

Stability and Bifurcation Analysis of Three Species in Yellowstone
Park Consisting of Prey, Predator and Competitor and the Effects of
Predator Reduction on Living Species in the Ecosystem

by

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Abstract

The interactions among wolves, deer, and beavers in Yellowstone National Park demonstrate intricate dynamics with implications for population growth and decline. By applying bifurcation theory, we analyze how subtle environmental or population changes can significantly impact ecosystem stability. Wolves, as apex predators, influence deer populations, which, in turn, affect the behaviour and habitat of beavers. Understanding these complex interconnections is crucial for effective ecosystem management and conservation. Through mathematical biology and bifurcation analysis, we gain insights into the coexistence and mutual influence of different species in natural environments. This research sheds light on the intricate relationships that shape ecological communities, emphasizing the importance of studying predator-prey and competitor interactions to comprehend and protect these ecosystems.

Dedication

This thesis is dedicated to my beloved grandparents, Abdul-Ali Bakhtiar, Zahra Raouf Haghighi, Hashem Tamjidi, and Masoumeh Raouf Haghighi, whose love and support have guided me towards academic excellence.

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“Rest in peace, Cyrus, for we are awake, and we will always stay awake.”

– Mohammad Reza Pahlavi, *Answer to History*

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List of Notation

r	deer population growth rate
k	deer population carrying capacity
s	beaver population growth rate
h	beaver population carrying capacity
c	wolf population growth rate
a	wolf-deer attack rate
m	wolf mortality rate
t	time
x	deer population
y	beaver population
z	wolf population
E_0	extinction equilibrium
E_1	deer-only equilibrium
E_2	beaver-only equilibrium
E_3	predator-free equilibrium
E_4	deer-wolf equilibrium
E_5	coexistence equilibrium
J	Jacobian matrix

Chapter 1

Introduction

1.1 Wolves and Their Impact on the Ecosystem

The complex relationship between a predator (wolves), its prey (deer), and the prey's competitor (beavers) in Yellowstone park excited me to have a better understanding of the dynamics of ecological communities. I found it very interesting to read about the dynamic changes of the wolf population, its direct effects on the survival of the deer population, and its indirect effects and possible extinction of the beaver population. Since the founding of Yellowstone Park a variety of plants, animals, and other living things have formed an ecological community, and they have coexisted, directly or indirectly affecting each other [7]. Wolves are the predators in Yellowstone Park, preying on deer, which affects the deer population. The decreasing deer population can lead to a decrease in grazing pressure on vegetation, allowing for more vegetation to grow. This is in favour of beavers, because there will be more food sources for the beavers as the deer population decreases. Mathematical models can be used to study and understand these interactions and help to inform conservation efforts and management strategies in the park.

The relationship between wolf populations and beaver populations is a crucial aspect of ecosystem dynamics, particularly in regions like Yellowstone Park. Although wolves do not prey on beavers directly, their presence significantly influences deer populations, which are the primary competitors of beavers for resources. As wolf populations decline due to human activities such as hunting and trapping, deer populations tend to increase. This growth in deer numbers poses a threat to beaver populations, as both species compete for limited resources. Therefore, declining wolf populations have both a direct impact on deer populations and an indirect effect on beaver populations, highlighting the extensive influence that predator presence can have on biodiversity and the overall health of an ecosystem. This balanced predator-prey relationship is essential for maintaining ecological stability, preventing overgrazing, and ensuring the coexistence of these three species within their habitat.

The conditions for the coexistence of species in the Yellowstone Park ecosystem depends on various factors, including competition for resources, predation, and environmental conditions. Predation plays a key role in maintaining the balance of species in an ecosystem by controlling the population of prey species. Species in an ecosystem must be able to share resources such as food to avoid direct competition with each other. In this battle, the species that is stronger and has access to food will survive. The coexistence of species in Yellowstone Parks is a complex and dynamic process that is influenced by various factors. This park helps to support the coexistence of different species by maintaining a healthy and diverse ecosystem.

This research addresses the following basic questions:

- What is the role of the wolves in stabilizing the ecosystem?
- Does the decline or extinction of wolves lead to the decline or extinction of the two other species?

- What are the coexistence conditions of these species in an ecosystem?

The research focuses on exploring the concept of a transcritical bifurcation, which occurs when there is a shift in stability between fixed points within a biological system. Specifically investigating the implications of transcritical bifurcations in the context of the relationship between the reduction of the wolf population and its impact on the populations of deer and beavers, this study aims to shed light on the dynamics of ecological systems. By delving into the stability and resilience of these interconnected populations, the research findings offer valuable insights that can help predict and elucidate observed patterns in nature, contributing to a deeper understanding of the intricate balance within ecosystems and the potential consequences of perturbations within them. By analyzing a mathematical model of the dynamics of the three species, we can better understand the effect of the removal of the wolf population from Yellowstone Park.

1.2 Direct and indirect effects on population

Our three study species, wolves, deer, and beaver, coexist in the same area, forming an ecological community. Different types of interactions between species in a community can effect populations. Competition and predator-prey relationships are among the factors having the most important effects on population sizes.

Species in competition share the same resources. For example, deer and beaver compete for the same food sources. Both populations will face declines in the absence of food. As deer population increases, beavers have difficulties finding food. The lack of food increases deaths of beavers. Competition is based on the existence of resources, and this feature is the secret of survival for all creatures in nature. All species need food to survive and the lack or absence of food can cause extinction.

Many creatures died of starvation due to the presence of stronger competitors.

On the other hand, in a predator-prey relationship, one population is a food source for another and changes in numbers of one population influence the other. For example, wolves are predators who need to hunt and feed on deer to survive. Understanding the relationship between prey and predators is one of the central topics in ecology [6].

The effects of prey and predators on populations are different from those of competition for food. The relationship between prey and predators have been the concern of biologists for a long time [2]. Over time, many living species became extinct. For example, indiscriminate hunting of the Mazandaran tiger in Iran drove this species to extinction about one hundred and fifty years ago [9]. The prey-predator model has provided a better understanding of changes in the dynamics of populations. Wolf mortality, from hunting for example, can lead to changes in the number of deer and beavers and change the balance of the community. Although predators have a direct impact on the population of prey species, in our three-species community, the indirect impact of declining or increasing deer populations affects beavers' access to food resources. Thus, the indirect effects of predators are a common feature of ecological systems. Although predators are seen as potential control factor for populations, it is reasonable to expect that all three populations react in ways that affect each other.

Chapter 2

Mathematical model

2.1 Assumptions

The purpose of this report is to provide a detailed analysis of a three-dimensional model capturing the competitive and predator-prey dynamics of an ecological community like the wolf-deer-beaver community of Yellowstone Park. We consider a mathematical model of predator, prey, and competitor dynamics in which the following assumptions are made.

- In the absence of predation by wolves, the deer and beaver populations increase logistically with growth rates r and s , respectively, and carrying capacities k and h , respectively.
- Competition between beaver and deer is modelled through the carrying capacities.
- Wolf predation on deer reduces the deer population at a rate a and in proportion to both wolf and deer populations.
- The wolf population increases at a rate c and in proportion to both the wolf

and deer populations. We neglect other resources the wolves may exploit when deer populations are low.

- The wolf population declines due to mortality at a rate m .
- External factors such as infectious diseases, drought, etc. are not explicitly included in this model.

The model expresses the relationships between wolf, deer, and beaver populations. By studying the model, we can have a better understanding of the behaviours of these species.

