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The Evolution of Stability in a Stochastic Predator-Prey System

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Abstract

This master's thesis aim to see if fluctuations in the environment can make a stable predator-prey system naturally evolve into an unstable system. In [1], Abrams and Matsuda uses numerical methods to investigate the stability properties of a predator-prey system and looks at the effect that the unstable population dynamics have on the mean population sizes and the mean predation pressure. After re-deriving some of their main results, I introduce white noise in the prey equation to model the fluctuations which occur in e.g. the weather. Using both algebraic and numerical methods I present how different sets of parameters will affect the evolution of the stability of the system. The evolution of the prey population is assumed to select through the trait that codes for the prey's vulnerability. The parameter describing the prey vulnerability is therefore used in the evaluation of the direction of the evolution, which is done using techniques from Adaptive Dynamics.

Unlike [1], I choose to separate the time scales of which the population dynamics and evolution occur on and evaluate the direction of the evolution by looking at the selection gradient. It is found out that the system can change its stability properties if the fluctuations reach a certain level. Based on numerical simulations, this level of fluctuations seems possible to exist in real ecological systems. The unstable evolution is possible since cycling dynamics have a negative effect on the mean predator population and positive on the prey dito.

Foreword

This report is my master's thesis for a degree in Master of Science in Engineering Physics at the Lund Institute of Technology (LTH). The project was performed within the Department of Biology at Lund University, during 20 weeks in the spring and part of the summer in 2013. Since this actually is a thesis in Ecology (TEK920), a certain exemption was made by the administrators for the Engineering Physics program, Johan Hugosson and Carina Fasth.

My supervisor for the project was Jörgen Ripa and examiner was Anders Brodin, both within the group of Evolutionary Ecology at the Department of Biology.

I specially want to thank Jörgen for his guidance when ever some difficulties have occurred and Johan and Carina for letting me do this project as my thesis.

4

Contents

Chapter 1

Introduction

1.1 Background

A predator-prey model system is as a mathematical system consisting of two or more time dependent entities which rates of change can be described by ordinary differential equations[1]. The entities are biologically interpreted as densities of e.g. animals or plants and their governing differential equations are often of non linear character. The non-linearity causes a complex structure of the resulting dynamical system which makes it often impossible to get closed form solutions. One must therefore consult numerical methods to solve the system of equations. However, much of the systems qualitative behavior can still be uncovered using algebraic tools only, i.e. "paper and pencil mathematics". When the system is within its stable region of the parameter space, the population densities will always converge towards the steady state, i.e. the stable fixed point. How the system behaves while reaching the fixed point depends on the eigenvalues of its Jacobian matrix. The Jacobian is a linearized version of the non linear system and is only a valid approximation close to the fixed point. If one or more parameter values are increased/decreased to the extent that the system no longer is stable, the system can no longer be linearly approximated hence computer simulations are the only way to get a good idea of the system's behavior[2]. That the system has become unstable does not mean that the populations we model will crash and die. In predator-prey systems it is common that when the border of the stable parameter space has been reached, a Hopf bifurcation occurs[4]. This is a fancy word of saying that a pair of complex conjugated eigenvalues gets positive real parts. This makes the fixed point unstable and the populations will start cycling in time, no longer reaching their steady

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[1]Predator-prey systems can also be described by difference equations, but the biological interpretation will be different as such model will give us discrete generations of fixed size. In a first order difference equation, we have that between the generations n and $n+1$, all individuals at n are assumed to die and immediately be replaced with new individuals of the next generation[4], something we don't consider here.

state values. That is, the fixed point is no longer an attractor of the system, but as the trajectories in phase space are bounded we end up with another attractor which is called a *limit cycle*[4][7].

Introducing stochasticity into the system by white noise in the prey population (specified below) will more or less disturb the system in terms of it not being able to settle at its steady state anymore (if the system originally was stable). In case of an unstable system, the phase diagram will no longer have its smooth, counter-clockwise cycles, see Figure 1.1. The fluctuations can be driven by changes in the environment of the predators and prey, e.g. the weather and food availability. Assuming that the prey are herbivores of some kind, their growth rate depends on the quality and amount of plants they have access to. "Bad" weather or low food availability will have negative effects on the prey population growth rate while "good" weather and high food availability will then have a positive dito. The fluctuations in the prey population will have an effect on the predator population as well, where a higher prey density would result in more predators and vice versa. It has been shown that unstable systems with cycling populations shifts the
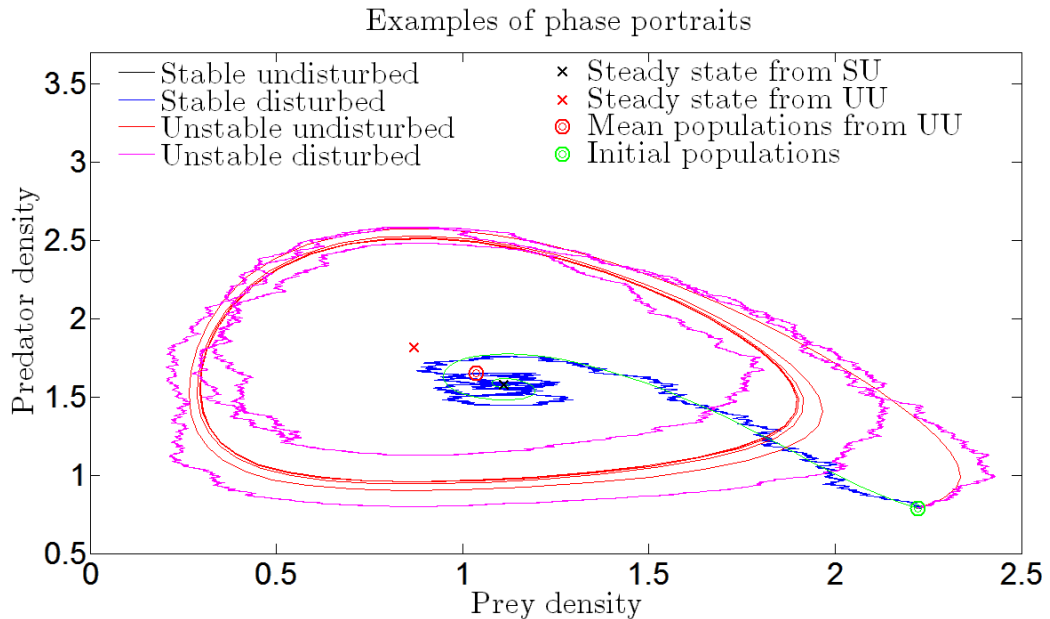

Figure 1.1: The prey population increases in size when the system gets unstable while the opposite is true for the predator population, which explains the South-East shift of the mean populations compared to the equilibrium populations.

mean population sizes in a South-East direction from the steady state in phase space[2], see Figure 1.1. This means that the mean predator popula-

tion decreases while the mean prey population increases with the instability of the system. Stochastic variations also have similar effect on the mean population sizes as unstable deterministic cycling systems have, which could possibly have an effect on the system's evolutionary dynamics[8]. This could make it possible for further evolution of a behavior, i.e. changing the value of a parameter to further increase fitness. As stochasticity doesn't change the stability regions of the parameters, we know that enough increase/decrease of their values will make the system unstable. This leads us to the main question; Can a two dimensional predator-prey system evolve into an unstable state if there are fluctuations in the prey population density? Another question is how the stochastic variations will effect an already unstable system. If further evolutionary change is possible, will this drive the system towards greater instability or could the amplitude of the oscillations perhaps be damped?

One could imagine a real biological system with two trophic levels that have existed for a long time with negligible deviations from their equilibrium densities. Both populations have with time co-evolved and the predators have specialized in hunting the preys while the preys have specialized in defense from the predators. Now if something happens which directly effects the prey's total growth rate, e.g. the mean temperature changes and causes irregular food availability for the prey, the prey population size will start to vary in a stochastic manner. A sudden drop in prey density will have a negative effect on the predator population, which will decrease. The lower predation pressure will in its turn have a positive effect on the prey population which will start to increase. If there instead is a sudden increase in prey density it will have a positive effect on the predator population, which will increase the predation pressure felt by the prey, and the prey population will start to decrease. As we assumed that the original deterministic system was stable, this should also be the case with the new stochastic system. However, as the new stochastic system has small fluctuations in the equilibrium populations, further optimization of their behavior(s) might be possible. If the prey population are able to evolve into an unstable parameter region, the whole system will get unstable. Hence the fluctuations have caused the predator-prey system to become evolutionary unstable.

The prey population are assumed to have a certain vulnerability which decides how hard or easy they are to catch in the eyes of the predators. Low vulnerability can be interpreted as the prey are less likely to take risks while foraging and thereby not bump into a predator as often as a prey individual with higher vulnerability. Biologically speaking, it is possible that the vulnerability of individuals could vary over the course of a year. If the prey species are such that they feed their young, this time of the year might encourage the parents to take higher risks while foraging, while other parts of

the year they are more careful. However, here we don't consider this kind of behavior, as an individual's vulnerability is assumed constant over its lifetime. The genetic trait that codes for the vulnerability of the prey is assumed to be inherited from the parent (asexual reproduction) to its young. Dealing with adaptive dynamics (an introduction to AD is given in the second next section) it is common to think of life as a game where the individuals are the players and their different genetic traits give raise to different life strategies[3]. In this context we think of the vulnerability as the strategy that different prey individuals play with. The individual with the best strategy compared to the others should have the greatest pay-off and those individuals with a poor strategy should have less. The pay-off in evolutionary games is called *fitness*. Prey individuals that are very likely to survive and reproduce have high fitness, while individuals that are not have low fitness. Thereby will the genetic traits of the high fitness individuals decide the direction of the evolution. In this case evolution acts on the vulnerability and should thereby be the parameter that is used in the evaluation of the fitness of the prey. In predator-prey systems, the fitness G of a population N is defined as its per capita growth rate and is thereby derived directly from the equation of its total growth rate, i.e. $G = \dot{N}/N$. The fitness is typically a function of one or more trait values and it could be thought of as a "fitness function". Intuitively one might in our case think that the fitness evaluation should be very simple as prey with low vulnerability take less risks and are thereby more likely to survive. However, as there are a certain trade-off built into the model, prey with low vulnerability also have a low rate of reproduction. We can think of this as they are not able to harvest the same amount of food as prey with higher vulnerability. To exemplify the effect of the trade-off one can think of two different parenting strategies within a population. If we assume that all prey get the same amount of offspring, strategy 1 is to give all offspring equal amounts of food and thereby have a high survival rate of the offspring, with the setback that the parents take a lot of risks and dies more often than those parents using strategy 2. Strategy 2 is then to focus on the raising of one (or few) offspring(s), which gives the offspring a low survival rate but the parents have a higher likelihood of surviving. If both parents die, independent of strategy used, the offspring will also die and this will of course happen most often for strategy 1-parents.

Using the fitness function, we want to find out whether in a prey population with a certain vulnerability, will a prey individual with slightly higher or lower vulnerability have a higher fitness than the average prey? To answer this, it is however often easier to use the *selection gradient*, which is the derivative of the fitness function with respect to the trait value. The selection gradient enables us to see the direction of the evolution in a simpler way than the fitness function. As the evolution selects for prey with high fitness, this corresponds in our model to either increase or decrease the vulnerability

of the prey population. If the selection is favorable for higher vulnerabilities, the selection gradient take a positive value, while a negative value indicates that selection is favorable for prey with lower vulnerabilities. This is a direct consequence of the shape of the fitness function at the specific point in time we look at, as the evolution will always push the populations in the uphill direction in the fitness landscape. When the population have reached its peek in the fitness landscape, this corresponds to a selection gradient that equals zero[3][6].

