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Date: 2025
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TU Delft

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to obtain the degree of Bachelor of Science
at the Delft University of Technology,
to be defended publicly on Tuesday July 15, 2025 at 13:00 PM.

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Layman's Abstract

Traditionally, populations have only been measured by direct counting, supplemented by mathematical models such as the Lotka–Volterra equations. However, these models of population dynamics generally do not consider random events in nature, such as unexpected births, sudden disease outbreaks or environmental changes, which can impact population size. This thesis improves upon this model by incorporating randomness (noise) through the use of Wiener processes, resulting in a more realistic outcome. Furthermore, it is proven for two species that the resulting model has a unique, global solution.

The Extended Kalman Filter (EKF) is used to handle incomplete and noisy data. It is proven here that the EKF has bounded expected error. Finally, it is demonstrated that population estimates can be determined for a different, related species even if data is only available for one species.

Abstract

Classically, population dynamics are described by the deterministic Lotka-Volterra equations. These equations do not accurately reflect reality, where stochastic influences have a big impact on populations of species, due to unpredictable environmental and biological factors. Using the Wiener process to include these influences allows for more realistic results, but means that solutions can deviate to unrealistic population numbers. This thesis provides a self-contained proof of the existence, uniqueness and boundedness of solutions of such systems.
In many cases, population data for all species is unavailable. To make accurate estimates for the unknown or hidden data, the extended Kalman filter can be applied. Which, through a combination of the data and the mathematical model, creates an estimate for the population. An exponential bound for the error of this estimation is derived in expectation

Summary

In order to model a population, data for that population is generally required. Models such as the Lotka-Volterra equations can be fitted to that data in order to obtain a specific set of equations that closely align to reality. Actual population estimates cannot always be done on basis of reliable data; sometimes only very noisy data is available, or even no data at all. In that case, it might be, that data from other species in close relationship with the former, is available. From this data, an estimate could be made for the population of the former.

In this thesis, a fundamental framework is introduced to enable the construction of a mathematical model which accurately reflects interactions between populations in nature. After the establishment of this model and proving the well-posedness of that model, a possible algorithm to deduce the unknown, or 'hidden' population, is proposed, and a bound for the error of this method is demonstrated. This is then applied to data in order to prove the usefulness of this combination of model and algorithm.

The commonly used Lotka-Volterra system of equations, describing the populations of interacting species, was expanded with a noise term, thus allowing the inclusion of stochastic effects, such as random births and deaths, but also diseases, floods and other random biological or environmental changes. Global existence and uniqueness of these equations were proven, thus determining that the stochastic differential equations are, mathematically, valid. This was done by proving the boundedness and nonnegativity of solutions, using equilibria, thereby also satisfying a biological constraint.

After establishing the necessary mathematical framework, the extended Kalman filter is formulated. This filter is used to determine the hidden state and filter out some of the noise from the data. As this filter only provides an estimate, an error most likely exists. An exponential bound in expectation for this specific set of equations was proven, generalising the proof from [Reif et al., 2000] in certain respects.

The reliability of the model, in combination with the extended Kalman filter is further substantiated by application to real and simulated data, thus reinforcing the usefulness of the model.

Contents

Nomenclature

Abbreviations

Abbreviation	Definition
EKF	Extended Kalman Filter
EV	Eigenvalue
KF	Kalman Filter
LV	Lotka-Volterra equations, an interaction model between species

Symbols

Symbol	Definition
$\mathrm{tr}(\cdot)$	the trace of a matrix
$\lvert \cdot \rvert$	the absolute value
$\lvert\lvert \cdot \rvert\rvert$	the Euclidian norm of a vector
$\lvert\lvert \cdot \rvert\rvert$	the spectral norm of a matrix
A^T	Transpose of matrix A
$\subset$	Strict inclusion

1 Introduction

Mathematical models are indispensable for understanding the numerous complex factors that influence changes in a species' population over time. Among the various variables influencing these changes, some common ones are birth and death rates [Kendall, 1948], competition, predation [Wangersky, 1978], environmental factors, such as climate, habitat loss [Johnston et al., 2019] or even seasonal variations [Fretwell, 1972], and genetic mutation, including evolutionary adaption [Turcotte et al., 2011]. Interspecific interactions consist mainly of competition [Tilman, 1982], predation and symbiosis [Bronstein, 2015], which includes both mutualistic and parasitic relationships.

Population models have a very long history. In 1202 an exercise in an arithmetic book written by Leonardo of Pisa (c. 1170–1250) involved building a mathematical model for a hypothetical scenario involving the growth of a rabbit population under ideal conditions, where each pair of rabbits produces a new pair each month. He provided an early and simple example of exponential population growth, known today as the Fibonacci sequence [University of Utah, 2009].

One of the earliest and best-known population models was introduced by Alfred Lotka in 1910. Lotka published a set of first-order nonlinear differential equations[Lotka, 1910] that later became known as the Lotka-Volterra equations or, more commonly, the predator-prey model. This describes a model in which the number of prey grows exponentially in the absence of predators, and the number of predators declines exponentially in the absence of prey [Murray, 2002]. A form of these equations is given in Equation 1.1, here n different species are modelled, and the population changes for each species i depend on interactions with all other species, including itself, at a rate of $a_{i,j}$ where j denotes the respective interacting species. The interaction constant $a_{i,j}$ describes the type of relationship, symbiotic, competition or predation, respectively; the death rate for $a_{i,i}$, and r_i describes the reproduction rate. The Lotka-Volterra equations for a system of n dimensions can be given by:

$$\begin{aligned}
\frac{dX_1}{dt} &= X_1\big(r_1 - \sum_{i=1}^{n} a_{1,i}X_i\big), \\
\frac{dX_2}{dt} &= X_2\big(r_2 - \sum_{i=1}^{n} a_{2,i}X_i\big), \\
&\vdots \\
\frac{dX_n}{dt} &= X_n\big(r_n - \sum_{i=1}^{n} a_{n,i}X_i\big).
\end{aligned} \tag{1.1}$$

Where $X_i(t)$ describes the population of species i at time t.

Since the publication of Lotka's original model, modifications have been made and new models have been developed. Although the basic idea has remained the same, integral equations are now often used. The Lotka–Volterra equations remain popular, partly because of their simplicity. However, a significant limitation to this is its deterministic character. Population changes are not solely dependent on the amount of a species, but are inevitably linked to uncertainty. Some of the unpredictable factors are environmental fluctuations[Louthan & Morris, 2021] and random genetic variation[Matic, 2019]. Incorporating one or more stochastic elements into this model provides a more realistic portrayal of population dynamics. Randomness in birth, death, and interaction rates, has a vast impact on ecological systems [Schnute, 1991]. A common approach is by adding noise, taken as standard Brownian motion, with the intensity dependent upon the total population of all species. The resulting stochastic integral equations can be solved using Wiener or Itô integration.

In practice, it is often challenging to model populations accurately, due to the frequent lack of complete real-time data for all species involved. Often, information regarding the population size of one or more of the species is unavailable, or unreliable. This lack of data can be remedied using filtering techniques, which mathematically estimate the unknown or "hidden" state of a system from noisy or incomplete observations.

Kalman filtering (KF) is a commonly used method applied to stochastic differential systems, subject to Gaussian noise or even with incomplete data [Akram et al., 2019]. Stochastic filtering, of which Kalman filtering is a part, can be defined as a way to estimate the state of a dynamic system from noisy observations [Kallsen, 2018]. The KF algorithm is recursive and thus continuously refines the estimation, facilitated by constant integration of new (partial) measurements and the subsequent updating of any preceding estimates[Kalman, 1960]. The extended Kalman Filter (EKF) is a widely used extension of the original algorithm. It allows nonlinear systems to be approximated through linearisation and is applied in a multitude of situations. Particularly it is widely used in localisation [Ullah et al., 2021], [Al Malkia et al., 2020]. But also in the prediction of pest outbreaks, for instance in the case of flies [Bono Rosselló et al., 2023]. However the applications for population estimates of a species remain comparatively limited. Some attempts have been made to predict the number of fish [Gudmundsson, 1995], [Ennola et al., 1998] or the weight of these fish [Aljehani et al., 2023]. In contrast, the EKF has been widely applied to model the prevalence and spread of viruses, for example, COVID-19 [Piccirillo, 2021], [Zhu et al., 2025]. Whilst Bayesian approaches have been used to estimate the parameters of the Lotka-Volterra system [Rahman et al., 2012], and other observers have been used, like state ratio dynamics, [Badri, 2022], the (extended) Kalman Filter remains a commonly used estimator. Recently the extended Kalman Filter has been used to approximate the parameters of fish stocks [Benz et al., 2021]. Although this is done using Lyapunov methods, which will not be used in this paper.

The objective of this report is to *clearly introduce a system of stochastic differential equations (SDEs) that can accurately describe different interacting populations, and prove that these SDEs are well-posed. The aim is to apply the extended Kalman filter to enable the use of partial and noisy observations while still obtaining an accurate population estimate. An asymptotic exponential error bound for estimations retrieved from this filter should be derived.*

In order to do this, first some fundamental knowledge will be introduced in Chapter 2, then the Lotka-Volterra model will be modified to include the stochastic elements, thus resulting in an SDE. This, as well as proving that this SDE has a unique, bounded solution will be done in Chapter 3. In the next Chapter, 4, the error of applying the extended Kalman filter will be determined in expectation. Lastly, the extended Kalman filter will be applied to example data, with the earlier determined model. Then, two examples for finding the hidden state will be given with simulated data, in Chapter 5. The results of this report are discussed in chapter 6, and ultimately a conclusion is drawn in chapter 7. Furthermore, data and the used code will be provided in the appendices A-E.

2

Preliminary Concepts

2.1. Biological Basis

In biology, interactions between species are generally categorized as either predatory or symbiotic. Symbiotic relations are then often subdivided into the following six divisions: Mutualism[Britannica, 2025b], Commensalism[Britannica, 2025a], Parasitism[Britannica, 2025c], Neutralism[Lidicker, 1979], Amensalism[Britannica, 2010] and Competition[Britannica, 2019]. This can be seen in Table 2.1

Species A $\downarrow$ \Species B $\rightarrow$	**Benefit**	**Neutral**	**Harm**
Benefit	Mutualism	Commensalism	Parasitism
Neutral	Commensalism	Neutralism	Amensalism
Harm	Parasitism	Amensalism	Competition

Table 2.1: Types of symbiotic relations between species A and B

Although it may seem from this table that parasitism and predation are the same, there is an important difference between them; the method of prey consumption. Parasites feed on living tissue, whereas predators kill their prey before or during the feeding process.

2.2. Remarks on Lotka Volterra model

As is done in the Introduction the general predator prey model used in this report is based on the Lotka-Volterra model, and given by Equation 2.1. Here $a_{i,j}$ describes the influence the population of j has on species i, the reproductive rate of species i is given by $r_i > 0$. Then, for a system of n different species, there are n equations describing the change in population for each individual species.
As the reproduction rate r_i only depends on the population of the respective species, it is scaled only by X_i; the interaction described by $a_{i,j}$ is multiplied by both X_i and X_j, expressing its dependence on the population of both species. This is because there are fewer interactions when there are fewer

individuals of one or both species.

$$
\begin{aligned}
\frac{dX_1}{dt} &= X_1\big(r_1 - \sum_{i=1}^{n} a_{1,i}X_i\big),\\
\frac{dX_2}{dt} &= X_2\big(r_2 - \sum_{i=1}^{n} a_{2,i}X_i\big),\\
&\vdots\\
\frac{dX_n}{dt} &= X_n\big(r_n - \sum_{i=1}^{n} a_{n,i}X_i\big).
\end{aligned} \tag{2.1}
$$

A symbiotic relationship between species i and species j exists if $a_{i,j} < 0$ and $a_{j,i} < 0$, competition between the species i, j is described by $a_{i,j} > 0$ and $a_{j,i} > 0$, and lastly a predator-prey model is described using $a_{i,j} < 0$ and $a_{j,i} > 0$ where species j would be the prey. If $a_{i,j} = 0$ then the population of species j has no effect on the growth or decline of the population of i.

2.2.1. Example: predation

This report will explore a predator-prey interaction between two species as an example. In such a relationship, one species, the predator, feeds on the other (the prey). This means, that the prey population supports the growth of the predator population, it exerts a positive influence. However, the latter has a negative influence on the prey population by reducing its numbers through predation.
For this example the interaction between moose and wolves in the Isle Royale National Park is chosen. The data used is given in Appendix A, plotting this data yields Figure 2.1

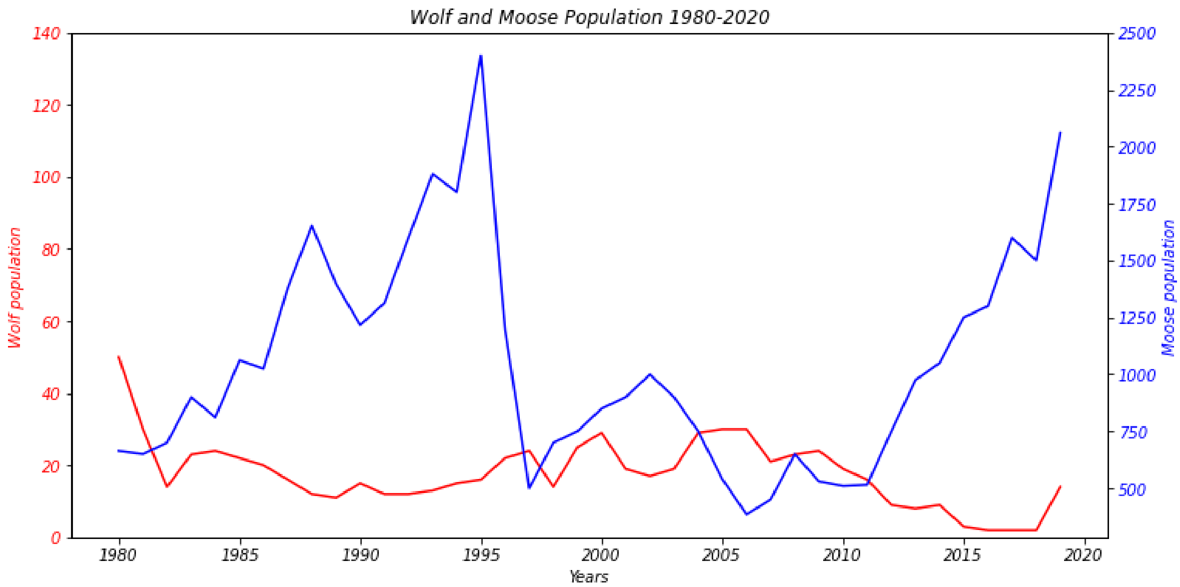

Figure 2.1: The population wolves (left vertical axis) and of moose (right vertical axis) in the Isle Royale National Park between 1980 and 2019

Here, a classic predator-prey dynamic is exemplified by an interaction between wolves and moose. At the outset of the graph, a lack of predators (wolves) allows the prey population (moose) to multiply quickly. The rapid resulting abundance of prey leads to an increase in the number of predators. As the wolf population grows, the predation of other species increases, resulting in a drastic reduction in the number of moose. In response to the decreased number of prey, the wolf population also declines, reducing the pressure on the prey and enabling the moose population to recover.

When fitting the Lotka-Volterra equations to this data, which is about only two populations, the equations simplify to just two:

$$\frac{dX_1}{dt} = X_1 r_1 - a_{1,2} X_1 X_2 \tag{2.2}$$
$$\frac{dX_2}{dt} = X_2 r_2 - a_{2,1} X_1 X_2 \tag{2.3}$$
$$\tag{2.4}$$

Then by inputting $r_1 = 0.466, a_{1,2} = 0.00819, r_2 = 0.0001, a_{2,1} = 0.107$ the LV equations achieve a result (Figure 2.2) that is close to the real data. Note that the estimation for the wolf population is always a little higher than in real life, this is mainly due to the severe difference in population sizes between the wolves and the moose.

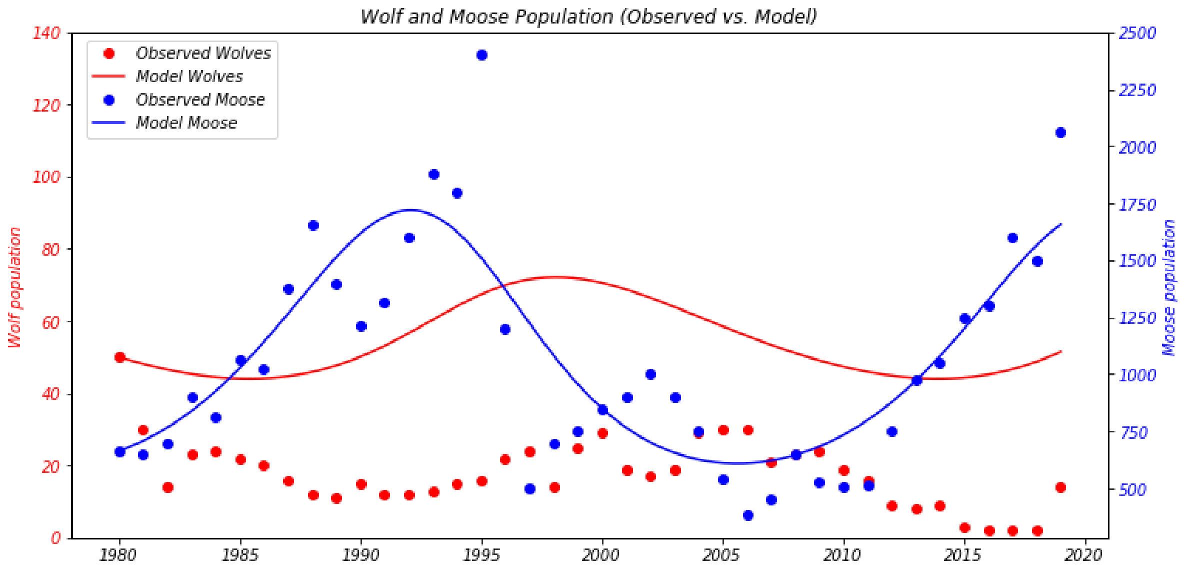

Figure 2.2: The population wolves (left vertical axis) and of moose (right vertical axis) in the Isle Royale National Park between 1980 and 2019. With the LV-equations for $r_1 = 0.466, a_{1,2} = 0.00819, r_2 = 0.0001, a_{2,1} = 0.107$.

2.3. Stochastic Noise

A stochastic process is a collection of random variables, often dependent on the time, describing the state of a process at for example a time t. This allows stochastic processes to describe systems experiencing random changes. Each random variable takes a value from a range of possibilities, with a certain probability [Ross, 1996][Gallager, 2013]. Or, if all possible outcomes are seen as a family of paths, then the stochastic process describes the probability of taking one of these paths[Mörters & Peres, 2010]

The noise added to the equations on population interaction (Equation 2.1) will be given by a Wiener process, which is sometimes called Brownian motion. Both names will be used interchangeably throughout this thesis.

Definition 2.3.1. ***Wiener process [Szabados, 1994]:***
A stochastic process W_t is called a Wiener process if the following holds:

1. $W(0) = 0$ *almost surely.*
2. $\forall s, t$ *with*: $0 \leq s \leq t$ *it holds that* $W(t) - W(s) \sim \mathcal{N}(0, t - s)$.
3. $\forall s, t, u, v$, *such that* $0 < s < t \leq u < v$, *it holds that* $W(s) - W(t)$ *is independent of* $W(u) - W(v)$.

4. *$t \mapsto W(t)$ is continuous, almost surely.*

The given probability density function of the Wiener process for $t > 0$ as presented in Equation 2.5 is:

$$f_{W_t}(x) = \frac{1}{\sqrt{2\pi t}} e^{-x^2/(2t)}. \quad (2.5)$$

The probability density function is the same as that of a normal distribution with mean 0 and standard deviation t. From this distribution function it immediately follows that $\mathbb{E}(W_t) = 0$, and Var $(W_t) = t$. Furthermore the increment $W_t - W_s$ is proportional to $\mathcal{N}(0, t-s)$, meaning it is normally distributed with mean zero and a variance of $t - s$.

