Stable Coexistence of a Predator-Prey model with a Scavenger

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Abstract

This thesis involves the study of a predator-prey model with a scavenger. The predator also preys upon the scavenger. The objectives are to develop a model for the three species and identify conditions for stable coexistence. The thesis also addresses the effects of extinction of a population. The initial model defined in this study did not produce relevant results and was therefore revised. The revised model sets conditions for a stable equilibrium and determines the impact on the remaining populations when one population goes extinct. Local stability analysis, numerical tests using the MATCONT software application and phase space diagrams were used to arrive at and highlight the findings. The model does not aim to be definitive. It may be refined further and can serve as a basis to study a variety of research issues.
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Chapter 1

Introduction and Basic Concepts

1.1 Introduction

Mathematical models are often used to examine the dynamics of complex interacting populations. In mathematical ecology a widely known and applied model is the classical Lotka-Volterra model. This model was formulated in 1926 by Vito Volterra and around the same time Alfred Lotka independently studied similar equations. The Lotka-Volterra model, also known as predator-prey model, consists of two coupled nonlinear differential equations and illustrates the interactions of one predator and one prey population. Although these predator-prey equations give insight into ecosystems and very good results, the model has its limitations and over the years they have been refined further to better approximate reality. Nowadays many variations of this model exist with applications in other disciplines[2].

Several studies have been done in which a third species is added to a predator prey model: two predators compete for one prey [4] or a predator may fall victim to another omnivore[2]. The Lotka-Volterra model has been extended further to include n species, with more predators and prey species being considered, and many studies on this n-dimensional system have been done [4]. By contrast only a few studies have been conducted on predator prey models that include scavengers. A scavenger is an animal that lives from consuming cadavers i.e. animals which starve naturally or are killed by other animals. Scavengers are important because they clean up the environment.

Several authors [7],[9],[10], have studied the model with different assumptions in relation to the presence of the scavenger. Ben Nolting et al [7], analyzed a three species population model namely a predator, its prey and a scavenger. An equation for the scavenger population is introduced into the classical Lotka-Volterra equations. In the presented model the scavenger doesn’t influence the predator and prey population. This assumption makes the mathematical analysis easier. That does not mean that the model is completely unrealistic because there are real life situations where scavengers have no impact on predators and preys. The authors also stated that with scavengers they meant carrion feeders such as hyenas, vultures, ravens etc. Conditions for persistence and extinction of the scavenger population are calculated. According to the authors this paper serves as a basis for further research on modeling populations with scavengers.
On the other hand Previte, J. P. and Hoffman, K.A. [9] discussed two scenarios of a predator prey model with the introduction of a third species, a scavenger of the prey. In the first scenario the scavenger is also a predator of the original prey and consumes the carcasses of the predator and benefits from both interactions, while in the second scenario the scavenger benefit from the interaction with the predator and inhibits the prey but has no benefit from that interaction.

In a later study Previte, J. P. and Hoffman, K.A.[10] introduced and studied a three-species model with a scavenger added to a predator prey system, namely: the scavenger eats the prey and also consumes the carcasses of the predator. Their model has the biologically relevant property of bounded trajectories for positive initial conditions. Furthermore their model exhibits Hopf bifurcations, bistability, and chaos, which indicates the complexity of the dynamics due to adding a scavenger to a classical predator prey system.

These studies have been taken into account for the current study. The main aim of the current study is to investigate an expanded Lotka-Volterra system, with a scavenger added to it. This study differentiates itself from other expanded predator-prey models due to the following assumptions related to the scavenger namely: 1) the scavenger is eaten by the predator, an assumption not previously observed or studied by other authors, thus far, as far as the author knows; 2) the scavenger only feeds itself with the carcasses of prey, ignoring the carcasses of the predator, for the purpose of simplification of the model. An example of such a triple can be a lion, zebra and hyena, where the lion is considered the predator, the zebra the prey and the hyena the scavenger.

The purpose of the study is to formulate a model that describes the dynamics of the prey, predator and scavenger populations and ultimately to present conditions that lead to stable coexistence. In this study stable coexistence is considered to be a stable equilibrium or a stable limit cycle of the populations. In addition, a special case scenario is considered namely the impact of the extinction of one of the populations. The study does not aim to validate the model with real life data, although the intention is to find results that may be relevant in ecological terms.

In order to find conditions for a stable coexistence a local stability analysis of the equilibria of a first model was done and an extensive number of numerical simulations were performed using the software package Matcont. The purpose of the computer simulations was to verify analytical calculations as well as to study the stability of non-hyperbolic equilibrium points of the model. Conditions for stable coexistence were found as will be discussed in detail in the thesis. Furthermore the study also shows that the extinction of all three populations only occurs if the prey dies out. After the analysis of the model it was concluded that the carrying capacity of the predator should be taken into account for more relevant results. Therefore an extension of the original model was formulated and analyzed.

The thesis is organized as follows. The first chapter deals with some basic concepts and theory relevant to understand the calculations done in future chapters. The second chapter gives the analysis of the model and chapter three describes the extended model.
In chapter three the conditions for stable coexistence of the three populations can be found. In the fourth chapter the effects are examined when one of the populations dies out. The last chapter deals with the conclusions and future research to be done with the model.
1.2 Basic Concepts

This paragraph contains some basic concepts, definitions and theorems to better understand the calculations made in future chapters.

1.2.1 The classical Lotka-Volterra system

A predator-prey system or Lotka-Volterra system is a system of coupled differential equations. The simplest form of the model is made up of one predator and one prey where the prey is the only food supply for the predator. If $x(t)$ is the prey population and $y(t)$ the predator population then the model consists of the following differential equations:

$$
\begin{align*}
&\frac{dx}{dt} = ax - bxy \\
&\frac{dy}{dt} = -cy + dxy
\end{align*}
$$ (1.1)

The parameters $a$, $b$, $c$, $d$, are all positive constants. The parameter $a$ is the natural growth rate of the prey and $c$ is the natural death rate of the predators. Parameter $b$ is called the predation rate coefficient and represents the effect of predation. And the parameter $d$ is the reproduction rate of predators per one eaten prey. In this model it is assumed that prey are the only food supply for predators and prey have enough food. Furthermore prey will grow exponentially in absence of predators and predators will go extinct (also exponentially) in absence of prey. Birth, death and migration are proportional with the size of the population. The encounters between predators and prey are proportional with the size of both populations.

The system cannot be solved analytically, and thus numerical methods must be used to find the solution of the model. But instead of solving the system, it is better to use graphical methods to analyze the behavior of the model. For autonomous systems, solutions in the $xy$-plane are analyzed. The $xy$-plane is called the phase plane and the solution curve is called trajectory or orbit of the system. Volterra has proven geometrically that solutions of system (1.1) in the positive space are closed curves with the exception of the equilibrium point [1]. Closed orbits correspond to periodic solutions [13]. Figure 1.1 is an example of closed curves in the phase space.
1.2.2 Definition and Stability Analysis of equilibrium points

An equilibrium point $x^*$ (sometimes called fixed points or steady states) of a dynamical system $\dot{x} = f(x)$, $x \in \mathbb{R}^n$ is a constant solution. That implies that the system at this point remain unchanged with time. The equilibrium points $x^*$ can be found by setting the derivatives of the equations to zero, and then solve for $x$.

Stability definitions of equilibrium points

**Definition 1.1.** An equilibrium point $x^*$ is **attracting** if there is a $\delta > 0$ such that $x(t) \to x^*$ as $t \to \infty$, whenever $|x(0) - x^*| < \delta$. Thus any trajectory that starts within a distance $\delta$ of $x^*$ is guaranteed to converge to $x^*$ eventually.

**Definition 1.2.** An equilibrium point $x^*$ is **Lyapunov stable** if for each $\epsilon > 0$, there is a $\delta > 0$ such that $|x(t) - x^*| < \epsilon$, whenever $t \geq 0$ and $|x(0) - x^*| < \delta$. Thus trajectories that start within $\delta$ of $x^*$ remain within a distance $\epsilon$ of $x^*$ for all positive time.

In figure 1.2 is shown that trajectories that start nearby an attracting equilibrium point must approach the equilibrium point eventually. In contrast if an equilibrium point is **Lyapunov stable**, trajectories remain close for all time.

![Figure 1.2: Attracting and Liapunov stable point (Strogatz, 1994, p. 142)](image)
Definition 1.3. An equilibrium point $x^*$ is **asymptotically stable** if it is both attracting and Lyapunov stable.

Definition 1.4. An equilibrium point is **neutrally stable** when it is Lyapunov stable but not attracting. Nearby trajectories are neither attracted to nor repelled from a neutrally stable equilibrium point.

If none of the above holds the equilibrium point is unstable.[13].

**Stability Analysis of equilibrium points**

To classify the equilibrium points the eigenvalues of Jacobian matrix of the corresponding dynamical system are computed. An equilibrium point $x = x^*$ of $\dot{x} = f(x)$, $x \in \mathbb{R}^n$ is a **hyperbolic fixed point** if none of the eigenvalues of the Jacobian matrix have a zero real part. Hyperbolic fixed points are robust, which means that the phase portrait near the equilibria does not change qualitatively. Moreover for such a fixed point the behavior of the system is qualitatively the same as the behavior of the linearized system. This is a consequence of the Hartman-Grobman Theorem. The Hartman-Grobman Theorem or linearization Theorem states that the local phase portrait of the system and its linearization are topologically equivalent in the neighborhood of a hyperbolic fixed point. Topologically equivalent means that there exists a homeomorphism that maps one local phase portrait to the other.

An equilibrium point $x = x^*$ of $\dot{x} = f(x)$, $x \in \mathbb{R}^n$ is **non-hyperbolic** if at least one eigenvalue of the Jacobian matrix is zero or has a zero real part. These equilibria are not robust which means that the system does change qualitatively under small changes. Non-hyperbolic equilibria with all eigenvalues having negative or zero real parts are considered to be critical because their stability cannot be determined using the eigenvalues of the Jacobian matrix.

**An equilibrium point is asymptotically stable if all eigenvalues of the Jacobian matrix have negative real parts and it is unstable if at least one eigenvalue has positive real part**

**Classification of equilibria in the three dimensional space**

The Jacobian matrix of a three dimensional system has 3 eigenvalues of which all three can be real or only one is real and the two others are complex conjugate. The sign of the real parts of the eigenvalues of the Jacobian evaluated at the equilibrium determines the local stability of that equilibrium point. Based on the sign of the eigenvalues and whether or not they are real, we can distinguish between four types of equilibriums: (see also Table 1.1)

- A hyperbolic fixed point is a **node** when all eigenvalues are real and have the same sign. The node is stable when the three eigenvalues are negative and unstable when the eigenvalues are positive.

- When all three eigenvalues are real with at least one of them positive and at least one of them negative than the fixed point is a **saddle**. A saddle is always unstable.
• When there are complex eigenvalues, the fixed point is either a focus-node or a saddle-focus. If all three eigenvalues have real parts of the same sign the fixed point is a **focus-node**, which is stable when the sign is negative and unstable when the sign is positive.

• If there is one real eigenvalue with the sign opposite to the sign of the real part of the complex-conjugate eigenvalues the fixed point is a **saddle-focus** and always unstable [3].