To provide answers to the different questions, I will scrutinize the system using both analytical and numerical methods. The algebraic tools used are on the level that an engineering student on his or her last years of studies should be able to follow. All the numerics and simulations used are implemented in MATLAB.

1.2 Defining the Equations

A two dimensional predator-prey system is defined by a set of equations on the form

$$\dot{N} = f_N(N, P) \tag{1.1a}$$

$$\dot{P} = f_P(N, P) \tag{1.1b}$$

where N is the density of the prey and P is the density of the predators. The term "density" means here the number of prey or predator individuals per area unit. The area unit can be different between the populations, e.g. we could measure the prey density in # prey per 100 m^2 and the predator density in # predators per 1 km^2 depending on what suits us best. The functions f_N and f_P describes the total growth rates of the prey respectively the predators. If these terms are positive it means that the populations are increasing in size whereas negative terms indicates decreasing populations. In this project the functions f_N and f_P are defined as

$$f_N = N[r(C) - kN - CP\alpha(C, N)] \tag{1.2a}$$

and

$$f_P = P[BCN\alpha(C, N) - d]. \tag{1.2b}$$

In the equation for the prey density (1.2a) there is one positive contribution and two negative. The positive contribution is called the intrinsic growth rate of the prey and is simply the birth of new prey individuals. The second term is restricting the total growth rate of the prey population by making it dependent the square of the current size and thereby introducing a maximum

size of the population. Biologically this could mean that there are limited amount of food and space for the prey population. This makes the population growth rate smaller as the population grows until it reaches a maximum value, the carrying capacity. The last term is the negative contribution from the predation on the prey population by the predators. The equation describing the change in predator density (1.2b) has only two terms, whereas the positive contribution is the birth rate of new predators as a result of the predation on the prey and the negative contribution is their death rate. The parameter C is the vulnerability of the prey population and is defined as the rate at which an unsatiated predator captures a prey during its active search time. Only strictly positive values on this parameter is of interest here and therefore it is further assumed that $C > 0$ always holds.

In system 1.2 we see that the birth rates of both populations and the predation mortality of the preys are all functions of the vulnerability. The birth rate of the preys is assumed to be linearly dependent on the vulnerability, i.e. $r(C) = R + qC$, where $R, q > 0$. The birth rate of the predators and the death rate of the prey are depending on the function $\alpha(C, N) = 1/(1+hCN)$ which is the rate at which the predators search for the prey. The constant h is known as the handling time of the predators and is the refractory period of the predators, i.e. when a prey has been caught; how long does the predators have to rest and digest their meal before hunting again.

The construction $CN\alpha(C, N)$ is called the predators' functional response and is here of the so called type II[2]. It is the functional response that gives the rate of prey consumption per predator. Vice versa tells $CP\alpha(C, N)$ how much preys that are consumed per time unit and prey. B is the yield factor that converts consumed prey into new predators and is a measure of how effective the predators take care of the caught prays.

In a realistic model, the total birth rate of the prey and the death rate of the predators should be depending on their current population sizes. This is achieved here by the products $r(C) \cdot N$ in Equation 1.2a and $d \cdot P$ in Equation 1.2b. Further, the chance of an encounter between the preys and predators is proportional to both their sizes, $N \cdot P$, which is seen in terms describing the predation of prey and birth of predators. Writing out all the ingoing functions gives us the following system of differential equations

$$\dot{N} = N\left(R + qC - kN - \frac{CP}{1 + hCN}\right) \tag{1.3a}$$

$$\dot{P} = P\left(\frac{BCN}{1 + hCN} - d\right), \tag{1.3b}$$

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[2]Having $\alpha(C, N) = 1$ would be a type I functional response.

where all the constants are assumed strictly positive. The time scale that these equations acts within is called *the ecological time scale*. This time scale is where the population dynamics occur and could thereby be considered as "small". The evolution on the other hand is assumed to act on a much larger time scale, *the evolutionary time scale*, and we can thereby use a constant C in our equations for the population dynamics.

1.3 Dimension Analysis

Working with dynamical systems, it is interesting to know how the parameters effects the properties of the system, i.e. how sensitive the system is to a certain change in the parameters and how the stability properties will be altered. Making a dimension analysis and re-define the parameters will reduce the number of parameters significantly, which will make this analysis easier. This means that the system should be rewritten on a dimensionless form. As C is the key parameter, we typically want to re-scale this parameter into having dimension 1. The same goes for parameters d, h and q. B, k and R are parameters that are used to normalize the system. By re-defining $C \rightarrow C^\star$, $d \rightarrow d^\star$, $h \rightarrow h^\star$ and $q \rightarrow q^\star$ as

$$C^\star = \frac{B}{k}C, \quad d^\star = \frac{1}{R}d, \quad h^\star = \frac{R}{B}h, \quad \text{and} \quad q^\star = \frac{k}{BR}q$$

the original system defined by 1.3 can now be rewritten on a dimensionless form. Our time dependent entities $N^\star$ and $P^\star$ are now $N^\star = NR/k$ respectively $P^\star = PBR/k$, while the time itself is $t^\star = t/R$. However, to get an easy notation the superscript stars are now dropped and from now on are all the entities and parameters on the dimensionless form presented here. The new dimensionless version of system 1.3 is

$$\dot{N} = N\left(1 + qC - N - \frac{CP}{1 + hCN}\right) \tag{1.4a}$$

$$\dot{P} = P\left(\frac{CN}{1 + hCN} - d\right), \tag{1.4b}$$

where now all the ingoing entities and parameters have dimension 1.

1.4 Adaptive Dynamics

This and the following section are meant as a brief introduction to some of the most general concepts within the field of adaptive dynamics (AD). The reader could for example consult [3] and [6] for a more thorough introduction to the subject.

AD is used to describe how populations will evolve on the evolutionary time scale by using a combination of population dynamics and game theory. It is closely related to what is known as quantitative genetics (QG), but is more easy to use, mathematically speaking. The main difference between AD and QG is how the trait values are distributed within the population. A trait value is typically represented by a real number. The different traits an individual has makes up its phenotype, which in turn decides the strategy the individual is playing. In this report we only have one trait, thus the trait and phenotype are equivalent.

In QG there are assumed a certain genetic variance within the population, centered around the most common value, e.g. a kind of normal distribution of trait values. If a trait slightly away from the mean is more preferable, i.e. gives higher fitness (the fitness concept is described in the next section) the whole distribution will slide towards this value, making it the new mean value. In contrast, AD assumes that all individuals of the population have the same trait value (plays the same strategy), i.e. a monomorphic population (a Dirac distribution). These individuals are called the *residents*. Among the residents there will on rare occasions show up individuals with different trait values, *mutants*. Having different genetic traits than the residents alters the strategy the mutant plays, for example while foraging or searching for a partner.

Both AD and QG are so called frequency dependent models, which means that the success of a certain strategy depends on frequency of which it is played and how common other alternative strategies are. This is where AD is more favorable, as the mutant's environment is defined only by the strategy played by the residents. This an effect of the assumption that we consider mutants rare in the population and should therefore not effect each other. The mathematical treatment now becomes easy as we only have to compare two strategies, one played by the resident population and one by the mutant. If the mutant's strategy is better than the residents', the mutant will be able to spread its genes in the population and thereby become more and more common. Finally, there will be no individual left playing the old resident strategy and all new individuals plays the mutant strategy. The mutant strategy have thereby become the new resident strategy. If a new mutant, with an even better strategy, shows up the same phenomenon occurs again. The process where a rare mutant strategy creates a new monomorphic population by dominating the old resident strategy is known as an *invasion*. The transition of resident strategies in AD is a discrete step from one strategy to another, while in QG the transition is continuous. Since the transitions happens on an evolutionary time scale, the populations are assumed to be at their equilibrium densities during the transitions.

To see if a mutant strategy can invade or not, the mutant's initial growth rate is calculated. The initial growth rate of a rare mutant will in the next section be given the name *invasion fitness*. If the resident strategy is so good that no mutants can invade (i.e. all other strategies than the residents' own will result in a lower fitness), the resident strategy is *uninvadable*, which in next section is known as an *evolutionary stable strategy*. The direction of the evolution is decided by the derivative of the invasion fitness, the *selection gradient*. A positive gradient will select for higher trait value while a negative gradient selects for a lower dito.

1.5 The Fitness Concept in AD

1.5.1 Stable dynamics

The *fitness*, G, is used as a of measure of how well adapted individuals are to their environment. An individual that has a high likelihood to survive and reproduce will have high fitness, while an individual which has lower dito likelihoods will have lower fitness[5]. Here, the environment is defined by the residents and the strategy they play. The individuals which fitness we are interested in calculating are the possible mutants. In the previous section it was stated that it was the invasion fitness (initial growth rate) of the mutants that had to be calculated to see if there could be any possible invasions. This invasion fitness will be a function that describes how the fitness landscape looks like for invading mutants given a certain resident strategy. The fitness is defined as the per capita growth rate, and here will the resident prey population with trait value C^* have the invasion fitness

$$G(C^*, C^*) = \frac{\dot{N}(C^*)}{N(C^*)} = 1 + qC^* - N^*(C^*) - \frac{C^* P^*(C^*)}{1 + hC^* N^*(C^*)}. \qquad (1.5)$$

Here we evaluated the populations at their steady state values as we now look at the evolutionary time scale and can assume constant population sizes. (The equations for the steady state populations, Eqn. 2.1a, is given in section 2.1.) However, the expression of the residents' fitness in Equation 1.5 must be equal zero for all C^*'s as the population otherwise would grow infinitely. This is not the case with a rare mutant, as the frequency of which the mutant's strategy is played is negligible compared to the frequency of the resident strategy. The predators should still be satiated by the residents, while the mutant's own strategy (trait value) should be used to calculate its intrinsic growth rate and risk of predation. The invasion fitness of a rare mutant with trait value C will therefore be

$$G(C, C^*) = 1 + qC - N^*(C^*) - \frac{CP^*(C^*)}{1 + hC^* N^*(C^*)}. \qquad (1.6)$$

So the invasion fitness of the rare mutant is here a linear function of the mutant's own trait value. The steady state populations are calculated using

the residents' trait value. Using the graph of $G(C, C^*)$ we can find out which strategies that can invade depending on which strategy the residents use. If $G(C, C^*)$ has positive slope at $C = C^*$, mutants with trait values $C > C^*$ are able to invade, while a negative slope at the resident trait value selects for mutants with $C < C^*$. As the slope at $G(C = C^*, C^*)$ is just the derivative of $G(C, C^*)$ with respect to C at C^*, we can get an analytical expression that tells us the current direction of the evolution. The derivative $\partial G / \partial C$ is called the selection gradient, g, and will after some simplifications[3] be

$$g(C) = \frac{d - C(1 - dh)}{C^2(1 - dh)}. \tag{1.7}$$

The C-value where $g(C)$ vanishes is called a *singular strategy* (SS). Solving Equation 1.7 for the intersection with the x-axis results in

$$C^{\mathrm{SS}} = \frac{d}{1 - dh}, \tag{1.8}$$

where the superscript SS emphasizes that this trait value represents a singular strategy. To tell whether the singular strategy lays on a maximum or minimum in the fitness landscape we have to check the sign of the second derivative of $G(C, C^*)$ with respect to the mutant's trait value, evaluated at C^{SS}. If the second derivative is negative, the trait value lays on a maximum in trait space. A trait value laying on a maximum will result in an unbeatable strategy, an *evolutionary stable strategy* (ESS). An ESS is a strategy, that if played by the residents, there is no better strategy to play which makes it an uninvadable strategy, as previously mentioned. The expression for the ESS criterion is

$$\left. \frac{\partial^2 G}{\partial C^2} \right|_{C^* = C^{\mathrm{SS}}} < 0. \quad \text{(Evolutionary stability criterion)} \tag{1.9}$$