Let the number of samples be 200, then a possible realisation of the Wiener process is given in Figure 2.3:

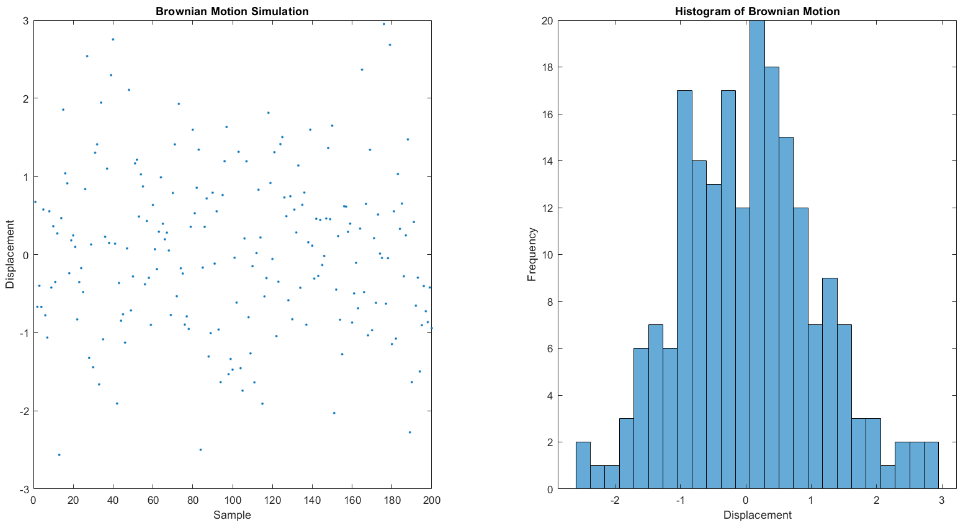

Figure 2.3: Brownian motion for 200 samples, to the left the vector with the samples, to the right the histogram of the values. It can be observed, that this histogram approximates that of a normal distribution, that the mean is zero.

A filtration is an increasing sequence of sigma algebras on the probability space. Increasing means the sequence is nested, thus a later filtration is a superset of an earlier one, it includes all earlier sets. It is used to depict knowing more about the outcome of a stochastic process as time progresses and more information is known. Informally, it contains all information known at time t, more formally it can be defined as:

Definition 2.3.2. ***Filtration****[Oksendal, 2000]:*
A family of σ-algebras, $\mathcal{F} = \{\mathcal{F}_t\}_{t\geq 0}$ is a filtration if, $\forall\ 0 \leq t \leq s$:

$$F_t \subseteq F_s.$$

The Wiener process which will be used in this paper is a F_t-Wiener process, meaning the wiener process is consistent with the available information at time t, as defined by the filtration F_t.

Definition 2.3.3. ***Adapted Process****[Oksendal, 2000]:*
Let $\{\mathcal{F}_t\}_{t\geq 0}$ denote a filtration with probability space Ω. A stochastic process $g(t,\omega) : [0,\infty) \times \Omega \to \mathbb{R}^n$ is said to be adapted to the filtration $\mathcal{F}_t$ if, $\forall t \geq 0$, the mapping $\omega \mapsto g(t,\omega)$ is measurable with respect to $\mathcal{F}_t$.

A stochastic process is adapted when the value of the process at any given time depends only on the information available up to the time it is happening and not on any future information. It is often used in stochastic modeling, for example, in finance and control theory, where decisions are based on current and past information.

A filtration denotes the information known until some time t. In certain contexts, only the minimal filtration, with respect to which the stochastic process is measurable, is required. This minimal filtration is equivalent to the filtration generated by that process. For Brownian motion, this specific filtration is termed the Brownian filtration. Formally, this can be defined as:

Definition 2.3.4. ***Brownian Filtration****[Kozdron, 2009]:*
On a probability space $(\Omega, \mathcal{F}, \mathbb{P})$ the Brownian Filtration with respect to the Wiener process W_t is given by

$$\mathcal{F}_t = \sigma(W_s, 0 \leq s \leq t). \tag{2.6}$$

From now on, W denotes a Wiener process with respect to the filtration $\mathcal{F}_t$, $\sigma(W_s, 0 \leq s \leq t)$ is the smallest σ-algebra where all W_s, for $0 \leq s \leq t$ are measurable.

2.3.1. Population dependent noise

Noise refers to stochastic events, which influence the population of one or more species. The random increase, or more often, decrease in population can happen due to a multitude of contrasting causes. Examples include accidental deaths, e.g. collisions with cars; diseases, e.g. viruses; environmental changes, especially climate change, which is an increasingly important cause of damage; and direct human activities, e.g. hunting, which has a major impact on noise, depending on the species.
A fundamental aspect of this noise is its dependence on the size of the affected species. However, it might also depend on the size of other species. For instance, one species might be the carrier of a disease deadly to another species. In such a case the probability of transmitting this disease to a susceptible species increases as the population size of the carrier species grows.
In order to prove boundedness this paper will assume the influence of the stochastic noise becomes zero, somewhere before the lower and upper bounds. Meaning, that if D is the maximum population capacity of some species i, that the support of the noise for some X_i is compact and a strict subset of $[0, D]$. If $S_{i,j}$ is the support of $\sigma_{i,j}$ then

$$S_{i,j} \subset (0, D)^n, \ \ \forall i, j \in (1, n). \tag{2.7}$$

This support condition will be formulated more specifically in later chapters, when this is necessary.
As the noise should not decrease too sharply, i.e. discontinuously, it is furthermore assumed that the function $\sigma_{i,j}$ is Lipschitz continuous for all $i, j = 1, \ldots, n$.

Both Wiener and Itô integration are methods of integration with respect to a stochastic process. Wiener integration can be considered a special case of Itô integration in that the latter permits integration over a wider range of functions and integrands. The Itô integral is a more general concept, allowing the integration of adapted stochastic processes with respect to semimartingales, e.g. Brownian motion. This paper will only define Itô integration.

Definition 2.3.5. ***Itô Integration[Kozdron, 2009]:***
Let L^2 denote the space where $\forall t \geq 0 : g(t)$ is adapted to $\mathcal{F}_t$, with $\mathcal{F}_t$ being the Brownian Filtration, and where $\forall\, T > 0 : \int_0^T \mathbb{E}\left[g^2(t)\right] \mathrm{d}t < \infty$. Then the following limit is well posed as a limit in $L^2(\Omega \times [0, T])$:

$$I_t(g)(\omega) = \int_0^t g(s, \omega) \mathrm{d}B_s(\omega) = \sum_{i=1}^{n} X_{i-1}(\omega) \left(B_{t_i}(\omega) - B_{t_{i-1}}(\omega)\right) \tag{2.8}$$

This integral is a random process in a way that it is a random variable in $L^2(\Omega)$, which also guarantees its existence and uniqueness as $L^2(\Omega \times [0, T])$ is a Hilbert space.
Furthermore, it is well known that the stochastic integral definition in this way is continuous almost surely [Kozdron, 2009].

2.4. Filtering

In 1949, Norbert Wiener introduced the Wiener filter, as a method to retrieve signals from noisy measurements. His solution was a significant improvement from earlier solutions to the filtering problem. Generally, the filtering problem can be stated as follows: given some stochastic (possibly noisy) signal $\mathbf{x}$, and $\mathbf{y}$ is the observable data. This means that when $\mathbf{x}$ is measured, it is possible that some noise is added to the original data, yielding $\mathbf{y}$ as an observation with noise. The filtering problem tries to calculate an estimate, $\hat{\mathbf{x}}$, as close as possible to the original, from $\mathbf{y}$. This is done by minimising the mean squared error between true and estimated data, meaning it tries to minimise:

$$\mathbb{E}\left[||\mathbf{x}-\hat{\mathbf{x}}||^2\right]. \tag{2.9}$$

Where $\hat{\mathbf{x}}$ depends only on $\mathbf{y}$ and not on $\mathbf{x}$.
Wiener assumed generalised noise, such as multiplicative or additive noise, meaning $\mathbf{y} = \mathbf{x} + \varepsilon$. Although this was a central condition to his solution, it was later let go, as different filters could solve the problem for any type of noise. Subsequent filtering techniques often only necessitate covariance matrices and means of $\mathbf{x}$ and $\mathbf{y}$.
Kalman filtering extends this problem to a dynamic system using partial and noisy observations. It gets results by combining the new observations with predictions. In this case, the predictions are done by applying the Predator-Prey equations. This means, that instead of the earlier mentioned minimisation of the mean square, which was given in Equation 2.9 the mean square error that is to be minimised by the Kalman filter, in the discrete case, is given by:

$$\mathbb{E}\left[||\mathbf{x_k}-\hat{\mathbf{x}}_{k|k}||^2\right], \tag{2.10}$$

where

$$\hat{\mathbf{x}}_{k+1|k} = \mathbb{E}\left[\mathbf{x}_{k+1}|\mathbf{y}_1,\ldots,\mathbf{y}_k\right]. \tag{2.11}$$

In this sense the Kalman filter is the best possible linear estimator [Reid, 2001].
In application, the (standard) Kalman filter assumes a linear relationship between data $\mathbf{x}$ and measurable data $\mathbf{y}$. The extended Kalman filter, which will be used in this thesis, removes this constraint, and is often applied to nonlinear systems. For completeness both cases will be given, both in continuous and discrete versions. The continuous case is mathematically more interesting, but due to the application of the filter later in the thesis, using code, the discrete case will also be given.

2.4.1. Continuous Kalman Filtering

Traditionally the Kalman filter has been used only in discrete cases, as data generally only comes in discrete time steps. Nevertheless the continuous Kalman filter is often used, as the situations described by the filter progress in continuous time. Modelling them accordingly provides more theoretical knowledge about the system and the filter.
The continuous Kalman, or often called the Kalman-Bucy filter provides a state-estimation method for continuous systems. The provided solution is a consistent solution to the linear Gaussian problem.
Although used less for real-world applications it provides a lot of insight into the more theoretical workings of a system. By giving a better understanding of the properties of the filter.
Assuming the model is of the form:

$$\begin{aligned} \mathrm{d}\mathbf{x} &= \mathbf{F}(t)\cdot\mathbf{x}(t)\mathrm{d}t \quad &+\mathrm{d}\mathbf{v}(t),\\ \mathrm{d}\mathbf{y}(t) &= \mathbf{H}(t)\cdot\mathbf{x}(t)\mathrm{d}t \quad &+\mathrm{d}\mathbf{w}(t). \end{aligned} \tag{2.12}$$

Where $\mathbf{Q}(t)$ and $\mathbf{R}(t)$ describe the variances of the noise, $\mathbf{v}(t) \sim \mathcal{N}(0,\mathbf{Q}(t))$ respectively $\mathbf{w}(t) \sim \mathcal{N}(0,\mathbf{R}(t))$.

The continuous Kalman filter can be derived from the discrete case by taking the limit of the timestep-size to zero. Doing so results in the following equations [Frank L. Lewis, 2007]:

$$\begin{aligned} \frac{\mathrm{d}}{\mathrm{d}t}\mathbf{P} &= \mathbf{F}(t)\cdot\mathbf{P}(t)+\mathbf{P}(t)\cdot\mathbf{F}^T(t)+\mathbf{Q}(t)-\mathbf{K}(t)\cdot\mathbf{R}(t)\cdot\mathbf{K}^T(t),\\ \mathbf{K}(t) &= \mathbf{P}(t)\cdot\mathbf{H}^T(t)\cdot\mathbf{R}^{-1}(t),\\ \mathrm{d}\hat{\mathbf{x}} &= \mathbf{F}(t)\cdot\hat{\mathbf{x}}(t)\mathrm{d}t+\mathbf{K}(t)(\mathrm{d}\mathbf{y}(t)-\mathbf{H}(t)\cdot\hat{\mathbf{x}}(t)\mathrm{d}t). \end{aligned} \tag{2.13}$$

2.4.2. Discrete Kalman Filtering

Discrete Kalman filtering is commonly used in the application of the Kalman filter. Although most systems are continuous, implementation, using for example real-life data, often demands a discrete filter. This is due to the fact that it is often not possible to measure data continuously. This is the case for this thesis because continuous population data is unavailable. This is because populations of species have to be counted.

In general Kalman filtering is based on data with a given uncertainty, the covariance. This means it is in the form

$$\begin{aligned} &\hat{x}_{k-2|k-2}, \hat{x}_{k-1|k-1}, \dots,\\ &\mathbf{P}_{k-2|k-2}, \mathbf{P}_{k-1|k-1}, \dots. \end{aligned}$$

Meaning the data at time $k-2$ is based on the state at time $k-2$. With this a prediction is made based on the data at time $k-1$ using the predator-prey equations:

$$\begin{aligned} &\hat{x}_{k|k-1},\\ &\mathbf{P}_{k|k-1}. \end{aligned}$$

This is combined (updated) with the new noisy and or partial measurement to yield

$$\begin{aligned} &\hat{x}_{k|k},\\ &\mathbf{P}_{k|k}. \end{aligned}$$

To give an approximate number of predators and prey at time k. The combination is made using the optimal Kalman gain; this sequence can be repeatedly done until the prediction is made for the desired time interval.
More formally, assume a model of the form:

$$\begin{aligned} \mathbf{x}_k &= \mathbf{F}_k\cdot\mathbf{x}_{k-1} \quad +\mathbf{v}_k,\\ \mathbf{y}_k &= \mathbf{H}_k\cdot\mathbf{x}_k \quad\quad +\mathbf{w}_k. \end{aligned} \tag{2.14}$$

Where

- $\mathbf{F_k}\in\mathbb{R}^{D\times D}$ is the state transition matrix,
- $\mathbf{H_k}\in\mathbb{R}^{M\times D}$ is the measurement matrix,
- $\mathbf{v_k}\in\mathbb{R}^{D\times 1}$ is the Gaussian noise vector with $\mathbf{v_k}\sim\mathcal{N}(0,\mathbf{Q_k}$,
- $\mathbf{w_k}\in\mathbb{R}^{M\times 1}$ is the Gaussian noise vector with $\mathbf{w_k}\sim\mathcal{N}(0,\mathbf{R_k}$.

Prediction

The prediction is then made by performing the following calculations [Kovvali et al., 2013]:

$$\begin{aligned} \hat{\mathbf{x}}_{k|k-1} &= \mathbf{F}_k\cdot\hat{\mathbf{x}}_{k-1|k-1},\\ \mathbf{P}_{k|k-1} &= \mathbf{F}_k\cdot\mathbf{P}_{k-1|k-1}\cdot\mathbf{F}_k^T \quad +\mathbf{Q}_k. \end{aligned} \tag{2.15}$$

Estimate

In order to compute the estimate $\hat{\mathbf{x}}_{n|n}$ the following has to be calculated[Kovvali et al., 2013]:

$$\begin{aligned}\mathbf{S}_k &= \mathbf{H}_k \mathbf{P}_{k|k-1} \mathbf{H}_k^T + \mathbf{R}_k, \\ \mathbf{K}_k &= \mathbf{P}_{k|k-1} \mathbf{H}_k^T \mathbf{S}_k^{-1}, \\ \hat{\mathbf{x}}_{k|k} &= \hat{\mathbf{x}}_{k|k-1} + \mathbf{K}_k (\mathbf{y}_k - \mathbf{H}_k \hat{\mathbf{x}}_{k|k-1}), \\ \mathbf{P}_{k|k} &= \mathbf{P}_{k|k-1} - \mathbf{K}_k \mathbf{H}_k \mathbf{P}_{k|k-1}.\end{aligned} \tag{2.16}$$

Here, of course, $\hat{\mathbf{x}}_{k|k}$ and $\mathbf{P}_{n|n}$ are the prediction respectively the uncertainty of the prediction. Using these two, and the model, a new prediction can be made, and subsequently a new estimate for time $n+1$.

2.4.3. Extended Kalman Filter

The extended Kalman filter(EKF) is used to estimate the states of a nonlinear dynamic system. The EKF is based on the traditional Kalman Filter, which works on linear dynamic systems with Gaussian noise, this use is extended by the EKF to nonlinear systems, by approximating the functions as linear. In the past the extended filter has been used in for example robotics, navigation and for GPS, which are systems that generally experience nonlinear behaviour.

Instead of the state transition and observational models being linear, they can now be any differentiable function. Again, first the continuous filter will be given and afterwards the discrete case.

2.4.4. Continuous Extended Kalman Filter

Instead of supposing that there is a linear relationship between $\mathbf{x}$ and $\mathbf{y}$

$$\begin{aligned}\mathrm{d}\mathbf{x}(t) &= f(\mathbf{x}(t)))\mathrm{d}t + G(\mathbf{x}(t))\mathrm{d}\mathbf{v}(t), \\ \mathrm{d}\mathbf{z}(t) &= h(\mathbf{x}(t))\mathrm{d}t + \mathrm{d}\mathbf{w}(t).\end{aligned} \tag{2.17}$$

With initial values at time t_0

$$\begin{aligned}\hat{\mathbf{x}}(t_0) &= \mathbb{E}[\mathbf{x}(t_0)], \\ \mathbf{P}(t_0) &= \mathrm{Var}[\mathbf{x}(t_0)].\end{aligned} \tag{2.18}$$

Where Var denotes the variance and $\mathbf{v}(t) \sim \mathcal{N}(0, \mathbf{Q}(t))$ and $\mathbf{w}(t) \sim \mathcal{N}(0, \mathbf{R}(t))$.

Let

$$\begin{aligned}F(t) &= \left.\frac{\partial f}{\partial \mathbf{x}}\right|_{\hat{\mathbf{x}}(t)}, \\ H(t) &= \left.\frac{\partial h}{\partial \mathbf{x}}\right|_{\hat{\mathbf{x}}(t)}.\end{aligned} \tag{2.19}$$

This allows for the approximation of the non-linear functions f and h by:

$$\begin{aligned}f(\mathbf{x}(t), t) &\approx f(\hat{\mathbf{x}}(t), t) + F(\hat{\mathbf{x}}(t), t)(\mathbf{x}(t) - \hat{\mathbf{x}}(t)), \\ h(\mathbf{x}(t), t) &\approx h(\hat{\mathbf{x}}(t), t) + H(\hat{\mathbf{x}}(t), t)(\mathbf{x}(t) - \hat{\mathbf{x}}(t)).\end{aligned} \tag{2.20}$$

With $\hat{\mathrm{x}}(t)$ being the current state estimate.

In the continuous case the predict and update steps are done simultaneously [Morrel, 1997]:

$$\begin{aligned}K(t) &= P(t)H(t)^T R(t)^{-1}, \\ \hat{\mathbf{x}}(t) &= f(\hat{\mathbf{x}}(t)) + K(t)(\mathbf{z}(t) - h(\hat{\mathbf{x}}(t))), \\ \frac{\mathrm{d}}{\mathrm{d}t}P(t) &= F(t) \cdot P(t) + P(t)F(t)^T - K(t)H(t)P(t) + GQ(t)G^T.\end{aligned} \tag{2.21}$$

Then lastly for the discrete extended Kalman filter.

2.4.5. Discrete Extended Kalman Filter

The assumed model is of the form:

$$\begin{aligned} \mathbf{x}_k &= f(\mathbf{x}_{k-1}) + \mathbf{v}_{k-1}, \\ \mathbf{z}_k &= h(\mathbf{x}_k) + \mathbf{w}_k. \end{aligned} \tag{2.22}$$

Again with $\mathbf{v}(t) \sim \mathcal{N}(0, \mathbf{Q}(t))$ and $\mathbf{w}(t) \sim \mathcal{N}(0, \mathbf{R}(t))$.