Let $x(t)$, $y(t)$, and $z(t)$ denote the populations, at time t , of deer, beaver, and wolves, respectively. Based on the assumptions and rates introduced above, we propose the following system of three differential equations to model of the dynamics of the wolf-deer-beaver ecosystem:

$$\frac{dx}{dt} = rx \left(1 - \frac{x+y}{k} \right) - azx \quad (2.1a)$$

$$\frac{dy}{dt} = sy \left(1 - \frac{x+y}{h} \right) \quad (2.1b)$$

$$\frac{dz}{dt} = czx - mz \quad (2.1c)$$

Equation (2.1a) deals with the changes in deer population. The first term models the logistic growth of the deer at rate r and with a carrying capacity k . Note the limit of growth depends on the sum of the deer and beaver populations, $x + y$. The first term of Equation (2.1b) has a similar form. There the beaver population increases at rate s , with a carrying capacity h . In both equations, the decrease in growth with both species models the competition over a common resource. If $h < k$, the deer have a competitive advantage, represented by their higher carrying capacity.

The second term of Equation (2.1a), $-azx$, models the decrease in the deer popu-

lation due to predation by wolves at rate a . Since the beavers are not subject to predation by wolves, there is no corresponding predation term in Equation (2.1b). Equation (2.1c) models the dynamics of the wolf population and explains the changes in population over time. The predator population increases in proportion to the predation term in (2.1a) and is reduced due to natural death of predators at rate mz . Declining deer populations and lack of food can help to reduce wolf populations.

My report focuses on the equilibrium dynamics of Model (2.1) with non-negative initial conditions:

$$x(0) \geq 0, \quad y(0) \geq 0, \quad z(0) \geq 0. \quad (2.2)$$

By design, all model parameters are positive.

Chapter 3

Model analysis

Population increases of prey can negatively impact the ecosystem of Yellowstone Park. The winner of the competition is the species that takes the food from its competitor. My analysis of Model (2.1) first establishes the equilibrium points and conditions for which they are nonnegative and then derives stability conditions for each equilibrium. My conclusions are based on the dependence of the equilibria and their stability on model parameters, specifically wolf mortality, m , and deer carrying capacity, k .

Factors such as birth rates, death rates, immigration rates, and refugee arrivals contribute to the dynamic balance of the population in Yellowstone National Park over time. These elements promote a relatively stable population within healthy ecosystems, resulting in populations that are generally consistent. [3].

Removal of one species can cause changes in the system and lead to the collapse of species in the ecosystems. The absence of wolves affects the increase in deer population. The increase in the population of deer has an effect on the reduction of vegetation grazing in Yellowstone National Park. With the reduction of grazing in the park, beavers face food shortages. The beaver population is decreasing due

to lack of food and this leads to beavers facing the risk of extinction. To preserve a healthy ecosystem, the importance of preserving all species is critical, as the decline of one species can significantly impact the population dynamics of other species within an ecosystem.

3.1 The predator-free and wolf-deer sub-systems

My model is built by combining simpler models. These can be seen as invariant sets of the model. We first consider a competition model where the dynamics of the deer, beaver, and wolf populations are analyzed in isolation. This analysis involves studying the behaviour of each species on their respective axes (deer-only axis, beaver-only axis, and wolf-only axis) when the other populations are zero. In the absence of wolves and beavers, $z(t) = y(t) = 0$, the deer population is governed by a simple logistic growth with carrying capacity k and per capita growth rate r . The size of the deer population is limited by such factors as adequate food, water, etc. If these needs are not met, the deer population will shrink until the source returns.

Similarly, in the absence of wolf and deer populations, the beaver population experiences logistic growth with carrying capacity h and growth rate s . The beaver can use food resources without a competitor and increase their population by a carrying capacity of h .

In the absence of deer and beaver populations, the dynamics of Model (2.1) simplify to $\frac{dz}{dt} = -mz$. The extinction of deer and beaver populations will inevitably result in the extinction of wolves.

In the scenario where beavers are absent, deer have exclusive access to abundant food resources. This ecological dynamic is manifested in the model through the stability of the deer-wolf plane at $y = 0$. The deer-wolf sub-model exemplifies a clas-

sical predator-prey system, showcasing equilibrium points including the extinction equilibrium, E_0 , the deer-only equilibrium, E_1 , and, when $m < ck$, the deer-wolf equilibrium, E_4 .

As the predator population diminishes, the prey population is afforded the opportunity to thrive. The expansion of the prey population supplies the predator with ample nourishment, fostering an increase in the predator population. However, this surge in the predator population poses a risk to the prey population, which becomes vulnerable to predation. Consequently, the rise in predator population can contribute to a reduction in the prey population.

A decline in food sources for the predator can present challenges in locating sustenance, resulting in a decrease in the predator population.

Deer-beaver plane: In the absence of wolves, $z(t) = 0$, dynamics of deer and beaver in Model (2.1) reduces to a classic competition model.

$$\frac{dx}{dt} = rx\left(1 - \frac{x+y}{k}\right) \quad (3.1)$$

$$\frac{dy}{dt} = sy\left(1 - \frac{x+y}{h}\right) \quad (3.2)$$

The populations of deer and beaver are influenced by their interactions, as seen in the equations. Deer and beavers share the same food resources, and the stronger competitor tries to out-compete the weaker competitor.

The competition model can be used to understand how deer populations compete for resources in the absence of wolves [1]. Differential equations represent competition for resources, where the growth of one population may inhibit the growth of another due to resource limitations.

Wolf-Deer Plane: In the absence of beavers, wolves primarily rely on deer as their food source, while deer benefit from the availability of abundant and exclusive food resources. This dynamic is illustrated in my model by the invariance of the wolf-deer plane at $y = 0$, indicating that the absence of beavers allows for the clear interaction between wolves and deer. The wolf-deer submodel exemplifies a classic predator-prey relationship, where the populations of wolves and deer are interdependent. As will be demonstrated in the subsequent section, this plane encompasses critical equilibrium points: the extinction equilibrium E_0 , where both populations are extinct; the deer-only equilibrium E_1 , where the deer population exists at its carrying capacity while the wolf population is absent; and, when $m < ck$, the wolf-deer equilibrium E_4 , representing a stable coexistence of both species.

When the beaver population is absent ($y = 0$), the dynamics of the deer and wolf populations can be analyzed through traditional predator-prey dynamics. The interaction between these populations is characterized as a prey-predator relationship, where the growth and survival of wolves depend on their ability to hunt and consume deer. In this scenario, Model (2.1) simplifies to a form analogous to the classic Lotka-Volterra model, which captures the essential dynamics of predator-prey interactions:

$$\frac{dx}{dt} = rx \left(1 - \frac{x}{k}\right) - azx, \quad (3.3)$$

$$\frac{dz}{dt} = czx - mz. \quad (3.4)$$

The equilibrium points can be summarized as follows:

1. $(0, 0)$: Both populations are extinct, indicating a collapse of the ecosystem where neither species can survive.

2. $(K, 0)$: The deer population is at its carrying capacity K , while the wolf population is absent. This scenario illustrates the potential for deer to thrive in the absence of predation, but it can lead to overpopulation and resource depletion.
3. $(\frac{m}{c}, \frac{r}{a}(1 - \frac{m}{K}))$: This point represents the stable coexistence of deer and wolves. Here, the deer population reaches a level where it can sustain both itself and a population of wolves. The equations reveal that the deer population grows at a rate determined by its own reproductive capacity and the predation pressure exerted by wolves.