In our case, Equation 1.9 cannot be used to verify that the singular strategy is an ESS, as $G(C, C^*)$ is linear in C, hence the second derivative in C is zero. One can use a second order method to check that this value actually is an ESS, but as the mathematical procedure would be very cumbersome such method is not used here. Instead we use a criterion that checks if the SS is able to attract populations that plays strategies close to it. If the SS is such an "evolutionary attractor", then we can argue that the SS also should be an ESS. In other words, populations with slightly lower/higher trait value than the SS should increase/decrease their trait value as the evolution goes by until they reach the SS. This means that the selection gradient must point towards the SS. This can only happen if the selection gradient is a decreasing function in the neighborhood of the SS. If the SS fulfills this criterion it is

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[3]Using the equations for the steady state populations in Equation 2.1a.

said to be *convergent stable*. The criterion is put mathematically as

$$\left.\frac{dg}{dC}\right|_{C=C^{\text{SS}}} < 0. \quad \text{(Convergence stability criterion)} \quad (1.10)$$

When a singular strategy is convergent stable it means that this is the end point of evolution of that strategy. If we calculate the convergent stability criterion we end up with

$$\left.\frac{dg}{dC}\right|_{C=C^{\text{SS}}} = -\left(\frac{1-dh}{d}\right)^2, \quad (1.11)$$

which clearly satisfy Equation 1.10. But how can knowing that the SS is convergent stable be used as an argument for that it should also be an ESS? Well, when the prey population have reached the SS the fitness landscape becomes flat which means that we will have neutral selection, i.e. every mutant (regardless of its trait value) will have equal fitness to the residents. However, if a mutant group with trait value C' will increase their size we can no longer use Eqn. 1.6 to calculate their fitness since that equation assumes that mutants are rare. Instead we could use the mean value of the traits C^* and C' to calculate the selection gradient. Since C^* is convergent stable, the selection gradient will once again point towards C^* and C'-mutants will have negative fitness compared to those with C^*.

There are still times when the SS is not an ESS but still attracts nearby strategies. Then the SS is said be a branching point. The populations will evolve towards it, increasing their fitness until they finally reach it. Then *any* different strategy will have greater fitness than the resident and the population will be going through disruptive selection. This kind of selection might split the former population into two new "morphs", whereof one evolves towards lower trait values and the other towards higher. Typically this happens when the SS lay on a convergent stable minimum in the fitness landscape. This is theoretically interesting e.g. when studying the formation of species pairs [Geritz et al. 1998].

In Figure 1.2, a hypothetical invasion fitness function is illustrated when evaluated at two different resident trait values; $C^* < C^{\text{ESS}}$ in 1.2(a) and $C^* = C^{\text{ESS}}$ in 1.2(b). As the direction of the evolution is determined by the selection gradient, mutants with a trait values $C > C^*$ will be able to invade as long as $g(C) > 0$. In the illustrated case we can only see that the SS in an ESS.

1.5.2 Unstable dynamics

When C generates a stable system, the calculation of Equations 1.6 and 1.7 are easy as we simply need the equilibrium densities of the populations,

The invasion fitness evaluated at a specific C^*

(a) G evaluated at $C^* < C^{\mathrm{ESS}}$ and with $g(C) > 0$.

The invasion fitness evaluated at an ESS

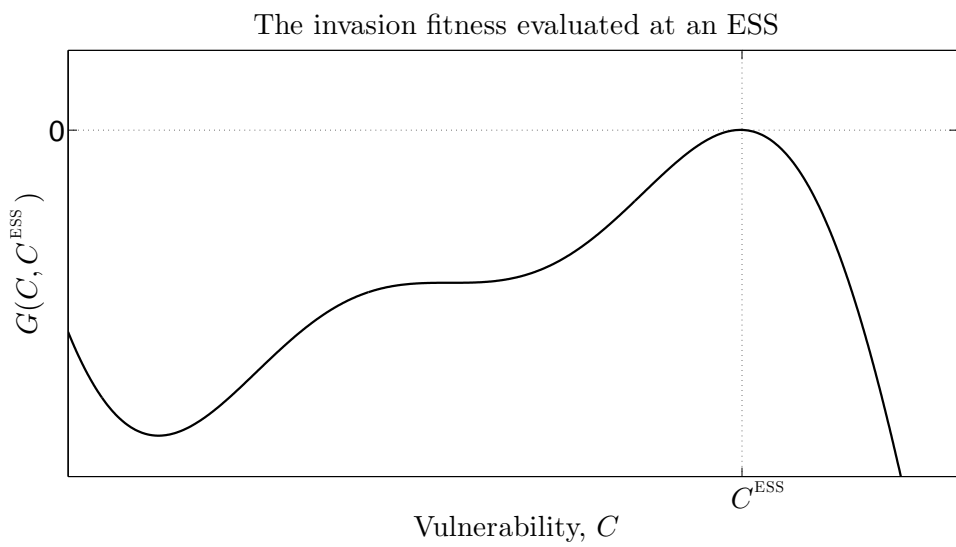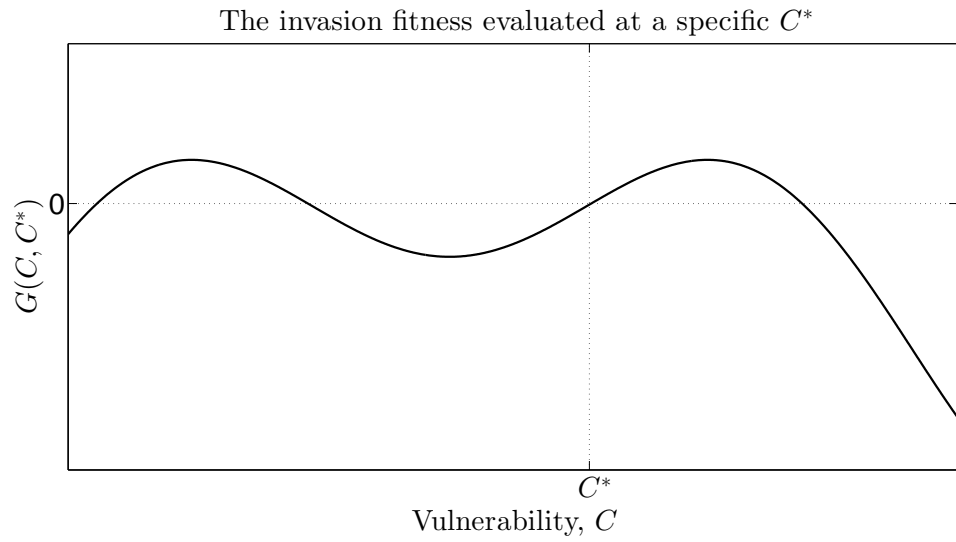(b) G evaluated at $C^* = C^{\mathrm{ESS}}$ and $g(C) = 0$.

Figure 1.2: A hypothetical fitness function evaluated at two different resident vulnerabilities.

which are constant. However, we are also interested in knowing how these functions behave for $C \geq C^i$. Knowing that when the system gets unstable, the population densities are no longer constant in time and cannot be used as predictions. Using data from real simulations is the only way to see how these functions will behave in the unstable region[2]. To calculate G and g outside the stable region we must therefore simulate the system over a long period of time and then calculate the mean of these functions. This will give us the mean invasion fitness as

$$\bar{G} = 1 + qC - \overline{N(\mathsf{t})} - \overline{\frac{CP(\mathsf{t})}{1 + hC^*N(\mathsf{t})}} \tag{1.12}$$

and the mean selection gradient as

$$\bar{g} = q - \overline{\frac{P(\mathsf{t})}{1 + hCN(\mathsf{t})}}. \tag{1.13}$$

The notation $N(\mathsf{t})$ and $P(\mathsf{t})$ indicates that these entities now are vectors from the result of a simulation. When the system is stable, Equations 1.12 and 1.13 are exactly equal 1.6 respectively 1.7, but the computing time for the latter equations are tremendously faster as they do not require any actual computer simulations.

1.6 The Mean Predation Pressure

The predation pressure or the risk of predation is determined by the current density of the predators, $P(t)$, and their search time, $1/(1 + hCN(t))$. The total search time itself also contains the current density of prey, which means that the MPP will vary over time if the populations themselves do this. Therefore, what is interesting is the *mean predation pressure*, (MPP) which is the predation pressure the prey experience over long time. When the MPP for $C \geq C^i$ we take the same approch as with the invasion fitness and selection gradient in the previous section. The actual MPP is therefore decided by simulating the system and taking the mean value of the predation pressure for every unstable C-value, i.e.

$$\mathrm{MPP} = \overline{\frac{P(\mathsf{t})}{1 + hCN(\mathsf{t})}}. \tag{1.14}$$

The MPP is strongly connected to the selection gradient and in this system almost completely decides what it will look like, i.e. compare with Eqn. 1.13.

Chapter 2

Methods

2.1 General Stability Analysis

The first step in the analysis of system 1.4 is to find its steady states (N_i^*, P_i^*), which are

$$(N_1^*, P_1^*) = \left(\frac{d}{C(1-dh)}, \frac{1+hCN_1^*}{C} \left(1 + qC - N_1^*\right) \right), \quad (2.1a)$$

$$(N_2^*, P_2^*) = (1 + qC, 0) \quad (2.1b)$$

and

$$(N_3^*, P_3^*) = (0,0). \quad (2.1c)$$

Here we assume that the condition $dh < 1$ is fulfilled, as 2.1a otherwise will have a negative stable prey population. As a positive stable predator population is also desired, we further assume that $1 + qC > N_1^*$ holds. This last condition can be formulated as a condition on the predator death rate d as

$$d < \frac{C(1+qC)}{1 + hC + hqC^2}, \quad (2.2)$$

which tells us that the predator death rate cannot be too high if the system should be stable. Since it is only 2.1a that gives non zero population sizes in both N and P, this is the steady state that the forthcoming analysis is concentrated on. For simplicity will this steady state therefore only be referred to as (N^*, P^*). The steady states in Equations 2.1 are equivalent to the systems fixed points, but future reference to the "fixed point" will only refer to the steady state 2.1a unless stated else.

The next step in the analysis is to bring forth the Jacobian matrix $\mathbf{J}$ of the system, which is

$$
\mathbf{J}(N,P) = \begin{pmatrix} 1 + qC - 2N - \dfrac{CP}{(1+hCN)^2} & -\dfrac{CN}{1+hCN} \\ \dfrac{CP}{(1+hCN)^2} & \dfrac{CN}{1+hCN} - d \end{pmatrix}. \quad (2.3)
$$

Evaluating $\mathbf{J}$ at the steady state (N^*, P^*) gives the sought after Jacobian[1]. One thing worth noting is that the term J_{22} will be equal zero at the steady state.