Then, for the prediction step, we have the following[Morrel, 1997]:

$$\begin{aligned} \hat{\mathbf{x}}_{k|k-1} &= f(\hat{\mathbf{x}}_{k-1|k-1}), \\ \mathbf{P}_{k|k-1} &= \mathbf{F}_k \cdot \mathbf{P}_{k-1|k-1} \cdot \mathbf{F}_k^T \quad + \mathbf{Q}_{k-1}. \end{aligned} \tag{2.23}$$

Let:

$$\begin{aligned} \mathbf{F}(t) &= \left.\frac{\partial f}{\partial \mathbf{x}}\right|_{\hat{\mathbf{x}}_{k-1|k-1}}, \\ \mathbf{H}(t) &= \left.\frac{\partial h}{\partial \mathbf{x}}\right|_{\hat{\mathbf{x}}_{k|k-1}}. \end{aligned} \tag{2.24}$$

Then the update step is then done in the following way:

$$\begin{aligned} \tilde{\mathbf{y}}_k &= \mathbf{z}_k - h(\hat{\mathbf{x}}_{k|k-1}) \\ \mathbf{S}_k &= \mathbf{H}_k \mathbf{P}_{k|k-1} \mathbf{H}_k^T + \mathbf{R}_k, \\ \mathbf{K}_k &= \mathbf{P}_{k|k-1} \mathbf{H}_k^T \mathbf{S}_k^{-1}, \\ \hat{\mathbf{x}}_{k|k} &= \hat{\mathbf{x}}_{k|k-1} + \mathbf{K}_k \tilde{\mathbf{y}}_k, \\ \mathbf{P}_{k|k} &= \mathbf{P}_{k|k-1} - \mathbf{K}_k \mathbf{H}_k \mathbf{P}_{k|k-1}. \end{aligned} \tag{2.25}$$

3

Stochastic Integral Equations for Population Models

In numerous ways, population dynamics are subject to unpredictable occurrences. Whilst births, deaths and interaction rates can be represented by fixed parameters on a grander level, there always will be an inherent probability that reality deviates from these averages. A particular deterministic model was discussed in Section 2.2, which describes population changes using average interaction and growth rates. However, this, and other models like it, do not account for stochastic influences on population size, which, depending on the scale, could significantly influence one or more species. Incorporating stochastic fluctuations or 'noise' into the mathematical models is a logical next step in describing population changes more accurately. This chapter will outline one approach to incorporating noise and prove that solutions to this model exist.

3.1. Stochastic noise in the LV model

The Lotka-Volterra equations, which form the basis of all subsequent equations in this report, were outlined in Section 2.2. For the incorporation of the stochastic elements into this equation, these equations will be rewritten into integral equations. This can simply be done by integrating all equations, as they are only first order differential equations. The results of this are given in equation 3.2.

$$
\begin{aligned}
\int_{t_0}^{t} \frac{dX_1}{ds}(s)\mathrm{d}s &= \int_{t_0}^{t} X_1(s)\big(r_1 - \sum_{i=1}^{n} a_{1,i}X_i(s)\big)\mathrm{d}s,\\
\int_{t_0}^{t} \frac{dX_2}{ds}(s)\mathrm{d}s &= \int_{t_0}^{t} X_2(s)\big(r_2 - \sum_{i=1}^{n} a_{2,i}X_i(s)\big)\mathrm{d}s,\\
&\vdots\\
\int_{t_0}^{t} \frac{dX_n}{ds}(s)\mathrm{d}s &= \int_{t_0}^{t} X_n(s)\big(r_n - \sum_{i=1}^{n} a_{n,i}X_i(s)\big)\mathrm{d}s.
\end{aligned}
\tag{3.1}
$$

$$\Leftrightarrow$$

$$
\begin{aligned}
X_1(t) &= X_1(t_0) + \int_{t_0}^{t} X_1(s)\big(r_1 - \sum_{i=1}^{n} a_{1,i}X_i(s)\big)\mathrm{d}s,\\
X_2(t) &= X_2(t_0) + \int_{t_0}^{t} X_2(s)\big(r_2 - \sum_{i=1}^{n} a_{2,i}X_i(s)\big)\mathrm{d}s,\\
&\vdots\\
X_n(t) &= X_n(t_0) + \int_{t_0}^{t} X_n(s)\big(r_n - \sum_{i=1}^{n} a_{n,i}X_i(s)\big)\mathrm{d}s.
\end{aligned}
\tag{3.2}
$$

Then in order to add the noise as described in section 2.3.1, Brownian motion, described by W_i, needs to be added. Furthermore, as this noise term does not have the same weight for each individual species, see Section 2.3.1, a noise term dependent on the populations of the species, $\sigma_{m,n}(t, X_1, \ldots, X_n)$, describing the stochastic influence of species n on species m will be added, which will be integrated with respect to the Brownian motion. Fully working this out yields equation 3.3.

$$
\begin{aligned}
X_1(t) &= X_1(t_0) + \int_{t_0}^{t} X_1(s)\big(r_1 - \sum_{i=1}^{n} a_{1,i}X_i(s)\big)\mathrm{d}s + \sum_{i=1}^{n}\int_{t_0}^{t} \sigma_{1,i}(s, X_1(s), \ldots, X_n(s))\mathrm{d}W_i(s),\\
X_2(t) &= X_2(t_0) + \int_{t_0}^{t} X_2(s)\big(r_2 - \sum_{i=1}^{n} a_{2,i}X_i(s)\big)\mathrm{d}s + \sum_{i=1}^{n}\int_{t_0}^{t} \sigma_{2,i}(s, X_1(s), \ldots, X_n(s))\mathrm{d}W_i(s),\\
&\vdots\\
X_n(t) &= X_n(t_0) + \int_{t_0}^{t} X_n(s)\big(r_n - \sum_{i=1}^{n} a_{n,i}X_i(s)\big)\mathrm{d}s + \sum_{i=1}^{n}\int_{t_0}^{t} \sigma_{n,i}(s, X_1(s), \ldots, X_n(s))\mathrm{d}W_i(s).
\end{aligned}
\tag{3.3}
$$

These equations can then be solved using the Itô integral as described in definition 2.3.5.

3.2. Properties

In this section, some properties for this system of equations will be proven; these will be important for biological realism and mathematical correctness. One of these properties is well-posedness, which is essential for validating the model, as it demonstrates the existence of a unique solution to Equation 3.3, which will now be written as:

$$
\begin{aligned}
\mathrm{d}X_1(t) &= X_1(s)\big(r_1 - \sum_{i=1}^{n} a_{1,i}X_i(s)\big)\mathrm{d}s + \sum_{i=1}^{n} \sigma_{1,i}(s, X_1(s), \ldots, X_n(s))\mathrm{d}W_i(s),\\
\mathrm{d}X_2(t) &= X_2(s)\big(r_2 - \sum_{i=1}^{n} a_{2,i}X_i(s)\big)\mathrm{d}s + \sum_{i=1}^{n} \sigma_{2,i}(s, X_1(s), \ldots, X_n(s))\mathrm{d}W_i(s),\\
&\vdots\\
\mathrm{d}X_n(t) &= X_n(s)\big(r_n - \sum_{i=1}^{n} a_{n,i}X_i(s)\big)\mathrm{d}s + \sum_{i=1}^{n} \sigma_{n,i}(s, X_1(s), \ldots, X_n(s))\mathrm{d}W_i(s).
\end{aligned}
\tag{3.4}
$$

Here $\mathbf{X} = (X_1, X_2, \ldots, X_n)^T \in \mathbb{R}^n$, the matrix $\Sigma \in \mathbb{R}^{n\times n}$ with elements $i, j = 1, \ldots, n$ being $\sigma_{i,j}$, and $r_i, a_{i,j} \in \mathbb{R}$ are constants with $a_{i,j}$ being the elements of matrix A. Let $\mathbf{W} = (W_1, \ldots, W_n)^T$. This allows a rewrite of Equation 3.4 to:

$$
\mathrm{d}\mathbf{X}(t) = \mathbf{X}(t)\left(\mathbf{r} - A\mathbf{X}(t)\right)\mathrm{d}t + \Sigma(\mathbf{X}(t), t)\mathrm{d}\mathbf{W}(t). \tag{3.5}
$$

The stochastic component is described using a Wiener process, within the filtered probability space $(\Omega, \mathcal{F}, \mathcal{F}_t, \mathbb{P})$, where Ω is the sample space, $\mathcal{F}$ is all σ-algebra's with respect to the whole process, $\mathcal{F}_t$ is the Brownian filtration, and lastly $\mathbb{P}$ is the Wiener probability measure. From now on, this probability space will be used, if no other is mentioned.

It is assumed, that $X_i(t_0)$ and $\mathcal{F}_t$ are measurable.
We define solutions in a similar fashion as strong solutions in [Evans, 2013], henceforth these type of solutions will just be referred to as solutions.

Definition 3.2.1. *Solution to a stochastic differential equation*
A stochastic process $\{\mathbf{X}(t) : t_0 \leq t \leq T\}$, with $\mathbf{X} \in \mathbb{R}^n$ and $\mathbf{X}(t_0)$ being the initial condition, is called a solution to a stochastic differential equation, like equation 3.4:

$$\mathbf{X}(t) = \mathbf{b}(\mathbf{X}(t), t)\mathrm{d}t + \Sigma(\mathbf{X}(t), t)\mathrm{d}\mathbf{W}(t), \tag{3.6}$$

where $\mathbf{b}$ is the vector $[b_1, b_2, \ldots, b_n]$, $b_i = X_i(t)(r_i - \sum_{j=1}^{n} a_{i,j}X_j(t))$, and $\mathcal{F}$ is the filtration, if the following conditions are satisfied:

1. *the process $\mathbf{X}$ is adapted to the filtration.*
2. *$\mathbf{b}$ satisfies the integrability condition*

$$\mathbb{E}\left[\int_{t_0}^{T} |\mathbf{b}(\mathbf{X}(s), s)| ds\right] < \infty.$$

3. *Σ, evaluated along the process $\mathbf{X}$, satisfies the integrability condition*

$$\mathbb{E}\left[\int_{t_0}^{T} |\Sigma(\mathbf{X}(s), s)|^2 ds\right] < \infty,$$

   where Σ denotes the matrix with elements $\sigma_{i,j}$.

4. *Almost surely the process $X(t)$ fulfills the integral equation:*

$$\mathbf{X}(t) = \mathbf{X}(t_0) + \int_{t_0}^{t} \mathbf{b}(\mathbf{X}(s), s) ds + \int_{t_0}^{t} \Sigma(\mathbf{X}(s), s) d\mathbf{W}(s),$$

   for all $t \in [t_0, T]$.

5. *The initial condition $\mathbf{X}(t_0)$ is $\mathcal{F}_{t_0}$ measurable.*

The following model assumptions are placed on the system and its variables in order to ensure that the real-life data and interactions between species can be described mathematically.
It is assumed that the effects of noise in positive as well as in negative sense can be seen as equivalent in expectation. Gaussian noise is a popular choice due to its mathematical properties.

Model Assumption 3.2.1.
Gaussian noise is assumed to accurately describe the influence of noise on the populations $1, \ldots, n$.

In nature, it is not expected that populations of species will change in any way other than through simple birth and death. However, in some less wild environments, such as many reserves, species are added or removed if their numbers become unsustainable (e.g. [U.S. National Park Service, 2015b]). This, of course, cannot be predicted by a mathematical model.

Model Assumption 3.2.2.
A key biological assumption is that the environment is isolated, except for stochastic effects. This means that no individuals are added to or removed from the system through large-scale external interventions, e.g. the reintroduction of species.

Lastly the assumptions that are already placed on the Lotka-Volterra system are naturally also applicable here. This means that the following is assumed:

Model Assumption 3.2.3.
The standard Lotka-Volterra assumptions are naturally applicable. These conditions for the model to work are:

- *The LV model assumes [Sandeep C H, 2019] that the prey population -which does not consume other species- always has enough food. However, predators only consume the prey described in this model, other food sources are not exploited.*
- *The rate of change of the population is entirely dependent on its size, i.e. an increase in the number of prey is directly proportional to an increase in the number of births of that species.*
- *There are no impactful environmental changes during the described time, and genetic adaptation is irrelevant.*
- *Lastly, no spatial or age aspects are considered; the population of each species is just that, no other attributes are included.*

Furthermore, some pure mathematical assumptions are also made about the coefficients in the equations. These will be used to prove the boundedness of solutions.

Assumption 3.2.1.
Local Lipschitz continuity[Searcóid, 2006] is assumed for the coefficients $b_i : [0,T] \times \mathbb{R} \mapsto \mathbb{R}$ and $\sigma_{i,k} : [0,T] \times \mathbb{R}^n \mapsto \mathbb{R}$. In other words, let $i = 1,\dots,n$, some constant $B \geq 0$, and $\forall x_i$ with $\mathbf{x} = (x_1 \dots, x_i, \dots, x_n)^T$, there exists a neighbourhood $S(\mathbf{x})$ such that $\forall \mathbf{y} \in S(\mathbf{x}),$ such that $\mathbf{y} = (y_1,\dots,y_i,\dots,y_n)^T$ the following inequality holds:

$$|b_i(t,\mathbf{x}(t)) - b_i(t,\mathbf{y}(t))| + \sum_{k=1}^{n} |\sigma_{i,k}(t,\mathbf{x}(t)) - \sigma_{i,k}(t,\mathbf{y}(t))| \leq B|x_i - y_i|, \ \forall t \in [0,T]. \tag{3.7}$$

From this assumption it easily follows that the coefficients experience local linear growth i.e. for some neighbourhood $S(\mathbf{x})$ around $\mathbf{x}$ there exists a constant $B \geq 0$, where $\forall \mathbf{y}(\mathbf{x})$ the following holds:

$$|b(t,\mathbf{y}(t))| + \sum_{k=1}^{n} |\sigma_{i,k}(t,\mathbf{y}(t))| \leq B(1 + |y_i|), \ i = 1,\dots,n. \tag{3.8}$$

Theorem 3.2.1. ***Boundedness of the quadratic LV system [Baigent, 2017]:***
For a system as in Equation 3.2 with $t \in [t_0,T]$, with $n = 2$, which can be written as:

$$\mathbf{X}(t) = \mathbf{b}(\mathbf{X}(t),t)\mathrm{d}t, \tag{3.9}$$

for $\mathbf{b}$ a vector with elements $b_i = X_i(t)(r_i - \sum_{j=1}^{n} a_{i,j}X_j(t))$ for $i = 1,\dots,n$, with $a_{i,j} > 0,\ r_i > 0$. Then $\forall i = 1,\dots,n$ there exists some $D_C \in \mathbb{R}$ such that $X_i(t) < D_C \forall t \in [t_0,T] \forall i = 1,\dots,n$.

Definition 3.2.2. ***Population Capacity:***
The constant D_C for a deterministic system as in Equation 3.4 with D_C the smallest upper bound as given by Theorem 3.2.1, will be referred to as the maximum population capacity or D_C.

As mentioned in the Preliminaries, Section 2.3.1, the support for σ is compact and a strict subset of $(0,D)^n$. From now on it will be assumed that the support of each $\sigma_{i,j}$ exists only on some bounded interval $[c,C]$ with $0 < c < C < D_C$ and $c, C, D_C \in \mathbb{R}$ for D_C an upper bound on the population capacity as in 3.2.1. Thus, ensuring that the support is a compact, strict subset of $[0,D_C]$.

Assumption 3.2.2.
Let $i = 1,\dots,n, c, C \in \mathbb{R}, 0 < c < C$ then the following holds

$$\forall X_i \notin [c,C] \Rightarrow \sigma_{i,j}(t,\mathbf{X}) = 0. \tag{3.10}$$

It should be noted again that the support condition formulated in Assumption 3.2.2 can be stated more generally. Hypothetically, the support for $\sigma_(i,j)$ could be a strict subset of the set $[0,D]$. The nature of the proofs in this chapter does not change and will be given with the support as in the assumption for simplicity.

3.3. Solutions

In mathematics, well-posedness is a fundamental requirement of a system that describes two conditions of a solution: its existence and its uniqueness. What constitutes as a solution was given earlier in Definition 3.2.1, now the existence and uniqueness of this solution will be proven. This is done by proving the boundedness of a solution.
Some important properties of the equations will be listed here, as they are important for the following theorems and proofs:

- In the defintion of a Wiener process 2.3.1 it was demanded that future increments are independent of past increments. This characteristic is called the Markov- or memory less -property.
- It is easily visible that local Lipschitz continuity holds for all coefficients of X_i, with $i = 1, \dots, n$, without any conditions for the growth factor $b_i = X_i(s)(r_n - \sum_{j=1}^n a_{i,j} X_j(s))$ which is quadratic, it also holds for all $\sigma_{i,j}(t, X_1(t), \dots, X_n(t)), i, j = 1, \dots, n$ by assumption.

First to look at the equilibria of the system, in the case of two species.
Lemma 3.3.1. ***Equilibria for a system of two species:***
Let $n = 2$, and let $T \in \mathbb{R}_{>0}, t_0 \in [0, T]$ denote times, $\mathbf{X} = (X_1, X_2)^T$ being a a local solution to Equation 3.6 with b and σ of this equation satisfying Assumption 3.2.1, with respect to the initial condition $\mathbf{X}(t_0) \in [0, D_C]^2$, with D_C as in Theorem 3.2.1 the maximum population capacity of a species.
The nondimensionalised equivalent of this system has the equilibria $(0,0), (1,0)$ and $(0,1)$, which are unstable if Assumption 3.2.2 holds, meaning the support for $\sigma_{i,j}(\mathbf{X}(t), t)$ doesn't exist at $0$and D and furthermore, if both

$$\frac{a_{1,2} r_2}{a_{2,2} r_1} < 1 \text{ and } \frac{a_{2,1} r_1}{a_{1,1} r_2} < 1. \tag{3.11}$$

Moreover, if $\exists\, p \in \mathbb{R}$:

$$\mathcal{B}_p(X_1^*, X_2^*) \cap \textit{supp}(\sigma_{i,j}(t, \mathbf{X})) = \emptyset,\ \forall i, j \in (1, \dots, n) \text{ and } t \in [t_0, T], \tag{3.12}$$

where $\mathcal{B}_p(\mathbf{X})$ denotes a ball with radius p, and centre $\mathbf{X} = (X_1, X_2)$, then a fourth equilibrium, $(X_1^*, X_2^*) = (\frac{a_{1,1}(a_{2,2} r_1 - a_{1,2} r_2)}{r_1(a_{1,1} a_{2,2} - a1,2 a_{2,1})}, \frac{a_{2,2}(a_{1,1} r_2 - a_{2,1} r_1)}{r_2(a_{1,1} a_{2,2} - a1,2 a_{2,1})})$ exists.
Furthermore, the eigenvectors of the equilibria $(0,0), (1,0), (0,1)$ are the unit vectors in $\mathbb{R}^2$.

