Internal Report 2010–17 August 2010

Universiteit Leiden
Opleiding Informatica

Dynamical Systems: Connected Predator-Prey Systems

Saskia Hiltemann

MASTER'S THESIS

Leiden Institute of Advanced Computer Science (LIACS)
Leiden University
Niels Bohrweg 1
2333 CA Leiden
The Netherlands

Dynamical Systems: Connected Predator-Prey Systems

Saskia Hiltemann (s0206180)
LIACS, Leiden University
Supervisors: Michael Emmerich, Patsy Haccou, Andre Deutz

August 11, 2010

Contents

1 Preface

This report comes with a number of supplementary files:

1. **Java program**
   This is the program used for the numerical simulations.

2. **Java program user manual**
   This is the manual for the program

3. **Simulation save-files**
   All save-files have the extension `.params`. These save-files can be loaded into the program. Some of the more interesting settings were stored in a file for the interested reader to explore.

4. **Mathematica notebooks**
   Some of the calculations were performed using Mathematica. The notebooks containing these calculations are provided. Hard copies of the notebooks can also be found in appendix B.

To keep this document readable, derivations of most results are not included in the main document. The derivations of selected equations and results can be found in appendix A. Those results which have derivations in this appendix are indicated by an asterisk behind the equation number.

2 Introduction

As the human population grows, the impact it has on the natural environment increases. Animal habitats become fragmented and species may become endangered. But we as humans are in the unique position of being able to influence our own environmental impact. For example we can build wildlife-bridges across highways, or use radar signals to steer birds away from wind turbines. We can plan the expansion of our own habitat, cities and infrastructure, in such a way as to minimize the negative effect on the surrounding wildlife habitats. In order to make the right planning decisions, it is important to know how and to what extent various factors influence the population dynamics of ecosystems and what the interaction between these factors is. Besides descriptive, statistical studies, the development of mechanistic models is of great importance for the understanding of these effects. However, existing mechanistic models are often rather simplistic and/or do not take spatial effects into account. Advanced modelling techniques as well as the availability of computer simulation and computer algebra systems make it possible to analyze more realistic, and complex, dynamical systems in ecology.

We construct an ordinary differential equations model of a one-predator-two-prey dynamical system, and derive equilibrium points and their stability analytically. We then extend the model, to one in which multiple such predator prey systems are connected to each other, that is, predator and/or prey are able to migrate between a small number of habitat patches. Based on numerical simulations we study the various effects the spatial aspect has on the overall dynamics of the system with a focus on phenomena that cannot occur in single patch dynamics, e.g. the effect of the creation of safe havens for an endangered prey species on the stability of its population.

3 Background

One of the earliest, and perhaps the most well-known examples of a predator-prey system is the Lotka-Volterra model. This model was independently developed by Alfred Lotka [3] and Vito Volterra [5][4] in 1925 and 1926 respectively. The model consists of two coupled non-linear differential equations which describe the dynamics of two interacting species, where one is the prey and one the predator:

$$\frac{dx}{dt} = x(\alpha - \beta y)$$
$$\frac{dy}{dt} = -y(\gamma - \delta x).$$

Here x denotes the prey, and y the predator. The prey is assumed to have an unlimited food supply and will grow exponentially unless they are subject to predation. This exponential growth is represented by the term αx in the equation for the prey. The term $-\beta yx$ represents the predation. This predation is assumed to be proportional to the rate at which predator and prey meet.

In the equation for the predator, the term δxy represents the growth in the predator population. Note that this term is similar to the predation term of the prey, apart from a constant factor. The term γy represent the decrease in predator population due to natural death or emigration. This leads to an exponential decay in the predator population in the absence of prey.

When we analyze this system, we find that it has two equilibrium points, one in which both predator and prey populations are zero, and one in which both are nonzero, and predator and prey coexist in equilibrium. The Lotka-Volterra system also yields the periodic cycles often observed in nature, where the populations of predator and prey oscillate with a certain regularity, and the peaks of the predator population lag behind the peaks in prey population (figure 3.1).

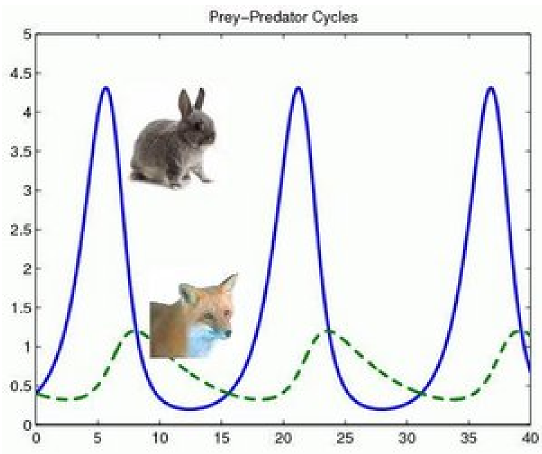


Figure 3.1: *Predator-prey cycles occurring in the Lotka-Volterra model*

While this simple model is able to capture some key properties of real predator-prey systems, it has a number of shortcomings. For instance, imagine a system in which there are a number of prey, but no predators. The population of the prey would now increase exponentially without limit. This would obviously not occur in nature; there is a limit on the maximum prey population an environment can support. Furthermore, the assumption that the predation rate is proportional to the encounter rate of predator and prey is also not a very realistic one. Predators have a maximum number of prey they can consume in a given time.

The Lotka-Volterra models were later extended in a great number of ways by many different researches. Most notably by C.S. Holling, who introduced the concept of a *functional response* [1] [2]. A functional response describes how the consumption rate of the predator varies with the abundance of the prey. Holling described three different types of functional response, which are depicted in figure 3.2.

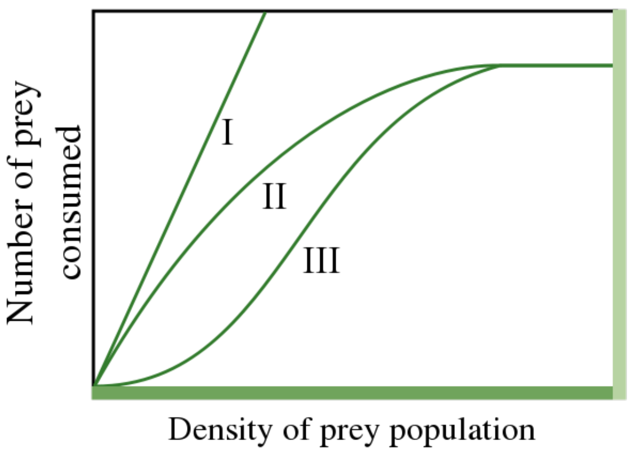
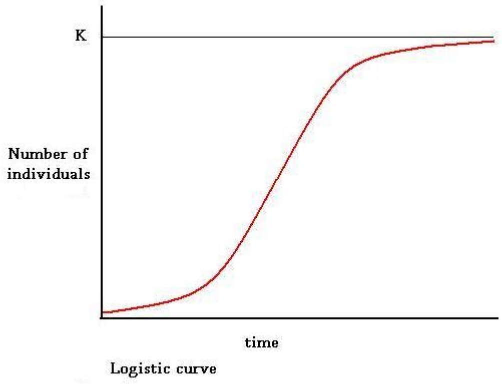


Figure 3.2: *Three types of functional responses described by C.S. Holling*

A type I functional response is characterized by a linear increase in consumption with increased prey density, with possibly a maximum, after which the intake rate of the predator remains constant despite increased prey populations. A type II functional response exhibits a decelerating intake rate as the prey population increases, until a saturation level is reached, then a further increase in prey population does not lead to a higher consumption rate by the predator. This is motivated by the idea that predators are limited in their capacity to process food; they need time to capture and digest the prey for instance. A type III functional response is similar to a type II, in that saturation occurs, but at low prey levels a accelerating intake rate is displayed.