In order for the fixed point to be stable, the trace of $\mathbf{J}$ has to be strictly less than zero and its determinant strictly positive[4][7]. As all the ingoing parameters are greater than zero, it is straight forward to show that the latter condition will be fulfilled. The first condition can either be rewritten as a restriction of the growth rate of the prey, or more elegant, be solved for the vulnerability. By setting the trace equal zero and solve for C we arrive at an expression for the vulnerability that makes the system go through a Hopf bifurcation and become unstable[2]. This value is here called C^i and is defined as

$$
C^i = \frac{1}{2q} \left(\sqrt{1 + \frac{4q}{h} \left(\frac{1+dh}{1-dh} \right)} - 1 \right). \quad (2.4)
$$

When $C \geq C^i$ the system is no longer attracted to the fixed point (N^*, P^*), but instead to a limit cycle. This means that the population densities are now cycling in time. Making the same analysis on the two other fixed points tells us that 2.1c will always be unstable with saddle node dynamics, while the stability of 2.1b is unknown as the determinant of the Jacobian matrix is equal to zero.

For a fixed point to be stable, both eigenvalues, λ_1 and λ_2, of the Jacobian at that point have to have negative real part[7]. In Figure 2.1(a) the eigenvalues of $\mathbf{J}$ are illustrated as functions of the vulnerability on a large interval. We see that it is only in a small region of C-space that we have stability in the system. Figure 2.1(b) show a close up view of this specific parameter interval. It is within this region that we assume that our initial system will be. Similar eigenvalue analysis are also done for the parameter regions Cd, Ch and Cq and is presented in the Results part.

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[1]Since the analytical expression of $\mathbf{J}(N^*, P^*)$ becomes very cumbersome I decide not to write it out explicitly as further analysis was done numerically.

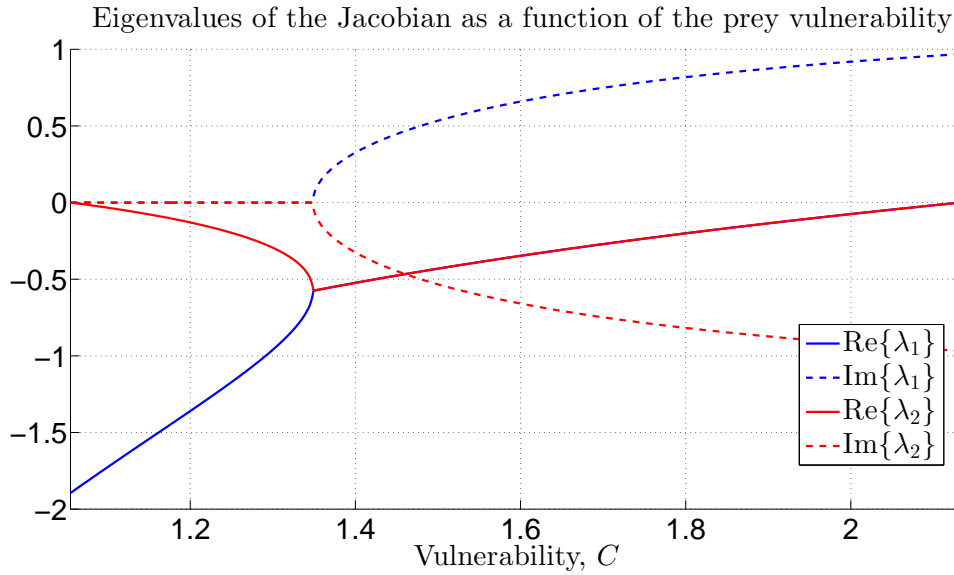[2]The calculation ends up with a second degree polynomial and we choose the root which is positive.
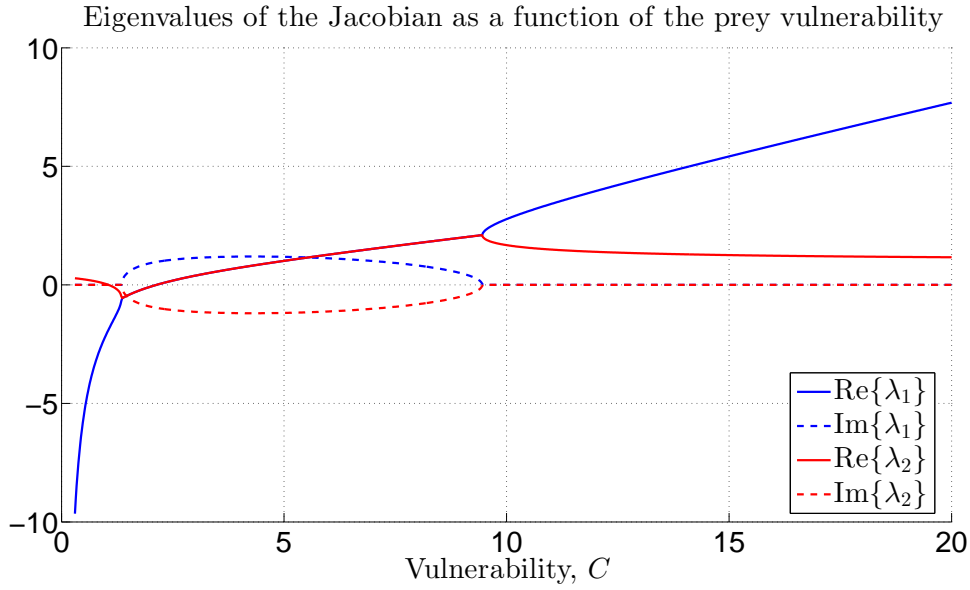
(a) The eigenvalues real and imaginary parts illustrated for a large C-interval.

(b) A close-up view on the parameter region where the system is stable.

Figure 2.1: As C increases from zero, $\mathrm{Re}\{\lambda_2\}$ will change sign from $+$ to $-$ at $\gtrapprox 1.05$ and the system will become stable. Further increase of C will destabilize the system, as the eigenvalues real parts will become positive one again at $C = C^i$. In other words, we start of the biological interesting parameter interval first when $C > 1.05$ and the system is stable. When $1.05 < C \lessapprox 1.35$, the eigenvalues are real and negative. In the region $1.35 < C < C^i$ we have a pair of complex conjugated eigenvalues which we also have in the unstable region $C^i \leq C \lessapprox 9.45$. Simulations suggest that when $C > 9.45$ $\mathrm{Re}\{\lambda_1\}$ increases in a linear manner. Other parameter values for this simulation was $d = 1.0$, $h = 0.5$ and $q = 0.85$.

2.2   Introducing Stochasticity

Consider a stochastic process $w(t)$, where

$$\Delta w = w(t + \Delta t) - w(t) \tag{2.5}$$

is independent of both w and t. Further assume that the expectation of Δw is zero and the variance is $\sigma^2 \Delta t$. The process $w(t)$ is a so called *random walk* or white noise and is introduced in the equation for the prey population density (Eqn. 1.4a) in order to model environmental fluctuations. If we let $\Delta t \to 0$ in Equation 2.5 we will be left with the differential of the random walk, dw, which has expectation zero and a variance equal $\sigma^2 dt$, where dt is the differential of t. To have realistic fluctuations, dw should have a density dependence and is therefore chosen as

$$dw = A\Gamma N^*, \tag{2.6}$$

with $0 < A \le 0.2$ and Γ a normal distributed variable with expectation value zero and variance dt. N^* is the steady state value of the prey population. To introduce dw in system 1.4, this system is also differentiated and will then look like

$$dN = f_N dt + dw \tag{2.7a}$$

$$dP = f_P dt. \tag{2.7b}$$

Now we are interested in finding out how this disturbed system will deviate from the system in 1.4 and what the effects will be on the selection gradient. Let x_1 and x_2 be the deviations the white noise causes from the steady state 2.1a. These deviations will then be given as

$$x_1 = N - N^*$$

and

$$x_2 = P - P^*.$$

Using matrix notation, the linearization of system 2.7 can be written as

$$d\mathbf{x} = \mathbf{J}\mathbf{x}dt + d\mathbf{w} \tag{2.8}$$

which can be regarded as a two dimensional Ornstein-Uhlenbeck process with $\mathbf{x} = [x_1\ x_2]^T$ and $d\mathbf{w} = [dw\ 0]^T$. The goal now is to make a complete second order Taylor approximation of the selection gradient and then calculate its mean value. The second order Taylor approximation of the selection gradient will be

$$\tilde{g} = g_0 + g_N' x_1 + g_P' x_2 + \frac{1}{2} g_{N,N}'' x_1^2 + g_{N,P}'' x_1 x_2 + \frac{1}{2} g_{P,P}'' x_2^2. \tag{2.9}$$

The subscript indices indicates the variable which g has been differentiated with respect to. Calculating the mean value of Equation 2.9 will require the mean deviations from the steady state and their variances since

$$\bar{g} = g_0 + g'_N \bar{x}_1 + g'_P \bar{x}_2 + \frac{1}{2} g''_{N,N} V(x_1)$$
$$+ g''_{N,P} C(x_1, x_2) + \frac{1}{2} g''_{P,P} V(x_2). \quad (2.10)$$

The calculation of Equation 2.10 is here performed in two steps. In Step 1 the variances are obtained by making a first order approximation of the population dynamics. In Step 2 the mean deviations from the steady state are calculated by first making a second order expansion of the expectation of dx_1 and dx_2, then calculating their mean values. Using that their mean values are equal zero and our expressions for the variances, the mean deviations can be calculated. Then we can finally calculate Eqn. 2.10.

Step 1

Making a first order Taylor expansion of the population growth functions and using that the expectation of $d\mathbf{x}$ and therefore also the expectation of $\mathbf{x}$ is zero, leads to the equation

$$\mathbf{VJ} + \mathbf{J}^T \mathbf{V} + \boldsymbol{\Sigma} = 0. \quad (2.11)$$

Here is $\mathbf{V}$ is the covariance matrix, containing the elements $V_{11} = V(x_1)$, $V_{22} = V(x_2)$ and $V_{12} = V_{21} = C(x_1, x_2)$, i.e. the variance of the prey and predator population densities and their covariance. $\mathbf{J}$ is still the regular Jacobian matrix and $\boldsymbol{\Sigma}$ is the covariance matrix of the white noise, thus containing only one non zero element σ_{11}^2 which is the variance of dw. Solving Equation 2.11 component wise gives the elements of $\mathbf{V}$ as

$$V(x_1) = -\frac{\sigma_{11}^2}{2 J_{11}}, \quad (2.12a)$$

$$V(x_2) = -\frac{J_{21}}{J_{12}} V(x_1) \quad (2.12b)$$

and

$$C(x_1, x_2) = 0. \quad (2.12c)$$

Looking at the expression of $V(x_1)$ we recognize J_{11} as the only term making up the trace of the Jacobian. However division with this component will make the variance go towards infinity as the system approaches the border of instability, reminding us that the linearized system is only a valid approximation close to the fixed point.