Proof: The system for two species is given by

$$\begin{aligned} \mathrm{d}X_1(t) &= X_1(t)\big(r_1 - a_{1,1} X_1(t) - a_{1,2} X_2(t)\big)\mathrm{d}s \\ &\quad + \sigma_{1,1}(s, X_1(t), X_2(t))\mathrm{d}W_1(t) + \sigma_{1,2}(s, X_1(t), X_2(t))\mathrm{d}W_2(t), \end{aligned} \tag{3.13}$$

$$\begin{aligned} \mathrm{d}X_2(t) &= X_2(t)\big(r_2 - a_{2,1} X_1(t) - a_{2,2} X_2(t)\big)\mathrm{d}s \\ &\quad + \sigma_{2,1}(s, X_1(t), X_2(t))\mathrm{d}W_1(t) + \sigma_{2,2}(s, X_1(t), X_2(t))\mathrm{d}W_2(t). \end{aligned} \tag{3.14}$$

Where, as mentioned in Chapter 2 and reiterated in a earlier Assumption (3.2.2) on the system, the support for all $\sigma_{i,j}$ with $i, j = 1, 2$ is limited to some c, C st. $0 < c < C < D_C$. In order to prove that the equilibria of the deterministic system also exist in the stochastic system remember that the support of the stochastic influence is limited by Assumption 3.2.2. If the stochastic part of the SDE is zero, then the equilibria of the deterministic system can be found; this allows the equations to simplify as:

$$\mathrm{d}X_1(t) = X_1(t)\big(r_1 - a_{1,1} X_1(t) - a_{1,2} X_2(t)\big)\mathrm{d}t, \tag{3.15}$$

$$\mathrm{d}X_2(t) = X_2(t)\big(r_2 - a_{2,1} X_1(t) - a_{2,2} X_2(t)\big)\mathrm{d}t. \tag{3.16}$$

To nondimensionalise this system, take the following: $L_1 = \frac{X_1 a_{1,1}}{r_1},\ L_2 = \frac{X_2 a_{2,2}}{r_2},\ \tau = r_1 t,\ \rho = \frac{r_2}{r_1},\ b_1 = \frac{a_{1,2} r_2}{a_{2,2} r_1},\ b_2 = \frac{a_{2,1} r_1}{a_{1,1} r_2}$ this results in the following system:

$$\frac{\mathrm{d}L_1}{\mathrm{d}\tau} = L_1(1 - L_1 - b_1 L_2), \tag{3.17}$$

$$\frac{\mathrm{d}L_2}{\mathrm{d}\tau} = \rho L_2(1 - b_2 L_1 - L_2). \tag{3.18}$$

The following equilibria: $(0,0),\ (1,0),\ (0,1),\ (\frac{1-b_1}{1-b_1b_2}, \frac{1-b_2}{1-b_1b_2})$ can be obtained by setting both equations to zero. Where the last one only exists if $b_1b_2 \neq 1 \Leftrightarrow \frac{a_{1,2}a_{2,1}}{a_{1,1}a_{2,2}} \neq 1$
The stability of the equilibria can be analysed by looking at the linearised system given by the Jacobian of equation 3.17, which is:

$$J = \begin{pmatrix} 1-2L_1-b_1L_2 & -b_1L_1 \\ -\rho b_2 L_2 & \rho(1-b_2L_1-2L_2) \end{pmatrix}. \tag{3.19}$$

Now the eigenvalues can be calculated by det $(J-\lambda I) = 0$.
In case of the equilibrium $(0,0)$ this equation results in $(1-\lambda)(\rho-\lambda) = 0$, meaning the eigenvalues are $\lambda_1 = 1, \lambda_2 = \rho$. This equilibrium is always unstable due to at least one of the eigenvalues being positive [Hirsch et al., 2012].
The equilibrium $(1,0)$ has the characteristic polynomial $0 = (-1-\lambda)(\rho(1-b_2)-\lambda)$ resulting in the eigenvalues $\lambda_1 = -1, \lambda_2 = \rho(1-b_2)$ this equilibrium is only unstable if $b_2 < 1$. Meaning the equilibrium is unstable since $\frac{a_{2,1}r_1}{a_{1,1}r_2} < 1$.
Similarly to the equilibrium $(1,0)$ the eigenvalues of the equilibrium $(0,1)$ can be calculated resulting in $\lambda_1 = -\rho, \lambda_2 = 1-b_1$ which is unstable if $b_1 < 1$, which is equivalent to saying $\frac{a_{1,2}r_2}{a_{2,2}r_1} < 1$ by filling in b_1.
The last equilibrium, $(\frac{1-b_1}{1-b_1b_2}, \frac{1-b_2}{1-b_1b_2}) = (L_1^*, L_2^*)$ has a more complex characteristic polynomial; its eigenvalues are given by

$$\lambda_{1,2} = \frac{-b_1 - b_2\rho + \rho + 1 \pm \sqrt{(b_1+b_2\rho-\rho-1)^2 - 4\rho(1-b_1b_2)(b_1-1)(b_2-1)}}{2(1-b_1b_2)}.$$

If the aforementioned conditions are met, meaning $b_1, b_2 < 1$, then these eigenvalues are real but not necessarily negative. Stability of this equilibrium, when both eigenvalues are negative [Hirsch et al., 2012] happens when:

$$\text{tr } J(L_1^*, L_2^*) < 0, \tag{3.20}$$
$$\det J(L_1^*, L_2^*) > 0. \tag{3.21}$$

Then this equilibrium can only be stable, if there are no stochastic fluctuations around the equilibrium, meaning $\exists p \in \mathbb{R}$ where for a ball $\mathcal{B}_p(L_1^*, L_2^*)$ with radius p, for $i,j = 1,2$ we have that if $\mathbf{X} \in \mathcal{B}_p(L_1^*, L_2^*)$ then $\sigma_{i,j}(\mathbf{X}, t) = 0$ for all t. Allowing that the system, around this equilibrium, is locally described by a deterministic equation.

Now to look at the eigenvectors, these can easily be calculated using matrix J and the already calculated eigenvalues by $(J-\lambda I)\mathbf{v} = \mathbf{0}$ for I being the identity matrix, $\mathbf{v}$ being the eigenvector corresponding to eigenvalue λ and $\mathbf{0}$ being the zero vector. Doing so results in the observation that for the equilibria $(0,0),\ (1,0)$ and $(0,1)$ the eigenvectors are all the same, and that they are the unit vectors $(1,0)^T,\ (0,1)^T$. Due to the matrix always having one zero on the diagonal and one zero on a off-diagonal.

□

Lemma 3.3.1 can be easily visualised if some values for the constants are chosen. Let $b_1 = 0,5, b_2 = 0,5$ and $\rho = 1$ for b_1, b_2 and ρ being the variables of the nondimensionalised system as defined in the lemma, then the conditions are met for a stable equilibrium in the first quadrant of the phase plane. This can be seen in Figure 3.1. Solutions beginning in the first quadrant tend toward the stable equilibrium. All other solutions do not cross into the positive quadrant.

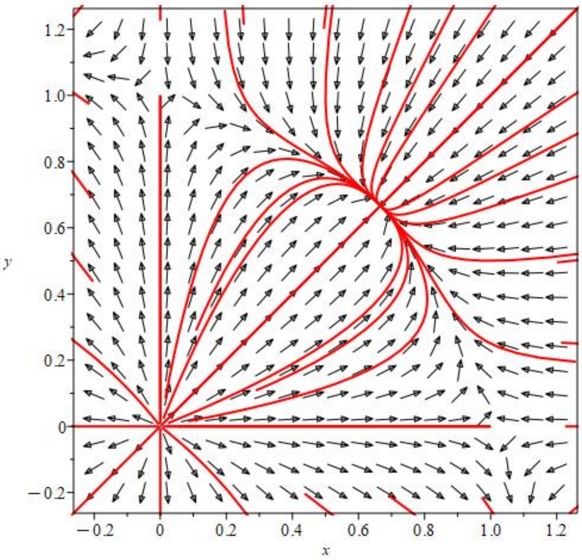

Figure 3.1: The phase plane of the system 3.17 with $b_1 = b_2 = 0,5$ and $\rho = 1$

Some other phase planes can also be constructed, in the case that the equilibrium (L_1^*, L_2^*) is a stable spiral sink or a centre. For readers unfamiliar with the terminology used in dynamical systems, formal definitions of these types of equilibria can be found in [Hirsch et al., 2012]. This happens in the case where $b_1 = 0.3, b_2 = -0.01$ and $\rho = 0.6$, which can be seen in Figure 3.2, respectively when $b_1 = 2, b_2 = 3$ and $\rho = -0.5$ which is given in Figure 3.3. Notice that solutions do not cross the boundary $[0,1]$ on both axes in the first two cases. The bounds are $[0,1]$ instead of $[0,D]$, for some $D \in \mathbb{R}$, due to the nondimensionalisation. The third case only has solutions that stay inside the boundary if the initial values satisfy $X_1(t_0)X_2(t_0) < 1$. This is due to the parameters $b_1, b_2 > 1$, they do not satisfy the conditions from Lemma 3.3.1.

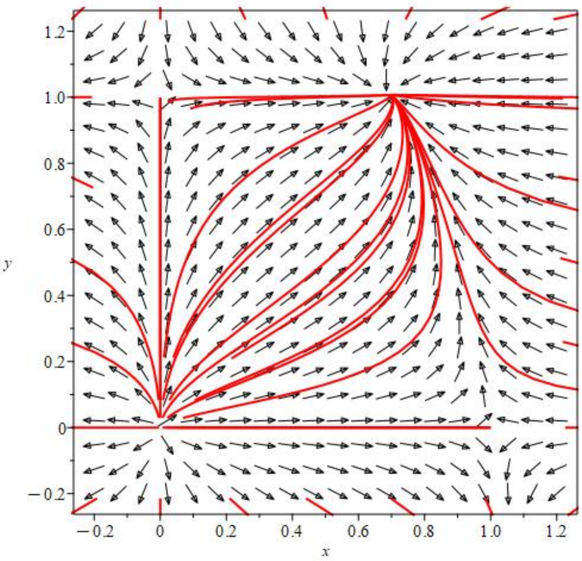

Figure 3.2: The phaseplane of the system 3.17 with $b_1 = 0.3, b_2 = -0.01$ and $\rho = 0.6$

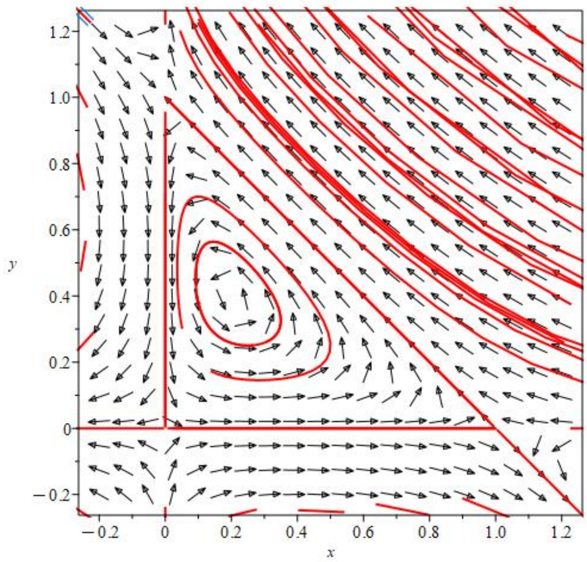

Figure 3.3: The phaseplane of the system 3.17 with $b_1 = 2, b_2 = 3$ and $\rho = -0.5$

In order to prove boundedness, some conditions have to be set. The following assumptions are recalled:

- It is again set as a condition that the coefficients $\sigma_{i,j}$ are locally Lipschitz continuous and experience local linear growth, meaning they satisfy Assumption 3.2.1.
- Similarly, the coefficients $\sigma_{i,j}$ are of the form as described by Assumption 3.2.2. Meaning for $0 < c < C < D_C$

$$\forall X_i \notin [c, C] := \sigma_{i,j}(t, \mathbf{X}) = 0,$$

with D_C being some population capacity.

Two new assumptions are established, firstly in order for Lemma 3.3.1 to hold the following is assumed:
Assumption 3.3.1. *The values of the variables are bounded in the following way for some $\varrho > 0$:*

$$\frac{a_{1,2}r_2}{a_{2,2}r_1} < 1 \qquad \frac{a_{2,1}r_1}{a_{1,1}r_2} < 1 \tag{3.22}$$

$$\frac{a_{1,2}a_{2,1}}{a_{1,1}a_{2,2}} \neq 1 \qquad \varrho > r_1 r_2 > 0. \tag{3.23}$$

Furthermore the second new assumption to be established, is due to the biological impossibility of $X_i < 0$, as the population of a species cannot be negative and as we are trying to prove that a population cannot be greater than some upper bound. Biologically, this is also impossible, as this would mean that there are more animals then could be sustained in nature. That means it can only happen, if more of that species are added by for example humans.
These bounds of course also hold for the initial condition, as such it is assumed:

Assumption 3.3.2.
Let for a constant $D_C > 0$, the initial condition $X_i(t_0)$ satisfy: $0 < X_i(t_0) < D_C$ for all $i = 1, \ldots, n$ almost surely.

Theorem 3.3.1. ***Boundedness:***
Let $0 < t_0 < T$, both denoting times and assume the abovementioned Assumptions, 3.2.1, 3.2.2, 3.3.1, are fulfilled where it is required that $0 < c < C < D_C$, where D_C is the maximum population capacity, given by Theorem 3.2.1. Let $X_i(t)$ denote a local solution to 3.4, $i = 1, 2$, for $t \in [t_0, t_1)$, for

$t_1 = t_1(\omega) \in (t_0, T)$, both denoting times, with $X_i(t_0)$ being the initial condition subject to Assumption 3.3.2.
It holds that for $i = 1, 2$ and a unique solution on $[t_0, t_1)$, there exists some $D \geq D_C$

$$0 \leq X_i(t) \leq D \text{ for } t \in [t_0, t_1).$$

Meaning the population of each species i is always nonnegative and bounded by D, which will subsequently be called the population maximum.

Proof: Fix an $\omega \in \Omega$ such that a solution exists for time $t \in [t_0, t_1(\omega))$. To prove that a solution exists globally it is enough to prove uniform boundedness of the solution, in $(\omega, t) \in \Omega \times [t_0, t_1(\omega))$, meaning the solution does not increase beyond a bound, in this case D, and is bounded from below, presently by 0. The existence and uniqueness of local solutions for equation 3.4 was established in Theorem 3.3.2 by proving that the coefficients of the equation are locally Lipschitz continuous. This property implies continuity for all $t \in [t_0, t_1)$, which is the domain in which solutions exist.
To substantiate the boundedness of solutions, individual cases for the initial condition will be analysed.

By assumption, any initial condition $X_i(t_0) < 0$ or $X_i(t_0) > D_C$ are ruled out. These cases will thus not be considered.

Consider the case where the initial condition is confined in a region where the stochastic variable has support, meaning $X_i(t_0) \in [c, C]$. Due to the continuity of solutions, it can be concluded that the solution either remains confined in the bounds of the support of the stochastic variable, thus proving global existence, or leaves one of the two deterministic regions $(0, c)$ or (C, D_C).

Case 1: $X_i(t_0) = 0$, for at least one $i \in (1, 2)$
When $X_i(t_0) = 0$, the difference equation is simply the deterministic equation, as for all j $\sigma_{i,j}$ is zero, when X_i is sufficiently small. The difference equation can be written as

$$\frac{\mathrm{d}X_i}{\mathrm{d}t}(t) = X_i(t)(r_i - \sum_{j=1}^{n} a_{i,j} X_j(t)), \tag{3.24}$$

for $i = 1, 2$. Following Theorem 3.3.2, a unique local solution exists on $[t_0, t_1)$. Given that $\mathrm{d}X_i(t) = 0$ for $t \in [t_0, t_1)$ it follows that this solution is $X_i(t) = 0 \ \forall t_1(\omega) \geq t \geq t_0$. By extension it is clear than that for all $t \in [t_0, T]$ we have $X_i(t) = 0$.

Case 2: $X_i(t_0) \in (0, c)$, for at least one $i \in (1, 2)$
In this case, the solution $X_i(t)$ is, at least initially, deterministic. By continuity, the solution satisfies the deterministic equation and is differentiable over some interval $[t_0, t_E]$, with its differential given by Equation 3.24 from t_0 until at least the later time t_E:

$$\frac{\mathrm{d}X_i}{\mathrm{d}t}(t) = X_i(r_i - \sum_{j=1}^{2} a_{i,j} X_j). \tag{3.25}$$

First to consider the possibility of the solution crossing into the negative domain. Assume that there exists some t_3 such that $X_i(t_3) < 0$, this means that there exists some $t_2 < t_3$ such that $X_i(t_2) > 0$ due to continuity. However, this means

$$\exists t_4 \in [t_2, t_3] : X_i(t_4) = 0.$$

Meaning when the equation is restarted at this point, it will stay there, i.e.

$$X_i(t) = 0, \text{ for } t > t_4.$$

Case 3: $X_i(t_0) \in (C, D_C)$, for at least one $i \in (1, 2)$

A similar argument holds to the case where $X_i(t_0) \in (0, c)$. Meaning that for X_i to leave (C, D_C) there must be a time t_2 such that either $X_i(t_2) = C$ or $X_i(t_2) = D_C$ which would either reduce it to Case 2 or Case 4 below.

Case 4: $X_i(t_0) = D_C$, for at least one $i \in (1, 2)$
Whenever $X_i(t_0) = D_C$, the solution is at the upper bound of the domain for the initial conditions. Similar to the case when $X_i(t_0) = 0$, the system is governed by the deterministic part of the equation, see Equation 3.24, as there is no support for the $\sigma-$functions. Solution will not increase far beyond D_C. This can be seen by looking at the nondimensionalised system as given in Lemma 3.3.1:

$$\frac{\mathrm{d}L_1}{\mathrm{d}\tau} = L_1(1 - L_1 - b_1 L_2), \tag{3.26}$$

$$\frac{\mathrm{d}L_2}{\mathrm{d}\tau} = \rho L_2(1 - b_2 L_1 - L_2). \tag{3.27}$$

By Assumption 3.3.1 $b_1, b_2 < 1$ and $\rho > 0$, ρ being bounded from above, because the system is nondimensionalised, L_1 and L_2 are not necessarily bounded by the same D_C but this does not change the proof, for the upper bound of the initial condition D_C will be taken, with $D_C = 1$ [Murray, 2002] and we allow $D > 1 = D_C$. Two cases need to be considered:
first, if $b_1 > 0$: then it is easily visible, that if $L_1 = D_C$ it holds that for any $L_2 \in [0, D_C]$:

$$\frac{\mathrm{d}L_1}{\mathrm{d}\tau} = D_C(1 - D_C - b_1 L_2) < 0 \tag{3.28}$$

thus, meaning that solutions do not increase permanently, they do not achieve values greater than D_C. This also holds similarly for $L_2 = D_C$ if $b_2 > 0$.
Then, if $b_1 < 0$, as $L_2 \in [0, D_C]$ it holds that

$$\frac{\mathrm{d}L_1}{\mathrm{d}\tau} = D_C(1 - D_C - b_1 L_2) \tag{3.29}$$

$$\leq D_C(1 - D_C - b_1 D_C). \tag{3.30}$$

This means the growth of L_1 is bounded, as $1 - L_1 - b_1 D_C < 0$ if $L_1 > 1 - b_1 D_C$, which is inevitable if L_1 is increasing, as $1 - b_1 D_C$ is some positive number greater than 1. Thus, proving that L_1 cannot be unbounded, as it has a negative differential if L_1 gets big enough, i.e. if $L_1 = D = 1 - b_1 D_C$. A similar argument holds for L_2, thus proving boundedness for both L_1 and L_2.
Boundedness for the nondimensionalised system of course also means boundedness of the original system.

□

Thus, it was proven that solutions move away from both $X_i = 0$ and $X_i = D$, enclosing the space between them. For the case of $n = 2$, which was proven, the solutions for $X_1, X, 2$ being respectively 0 or D, can be seen as a box enclosing the space.

Using this result the global existence and uniqueness of a solution in the case $n = 2$ can be proven. This proof is short as it almost entirely follows from theorem 3.3.1.

Local existence and uniqueness will be proven using a theorem from [Evans, 2013], which states the following:

Theorem 3.3.2. ***Existence and Uniqueness****:*

For $\mathbf{X}(t) \in \mathbb{R}^n$, $t \in [t_0, T]$, the Wiener process $\mathbf{W}(t)$ and $\mathbf{r} \in \mathbb{R}^n, A, \Sigma \in \mathbb{R}^{n \times n}$ let the stochastic differential equation be,

$$\mathrm{d}\mathbf{X}(t) = \mathbf{X}(t)(\mathbf{r} - A\mathbf{X}(t))\mathrm{d}t + \Sigma(\mathbf{X}(t), t)\mathrm{d}\mathbf{W}(t). \tag{3.31}$$

With the matrix A having elements $a_{i,j}$ and matrix Σ having elements $\sigma_{i,j}$.
Let $\mathbf{X}(t_0)$ be the initial condition, such that $\mathbf{X}(t_0)$ is $\mathcal{F}_{t_0}$ measurable. Then if the following conditions hold:

- *The second moment of the initial condition is bounded,*

$$\mathbb{E}\left[|\mathbf{X}(t_0)|^2\right] < \infty.$$

- *The initial condition is independent of the Wiener process.*

Then, by assumption 3.2.1, for almost all $\omega \in \Omega$ a unique local solution exists to Equation 3.31, i.e. a solution exists on $[t_0, t_1)$ for some time t_1 where $t_1 = t_1(\omega) \in [t_0, T]$.