**Table 1.1: Classification of three dimensional equilibrium points**

<table>
<thead>
<tr>
<th>Eigenvalues</th>
<th>Fixed point and stability</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Real eigenvalues</strong></td>
<td></td>
</tr>
<tr>
<td>$\lambda_1, \lambda_2, \lambda_3$ negative</td>
<td>Stable node</td>
</tr>
<tr>
<td>$\lambda_1, \lambda_2, \lambda_3$ positive</td>
<td>Unstable node</td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td>Real eigenvalues and at least one positive and one negative</td>
<td>Saddle (unstable)</td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Complex eigenvalues</strong></td>
<td></td>
</tr>
<tr>
<td>$\lambda_1, \lambda_2, \lambda_3$ negative real parts</td>
<td>Stable focus-node</td>
</tr>
<tr>
<td>$\lambda_1, \lambda_2, \lambda_3$ positive real parts</td>
<td>Unstable focus-node</td>
</tr>
<tr>
<td>One real eigenvalue with sign opposite to the sign of the real part of the complex eigenvalues</td>
<td>Saddle-focus (unstable)</td>
</tr>
</tbody>
</table>

**Routh’s criterion**

Sometimes it is difficult (or nearly impossible) to calculate the eigenvalues. In such cases the Routh Hurwitz method is a useful option for evaluating the stability of fixed points. With this method it can be determined whether the roots of all the eigenvalues have negative real parts. The roots of the polynomial $a_n s^n + a_{n-1}s^{n-1} + \ldots + a_1 s + a_0$, with $a_n \neq 0$, all have a negative real part if and only if the Routh table consists of $n+1$ rows and all the elements in the first column of the table have the same sign, i.e., all elements of this column are either positive or negative. In the Routh table coefficients are arranged as follows:

$$
\begin{array}{ccc}
 a_n & a_{n-2} & a_{n-4} \\
 a_{n-1} & a_{n-3} & a_{n-5} \\
 b_{n-2} & b_{n-4} & b_{n-6} \\
\end{array}
$$
where the coefficients $b_i$, $c_i$, $d_i$ are defined as follows:

\[
b_{n-2} = \frac{a_{n-1}a_{n-2} - a_{n}a_{n-3}}{a_{n-1}} \quad b_{n-4} = \frac{a_{n-1}a_{n-4} - a_n a_{n-5}}{a_{n-1}}
\]

\[
c_{n-3} = \frac{b_{n-2}a_{n-3} - a_{n-1}b_{n-4}}{b_{n-2}} \quad c_{n-5} = \frac{b_{n-2}a_{n-5} - a_{n-1}n_{n-6}}{b_{n-2}}
\]

\[
d_{n-4} = \frac{c_{n-3}b_{n-4} - b_{n-2}c_{n-5}}{c_{n-3}} \quad d_{n-6} = \frac{c_{n-3}b_{n-6} - b_{n-2}c_{n-7}}{c_{n-3}}
\]

If coefficients are found with a negative index then these coefficients are set to be zero. When a zero in the first column is encountered the table is finished. The Routh table contains at most $n + 1$ rows [8]

Suppose there is a third degree characteristic polynomial $a_3 \lambda^3 + a_2 \lambda^2 + a_1 \lambda + a_0 = 0$. The corresponding Routh table is:

\[
\begin{array}{cccc}
a_3 & a_1 \\
a_2 & a_0 \\
b_1 & \\
c_0 & \\
\end{array}
\]

where $b_1 = \frac{a_2a_1 - a_3a_0}{a_2} = a_1 - \frac{a_3a_0}{a_2}$ and $c_0 = \frac{b_1a_0 - a_2b_{-1}}{b_1} = a_0$
1.3 Stable, unstable and center manifolds

Definition 1.5. A set $S \in \mathbb{R}^n$ is an invariant set of a dynamical system if
\[ \forall x_0 \in S \text{ and } \forall t \geq 0, \ x(t) \in S \] [5]

Definition 1.6. The stable eigenspace $V^s$ is the space spanned by the eigenvectors whose corresponding eigenvalues have negative real parts. The unstable eigenspace $V^u$ is the space spanned by the eigenvectors whose corresponding eigenvalues have positive real parts. The centre eigenspace $V^c$ is the space spanned by the eigenvectors whose corresponding eigenvalues have a real part of zero.

Definition 1.7. The stable manifold $W^s$ of an equilibrium point $E$ is a set of points in the phase space with the following two properties:

1. For $x \in W^s$, $\phi'(x) \rightarrow E$ as $t \rightarrow \infty$, and $\phi'(x)$ denotes the solution of the system.
2. $W^s$ is tangent to $V^s$ at $E$.

Definition 1.8. The unstable manifold $W^u$ of an equilibrium point $E$ is a set of points in the phase space with the following two properties:

1. For $x \in W^u$, $\phi'(x) \rightarrow E$ as $t \rightarrow -\infty$
2. $W^u$ is tangent to $V^u$ at $E$.

Definition 1.9. The center manifold of an equilibrium point $E$ is an invariant manifold of the differential equations with the added property that the manifold is tangent to $V^c$ at $E$.

The centre manifold theorem

The Center Manifold Theorem states that associated with each equilibrium $(x_0, y_0, z_0)$ there exist invariant sets containing $(x_0, y_0, z_0)$, called the stable manifold, the unstable manifold, and a center manifold. The stable and unstable manifolds are unique, but there may be more than one center manifold. The dimensions of these sets are given by the number of eigenvalues of the Jacobian at $J(x_0, y_0, z_0)$ having negative, positive, and zero real part, respectively. Moreover, each such manifold is tangent to the real space that is spanned by the eigenvectors associated with that manifold. On the stable manifold all trajectories tend toward the equilibrium as $t \rightarrow \infty$, and on the unstable manifold all trajectories tend away from the equilibrium as $t \rightarrow \infty$. However, the theorem gives no conclusion concerning the direction of the flow of trajectories on a center manifold [12].

1.4 Limit cycles and Andronov-Hopf bifurcations

Sometimes trajectories turn out to be closed curves. That means the solution is periodic. An isolated closed curve is called a limit cycle. A limit cycle could be stable, unstable or semistable. A limit cycle is stable or attracting when nearby trajectories
spiral towards it and unstable when limit cycles spiral away from it. The limit cycle is semistable when some nearby curves approach towards it while others move away from it.

Bifurcation is the qualitative change of a system due to the change of parameter values. For example, if parameter values are changed a stable equilibrium can become unstable and vice versa. Bifurcation occurs only in non-hyperbolic equilibrium points, because according to the Hartman-Grobman Theorem the structure of the system and the linearized system are the same near a hyperbolic equilibrium point. A very important bifurcation is the Andronov-Hopf bifurcation mostly referred to as Hopf bifurcation and occurs when a stable equilibrium more specifically a stable focus becomes an unstable focus and a limit cycle arises. The bifurcation is called supercritical when a stable equilibrium becomes unstable and a stable limit cycle is born. When an unstable limit cycle arises from an unstable focus that becomes stable the bifurcation is called subcritical [13]

1.5 Carrying capacity in an ecosystem

In ecological terms, the carrying capacity of an ecosystem is the size of the population or community that can be supported indefinitely upon the available resources and services of that ecosystem. Living within the limits of an ecosystem depends on three factors: the amount of resources available in the ecosystem; the size of the population or community; and the amount of resources each individual within the community is consuming [14].

1.6 The system in the dimensionless form

A model can be transformed into a dimensionless form. That is rewriting the system in terms of dimensionless quantities. One of the advantages of a system in the dimensionless form is that the number of parameters is reduced to a minimum. That makes the analysis easier. Furthermore parameters can be better compared with each other, in terms of small and large and thus one gets more insight into the system. It is also possible to make a comparison between different systems. The dynamics of the transformed model will be the same as in the original system [6].
Model I
The predator-prey-scavenger model without the carrying capacity of the predator

2.1 Introduction

In this chapter, the development of the model, its analysis and the findings will be discussed in order to study possible conditions for a stable coexistence of the predator, prey and scavenger populations. The model in this chapter will be referred to as Model I or First Model.

The development of Model I consists of the construction of the equations based on the intended assumptions and the transformation of the system in the dimensionless form. In order to develop and analyse the model, a brief literature review was carried out, followed by a study of theorems and concepts of non-linear dynamical systems to achieve a clear understanding of: 1) how the equations should be written and the model be constructed; 2) the importance of writing the model in the dimensionless form; 3) the stability analysis of equilibrium points.

The analysis includes the calculation and determination of the stability of all equilibrium points. The analysis of Model I also involves numerical simulations. The findings consist of an interpretation of the analytical and numerical outcomes.

2.2 Description of Model I

Assumptions of Model I

- The prey has enough food and will grow exponentially in the absence of predators. The exponential growth is illustrated by the term $AX$.

- The rate of predation upon the prey is proportional to the encounters of predators and prey. This assumption is modeled by the term $-BXY$. 
• The scavenger population has no impact on the prey population. There is no $Z$ term in the first equation.

• Predators will die out exponentially in the absence of prey and scavengers. This assumption is represented by the term $-CY$.

• The predator population increases, due to predation upon prey and scavengers. The terms $DXY$ and $EXY$ are illustrating this assumption.

• Without predators and prey the scavengers will also go extinct. The terms that represented this assumption are $-FZ$ and $-JZ^2$.

• The term $JZ^2$ ensures that the scavenger population does not grow endlessly.

• The scavenger population benefits from prey that die naturally or prey killed by predators. The terms representing that are $GXZ$ and $IXYZ$ respectively.

• The rate of predation upon the scavenger is proportional to the encounters of predators and scavengers. This assumption is modeled by the term $-HYZ$.

• Predators prey and scavengers will come across each other randomly in the environment.

• The populations live in a closed environment, so there will be neither immigration nor emigration and there will be no change benefiting a particular species.

The model consists of three species, namely a predator, a prey and a scavenger and is made up of the following nonlinear, autonomous differential equations:

\[
\begin{align*}
\frac{dX}{dt} &= AX - BXY \\
\frac{dY}{dt} &= -CY + DXY + EYZ \\
\frac{dZ}{dt} &= -FZ + GXZ - HYZ + IXYZ - JZ^2
\end{align*}
\]

where $X(t)$ represents the prey population, $Y(t)$ the predator population and $Z(t)$ represent the scavenger species. There are ten parameters and all are assumed to be positive constants. Variables are non-negative.

Model I can be classified as a continuous, deterministic, unstructured population model. The model is represented by differential equations and thus continuous. For any set of initial conditions there is only one solution. There is no randomness in the result. That makes the system a deterministic model. With unstructured population is meant that all members of a certain population are considered identical.[11].
2.2.1 Parameters of Model I

The parameters of Model I are presented in Table 2.1.

The parameter $A$ represents the natural growth rate of prey and is proportional to the prey population. The parameter $B$ represents the effect on the prey because of the predation of the predator.

In the second equation parameter $C$ represents the natural death rate of the predators. The predator population benefits from the prey and that result in an increase in the predator population. Parameter $D$ is associated with the increase and is called the reproduction rate of predators per one eaten prey. But the predators are also benefiting from the scavengers and parameter $E$ represents the effect of predation from the scavengers.

The parameter $F$ in the last equation is the natural death rate of the scavengers and the parameter $J$ ensures that the scavenger population cannot grow infinitely. The parameter, $G$ represents the benefit to scavengers from prey that die naturally while the parameter $I$ is the benefit when prey are killed by predators. The effect on the scavenger because of the predator is represented by the parameter $H$.