$\square$

Step 2

Making a second order Taylor expansion of the deviation differentials and taking their mean results in the equations

$$0 = J_{11}\bar{x}_1 + J_{12}\bar{x}_2 + \frac{1}{2}(f_N)''_{N,N}V(x_1)+$$
$$+ (f_N)''_{N,P}C(x_1, x_2) + \frac{1}{2}(f_N)''_{P,P}V(x_2)$$

and

$$0 = J_{21}\bar{x}_1 + J_{22}\bar{x}_2 + \frac{1}{2}(f_P)''_{N,N}V(x_1)+$$
$$+ (f_P)''_{N,P}C(x_1, x_2) + \frac{1}{2}(f_P)''_{P,P}V(x_2).$$

Identifying that $J_{22} = (f_N)''_{P,P} = (f_P)''_{P,P} = 0$, the equations are simplified to

$$J_{11}\bar{x}_1 + J_{12}\bar{x}_2 + \left(\frac{hC^2P^*}{(1+hCN^*)^3} - 1\right)V(x_1) = 0$$

respectively

$$J_{21}\bar{x}_1 - \frac{hC^2P^*}{(1+hCN^*)^3}V(x_1) = 0.$$

Solving this system of equations is straight forward and will give the mean deviations as

$$\bar{x}_1 = \frac{C^2hP^*}{(1+hCN^*)^3}\frac{V(x_1)}{J_{21}} \tag{2.13a}$$

and

$$\bar{x}_2 = \frac{1}{J_{12}}\left(\left(1 - \frac{hC^2P^*}{(1+hCN^*)^3}\right)V(x_1) - J_{11}\bar{x}_1\right). \tag{2.13b}$$

$\square$

Now we have got everything to successfully calculate the mean of the Taylor expanded selection gradient,

$$\bar{g} = q - \frac{P^*}{1+hCN^*} + \frac{hCP^*}{(1+hCN^*)^2}\bar{x}_1-$$
$$- \frac{1}{1+hCN^*}\bar{x}_2 - \frac{2h^2C^2P^*}{(1+hCN^*)^3}V(x_1). \tag{2.14}$$

This analytical expression is correct to the order of x_1^2, x_2^2 and x_1x_2. Equation 2.14 is compared with the selection gradient that can be calculated

directly from the numerical simulations. The numerical simulations of system 2.7 are performed using a basic forward Euler method, i.e.

$$N_{i+1} = N_i + N_i \left(1 + qC - N_i - \frac{CP_i}{1 + hCN_i} \right) dt + dw_i \qquad (2.15a)$$

$$P_{i+1} = P_i + P_i \left(\frac{CN_i}{1 + hCN_i} - d \right) dt. \qquad (2.15b)$$

The resulting vectors $N(\mathbf{t})$ and $P(\mathbf{t})$ are now used in the calculation of the mean selection gradient $\overline{g}_j$ for every vulnerability C_j,

$$\overline{g}_j = q - \overline{\frac{P(\mathbf{t})}{1 + hC_jN(\mathbf{t})}}. \qquad (2.16)$$

However, the undisturbed system 1.4 should also be simulated for the same C-interval in order for us to have anything to compare the disturbed system with. The numerical simulations of system 1.4 are made using MATLAB's own built-in ode solver called ode23t. The calculations of the system's mean selection gradients are done using Equation 1.13.
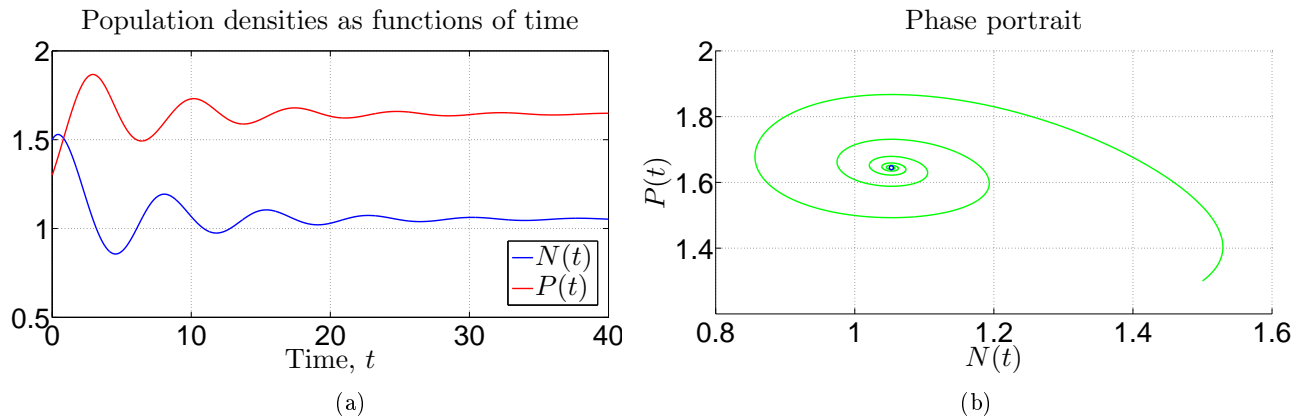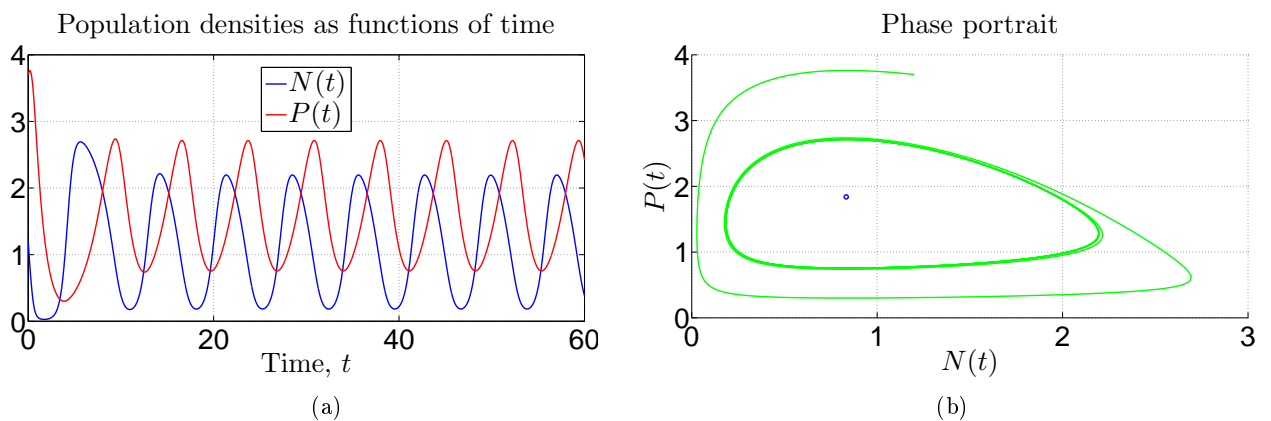
Chapter 3

Results

In all simulations, unless stated else, the values of the dimensionless constants have been: $d = 1.0$, $h = 0.5$, $q = 0.85$ and $dt = 10^{-3}$.

3.1 Basic Simulations

Simulating system 1.4, there are basically three different outcomes depending on the value of C. In the first and second, the system is stable but have either real or imaginary eigenvalues. In the third case the system is unstable and have gone through a Hopf bifurcation. In Figures 3.1(a), 3.2(a) and 3.3(a) the prey and predator densities in the different cases are shown as functions of the time and in Figures 3.1(b), 3.2(b) and 3.3(b) are their corresponding phase portraits. In the phase portraits the steady state 2.1a have been marked in each figure by a circle.

The numerical value on C where the system gets unstable was found via Equation 2.4 to be $C^i = 2.1329$, using five significant digits and the default parameter values. To get a qualitative idea of how the instability affects the system, the population densities predicted by the steady state values was compared with the mean densities from actual simulations, see Figure 3.4. It shows clearly that while the system is stable, the steady state predictions and mean values gives the same population densities, while for $C \geq C^i$ they differ quite dramatically. One sees that the prey population benefits from the now oscillating dynamics while the opposite is true for the predators, speaking in terms of their mean population densities.

Population densities as functions of time

Phase portrait

(a)

(b)
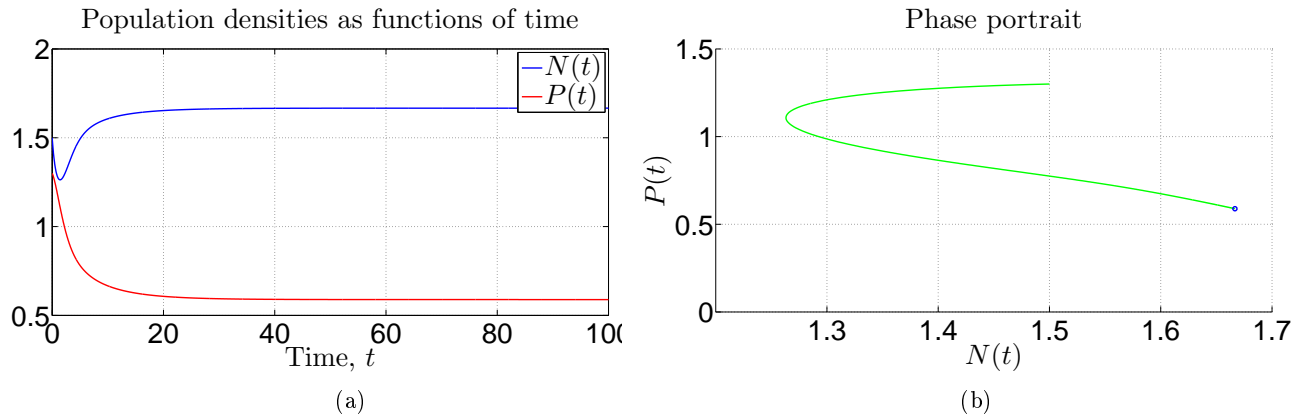
Figure 3.1: Stable system with real eigenvalues at $C = 1.2$.

Population densities as functions of time

Phase portrait

(a)

(b)

Figure 3.2: Stable system with imaginary eigenvalues at $C = 1.9$.

Population densities as functions of time

Phase portrait

(a)

(b)

Figure 3.3: Unstable system with imaginary eigenvalues at $C = 2.4$.