The use of a functional response makes the predator prey system a bit more realistic. To address the problem of unlimited prey growth in absence of predators, we can use a logistic growth model instead of the exponential growth employed in the Lotka-Volterra model. A logistic growth function is of the form:

$$\frac{dx}{dt} = rx(1 - \frac{x}{k}) \tag{3.1}$$



In absence of predators, the prey population will increase up to a maximum, referred to as the *carrying capacity*, k. This carrying capacity is an indication of the resources available in the environment to sustain the prey population.

A great number of additional changes may be made to the system. For instance we could extend the system to include several prey or predator species. Then we could also introduce interactions, for example competition, between two predators species or between two prey species. Or we could explicitly model the available resources of the prey (e.g. plant life). The exact model we employ also depends on the system we are attempting to model, different predator or prey species may exhibit different characteristics.

In the next section we construct our own predator-prey system, involving a single predator and two prey species. We then analyze this system, both analytically and numerically, and then introduce a spatial component to the model, by creating a network of predator-prey systems, between which the predator and/or prey are able to travel.

4 Predator-Prey System

The predator-prey system we developed consists of one predator species, denoted by y, and two prey species, denoted by x and z. Each of the prey species have a certain energy content, E, which the predator can use to sustain itself and produce offspring. The prey also have associated with them a certain handling time, h, which denotes the time the predator needs for capturing, killing, eating and digesting the prey. The *profitability* of the prey item is now defined as the ratio E/h; the energy intake from consuming the prey divided by the amount of time needed to obtain that energy from the prey.

We define prey x as being the more profitable prey. In other words, we require that

$$\frac{E_x}{h_x} > \frac{E_z}{h_z}. \tag{4.1}$$

Furthermore, prey is encountered at a rate of λ.

4.1 Optimal Foraging

Optimal foraging theory states that organisms forage (or hunt) in such a way as to maximize their energy intake rate. Since x is the more profitable prey, the predator will prefer x over z wherever possible.
If our predator consumes only prey x, and not z, the energy intake per unit time is given by:

$$\frac{T \cdot \lambda_x \cdot E_x}{T + T \cdot \lambda_x \cdot h_x} = \frac{\textit{Energy gained}}{\textit{Time spent hunting + time spent handling the prey}},$$

where T is the time spent foraging (hunting). Since T appears in every factor of the equation, it can be simplified as:

$$\frac{\lambda_x E_x}{1 + \lambda_x h_x} \tag{4.2}$$

Now we compare this to the situation where prey z is included in the predator's diet. The energy intake per unit time then becomes:

$$\begin{aligned} &\frac{T\lambda_x E_x + T\lambda_z E_z}{T + T\lambda_x h_x + T\lambda_z h_z} \\ &= \frac{\lambda_x E_x + \lambda_z E_z}{1 + \lambda_x h_x + \lambda_z h_z} \end{aligned} \tag{4.3}$$

According to the optimal foraging theory, the predator will only include prey z in its diet if this leads to an increase in the energy intake rate. For example it may be that prey z has such a high handling time, that it is more efficient to ignore prey z when it is encountered, and continue hunting for prey x. Only when prey x is very scarce (and thus would take a long time to find), would it be beneficial to consume z.

In order for the predator to include prey z in its diet, the following inequality must hold:

$$\begin{aligned} \textit{Energy intake rate without } z \; &< \textit{Energy intake rate when } z \textit{ is included} \\ \Rightarrow \frac{\lambda_x E_x}{1+\lambda_x h_x} \; &< \frac{\lambda_x E_x + \lambda_z E_z}{1+\lambda_x h_x + \lambda_z h_z} \end{aligned} \tag{4.4}$$

which leads to the requirement:

$$\frac{\lambda_x E_x}{1+\lambda_x h_x} < \frac{E_z}{h_z}. \tag{4.5*}$$

If this requirement holds, prey z is included in the diet, and otherwise it is not. Notice that whether or not z is consumed depends only on the encounter rate of the primary prey x, not on the encounter rate of prey z itself. Thus there is a threshold value of the encounter rate λ_x, under which the predator will include prey z in their diet, and above which they will not.

We can incorporate this threshold into our description of the energy intake rate of the predator:

$$\frac{\lambda_x E_x + \delta\lambda_z E_z}{1+\lambda_x h_x + \delta\lambda_z h_z}, \tag{4.6}$$

where

$$\delta = \begin{cases} 1 & \text{if} \quad \dfrac{\lambda_x E_x}{1+\lambda_x h_x} < \dfrac{E_z}{h_z} \\ 0 & \text{otherwise} \end{cases}$$

4.2 Predator Dynamics

Predators consume the prey, and use the energy to create offspring. The predators are modelled to have a type II functional response. A functional response describes how the consumption rate of an individual predator changes with respect to prey density. A type II functional response is characterized by a decelerating consumption rate with increased prey density, until finally it becomes constant at a saturation point (see figure 4.1). This follows from the assumption that the consumer is limited by its capacity to process food.

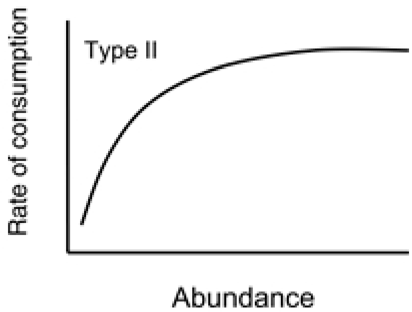


Figure 4.1: *A type II functional response*

This type of functional response can be described by the following (Holling's disk) equation:

$$f(x) = \frac{ax}{1 + ah_x x}. \tag{4.7}$$

Here h_x is the handling time, and a is the *attack rate*. The attack rate, also referred to as the *searching efficiency*, is the number of prey encountered by the predator per unit of prey density.

In our system, the predator also has alternative prey options, so we alter equation 4.7 to include prey z:

$$f(x) = \frac{ax + \delta az}{1 + ah_x x + \delta ah_z z}. \tag{4.8}$$

Here we have assumed the attack rate, a, is equal for both prey types. That is, we take the attack rate to be a characteristic of the landscape; a measure of the ability to take cover in the landscape and escape the predators.

The change in predator population size per unit time can be described with the following differential equation.

$$\frac{dy}{dt} = -\mu y + \gamma_x \frac{ax}{1 + ah_x x + \delta ah_z z} y + \gamma_z \frac{\delta az}{1 + ah_x x + \delta ah_z z} y.$$

Here μ is the mortality rate. γ_x and γ_z are constants describing the rate at which prey (energy) are converted into offspring. The first term describes predator death, proportional only to its own population size. The second term describes the increase in predator population due to the consumption of prey x, and the last term describes the increase in population size due to the consumption of prey z.