It is important to mention that the system is not a generalized Lotka-Volterra system because of the term $IXYZ$ that is associated with the interaction of the three species.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Interpretation</th>
</tr>
</thead>
<tbody>
<tr>
<td>$A$</td>
<td>natural growth rate of $X$</td>
</tr>
<tr>
<td>$B$</td>
<td>effect on $x$ due to predation of $Y$</td>
</tr>
<tr>
<td>$C$</td>
<td>natural death rate of $Y$</td>
</tr>
<tr>
<td>$D$</td>
<td>benefit to $Y$ from $X$</td>
</tr>
<tr>
<td>$E$</td>
<td>benefit to $Y$ from $Z$</td>
</tr>
<tr>
<td>$F$</td>
<td>natural death rate of $Z$</td>
</tr>
<tr>
<td>$G$</td>
<td>benefit to $Z$ from $X$ (natural death)</td>
</tr>
<tr>
<td>$H$</td>
<td>effect on $Z$ due to predation of $Y$</td>
</tr>
<tr>
<td>$I$</td>
<td>benefit to $Z$ from $X$ killed by $Y$</td>
</tr>
<tr>
<td>$J$</td>
<td>relates to the carrying capacity of $Z$</td>
</tr>
</tbody>
</table>

1Generalized Lotka Volterra systems contain only quadratic terms
2.2.2 The dimensionless form of Model I

The original system (see equation 2.1) contains ten parameters. With four variable changes the number of parameters can be reduced to six. The dynamics of the new model will be the same as in the original system.

System (2.1) can be written as

\[
\begin{align*}
\frac{dX}{dt} &= AX(1 - \frac{B}{A}Y) \\
\frac{dY}{dt} &= AY(-\frac{C}{A} + \frac{D}{A}X + \frac{E}{A}Z) \\
\frac{dZ}{dt} &= AZ(-\frac{F}{A} + \frac{G}{A}X - \frac{H}{A}Y + \frac{I}{A}XY - \frac{J}{A}Z)
\end{align*}
\] (2.2)

The variable changes are as follows:

\[
\begin{align*}
\tau &= At \Rightarrow d\tau = A \ dt \Rightarrow dt = \frac{d\tau}{A} \quad (2.3) \\
y &= \frac{B}{A}Y \Rightarrow Y = \frac{A}{B}y \Rightarrow \frac{dY}{dt} = \frac{A}{B} \frac{dy}{dt} \quad (2.4) \\
x &= \frac{D}{A}X \Rightarrow X = \frac{A}{D}x \Rightarrow \frac{dX}{dt} = \frac{A}{D} \frac{dx}{dt} \quad (2.5) \\
z &= \frac{E}{A}Z \Rightarrow Z = \frac{A}{E}z \Rightarrow \frac{dZ}{dt} = \frac{A}{E} \frac{dz}{dt} \quad (2.6)
\end{align*}
\]

Substituting (2.3), (2.4) and (2.5) in the first equation of system (2.2) gives

\[
\frac{A}{D} \frac{dx}{d\tau} A = A \frac{A}{D} x(1 - y) \Rightarrow \frac{dx}{d\tau} = x(1 - y) \quad (2.7)
\]

Substituting (2.3) to (2.6) in the second equation of system (2.2) gives

\[
\frac{A}{B} \frac{dy}{d\tau} A = A \frac{A}{B} y(-\frac{C}{A} + x + z) \Rightarrow \frac{dy}{d\tau} = y(-\frac{C}{A} + x + z) \quad (2.8)
\]

Substituting (2.3) to (2.6) in the third equation of system (2.2) gives

\[
\frac{A}{E} \frac{dz}{d\tau} A = A \frac{A}{E} z(-\frac{F}{A} + \frac{G}{A}x - \frac{H}{A}y + \frac{I}{A}A\frac{A}{A}xxy - \frac{J}{A}A\frac{A}{E}z) \Rightarrow \frac{dz}{d\tau} = z(-\frac{F}{A} + \frac{G}{A}x - \frac{H}{B}y + \frac{I}{A}A\frac{A}{D}xxy - \frac{J}{E}z) \quad (2.9)
\]

\[
\frac{dz}{d\tau} = z(-\frac{F}{A} + \frac{G}{A}x - \frac{H}{B}y + \frac{I}{A}A\frac{A}{D}xxy - \frac{J}{E}z) \quad (2.10)
\]
Hence system (2.2) becomes

\[
\begin{align*}
\frac{dx}{d\tau} &= x(1 - y) \\
\frac{dy}{d\tau} &= y\left(\frac{-C}{A} + x + z\right) \\
\frac{dz}{d\tau} &= z\left(\frac{-E}{A} + \frac{G}{B}x - \frac{H}{B}y + \frac{I*A*D}{B*D}xy - \frac{J}{E}z\right)
\end{align*}
\] (2.11)

or

\[
\begin{align*}
\frac{dx}{dt} &= x(1 - y) \\
\frac{dy}{dt} &= y(-c + x + z) \\
\frac{dz}{dt} &= z(-d + ex - fy + gxy - hz)
\end{align*}
\] (2.12)

with \(c = \frac{C}{A}; \ d = \frac{F}{A}; \ e = \frac{G}{D}; \ f = \frac{H}{B}; \ g = \frac{I*A}{B*D}; \ h = \frac{J}{E}; \) and \(\tau\) may be replaced by \(t\).

Model I is represented by the equations of system (2.12) and this system will be used for further calculations.

### 2.3 Methods

In this paragraph the applied methods with the aim to find conditions for a stable coexistence of the predator, prey and scavenger populations, are presented. Taking into account the theorems and concepts introduced in Chapter one, the findings of authors [7],[9],[10], and the comprehension achieved on the object in study, the following research steps were defined and carried out:

- Calculation and local stability analysis of all equilibrium points using the Jacobian matrix. The matrix and the coefficients of the characteristic polynomial were computed using the Maple computer algebra system. In case eigenvalues could not be calculated, the stability of equilibrium points was determined using the Rouths method. The stability of non-hyperbolic equilibrium points was investigated numerically.

- Calculation of the stable and unstable manifolds in order to better understand the local behavior near the equilibrium point was carried out only for those cases where the eigenvalues were calculated.

- An extensive number of numerical simulations was performed using the software package Matcont, a graphical Matlab package for the analysis of dynamical systems, in order to verify analytical calculations as well as to study the stability of non-hyperbolic equilibrium points of the model.

- Model improvement taking into account the carrying capacity principle.
2.4 Results for equilibrium calculation and stability analysis

2.4.1 Results for the calculation of the equilibrium points

The equilibrium points of the system in equation (2.12) can be found by setting all equations equal to zero and solving the system for x, y and z.

Thus the system

\[
\begin{align*}
\frac{dx}{dt} &= x(1 - y) = 0 \\
\frac{dy}{dt} &= y(-c + x + z) = 0 \\
\frac{dz}{dt} &= z(-d + ex - fy + gxy - hz) = 0
\end{align*}
\]

must be solved.

That is equivalent to solving eight subsystems. Three subsystems have no solutions and therefore there are five equilibrium points.

The five equilibrium points are $(0, 0, 0)$, $(c, 1, 0)$, $\left(0, 0, -\frac{d}{h}\right)$, $\left(0, -\frac{hc + d}{f}, c\right)$ and

\[
\left(\frac{d + f + hc}{e + g + h}, 1, \frac{ce + cg - d - f}{e + g + h}\right)
\]

The prey, predator and scavenger populations are represented by non negative numbers. Therefore the equilibrium points $\left(0, 0, -\frac{d}{h}\right)$, $\left(0, -\frac{hc + d}{f}, c\right)$ are not realistic because $-\frac{d}{h} < 0$ and $-\frac{hc + d}{f} < 0$.

Thus only three equilibrium points will be considered:

$E_1 = (0, 0, 0)$

$E_2 = (c, 1, 0)$ and

$E_3 = (\alpha, 1, \beta)$ with $\alpha = \frac{d + f + hc}{e + g + h}$ and $\beta = \frac{ce + cg - d - f}{e + g + h}$

Evaluating the fixed point $E_3 = (\alpha, 1, \beta)$ the x-coordinate $\alpha$ is always positive. To force the z-coordinate $\beta$ to be positive or zero the condition $ce + cg - d - f \geq 0$ must be satisfied.

If $\beta = 0$ then $ce + cg = d + f$ and $\alpha = \frac{d + f + hc}{e + g + h} = \frac{ce + cg + hc}{e + g + h} = \frac{c(e + g + c)}{e + g + h} = c$

That implies that the point $E_3 = (\alpha, 1, \beta)$ coincides with the point $E_2 = (c, 1, 0)$.

Hence if $ce + cg = d + f = 0$ there will be two equilibrium points. If on the other hand $ce + cg = d + f > 0$ then there exists three equilibrium points and the point $E_3 = (\alpha, 1, \beta)$ lies in the positive octant.

\footnote{A detailed calculation of the equilibrium points is given in Appendix A.1}
2.4.2 Results of the stability analysis of the point $E_1 = (0, 0, 0)$

The Jacobian matrix of system (2.12) is:

$$\begin{bmatrix}
1 - y & -x & 0 \\
y & -c + x + z & y \\
z(e + gy) & z(-f + gx) & -d + ex - fy + gxy - 2hz
\end{bmatrix}$$  \hspace{1cm} (2.14)

Evaluating the Jacobian for $E_1$ gives the matrix $M_1 = \begin{bmatrix} 1 & 0 & 0 \\ 0 & -c & 0 \\ 0 & 0 & -d \end{bmatrix}$

Calculation of the eigenvalues of the system requires solving the equation $\text{Det}(\lambda I - M_1) = 0$, where $I$ is the identity matrix.

This results in the matrix $\lambda I - M_1 = \begin{bmatrix} \lambda - 1 & 0 & 0 \\ 0 & \lambda + c & 0 \\ 0 & 0 & \lambda + d \end{bmatrix}$

The characteristic equation becomes $(\lambda - 1)(\lambda + c)(\lambda + d) = 0$, which results in three real eigenvalues: $\lambda = 1$, $\lambda = -c$, $\lambda = -d$. The conclusion is that the equilibrium is a saddle point and thus an unstable equilibrium point.

**Stable, unstable and center manifolds**

The eigenvector for $\lambda = 1$ is $(1, 0, 0)$. Hence the unstable eigenspace is the one dimensional space spanned by $(1, 0, 0)$. According to the center manifold theorem there exists a one dimensional manifold (curve) tangent to $(1, 0, 0)$ at the equilibrium point $(0, 0, 0)$. This unstable manifold is the x-axis. Trajectories starting on the x-axis do not approach the equilibrium point $(0, 0, 0)$ but tend to infinity. Figure 2.1 gives an example of a trajectory starting on the x-axis and approaching infinity.

The eigenvectors for $\lambda = -c$ and $\lambda = -d$ are $(0, 1, 0)$ and $(0, 0, 1)$. The stable eigenspace is the yz-plane and the corresponding invariant stable manifold is a two dimensional space tangent to the yz-plane at the equilibrium point $(0, 0, 0)$. This invariant stable manifold is the yz-plane itself. There are no center manifolds in this case. Trajectories starting in the yz-plane will be limited to the equilibrium point $(0, 0, 0)$. Figure 2.2 gives an example of a trajectory starting in the yz-plane and limiting to the equilibrium point.
Figure 2.1: The x-axis is an unstable manifold. A trajectory starting on the x-axis does not limit to the equilibrium point (0, 0, 0) but tends to infinity. The initial values are (0.001, 0, 0) and parameter values are \( c=0.5, \ d=0.5, \ e=1, \ f=0.5, \ g=1, \ h=0.5 \).

Figure 2.2: The yz-plane is a stable manifold. A trajectory starting in the yz-plane is approaching the equilibrium point (0, 0, 0). Initial conditions are (0, 2, 2) and parameter values are \( c=0.5, \ d=0.5, \ e=1, \ f=0.5, \ g=1, \ h=0.5 \).

2.4.3 Results of the stability analysis of the point \( E_2 = (c, 1, 0) \)

The same calculations that are performed for the point \( E_1 \) can be done for the fixed point \( E_2 = (c, 1, 0) \).