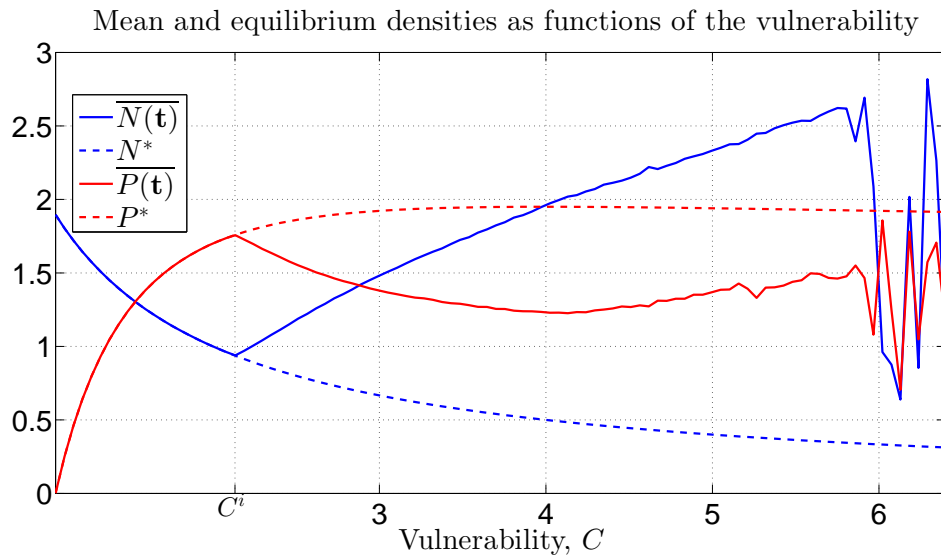Mean and equilibrium densities as functions of the vulnerability

Figure 3.4: The population densities as mean values from simulations and as predicted from the steady state as functions of the vulnerability. The C-interval for the simulation was $[1.055, 6.4]$. Note that N^* and P^* are partially covered by $\overline{N(\mathbf{t})}$ respectively $\overline{P(\mathbf{t})}$.
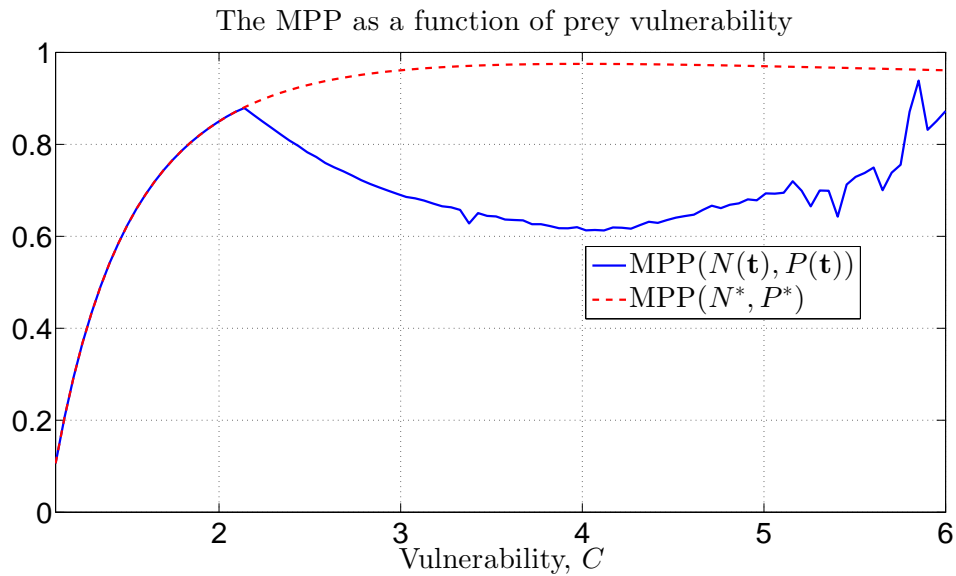
The MPP as a function of prey vulnerability

Figure 3.5: The mean predation pressure predicted by the steady state densities is equal to the actual risk of predation as long as the system is stable. When $C \geq C^i$ the actual risk of predation is reduced as the vulnerability increases.

3.2   The Mean Predation Pressure

Comparing the MPP predicted by the steady state populations with the
MPP from the actual risk of predation reveals that when the system has be-
come unstable, the actual risk of predation is reduced as the prey increases
their vulnerability, see Figure 3.5. When C just has passed 4 the actual
MPP starts to increase a little bit again. Between 5–6 the system are ex-
tremely unstable which leads to much inaccuracy in the numerical methods.
Simulations suggests that the accuracy is greatly decreased when $C > 5.92$
as it no longer predicts stable oscillations. However, already at $C = 2.70$ the
prey population reaches 2 % of its steady state value during the oscillations
and studying C-values that generates population densities that reaches this
low are not of any real biological interest. Therefore an upper "realistic"
limit is set to $C_{max} = 2.3$. This value on C generates variations in the prey
population between 53 % to 167 % of N^* and between 70 % to 126 % of P^*
in the predator population.

3.3   The Invasion Fitness and Selection Gradient

To illustrate the invasion fitness (Eqn. 1.6), we simply select an arbitrary
stable value on C^* and plot the invasion fitness as a function of C. As the
resulting function is linear in C, a positive slope indicates that mutants with
$C^* < C$ will have a higher fitness than the resident prey population and
thereby be able to invade. When the slope is zero, the ESS has been reached
and we have "zero selection". Finally, a negative slope will give mutants with
$C < C^*$ ability to invade. In Figure 3.6, these linear functions has been
generated for a number of different stable C^*-values and plotted on top of
each other. The red and blue lines represents selection for higher respectively
lower vulnerability. As C^* increases, the selection gradient decreases, until
$C^* = C^{ESS}$ and it vanishes. Increasing C^* further will then change the sign
of the selection gradient as the slope of $G(C, C^*)$ becomes negative. The
horizontal black line indicates where the slope of the invasion fitness is zero
and the black dot represents C^{ESS}, which becomes the center of rotation
once the invasion fitness function "hits" it.

Figure 3.7 is a so-called pairwise-invasibility plot which shows how the inva-
sion fitness looks in C^*C-space. The whole stable, and some of the unstable,
region is illustrated. The regions indicated with a + sign are regions in trait
space where a rare mutant with trait value C has positive initial growth rate,
while the − signs indicates regions where the mutant has negative dito. As
when $C^* = C^{ESS}$ generates a completely vertical line means that when the
population has reached the ESS, an invading mutant with *any* other vulner-
ability will have the same fitness as the residents. However, as our model is
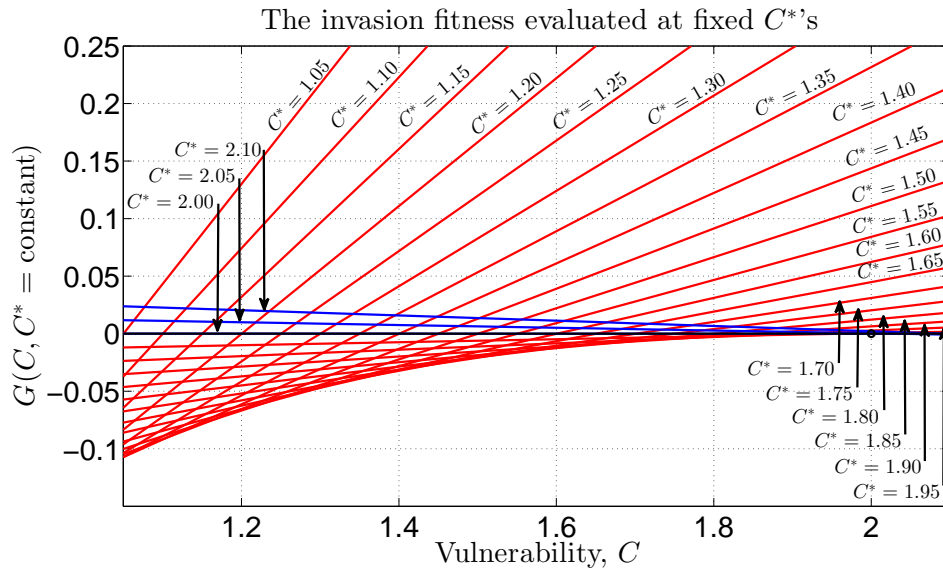
Figure 3.6: Different resident vulnerabilities generates different invasion fitness for the potential mutants. Increasing C^* will only be favorable once the invasion fitness function "hits" C^{ESS} as the slope of the fitness function afterwards will become negative with further increase in C^*.
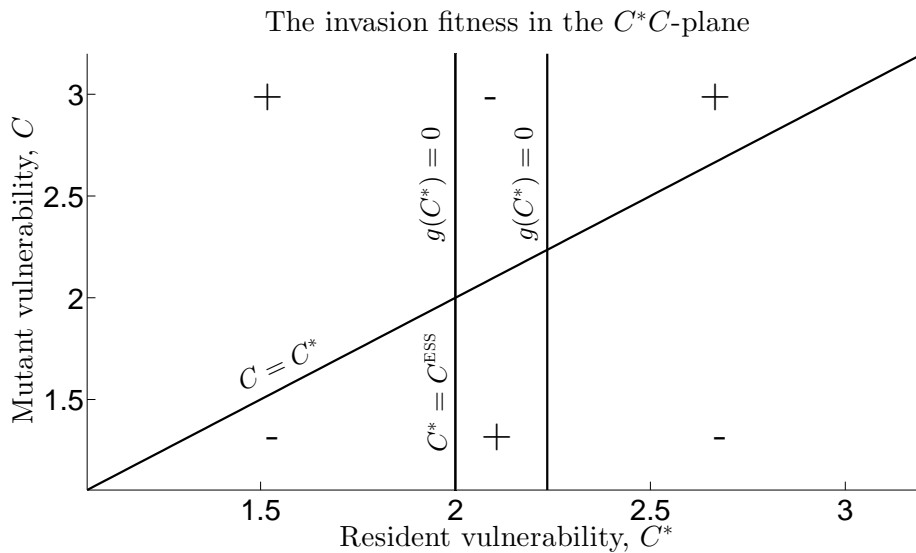
Figure 3.7: A two dimensional illustration of the invasion fitness. The + and -'s signs indicates the sign of the selection gradient, i.e. positive respectively negative initial growth rate of the mutant.

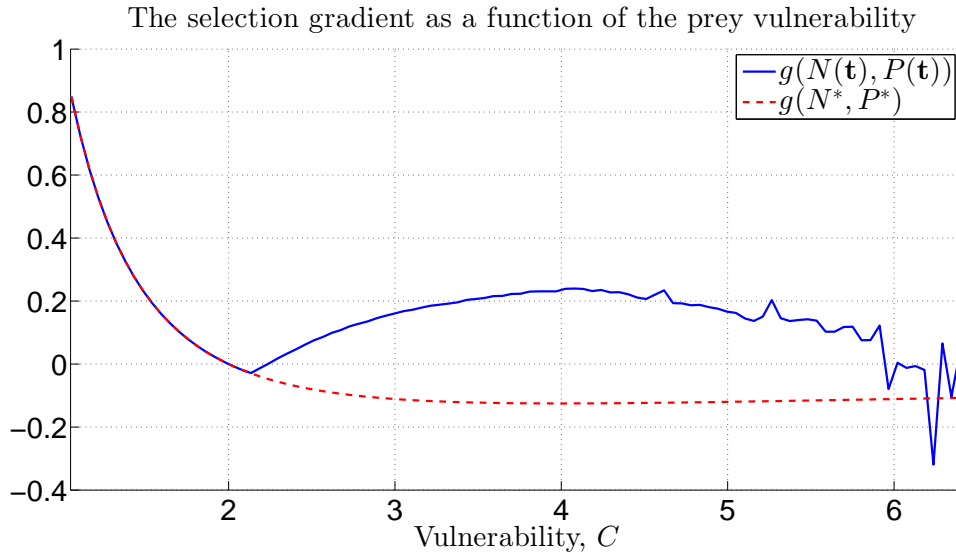The selection gradient as a function of the prey vulnerability

Figure 3.8: The selection gradient illustrated as a function of the vulnerability using two different methods of calculation, Equation 1.7 (red) respectively 1.13 (blue).

frequency dependent, a mutant that becomes "common" among the resident ESS-population will soon get negative growth rate and decrease in number (as argued in section 1.5.1).