Proof: of Theorem 3.3.2 globally:
This proof will be done by contradiction. Assume there exists some final time $t_f < T$ so that $\mathbf{X}(t)$ only has a solution for $t \in [t_0, t_f)$.

Earlier, it was assumed that the coefficients b_i and $\sigma_{i,j}$ for $i, j = 1, 2$ are locally Lipschitz continuous. This means, that for a set S, with $\mathbf{x}, \mathbf{y} \in S$ and $i = 1, 2$ there exists a B such that:

$$|b_i(t, \mathbf{x}(t)) - b_i(t, \mathbf{y}(t))| + \sum_{k=1}^{n} |\sigma_{i,k}(t, \mathbf{x}(t)) - \sigma_{i,k}(t, \mathbf{y}(t))| \leq B|x_i(t) - y_i(t)|. \tag{3.32}$$

Due to this local Lipschitz continuity, it is then known that a local solution exists on $[t_0, t_1)$, $t_1 = t_1(\omega)$. At this time, the solution, $\mathbf{X}(t)$ is still in the box $[0, D]$ for all $t \in [t_0, t_1)$ as was just proven in Lemma 3.3.1. Assume that this $t_1 = t_f$, thus that no solutions exist after this t_1.
Take $\mathbf{X}(t_1) := \lim_{t \uparrow t_1} \mathbf{X}(t)$, which exists due to the boundedness of $\mathbf{X}(t)$ on the aforementioned interval. Restart the equation at $t = t_1$, with $\mathbf{X}(t_1)$ being the new initial condition. Then this means that at this point, there will still be a solution, as the conditions are still fulfilled due to the boundedness of $\mathbf{X}$ at t_1, meaning a solution exists on $[t_1, t_2)$ for some $t_2 = t_2(\omega)$. But this $t_2 > t_f$, hence a solution exits until T, in other words, $t_f = T$.

□

It can be remarked, that a proof for global well-posedness could be made by setting the coefficients to only exist on $[0, D]$, by letting $b_i(t, \mathbf{x}(t)) = \tilde{b_i}(t, \mathbf{x}(t))\mathbb{1}_{[0,D]}$. However, this brings a new problem, as this would mean that the coefficients are not continuous anymore, which is why the possibility was not considered.

4

Bounding the estimation error of the Extended Kalman Filter

The extended Kalman filter, described in Chapter 2.4.3, is a widely used tool to estimate the state of nonlinear systems. It is broadly used, most often with economic or navigation purposes [Kovvali et al., 2013]. Although the usefulness of the filter is proven repeatedly for many applications and its performance is generally robust [Lu & Niu, 2014], understanding its faults and possible errors is of high importance to further substantiate its findings.

In this chapter, the stability of the continuous time EKF will be studied under the specific conditions of population dynamics. The analysis will be based on the error bounds found by Konrad Reif [Reif et al., 2000], who detailed conditions ensuring the boundedness of the error. However, in contrast to Reif's general proof and conditions, this chapter will simplify this analysis due to the more specific nature of the SDE model, as described in Equation 3.4. Consequently, the stability proof here does not require a smallness condition for the initial error. Furthermore, the proof does not require the use of Lyapunov functions or general assumptions, as some of them become redundant due to the conditions already placed on the model.
Although the Lotka-Volterra equations are generally only given for two species, the proof given in this chapter will hold for the general case with n species. The specific conditions for when $n = 2$, for example, when there is just one predator and one prey, will be worked out in the corollary (see 4.0.1.1).

The same SDE will be used, as in the previous chapters, it is given by Equation 3.4 and writing it in terms of vectors and matrices yields:

$$\mathrm{d}\mathbf{X}(t) = \mathbf{X}(t)(\mathbf{r} - A\mathbf{X}(t))\mathrm{d}t + \Sigma(\mathbf{X}(t), t)\mathrm{d}\mathbf{W}(t). \tag{4.1}$$

Where $\mathbf{X}(t) \in \mathbb{R}^n$, $t \geq 0$ describes the time, $\mathbf{X}(t_0)$ is the initial condition , $\mathbf{W}(t) \sim \mathcal{N}(0, Q(t))$ is the Wiener process in $\mathbb{R}^n$ and $\mathbf{r} \in \mathbb{R}^n$ is the vector of r_i's, $A \in \mathbb{R}^{n\times n}$ the matrix with row i having elements $a_{i,j}$ where j is the respective column, lastly $\Sigma \in \mathbb{R}^{n\times n}$ has the elements $\sigma_{i,j}(\mathbf{X}, t)$ on the ith row and jth column. The functions $\sigma_{i,j}$ can take on any form; they are not limited to the functions with compact, bounded support that were previously examined. This allows the following theorems to be stated for more general functions, although the existence and uniqueness of these systems have not been proven; they are nonetheless assumed to hold. Meaning unique solutions $\mathbf{X}(t)$ to equation 4.1 are assumed to exist globally.
The observation is given by

$$\mathrm{d}\mathbf{Y}(t) = h(\mathbf{X})\mathrm{d}t + \Phi(\mathbf{X}(t), t)\mathrm{d}\mathbf{V}(t). \tag{4.2}$$

Here $\mathbf{Y}(t) \in \mathbb{R}^m$, h describes the observation, with initial condition $\mathbf{Y}(t_0)$, $\Phi \in \mathbb{R}^{m\times m}$ the matrix describing the intensity of the measurement noise and $\mathbf{V}(t) \in \mathbb{R}^m$ a Wiener process independent of $\mathbf{W}$ and

$\mathbf{V}(t) \sim \mathcal{N}(0, R(t))$. For $h(\mathbf{X})$, a function describing the change in observation of $\mathbf{X}(t)$ whose differential is quadratic, it is assumed that h is a polynomial of at most second order in space and smooth in time.

This system will be assessed using the following state estimator, which was generally given by Equation 2.21 in an earlier chapter:

$$\mathrm{d}\hat{\mathbf{X}}(t) = \hat{\mathbf{X}}(t)(\mathbf{r} - A\hat{\mathbf{X}}(t))\mathrm{d}t + K(t)(\mathrm{d}\mathbf{Y}(t) - h(\hat{\mathbf{X}}(t), t)). \tag{4.3}$$

Here K is the Kalman gain, also described in Equation 2.21. The error of this estimation is then given by

$$\eta(t) = \mathbf{X}(t) - \hat{\mathbf{X}}(t). \tag{4.4}$$

By linearizing equation 4.1 by letting $B(\mathbf{X} = \frac{\mathrm{d}}{\mathrm{d}\mathbf{X}} b(\mathbf{X})$ and equation 4.2 by setting $H(\mathbf{X}) = \frac{\mathrm{d}}{\mathrm{d}\mathbf{X}} h(\mathbf{X})$, and letting $\psi(\mathbf{X}(t), \hat{\mathbf{X}}(t)), \chi(\mathbf{X}(t), \hat{\mathbf{X}}(t))$ be the remaining nonlinear terms from$f(\mathbf{X}(t)) - f(\hat{\mathbf{X}}(t))$ respectively $h(\mathbf{X}) - h(\hat{\mathbf{X}})$, i.e.

$$\psi(\mathbf{X}(t), \hat{\mathbf{X}}(t)) = b(\mathbf{X}(t)) - b(\hat{\mathbf{X}}(t)) - B(\mathbf{X}(t))[\mathbf{X}(t) - \hat{\mathbf{X}}(t)], \tag{4.5}$$

$$\chi(\mathbf{X}(t), \hat{\mathbf{X}}(t)) = h(\mathbf{X}(t)) - h(\hat{\mathbf{X}}(t)) - H(\mathbf{X})[\mathbf{X}(t) - \hat{\mathbf{X}}(t)]. \tag{4.6}$$

Where, as earlier $b(\mathbf{X}(t)) = \mathbf{X}(t)(\mathbf{r} - A\mathbf{X}(t))$ thus ψ is a vector with its i-th element being

$$\psi_i(t) = (x_i(t) - \hat{x}_i(t)) \left(\sum_{j=1}^{n} a_{i,j}(x_j(t) + \hat{x}_j(t)) \right). \tag{4.7}$$

The vector $\chi(t)$ depends on the choice of $h(\mathbf{X})$.
From now on, instead of writing $B(\mathbf{X}(t))$ notation will be simplified and $B(t)$ will be written.
Both of these functions, ψ, χ are quadratic as the functions described by them are polynomial function of at most power two. Lastly set $\ell(t) = \psi(\mathbf{X}(t), \hat{\mathbf{X}}(t)) - K(t)\chi(\mathbf{X}(t), \hat{\mathbf{X}}(t))$ in order to rewrite $\eta(t)$ as

$$\mathrm{d}\eta(t) = [(B(t) - K(t)H(t))\eta(t) + \ell(t)]\,\mathrm{d}t + (\Sigma(\mathbf{X}(t), t)\mathrm{d}\mathbf{W}(t) - K(t)\Phi(\mathbf{X}(t), t)\mathrm{d}\mathbf{V}(t)). \tag{4.8}$$

Let this system be rewritten as:

$$\mathrm{d}\eta(t) = f(\eta(t), t)\mathrm{d}t + G(\eta(t), t)\mathrm{d}\tilde{\mathbf{W}}(t). \tag{4.9}$$

Meaning $f : \mathbb{R}^n \times [t_0, T] \to \mathbb{R}^n$, $f(\eta(t), t) = B - K(t)H(t))\eta(t) + \ell(t)$, $G(\eta(t), t) = \Sigma(\mathbf{X}(t), t) - K(t)\Phi(\mathbf{X}(t), t)$ and $\tilde{\mathbf{W}}$ is the vector with $\mathbf{W}$ and $\mathbf{V}$.
Let $K(t)$ be locally Lipschitz continuous, then f, G are locally Lipschitz continuous and experience local linear growth as the other coefficients already satisfy this criterion. Furthermore, assume that the coefficients of the derivative of f with respect to t are again Lipschitz continuous, that is, $\frac{\partial}{\partial t} f$ has Lipschitz continuous coefficients in space.

Lemma 4.0.1. ***Itô's lemma[Kozdron, 2009]:***
Let $\eta(t) : [t_0, \infty) \mapsto \mathbb{R}$ be a diffusion satisfying the SDE (equation 4.9) with initial condition $\eta(t_0)$

$$\mathrm{d}\eta(t) = f(\eta(t), t)\mathrm{d}t + G(\eta(t), t)\mathrm{d}\tilde{\mathbf{W}}(t). \tag{4.10}$$

Then, for all $V \in C^2(\mathbb{R}^n) \times C^1(\mathbb{R})$ almost surely for $t \in [t_0, T]$:

$$\mathrm{d}V(\eta(t), t) = \mathcal{L}V(\eta(t), t)\mathrm{d}t + G(\eta(t), t)\nabla_\eta V(\eta(t), t)\mathrm{d}\tilde{\mathbf{W}}, \tag{4.11}$$

with

$$\mathcal{L}V(\eta(t), t) = \frac{\partial V}{\partial t}(\eta(t), t) + f(\eta(t), t)(\nabla_\eta V(\eta(t), t)) + \frac{1}{2}\mathit{tr}(G^T(\eta(t), t)H_\eta(V(\eta(t), t))G(\eta(t), t)). \tag{4.12}$$

Here $\nabla_\eta V$ is the gradient of V with respect to η, just as $H_\eta(V)$ is the Hessian matrix of V with respect to η, lastly tr denotes the trace of a matrix.

Due to the earlier assumptions, a solution exists until some later time T, meaning an infinitesimal generator can be defined. An infinitesimal generator, sometimes called a differential generator provides a bridge between stochastic differential equations and deterministic equations, by describing the movement of a process for a short time interval. In Itô's lemma, this differential generator for some stochastic process V is given by $\mathcal{L}V$. This will be used to calculate the estimation error.

Lemma 4.0.2. ***Bound on a determinate part:***
Let $\mathbf{X}(t), \hat{\mathbf{X}}(t)$ be global solutions to Equations 4.1 respectively 4.3, P the covariance matrix and R the variance of the observer's noise, as per Section 2.4.3. Assume the following conditions: $\exists \underline{p}, \underline{r}, \in \mathbb{R}_{>0}$ such that:

$$\underline{p}I \leq P(t),\ P \text{ invertible,} \tag{4.13}$$

$$\underline{r}I \leq R(t), \tag{4.14}$$

for $t \in [t_0, T]$.

Then the following inequality holds for all times $t \in [t_0, T]$ almost surely:

$$2(\mathbf{X} - \hat{\mathbf{X}})^T P^{-1} \ell(t) \leq 2\left(\frac{\kappa_\psi}{\underline{p}} + \frac{\overline{h}\kappa_\chi}{\underline{r}}\right) ||(\mathbf{X}(t) - \hat{\mathbf{X}}(t))||^2, \tag{4.15}$$

Where $\ell(t), \hat{\mathbf{X}}(t)) = \psi(\mathbf{X}(t), \hat{\mathbf{X}}(t)) - K(t)\chi(\mathbf{X}(t), \hat{\mathbf{X}}(t))$.

Proof: First, it is good to remember that due to the condition of local linear growth it is known that for some $\epsilon_\psi, \epsilon_\chi, \kappa_\psi, \kappa_\chi \in \mathbb{R}_{>0}$ the following holds:

$$\forall \mathbf{X}(t), \hat{\mathbf{X}}(t) : ||\mathbf{X}(t) - \hat{\mathbf{X}}(t)|| \leq \epsilon_\psi \text{ it holds } ||\psi(\mathbf{X}(t), \hat{\mathbf{X}}(t))|| \leq \kappa_\psi ||\mathbf{X}(t) - \hat{\mathbf{X}}(t)||, \tag{4.16}$$

$$\forall \mathbf{X}(t), \hat{\mathbf{X}}(t) : ||\mathbf{X}(t) - \hat{\mathbf{X}}(t)|| \leq \epsilon_\chi \text{ it holds } ||\chi(\mathbf{X}(t), \hat{\mathbf{X}}(t))|| \leq \kappa_\chi ||\mathbf{X}(t) - \hat{\mathbf{X}}(t)||. \tag{4.17}$$

For $\mathbf{X}(t), \hat{\mathbf{X}}(t)$ being solutions of equation 4.1 respectively 4.3 on $t \in [t_0, T]$.
This works for example for $\kappa_\psi = 2D\sqrt{\sum_{i=1}^n \left(\sum_{j=1}^n a_{i,j}\right)^2}$, due to the bounds on $\mathbf{X}(t)$ by Theorem 3.3.1 and Equation 4.7.
Again, for χ it depends on the chosen function h.

By definition (Equation 2.21) it is given that $K(t) = P(t)H^T(t)R^{-1}(t)$, filling this in into the left side of Equation 4.15 yields:

$$\begin{aligned} &2(\mathbf{X}(t) - \hat{\mathbf{X}}(t))^T(t)P^{-1}\ell(t) \\ &\quad = 2(\mathbf{X}(t) - \hat{\mathbf{X}}(t))^T(P^{-1}(t)\psi(\mathbf{X}(t), \hat{\mathbf{X}}(t)) - H^T(t)R^{-1}(t)\chi(\mathbf{X}(t), \hat{\mathbf{X}}(t))), \quad (4.18) \\ &\quad \leq 2(\mathbf{X}(t) - \hat{\mathbf{X}}(t))^T(\frac{1}{\underline{p}}\psi(\mathbf{X}(t), \hat{\mathbf{X}}(t)) - H^T(t)\frac{1}{\underline{r}}\chi(\mathbf{X}(t), \hat{\mathbf{X}}(t))). \quad (4.19) \end{aligned}$$

Here R^{-1} exists, as R is diagonal and greater than zero. As X is bounded, so is the observer matrix H, as this matrix discribes observing a bounded value. Thus it is given that $\exists \overline{h} \in \mathbb{R}_{>0}$ such that:

$$||H(t)|| \leq \overline{h} \tag{4.20}$$

By filling in Assumptions 4.13 and 4.14. Then taking the norm of this equation and filling in Equation

4.20

$$||2(\mathbf{X}(t)-\hat{\mathbf{X}}(t))^T P^{-1}\ell(t)|| = ||2(\mathbf{X}(t)-\hat{\mathbf{X}}(t))^T(\frac{1}{\underline{p}}\psi(\mathbf{X}(t),\hat{\mathbf{X}}(t)) - H^T(t)\frac{1}{\underline{r}}\chi(\mathbf{X}(t),\hat{\mathbf{X}}(t)))||, \tag{4.21}$$

$$\leq ||2(\mathbf{X}(t)-\hat{\mathbf{X}}(t))|| \left(||\frac{1}{\underline{p}}\psi(\mathbf{X}(t),\hat{\mathbf{X}}(t))|| + ||H^T(t)|| \cdot ||\frac{1}{\underline{r}}\chi(\mathbf{X}(t),\hat{\mathbf{X}}(t))||\right), \tag{4.22}$$

$$\leq 2||(\mathbf{X}(t)-\hat{\mathbf{X}}(t))|| \left(\frac{1}{\underline{p}}||\psi(\mathbf{X}(t),\hat{\mathbf{X}}(t))|| + \frac{\overline{h}}{\underline{r}}||\chi(\mathbf{X}(t),\hat{\mathbf{X}}(t))||\right). \tag{4.23}$$

And then by filling in the last two inequalities 4.16 and 4.17, taking $\epsilon_{\psi,\chi} = \min(\epsilon_\psi, \epsilon_\chi)$ it holds for $\mathbf{X}(t), \hat{\mathbf{X}}(t) : ||\mathbf{X}(t) - \hat{\mathbf{X}}(t)|| \leq \epsilon_{\psi,\chi}$:

$$||2(\mathbf{X}(t)-\hat{\mathbf{X}}(t))^T P^{-1}\ell(t)|| \leq 2||(\mathbf{X}(t)-\hat{\mathbf{X}}(t))|| \left(\frac{\kappa_\psi}{\underline{p}} + \frac{\overline{h}\kappa_\chi}{\underline{r}}\right) ||(\mathbf{X}(t)-\hat{\mathbf{X}}(t))||. \tag{4.24}$$

Which can easily be rewritten into Equation 4.15. □

The following lemma holds for general Σ, although later it will be used for the specific Σ, as used all throughout the paper.

Lemma 4.0.3.
For $K(t)$ being the Kalman gain, $P(t)$ the covariance matrix as described in Section 2.4.3, equation 2.21 and Σ, Φ time varying matrices on $t \in [t_0, T]$, fulfilling the following conditions: $\exists \underline{p}, \overline{k}, \omega_\Phi \in \mathbb{R}_{>0}$ I being the identity matrix, n,m being the number of rows of Σ and Φ respectively:

$$\underline{p}I \leq P(t), \tag{4.25}$$

$$||K(t)|| \leq \overline{k}, \tag{4.26}$$

$$||\Sigma(t)|| \leq \varsigma(t), \text{ for some function } \varsigma(t), \tag{4.27}$$

$$||\Phi(t)\Phi^T(t)|| \leq \omega_\Phi, \tag{4.28}$$

then:

$$\text{tr}\left[(\Sigma(t)\Sigma^T(t) + K(t)\Phi(t)\Phi^T(t)K^T(t))P^{-1}\right] \leq (\varsigma^2(t) + \overline{k}^2\omega_\Phi m)\frac{1}{\underline{p}}. \tag{4.29}$$

Proof: A $\overline{p} \in \mathbb{R}_{>0} : P(t) \leq \overline{p}I$ exists as P only has a bounded support and X_i being bounded above (see Chapter 3).
Just as in Lemma 4.0.2 P^{-1} exists with probability 1, as due to 4.25 P is bounded on the diagonal by $\underline{p}$ as a lower bound and all other elements are 0. As $\overline{p} > 0$ no eigenvalue can be zero, thus P is invertible [de Groot, 2021] with probability 1.
Due to $||\Sigma(t)||$ being bounded by $\varsigma(t)$, the following equalities hold:

$$||\Sigma(t)\Sigma^T(t)|| \leq ||\Sigma(t)|| \cdot ||\Sigma^T(t)|| \leq ||\Sigma(t)||^2 \leq \varsigma^2(t). \tag{4.30}$$

Due to the bound on $||\Phi(t)\Phi^T(t)||$ its trace is bounded by $\omega_\Phi \text{tr}[I^{m\times m}]$ with $I^{m\times m}$ being the identity matrix with m rows, which results in the following bound on the trace: tr $\left(\Phi(t)\Phi^T(t)\right) \leq m\omega_\Phi$.