The dynamics of the deer population and the maintenance of ecosystem stability between predator and prey underscore the interconnectedness of species and highlight the importance of preserving a sustainable equilibrium. The presence of wolves helps regulate deer populations, preventing overgrazing and enabling the ecosystem to maintain biodiversity. Conversely, if wolf populations decline due to a lack of food resources like deer, this can lead to an unchecked increase in deer populations, which may result in habitat degradation and further ecological imbalances.

From a mathematical perspective, the survival of wolf populations is contingent upon their ability to secure sustenance from deer. Therefore, a decline in prey availability could potentially jeopardize the stability of the predator-prey relationship, leading to the risk of extinction for both species. Understanding these dynamics is crucial for effective wildlife management and conservation strategies aimed at maintaining ecological balance.

Wolf-Beaver Plane: In the absence of deer ($x = 0$), Model (2.1) simplifies to the following system of equations:

$$\frac{dy}{dt} = sy \left(1 - \frac{y}{h}\right), \quad (3.5)$$

$$\frac{dz}{dt} = -mz. \quad (3.6)$$

This three-species model focuses on the dynamics of the wolf-beaver system when deer are absent, allowing us to explore the implications of these populations for ecosystem stability. In this context, it is assumed that wolves primarily rely on deer as their prey and do not directly interact with beavers. Consequently, the survival of the wolf population hinges entirely on the availability of deer; without deer, wolves face potential extinction due to a lack of food resources.

Conversely, beavers can thrive independently as long as their habitat and food sources are sufficient, primarily feeding on vegetation. This independence can enhance biodiversity within the ecosystem. Although there are no direct interactions between wolves and beavers, the dynamics of their populations are interconnected through their respective ecological roles. The absence of deer may lead to increased beaver populations, which could alter the habitat structure and availability of resources, potentially impacting other species within the ecosystem. This relationship underscores the delicate balance within the ecosystem and highlights the potential consequences of deer absence, which could adversely affect both wolf and beaver populations indirectly through changes in habitat dynamics.

3.2 Equilibria and Stability

In this section, I outline the existence and stability of the equilibrium points of Model (2.1). Equilibrium points are solutions that do not change over time. That is, the

right hand sides of Equations (2.1) are zero at equilibrium points. Studying equilibrium solutions is important in mathematical biology in order to predict long-term behaviours of a system. The equilibrium solutions satisfy the following conditions:

1. from (2.1a), either $x = 0$ or $z = \frac{r}{a}(1 - \frac{x+y}{k})$;
2. from (2.1b), either $y = 0$ or $x + y = h$;
3. from (2.1c), either $z = 0$ or $x = \frac{m}{c}$.

These three pairs of conditions imply eight possibilities based on the eight choices of zeros for the three species.

A straightforward analysis reveals that only five choices lead to nonnegative equilibria. However, one choice leads to a continuum of equilibria. Thus, Model (2.1) has up to four isolated equilibrium points: the trivial equilibrium, $E_0 = (0, 0, 0)$, the deer-only equilibrium, $E_1 = (k, 0, 0)$, the beaver-only equilibrium, $E_2 = (0, h, 0)$, the beaver-free equilibrium, $E_4 = (\frac{m}{c}, 0, \frac{r}{a}(1 - \frac{m}{ck}))$, and the coexistence equilibrium, $E_5 = (\frac{m}{c}, \frac{ch-m}{c}, \frac{r}{a}(1 - \frac{h}{k}))$. In the special case $k = h$, the model has a line of predator-free equilibria, $E_3 = (k - y_3, y_3, 0)$, $0 < y_3 \leq k = h$.

Equilibria can be classified as stable or unstable. In mathematics, a stable equilibrium point is a point in a dynamical system where the system returns to it if it is perturbed. This means that if the system is slightly disturbed from its equilibrium, it will eventually return to the equilibrium point without further external influence. In other words, the system returns to rest after being disturbed.

In Yellowstone National Park, the relationship between wolves, deer, and beavers can be complex and interconnected. Wolves are predators of deer, which are prey animals. Beavers, on the other hand, can have indirect effects on vegetation. A stable equilibrium in this system would involve a balance where all three species can

coexist without any one species drastically overpopulating or declining. Here is a simplified explanation of how this equilibrium might work.

To maintain a stable equilibrium in this system, factors such as food availability, habitat quality, predation pressure, and competition for resources all play a role. Natural fluctuations in populations are normal, but if any one species experiences a drastic increase or decrease in numbers, it can disrupt the balance and potentially lead to cascading effects throughout the ecosystem.

A stable equilibrium is represented as a point on a graph where the rate of change of an ecosystem is zero and any deviations from this point result in return to the equilibrium state. In the mathematical model for predator-prey dynamics, the equilibrium point $(0,0,0)$ signifies that all species populations are at zero. This indicates a state where no species can sustain a viable population, resulting in an unsustainable ecosystem. At this equilibrium, the absence of surviving species highlights the importance of balanced interactions and sufficient populations for the ecosystem's functionality. In the context of dynamical systems, a stable equilibrium point is a point where a system will return to after being perturbed.

Mathematically, a stable equilibrium point is defined as follows: an equilibrium point x^* of a dynamical system is said to be stable if, for every $\epsilon > 0$, there exists a $\sigma > 0$ such that if $\|x(0) - x^*\| < \sigma$, then $\|x(t) - x^*\| < \epsilon$ for all $t \geq 0$ [8].

This definition is useful for analyzing the behaviour of dynamical systems near equilibrium points, as it aids in determining long-term system behaviour and predicting how changes in one population may affect others and how the ecosystem as a whole may respond to disturbances or management interventions, thereby providing insights into the interactions and dynamics of species in Yellowstone National Park.

The phenomenon of unstable equilibria, characterized by recurring invasions, underscores the dynamic nature of the ecosystem, where the introduction of new species

can significantly alter existing species interactions. In contrast, stable equilibria illustrate the consequences of intense interspecies competition and resource constraints, which ultimately shape the long-term viability of populations within the ecosystem. These dynamics emphasize the intricate interplay between species interactions and environmental factors in determining the stability and resilience of the ecosystem.

In the context of the Yellowstone wolf-deer-beaver ecosystem, an unstable equilibrium point could occur if there is an imbalance in the population dynamics of these species. For example, if the wolf population decreases significantly due to disease or hunting, the deer population may increase rapidly without their main predator to keep their numbers in check. This could lead to overgrazing of vegetation, which in turn affects the beaver population that relies on certain plant species for food and habitat. In this scenario, the ecosystem may reach an unstable equilibrium point where the populations of deer and beavers are unsustainable due to lack of predation pressure from wolves. This could lead to a collapse of the ecosystem as the resources become depleted and the populations of deer and beavers decline drastically. In such a case, ecosystem management strategies would need to be implemented to restore balance and prevent the system from collapsing. This could involve reintroducing wolves to the ecosystem, implementing hunting regulations, or restoring habitat for beavers to thrive. By addressing the underlying imbalances, the ecosystem can potentially stabilize and reach a more sustainable equilibrium point.

The stability of each equilibrium point is analyzed by calculating its Jacobian matrix and finding the eigenvalues at each equilibrium point. The equilibrium is considered locally asymptotically stable if all eigenvalues of the Jacobian have negative real parts. Therefore, for stability of the equilibrium, the real parts of all eigenvalues of the Jacobian matrix must be negative [11]. Using the eigenvalues, we can determine the basic behaviour of solutions near the equilibrium point.