This can be rewritten more compactly as:

$$\frac{dy}{dt} = y \left[-\mu + \frac{a(\gamma_x x + \delta \gamma_z z)}{1 + a(h_x x + \delta h_z z)} \right]. \tag{4.9}$$

If we assume that the prey-into-offspring conversion rates γ_x and γ_z depend only of the amount of energy gained from the prey, we can say that

$$\gamma_x = \gamma E_x \tag{4.10}$$
$$\gamma_z = \gamma E_z. \tag{4.11}$$

We can also relate the encounter rates λ_x and λ_z with the attack rate a through

$$\lambda_x = ax \tag{4.12}$$
$$\lambda_z = az. \tag{4.13}$$

Using these relations, we can rewrite our definition of δ in terms of a instead of λ_x and λ_z, and in terms of γ_x and γ_z instead of E_x and E_z, as:

$$\delta = \begin{cases} 1 & \text{if} \quad \dfrac{a\gamma_x x}{1 + ah_x x} < \dfrac{\gamma_z}{h_z} \\ 0 & \text{otherwise} \end{cases} \tag{4.14}$$

We can also use relations 4.10 and 4.11 to rewrite the requirement that x be the primary prey (requirement 4.1), in terms of γ_x and γ_z instead of the energy values of the two prey:

$$\frac{\gamma_x}{h_x} > \frac{\gamma_z}{h_z} \tag{4.15}$$

4.3 Prey Dynamics

In the absence of predators, the prey will exhibit a logistic growth:

$$\frac{dx}{dt} = r_x x(1 - \frac{x}{k_x}). \tag{4.16}$$

Here k_x is the carrying capacity, and r_x is the growth (birth) rate of prey x. But in the presence of predators, prey numbers will decrease proportional to the number of predators, and according to the functional response of the predators, yielding the following full equation for the prey:

$$\frac{dx}{dt} = r_x x(1 - \frac{x}{k_x}) - \frac{ax}{1 + ah_x x + \delta ah_z z} y. \tag{4.17}$$

The expression for z is completely analogous to that of x, except for the fact that prey z is not always predated on by y:

$$\frac{dz}{dt} = r_z z(1 - \frac{z}{k_z}) - \frac{\delta az}{1 + ah_x x + \delta ah_z z} y. \tag{4.18}$$

We assume that there is a virtually unlimited supply of alternative resource z, which we model by setting $k_z \gg k_x$.

4.4 Change in Diet

When will the predator include the alternative prey, z, in its diet? In other words, when does δ change from 0 to 1? From the definition of δ,

$$\delta = \begin{cases} 1 & \text{if} \quad \dfrac{a\gamma_x x}{1 + ah_x x} < \dfrac{\gamma_z}{h_z} \\ 0 & \text{otherwise} \end{cases}, \tag{4.19}$$

we can see that this only depends on the abundance of prey x, not on the abundance of prey z.

If the density of prey x falls below a certain threshold, the predator will include prey z in its diet. We now determine this threshold by determining when δ will have a value of 1:

$$\begin{aligned} \frac{a\gamma_x x}{1 + ah_x x} &< \frac{\gamma_z}{h_z} \\ \Leftrightarrow x &< \frac{1}{a(h_z \frac{\gamma_x}{\gamma_z} - h_x)}, \end{aligned} \tag{4.20*}$$

and zero otherwise. This means that we can define δ in terms of the density of prey x:

$$\boxed{\delta = \begin{cases} 1 & \text{if} \quad x \leq \dfrac{1}{a\left(h_z \dfrac{\gamma_x}{\gamma_z} - h_x\right)} \\ 0 & \text{otherwise} \end{cases}} \tag{4.21}$$

4.5 Full System

Putting everything together gives us the following full description of our predator-prey system:

$$
\begin{aligned}
\frac{dy}{dt} &= y\left[-\mu + \frac{a(\gamma_x x + \delta\gamma_z z)}{1 + a(h_x x + \delta h_z z)}\right] \\
\frac{dx}{dt} &= x\left[r_x(1 - \frac{x}{k_x}) - \frac{ay}{1 + a(h_x x + \delta h_z z)}\right] \\
\frac{dz}{dt} &= z\left[r_z(1 - \frac{z}{k_z}) - \frac{\delta ay}{1 + a(h_x x + \delta h_z z)}\right] \\
\delta &= \begin{cases} 1 & \text{if} \quad x \le \dfrac{1}{a\left(h_z \dfrac{\gamma_x}{\gamma_z} - h_x\right)} \\ 0 & \text{otherwise} \end{cases} \\
\frac{\gamma_x}{h_x} &> \frac{\gamma_z}{h_z} \\
k_z &\gg k_x \\
a &= \text{attack rate} \\
h &= \text{handling time} \\
r &= \text{growth rate} \\
k &= \text{carrying capacity} \\
\mu &= \text{mortality rate} \\
\gamma &= \text{prey-to-offspring conversion rate} \\
a, h, r, k, \mu, \gamma &\ge 0
\end{aligned}
\tag{4.22}
$$

5 Analysis

To analyze this system, we will first look at the situation where the preferred prey x is extinct (section 5.1), and then study the dynamics when we add prey x to the system (section 5.2).

5.1 System Without Prey x

If the primary prey is extinct ($x = 0$), δ will be 1. This leads to the following description of the system in absence of prey x:

$$\begin{aligned} \frac{dy}{dt} &= y\left[-\mu + \frac{a\gamma_z z}{1 + ah_z z}\right] \\ \frac{dz}{dt} &= z\left[r_z(1 - \frac{z}{k_z}) - \frac{ay}{1 + ah_z z}\right] \end{aligned} \tag{5.1}$$

In order to determine the equilibria of this system, we determine the zero-isoclines (regions of zero growth) for predator and prey. The prey zero-isocline is obtained by setting $\frac{dz}{dt} = 0$ and the predator zero-isocline is found by setting $\frac{dy}{dt} = 0$. This leads to the following zero-isoclines:

Prey zero-isoclines:

$$\frac{dz}{dt} = 0 \Rightarrow \quad y = \frac{r_z}{a}\left(1 - \frac{z}{k_z}\right)(1 + ah_z z) \qquad (a)$$

$$z = 0 \qquad (b)$$

(5.2*)

Predator zero-isoclines:

$$\frac{dy}{dt} = 0 \Rightarrow \quad z = \frac{\mu}{a\left(\gamma_z - \mu h_z\right)} \qquad (c)$$

$$y = 0 \qquad (d)$$

Note that the predator isocline 5.2*c, is a constant, and independent of predator numbers. The prey zero-isocline 5.2*a describes a truncated parabola. Figure 5.1 shows these isoclines in $y - z$ phase space.

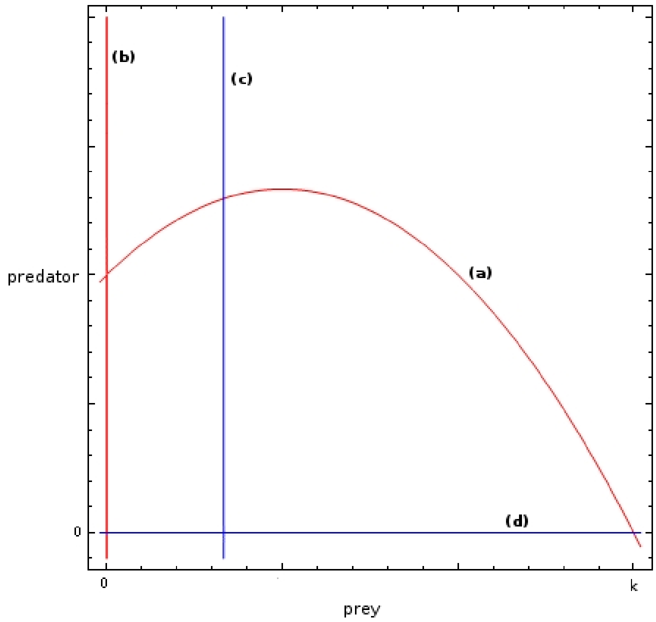


Figure 5.1: *Zero-isoclines plotted in phase space. Prey isoclines are given in red (a and b(, and predator isoclines in blue (c and d).*

Equilibria

Wherever a predator isocline and a prey isocline intersect we have an equilibrium point, as both predator and prey population densities remain stable over time.