Then, again by condition 4.25 the following holds:

$$\overline{p}^{-1}I \leq P^{-1}(t) \leq \underline{p}^{-1}I \tag{4.31}$$

Furthermore, by conditions 4.26,4.27 and 4.28

$$\text{tr}\left[(\Sigma(t)\Sigma^T(t) + K(t)\Phi(t)\Phi^T(t)K^T(t))P^{-1}(t)\right] \tag{4.32}$$

$$\leq \left(\text{tr}\left[(\Sigma(t)\Sigma^T(t)\right] + \overline{k}\text{tr}\left[\Phi(t)\Phi^T(t)\right]\overline{k}\right)\frac{1}{\underline{p}}, \tag{4.33}$$

$$\leq (\varsigma^2(t) + \overline{k}\omega_\Phi m\overline{k})\frac{1}{\underline{p}}. \tag{4.34}$$

□

Lemma 4.0.4. ***Gronwall inequality[Tao, 2006]:***
Let $u : [t_0, T] \to \mathbb{R}$ be continuous and nonnegative and suppose u fulfils the following inequality for all $t \in [t_0, T]$, $\alpha \geq 0, \beta(t) : [t_0, T] \in \mathbb{R}_{>0}$ continuous:

$$u(t) \leq \alpha + \int_{t_0}^{t} \beta(s)u(s)\mathrm{d}s, \tag{4.35}$$

then $\forall t \in [t_0, T]$

$$u(t) \leq \alpha \exp\left(\int_{t_0}^{t} \beta(s)\mathrm{d}s\right). \tag{4.36}$$

The following theorem proves the asymptotic boundedness of the extended Kalman filter error, denoted by $\eta(t)$, in expectation. This proof is based on Reif's proof [Reif et al., 2000], which has been expanded through generalisation and specification in certain parts. This is done by using a more general function for the estimated covariance matrix P, as well as relaxing the bound on $||\Sigma(\mathbf{X}(t), t)||$. Due to the nature of the system of equations, as described in Equation 4.1 and the earlier conditions, some of the constraints could be relaxed. Furthermore, this proof does not use Lyapunov functions and is fully worked out, which simplifies it.

Theorem 4.0.1. ***Exponential bound of the squared error in expectation:***
Let $\mathbf{X}(t), \hat{\mathbf{X}}(t)$ be solutions of equation 4.1 respectively 4.3 on $t \in [t_0, T]$ such that $\mathbb{E}[\mathbf{X}(t_0)]^2 + \mathbb{E}[\hat{\mathbf{X}}(t_0)]^2 < \infty$ for all $t \in [t_0, T]$.
For the stochastic equation as in 3.4 let the following assumptions hold: $\exists \underline{p}, \underline{r}, \underline{q}, \omega_\Phi \in \mathbb{R}_{>0}$ and let I be the identity matrix

$$\underline{p}I \leq P(t), \text{ for all } t \in [t_0, T], \tag{4.37}$$

$$\underline{r}I \leq R(t), \text{ for all } t \in [t_0, T] \text{ and subsequently } R(t) \text{ being invertible}, \tag{4.38}$$

$$\underline{q}I \leq Q(t), \text{ for all } t \in [t_0, T], \tag{4.39}$$

$$||\Sigma(\mathbf{X}(t), t)|| \leq \varsigma(t),\ \varsigma \in L^2, \text{ for all } t \in [t_0, T],\ \mathbf{X}(t) \in \mathbb{R}^n \tag{4.40}$$

$$||\Phi(\mathbf{X}, t)\Phi^T(\mathbf{X}, t)|| \leq \omega_\Phi, \text{ for all } t \in [t_0, T],\ \mathbf{X}(t) \in \mathbb{R}^n. \tag{4.41}$$

Then, for all $t \in [t_0, T]$:

$$\mathbb{E}\left[||\eta(t)||^2\right] \leq \mathbb{E}[||\eta(t_0)||^2]\exp(-\int_{t_0}^{t}\left(-\mu\varsigma^2(t) + \underline{p}\mu_d + \mu_n(t)\right)\mathrm{d}s). \tag{4.42}$$

Proof: First, remember, due to the condition of local linear growth, $\exists \epsilon_\psi, \epsilon_\chi, \kappa_\psi, \kappa_\chi \in \mathbb{R}$

$$\forall \mathbf{X}(t), \hat{\mathbf{X}}(t) : ||\mathbf{X}(t) - \hat{\mathbf{X}}(t)|| \leq \epsilon_\psi \text{ it holds } ||\psi(\mathbf{X}(t), \hat{\mathbf{X}}(t))|| \leq \kappa_\psi ||\mathbf{X}(t) - \hat{\mathbf{X}}(t)||, \tag{4.43}$$

and

$$\forall \mathbf{X}(t), \hat{\mathbf{X}}(t) : ||\mathbf{X}(t) - \hat{\mathbf{X}}(t)|| \leq \epsilon_\chi \text{ it holds } ||\chi(\mathbf{X}(t), \hat{\mathbf{X}}(t))|| \leq \kappa_\chi ||\mathbf{X}(t) - \hat{\mathbf{X}}(t)||. \tag{4.44}$$

Again, this holds for a specific κ_ψ as described in Lemma 4.0.2, κ_χ depends on the choice of h. Also remember, that just as in Lemma 4.0.2 $\exists \overline{h} \in \mathbb{R}_{>0}$:

$$||H(t)|| \leq \overline{h}. \tag{4.45}$$

As well as a $\overline{p} \in \mathrm{R}_{>0}$ such that:

$$P(t) \leq \overline{p} I, \tag{4.46}$$

exists as P is bounded, due to X_i being bounded above (see Chapter 3).
Now let $V(\eta, t) = \eta^T(t) P^{-1}(t) \eta(t)$, again assuming P^{-1} exists as in the Lemmas 4.0.2 and 4.0.3. Remember by Equation 4.9 η satisfies $\mathrm{d}\eta(t) = [(B(t) - K(t)H(t))\eta(t) + \ell(t)]\,\mathrm{d}t + (\Sigma(\mathbf{X}(t), t)\mathrm{d}\mathbf{W}(t) - K(t)\Phi(\mathbf{X}(t), t)\mathrm{d}\mathbf{V}(t))$, then:

$$\frac{\partial V}{\partial t}(\eta, t) = \frac{\mathrm{d}(\eta^T(t) P^{-1}(t) \eta(t))}{\mathrm{d}t}(t) = \eta^T(t) \frac{\mathrm{d}P^{-1}(t)}{\mathrm{d}t}(t)\eta(t). \tag{4.47}$$

And as for almost all $t \in [t_0, T]$, with f from Equation 4.9: $f(\eta, t) = (B(t) - K(t)H(t))\eta(t) + \ell(t)$, remember that by equation 2.21 P is defined by $\frac{\mathrm{d}}{\mathrm{d}t}P(t) = F(t) \cdot P(t) + P(t)F(t)^T - K(t)H(t)P(t) + GQ(t)G^T$, then:

$$\begin{aligned}
f(\eta(t), t)(\nabla_\eta V) &= [(B(t) - K(t)H(t))\eta(t) + \ell(t)]\,(\nabla_\eta V), &(4.48)\\
&= [(B(t) - K(t)H(t))\eta(t) + \ell(t)]\,(\nabla_\eta(\eta^T(t) P^{-1}(t) \eta(t))), &(4.49)\\
&= [(B(t) - K(t)H(t))\eta(t) + \ell(t)]\,(I P^{-1}(t)\eta(t) + \eta^T(t) P^{-1} I), &(4.50)\\
&= [(B(t) - K(t)H(t))\eta(t) + \ell(t)]\,(2\eta^T(t) P^{-1}(t)), &(4.51)\\
&= \eta^T(t)(B(t) - K(t)H(t))^T P^{-1}(t)\eta(t)\\
&\quad + \eta^T(t) P^{-1}(t)(B(t) - K(t)H(t))\eta(t)\\
&\quad + \ell(t) 2\eta^T(t) P^{-1}(t), &(4.52)
\end{aligned}$$

with $\ell(t) = \psi(\mathbf{X}(t), \hat{\mathbf{X}}(t)) - K(t)\chi(\mathbf{X}(t), \hat{\mathbf{X}}(t))$, and $(P^{-1})^T(t) = P^{-1}(t)$ as $P^{-1}(t)$ is diagonal due to condition 4.37 and 4.46. Also $\ell(t)2\eta^T(t)P^{-1}(t) = 2\eta^T(t)P^{-1}(t)\ell(t)$ and

$$\frac{1}{2}\mathrm{Tr}(G^T(\eta(t), t) H_\eta(V) G(\eta(t), t)) = \frac{1}{2}\mathrm{Tr}(G^T(\eta(t), t) 2P^{-1}(t) G(\eta(t), t)) = \mathrm{Tr}(G^T(\eta(t), t) G(\eta(t), t) P^{-1}(t)). \tag{4.53}$$

As $V(\eta, t) = \eta^T P(t)^{-1} \eta = P^{-1}(t)||\eta||^2$ due to diagonality of P^{-1} then the Hessian with respect to η is $H_\eta(P^{-1}(t)||\eta||^2) = 2P^{-1}(t)$. Filling in $G = \Sigma(\mathbf{X}(t), t) - K(t)\Phi(t)$ then results in the following equation:

$$\begin{aligned}
\frac{1}{2}\mathrm{tr}(G^T(\eta(t), t) H_\eta(V) G(\eta(t), t)) =&\mathrm{tr}\left((\Sigma^T(\mathbf{X}, t)\Sigma(\mathbf{X}, t) - \Sigma^T(\mathbf{X}, t) K(t)\Phi(t)\right.\\
&\left. - (K(t)\Phi(t))^T \Sigma(\mathbf{X}, t) + K(t)\Phi(t)\Phi^T(t) K^T(t)) P^{-1}\right). \qquad (4.54)
\end{aligned}$$

By filling in $V(\eta, t) = \eta^T(t) P^{-1}(t) \eta(t)$ in the differential generator, Equation 4.12 from Itô's lemma, Lemma 4.0.1, combining this with Equations 4.47, 4.52 and 4.54 yields:

$$\begin{aligned}
\mathcal{L}V(\eta(t), t) = &\eta^T(t) \frac{\mathrm{d}P^{-1}}{\mathrm{d}t}(t)\eta(t)\\
&+ \eta^T(t)(B(t) - K(t)H(t))^T P^{-1}(t)\eta(t)\\
&+ \eta^T(t) P^{-1}(t)(B - K(t)H(t))\eta(t)\\
&+ \ell(t) 2\eta^T(t) P^{-1}(t)\\
&+ \mathrm{tr}\left((\Sigma^T(\mathbf{X}(t), t)\Sigma(\mathbf{X}(t), t) + K(t)\Phi(t)\Phi^T(t) K^T(t)) P^{-1}\right). \qquad (4.55)
\end{aligned}$$

Using Lemma 4.0.2 it is known that: $2(\mathbf{X}-\hat{\mathbf{X}})^T P^{-1}\ell(t) \leq 2\left(\frac{\kappa_\psi}{\underline{p}} + \frac{\overline{h}\kappa_\chi}{\underline{r}}\right)||(\mathbf{X}-\hat{\mathbf{X}})||^2$, due to conditions 4.37 and 4.38 as well as that R is invertible, on $\epsilon_{\psi,\chi} = \min(\epsilon_\psi, \epsilon_\chi)$. Let $\mu_d = 2\left(\frac{\kappa_\psi}{\underline{p}} + \frac{\overline{h}\kappa_\chi}{\underline{r}}\right)$.

Furthermore from Lemma 4.0.3, whose conditions are satisfied by 4.37, 4.40 and 4.41, as the bound on K is given by then $||K|| = ||P(t)H^T(t)R^{-1}(t)|| \leq \frac{\overline{p}\overline{h}}{\underline{r}} = \overline{k}$, due to 4.38, 4.45 and 4.46 it is known that: tr $\left((\Sigma^T(\mathbf{X},t)\Sigma(\mathbf{X},t) + K(t)\Phi(t)\Phi^T(t)K^T(t))P^{-1}\right) \leq \frac{1}{\underline{p}}(\varsigma^2(t) + \overline{k}^2\omega_\Phi^2 m^2)$ Let $\mu_n(t) = \frac{1}{\underline{p}}(\varsigma^2(t) + \overline{k}^2\omega_\Phi m)$

Combining this with Equation 4.55 yields:

$$\begin{aligned}\mathcal{L}V(\eta(t),t) \leq\ & \eta^T(t)\frac{\mathrm{d}P^{-1}}{\mathrm{d}t}(t)\eta(t)\\ &+ \eta^T(t)(B(t)-K(t)H(t))^T P^{-1}(t)\eta(t)\\ &+ \eta^T(t)P^{-1}(t)(B-K(t)H(t))\eta(t)\\ &+ \mu_d||(\mathbf{X}(t)-\hat{\mathbf{X}}(t))||^2 + \mu_n(t).\end{aligned} \tag{4.56}$$

By utilizing $K(t) = P(t)H^T(t)R^{-1}(t)$, and given that $R^{-1}(t)$ and $P^{-1}(t)$ are diagonal, due to $R(t)$ and $P(t)$ being diagonal the following holds:

$$\eta^T(t)\frac{\mathrm{d}P^{-1}}{\mathrm{d}t}(t)\eta(t) + \eta^T(t)(B(t)-K(t)H(t))^T P^{-1}(t)\eta(t) + \eta^T(t)P^{-1}(t)(B(t)-K(t)H(t))\eta(t) \tag{4.57}$$

$$=\eta^T(t)\left(\frac{\mathrm{d}P^{-1}}{\mathrm{d}t}(t) + (B(t)-K(t)H(t))^T P^{-1}(t) + P^{-1}(t)(B(t)-K(t)H(t))\right)\eta(t) \tag{4.58}$$

$$=\eta^T(t)\left(\frac{\mathrm{d}P^{-1}}{\mathrm{d}t}(t) + B^T(t)P^{-1}(t) - H^T(t)K^T(t)P^{-1}(t) + P^{-1}(t)B(t) - P^{-1}(t)K(t)H(t)\right)\eta(t) \tag{4.59}$$

$$=\eta^T(t)\left(\frac{\mathrm{d}P^{-1}}{\mathrm{d}t}(t) + B^T(t)P^{-1}(t) - H^T(t)(R^{-1}(t))^T H(t) + P^{-1}(t)B(t) - H^T(t)R^{-1}(t)H(t)\right)\eta(t) \tag{4.60}$$

$$=\eta^T(t)\left(\frac{\mathrm{d}P^{-1}}{\mathrm{d}t}(t) + B^T(t)P^{-1}(t) + P^{-1}(t)B(t) - 2H^T(t)R^{-1}(t)H(t)\right)\eta(t). \tag{4.61}$$

The derivative of a matrix by a scalar is given by $\frac{\mathrm{d}}{\mathrm{d}t}P^{-1}(t) = -P^{-1}(t)\frac{\mathrm{d}}{\mathrm{d}t}P(t)P^{-1}(t)$[Pawel, 2006], in combination with $\frac{\mathrm{d}}{\mathrm{d}t}P = B(t)P(t) + P(t)B^T(t) - P(t)H(t)^T R(t)^{-1}H(t)P(t) + \Sigma Q(t)\Sigma^T$ from Equation 2.21, this yields the following equivalence:

$$\eta^T(t)\left(\frac{\mathrm{d}P^{-1}}{\mathrm{d}t}(t) + B^T(t)P^{-1}(t) + P^{-1}(t)B(t) - 2H^T(t)R^{-1}(t)H(t)\right)\eta(t) \tag{4.62}$$

$$=\eta^T(t)\left(-H^T(t)R^{-1}(t)H(t) - P^{-1}(t)\Sigma(t)Q(t)\Sigma^T(t)P^{-1}(t)\right)\eta(t). \tag{4.63}$$

Combining equation 4.63 with 4.56 yields

$$\begin{aligned}\mathcal{L}V(\eta(t),t) \leq\ & \eta^T(t)\left(-H^T(t)R^{-1}(t)H(t) - P^{-1}(t)\Sigma(t)Q(t)\Sigma^T(t)P^{-1}(t)\right)\eta(t)\\ &+ \mu_d||\eta(t)||^2 + \mu_n(t).\end{aligned} \tag{4.64}$$

By using Equations 4.39 and 4.46, as well as using $H^T(t)R^{-1}(t)H(t) \geq 0$, due to 4.38, R being diagonal and 4.40 it is given that

$$\begin{aligned}\mathcal{L}V(\eta(t),t) &\leq -\frac{q}{\overline{p}^2}\left(\eta^T\Sigma(t)\Sigma^T(t)\eta(t)\right) + \mu_d||\eta(t)||^2 + \mu_n(t),\\ &\leq \left(-\frac{q}{\overline{p}^2}||\Sigma^T(t)||^2 + \mu_d\right)||\eta(t)||^2 + \mu_n(t).\end{aligned} \tag{4.65}$$

The following holds

$$\mathcal{L}V(\eta(t),t) \leq \left(-\frac{q}{\overline{p}^2}\varsigma^2(t) + \mu_d\right)\frac{p}{\underline{p}}||\eta(t)||^2 + \mu_n(t), \tag{4.66}$$

$$\leq \left(-\mu\varsigma^2(t) + \underline{p}\mu_d\right)V(\eta(t),t) + \mu_n(t). \tag{4.67}$$

Due to $V(\eta(t),t) = \eta(t)P^{-1}(t)\eta(t)$, inequalities 4.37, 4.40, 4.46 and by taking $\mu = \frac{qp}{\overline{p}^2}$.