In the context of dynamical systems, particularly in nonlinear dynamics and chaos theory, a foundational result concerns the characterization of solutions to linear systems represented by the equation:

$$\frac{dx}{dt} = Ax,$$

where x is a vector of state variables and A is a square matrix that defines the system's dynamics. The equilibrium point x^* of the system is defined as a point satisfying the condition

$$Ax^* = 0.$$

For the analysis of the stability of this equilibrium point, it is assumed that all eigenvalues λ of the matrix A possess negative real parts, expressed mathematically as

$$\text{Re}(\lambda) < 0 \quad \forall \lambda.$$

Under the specified conditions, the general solution $x(t)$ of the system can be expressed as a linear combination of the eigenvectors v_i corresponding to each eigenvalue λ_i :

$$x(t) = c_1 e^{\lambda_1 t} v_1 + c_2 e^{\lambda_2 t} v_2 + \dots + c_n e^{\lambda_n t} v_n,$$

where c_i are constants determined by the initial conditions of the system.

In this context, let A denote the system matrix, which is a square matrix whose eigenvalues λ_i and corresponding eigenvectors v_i characterize the behaviour of the

linear system described by the differential equation

$$\frac{dx}{dt} = Ax.$$

The Jacobian matrix J refers to the matrix of first-order partial derivatives of the system's equations, evaluated at an equilibrium point. For a linear system, the Jacobian is equivalent to the system matrix A . The eigenvalues of the Jacobian matrix J are used to analyze the stability of the equilibrium point.

The significance of the assumption regarding the eigenvalues is critical: as t approaches infinity, the exponential terms $e^{\lambda_i t}$ decay to zero due to their negative real parts. Consequently, the solution $x(t)$ converges to the equilibrium point x^* :

$$\lim_{t \rightarrow \infty} x(t) = x^*.$$

An equilibrium point is considered locally asymptotically stable if all eigenvalues of the Jacobian matrix associated with the system have negative real parts. Conversely, the equilibrium point is deemed unstable if any eigenvalue has a positive real part. Therefore, the stability of an equilibrium point in a linear system is assured when all eigenvalues exhibit negative real parts.

This result not only demonstrates the stability of the equilibrium point but also provides valuable insights into the dynamic behaviour of the system in the vicinity of that point.

It is important to note that this conclusion does not directly arise from the definitions of eigenvalues and eigenvectors; rather, it stems from the properties of linear differential equations and the associated stability criteria, which reveal how the dynamics of the system are influenced by the eigenvalues of the Jacobian matrix and

their implications for the behaviour of solutions over time.

The Jacobian matrix of System (2.1) about an equilibrium (x, y, z) is given by

$$J_{x,y,z} = \begin{bmatrix} -az - \frac{r(2x+y)}{k} + r & \frac{-rx}{k} & -ax \\ \frac{-sy}{h} & \frac{s(h-x-2y)}{h} & 0 \\ cz & 0 & cx - m \end{bmatrix}$$

Population biologists frequently refer to J as the community matrix.

The first three predator-free equilibria, E_0 , E_1 , and E_2 , are nonnegative for all non-negative values of parameters. These represent, respectively, the absence of all three species, the deer-only equilibrium, and the beaver-only equilibrium.

The trivial equilibrium, $E_0 = (0, 0, 0)$, or extinction equilibrium represents the absence of all three species. Evaluating the Jacobian matrix at E_0 , we obtain the matrix

$$J_0 = \begin{bmatrix} r & 0 & 0 \\ 0 & s & 0 \\ 0 & 0 & m \end{bmatrix}$$

where r , s , and b are parameters representing the intrinsic growth rates and interaction coefficients of the species involved.

All parameters r , s , and b are positive, we can find the eigenvalues of the Jacobian matrix from its diagonal form. The eigenvalues are:

$$\lambda_1 = r, \quad \lambda_2 = s, \quad \lambda_3 = m.$$

Since λ_1 and λ_2 are positive, and λ_3 is negative, the equilibrium point E_0 is classified

as a saddle point.

A saddle point is characterized by having both stable and unstable manifolds. Specifically, the unstable manifold is two-dimensional and corresponds to the directions associated with the positive eigenvalues λ_1 and λ_2 .

The deer-only equilibrium, $E_1 = (k, 0, 0)$

is nonnegative for all feasible parameter values. The Jacobian matrix at E_1 is easily shown to be

$$J_{(k,0,0)} = \begin{bmatrix} -r & -r & -ak \\ 0 & s(1 - \frac{k}{h}) & 0 \\ 0 & 0 & ck - m \end{bmatrix}$$

The three eigenvalues are $-r$, $s(1 - \frac{k}{h})$, and $ck - m$. Hence, E_1 is stable if $\frac{m}{c} > k > h$ and unstable if $k < \min\{h, \frac{m}{c}\}$. A further calculation shows that the eigenspaces associated with the three eigenvalues are the deer-only, beaver-only, and wolf-only axes respectively. Hence the bifurcations occurring as $k - h$ or $ck - m$ change sign involve changes in the stability of E_1 to invasion by beaver or wolves respectively.

The beaver-only equilibrium, $E_2 = (0, h, 0)$, is also nonnegative for all feasible parameter values. The Jacobian matrix at E_2 is

$$J_{(0,h,0)} = \begin{bmatrix} r(1 - \frac{h}{k}) & 0 & 0 \\ -s & -s & 0 \\ 0 & 0 & -m \end{bmatrix}$$

The eigenvalues of $J_{(0,h,0)}$ are $r(1 - \frac{h}{k})$, $-s$, and $-m$. Hence E_2 is stable if $h > k$ and

unstable if $h < k$. A further calculation shows that the eigenspaces associated with the second two eigenvalues are the beaver-only and wolf-only axes respectively, and the eigenspace for the first eigenvalue is a line in the deer-beaver plane. Hence the bifurcation occurring as $k - h$ changes sign involves changes in the stability of E_2 to competition by deer.

The deer-beaver equilibria, $E_3 = (k - y_3, y_3, 0)$, where $y_3 \in (0, k)$, exist only in the special case where $h = k$. In this scenario, the carrying capacity of the beavers is equal to that of the deer, leading to a balanced competition between the two species. As a result, there is a set of equilibrium solutions, denoted by E_3 , along the line $x + y = h = k$.

The Jacobian matrix for any equilibrium in E_3 is given by

$$J_3 = \begin{bmatrix} -r \left(1 - \frac{y_3}{k}\right) & -r \left(1 - \frac{y_3}{k}\right) & -a(k - y_3) \\ -\frac{sy_3}{k} & -\frac{sy_3}{k} & 0 \\ 0 & 0 & c(k - y_3) - m \end{bmatrix}.$$

The eigenvalues of J_3 are $c(k - y_3) - m$, 0, and $-\frac{r(k - y_3) + sy_3}{k}$.

The eigenvalue $\lambda_1 = c(k - y_3) - m$ can have positive, negative, or zero values depending on the parameters and the specific value of y_3 . If $c(k - y_3) - m < 0$, this indicates stability in the direction associated with λ_1 , suggesting that perturbations away from the equilibrium will decay back towards the equilibrium along that axis.