Evaluating the Jacobian for \( E_2 \) gives the matrix \( M_2 = \begin{bmatrix} 0 & -c & 0 \\ 1 & 0 & 1 \\ 0 & 0 & -d + ec - f + gc \end{bmatrix} \).
The matrix \( \lambda I - M_2 \) is

\[
\begin{bmatrix}
\lambda & c & 0 \\
-1 & \lambda & -1 \\
0 & 0 & \lambda + d - ec + f - gc
\end{bmatrix}
\]

The characteristic equation becomes \((\lambda + d - ec + f - gc)(\lambda^2 + c) = 0\) resulting in one real eigenvalue and a pair of pure imaginary eigenvalues: \(\lambda_1 = ce + cg - d - f\) or \(\lambda_{2,3} = \pm \sqrt{c}i\).

The point \(E_2 = (c, 1, 0)\) is considered a non-hyperbolic fixed point because there are eigenvalues with zero real part. Depending on the parameter values two cases can be distinguished: \(\lambda_1 = 0\) or \(\lambda_1 > 0\). Note that \(\lambda_1 = ce + cg - d - f\) and as stated before \(ce + cg - d - f \geq 0\), otherwise the scavenger species becomes negative.

If at least one of the eigenvalues is positive then the equilibrium point is unstable. Hence if \(\lambda_1\) is positive, the point \(E_2 = (c, 1, 0)\) is unstable.

If on the other hand \(\lambda_1 = 0\), then all three eigenvalues have zero real parts. The stability cannot be determined using the Jacobian matrix and therefore numerical simulations will be carried out to gain some understanding of the stability. Several numerical simulations for different parameter values were performed. All the computer experiments where the stability of the equilibrium point \((c, 1, 0)\) is studied showed similar results, namely the scavenger population is tending to zero, but the other two populations are not approximating to the equilibrium coordinates. Therefore the equilibrium point \((c, 1, 0)\) is considered unstable.

Figure 2.3 displays an example of the three populations and also a trajectory in the positive octant. It can be seen that the scavenger population approximates zero but the predator and prey population are not limiting to the equilibrium coordinates.

**Stable, unstable and center manifolds**

For the case that \(\lambda_1 = 0\) all three eigenvalues have zero real parts. Therefore, according to the center manifold theorem there exists a three dimensional center manifold, however nothing can be concluded about the behavior on the center manifold.

If \(\lambda_1 = ce + cg - d - f > 0\) then the corresponding eigenvector is \(\alpha = \left(1, \frac{ce + cg - d - f}{c}, -\frac{1}{c}(c + d^2 - 2dec + 2df - 2dgc + e^2c^2 - 2ecf + 2ec^2g + f^2 - 2fge + g^2c^2)\right)\)

The eigenspace is the one dimensional space spanned by the eigenvector \(\alpha\).

According to the center manifold theorem if \(\lambda_1 > 0\), there is an unstable one dimensional manifold (curve) tangent to \(\alpha\) at the equilibrium point \((c, 1, 0)\).

For the eigenvalues \(\lambda_{2,3} = \pm \sqrt{c}i\) the corresponding eigenvectors are \((\sqrt{c}i, 1, 0)\) and \((-\sqrt{c}i, 1, 0)\). Associated with these two eigenvalues, there exists a two-dimensional invariant center manifold, passing through the point \((c, 1, 0)\) and tangent to the two-dimensional real subspace associated with the complex eigenvectors. This invariant center manifold is the xy-plane itself.
The prey population

The predator population

The scavenger population

A trajectory in the positive octant

Figure 2.3:
The parameter values are $c = 0.6; d = 1; e = 1.9; f = 0.2; g = 1; h = 0.5$;
The initial condition is $(0.5, 0.9, 0.1)$

2.4.4 Results of the stability analysis of the point $E_3 = (\alpha, 1, \beta)$ in the positive octant

The Jacobian matrix and the corresponding characteristic polynomial are computed but eigenvalues could not be calculated and therefore Routh’s method will be used to determine the stability of the equilibrium point. The characteristic polynomial is of third order and hence can be written as $a_3 s^3 + a_2 s^2 + a_1 s + a_0 = 0.$

The first column of the Routh table consists of the coefficients $a_3, a_2, b_1$ and $c_0$, where

$$b_1 = \frac{a_2 a_1 - a_3 a_0}{a_2} = a_1 - \frac{a_3 a_0}{a_2}$$

and

$$c_0 = \frac{b_1 a_0 - a_2 b_{-1}}{b_1}.$$ 

After simplification the Routh coefficients are:

$a_3 = 1$
\[ a_2 = \frac{h(ce + cg - d - f)}{e + g + h} \]

\[ b_1 = \frac{-1}{(e + g + h)^2 h} \left( hcg^2d - ce fh^2 + hdef + c^2 egh^2 - 2 c e f h^2 - hce^2 f + 2 hecg + hef - hfdg + gh^2 c + he f^2 + hce^2 + 2 f e g + hdg + dg^2 + f e^2 + f g^2 + hcedg - hc e g f + de^2 - dgh^2 c + f^2 h^2 + hfg + hcg^2 + c^2 g^2 h^2 + 2 deg + df h^2 + hde + eh^2 c - hd^2 g \right) \]

\[ c_0 = \frac{(d + f + hc)(ce + cg - d - f)}{e + g + h} \]

**Evaluating the Routh coefficients**

The third equilibrium point \((\alpha, 1, \beta)\) is stable if all coefficients of the first column have the same sign. Because \(a_3 = 1\) is positive all the other coefficients must be positive. All parameters are positive constants and the condition \(ce + cg - d - f > 0\) must be satisfied otherwise the fixed point is not in the positive space. Hence the coefficients \(a_2\) and \(c_1\) are positive. If the coefficient \(b_1\) would be positive then according to Rouths criterion all eigenvalues have negative real part and the point \((\alpha, 1, \beta)\) is a stable equilibrium point.

**Lemma 2.1.** The Routh coefficient \(b_1\) is always negative.

*Proof.*

The condition \(ce + cg - d - f > 0\) is satisfied. That is equivalent with \(d < ce + cg - f\).

If \(d = ce + cg - f\) is substituted in the coefficient \(b_1\), the result is \(-\frac{(e + g)c}{h}\).

The number \(-\frac{(e + g)c}{h}\) is negative because all parameters are positive constants.

Now if \(d < ce + cg - f\) the coefficient \(b_1\) must be less than \(-\frac{(e + g)c}{h}\).

Consequently if \(b_1\) is less than this value, then \(b_1\) is always negative. \(\Box\)

From the finding that \(b_1\) is always negative, the equilibrium point in the positive octant consequently also will be unstable.

Table 2.2 gives an overview of the equilibrium points, their stability and the corresponding eigenvalues. All equilibrium points are unstable.
<table>
<thead>
<tr>
<th>Parameter values</th>
<th>Fixed point</th>
<th>Eigenvalues and Stability</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Case 1</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( ce + cg - d - f = 0 )</td>
<td>(0,0,0) Saddle</td>
<td>( \lambda_1 = 1 ), ( \lambda_2 = -c ), ( \lambda_3 = -d ) Unstable</td>
</tr>
<tr>
<td></td>
<td>(c,1,0) non-hyperbolic</td>
<td>( \lambda_1 = 0 ), ( \lambda_2,3 = \pm \sqrt{c} ) i Unstable</td>
</tr>
<tr>
<td><strong>Case 2</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( ce + cg - d - f &gt; 0 )</td>
<td>(0,0,0) Saddle</td>
<td>( \lambda_1 = 1 ), ( \lambda_2 = -c ), ( \lambda_3 = -d ) Unstable</td>
</tr>
<tr>
<td></td>
<td>(c,1,0) non-hyperbolic</td>
<td>( \lambda_1 = ce + cg - d - f &gt; 0 ), ( \lambda_{2,3} = \pm \sqrt{c} ) i Unstable</td>
</tr>
<tr>
<td></td>
<td>(( \alpha ), 1, ( \beta ))</td>
<td>Eigenvalues not calculated Unstable</td>
</tr>
</tbody>
</table>

### 2.4.5 Results of the simulations with the point \( E_3 = (\alpha, 1, \beta) \)

To further examine the behavior of the system numerical simulations were necessary. The equilibrium point of interest is the point in the positive space \((\alpha, 1, \beta)\) and therefore the condition \( ce + cg - d - f > 0 \) must be satisfied. A large number of simulations was performed. Two examples (see figures 2.4 and 2.5) are presented below. It is worth mentioning that in both examples certain values assumed by the prey and scavenger population were too small to be taken into consideration.

**Example 1**

The parameter values are \( c = 0.2, d = 0.1, e = 0.9; f = 0.1, g = 0.2, h = 0.1 \). Different initial conditions were tested and all give similar results, namely the values of the prey and scavenger populations become too low to consider. In figure 2.4 a graph of each of the populations is displayed. The initial point is \((0.1, 1, 0.1)\). The equilibrium point is calculated: \((0.1833, 1, 0.0166)\) and is not stable as was calculated analytically.
Example 2
The parameter values are \( c = 1.05; d = 1; e = 1; f = 1; g = 1; h = 1 \). For these parameter values different initial points were tested and again populations assume values too low to consider. Figure 2.5 gives a clear picture of the three populations when the initial conditions are \((1, 1, 0.1)\). It can be seen that the equilibrium point \((1.0166, 1, 0.0333)\) is not stable.

---

**Figure 2.4: The three populations in the positive octant**
The parameter values are \( c=0.2, d=0.1, e=0.9, f=0.1, g=0.2, h=0.1 \). The initial point is \((0.1, 1, 0.1)\)

**Figure 2.5: The three populations in the positive octant**
The parameter values are \( c=1.05, d=1, e=1, f=1, g=1, h=1 \). The initial point is \((1, 1, 0.1)\)
2.5 Discussion and conclusion

The findings above have shown that no stable equilibrium points could be achieved for the system under study. Model I contains two or three equilibrium points depending on the value of the condition: \( ce + cg - d - f \). In case the condition \( ce + cg - d - f > 0 \) there exists three non negative equilibrium points and one is in the positive space. On the other hand, if \( ce + cg - d - f = 0 \) there are two non negative equilibrium points neither of which is in the positive octant. All equilibrium points are unstable. For the the equilibrium points \((0,0,0)\) and \((c,1,0)\) the existence of the stable, unstable and center manifolds is studied, and if possible also been calculated.

These results were confirmed numerically with computer simulations. In almost all the numerical experiments, the values of the prey and scavenger populations were far too small to be taken into consideration, in comparison to the values of \( y \). It is also worth mentioning that the values of each individual population, assumed in a certain time range, were not compatible in terms of magnitude, in other words, the values presented different orders of magnitude.

It was not possible to obtain a set of parameter values showing some reasonable values about the coexistence of the three populations for Model I. The predator population was assuming large values in comparison to the values of the prey and the scavenger population.

In the scavenger models in the previously mentioned papers [7],[9],[10], stable equilibria have been found. In those models a carrying capacity for the scavenger population was included and in some of the models also a carrying capacity for the prey population. But there was no carrying capacity included for the predator population. In the current study there was no carrying capacity incorporated for the prey and predator populations only for the scavenger population. In contrast to previous studies the predator population in this study benefits from two populations namely the scavenger and the prey population. Consequently, the predator population grew substantially and because no carrying capacity was considered the predator population grew without bounds. It may be concluded that the model as defined in (2.12) does not show reasonable values for the three populations and requires the inclusion of the carrying capacity of the predator population. In the next chapter, an improvement of Model I will be presented, i.e. Model II or Improved Model, which takes into consideration the carrying capacity of the predator population.
Chapter 3

Model II
The predator-prey-scavenger model with the inclusion of a carrying capacity for the predator population

3.1 Introduction

This chapter will describe an extension of Model I. The findings of the previous chapter suggested that the model should be modified to include the carrying capacity of the predator population. For that reason, Model I was expanded to include the carrying capacity of the predator population. That improved model will be referred below as Model II or Improved Model.