The intersection of isoclines b and d gives us the trivial fixed point $(y, z) = (0, 0)$, which is the situation where both species have become extinct. The intersection of isoclines a and d give us two fixed points. The first is

$$(y, z) = (0, -\frac{1}{ah_z}), \tag{5.3*}$$

which is infeasible since it requires a negative prey population z. The second fixed point is

$$(y, z) = (0, k_z), \tag{5.4*}$$

which describes the situation where the predator has become extinct and prey z is able to grow to its carrying capacity k_z. Isoclines b and c never intersect, so the only remaining fixed point is the one given by the intersection of isoclines a and c.

This intersection between the nontrivial zero-isoclines of predator and prey (c and a respectively), only produces a feasible fixed point when the predator zero-isocline is located between 0 and k_z

(see Figure 5.1). If this is not the case, the intersection occurs in an area where either the predator or prey densities (or both) are negative, which obviously cannot occur in nature. From 5.2*c we can determine that the predator isocline is only positive if it holds that:

$$\mu < \frac{\gamma_z}{h_z} \tag{5.5}$$

The expression on the right-hand side of this inequality denotes the profitability of the prey. This requirement thus states that the death rate should be smaller than the rate at which new offspring are produced from the consumption of prey. If the predators would die at a higher rate than that they reproduce, their numbers would always decline.

The prey isocline falls to the left of k_z iff:

$$k_z > \frac{\mu}{a\left(\gamma_z - \mu h_z\right)}. \tag{5.6}$$

Whenever both 5.5 and 5.6 are satisfied, then there is an additional, non-trivial, fixed point, namely the one where isoclines 5.2*a and 5.2*c intersect. Since the predators isocline is a vertical line, we know that the value of z at the equilibrium point, $\hat{z}$, is:

$$\hat{z} = \frac{\mu}{a(\gamma_z - \mu h_z)}$$

Plugging this into the equation for the prey's isocline gives us the value of y at the equilibrium point ($\hat{y}$):

$$\hat{y} = \frac{r_z}{a}\left(1 - \frac{\mu}{ak_z(\gamma_z - \mu h_z)}\right)\left(1 + \frac{\mu h_z}{\gamma_z - \mu h_z}\right) \tag{5.7}$$

In summary, the equilibria of our system are given by:

trivial:

$(\hat{y}, \hat{z}) = (0, 0)$

$(\hat{y}, \hat{z}) = (0, k_z)$

nontrivial:

$(\hat{y}, \hat{z})$ with

$$\hat{y} = \frac{r_z}{a}\left(1 - \frac{\mu}{ak_z(\gamma_z - \mu h_z)}\right)\left(1 + \frac{\mu h_z}{\gamma_z - \mu h_z}\right)$$

$$\hat{z} = \frac{\mu}{a(\gamma_z - \mu h_z)}$$

which exists iff

$$\mu < \frac{\gamma_z}{h_z} \quad \text{and} \quad k_z > \frac{\mu}{a\left(\gamma_z - \mu h_z\right)} \tag{5.8}$$

5.1.1 Stability of Fixed Points

We now want to find out if these fixed points are stable or unstable. If a fixed point is unstable, small perturbations from the fixed point can cause the system to move away from the fixed point. If a fixed point is stable, the system will return to it after it has undergone small perturbations. First we will give a graphical argument for the stability of the fixed points, which we will later prove analytically.

Graphical Approach

We know that at the fixed points, the predator and prey numbers remain the same over time, but what happens if we are not at a fixed point? If $\frac{dz}{dt} < 0$, the prey population will decline, and if $\frac{dz}{dt} > 0$ it will grow. We can determine that there is a positive growth if

$$y < \frac{r_z}{a}\left(1 - \frac{z}{k_z}\right)(1 + ah_z z), \tag{5.9}$$

which corresponds to the area under the parabola. In figure 5.2, the shaded area indicates the region of growth for the prey, and the unshaded area indicates the area of decline.

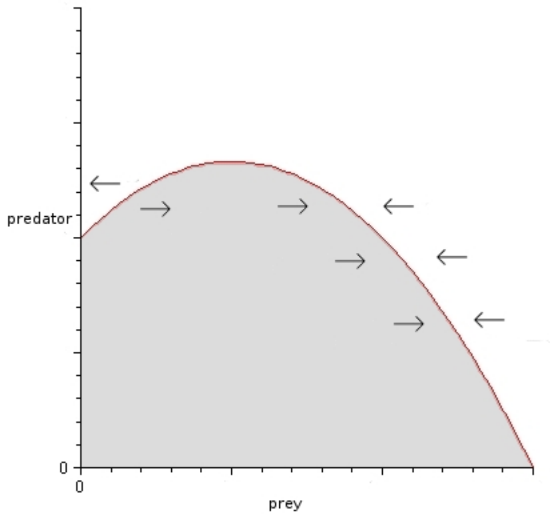


Figure 5.2: *Regions of growth and decline of the prey.*

The arrows indicate this growth and decline in prey numbers. From the arrows we can see that for points near the right half of the parabola, the system always moves toward the isocline, whereas for points near the left half of the parabola, the system always moves away from the isocline. This leads us to believe that if the nontrivial equilibrium falls to the right of the peak of the prey zero-isocline, it will be stable, and that if the fixed point falls to the left of the peak, it will be unstable. We can determine the peak of the prey zero-isocline to be located at:

$$z = \frac{1}{2}\left(k_z - \frac{1}{ah_z}\right) \tag{5.10*}$$

But for the full dynamics, we also need to consider the area of growth or decline of the predator. We can determine that there is positive predator growth, $\frac{dy}{dt} > 0$, if

$$z > \frac{\mu}{a\left(\gamma_z - \mu h_z\right)}. \tag{5.11}$$

(Assuming that the predator isocline is positive, i.e. $\mu < \frac{\gamma_z}{h_z}$.) In figure 5.3 this region of growth is indicated by a red shading.

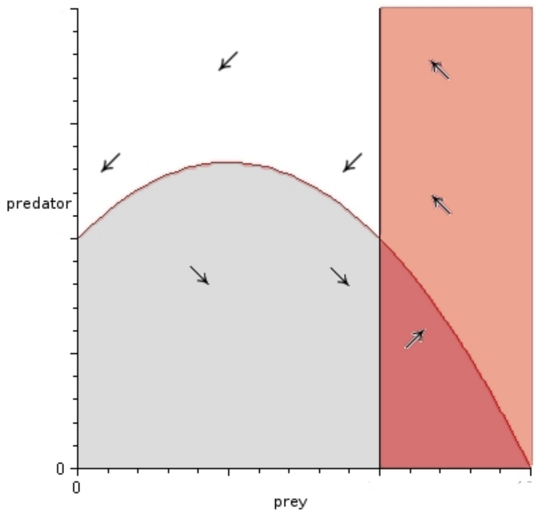
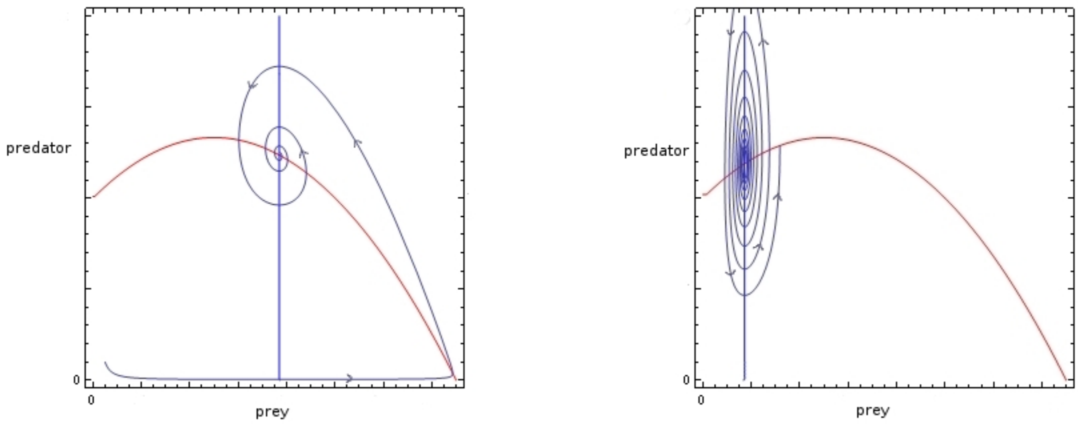