The second eigenvalue $\lambda_2 = 0$ indicates a neutral direction, suggesting that perturbations along this direction do not lead to decay or growth, and the system's behaviour in this direction requires further analysis to determine stability.

The third eigenvalue $\lambda_3 = -\frac{r(k - y_3) + sy_3}{k}$ is always negative, indicating stability in

that direction. This suggests that perturbations away from the equilibrium in the direction associated with λ_3 will also decay back towards the equilibrium, ensuring that the population dynamics return to the equilibrium point along that axis.

Overall, the dynamics around the deer-beaver equilibrium E_3 depend critically on the nature of the eigenvalues, particularly the stability indicated by λ_1 and λ_3 , while λ_2 requires further exploration to fully understand the behaviour of the system.

The wolf-deer equilibrium, $E_4 = \left(\frac{m}{c}, 0, \frac{r}{a}\left(1 - \frac{m}{ck}\right)\right)$ is nonnegative if $m < ck$.

The Jacobian at E_4 is

$$J_4 = \begin{bmatrix} \frac{-rm}{ck} & -\frac{rm}{ck} & \frac{-am}{c} \\ 0 & s\left(1 - \frac{m}{ch}\right) & 0 \\ cr\left(\frac{1-\frac{m}{ck}}{a}\right) & 0 & 0 \end{bmatrix}$$

The characteristic polynomial of J_4 can be factored as $(\lambda - s(1 - \frac{m}{ch}))(\lambda^2 - \lambda\tau + \Delta)$, with $\tau = -\frac{mr}{ck} < 0$, and $\Delta = mr(1 - \frac{m}{ck}) > 0$. It follows that the zeros of the quadratic factor have negative real parts. The other eigenvalue, $s(1 - \frac{m}{ch})$, is negative for $m < ch$. Hence, E_4 is stable if $m < ch$ and unstable if $m > ch$.

The coexistence equilibrium, $E_5 = \left(\frac{m}{c}, \frac{ch-m}{c}, \frac{r}{a}\left(1 - \frac{h}{k}\right)\right)$ is positive if and only if $m < ch$ and $h < k$. The Jacobian evaluated at E_5 is

$$J_{\left(\frac{m}{c}, \frac{ch-m}{c}, \frac{r}{a}\left(1 - \frac{h}{k}\right)\right)} = \begin{bmatrix} \frac{-mr}{ck} & \frac{-mr}{ck} & \frac{-am}{c} \\ \frac{s(-ch+m)}{ch} & \frac{s(-ch+m)}{ch} & 0 \\ \frac{-cr(-k+h)}{ak} & 0 & 0 \end{bmatrix}$$

At first glance, this matrix may seem complicated, but as you can see $\frac{mr}{ck}$ is repeated

Symbol	x	y	z	Nonnegativity Conditions	Stable region
E_0	0	0	0	none	always unstable
E_1	k	0	0	none	$\frac{m}{c} > k > h$
E_2	0	h	0	none	$h > k$
E_3	$k - y_3$	y_3	0	$0 < y_3 < k = h$	$y_3 > k - \frac{m}{c}$
E_4	$\frac{m}{c}$	0	$\frac{r}{a}(1 - \frac{m}{ck})$	$m < ck$	$m > ch$
E_5	$\frac{m}{c}$	$\frac{ch-m}{c}$	$\frac{r}{a}(1 - \frac{h}{k})$	$\frac{m}{c} < h < k$	always stable

Table 3.1: Equilibria and stability conditions. Note E_3 represents a line of equilibria.

twice in the first row and $\frac{s(-ch+m)}{ch}$ is repeated twice in the second row.

This analysis demonstrates the effectiveness of the Routh-Hurwitz criterion in determining the stability of equilibria in ecological models [10].

To simplify the computations, let

$$\begin{aligned}
b &= \frac{mr}{ck} \\
e &= \frac{am}{c} \\
f &= \frac{s(ch-m)}{ch} \\
g &= \frac{cr(k-h)}{ak}
\end{aligned}$$

so that

$$J_5 = \begin{bmatrix} -b & -b & -e \\ -f & -f & 0 \\ g & 0 & 0 \end{bmatrix}$$

The characteristic polynomial of J_5 is $\lambda^3 + \lambda^2(b+f) + \lambda eg + feg$. All coefficients are positive, hence, by the Routh-Hurwitz stability criterion, the equilibrium is stable if $(b+f)eg > feg$, which is easily seen to hold true under the conditions for the nonnegativity of the equilibrium. Therefore, E_5 is a stable equilibrium.

Chapter 4

Bifurcation diagram

The transcritical bifurcation diagram serves as a valuable tool for elucidating changes in the stability of equilibrium points and their implications for population dynamics within Yellowstone National Park. In mathematical terms, a bifurcation occurs when a change in a parameter induces a qualitative change in the system's behaviour. The beauty of bifurcation analysis lies in its ability to illustrate how, through parameter adjustments, equilibrium points may lose stability or even vanish altogether. Essentially, bifurcation describes a process in which a system undergoes a sudden qualitative change in behaviour as a result of slight modifications in a parameter, thereby highlighting the intricate relationships between ecological factors and population dynamics [4].

A bifurcation in a nonlinear differential equation occurs when a small parameter change results in a qualitative alteration of the long-term solution, including the creation or destruction of fixed points and shifts in their stability. This highlights the conditions that lead to sudden transformations in dynamic systems [5].

Bifurcations are important in understanding ecological stability and resilience, as well as predicting the effects of environmental disturbances or management interventions.

Stability is very important in an ecological system. One of the important mathematical tools that help us to have a better understanding of the story of creatures of Yellowstone's Park is bifurcation theory.

In biology, a bifurcation diagram serves as a visual representation that illustrates the behaviour of a biological system as a parameter is altered, commonly used to analyze the dynamics of systems like population growth or ecological interactions. By providing insight into how a system's behaviour changes with variations in external conditions or internal parameters, bifurcation diagrams aid biologists in understanding the complex relationships and interactions within biological systems, helping to predict and interpret the responses of these systems to different stimuli or changes.

4.1 Beaver Population Response to Wolf Mortality: Bifurcation Analysis in Mathematical Biology

The conditions for nonnegativity and stability of the equilibria involve four parameters: m , k , h , and c (see Table 3.1). However, each condition can be expressed in terms of two dimensionless ratios: $\frac{m}{ch}$ and $\frac{k}{h}$. Hence, it is sufficient and convenient to summarize the bifurcations of equilibria in terms of the two parameters m and k .