First Model I will be reformulated taking into account the carrying capacity of the predator population. The study of Model II is similar to that of Model I. Model II will be reduced to the dimensionless form, a local stability analysis of all equilibrium points will be carried out and numerical experiments will be conducted.

3.2 Description of Model II

The assumptions and parameters of Model II are almost the same as in Model I. The only difference with Model I is that the carrying capacity of the predator population will be included in model II. A new parameter, $K$, which is associated with the carrying capacity, is introduced to prevent the predator population from growing endlessly. The second equation of the original system will contain one more term namely $KY^2$. This results in model II given below:
\[
\begin{align*}
\frac{dX}{dt} &= AX - BXY \\
\frac{dY}{dt} &= -CY + DXY + EYZ - KY^2 \\
\frac{dZ}{dt} &= -FZ + GXZ - HYZ + IXYZ - JZ^2
\end{align*}
\] (3.1)

Model II can be reduced to its dimensionless form:
\[
\begin{align*}
\frac{dx}{dt} &= x(1 - y) \\
\frac{dy}{dt} &= y(-c + x + z - ky) \\
\frac{dz}{dt} &= z(-d + ex - fy + gxy - hz)
\end{align*}
\] (3.2)

with \( c = \frac{c}{A} \); \( d = \frac{d}{A} \); \( e = \frac{e}{B} \); \( f = \frac{f}{B} \); \( g = \frac{g}{B} \); \( h = \frac{h}{B} \); \( k = \frac{k}{B} \);

Model II as defined in equation(3.2) contains 7 parameters, while Model I had only 6 parameters.

3.3 Methods

In order to find conditions for stable coexistence of the three populations the following research steps were carried out:

- The calculation and stability analysis of all equilibrium points using the Jacobian or using Routh’s method;
- Numerical simulations in order to determine the stability of non-hyperbolic equilibrium points and to verify analytical calculations.

Due to the complexity of Model II there are no stable, unstable and center manifolds calculated.

3.4 Results for equilibrium calculation and stability analysis

3.4.1 Results for the calculation of the equilibrium points

The equilibrium points of Model II are:

- \( f_1 = (0, 0, 0) \)
- \( f_2 = (c + k, 1, 0) \)
- \( f_3 = (\alpha_1, 1, \beta_1) \), with \( \alpha_1 = \frac{d + f + h(c + k)}{e + g + h} \) and \( \beta_1 = \frac{(c + k)(e + g) - d - f}{e + g + h} \)

\(^1\text{Detailed calculations of the equilibrium points are given in Appendix A.2} \)
Equilibrium point \( f_3 \) lies in the positive space if the condition \((c + k)(e + g) - d - f > 0\) is satisfied. If however the condition \((c + k)(e + g) - d - f = 0\) is met, the equilibrium points \( f_2 \) and \( f_3 \) coincide.

### 3.4.2 Results of the stability analysis of the point \((0, 0, 0)\)

The eigenvalues of the Jacobian matrix for the point \( f_1 \) are \( \lambda = 1, \lambda = c, \lambda = d \). Consequently the equilibrium point \( f_1(0, 0, 0) \) is a saddle point and thus unstable. \(^2\)

### 3.4.3 Results of the stability analysis of the point \((c + k, 1, 0)\)

The stability of the equilibrium point \( f_2 = (c + k, 1, 0) \) depends on the condition \((c + k)(e + g) - d - f\). The eigenvalues of the Jacobian matrix are

\[
\lambda_{1,2} = -\frac{1}{2}k \pm \frac{1}{2}\sqrt{k^2 - 4c - 4k} \quad \text{and} \quad \lambda_3 = (c + k)(e + g) - d - f
\]

If the condition \((c + k)(e + g) - d - f > 0\) is met, then the point \( f_2 = (c + k, 1, 0) \) is unstable because there exists a positive eigenvalue.

If, however the condition \((c + k)(e + g) - d - f = 0\) holds, the point \((c+k, 1, 0)\) is a non-hyperbolic point. The stability of the non-hyperbolic point is numerically examined.

**Numerical study of the stability of the non-hyperbolic point \((c + k, 1, 0)\)**

In the case that \((c + k)(e + g) - d - f = 0\), the equilibrium \((c + k, 1, 0)\) is a non-hyperbolic point. The characteristic polynomial has one zero eigenvalue and two eigenvalues with negative real parts and thus is there a possibility that the equilibrium point is stable. Determination of the stability using analytical techniques is complex and therefore several numerical simulations are studied.

The following eigenvalues with negative real part are obtained:

\[
\lambda_{1,2} = -\frac{1}{2}k \pm \frac{1}{2}\sqrt{k^2 - 4c - 4k}
\]

Depending on the value of \(k^2 - 4c - 4k\) three cases can be distinguished:

1. If \(k^2 - 4c - 4k = 0\) then there will be two real and equal eigenvalues.
2. If \(k^2 - 4c - 4k < 0\) then there will be two complex eigenvalues.
3. If \(k^2 - 4c - 4k > 0\) then there will be two real and different eigenvalues.

An example of each of the three cases is presented below. For each case the condition \((c + k)(e + g) - d - f\) is satisfied.

\(^2\)Detailed calculations of the eigenvalues and the stability of the point \( f_1 \) are given in Appendix B
Example 1
Let $c = \frac{5}{2}$, $d = \frac{13}{4}$, $e = \frac{1}{2}$, $f = 3$, $g = \frac{1}{2}$, $h = 1$ and $k = 5$. Then the condition $k^2 - 4c - 4k = 0$ is satisfied. The equilibrium point is calculated and is $(6\frac{1}{2}, 1, 0)$.
Different initial conditions are tested and all solution trajectories were limiting to the equilibrium point. Figure 3.1 provides a clear picture of the stability of the three populations as well as a trajectory in the phase space converging to the equilibrium point. The initial point is $(1, 1, 1)$. It can be seen that each of the three populations is converging to the corresponding equilibrium coordinate. In figure 3.2, a trajectory in the positive octant limiting to the equilibrium, is displayed.

Example 2
Let $c = 1$, $d = 2$, $e = 1$, $f = 2$, $g = 1$, $h = 1$ and $k = 1$. Then the condition $k^2 - 4c - 4k < 0$ is satisfied. The equilibrium point is calculated and is $(2, 1, 0)$. Various simulations with different initial conditions were conducted and all solution trajectories were tending to the equilibrium point. In figure 3.3, a trajectory tending to the equilibrium point when the initial point is $(1, 1, 1)$, is displayed.

Example 3
Let $c = 1$, $d = 2$, $e = \frac{1}{4}$, $f = 1$, $g = \frac{1}{4}$, $h = 1$ and $k = 5$. Then the condition $k^2 - 4c - 4k > 0$ is satisfied. The equilibrium point is calculated and is $(6, 1, 0)$.
The simulations were carried out with different initial values. For all these initial conditions, the solution trajectories were limiting to the equilibrium point. Figure 3.3 shows a trajectory limited to the equilibrium point when the initial point is $(10, 10, 10)$. 
Figure 3.1: All three populations are limiting to the equilibrium coordinates
Figure 3.2: Example 1: A trajectory limiting to a stable equilibrium point. The parameter values are $c = \frac{5}{4}$, $d = \frac{13}{4}$, $e = \frac{1}{2}$, $f = 3$, $g = \frac{1}{2}$, $h = 1$ and $k = 5$. The initial conditions are $(1, 1, 1)$.

Figure 3.3: Example 2: A trajectory limiting to a stable equilibrium point. The parameter values are $c =1$, $d = 2$, $e = 1$, $f = 2$, $g=1$, $h = 1$ and $k = 1$. The initial conditions are $(1, 1, 1)$. 
Figure 3.4: Example 3: A trajectory limiting to a stable equilibrium point.
The parameter values are $c = 1$, $d = 2$, $e = \frac{1}{4}$, $f = 1$, $g = \frac{1}{4}$, $h = 1$ and $k = 5$.
The initial conditions are $(10, 10, 10)$.

### 3.4.4 Results of the stability analysis of the point $(\alpha_1, 1, \beta_1)$

The equilibrium point $f_3 = (\alpha_1, 1, \beta_1)$ is in the positive octant if the condition $(c + k)(e + g) - d - f > 0$ is satisfied. As in Model I the stability of the equilibrium point in the positive octant can be determined using Routh’s method.

The Routh coefficients are calculated and simplified using Maple and are:

\[
a_3 = 1 \\
a_2 = \frac{k(e + g + h) + h[(c + k)(e + g) - d - f]}{e + g + h} \\
c_0 = \frac{(d + f + hc)[(c + k)(e + g) - d - f]}{e + g + h}
\]

The coefficient $b_1$ is displayed on the next page.

According to Routh’s method the stability of the equilibrium point is guaranteed when all the Routh coefficients have the same sign. The coefficient $a_3 = 1$ and thus positive. The coefficients $a_2$ and $c_0$ are positive because all parameters are positive and the factor $[(c + k)(e + g) - d - f]$ is also positive. Therefore the equilibrium point $(\alpha_1, 1, \beta_1)$ will be stable when the coefficient $b_1$ is positive.

**Lemma 3.1.** The Routh coefficient $b_1$ of Model II can be positive, negative or zero.

**Proof.**
The condition $(c + k)(e + g) - d - f > 0$ is satisfied.
That is equivalent with $d < (c + k)(e + g) - f$.
If $d = ce + cg - f$ is substituted in the coefficient $b_1$, the result is $c + k$ and $c + k > 0$.
Now if $d < ce + cg - f$ the coefficient $b_1$ must be less than $c + k$.
Consequently if $b_1$ is less than $c + k$ then the coefficient $b_1$ can be positive, negative or zero.

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The equilibrium point \( f_3 = (\alpha_1, 1, \beta_1) \) is stable if \( b_1 > 0 \) and unstable if \( b_1 < 0 \). If \( b_1 = 0 \) then a Hopf bifurcation occurs, which means that a limit cycle exists. It is complicated to further refine the condition \( b_1 > 0 \) in terms of parameter values and therefore, in the next section various examples are studied numerically.

In Table 3.2 an overview of the equilibrium points and their stability is given.
### Table 3.1: Stability of equilibrium points of Model II

<table>
<thead>
<tr>
<th>Parameter values</th>
<th>Fixed point</th>
<th>Eigenvalues and Stability</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Case 1</strong></td>
<td>(0,0,0)</td>
<td>$\lambda_1 = 1$ , $\lambda_2 = -c$ , $\lambda_3 = -d$</td>
</tr>
<tr>
<td></td>
<td>Saddle</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(c+k,1,0)</td>
<td>$\lambda_{1,2} = -\frac{1}{2}k \pm \frac{1}{2}\sqrt{(k^2 - 4c - 4k)}$</td>
</tr>
<tr>
<td></td>
<td>Non-hyperbolic point</td>
<td>$\lambda_3 = 0$</td>
</tr>
<tr>
<td><strong>Case 2</strong></td>
<td>(0,0,0)</td>
<td>$\lambda_1 = 1$ , $\lambda_2 = -c$ , $\lambda_3 = -d$</td>
</tr>
<tr>
<td></td>
<td>Saddle</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(c+k,1,0)</td>
<td>$\lambda_{1,2} = -\frac{1}{2}k \pm \frac{1}{2}\sqrt{(k^2 - 4c - 4k)}$</td>
</tr>
<tr>
<td></td>
<td>Saddle</td>
<td>$\lambda_3 = (c+k)(e+g) - d - f &gt; 0$</td>
</tr>
<tr>
<td></td>
<td>$(\alpha_1, 1, \beta_1)$</td>
<td>Stable if $b_1 &gt; 0$ ( $b_1$ as defined above)</td>
</tr>
</tbody>
</table>

#### 3.4.5 Results of the simulations with the point $({\alpha_1}, 1, {\beta_1})$

In this section three numerical examples of Model II will be presented. The purpose of the numerical study is to examine the stability of the equilibrium point in the positive space and to determine whether a limit cycle could be found. From the previous section it is known that a stable equilibrium point exists if the Routh coefficient $b_1$ is positive. Furthermore the condition $(c+k)(e+g) - d - f > 0$ must be satisfied, otherwise there will be no equilibrium point in the positive space. The coefficient $b_1$ consists of many terms (about 80) and as stated earlier it is not possible to further refine the condition $b_1 > 0$ expressed in parameter values. For this reason the coefficient $b_1$ will not be evaluated.