Then due to $\mathcal{L}$ being the differential operator and rewriting 4.67 using 4.11 from Lemma 4.0.1:

$$V(\eta(t),t) \leq V(\eta(t_0),t_0) - \int_{t_0}^{t}\left(\left[-\mu\varsigma^2(t) + \underline{p}\mu_d\right]V(\eta(s),s) + \mu_n(t)\right)\mathrm{d}s + \int_{t_0}^{t} G\mathrm{d}\tilde{\mathbf{W}}. \tag{4.68}$$

Recall that $G(t) = [\Sigma(\mathbf{X}(t),t), -K(t)\Phi(t)]$ and that $||\Sigma(\mathbf{X}(t),t)|| \leq \varsigma(t)$, $\varsigma \in L^2$, $||K(t)|| \leq \overline{k}$ and $||\Phi(\mathbf{X}(t),t)\Phi^T(\mathbf{X}(t),t)|| \leq \omega_\phi$ thus $||\Phi(\mathbf{X}(t),t)||$ is bounded. As such $\int_0^T \mathbb{E}[||G(t)||^2]\mathrm{d}t$ exists and is bounded meaning the expected value of the martingale can be calculated, using Itô integration as outlined in Definition 2.3.5. This expected value is zero as

$$\int_{t_0}^{t} G(t)d\tilde{\mathbf{W}} = \lim_{m\to\infty}\sum_{i=1}^{m} G(t_{i-1})(\tilde{\mathbf{W}}(t_i) - \tilde{\mathbf{W}}(t_{i-1})). \tag{4.69}$$

By Definition 2.3.1 $\mathbb{E}\left[\tilde{W}(t_i) - \tilde{W}(t_{i-1})\right] = 0$, then:

$$\mathbb{E}\left[V(\eta(t),t)\right] \leq \mathbb{E}\left[V(\eta(t_0),t_0)\right] - \mathbb{E}\left[\int_{t_0}^{t}\left(\left[-\mu\varsigma^2(t) + \underline{p}\mu_d\right]V(\eta(s),s) + \mu_n(t)\right)\mathrm{d}s\right]. \tag{4.70}$$

By Fubini's theorem, see [Halmos, 1950], this is equivalent to

$$\mathbb{E}\left[V(\eta(t),t)\right] \leq \mathbb{E}\left[V(\eta(t_0),t_0)\right] - \int_{t_0}^{t}\left(\left[-\mu\varsigma^2(t) + \underline{p}\mu_d\right]\mathbb{E}\left[V(\eta(s),s)\right] + \mu_n(t)\right)\mathrm{d}s. \tag{4.71}$$

Where $\int_{t_0}^{t}\mu_n(t)\mathrm{d}s$ is bounded, as $\varsigma(t)$ is in L^2. Then, by Gronwall's inequality, Lemma 4.0.4, and $V(\eta(t),t) = \eta^T(t)P^{-1}(t)\eta(t)$ the exponential bound on the error η is proven in expectation, and we have

$$\mathbb{E}\left[||\eta(t)||^2\right] \leq \mathbb{E}\left[||\eta(t_0)||^2\right]\exp(-\int_{t_0}^{t}\left(-\mu\varsigma^2(t) + \underline{p}\mu_d + \mu_n(t)\right)\mathrm{d}s). \tag{4.72}$$

□

One of the main differences between this proof and the one from Reif, is that this one allows a closer bound on $||\Sigma(\mathbf{X}(t),t)||$, as the bound can depend on time, and only has to be in L^2. For example, if Σ is of the following form:

$$\Sigma(\mathbf{X}(t),t) = \begin{pmatrix} 1/t^{\frac{1}{4}} & 0 \\ 0 & 1/t^{\frac{1}{4}} \end{pmatrix} \tag{4.73}$$

then, $||\Sigma(\mathbf{X}(t),t)|| = t^{-\frac{1}{4}}$, the square of which is integrable, but the function is unbounded. Thus allowed by this theorem, but not in the one from Reif's paper [Reif et al., 2000].

In practice, and historically, most systems that describe the interaction between animals consist of just two species, typically, a predator and its prey. In the following corollary, the necessary conditions for Theorem 4.0.1 to hold will be worked out for the case where $i = 1, 2$ meaning there are just two animals.

Corollary 4.0.1.1. ***Bound on error in expectation in 2D case***
Let $\mathbf{X}(t) = (X_1(t), X_2(t))^T$ be the solution of a system as in 4.1 for $n = 2$, satisfying the same local Lipschitz conditions on the coefficients as given in Assumption 3.2.1, with a solution on $[t_0, T]$. The system is then given by:

$$\begin{aligned} \mathrm{d}X_1(t) &= X_1(t)\big(r_1 - a_{1,1}X_1(t) - a_{1,2}X_2(t)\big)\mathrm{d}s \\ &\quad + \sigma_{1,1}(s, X_1(t), X_2(t))\mathrm{d}W_1(t) + \sigma_{1,2}(s, X_1(t), X_2(t))\mathrm{d}W_2(t), \quad (4.74) \\ \mathrm{d}X_2(t) &= X_2(t)\big(r_2 - a_{2,1}X_1(t) - a_{2,2}X_2(t)\big)\mathrm{d}s \\ &\quad + \sigma_{2,1}(s, X_1(t), X_2(t))\mathrm{d}W_1(t) + \sigma_{2,2}(s, X_1(t), X_2(t))\mathrm{d}W_2(t). \quad (4.75) \end{aligned}$$

If the absolute value of $\sum_{k=1}^{2} \sigma_{i,k}\sigma_{j,k}$ is bounded for all $i, j = 1, 2$ i.e.

$$\left|\sum_{k=1}^{2} \sigma_{i,k}\sigma_{k,j}\right| < \alpha_\sigma,\ i, j \in (1, 2), \tag{4.76}$$

for some $\alpha_\sigma \in \mathbb{R}_{>0}$. A similar condition for the elements of Φ, $\phi_{i,j}$ should hold: $\exists\, \alpha_\phi \in \mathbb{R}_{>0}$ such that

$$\left|\sum_{k=1}^{2} \phi_{i,k}\phi_{k,j}\right| < \alpha_\phi,\ i, j \in (1, 2). \tag{4.77}$$

Lastly $\exists\, \underline{r}, \underline{q} \in \mathbb{R}_{>0}$:

$$\underline{r}I \leq R(t) \text{ and } R \text{ being invertible,} \tag{4.78}$$

$$\underline{q}I \leq Q(t),\ \text{ for all } t \in [t_0, T]. \tag{4.79}$$

Then Theorem 4.0.1 holds; there exists an exponential bound on the expectation of the error between the real data and the resulting estimate from the extended Kalman filter. Meaning

$$\mathbb{E}\left[||\eta(t)||^2\right] \leq \mathbb{E}\left[||\eta(t_0)||^2\right] \exp(-\int_{t_0}^{t} \big(-\mu\varsigma^2(t) + \underline{p}\mu_d + \mu_n(t)\big)\,\mathrm{d}s). \tag{4.80}$$

Proof: The random fluctuations at all times ensure that the covariance matrix is never zero on the diagonal, although it might be for all other values of the matrix. This ensures Condition 4.37.
Conditions 4.38, 4.39 are given in the same way, and as such, they hold.
All values of $\Sigma\Sigma^T$ can be described by $\sum_{k=1}^{2} \sigma_{i,k}\sigma_{j,k}$, where this is the element $(\Sigma\Sigma^T)_{i,j}$. As all these elements are bound, so is the determinant. Meaning conditions 4.40 and 4.41 are given, and the Theorem holds.

□

5
Filtering Stochastic Population Models

In this chapter, the model described in Chapter 3 will be implemented using the Extended Kalman Filter with the data as in Section 2.2.1. Furthermore, data will be simulated using the Lotka-Volterra equation, and noise will be applied. On this data, the model will again be applied, and an implementation will be done simulating the case when just one of the two species has population data. All implementations are done using Python; the data can be found in Appendix A, respectively Appendices D and E for the simulated data, and the respective code can be found in Appendices B and C.

5.1. Example Implementation

Using the discrete extended Kalman filter as described in Section 2.4.3, the equations described in Equation 3.4 can be fitted to the data from the Isle Royale National Park (Appendix A). The implementation of the EKF was done using Python; the code can be found in Appendix B.

Equation 3.4 simplifies to just two dimensions, thus:

$$\begin{aligned}
\mathrm{d}X_w(t) = X_w(t_0) &+ \int_{t_0}^{t} X_w(s)\big(r_w - a_{w,w}X_w(s) - a_{w,m}X_m(s)\big)\mathrm{d}s \\
&+ \int_{t_0}^{t} \big(\sigma_{w,w}(s, X_w(s), X_m(s))\mathrm{d}W_w(s) + \sigma_{w,m}(s, X_w(s), X_m(s))\mathrm{d}W_m(s)\big), \qquad (5.1)\\
\mathrm{d}X_m(t) = X_m(t_0) &+ \int_{t_0}^{t} X_m(s)\big(r_m - a_{m,w}X_w(s) - a_{m,m}X_m(s)\big)\mathrm{d}s \\
&+ \int_{t_0}^{t} \big(\sigma_{m,w}(s, X_w(s), X_m(s))\mathrm{d}W_w(s) + \sigma_{m,m}(s, X_w(s), X_m(s))\mathrm{d}W_m(s)\big). \qquad (5.2)
\end{aligned}$$

Here t_0 is of course the first time the number of wolfs and moose was recorded, being in this case 1980. The wolf population is described by X_w, and the population of the moose by X_m. By taking the following interaction and reproduction values:

$$r_w = 0.2 \qquad r_m = 0.1 \qquad a_{w,w} = 0.01 \qquad (5.3)$$

$$a_{w,m} = 0.001 \qquad a_{m,w} = 0.0002 \qquad a_{m,m} = 0.00005. \qquad (5.4)$$

Let $\sigma_{i,j}(X_m, X_w) = \tilde{\sigma}_{i,j}(X_m, X_w)\mathbb{1}_{X_i \in (c_m, C_m)}$ for i, j being w or m, with $\tilde{\sigma}_{m,m}(X_m, X_w) = -(X_m - c_m)(X_m - C_m)$, similar for $\tilde{\sigma}_{w,w}(X_m, X_w) = -(X_w - c_w)(X_w - C_w)$ and let $\tilde{\sigma}_{m,w}(X_m, X_w) = 0$ same as $\tilde{\sigma}_{w,m}(X_m, X_w) = 0$. This includes that $\sigma_{m,m}(X_m, X_w)$ and $\sigma_{w,w}(X_m, X_w)$ are zero, when X_m respectively X_w not in $[c, C]$. The following values are taken for c, C:

$$c_m = 100 \qquad C_m = 2000 \tag{5.5}$$
$$c_w = 1 \qquad C_w = 20 \tag{5.6}$$

And by taking the observation matrix H to be the identity matrix, as the observations are X_w, respectively X_m, meaning

$$h(\mathbf{X}(t)) = \begin{pmatrix} X_m & 0 \\ 0 & X_w \end{pmatrix}, \tag{5.7}$$

the differential of which is $I \in \mathbb{R}^{2\times 2}$ the following result is achieved:

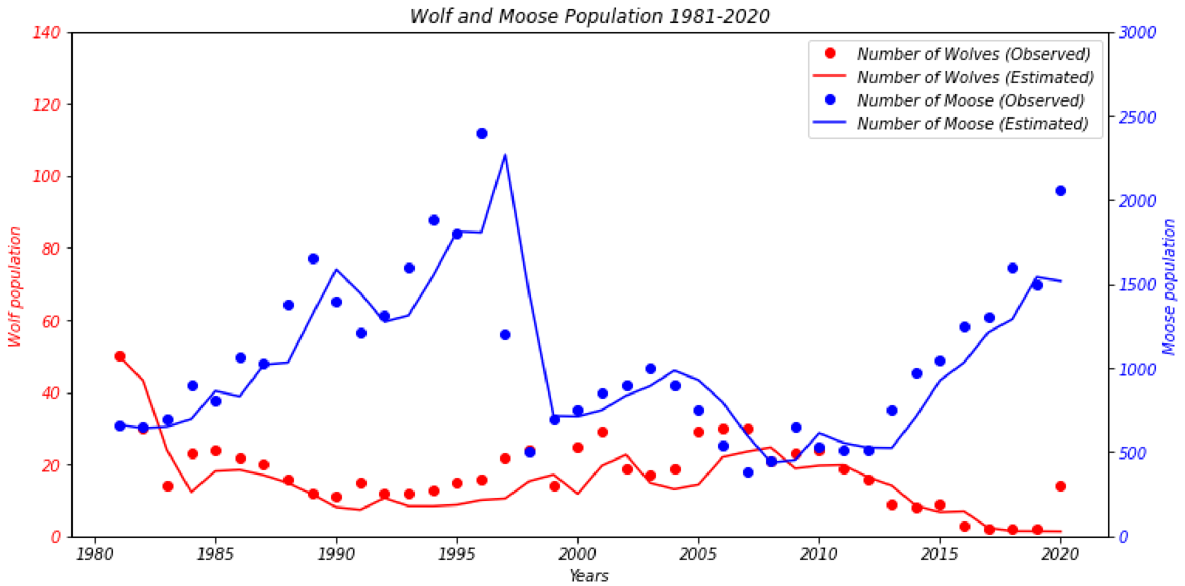

Figure 5.1: The extended Kalman filter applied to the recorded number of moose and wolves in the Isle Royale national park where the populations were described using Equation 5.1

A visual comparison of this result with the Lotka-Volterra system implementation shown in Figure 2.2 reveals that, even if a better LV fit were possible, this solution is much closer to the data points. This is because the EKF solution allows for a fitted curve that is more irregular, which aligns more with the data.

5.2. Finding the hidden state

This section presents an implementation of the Extended Kalman Filter (EKF), which is used to estimate the 'hidden' state. This implementation demonstrates how the model can be used in combination with the EKF when only limited and noisy data is available.

To simulate a realistic scenario, data is generated using the Lotka-Volterra equations for two species as given in Equation 3.2. Afterwards, random, normally distributed noise is added.

Then the model as described in Chapter 3 will be applied using the EKF, with the important difference that it is assumed that only the number of wolves is known. This means that the filter does not know how many moose are there, except for the initial number. The observation matrix is thus $H = [0, 1]$ instead of the identity matrix, which would be the case if both species are separately counted. In ecology, it is often the case that reliable data is only available for just one species, although knowing the number of both species could be desired. The EKF can then be used to estimate the other species, in this case, the number of moose.

The code for this implementation can be found in Appendix C, and was done using Python. The packages used were `NumPy`, for linear algebra and computations, `Matplotlib.pyplot` for plotting the results, `SciPy` for integrating the differential equations, and `Math`, for computations.

Although the results may vary, due to the added stochastic noise, a possible result will be given here. Two cases will be examined, the first being a predator-prey relationship, similar to the Wolf and Moose interactions from earlier. The second examined case will be that of a competition relationship, where both species curb the population growth of the other.

5.2.1. Predator-Prey Example:

The predator-prey relationship is characterised by one species hunting the other. This means that one species directly hurts the growth of the other, whilst the latter is the basis for the population growth of the former.
As described in Chapter 2, the predator prey relationship necessitates that the influence of the prey on the predator population is positive, in the case of wolves and moose this means $a_{m,w} > 0$ whilst the influence of the predator on the prey population is negative i.e. $a_{w,m} < 0$.
In this case, it will still be assumed that populations of moose and wolves are modelled, the variables were assumed to be the following:

$$r_w = 1 \qquad r_m = -1 \qquad a_{w,w} = -0.01$$
$$a_{w,m} = 1 \qquad a_{m,w} = -1 \qquad a_{m,m} = -0.01.$$

The added normally-distributed noise had a standard deviation of 0.5 and a mean of zero do to the sigma functions outlined below; furthermore,

$$Q = \begin{pmatrix} 0.1 & 0 \\ 0 & 0.1 \end{pmatrix}, \; R = 0.5^2, \; P = \begin{pmatrix} 0.1 & 0 \\ 0 & 0.1 \end{pmatrix}. \tag{5.8}$$

For both the predator and the prey the bounds of the noise are the same, $c = 0,5$ and $C = 5$. The assumption is made that the σ-functions are the same as before, i.e. $\sigma_{i,j}(X_m, X_w) = \frac{0.5}{t}\tilde{\sigma}_{i,j}(X_m, X_w)\mathbb{1}_{X_i \in (c_m, C_m)}$ for i, j being w or m. with $\tilde{\sigma}_{m,m}(X_m, X_w) = -(X_m - c_m)(X_m - C_m)$, $\tilde{\sigma}_{m,w}(X_m, X_w) = 0$, $\tilde{\sigma}_{w,w}(X_m, X_w) = -(X_w - c_w)(X_w - C_w)$ and $\tilde{\sigma}_{w,m}(X_m, X_w) = 0$ where $c_m = c_w, C_m = C_w$.
The simulated data is provided in Appendix D.

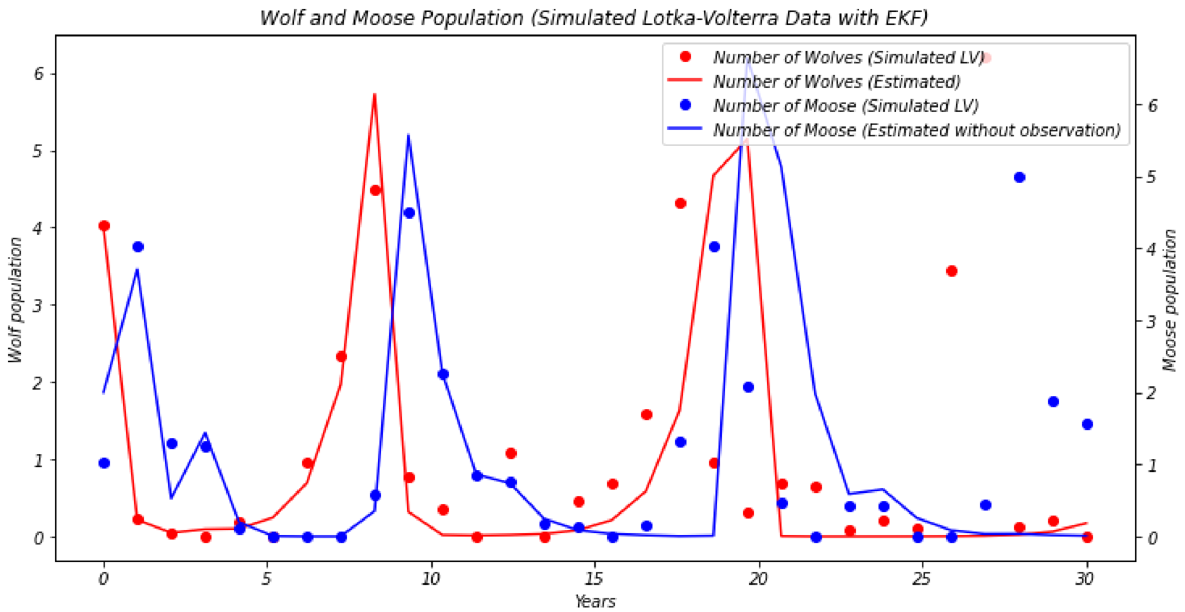

Figure 5.2: The extended Kalman filter applied to simulated data estimating the 'hidden' number of moose, using equations 5.1

5.2.2. Competition Example:

Competition between species occurs when both species rival for the same resource. In nature, there are many examples where two species compete for the same food sources, but this is not limited to different species. Two groups of the same species might also be seen as two competing populations. Some well known examples are lions and cheetahs, but also woodpeckers and squirrels. The only thing all these have in common is that they compete for food, water, habitats, etc..

By using the same code as for the last example, which is given in Appendix C, but changing the variables a simulation of such a relationship can be made for two species, S_1 and S_2, here of course, as the influence of each species on the other is negative, it is necessitated that for competition to exist $a_{1,2}, a_{2,1} < 0$.

Take the following variables:

$$r_1 = 0.1 \qquad r_2 = 0.1 \qquad a_{1,1} = 0.001$$
$$a_{1,2} = 0.00075 \qquad a_{2,1} = 0.0005 \qquad a_{2,2} = 0.00125.$$

With the same matrices and values for Q, R, P as in the last example, given in 5.2.1. But changing the standard deviation of the noise, added to the data to 4 for species S_1 and 1 for species S_2. With $c_1 = 1, C_1 = 80$ for species 1, and for species 2 $c_2 = 1, C_2 = 32$.
The functions taken for σ are the same as before.

The generated data is given in Appendix E, the resulting plot can be seen in Figure 5.3.