We first study the bifurcations occurring as the mortality rate of wolves, m , increases. There are two cases to consider. If $h > k$, E_2 is stable for all values of m and all other equilibria are either unstable or have negative components. In this case, the beavers always out-compete the deer for the primary resource, and both deer and wolf populations decline to zero over time (see Figure 4.1b). If $k > h$, the equilibria undergo two bifurcations as m increases: E_5 is stable for $0 < m < ch$, E_4 is stable

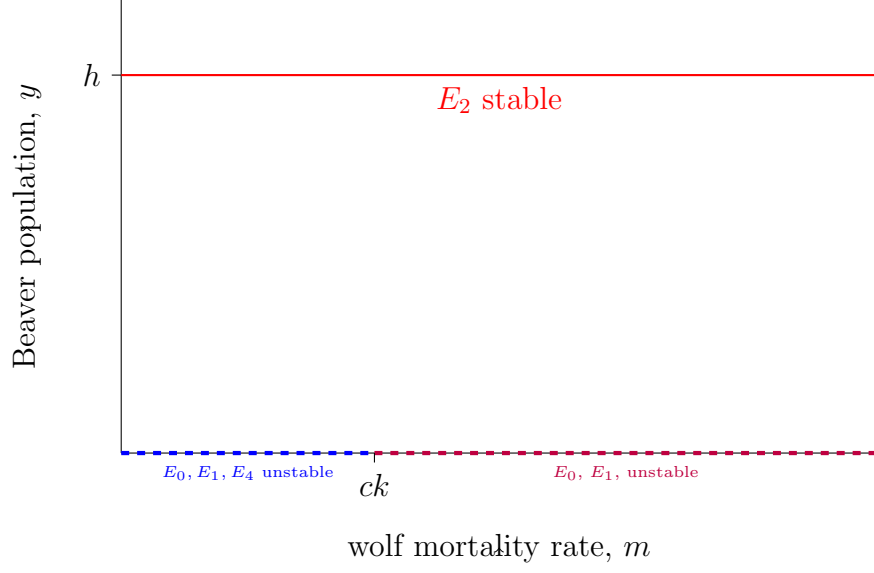
for $ch < m < ck$, and E_1 is stable for $m > ck$ (see Figure 4.1a). In each case, only one of the equilibria is both stable and nonnegative at any point in parameter space.

In the second case, as m increases from 0 to ch , the beaver population at the stable equilibrium, E_5 , decreases from the beaver carrying capacity, h , to zero (see Figure 4.1a). As m increases through ch , E_5 loses stability and E_4 becomes stable through a transcritical bifurcation. Only prey and predator remain in the ecosystem. The wolf-deer equilibrium, E_4 lies in the invariant wolf-deer plane representing the predator prey relationship between wolves and deer. As m increases from ch to ck , the equilibrium beaver population remains at zero and the deer population increases from h to the deer carrying capacity k (see Figure 4.2a). As m increases through ck , E_4 exchanges stability with E_1 in a second transcritical bifurcation. At E_1 , only the deer population remains: the wolf and beaver populations are zero and the deer population remains at the carrying capacity k . By increasing the mortality rate first the beaver and then the wolf populations collapsed and the deer population stabilized.

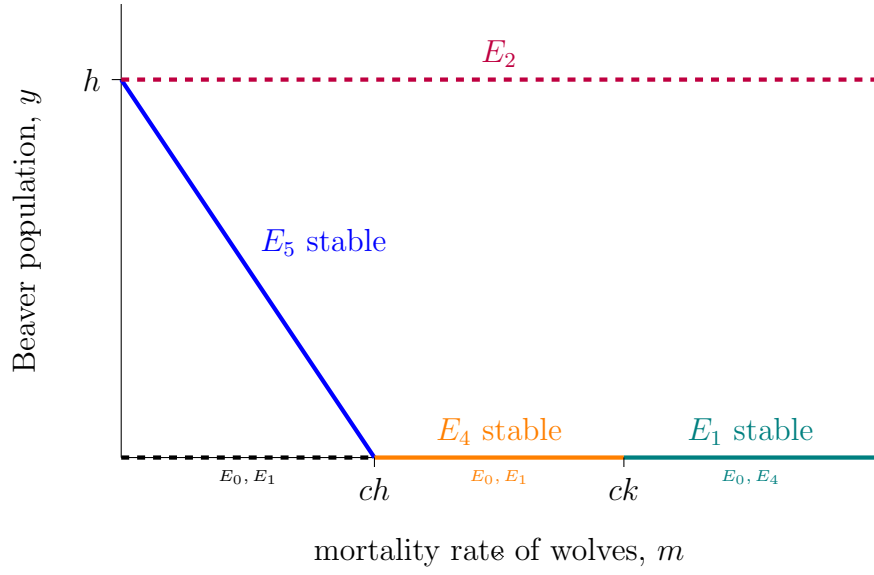
4.2 Bifurcation diagram of carrying capacity of the deer vs beaver population

The dependence of the equilibrium populations of deer, beaver, and wolves on the deer carrying capacity can be seen in several aspects. When the carrying capacity of the deer increases, it gives the deer a competitive advantage over the beavers, but it also leads to an increase in the wolf population. This results in several possible shifts in population dynamics and interactions.

When the deer carrying capacity is less than the beaver carrying capacity, the beaver-only equilibrium, E_2 is stable: the beavers out-compete the deer and the wolf population can not persist in absence of deer. In contrast, when the deer carrying capacity

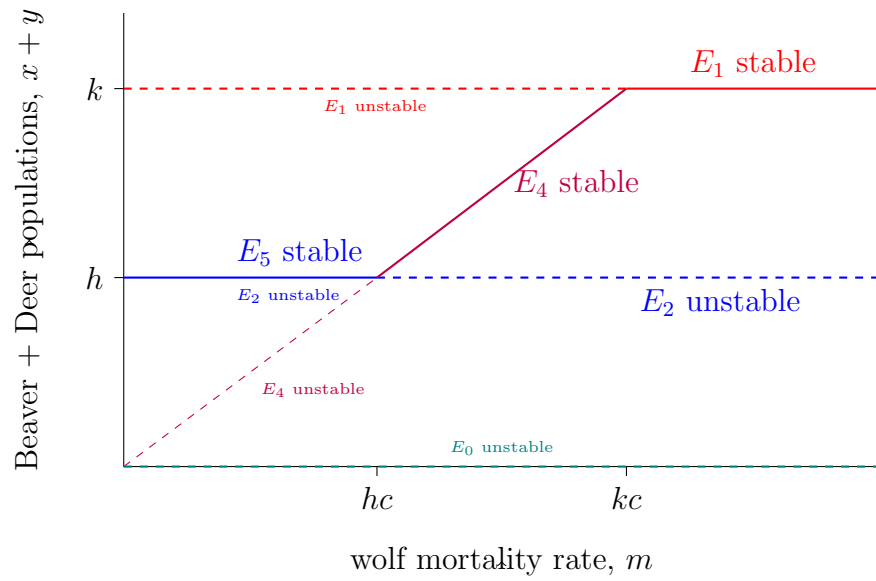


(a) Case I, $k < h$

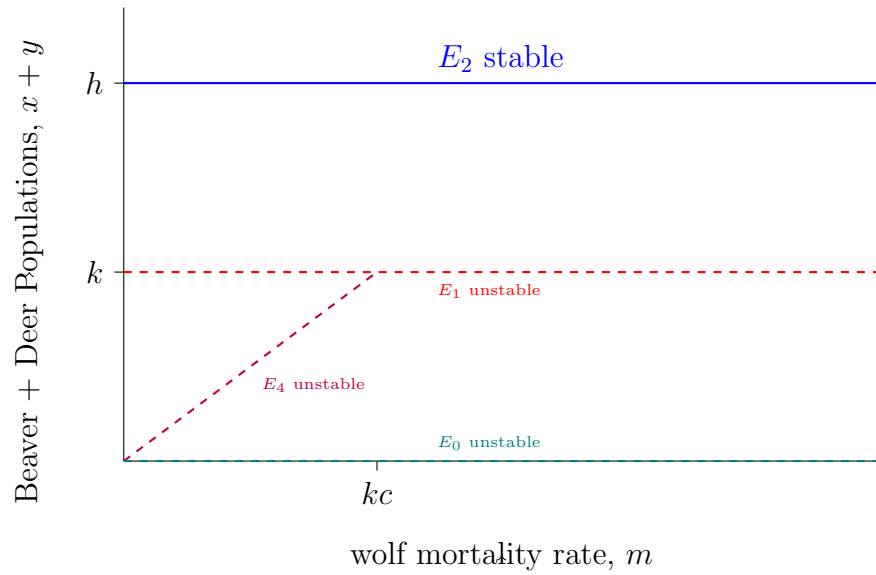


(b) Case II, $k > h$

Figure 4.1: Bifurcations of equilibrium states with changes in the mortality rate: (a) Case I, $k < h$; (b) Case II, $k > h$