The approach regarding the simulations is to select a parameter to be varied while the other parameters remain constant, in order to examine the stability of the positive equilibrium point. The system (3.2) contains 7 different parameters. Not all of the parameters can be addressed within the scope of this study. There is opted for three parameters of the scavenger equation because many studies are already conducted on the predator-prey equations. The parameters $e$, $f$ and $h$ of the scavenger equation will be taken into account. Parameter $e$ benefits the scavenger population, parameter $f$ is a disadvantage to it, and parameter $h$ has no influence on the condition $(c+k)(e+g) - d - f > 0$ . In each
simulation only one of the parameters will be varied and the other parameters will remain fixed. Various simulations are conducted varying the parameters e, f and h and holding the other parameters constant. For the other parameters, c, k, d and g, a set of different values was tested and all with various initial conditions. In the following examples some results are presented, from simulations with the parameter e, f and h.

**Example 1**
Example 1 involves varying parameter f. In this example all other parameters are fixed and set to one. The initial point is (1, 1, 1). The condition \((c + k)(e + g) - d - f > 0\) will be satisfied if \(0 < f < 3\). A Hopf bifurcation is detected at \(f = 0.722431\). Hence, for this value a limit cycle appears. Furthermore a stable equilibrium point is found for \(0.72234 < f < 3\) and for \(0 < f < 0.72234\) there is an unstable equilibrium point and the coexistence of all three populations is not guaranteed. In figure 3.5 (a), a trajectory limiting to the equilibrium, is shown. In figure 3.5(b) a limit cycle is displayed and in figure 3.5(c) an unstable equilibrium point is shown.

**Example 2**
Example 2 involves varying parameter h. In this example all other parameters are set to one. The value of h does not influence the condition \((c + k)(e + g) - d - f > 0\). The initial point is (1, 1, 1). A stable equilibrium point was found for \(h > 0.780773\) and for \(h = 0.780773\) a Hopf bifurcation occurs. Hence there exists a limit cycle for \(h = 0.780773\). If \(0 < h < 0.780773\), there is no stable equilibrium point. The populations take on very small values. This situation is not desirable because certain population values are too small in comparison to the other two populations, making the model completely unrealistic. In figure 3.6 (a), (b) and (c) an example of a stable equilibrium point, a limit cycle and an unstable equilibrium point are shown.

**Example 3**
In example 3 the parameter e is studied. All parameters, except the parameter e are chosen to be less than zero. Let \(c = 0.6, d = 0.5, f = 0.5, g = 0.25, h = 0.25\) and \(k = 0.4\). In order to satisfy the inequality \((c + k)(e + g) - d - f > 0\), parameter e must be greater than 0.75. The initial point is (1, 1, 1). A stable equilibrium point is found for \(0.75 < e < 1.322431\) and for \(e > 1.322431\) the equilibrium point loses its stability. Furthermore for \(e = 1.322431\) a Hopf bifurcation is detected resulting in a limit cycle for this value. In figure 3.7 (a), (b) and (c) an example of an stable equilibrium point, a limit cycle and an unstable equilibrium point are shown.
(a) Stable equilibrium point. $f = 2.9$

(b) Limit cycle. $f = 0.722431$

(c) Unstable equilibrium point. $f=0.5$. 

Figure 3.5: All parameters are set to one with the exception of parameter $f$. The initial point is $(1, 1, 1)$. 
(a) Stable equilibrium point. $h = 2$

(b) Limit cycle. $h = 0.780733$

(c) Unstable equilibrium point. $h = 0.4$.

Figure 3.6: All parameters are set to one with the exception of parameter $h$. The initial point is $(1, 1, 1)$. 

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(a) Stable equilibrium point. \( e = 0.8 \)

(b) Limit cycle. \( e = 1.322431 \)

(c) Unstable equilibrium point. \( e = 2 \).

Figure 3.7: The parameter values are: \( c = 0.6 \), \( d = 0.5 \), \( f = 0.25 \), \( h = 0.25 \), \( k = 0.4 \). The initial point is \((1, 1, 1)\).
3.5 Discussion and conclusion

In this chapter the carrying capacity of the predator population is incorporated into the original model and conditions for a stable coexistence of the three populations are established. Model II contains two or three equilibrium points depending on the condition \((c + k)(e + g) - d - f\). If the condition \((c + k)(e + g) - d - f > 0\) is satisfied then three equilibrium points are found and one lies in the positive octant. Furthermore the equilibrium point in the positive space is stable if the Routh coefficient \(b_1 > 0\). If the Routh coefficient \(b_1 = 0\) then there will be a limit cycle. From these findings it can be concluded that when the Routh coefficient \(b_1 \geq 0\) there will be a stable coexistence of the three populations. The other two equilibrium points are unstable.

On the other hand, if the condition \((c + k)(e + g) - d - f = 0\) holds, two equilibrium points were found and neither of them is in the positive octant. One of the equilibrium points turned out to be a non-hyperbolic point namely \((c + k, 1, 0)\). All the numerical simulations carried out with the non-hyperbolic equilibrium point \((c + k, 1, 0)\), showed a stable equilibrium point which means that the scavenger population will die out. But further proof is needed to confirm that the non-hyperbolic point \((c + k, 1, 0)\) is always a stable point. The other equilibrium point is unstable.

Several numerical simulations with the parameters e, f and h were conducted. Through the simulations it was possible to find values where Hopf bifurcations occurred and to find values leading to a stable equilibrium in the positive space.

The inclusion of the carrying capacity for the predator population is indeed an improvement because Model II produced acceptable results for the coexistence of the three populations. However, a drawback of the Model II is that the corresponding system (3.2) holds seven parameters, which makes analysis and computer simulations complex.

Model II can be simplified in such a way that it holds five parameters. In the third equation of Model II, represented by equation 3.2, the three terms \(exz\), \(fyz\) and \(gxyz\) can be substituted by one cubic term \(mxyz\). The cubic term, \(mxyz\), means that the scavenger benefits in a way proportional to the interactions among predator prey and scavenger. The first and second equation of Model II remains unchanged. The simplified model will be referred to as Model III and is defined as follows:

\[
\begin{align*}
\frac{dx}{dt} &= x(1 - y) \\
\frac{dy}{dt} &= y(-c + x + z - ky) \\
\frac{dz}{dt} &= z(-d + mxy - hz)
\end{align*}
\]  
\hspace{1cm} \text{(3.3)}

Because the number of parameters is lower, the analysis is easier to conduct and numerical experiments are easier. Model III will not be analyzed in this thesis. The next chapter will continue with Model II and discuss a special case of this model, namely the impact on the two remaining populations if one of the populations goes extinct.
Chapter 4

Special Case
What happens to the model in case one population dies out?

4.1 Introduction

In this chapter the influence on the two remaining populations if one of the populations dies out will be studied. The key question is: "Does the extinction of one population lead to the extinction of the two remaining populations?" This question is not only interesting from a biological point of view but can be seen as a special case scenario of the system described in Chapter 3, with one of the populations set to zero and therefore not considered in the resulting system.

We are therefore studying the dynamics of three two dimensional systems, namely: 1) a predator-scavenger system; 2) a prey-scavenger system; and 3) a predator-prey system. For all three systems we first formulate the model, calculate the equilibria and perform local and global stability analysis of equilibrium points as well as computer simulations to compare with analytical results.

4.2 Special case I: Extinction of the prey population

Here we consider the case where the prey population goes extinct. If the prey population dies out, the remaining model consists of the predator, \( y \), and scavenger population, \( z \), and is given by the following system:

\[
\begin{align*}
\frac{dy}{dt} &= y(-c + z - ky) \\
\frac{dz}{dt} &= z(-d - fy - hz)
\end{align*}
\] (4.1)

The only non-negative equilibrium point of this system is \((0, 0)\) and it is a stable node. \(^1\)

\(^1\) Detailed calculations of the equilibrium point \((0,0)\) are in Appendix C.1.
Results: Dynamics of the predator and scavenger populations

Given the fact that $y > 0$, the first equation of (4.1) shows that if $-c + z - ky > 0$ then $\frac{dy}{dt} > 0$ Therefore, $y$ will increase if $-c + z - ky > 0$ and $y$ will decrease if $-c + z - ky < 0$. Similarly from the second equation of (4.1) $z$ will increase if $-d - fy - hz > 0$ and $z$ will decrease if $-d - fy - hz < 0$.

Figure 4.1: Phase Plane diagram of the predator and scavenger population

Figure 4.1 displays the phase plane of $y$ and $z$ and it can be seen that there are two regions in the positive space. Region I is the region above the green line and under the red line. Region II is the region in the positive space above both lines. In region I the following two inequalities $-c + z - ky < 0$ and $-d - fy - hz < 0$ are satisfied. Therefore in this region, $y$ will decrease and $z$ will also decrease. Both populations will go extinct.

Points in region II satisfy the inequalities $-c + z - ky > 0$ and $-d - fy - hz < 0$. In this region, $y$ will increase and $z$ will decrease. As $y$ increases it will eventually reach values that satisfy the line $-c + z - ky = 0$ (red line). When the value of $y$ crosses the line, it is no longer in region II and will no longer increase. Both the predator and scavenger populations will decrease until the stable equilibrium $(0, 0)$ (displayed by a red dot) is reached. Therefore, solutions with initial conditions starting in the region II will "move" to region I and as populations with initial conditions in Region I, these will eventually go extinct. Therefore the equilibrium point $(0, 0)$ is a globally stable equilibrium point. The scavenger and predator population cannot survive without the prey population.

In figure 4.2 an example of the phase space of predators and scavengers is given. Trajectories are converging to the stable equilibrium $(0,0)$. 
4.3 Special case II:

Extinction of the predator population

If the predator population dies out, the remaining model consists of the prey, $x$, and scavenger population, $z$, and is given by the system below:

\[
\begin{align*}
\frac{dx}{dt} &= x \\
\frac{dz}{dt} &= z(-d + ex - hz)
\end{align*}
\] (4.2)

The only non-negative equilibrium point of this system is $(0, 0)$. The point $(0,0)$ is a saddle thus unstable. ²

Results: Dynamics of the prey and scavenger populations

From the first equation of (4.2) it can be concluded that the prey population will increase if $x > 0$. That means that the prey population always persists because $x$ is non negative. The scavenger population will increase if the inequality $-d + ex - hz > 0$ is satisfied and decrease if the condition $-d + ex - hz < 0$ holds.