Plotting the selection gradient as a function of the vulnerability gives us, in the stable region, a graph with negative slope which intersects the x-axis at $C = C^{\text{ESS}}$. Exploring the system outside its stable region is done easiest by looking at the selection gradient since it is depending only on C. In Figure 3.8 the selection gradient is presented both and as the average (Eqn. 1.13) and as predicted by the steady states (Eqn. 1.7). It is obvious that Equation 1.7 fails when $C \geq C^i$, which was suspected since that prediction is based on the steady state populations rather that the actual ones. Since $g(C)$ is positive for $C < C^{\text{ESS}}$ and $C > C^i$ the prey population will evolve towards *higher* vulnerability in these regions. Between these regions is an interval where the selection gradient is negative. This means that populations with resident vulnerabilities in this area will evolve towards *lower* vulnerability. Therefore will populations with vulnerabilities close to the ESS evolve towards it. This illustrates the convergence stability of the ESS, which was expected from Equation 1.11. The second time $g(C)$ crosses the x-axis C has entered the unstable region. This point is thus also a singular strategy, but neither an ESS nor convergent stable. Since we have negative selection to the left of this point and positive on the right, resident populations with vulnerabilities in these nearby regions will evolve away from this point, making it "unstable".
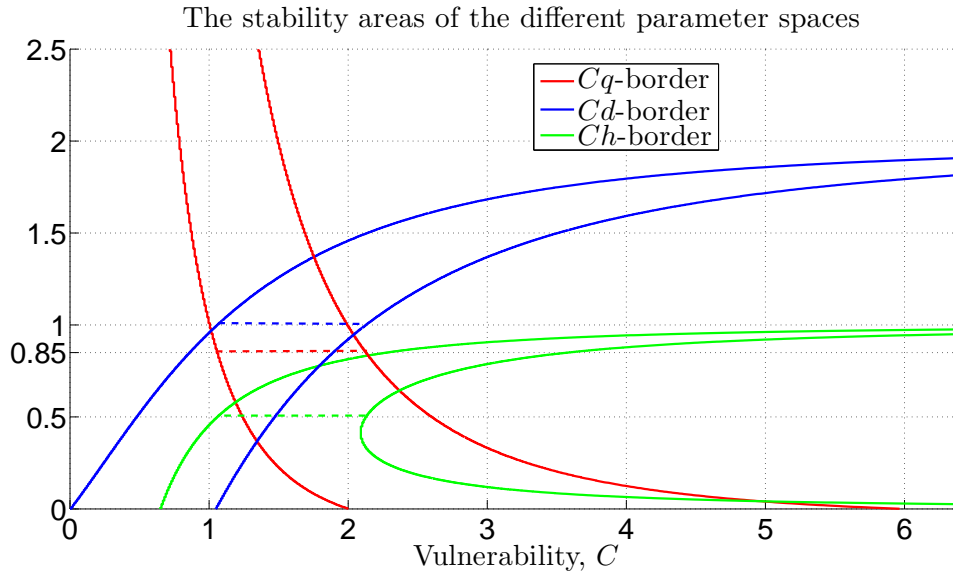
Figure 3.9: Stability areas of the parameter spaces Cd, Ch and Cq. The stable parameter region are the one that lies between the respectively colored lines. Note that since all parameters are drawn in the same graph, the y-axis has different units depending on the which of the lines you follow. The horizontal lines represent the default parameter values $q = 0.85$, $d = 1.0$ and $h = 0.5$.

From Figures 3.6 and 3.7 it is obvious that the selection gradient changes sign at $C = 2$ and thereby is $C^{\text{ESS}} = 2$. However, this can also be shown by inserting the values of the constants in Equation 1.8.

3.4 Parameter Choices Effect on the Stability

The upper boundary of the stable C-region was earlier told to be equal 2.1329. To estimate the lower limit, Figure 2.1(b) was used to see where $\text{Re}\{\lambda_2\} = 0$ which was at $C = 1.0546$. Biologically relevant C-values are therefore $C > 1.0546$. To calculate the stability region of the parameter d, both h and q was fixed to their default values while d and C varied during an eigenvalue analysis. Repeating this procedure with h and q, and plotting the stability boundaries in Cd-, Ch- and Cq-space resulted in Figure 3.9.

Increasing the death rate of the predators require that the vulnerability of the prey is increased in order to maintain stability. The opposite goes for q which if increased demands a decrease in prey vulnerability. Perhaps the strangest result is how the stability of the system is effected by variations in

the predators' handling time. As C increases beyond roughly 2, the predators will either need a high or a low handling time if the system should maintain its stability, see Fig. 3.9. If the predators have an intermediate handling time, the populations will start oscillating as the result of the instability. The parameter q has an interesting feature since it is only effecting C^i and not C^{ESS}. With the default parameter values we have $C^{\text{ESS}} < C^i$, but increasing q enough will turn the inequality sign and the system will naturally evolve into the unstable region of C-space. The critical value q^i for which $C^{\text{ESS}} = C^i$ is

$$q^i = \frac{1 - dh}{d^2 h}, \tag{3.1}$$

and is equal to 1.000, using the default parameter values. Changes in the parameters d and h have a more complex impact on the system as both C^{ESS} and C^i depend on these parameters. Decreases in either d or h will generate a smaller C^{ESS} and C^i, but since there is stronger dependence of d and h in C^{ESS} than in C^i, the ESS value will decrease proportionally more. This causes the selection gradient over the whole C-interval to decrease. The stronger parameter dependence in C^{ESS} also has noticeable effect when increases are made in these parameters. The ESS will increase faster than C^i and create an over all increase in g until $C^{\text{ESS}} = C^i$. From here we now have the same phenomenon as with the increase in q.

3.5   The Effects of a Variable Environment

The first noticeable effect of the introduction of the variable environment is an over all decrease in the MPP felt by the prey population, which results in an over all increase in the selection gradient. How much the selection gradient increases depends on the parameter A. Figure 3.10 shows how the selection gradient increases with A, calculated using Equation 2.16. The lower values on A do not increase the selection gradient significantly and it still changes sign two times, which means that the system is still evolutionary stable. As A increases, the population dynamics will experience stronger fluctuations, which inevitably will crash the populations earlier and earlier as both A and C increases. To get an intuitive grip on the realistic upper limit of A we define the "crash risk" for a specific A-value as the number of population crashes in a simulation[1], independent on the value on C, divided by the total number of simulations. In Table 3.1 the crash risk before and after reaching the unstable value on C is presented. The system was simulated for even numbers of A and the crash risk for the odd values was found by linear interpolation. At $0.0 \leq A \leq 0.12$ there is not a single population

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[1]Using $0 \leq t \leq 10^3$ with steps $\Delta t = 10^{-3}$.

crash before reaching C^i and at $0.0 \leq A \leq 0.10$ also very low crash risk afterwards. The crash risk in the stable region is regarded as acceptable while $A \leq 0.16$ and for $A \geq 0.17$ the crash risk is unrealistically high. At $A = 0.12$ it seems possible that the prey population naturally could evolve into the unstable region, as in Figure 3.10 the selection gradient is positive at the majority of the points nearby C^i and there is zero crash risk in the stable region. Worth noting is that it is always the prey population that causes the crashes, as it is here we have the primary disturbance. Table 3.1 further shows two columns with the average drop in the MPP between the disturbed and undisturbed system at two different values on the vulnerability parameter, simulated for twenty-two values of A. The drop in the MPP is higher at C^i than at C^{ESS} and as Equation 1.14 is very similar Equation 1.13, one can look at Figure 3.10 to confirm that also the selection gradient increases proportionally more at C^i than at C^{ESS}.

At $A = 0.12$ there is a 1.83 % drop in the MPP at the ESS, but is still where it seems possible for unstable evolution. Over all, the stability of the system is very sensitive to drops in the MPP. Since two different numerical methods was used, `ode23t` to calculate the undisturbed system and the explicit Euler method to calculate the disturbed, simulations with the latter was also done with no disturbance at all. The absolute value of the difference between the two methods at C^{ESS} was $0.555 \cdot 10^{-5}$ and at C^i it was $2.257 \cdot 10^{-5}$. With the chosen accuracy, this resulted in no measurable uncertainty either at C^{ESS} nor at C^i.

Comparing the Taylor expansion of g with the simulated result (Equation 2.14 and 2.16) showed that the maximum difference was about 1.0 % in the stable region of C, exept when $C \lesssim C^i$. Close to the unstable region, the Taylor expansion breaks down as the variances 2.12a and 2.12b goes towards infinity as a result of the trace of the Jacobian going towards zero. Looking at the ingoing quantities of the expansion individually, it was obvious that within the stable region, the largest negative contribution came from g'_P followed by $g''_{N,N}$. The largest positive contribution came from g'_N followed by $g''_{N,P}$.

	A	Crash risk (%)		Drop in MPP (%) at	
		$C < C^i$	$C \geq C^i$	C^{ESS}	$\lessapprox C^i$
Very low	0.00	–	–	$0.000^{\triangle}$	$0.003^{\triangle}$
	0.01	0	0	0.01	0.20
	0.02	0	0	0.05	0.42
	0.03	0	0	0.11	0.65
	0.04	0	0	0.20	0.90
	0.05	0	0	0.32	1.13
Low	0.06	0	0	0.43	1.37
	0.07	0	$0.300^{\diamond}$	0.61	1.71
	0.08	0	0.600	0.79	2.00
	0.09	0	$3.870^{\diamond}$	1.04	2.28
	0.10	0	7.140	1.24	2.63
Medium	0.11	0	$22.62^{\diamond}$	1.49	3.04
	0.12	0	38.10	1.83	3.48
	0.13	$0.900^{\diamond}$	$48.81^{\diamond}$	2.05	3.85
	0.14	1.800	59.52	2.42	4.45
High	0.15	$6.600^{\diamond}$	$71.43^{\diamond}$	2.72	4.84
	0.16	11.41	83.33	3.07	5.40
	0.17	$21.32^{\diamond}$	$90.18^{\diamond}$	3.58	6.09
	0.18	31.23	97.02	4.13	6.35
Very high	0.19	$43.85^{\diamond}$	$98.21^{\diamond}$	4.66	6.78
	0.20	56.46	99.40	5.16	7.60
	0.21	$65.02^{\diamond}$	$99.70^{\diamond}$	5.73	8.08
	0.22	73.57	100.00	6.35	8.57

Table 3.1: A table showing the crash risk within the prey population as a result of the introduction of the white noise in the prey population. 501 simulations was done on the interval $1.8 \leq C \leq 2.3$, each with time interval $0 \leq t \leq 10^3$ and time step $\Delta t = 10^{-3}$. 333 of the simulations was in the stable region and while 168 was in the unstable region. A 0 (zero) means that there wasn't a single crash during the whole simulation. Further, the table shows the mean relative drop in MPP between the disturbed and undisturbed system, calculated both at the ESS and when it is very close to C^i on the stable side[†]. 100 simulations for each A-value was done in order to calculate the mean drop in the MPP. Same time interval as before.