(a) Case I, $h < k$



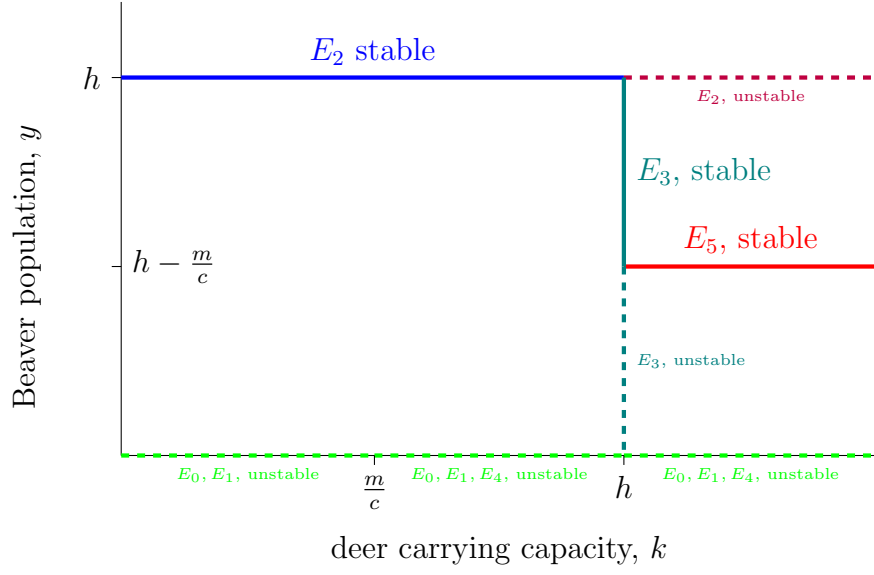
(b) Case II, $h > k$

Figure 4.2: The effect of wolf mortality on equilibrium prey populations: (a) Case I, $h < k$; (b) Case II, $k < h$

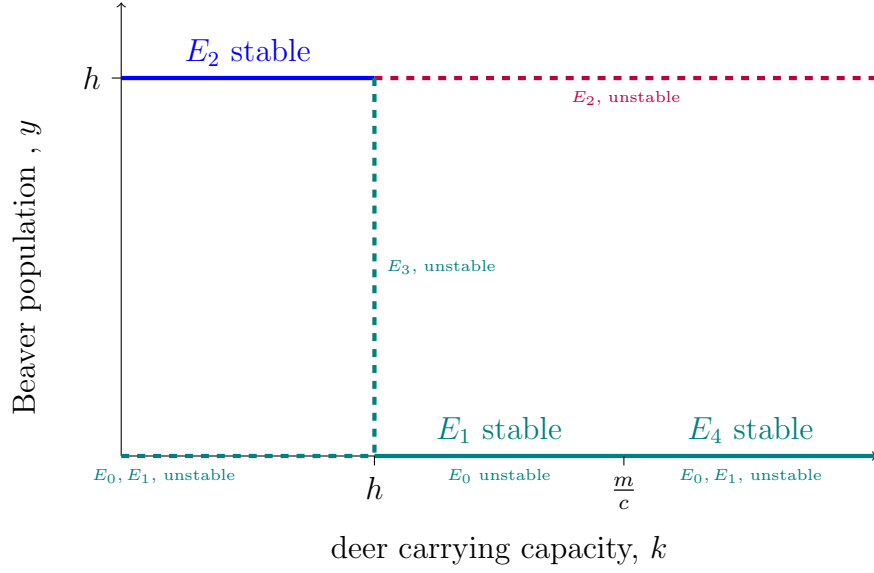
is larger than the beaver carrying capacity, the deer out-compete the beaver. Two outcomes are possible. If $m > hc$, the deer-only equilibrium, E_1 , is stable: the wolf population does not persist (see Figure 4.3a). If $m < hc$, the coexistence equilibrium, E_5 , is stable: the wolves persist, keeping the deer population low enough for the beaver population to persist (see Figure 4.3b).

At the point when the carrying capacity of the deer and the carrying capacity of the beaver are equal to each other, the line of deer-beaver equilibria, E_3 , appears. This is very unique situation. The set E_3 contains so many equilibrium points. Some of the equilibrium points are stable and some are unstable. The coexistence equilibrium, E_5 , is stable when the carrying capacity of the beaver is bigger than the carrying capacity of the deer. This shift of stability is a bifurcation between E_3 and E_5 by increasing the carrying capacity of the deer.

A second bifurcation occurs in the case $m > hc$. As we mentioned before, E_2 is the beaver-only equilibrium. When the carrying capacity of the deer is smaller than the carrying capacity of the beaver, E_2 is stable. When the carrying capacity of the deer becomes bigger than the carrying capacity of the beaver, E_2 loses stability and E_1 appears and is stable. By increasing the carrying capacity of the deer above $\frac{m}{c}$, E_1 loses stability. When E_1 is stable, if we introduce wolves, the wolf population decreases and stays at E_1 . When E_1 loses stability and is unstable if we introduce wolves population then E_4 appears and stable. E_4 is prey predator between wolves and deer populations in absence of beaver populations.



(a) Case I, $m < ch$



(b) Case II, $m > ch$

Figure 4.3: The effect of deer carrying capacity on equilibrium beaver populations: (a) Case I, $m < ch$; (b) Case II, $m > ch$