Figure 4.3 displays the phase plane of $x$ and $z$ and there are two regions in the positive space. Points in region I, that are the points above the line $-d + ex - hz = 0$, satisfy the inequality $-d + ex - hz < 0$, while the points in region II, (that are the points under the line) satisfy the inequality $-d + ex - hz > 0$.

²Detailed calculations of the equilibrium point $(0,0)$ are in Appendix C.2

Figure 4.2: Two trajectories are limiting to the stable equilibrium point $(0,0)$. The parameter values are $c=1$, $d=1$, $f=1$, $h=1$, $k=1$. The initial points are $(1,8)$ and $(8,4)$.
In region I the prey population increases and the scavenger population decreases. But the point \((0, 0)\) (displayed by a red dot) is not a locally stable equilibrium point. Therefore, initial points starting in the region I will “move” to region II. In region II both \(x\) and \(z\) are increasing and that means that both populations persist. The scavenger population will indeed decrease in the beginning and become close to zero, but as the point \((0, 0)\) is not an attracting equilibrium point, the points nearby move away from it, which results in the growth of the scavengers.

In figure 4.4 a trajectory starting in region I is displayed. In the beginning \(z\) is decreasing, reaching very low values, but at a certain point \(z\) is in region II and starts increasing,
which guarantees the survival of both populations.

### 4.4 Special case III: Extinction of the scavenger population

If the scavenger population dies out, the remaining model reverts back to the classical predator-prey model (see equation 1.1, page 4), with the only difference that a carrying capacity for the predator population is included. The model is given by the system below:

\[
\begin{align*}
\frac{dx}{dt} &= x(1 - y) \\
\frac{dy}{dt} &= y(-c + x - ky)
\end{align*}
\]  

(4.3)

**Results: Dynamics of the prey and predator populations**

The system (4.3) contains two non negative equilibrium points: (0, 0), which is unstable and the stable equilibrium point (c+k, 1).

In figure 4.5, the phase plane is given for this predator-prey system. It can be seen that the positive plane consists of four regions. In region I, that is the region under both lines and satisfying the inequalities \( y < 1 \) and \( -c + x - ky > 0 \), \( x \) and \( y \) are increasing. Region II is above the line \( y = 1 \) and under the line \( -c + x - ky = 0 \). In this region \( x \) is decreasing and \( y \) is increasing. Points in the region III are satisfying the inequalities \( y > 1 \) and \( -c + x - ky < 0 \). Both \( x \) and \( y \) are decreasing in region III. In the region IV \( x \) is increasing and \( y \) is decreasing.

The blue arrows in figure 4.5 show that both populations are moving toward the stable equilibrium point (*displayed by a red dot in the positive plane*). Solutions with initial points starting in any region will converge to the point \( (c+k, 1) \). Hence, the equilibrium point is a globally stable fixed point. That means that predators and prey will coexist if the scavenger population goes extinct.

In figure 4.6 two trajectories are displayed. One trajectory is starting in region I and the other is starting in region III. Both trajectories are converging to the equilibrium point.

\[\text{3 Detailed calculations of the equilibrium points are in Appendix C.3}\]
Figure 4.5: Phase Plane diagram of the prey and predator population

Figure 4.6: Two trajectories converging to the stable equilibrium point. The parameter values are $c = 1$, $k=1$
Trajectories starting at $(6, 0.5)$ in region I and $(2,10)$ in region III.
4.5 Discussion and Conclusions

The predator scavenger model, as defined in (4.1), has the globally stable equilibrium point $(0, 0)$. Therefore, it can be concluded that both populations die out. The prey scavenger model, as defined in (12) has the unstable equilibrium point $(0, 0)$. Furthermore, it can be derived from the phase plane diagrams that scavengers and prey will survive. Predators and prey will always persist in the absence of scavengers, because the predator prey model, as defined in (13) has a globally stable equilibrium point in the positive plane.

For special case I where the prey population dies out, the scavengers and predators cannot survive. This result was to be expected because we assumed in our model that the scavengers only live on carcasses of the prey. Without prey the scavenger population will die out and consequently the predator population, who only lives off the scavenger population, will eventually not have any scavenger to eat and thus will also go extinct.

If the scavenger population dies out, as in special case II, the predators and prey will coexist. This result is comparable to the classical Lotka-Volterra model, which the remaining model resembles closely. The main difference between the two models is that a carrying capacity for the predator population is included. A consequence of incorporating the predator carrying capacity is that the equilibrium point in the positive space becomes stable, whereas the positive equilibrium point of the classical predator-prey model is a center, which is neutrally stable. This is of course a direct result of the findings in chapter three, namely that the equilibrium point in the positive space is stable when the predator carrying capacity is included.

Prey and scavengers will also persist if the predator dies out. That result is logical, because the prey population has enough food to survive and grow, as do the scavengers living of the carcasses of prey that have died naturally. In this model neither of the two populations have enemies that decrease their numbers.

In chapter three conditions were found for the extinction of the scavenger population. The question arises whether it is likely that extinction of the prey or predator population also could happen. Intuitively, it seems that the predator population will not die out, but the prey population can go extinct. But only further study can provide a reliable answer.
General discussion

This thesis presented a model for three species, namely a prey, a predator and a scavenger. What makes this model different from other studies is that the scavenger species is also a victim of the predator. This can happen in nature. The purpose of the study was to formulate a reasonable model for the three populations and set conditions for the continued existence of all three populations. Furthermore, it is examined what happens to the remaining populations when one of the species dies out.

A first model was defined, but did not meet any relevant values for the prey, predator and scavenger populations. Therefore the original system was improved by including the carrying capacity of the predator population. For the improved model constraints for a positive and stable equilibrium point are found. Namely the findings in chapter three showed that when the Routh coefficient $b_1 \geq 0$ there will be a stable coexistence of the three populations. Several numerical examples show acceptable results for stable coexistence of the three populations. If conditions for the coexistence are not met it could be that one population dies out. The model also predicts satisfactory results on this namely populations only die out when the prey dies out. For the other cases the remaining populations persists. Again, the results are confirmed by numerical simulations.

The study in this thesis can be viewed as a first step in modeling a prey, predator and scavenger where the scavenger is consumed by the predator. The model can be further improved and numerous interesting research questions can be studied. The improved system in this thesis holds seven parameters. An option is to simplify the model even further, in such a way that it holds five parameters. This simplified model is briefly described in paragraph 3.5. Experimenting numerically with this model will be easier and from the simulations a variety of interesting questions can arise. For example, one can try to further refine the study in this thesis and find a range of parameter values that lead to the stable coexistence of the three populations. Or one can try to find a range of parameter values that lead to bounded orbits. This is biologically relevant because no population grows endlessly. Another interesting issue is to find conditions that lead to the extinction of the prey or predator population.
Bibliography


Calculation of equilibrium points

A.1 The equilibrium points of Model I

The equilibrium points can be determined by solving the system

\[
\begin{align*}
    x(1 - y) &= 0 \\
    y(-c + x + z) &= 0 \\
    z(-d + ex - fy + gxy - hz) &= 0
\end{align*}
\]  

That is equivalent to solving the following subsystems:

\[
\begin{align*}
    \begin{cases}
        x = 0 \\
        y = 0 \\
        z = 0
    \end{cases} \quad \text{The solution is (0,0,0)}
\end{align*}
\]

\[
\begin{align*}
    \begin{cases}
        x = 0 \\
        y = 0 \\
        -d + ex - fy + gxy - hz = 0
    \end{cases} \quad \text{The solution is (0,0,-}\frac{d}{h})
\end{align*}
\]

\[
\begin{align*}
    \begin{cases}
        x = 0 \\
        -c + x + z = 0 \\
        z = 0
    \end{cases} \quad \text{The system has no solution}
\end{align*}
\]

\[
\begin{align*}
    \begin{cases}
        x = 0 \\
        -c + x + z = 0 \\
        -d + ex - fy + gxy - hz = 0
    \end{cases} \quad \text{The solution is } \left(0, -\frac{hc+d}{f}, c\right)
\end{align*}
\]

\[
\begin{align*}
    \begin{cases}
        y = 1 \\
        y = 0 \\
        z = 0
    \end{cases} \quad \text{The system has no solution}
\end{align*}
\]

\[
\begin{align*}
    \begin{cases}
        y = 1 \\
        y = 0 \\
        -d + ex - fy + gxy - hz = 0
    \end{cases} \quad \text{The system has no solution}
\end{align*}
\]
The solution is \((c,1,0)\)

\[
\begin{cases}
y = 1 \\
-c + x + z = 0 \\
z = 0
\end{cases}
\]

The solution is \((\frac{d+f+hc}{e+g+h}, 1, \frac{ce+cg-d-f}{e+g+h})\)

Considering only positive coordinates: \((0,0,0)\); \((c+k,1,0)\) ; \((\frac{d+f+hc}{e+g+h}, 1, \frac{ce+cg-d-f}{e+g+h})\), \(\text{(with } ce + cg - d - f > 0\text{)}\)

\section*{A.2 The equilibrium points of Model II}

The calculation of the equilibrium points is similar to that of model I. Thus the system

\[
\begin{cases}
x(1-y) = 0 \\
y(-c + x + z - ky) = 0 \\
z(-d + ex - fy + gxy - hz) = 0
\end{cases}
\]  

(A.2)

must be solved.

The equilibrium points are:

1. \((0,0,0)\)
2. \((0,0,-\frac{d}{h})\)
3. \((c+k,1,0)\)
4. \((0,-\frac{d+ch}{f+hk}, \frac{fc-kd}{f+hk})\)
5. \((\frac{d+f+h(c+k)}{e+g+h}, 1, \frac{(c+k)(e+g) - d - f}{e+g+h})\)

The points (1), (3) and (5) will be considered. \(\text{(with } (c+k)(e+g) - d - f > 0\text{)}\)

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Stability of equilibrium points of Model II

The Jacobian matrix of system (3.2) is:

\[
\begin{bmatrix}
1 - y & -x & 0 \\
y & -c + x + z - 2ky & y \\
z(e + gy) & z(-f + gx) & -d + ex - fy + gxy - 2hz
\end{bmatrix}
\]  \hspace{1cm} (B.1)

The equilibrium point (0,0,0)

Evaluating the Jacobian for (0,0,0) ⇒ \( B_1 = \begin{bmatrix} 1 & 0 & 0 \\ 0 & -c & 0 \\ 0 & 0 & -d \end{bmatrix} \)

The matrix \( (\lambda I - B_1) \) =

\[
\begin{bmatrix}
\lambda - 1 & 0 & 0 \\
0 & \lambda + c & 0 \\
0 & 0 & \lambda + d
\end{bmatrix}
\]

Calculating the eigenvalues ⇒ \( \text{Det}(\lambda I - B_1) = 0 \Rightarrow (\lambda - 1)(\lambda + c)(\lambda + d) \Rightarrow \)

Eigenvalues: \( \lambda = 1, \lambda = -c, \lambda = -d. \)

Hence (0,0,0) is unstable.