Figure 5.3

The arrows again indicate the direction in which the system moves in the different regions. Near the point where the two isoclines meet, the system spirals around the fixed point. If the fixed point falls on the right half of the parabola, we suspect the system is attracted to the (stable) fixed point, and if the fixed point is located on the left half of the parabola, we suspect it is repelled by the (unstable) fixed point. To see if this is indeed what happens, we plot trajectories for both cases:



(a) *Isoclines intersect in the right half of the parabola*

(b) *Isoclines intersect in the left half of the parabola*

Figure 5.4: *Examples of trajectories*

From figure 5.4, we see that for these example trajectories, it is indeed the case that the fixed point located on the right half of the parabola is attractive (stable), and the fixed point located on the left half is repellent (unstable). In the next section, we will prove analytically that this is also true in general.

Let us have a look at what happens if the predator isocline is negative, or falls to the right of k_z. In this case there is no (realistic) nontrivial fixed point, since at the intersection either the prey or the predator or both have negative population numbers. If the predator isocline is negative, there is positive predator growth only if:

$$z < \frac{\mu}{a(\gamma_z - \mu h_z)} \tag{5.12}$$

Since the right side of this inequality is a negative number, this means that for realistic situations, the predator population is always declining. This means the predator will become extinct, and the prey will grow towards carrying capacity. The fixed point $(0, k_z)$ is now stable, and the fixed point $(0, 0)$ is a saddle point (unstable). Small increase in y will cause the system to go back to the fixed point, but a small increase in z will cause the system to move away from the origin, to eventually end up in the point $(0, k_z)$.

If the predator isocline falls to the right of the carrying capacity k_z, i.e.

$$k_z < \frac{\mu}{a\,(\gamma_z - \mu h_z)} \tag{5.13}$$

we again have a situation for which in all feasible situations (z and y nonnegative and $z < k_z$), the predator numbers will decline, implying that again the predator will always become extinct eventually, and that the fixed point $(0, 0)$ is unstable, while the fixed point $(0, k_z)$ is stable.

Analytical Approach

We would now like to give analytical proof for the conditions for stability of the fixed points. To this end we perform an eigenvalue analysis. Recall that our system is given by:

$$\begin{aligned} \frac{dy}{dt} &= y\left[-\mu + \frac{a\gamma_z z}{1+ah_z z}\right] \\ \frac{dz}{dt} &= z\left[r_z(1-\frac{z}{k_z}) - \frac{ay}{1+ah_z z}\right], \end{aligned} \tag{5.14}$$

which we can write in a more general form as:

$$\frac{dy}{dt} = yg_y(y,z) \tag{5.15}$$

$$\frac{dz}{dt} = zg_z(y,z). \tag{5.16}$$

Here $g_y(y,z)$ and $g_z(y,z)$ correspond to the expressions in the square brackets of 5.14.

In order to investigate the stability of the equilibria, we look at the Jacobian of this system. The Jacobian is given by:

$$\mathbf{J} = \begin{bmatrix} y\frac{dg_y}{dy} + g_y & y\frac{dg_y}{dz} \\ z\frac{dg_z}{dy} & z\frac{dg_z}{dz} + g_z \end{bmatrix}, \tag{5.17}$$

Stability of the nontrivial fixed point

We can use equations 5.15 and 5.16 to simplify the Jacobian given in 5.17. Equation 5.15 implies $y = 0 \ \vee \ g_y(y,z) = 0$, and since we are looking at the nontrivial equilibria, we say y is nonzero, which means that $g_y(y,z)$ must be zero. In the same manner we get that $g_z(y,z) = 0$. Plugging this into the expression for the Jacobian gives us:

$$\mathbf{J} = \begin{bmatrix} y\frac{dg_y}{dy} & y\frac{dg_y}{dz} \\ z\frac{dg_z}{dy} & z\frac{dg_z}{dz} \end{bmatrix}.$$

Computing the remaining partial derivatives leads to:

$$\mathbf{J} = \begin{bmatrix} 0 & y\left(\frac{a\gamma_z}{1+ah_z z} - \frac{\gamma_z a^2 h_z z}{(1+ah_z z)^2}\right) \\ -\frac{az}{1+ah_z z} & z\left(-\frac{r_z}{k_z} + \frac{a^2 h_z y}{(1+ah_z z)^2}\right) \end{bmatrix}, \tag{5.18*}$$

Using the equation

$$y = \frac{r_z}{a}(1 - \frac{z}{k_z})(1 + ah_z z) \tag{5.19}$$

for equilibrium points, we can further simplify the Jacobian as follows:

$$\mathbf{J} = \begin{bmatrix} 0 & \gamma_z r_z(1 - \frac{z}{k_z}) - \frac{\gamma_z a h_z r_z z (1 - \frac{z}{k_z})}{1 + a h_z z} \\ \\ -\frac{az}{1 + a h_z z} & z\left(-\frac{r_z}{k_z} + \frac{a h_z r_z (1 - \frac{z}{k_z})}{1 + a h_z z}\right) \end{bmatrix}. \tag{5.20*}$$

Finding the eigenvalues of a 2×2 Jacobian, involves solving the *characteristic equation*,

$$\lambda^2 - \mathrm{Tr}(\mathbf{J})\lambda + \det(\mathbf{J}) = 0, \tag{5.21}$$

for λ. The solutions to this equation give us the eigenvalues. The stability of a fixed point can be determined in general from the signs of the eigenvalues as follows:

- All eigenvalues negative $\rightarrow$ fixed point is stable (attractor)
- All eigenvalues positive $\rightarrow$ fixed point is unstable (repeller)
- There are both positive and negative eigenvalues $\rightarrow$ fixed point is a *saddle point.*

The trace is simply the sum of the eigenvalues, while the determinant is the product of the eigenvalues. For a 2×2 Jacobian, we can also use the signs of the trace and determinant to classify the stability of fixed points:

- Trace negative, determinant positive $\rightarrow$ fixed point is stable (attractor)
- Trace positive, determinant positive $\rightarrow$ fixed point is unstable (repeller)
- Determinant negative $\rightarrow$ fixed point is a *saddle point.*

We would now like to determine the conditions for the stability of the nontrivial equilibrium point $(\hat{y}, \hat{z})$ in our system.

Requiring that the determinant be positive leads to the requirement that

$$0 < \hat{z} < k_z, \tag{5.22*}$$

which exactly describes the situation for which the nontrivial fixed point is biologically realistic (both predator and prey numbers nonnegative). This requirement is met if it holds that:

$$\mu < \frac{\gamma_z}{h_z} \quad \wedge \quad k_z > \frac{\mu}{a(\gamma_z - \mu h_z)}. \tag{5.23*}$$

This describes the situation for which the nontrivial fixed point exists (see equations 5.5 and 5.6). Thus, whenever the fixed point exists, the determinant is positive. This means we only need to worry about the trace when determining the stability of the fixed point.