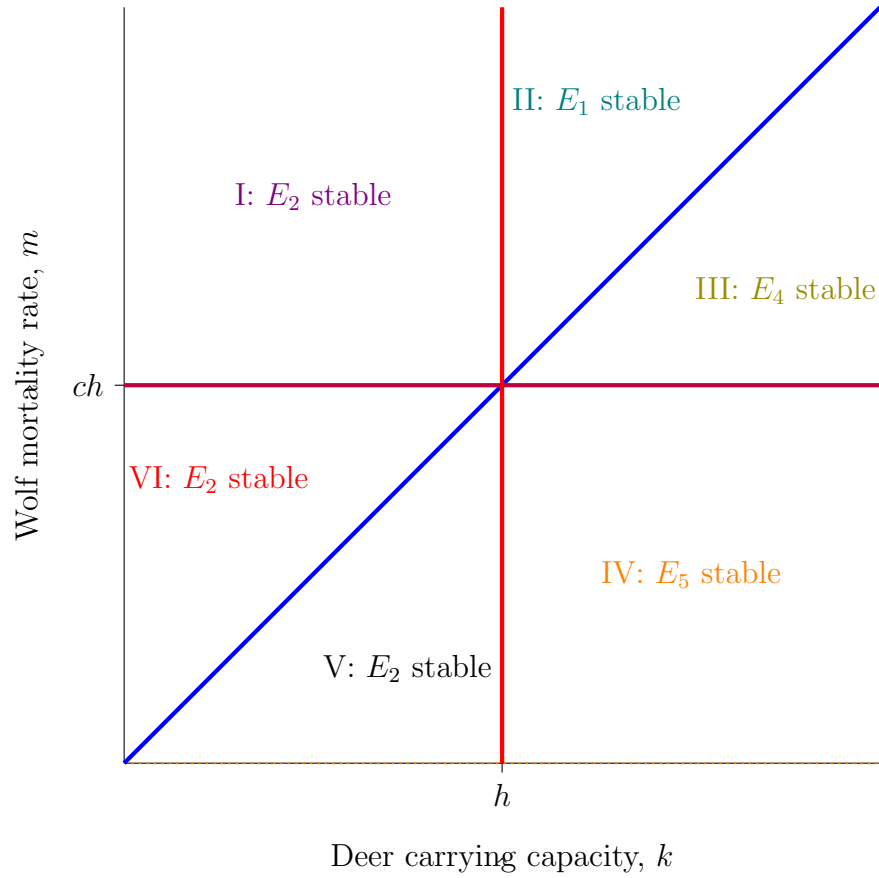


Figure 4.4: Bifurcations of equilibrium states with changes in the deer carrying capacity, k .

4.3 Impact of Wolf Mortality and Carrying Capacity

The complete dynamics of the system can be illustrated in the m - k plane (see Figure 4.4). As you can see, there are six parts, in each of these parts there will be a stable equilibrium point.

We begin our analysis in Region IV, where all species — wolves, deer, and beavers — coexist within the ecosystem. As we increase the mortality rate of wolves, a

significant shift occurs, leading us to Region III. In this new region, the population of beavers experiences a decline, resulting in a predator-prey dynamic that involves only wolves and deer. This transition highlights the complex interactions within the ecosystem, demonstrating how alterations in predator mortality can influence the population dynamics of prey species and potentially disrupt the balance of the ecological community.

Now if we travel from region III to region II by a mortality rate increase or a deer carrying capacity decrease, the population of wolves decreases and we end up with the deer-only equilibrium E_1 . By travelling from region II to region I by decreasing the carrying capacity of the deer, the beavers can find food more easily and their population increases to the beaver-only equilibrium, E_2 . Travelling from region I to region VI and then to region V by decreasing wolf mortality, the system remains at the beaver-only equilibrium. Travelling from region V to region IV again by increasing the deer carrying capacity, the three species can be existing in the ecosystem. These changes that occur as the carrying capacity and mortality rate are increased or decreased explain how the beaver population is affected by the carrying capacity of the deer and the mortality rate of the wolves.

Chapter 5

Discussion and Conclusions

5.1 General observations

This model introduces predators, i.e. wolf populations, and in particular, examines the indirect effect of their presence on beaver populations. In fact, predator populations only depend on one source, the deer population, and although they do not have direct contact with beavers, decreasing the predators will be a major risk to the beaver populations.

Deer and beavers are in competition to meet their basic needs. Increasing deer populations is a major threat to beavers in terms of finding food. In Yellowstone National Park, the dynamic relationship between wolves, deer, and beavers can be described using mathematical models, specifically predator-prey and competition models. Mathematical models, such as the Lotka-Volterra predator-prey model and the competition model, provide a framework for understanding and predicting the complex relationships between these species.

Similarly, the competition dynamics between deer and beavers highlight the potential for resource competition to affect population sizes.

The relationships between wolves, deer, and beavers in Yellowstone are complex and interconnected. These models enhance understanding and prediction of how changes in one population may impact the others, ultimately aiding in the conservation and management of this unique ecosystem.

This complex relationship between predator and prey highlights the interconnectedness of species and stresses the importance of preserving a sustainable equilibrium. From a mathematical perspective, the survival of wolf populations relies on their ability to obtain sustenance from deer, and a decline in prey availability could potentially lead to the extinction of the predator species. It is important to note that Yellowstone's ecosystem is complex, and many other factors can influence the dynamics between wolves, deer, beavers, and other species in the park. Management efforts, such as reintroducing wolves to the park in the 1990s, have aimed to restore balance and promote a healthy ecosystem in Yellowstone.

Our findings suggest that in order to ensure the survival of our ecological community, biologists should pay close attention to monitoring and managing the predator mortality rate. This parameter has the greatest impact on the stability of the system, and small changes in this value could lead to drastic consequences for the entire community. By focusing efforts on monitoring and managing this parameter, we can help to ensure the long-term survival of wolves, deer, and beaver in Yellowstone National Park.

Overall, our research highlights the importance of using mathematical models and bifurcation analysis in ecological studies. By combining theory with mathematical approximations, we can gain a better understanding of the complex interactions within ecosystems and make informed decisions to help protect and preserve species for future generations.

In studying the transcritical bifurcation of the three species (beaver, deer, and wolf)

in Yellowstone Park, it is evident that the dynamics of their interactions are highly complex and can lead to critical shifts in the stability of the ecosystem. The transcritical bifurcation occurs when the equilibrium state of the system changes qualitatively as a parameter, such as carrying capacity or mortality rates, is varied.

By increasing the mortality rate, m , the population of wolves decreases and the system approaches equilibrium E_1 , where both the populations of beavers and wolves are zero and only the deer live in Yellowstone park. This is what happened with hunting of wolves in Yellowstone Park and now we can have better understanding of their story.

The carrying capacity of the deer population and the mortality rates of the wolf population are crucial factors that influence the transcritical bifurcation in this ecological system.

Similarly, variations in the mortality rates of the wolf population, which are dependent on the availability of prey, particularly the deer population, can also trigger a transcritical bifurcation. Changes in the mortality rates of the wolf population can have cascading effects on the entire ecosystem, impacting the populations of both the deer and beaver species.

It is essential to closely monitor and manage the populations of the three species in Yellowstone Park to prevent the system from reaching a critical tipping point that could result in irreversible changes to the ecosystem. Understanding the dynamics of the transcritical bifurcation and its implications for the interactions between the beaver, deer, and wolf populations is crucial for the long-term health and sustainability of the ecosystem.

5.1.1 Final Thoughts

The interactions among wolves, deer, and beavers in Yellowstone National Park exemplify the intricate dynamics of ecological systems and their implications for population growth and decline. Through the application of bifurcation theory, specifically transcritical bifurcation, we can analyze how even minor environmental or population changes can have significant impacts on ecosystem stability. While wolves, as apex predators, control deer populations and influence beaver behaviour and habitat, the indirect consequences of declining wolf populations can adversely impact beaver populations. This disruption underscores the complex dynamics at play within the ecosystem. Understanding these indirect effects is essential for ecosystem management and conservation efforts. By employing transcritical bifurcation theory, we can gain deeper insights into these interactions and develop strategies to maintain the balance and resilience of Yellowstone's

Understanding these interconnections is vital for effective ecosystem management and conservation. By employing mathematical biology and conducting transcritical bifurcation analyses, we can gain insights into the coexistence and mutual influence of different species in their natural environments. This research sheds light on the intricate relationships that shape ecological communities, emphasizing the importance of studying predator-prey and competitor interactions to safeguard these ecosystems.

The incorporation of transcritical bifurcation theory enhances our understanding of the tipping points and critical thresholds within these ecosystems, highlighting the delicate balance required for their preservation. By unravelling the dynamics of these interactions, we can better inform conservation strategies and ensure the long-term sustainability of Yellowstone National Park and other natural habitats.

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