab")
install.packages("e1071")
install.packages("xlsx")
install.packages("WriteXLS")
install.packages("ggplot2")

library("WriteXLS")
library("xlsx")
library("R.matlab")
library("e1071")
library("ggplot2")
setwd("~/Desktop/Thesis-2017/R")

##### Importing datasets from matlab with autumn values for all three species #####

lemming2 <- readMat('lem2series.mat')    # Autumn values for Norwegian Lemming
lemming2 <- data.frame(matrix(unlist(lemming2), nrow=101, byrow=1)) #unlisting
data to create data frame
vole2 <- readMat('vole2series.mat')    # Autumn values for Grey-Sided Vole
vole2 <- data.frame(matrix(unlist(vole2), nrow=101, byrow=1))
#stoat2 <- readMat('stoat2series.mat')    # Autumn values for Stoat
#stoat2 <- data.frame(matrix(unlist(stoat2), nrow=101, byrow=25))
```

```
plot(lemming2$X1, type="l")
lines(vole2$X1, type="l", col="red")

lemminglog2<-log10(lemming2+1)
volelog2<-log10(vole2+1)



ggplot(lemminglog2, aes(y = X8, x = seq(1, length(lemminglog2$X8)))) + geom_line()

ggplot() +
  geom_line(aes(seq(1, length(lemminglog2$X8)), X8), lemminglog2, color="red") +
  geom_line(aes(seq(1, length(volelog2$X8)), X8), volelog2,color="blue")


plot(lemminglog2$X8, type="l")
lines(volelog2$X8, type="l", col="red")

##### Using cross-correlation analysis to look at synchronicity #####

par(mfrow=c(3,5))
ccf2<-sapply(1:ncol(lemminglog2), function(i) ccf(lemminglog2[,i],
volelog2[,i],lag.max=3,"correlation", main=colnames(lemminglog2)[i]))
ccf2
ccfvalues2<-ccf2
ccfvalues2<-ccfvalues2[1,]
#ccfvaluestable2 <- matrix(unlist(ccfvalues2), nrow=7, byrow=25)



##### Using the s-index to look at changes in amplitude (adding 1 due to presence
of zeros) #####

SDD1<-sapply(1:ncol(lemminglog2), function(i) sd(lemminglog2[,i]))
SDD1
SDD2<-sapply(1:ncol(volelog2), function(i) sd(volelog2[,i]))
SDD2

sd(SDD1)
sd(SDD2)

##### Calculating growth rates post- and pre-peak: symmetry #####


## Norwegian Lemming ##


## Sim 1 ##
LX1<-lemming2$X1
localMaximalem2x1 <- function(LX1)
```

```
{
# Use -Inf instead if x is numeric (non-integer)
y <- diff(c(-.Machine$integer.max, LX1)) > 0L
rle(y)$lengths
y <- cumsum(rle(y)$lengths)
y <- y[seq.int(1L, length(y), 2L)]
if (LX1[[1]] == LX1[[2]]) {
  y <- y[-1]
}
y
}
localMaximalem2x1(LX1)
lemminggrowth2.1<-diff(lemminglog2$X1+1)/(lemminglog2$X1+1)[-
length(lemminglog2$X1+1)]
lemdiff1.1<-(lemminggrowth2.1[2]-lemminggrowth2.1[3])
lemdiff1.2<-(lemminggrowth2.1[8]-lemminggrowth2.1[9])
lemdiff1.3<-(lemminggrowth2.1[18]-lemminggrowth2.1[9])
lemdiff1.4<-(lemminggrowth2.1[26]-lemminggrowth2.1[27])
lemdiff1.5<-(lemminggrowth2.1[33]-lemminggrowth2.1[34])
lemdiff1.6<-(lemminggrowth2.1[44]-lemminggrowth2.1[45])
lemdiff1.7<-(lemminggrowth2.1[53]-lemminggrowth2.1[54])
lemdiff1.8<-(lemminggrowth2.1[60]-lemminggrowth2.1[61])
lemdiff1.9<-(lemminggrowth2.1[68]-lemminggrowth2.1[69])
lemdiff1.10<-(lemminggrowth2.1[75]-lemminggrowth2.1[76])
lemdiff1.11<-(lemminggrowth2.1[84]-lemminggrowth2.1[85])
lemdiff1.12<-(lemminggrowth2.1[93]-lemminggrowth2.1[94])


sim1growth<-c(lemdiff1.1,lemdiff1.2,lemdiff1.3,lemdiff1.4,lemdiff1.5,lemdiff1.6,
        lemdiff1.7,lemdiff1.8,lemdiff1.9,lemdiff1.10,lemdiff1.11,lemdiff1.12)
sim1growtlemming<-mean(sim1growth)   ##Performed on all 25 scenarios.
```

X6: Spectral analysis

```
%%%%%%%%%% Spectral Analysis %%%%%%%%%%%%

domP = zeros(25, 1)
siP = zeros(25, 1)
for j=1:25
Y=fft(y1matmAred(:,j));
N = length(Y);
Y(1) = [];
nyquist = 1/2;
freq = (1:N/2)./(N/2)*nyquist;
period = 1./freq;
power = abs(Y(1:fix(N/2))).^2;


%%%
figure(105)          % figure of freq vs power.
subplot(5,5,j)
plot(freq,power), grid on
```

```matlab
xlabel('cycles/year')
%title(TSnames(j))
%%%

%%%
figure(106)          % figure of period vs power.
subplot(5,5,j)
plot(period,power),axis([0 10 0 max(power)+1]), grid on
ylabel('Power')
xlabel('Period(Years/Cycle)')
%title(TSnames(j))
%%%

[mp,index(:,j)] = max(power);
siP(j)  =1-(1-exp(-mp)).^N; % estimates the significance of the dominant power
%siP=[];
%siP=[siP P];
domP(j) = period(index(:, j))
%domP=[domP period(index(:,j))];

end


i=siP<0.05; % within significance level
Psign=siP(i); %
period=domP(i)'; % dominant and significant period
%tsNames=TSnames(i)';
signP=(period>2.7 & period<6.4); % period selected for dominant period between 2.9 and 6
PERIOD=period(signP);
%Location=tsNames(signP);
```