If we require that the trace be negative gives us the additional requirement that:

$$\hat{z} > \frac{1}{2}\left(k_z - \frac{1}{ah_z}\right). \tag{5.24*}$$

Recall that the right side of expression 5.24*, is exactly the location of the peak of the prey zero-isocline, z_p, in the phase portrait. This means that, as we suspected from the graphical approach, the equilibrium is stable if the fixed point falls to the right of the peak (i.e. $z_p < \hat{z} < k_z$). If the the fixed point falls to the left of the peak, that is if $0 < \hat{z} < z_p$, the trace is positive, which means the fixed point is *unstable*. We can show that requirement 5.24* is met if it holds that:

$$k_z < \frac{\gamma_z + \mu h_z}{ah_z(\gamma_z - \mu h_z)} \tag{5.25*}$$

Stability of the trivial fixed points
What of the stability of the trivial fixed points? We again start with the Jacobian,

$$\mathbf{J} = \begin{bmatrix} y\frac{dg_y}{dy} + g_y & y\frac{dg_y}{dz} \\ z\frac{dg_z}{dy} & z\frac{dg_z}{dz} + g_z \end{bmatrix}. \tag{5.26}$$

At the trivial fixed point $(\hat{y}, \hat{z}) = (0, 0)$, the Jacobian becomes:

$$\mathbf{J} = \begin{bmatrix} g_y & 0 \\ 0 & g_z \end{bmatrix}, \tag{5.27}$$

where

$$\begin{aligned} g_y &= -\mu + \frac{a\gamma_z z}{1 + ah_z z} \\ g_z &= r_z(1 - \frac{z}{k_z}) - \frac{ay}{1 + ah_z z}. \end{aligned}$$

Filling in the fixed point $(\hat{y}, \hat{z}) = (0, 0)$ leads to the Jacobian

$$\mathbf{J} = \begin{bmatrix} -\mu & 0 \\ 0 & r_z \end{bmatrix}, \tag{5.28}$$

which has eigenvalues $-\mu$ and r_z. Thus we see that the system has one positive and one negative eigenvalue, which means that $(0, 0)$ is a *saddle point*, and thus unstable. Intuitively we can see this as well; suppose both predator and prey are extinct (we are at fixed point $(0, 0)$), then a small perturbation from this point, may cause the system to move away from this equilibrium. For example the appearance of a few prey z, will cause z to grow logistically towards k_z because there are no predators. Thus the system moves away from the fixed point (0,0), which means this is an unstable fixed point.

Next we determine the stability of the other trivial fixed point, $(\hat{y}, \hat{z}) = (0, k_z)$ in a similar manner. The Jacobian now becomes:

$$\mathbf{J} = \begin{bmatrix} -\mu + \frac{a\gamma_z k_z}{1+ah_z k_z} & 0 \\ -\frac{ak_z}{1+ah_z k_z} & -r_z \end{bmatrix}. \tag{5.29}$$

The eigenvalues of this matrix are

$$-r_z \qquad \text{and} \qquad -\mu + \frac{a\gamma k_z}{1+ah_z k_z} \tag{5.30}$$

The first of these is always negative. The second is negative only if it holds that

$$\mu > \frac{\gamma_z}{h_z} \tag{5.31*}$$

or,

$$\mu < \frac{\gamma_z}{h_z} \quad \text{and} \quad k_z < \frac{\mu}{a(\gamma_z - \mu h_z)}. \tag{5.32*}$$

The first of these cases corresponds to a negative value of the predator isocline, and the second corresponds to a predator isocline located to the right of the carrying capacity k_z. This means that, for the situations we are interested in, namely those in which a nontrivial equilibrium exists, there is one negative and one positive eigenvalue, which means $(0, k_z)$ is a saddle point, and unstable. As soon as the predator is introduced in the system, it will start to reduce the prey population until another equilibrium is reached.

In summary, the stability of the fixed points are given by:

trivial:

$(\hat{y}, \hat{z}) = (0, 0)$ *unstable*

$(\hat{y}, \hat{z}) = (0, k_z)$ *unstable* if a nontrivial equilibrium exists.

stable otherwise

nontrivial:

$(\hat{y}, \hat{z})$ with

$$\begin{aligned}
\hat{y} &= \frac{r_z}{a}\left(1 - \frac{\mu}{ak_z(\gamma_z - \mu h_z)}\right)\left(1 + \frac{\mu h_z}{\gamma_z - \mu h_z}\right) \\
\hat{z} &= \frac{\mu}{a(\gamma_z - \mu h_z)}
\end{aligned} \tag{5.33}$$

which exists iff

$$\mu < \frac{\gamma_z}{h_z} \quad \wedge \quad k_z > \frac{\mu}{a\,(\gamma_z - \mu h_z)}$$

and is *stable* if $\quad k_z < \dfrac{\gamma_z + \mu h_z}{ah_z(\gamma_z - \mu h_z)}$

and *unstable* otherwise.

5.2 System Including Prey x

We now introduce the primary prey, which we denote by the variable x, into the system. Recall from box 4.22, that the system can be described by the following set of differential equations:

$$\frac{dy}{dt} = y\left[-\mu + \frac{a(\gamma_x x + \delta\gamma_z z)}{1 + a(h_x x + \delta h_z z)}\right] \tag{5.34}$$

$$\frac{dx}{dt} = x\left[r_x(1 - \frac{x}{k_x}) - \frac{ay}{1 + a(h_x x + \delta h_z z)}\right] \tag{5.35}$$

$$\frac{dz}{dt} = z\left[r_z(1 - \frac{z}{k_z}) - \frac{\delta ay}{1 + a(h_x x + \delta h_z z)}\right] \tag{5.36}$$

with

$$\delta = \begin{cases} 1 & \text{if} \quad x \leq \dfrac{1}{a\left(h_z\dfrac{\gamma_x}{\gamma_z} - h_x\right)} \\ 0 & \text{otherwise} \end{cases} \tag{5.37}$$

5.2.1 Equilibria

In order to determine the equilibria of this system, we again look at the isoclines, which are given by:

$$\begin{array}{llll}
\dfrac{dy}{dt} = 0 \Rightarrow & x = \dfrac{\mu - \delta az(\gamma_z - \mu h_z)}{a(\gamma_x - \mu h_x)} & & (a) \\
& y = 0 & & (b) \\
\dfrac{dx}{dt} = 0 \Rightarrow & y = \dfrac{r_x}{a}(1 - \dfrac{x}{k_x})(1 + ah_x x + \delta ah_z z) & & (c) \\
& x = 0 & & (d) \\
\dfrac{dz}{dt} = 0 \Rightarrow & y = \dfrac{r_z}{\delta a}(1 - \dfrac{z}{k_z})(1 + ah_x x + \delta ah_z z) & \wedge\ \delta = 1 & (e) \\
& z = 0 & & (f) \\
& z = k_z \ \wedge\ \delta = 0 & & (g)
\end{array} \tag{5.38*}$$

The isoclines are now surfaces in 3D phase space, and therefore harder to visualize. Anywhere that isoclines from all three species intersect, we have a fixed point. We will now discuss the equilibria that arise for all 12 possible combinations of the isoclines of the three species.

1. Isoclines (b),(d) and (f) intersect at the point $(\hat{x}, \hat{y}, \hat{z}) = (0, 0, 0)$, which describes the situation where all three species are extinct.

2. Isoclines (b),(d), and (e) meet at the point

$$(\hat{x}, \hat{y}, \hat{z}) = (0, 0, k_z), \tag{5.39*}$$

which describes the situations where the predator and its preferred prey, x, are extinct, and z can grow to its carrying capacity.

3. Isoclines (b),(c) and (f) intersect at the point

$$(\hat{x}, \hat{y}, \hat{z}) = (k_x, 0, 0), \tag{5.40*}$$

which describes the situation where the predator and the alternative prey are extinct, and prey x can grow to capacity.