$\diamond$ Linear interpolated value.
$\triangle$ Simulations to estimate the difference between the explicit Euler method and `ode23t`.
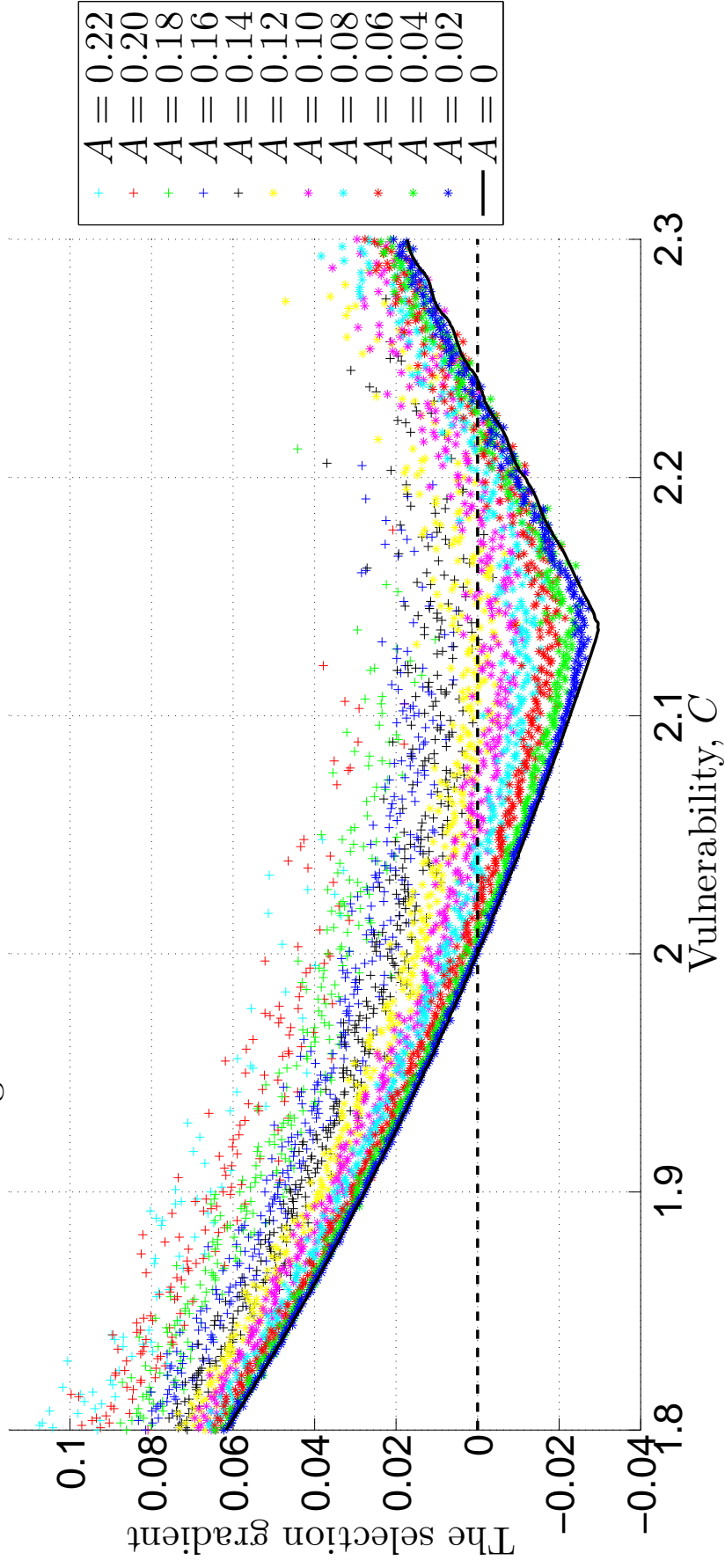[†] The simulated value was $C^i - 10^{-5}$.

Figure 3.10: The selection gradient of the disturbed system plotted for different values on the parameter A. The reason why there is fewer points in the simulations for high-value A's is that the populations crashes more frequently and earlier during the course of evolution.

Chapter 4

Discussion

4.1 The MPP

The mean predation pressure drop in the deterministic system is a direct result of the effect that cyclic dynamics have on the mean predator and prey populations. Once the system gets unstable, increasing C will lead to a decreased mean predator density while the prey density will increase. A decreased MPP is equivalent to a increased selection gradient (compare Figs. 3.5 and 3.8). Therefore will prey populations with positive selection gradient on the right hand side of C^i go on a never ending journey of evolution towards higher vulnerability. Still there are no environmental fluctuations and therefore will the completely deterministic system never crash, even though the population densities will reach extremely small values during the oscillations.

Introducing white noise in the prey population while the system was stable also resulted in a decreased MPP. The reason why the MPP drops was again that cycling dynamics, although stochastic in stable C-space, had the same effect on the mean population densities as with the deterministic unstable system.

4.2 Parameter Choices Effect on the Stability

The stability region in Ch-space is quite interesting, as at high prey vulnerabilities the predators have to have either very high or low handling time in order to have stable dynamics. Looking at the equilibrium value of the predator population (Eqn. 2.1a), we can conclude that this is a function which actually is increasing with h.

Making two simulations with one extremely low respectively high value on h reveals that the lower value generates very much oscillations before reaching its steady state, indicating that the eigenvalues have a small (negative)

real part. On the other hand, a high handling time gives almost no oscillations at all, indicating that the eigenvalues now have a large (negative) real part. Biologically this result tells us that if a predator population can catch and digest prey quickly, the mean predation pressure the prey population are experiencing will be high and their population size will thereby reduce quickly. The opposite happens when the predators take long time between their catches, even though the prey vulnerability still is very high. Continuing on the biological perspective, one could imagine an ecological system containing two predator types that coexists, preying on the same prey, but having completely different handling times and still might be close to their respectively equilibrium density. For example one could think of a forest where both snakes (high h) and small felines (low h) prey on the same bird species. However, a realistic model of this scenario would probably also require changing the other parameters. Another result from the same analysis is that if a predator population has co-evolved with the prey, decreasing the handling time as the prey increases their vulnerability, the stable dynamics are remained. Any invading predator phenotype with higher handling time will have higher fitness than the residents, but if the predators were to evolve towards higher handling times, the system itself will become unstable if not the prey population decreases their vulnerability to maintain the system within the stable region of Ch-space. Stable dynamics are also remained if the predators respond with increasing the handling time as the prey vulnerability increases. This seems however less biologically likely too me, as this means that when the prey becomes more and more easy to catch, the predators starts to catch fewer and fewer of them.

4.3   The Effect of a Variable Environment

Looking at the stable region of C-space in Figure 2.1(b), we see that a large interval here generates imaginary eigenvalues and particularly at the ESS-value. This means that if the system would get disturbed while at its ESS, the population densities will start cycle. If the amplitude of the disturbance is not that high that the populations immediately crashes, the oscillations will be damped. However if the system gets disturbed constantly, there will always be small fluctuations in the populations. When these fluctuations are very small their only effect is an insignificant increase of the selection gradient at the ESS, which still is the trait value that stable prey populations will evolve towards. In a real ecological system there could be numerous different sources that disturbs the prey (and predator) population(s). High amplitude disturbance could for example be habitat destruction, forest fires or releases of chemical toxins e.g. oil spill, which can cause the whole system to break down, even if it is stable. There are also very many sources that could create low amplitude disturbance themselves e.g. parasites, diseases or injuries and

adding them up together with the fickle weather and varying availability of food for the prey, it should be safe to assume that medium amplitude disturbances should be very common in ecological systems. Of course one can not directly translate the vague terms low, medium and high amplitude disturbance to the specific A-values that I choose to simulate the system for. But I do believe that making a connection where $0.01 \leq A \leq 0.05$ corresponds to very low amplitude disturbances, $0.06 \leq A \leq 0.10$ low, $0.11 \leq A \leq 0.14$ medium, $0.15 \leq A \leq 0.18$ high and $0.19 \leq A \leq 0.22$ very high, is not completely unrealistic. Specifically as the findings in table 3.1 showed that up to medium amplitude disturbances had very little chance, if any, to crash the populations when their dynamics are stable. And we certainly do not expect any real ecological system to break down completely because of bad weather like pouring rain, thunderstorms or drought. Because as long as there has been life on earth there have also been different types of weather and the organisms have still managed to evolve to this day. Major environmental changes, like the ice age, should be corresponding to the higher A-values. What is not quite realistic with the model is that it is only the prey population that causes the crashes. In a real ecological system one might would expect that the prey density might get so low that all the predators died out, causing an accelerated increase in the prey population[9]. Perhaps this type of dynamical behavior could be incorporated in the model if the fluctuations had higher density dependence which and/or was correlated to the population density at a specific point in time. In the simulations presented here the fluctuations was only correlated with the steady state population of the prey, completely disregarding the current population size. This caused situations where the cycling prey population could get very small disturbances when there is high density while get big disturbances when low density, where the latter causes a crash. Still it is not an unrealistic white noise parameter.

A negative selection gradient indicates that lower trait values are evolutionary favorable. In Figure 3.10 we see that for $A < 0.12$ there exists a negative selection gradient and these systems are thereby evolutionary stable as they evolve towards the CSS. We also see (Figs. 3.8 and 3.10) that there exists trait values C' which fulfills both $C' \geq C^i$ and $g(C') < 0$. This means that just because the deterministic system is unstable on the ecological time scale does not mean that the system is evolutionary unstable with run-away evolution. However, for this scenario to be interesting we must assume that a population "starts" with a trait value such as C' which then should decrease on the evolutionary time scale. Contrary to the initial assumption, that a population starts with a low dynamically stable trait value which increases. Or perhaps this region could be reached if the system first is experiencing high fluctuations and thereby run-away evolution, but when $C > C^i$ the fluctuations in the environment decreases and making $g(C) < 0$. Wich ever the case, I do believe that it is possible that a real ecological system, with

proven limit cycles, could exist within such a region. But for the system to maintain in this region for a long time (evolutionary speaking), there must be some other parameters that changes simultaneously, preventing the system from reaching ecological stability, or, again having different strength of the fluctuations on the evolutionary time scale.

Many ecological systems in nature already have oscillating dynamics, which indicates dynamical instability. They also have fluctuations, and not just on one trophic level as here, but rather on all. Although the fluctuations' strength surely differ between trophic levels, the predator population is also effected by diseases and various environmental changes and according to the results, systems with high environmental fluctuations should be expected to have unstable dynamics. It should therefore not be surprising if an ecological system shows high variations in the population densities.

Since the mathematical model is very simple, the results from it can suffer from certain remoteness of nature[10]. Therefore it is not anticipated that natural systems should have this "run-away evolution" that my results suggest. In reality this certainly does not happen to all species, as many have already lived and evolved for billions of years without going extinct. Still, populations that have evolved to extinction could have occurred in reality. I think however that it is probable that the predator population co-evolves with the prey, changing the evolutionary outcome by putting an upper limit on C. The interesting result is that populations could evolve from a stable ecological system into an unstable one, naturally. In a predator-prey model as the one I have investigated, one would probably expect an upper limit on the vulnerability for which the evolution stops. Perhaps my upper realistic limit of $C^{\mathrm{max}} = 2.3$ is not enough and the prey should actually be able to evolve towards even greater vulnerabilities?

4.4   Closing Comments

One of the downsides with using the vulnerability as evolutionary parameter was briefly mentioned in 1.1, p.9. This was that the vulnerability of the prey might have natural cycles, which in that case would demand the vulnerability to be a function depending on the time, e.g. some sinusoidal function. This would complicate the analytical analysis, but should be straight forward to implement and simulate. Another interesting study would be to estimate the vulnerability parameter with statistical methods using real data, then compare the findings with the results from this report.

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