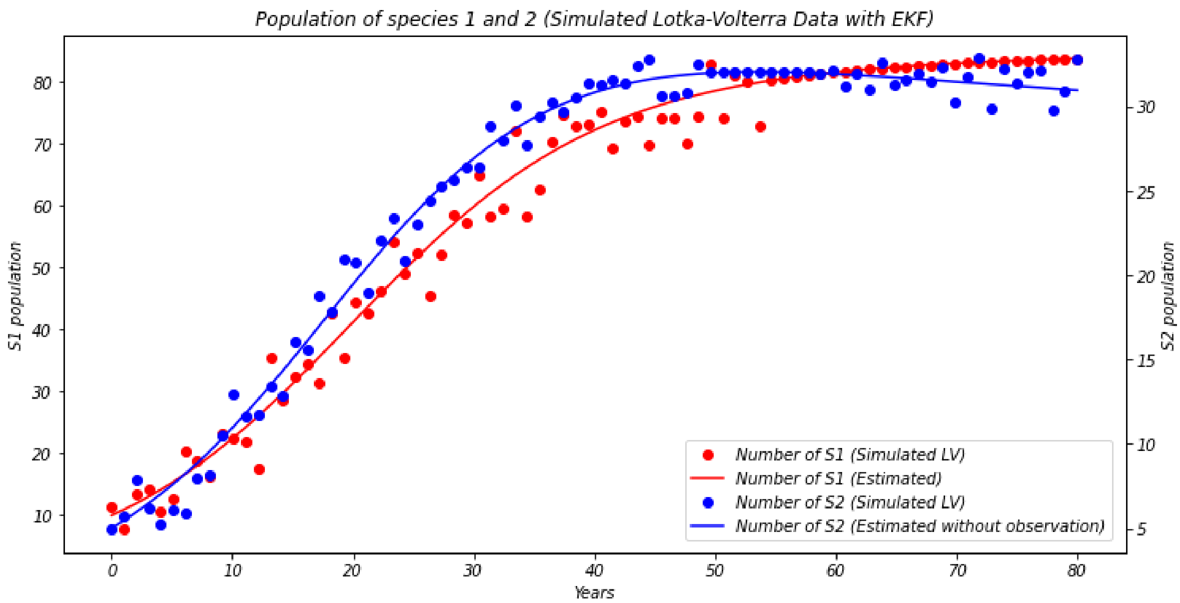

Figure 5.3: The extended Kalman filter applied to simulated data estimating the 'hidden' number of species 2 (S_2), using equations 5.1 and data from species 1 (S_1), when both species are in competition

It should be mentioned, that instead of the earlier simulated 30-year interval, now 80 years have been simulated. This is due to the population of the two species stabilising at that point. It can be observed that both increase to a maximum at approximately 80 and 35 animals for species 1, respectively, species 2.

6
Discussion

In this paper, a model describing the populations of n different species was made. This was done on the basis of the Lotka-Volterra equations, which were enhanced with a stochastic component describing the noise. The well-posedness of solutions of these equations was proven, and the extended Kalman filter was applied to this model, in order to estimate the populations based on partial and noisy data.

6.1. Model Realism

Although the simple Lotka-Volterra equations are already able to describe the populations of a predator and a prey species approximately, there are some well-known problems with using the model. One of the main problems, the randomness of interactions, was solved by adding Brownian motion. Making this noise term dependent on the population of the species addressed the randomness in birth and death, but also disease outbreaks, climate change or mutations.

However, the assumption that Gaussian noise describes the stochastic influence on one or more species might not accurately capture the complex interactions. Assuming Gaussian noise is a common mathematical assumption, but it may not fully describe the noise in practice. One possible problem could be that the noise is independent of the past, meaning random deaths cannot depend on random births, although this might seem logical. Furthermore, assuming that the support of the noise exists only on some bounded interval between the population maximum and minimum, ensures that the population is bounded, but might be a simplification from real life, where population bounds might be violated.

The environment in which the species populations are described is also assumed to be isolated. In practice, in a world less isolated from humans, many interventions are staged to prevent one or more species from going extinct. These events cannot be predicted by any mathematical model, which means that the accuracy of a prediction is reduced in such cases.

Furthermore, a population capacity was assumed. This was mainly done for mathematical purposes, to ensure a prediction could be made. But also because, in practice, a very large population cannot be sustained, due to food becoming scarce. This term is questionable to some [Dhondt, 1988] and might oversimplify the complex interactions between species and their environment. Further including the environment into the mathematical model might more accurately reflect these influences.

The proof for boundedness and nonnegativity, and thus existence and uniqueness of solutions, which follows from it, was also only done in the case of two species. This means that solutions might not exists for n or might be unbounded or negative. Although a mathematical proof for n species does not immediately follow, it is reasonable to assume that a similar approach could be used.

6.2. Filtering Accuracy

The extended Kalman filter (EKF) is a central element of this thesis. It is used to estimate nonlinear population dynamics and fitting the model to data. The algorithm works recursively to estimate the (hidden) states from noisy or missing data. The model shows promising results when applied to simulated data.

A significant finding of this thesis is the asymptotic exponential convergence of the estimation error of the EKF in expectation. This proves that the results obtained with the EKF, when applied to this model, are improving quickly when time progresses. By refraining from using Lyaponov functions or heavy assumptions on the coefficients, the result was generalised in some directions. But this does not mean that there are no drawbacks. For the proof, certain assumptions have been made, such as bounded covariance matrices and invertible observation noise matrices. In practice, these condtions might not always be met, even though they are commonly imposed in filtering theory.

6.3. Application

Although the model was applied to real-life data using the EKF, it has not been tested with many datasets. Furthermore, issues may arise when applying the model to real-life data, as the data was simulated when the model was tested in the case of observing just one of the species. Estimating the parameters of the model can cause significant issues when using models of this kind in practice. This might also be the case when applying this model.

7 Conclusion

In this report, the Extended Kalman Filter was applied to a stochastic population model. This was done by first introducing the mathematical framework necessary, including the Lotka-Volterra equations, which were expanded to include a stochastic component. This stochastic noise was described using the Wiener process. To this stochastic model, the EKF was applied, in order to investigate the possibility of finding 'hidden' states of population, i.e. determining the number of one species, if only the amount of another species is known.

Following a thorough mathematical analysis, it has been demonstrated that the constructed model has a unique and bounded solution for two species. This is essential if the model is to be used. In addition, the biological basis of the model was explained, including the necessity of a bounded solution for the model to be realistic.

For the extended Kalman filter, it was proven that any estimation using this filter has an error which is exponentially asymptotic in expectation. This was proven for the specific population equations earlier established in this report, which allowed for simplification of the proof and clearer, less restrictive assumptions furthermore the proof was generalised in some small ways.

Lastly, the model was applied to real-life data, using the Kalman filter, and the hidden states were determined for simulated data. Thereby proving that, even lacking data of one of the species, and only having noisy data for the other, an estimation can be made for the population of both species.

In summary, this thesis presents the mathematical framework for establishing stochastic differential equations that describe the population dynamics of multiple species. It proves that these equations, combined with the extended Kalman filter, provide a great tool for estimating the population of animals in the wild.

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A

Example: Population Data of Wolves and Moose on Isle Royale

Since 1980 the number of wolves and moose have been tracked on Isle Royale National Park. This data showcases classical cycles of an increase in the number of wolves yielding a decrease in the number of moose following an increase in the number of moose. The data is retrieved from the United States National Park Service [U.S. National Park Service, 2015a]

Year	Number of Wolves	Number of Moose
1980	50	664
1981	30	650
1982	14	700
1983	23	900
1984	24	811
1985	22	1062
1986	20	1025
1987	16	1380
1988	12	1653
1989	11	1397
1990	15	1216
1991	12	1313
1992	12	1600
1993	13	1880
1994	15	1800
1995	16	2400
1996	22	1200
1997	24	500
1998	14	700
1999	25	750
2000	29	850
2001	19	900
2002	17	1000
2003	19	900
2004	29	750
2005	30	540
2006	30	385
2007	21	450
2008	23	650
2009	24	530
2010	19	510
2011	16	515
2012	9	750
2013	8	975
2014	9	1050
2015	3	1250
2016	2	1300
2017	2	1600
2018	2	1500
2019	14	2060

B

Example: Extended Kalman Filter for wolves and moose on Isle Royale

```python
# -*- coding: utf-8 -*-
"""
Created on Tue May 13 18:35:18 2025

@author: olavv
"""
import numpy as np
import matplotlib.pyplot as plt

def EKF(initstate,initcov,wolvesdat,moosedat,procnoisecov,mnoisecov,rw,rm,aww,awm,amw,amm,dt):
    #assumes H=I
    n=len(wolvesdat)
    estdat=[initstate]
    estcov=[initcov]
    jetztest=initstate
    jtztcovest=initcov
    for k in range(n):
        predictedstate=np.array([
            jetztest[0]+dt*jetztest[0]*(rw-aww*jetztest[0]-awm*jetztest[1]),
            jetztest[1]+dt*jetztest[1]*(rm-amw*jetztest[0]-amm*jetztest[1])
        ])

        F=np.array([[1+dt*(rw-2*aww*jetztest[0]-awm*jetztest[1]),-dt*awm*jetztest[0]],
            [-dt*amw*jetztest[1],1+dt*(rm-amw*jetztest[0]-2*amm*jetztest[1])]])
        #Assume sigma is -(x_i-c)(x_i-C)
        F[:,0]=[i-(i-0.5)*(i-5)*np.random.normal(0,processnoisewolf) if 5>i>0.5 else i for i in F[:,0]]
        F[:,1]=[i-(i-0.5)*(i-5)*np.random.normal(0,processnoisemoose) if 5>i>0.5 else i for i in F[:,1]]


        #cov
        predcov=np.matmul(np.matmul(F,jtztcovest),np.transpose(F))+procnoisecov

        #Kalman ggain
        H=np.eye(2)
        S=np.matmul(np.matmul(H,predcov),np.transpose(H))+mnoisecov
        K=np.matmul(np.matmul(predcov,np.transpose(H)),np.linalg.inv(S))

        #update
        meas=np.array([wolvesdat[k],moosedat[k]])
        In=meas-np.matmul(H,predictedstate)
        updatestat=predictedstate+np.matmul(K,In)
        I=np.eye(2)
        updatecov=np.matmul((I-np.matmul(K,H)),predcov)
```

```

        estdat.append(updatestat)
        estcov.append(updatecov)
        jetztest=updatestat
        jtztcovest=updatecov
    return estdat,estcov

wolves=np.array
    ([50,30,14,23,24,22,20,16,12,11,15,12,12,13,15,16,22,24,14,25,29,19,17,19,29,30,30,21,23,24,19,16,9,8,9,3

moose=np.array
    ([664,650,700,900,811,1062,1025,1380,1653,1397,1216,1313,1600,1880,1800,2400,1200,500,700,750,850,900,100

years=np.arange(1981,2021)
initval=np.array([wolves[0], moose[0]])
initcov=np.diag([100,10000])

#parameters
rw=0.2
rm=0.1
aww=0.01
awm=0.001
amw=0.0002
amm=0.00005
timestep=1
dim=2

processnoisewolf=5
measurementnoisewolf=3
processnoisemoose=50
measurementnoisemoose=30
pnoisecov = np.diag([processnoisewolf**2,processnoisemoose**2])
measurenoisecov=np.diag([measurementnoisewolf**2,measurementnoisemoose**2])


stateest,covest=EKF(initval,initcov,wolves[:-1],moose[:-1],pnoisecov,measurenoisecov,rw,rm,
    aww,awm,amw,amm,timestep)
estw=np.array([i[0] for i in stateest])
estm=np.array([i[1] for i in stateest])

#plot
plt.figure()
fig,ax1=plt.subplots(figsize=(12,6))
ax1.plot(years,wolves,'ro',label="Number␣of␣Wolves␣(Observed)")
ax1.plot(years,estw,'r-',label="Number␣of␣Wolves␣(Estimated)")
ax1.set_xlabel("Years")
ax1.set_ylabel("Wolf␣population",color='r')
ax1.tick_params(axis='y',labelcolor='r')
ax1.set_ylim(0,140)

ax2 = ax1.twinx()
ax2.plot(years,moose,'bo',label="Number␣of␣Moose␣(Observed)")
ax2.plot(years,estm,'b-',label="Number␣of␣Moose␣(Estimated)")
ax2.set_ylabel("Moose␣population",color='b')
ax2.tick_params(axis='y',labelcolor='b')
ax2.set_ylim(0,3000)

plt.title("Wolf␣and␣Moose␣Population␣1981-2020")
fig.legend(loc="upper␣left", bbox_to_anchor=(0.67,0.88))
plt.show()
```

C

Example: Extended Kalman Filter for Estimating a Hidden State, Using Simulated Data

```
# -*- coding: utf-8 -*-
"""
Created on Wed Jun  4 11:38:33 2025

@author: olavv
"""

import numpy as np
import matplotlib.pyplot as plt
from scipy import integrate
import math

def LV(z,t,a,b,c,d,e,f):
    x,y=z
    dx=x*(a+b*y+e*x)
    dy=y*(c+d*x+f*y)
    return np.array([dx,dy])

a=1
b=-1
c=-1
d=1
e=0.01
f=0.01
x0=4
y0=2


def EKF(param,times,initval,initcov,R,Q,obs,x1datstd,x2datstd):
    #Calculating the EKF for the interval 'times' using provided data
    #Due to the randomness of the data it might be necessary to run more than once to get a '
        good' result. It might flatline otherwise. A solution can also be to reduce the noise
        .
    a,b,c,d,e,f=param
    t=len(times)
    Sest=np.array(initval)
    P=np.array(initcov)
    pred=[Sest]

    for k in range(1,t):
        dt=times[k]-times[k-1]
        val=integrate.odeint(LV,Sest,[times[k-1],times[k]],args=(a,b,c,d,e,f))
        Sestpred=val[1]
```

```
        F=np.array([[a+b*Sest[1]+2*e*Sest[0],b*Sest[0]],[d*Sest[1],c+d*Sest[0]+2*f*Sest[1]]])
        #Assume sigma is -(x_i-c)(x_i-C)
        F[:,0]=[i-(i-1)*(i-20)*np.random.normal(0,processnoisewolf) if 1>i>20 else i for i in
             F[:,0]]
        F[:,1]=[i-(i-100)*(i-2000)*np.random.normal(0,processnoisemoose) if 100>i>2000 else i
             for i in F[:,1]]

        Ppred=np.matmul(F,np.matmul(P,np.transpose(F)))+Q

        zk=np.array(obs[k,1])
        H=np.array([[0,1]])
        #H=only observe second species
        hkpred=np.array([Sestpred[1]])
        yk=zk-hkpred
        Sk=np.matmul(H,np.matmul(P,np.transpose(H)))+R
        Kk=np.matmul(P,np.matmul(np.transpose(H),np.linalg.inv(Sk)))
        Sest=Sestpred+np.matmul(Kk,yk)
        P=P-np.matmul(Kk,np.matmul(H,Ppred))

        pred.append(Sest)
    return np.array(pred)

#Time
tms=np.linspace(0,30,30)
init=[x0,y0]

dat=integrate.odeint(LV,init,tms,args=(a,b,c,d,e,f))

#Adding noise to data & ensuring all species are greater than zero in population
#c=0.5, C=5 here, c,C the same for both species
x1datstd=0.5
x2datstd=0.5
ndat=dat.copy()
ndat[:,0]=[i+np.random.normal(0,x1datstd) if 5>i>0.5 else i for i in ndat[:,0]]
ndat[:,1]=[i+np.random.normal(0,x2datstd) if 5>i>0.5 else i for i in ndat[:,1]]
ndat[:,0]=np.maximum(0,ndat[:,0])
ndat[:,1]=np.maximum(0,ndat[:,1])

#covariance
initcov=np.eye(2)
initcov=initcov*0.1
Q=np.array([[0.1,0],[0,0.1]])
R=np.array([[x1datstd*x1datstd]])
syspar=(a,b,c,d,e,f)

#Running EKF
pred=EKF(syspar,tms,init,initcov,R,Q,ndat,x1datstd,x2datstd)

#Plto
plt.figure()
fig,ax1=plt.subplots(figsize=(12,6))
ax1.plot(tms,ndat[:,0],'ro',label="Number of Wolves (Simulated LV)")
ax1.plot(tms,pred[:,0],'r-',label="Number of Wolves (Estimated)")
ax1.set_xlabel("Years")
ax1.set_ylabel("Wolf population")
ax1.tick_params(axis='y')
ax2=ax1.twinx()
ax2.plot(tms,ndat[:,1],'bo',label="Number of Moose (Simulated LV)")
ax2.plot(tms,pred[:,1],'b-',label="Number of Moose (Estimated without observation)")
ax2.set_ylabel("Moose population")
ax2.tick_params(axis='y')
plt.title("Wolf and Moose Population (Simulated Lotka-Volterra Data with EKF)")
fig.legend(loc="upper left",bbox_to_anchor=(0.555,0.88))
plt.show()
```

D

Simulated Data Used for Estimating a Hidden State, Example 1

In Chapter 5 data is simulated using the code in Appendix C, describing a predator-prey relationship between wolves and moose. This data is provided here.

Number of wolves	Number of moose
4.03394839	1.02070638
0.22050573	4.0255511
0.04609823	1.3100197
0.	1.26167582
0.19648357	0.10968117
0.	0.
0.95907669	0.
2.3345745	0.
4.4960925	0.5709021
0.77608162	4.50582849
0.35441753	2.26430123
0.	0.86030374
1.07797034	0.76343685
0.	0.17301601
0.45604967	0.13183278
0.69436303	0.
1.57929202	0.15276637
4.3132668	1.32460344
0.95027605	4.0286377
0.31589197	2.09064807
0.67955523	0.4768965
0.64319417	0.
0.08719057	0.42942849
0.20994507	0.43430752
0.10239324	0.
3.44742043	0.
6.19153986	0.45853177
0.12036848	5.00341178
0.21173942	1.87439746
0.	1.57811827

E

Simulated Data Used for Estimating a Hidden State, Example 2

In Chapter 5 data is simulated using the code in Appendix C, the data describes a competition relationship between species 1 and 2. This data is provided here.

Number of species 1	Number of species 2
10.00000000	5.00000000
10.92025417	5.45292056
11.91083468	5.93902597
12.97446300	6.45930774
14.11347875	7.01451952
15.32974498	7.60512852
16.62454868	8.23126586
17.99850306	8.89267952
19.45145093	9.58868970
20.98237626	10.31815056
22.58932775	11.07942040
24.26935965	11.87034305
26.01849449	12.68824276
27.83171241	13.52993458
29.70297045	14.39175184
31.62525449	15.26959105
33.59066430	16.15897409
35.59053099	17.05512611
37.61556441	17.95306709
39.65602375	18.84771261
41.70190650	19.73398044
43.74314823	20.60689853
45.76982377	21.46170899
47.77234138	22.29396367
49.74162383	23.09960835
51.66926504	23.87505020
53.54766126	24.61720853
55.37011148	25.32354713
57.13088654	25.99208894
58.82526358	26.62141205
60.44953132	27.21063114

62.00096783	27.75936591
63.47779481	28.26769923
64.87911286	28.73612790
66.20482288	29.16550902
67.45553828	29.55700430
68.63249184	29.91202461
69.73744159	30.23217658
70.77257849	30.51921258
71.74043872	30.77498527
72.64382180	31.00140678
73.48571669	31.20041357
74.26923557	31.37393635
74.99755647	31.52387522
75.67387416	31.65207972
76.30135872	31.76033303
76.88312207	31.85034037
77.42219103	31.92372064
77.92148641	31.98200108
78.38380765	32.02661434
78.81182192	32.05889764
79.20805723	32.08009354
79.57489874	32.09135183
79.91458781	32.09373287
80.22922295	32.08821091
80.52076327	32.07567884
80.79103196	32.05695219
81.04172223	32.03277449
81.27440239	32.00382145
81.49052298	31.97070628
81.69142256	31.93398386
81.87833513	31.89415569
82.05239623	31.85167381
82.21464995	31.80694519
82.36605499	31.76033533
82.50749108	31.71217210
82.63976467	31.66274890
82.76361469	31.61232794
82.87971765	31.56114301
82.98869274	31.50940219
83.09110644	31.45729031
83.18747680	31.40497115
83.27827754	31.35258951
83.36394166	31.30027306
83.44486504	31.24813406
83.52140949	31.19627089
83.59390577	31.14476946
83.66265625	31.09370452
83.72793737	31.04314073
83.79000195	30.99313380