The equilibrium point (c+k,1,0)

Evaluating the Jacobian for (0,0,0) ⇒ \( B_2 = \begin{bmatrix} 0 & -(c+k) & 0 \\ 1 & -k & 1 \\ 0 & 0 & (e+g)(c+k) - d - f \end{bmatrix} \)

The matrix \( (\lambda I - B_2) \) =

\[
\begin{bmatrix}
\lambda & c + k & 0 \\
-1 & \lambda + k & -1 \\
0 & 0 & \lambda + d + f - (e + g)(c + k)
\end{bmatrix}
\]

Calculating the eigenvalues ⇒ \( \text{Det}(\lambda I - B_2) = 0 \Rightarrow \)

\( (\lambda + d + f - (e + g)(c + k)(\lambda^2 + k\lambda + c + k) \Rightarrow \)

Eigenvalues: \( \lambda_{1,2} = \frac{1}{2}k \pm \frac{1}{2}\sqrt{k^2 - 4c - 4k} \text{ and } \lambda_3 = (c + k)(e + g) - d - f \)
Stability of equilibrium points special case

C.1 Equilibrium points and stability when the prey dies out

Calculation of the equilibrium points of system (4.1)

\[
\begin{align*}
\frac{dy}{dt} &= y(-c + z - ky) \\
\frac{dz}{dt} &= z(-d - fy - hz)
\end{align*}
\]

The equilibrium points can be derived from the equilibrium points of Model II. (see page Par 3.4.1 page 26)
If \( x = 0 \) then the only non negative equilibrium point is \((0,0)\).

The corresponding Jacobian matrix is

\[
\begin{bmatrix}
-c + z - 2ky & 2ky \\
-fz & -d - fy - 2hz
\end{bmatrix}
\] (C.1)

Evaluating the Jacobian for \((0,0)\) \(\Rightarrow A_1 = \begin{bmatrix} -c & 0 \\ 0 & -d \end{bmatrix}\)

\[
\lambda I - A_1 = \begin{bmatrix} \lambda + c & 0 \\ 0 & \lambda + d \end{bmatrix} \Rightarrow \text{Characteristic polynomial is: } (\lambda + c)(\lambda + d) = 0 \Rightarrow
\]

Eigenvalues: \( \lambda = -c \); \( \lambda = -d \) \(\Rightarrow (0,0) \) is a stable node.

C.2 Equilibrium points and stability when the predator dies out

Calculation of the equilibrium points of system (4.2)

\[
\begin{align*}
\frac{dx}{dt} &= x \\
\frac{dz}{dt} &= z(-d + ex - hz)
\end{align*}
\]

The equilibrium points can be derived from the equilibrium points of Model II. (see page Par 3.4.1 page 26)
If \( y = 0 \) then the only non negative equilibrium point is \((0,0)\).
The corresponding Jacobian matrix is

\[
\begin{bmatrix}
1 & 0 \\
e z & -d + ex - 2hz
\end{bmatrix}
\]  
(C.2)

Evaluating the Jacobian for \((0,0)\) \(\Rightarrow A_2 = \begin{bmatrix} 1 & 0 \\ 0 & -d \end{bmatrix} \)

\[\lambda I - A_2 = \begin{bmatrix} \lambda - 1 & 0 \\ 0 & \lambda + d \end{bmatrix} \Rightarrow \text{Characteristic polynomial is: } (\lambda - 1)(\lambda + d) = 0 \Rightarrow\]
Eigenvalues: \( \lambda = 1 ; \lambda = -d \Rightarrow (0,0) \) is a saddle, thus unstable.

### C.3 Equilibrium points and stability when the scavenger dies out

Calculation of the equilibrium points of system (4.3)

\[
\begin{align*}
\frac{dx}{dt} &= x(1 - y) \\
\frac{dy}{dt} &= y(-c + x - ky)
\end{align*}
\]

There are two equilibrium points if \( z = 0 \): \((0,0)\) and \((c+k,1)\)  
(see page Par 3.4.1 page 26)

The corresponding Jacobian matrix is

\[
\begin{bmatrix}
1 - y & -x \\
y & -c + x - 2ky
\end{bmatrix}
\]  
(C.3)

The equilibrium point \((0,0)\)

Evaluating the Jacobian for \((0,0)\) \(\Rightarrow A_3 = \begin{bmatrix} 1 & 0 \\ 0 & -c \end{bmatrix} \)

\[\lambda I - A_3 = \begin{bmatrix} \lambda - 1 & 0 \\ 0 & \lambda + c \end{bmatrix} \Rightarrow \text{Characteristic polynomial is: } (\lambda - 1)(\lambda + c) = 0 \Rightarrow\]
Eigenvalues: \( \lambda = 1 ; \lambda = -c \Rightarrow (0,0) \) is a saddle, thus unstable.

The equilibrium point \((c+k,1)\)

Evaluating the Jacobian for \((c+k,1)\) \(\Rightarrow A_3 = \begin{bmatrix} 0 & -(c + k) \\ 1 & -k \end{bmatrix} \)
\[ \lambda I - A_4 = \begin{bmatrix} \lambda & c + k \\ 1 & \lambda + k \end{bmatrix} \Rightarrow \text{Characteristic polynomial is: } \lambda^2 + k\lambda - (c + k) \Rightarrow \]

Eigenvalues: \( \lambda_{1,2} = -\frac{1}{2}k \pm \frac{1}{2}\sqrt{k^2 - 4c - 4k} \)

**Lemma C.1.**

*The eigenvalues \( \lambda_{1,2} = -\frac{1}{2}k \pm \frac{1}{2}\sqrt{k^2 - 4c - 4k} \) have negative real parts \( \forall c, k > 0 \)*

**Proof.**

\[ \lambda_1 = -\frac{1}{2}k + \frac{1}{2}\sqrt{k^2 - 4c - 4k} \]
\[ \lambda_2 = -\frac{1}{2}k - \frac{1}{2}\sqrt{k^2 - 4c - 4k} \]

Three cases can be distinguished:

Case 1: \( k^2 - 4k - 4c = 0 \Rightarrow \lambda_1 = \lambda_2 = -\frac{1}{2}k \)

Case 2: \( k^2 - 4k - 4c < 0 \Rightarrow \) Both eigenvalues are complex with negative real part \( -\frac{1}{2}k \)

Case 3: \( k^2 - 4k - 4c > 0 \Rightarrow \) Both eigenvalues are negative.

For case 3 it can be seen that \( \lambda_2 \) is negative.

\[ \lambda_1 = -\frac{1}{2}k + \frac{1}{2}\sqrt{k^2 - 4c - 4k} \text{ and can be written as } -\frac{1}{2}k\left(1 - \frac{1}{\sqrt{1 - (\frac{4c}{k^2} - \frac{4}{k})}}\right) \]

Furthermore, for case 3 the following holds:

\[ k^2 - 4k - 4c > 0 \]
\[ \Rightarrow k^2\left(1 - \frac{4c}{k^2} - \frac{4}{k}\right) > 0 \]
\[ \Rightarrow 1 - \frac{4c}{k^2} - \frac{4}{k} > 0 \]
\[ \Rightarrow \frac{4c}{k^2} + \frac{4}{k} < 1 \]
\[ \Rightarrow \sqrt{1 - (\frac{4c}{k^2} + \frac{4}{k})} < 1 \]
\[ \Rightarrow 1 - \sqrt{1 - (\frac{4c}{k^2} - \frac{4}{k})} > 0 \]

Therefore \( \lambda_1 \) is the product of a positive and a negative factor and hence \( \lambda_1 < 0 \).

And thus it is proven that for all three cases the eigenvalues have negative real parts.

\[ \Box \]

And because all three eigenvalues have negative real part the equilibrium point \((c+k,1)\) is stable.
Appendix D

Proof of Lemma's

A complete proof of lemma 2.1 of paragraph 2.4.4 using the Maple software package.

The Routh coefficient $b_1$ is always negative.

\[
\begin{align*}
\text{Proof of Lemma 2.1 done using Maple} \\
> b_1 &:= -\frac{1}{(e+g+h)^2} \left( h c g^2 d - c e f h^2 + h d e f + c^2 e g h^2 \\
&\quad - 2 c g f h^2 - h c e^2 f + 2 h c e g + h e f - h f d g + g h^2 c \\
&\quad + h e f^2 + h c e^2 + 2 f e g + h d g + d g^2 + f e^2 + f g^2 \\
&\quad + h c e d g - h c g e f + d e^2 - d g h^2 c + f^2 h^2 + h f g \\
&\quad + h c g^2 + c^2 g^2 h^2 + 2 d e g + d f h^2 + h d e + e h^2 c \\
&\quad - h d^2 g \right) \\
> &\quad \text{Substituting } d = c e + c g - f \text{ and simplifying} \\
> &\quad \text{subs} (d = c e + c g - f, b_1) \\
&\quad -\frac{1}{(e+g+h)^2} \left( e h^2 c + h e f + h c g^2 + g h^2 c + h f g \\
&\quad - h c e^2 f + 2 h c e g - 2 c g f h^2 + h e f^2 + f g^2 + h e c (c e \\
&\quad + c g - f) g + (c e + c g - f) g^2 + c^2 e g h^2 + (c e + c g \\
&\quad - f) e^2 + f e^2 + h c e^2 - h (c e + c g - f)^2 g + h (c e + c g \\
&\quad - f) e + h (c e + c g - f) g + 2 f e g - c e f h^2 - h c g e f \\
&\quad + h (c e + c g - f) e f - h f (c e + c g - f) g - (c e + c g \\
&\quad - f) g h^2 c + h c g^2 (c e + c g - f) + 2 (c e + c g - f) e g \\
&\quad + (c e + c g - f) f h^2 + f^2 h^2 + c^2 g^2 h^2 \right) \\
> &\quad \text{simplify (1)} \\
&\quad -\frac{(e + g) c}{h} \\
> &\quad \text{Because } d < c e + c g - f, \text{ the coefficient } b_1 \text{ must be less than} \\
&\quad -\frac{(e + g) c}{h} \\
> &\quad \text{And because} \\
&\quad -\frac{(e + g) c}{h} \text{ is a negative number the coefficient } b_1 \text{ is always negative.}
\end{align*}
\]

Proof of Lemma 2.1 done using Maple
A complete proof of lemma 3.1 of paragraph 3.4.4 using the Maple software package.

The Routh coefficient $b_1$ can be positive, negative or zero.

$$b_1 := \frac{1}{(e+g+h)^2} \left( f d g + e c h + e k h + k^2 e^2 h + f g - c g^2 a \
- d f h + g k h - c^2 g^2 h + k^2 h^2 e + c e^2 f - k h^2 d - k g^2 a \
- k h^2 f + g c h + k e^2 f + f h + d e - d e f - f^2 h + c h^2 \
+ e f + c g e f + 2 c g f h - k e d g - c e d g - c^2 e g h + d \
+ k h^2 e c + k h^2 g c - k e d h + k e^2 c h + k^2 e g h + k g f h \
- k g^2 c h + d g c h + d g + k h^2 - e f^2 + k g e f + d^2 g \
+ k^2 h^2 g + c e f h - (-2 f d g + k e^2 h + c g^2 d \
+ c g^2 f - c h^2 f - 2 d f h - c h^2 d + c^2 g^2 h + c^2 h^2 e \
+ k^2 h^2 e + c e^2 f - k h^2 d + 4 k e g c h + k g^2 d + c e^2 d \
- k h^2 f + k e^2 f + k^2 g^2 h - d^2 h - 2 d e f - f^2 h + c^2 h^2 g \
+ 2 c g e f + 2 k e d g + c^2 e^2 h - f^2 g - d^2 e + 2 c e d g \
+ 2 c^2 e g h + 2 k h^2 e c + 2 k h^2 g c + 2 k e^2 c h + 2 k^2 e g h \
+ 2 k g^2 c h + k e^2 d - e f^2 + 2 k g e f - d^2 g + k^2 h^2 g \
+ k g^2 f \right) \left( (e+g+h) (e c h + e k h + g c h + g k h - d h \
- f h + k h + k e + k g) \right)$$

$> \ simplify(subs(d=(e+k)\cdot(e+g)-f,b1))$

$$c+k$$

$> \text{Consequently if } b_1 \text{ is less than } c+k$

then the coefficient $b_1$ can be positive, negative or zero.

Proof of Lemma 3.1 done using Maple