4. The intersection of isoclines (b),(c), and (e) gives us the equilibrium

$$(\hat{x}, \hat{y}, \hat{z}) = (k_x, 0, k_z), \tag{5.41*}$$

which is the situation in which the predator is extinct, and both prey species can grow to their carrying capacity.

5. The intersection of isoclines (a), (d) and (e) describes the situation in which prey x is extinct, and yields the fixed point

$$\begin{aligned} &(0, \hat{y}, \hat{z}) \qquad \text{with} \\ &\hat{y} = \frac{r_z}{a}(1 - \frac{\mu}{ak_z(\gamma_z - \mu h_z)})(1 + \frac{\mu h_z}{\gamma_z - \mu h_z}) && (5.42^*) \\ &\hat{z} = \frac{\mu}{a(\gamma_z - \mu h_z)} && (5.43^*) \end{aligned}$$

provided that

$$\delta = 1\ , \qquad \mu < \frac{\gamma_z}{h_z}\ , \qquad k_z > \frac{\mu}{a\,(\gamma_z - \mu h_z)}. \tag{5.44*}$$

the requirement that δ be 1 translates to the requirement that

$$\begin{aligned} \hat{x} &< \frac{1}{a(h_z\frac{\gamma_x}{\gamma_z} - h_x)} \\ 0 &< \frac{1}{a(h_z\frac{\gamma_x}{\gamma_z} - h_x)} \\ \frac{\gamma_x}{h_x} &> \frac{\gamma_z}{h_z} \end{aligned} \tag{5.45*}$$

This is the requirement that x is the preferred (more profitable) prey (see 4.15), which is always the case in our system. Thus we see that whenever $x = 0$, δ will always be 1. This is what we would expect, since it simply means that if prey x is extinct, the predator will consume prey z.

6. The intersection of isoclines (a), (c) and (f) describes the situation in which prey z is extinct, and yields the fixed point

$$(\hat{x}, \hat{y}, \hat{z}) = (\hat{x}, \hat{y}, 0) \quad \text{with}$$
$$\hat{x} = \frac{\mu}{a(\gamma_x - \mu h_x)} \tag{5.46*}$$
$$\hat{y} = \frac{r_x}{a}(1 - \frac{\mu}{ak_x(\gamma_x - \mu h_x)})(1 + \frac{\mu h_x}{\gamma_x - \mu h_x}), \tag{5.47*}$$

provided that

$$\mu < \frac{\gamma_x}{h_x} \; , \qquad \text{and} \qquad k_x > \frac{\mu}{a\,(\gamma_x - \mu h_x)}. \tag{5.48*}$$

7. The intersection of isoclines (a), (c) and (g) describes the situation in which y and x are in equilibrium at a point where z is not included in the diet ($\delta = 0$). This means z can grow to its carrying capacity. The location of this fixed point is given by:

$$(\hat{x}, \hat{y}, \hat{z}) = (\hat{x}, \hat{y}, k_z) \quad \text{with}$$
$$\hat{x} = \frac{\mu}{a(\gamma_x - \mu h_x)} \tag{5.49*}$$
$$\hat{y} = \frac{r_x}{a}(1 - \frac{\mu}{ak_x(\gamma_x - \mu h_x)})(1 + \frac{\mu h_x}{\gamma_x - \mu h_x}) \tag{5.50*}$$

which only exists if

$$\delta = 0 \; , \qquad \mu < \frac{\gamma_x}{h_x} \;\; \text{and} \;\; k_x > \frac{\mu}{a\,(\gamma_x - \mu h_x)} \tag{5.51*}$$

the requirement that δ be zero at this point translates to the requirement that

$$\frac{\gamma_z}{h_z} < \mu < \frac{\gamma_x}{h_x} \tag{5.52*}$$

Thus we can say that this fixed point exists if it holds that:

$$\frac{\gamma_z}{h_z} < \mu < \frac{\gamma_x}{h_x} \;\; \text{and} \;\; k_x > \frac{\mu}{a\,(\gamma_x - \mu h_x)} \tag{5.53}$$

8. The point where isoclines (a), (c) and (e) intersect describes the situation where all three species coexist in equilibrium and z is included in the predators diet. We can show this fixed point to occur at

$$x = \frac{k_x}{a}\left[\frac{\alpha_z(r_x - r_z) + \mu r_z}{\beta}\right] \tag{5.54*}$$

$$y = \frac{r_x r_z}{a^2}\left[\frac{[\mu - \alpha_x - \alpha_z][\gamma_x k_x(-r_z + a h_z k_z(r_x - r_z)) - \gamma_z k_z(r_x + a h_x k_x(r_x - r_z))]}{\beta^2}\right] \tag{5.55*}$$

$$z = -\frac{k_z}{a}\left[\frac{\alpha_x(r_x - r_z) - \mu r_x}{\beta}\right] \tag{5.56*}$$

where

$$\alpha_x = a k_x(\gamma_x - \mu h_x) \tag{5.57}$$

$$\alpha_z = a k_z(\gamma_z - \mu h_z) \tag{5.58}$$

$$\beta = r_z k_x(\gamma_x - \mu h_x) + r_x k_z(\gamma_z - \mu h_z) \tag{5.59}$$

We would now like to know when this fixed point exists. In order for this fixed point to exist, x, y and z must all be positive numbers, and δ at this point must be 1 (z must be included in the diet). Let

$$I = \frac{\mu r_x}{a(\gamma_x - \mu h_x)(r_x - r_z)} \tag{5.60}$$

$$II = \frac{-\mu r_z}{a(\gamma_z - \mu h_z)(r_x - r_z)} \tag{5.61}$$

$$III = \frac{\mu - a k_x(\gamma_x - \mu h_x)}{a(\gamma_z - \mu h_z)} \tag{5.62}$$

$$IV = \frac{\mu - a k_z(\gamma_z - \mu h_z)}{a(\gamma_x - \mu h_x)} \tag{5.63}$$

$$V = \frac{\mu}{a(\gamma_x - \mu h_x)} \tag{5.64}$$

$$VI = \frac{\mu}{a(\gamma_z - \mu h_z)} \tag{5.65}$$

The following table shows the parameter ranges for which this fixed point exists:

9*. All other combinations of isoclines either never intersect, or yield duplicates of fixed points already mentioned above.

In summary, the fixed points of the 3-species system are given by:

<table>
<tr><td rowspan="6">$\mu < \dfrac{\gamma_z}{h_z}$</td><td rowspan="2">$r_x < r_z$</td><td>$k_x < V$</td><td>$III < k_z < II$</td></tr>
<tr><td>$k_x \geq V$</td><td>$k_z < II$</td></tr>
<tr><td rowspan="2">$r_x = r_z$</td><td>$k_x \leq V$</td><td>$k_z > III$</td></tr>
<tr><td colspan="2">$k_x > V$</td></tr>
<tr><td rowspan="2">$r_x > r_z$</td><td>$k_z < VI$</td><td>$IV < k_x < I$</td></tr>
<tr><td>$k_z \geq VI$</td><td>$k_x < I$</td></tr>
</table>

Table 5.1*: *The parametric ranges for which fixed point $(\hat{x}, \hat{y}, \hat{z})$ exists.*

trivial:

1). $(\hat{x}, \hat{y}, \hat{z}) = (0, 0, 0)$
2). $(\hat{x}, \hat{y}, \hat{z}) = (k_x, 0, 0)$
3). $(\hat{x}, \hat{y}, \hat{z}) = (0, 0, k_z)$
4). $(\hat{x}, \hat{y}, \hat{z}) = (k_x, 0, k_z)$

nontrivial:

5). $(\hat{x}, \hat{y}, \hat{z}) = (0, \hat{y}, \hat{z})$ with

$$\hat{y} = \frac{r_z}{a}(1 - \frac{\mu}{ak_z(\gamma_z - \mu h_z)})(1 + \frac{\mu h_z}{\gamma_z - \mu h_z})$$
$$\hat{z} = \frac{\mu}{a(\gamma_z - \mu h_z)}$$

exists if

$$\mu < \frac{\gamma_z}{h_z}, \quad \text{and} \quad k_z > \frac{\mu}{a\,(\gamma_z - \mu h_z)}$$

6). $(\hat{x}, \hat{y}, \hat{z}) = (\hat{x}, \hat{y}, 0)$ with

$$\hat{x} = \frac{\mu}{a(\gamma_x - \mu h_x)}$$
$$\hat{y} = \frac{r_x}{a}(1 - \frac{\mu}{ak_x(\gamma_x - \mu h_x)})(1 + \frac{\mu h_x}{\gamma_x - \mu h_x})$$

exists if

$$\mu < \frac{\gamma_x}{h_x} \quad \text{and} \quad k_x > \frac{\mu}{a\,(\gamma_x - \mu h_x)}$$

7). $(\hat{x}, \hat{y}, \hat{z}) = (\hat{x}, \hat{y}, k_z)$ with

$$\hat{x} = \frac{\mu}{a(\gamma_x - \mu h_x)}$$
$$\hat{y} = \frac{r_x}{a}(1 - \frac{\mu}{ak_x(\gamma_x - \mu h_x)})(1 + \frac{\mu h_x}{\gamma_x - \mu h_x})$$

exists if

$$\frac{\gamma_z}{h_z} < \mu < \frac{\gamma_x}{h_x} \quad \text{and} \quad k_x > \frac{\mu}{a\,(\gamma_x - \mu h_x)}$$

8). $(\hat{x}, \hat{y}, \hat{z})$ with:

$$\hat{x} = \frac{k_x}{a}\left[\frac{\alpha_z(r_x - r_z) + \mu r_z}{\beta}\right]$$

$$\hat{y} = \frac{r_x r_z}{a^2}\left[\frac{[\mu - \alpha_x - \alpha_z][\gamma_x k_x(-r_z + a h_z k_z(r_x - r_z)) - \gamma_z k_z(r_x + a h_x k_x(r_x - r_z))]}{\beta^2}\right]$$

$$\hat{z} = -\frac{k_z}{a}\left[\frac{\alpha_x(r_x - r_z) - \mu r_x}{\beta}\right]$$

where

$$\alpha_x = a k_x(\gamma_x - \mu h_x)$$
$$\alpha_z = a k_z(\gamma_z - \mu h_z)$$
$$\beta = r_z k_x(\gamma_x - \mu h_x) + r_x k_z(\gamma_z - \mu h_z)$$

which exists for:

$\mu < \frac{\gamma_z}{h_z}$	$r_x < r_z$	$k_x < V$	$III < k_z < II$
		$k_x \geq V$	$k_z < II$
	$r_x = r_z$	$k_x \leq V$	$k_z > III$
		$k_x > V$	
	$r_x > r_z$	$k_z < VI$	$IV < k_x < I$
		$k_z \geq VI$	$k_x < I$

where

$$I = \frac{\mu r_x}{a(\gamma_x - \mu h_x)(r_x - r_z)}$$
$$II = \frac{-\mu r_z}{a(\gamma_z - \mu h_z)(r_x - r_z)}$$
$$III = \frac{\mu - a k_x(\gamma_x - \mu h_x)}{a(\gamma_z - \mu h_z)}$$
$$IV = \frac{\mu - a k_z(\gamma_z - \mu h_z)}{a(\gamma_x - \mu h_x)}$$
$$V = \frac{\mu}{a(\gamma_x - \mu h_x)}$$
$$VI = \frac{\mu}{a(\gamma_z - \mu h_z)}$$

5.2.2 Stability Analysis

In the 3-species system, we now have a 3×3 Jacobian which we use to determine the stability of the fixed points. We rewrite equations 5.34-5.36 as:

$$\frac{dy}{dt} = yg_y(x, y, z) \tag{5.66}$$
$$\frac{dx}{dt} = xg_x(x, y, z) \tag{5.67}$$
$$\frac{dz}{dt} = zg_z(x, y, z), \tag{5.68}$$

where

$$g_y = -\mu + \frac{a(\gamma_x x + \delta\gamma_z z)}{1 + a(h_x x + \delta h_z z)} \tag{5.69}$$
$$g_x = r_x(1 - \frac{x}{k_x}) - \frac{ay}{1 + a(h_x x + \delta h_z z)} \tag{5.70}$$
$$g_z = r_z(1 - \frac{z}{k_z}) - \frac{\delta ay}{1 + a(h_x x + \delta h_z z)} \tag{5.71}$$

We can now express the Jacobian as:

$$\mathbf{J} = \begin{bmatrix} y\frac{dg_y}{dy} + g_y & y\frac{dg_y}{dx} & y\frac{dg_y}{dz} \\ x\frac{dg_x}{dy} & x\frac{dg_x}{dx} + g_x & x\frac{dg_x}{dz} \\ z\frac{dg_z}{dy} & z\frac{dg_z}{dx} & z\frac{dg_z}{dz} + g_z \end{bmatrix}, \tag{5.72}$$

We determine the partial derivatives to be:

$$\frac{dg_y}{dy} = 0 \tag{5.73*}$$
$$\frac{dg_y}{dx} = \frac{a\gamma_x}{1 + a(h_x x + \delta h_z z)} - \frac{a^2 h_x(\gamma_x x + \delta\gamma_z z)}{(1 + a(h_x x + \delta h_z z)^2} \tag{5.74*}$$
$$\frac{dg_y}{dz} = \frac{\delta a\gamma_z}{1 + a(h_x x + \delta h_z z)} - \frac{\delta a^2 h_z(\gamma_x x + \delta\gamma_z z)}{(1 + a(h_x x + \delta h_z z)^2} \tag{5.75*}$$

$$\frac{dg_x}{dy} = -\frac{a}{1 + a(h_x x + \delta h_z z)} \tag{5.76*}$$
$$\frac{dg_x}{dx} = -\frac{r_x}{k_x} + \frac{a^2 h_x y}{(1 + a(h_x x + \delta h_z z))^2} \tag{5.77*}$$
$$\frac{dg_x}{dz} = \frac{\delta a^2 h_z y}{(1 + a(h_x x + \delta h_z z))^2} \tag{5.78*}$$
$$\tag{5.79*}$$

$$\frac{dg_z}{dy} = -\frac{\delta a}{1 + a(h_x x + \delta h_z z)} \tag{5.80*}$$

$$\frac{dg_z}{dx} = \frac{\delta a^2 h_x y}{(1 + a(h_x x + \delta h_z z))^2} \tag{5.81*}$$

$$\frac{dg_z}{dz} = -\frac{r_z}{k_z} + \frac{\delta^2 a^2 h_z y}{(1 + a(h_x x + \delta h_z z))^2} \tag{5.82*}$$

Trivial Fixed Points

There are four trivial fixed points in this system, which describe situations in which the predator is extinct. Since the two prey species do not interact, they will be either extinct or at carrying capacity. We will now discuss them and determine their stability:

1). $(\hat{\mathbf{x}}, \hat{\mathbf{y}}, \hat{\mathbf{z}}) = (\mathbf{0}, \mathbf{0}, \mathbf{0})$
At this fixed point, all species are extinct. Intuitively, we can see that this equilibrium is a saddle point; if there were a small increase in the population of x, the absence of a predator will allow them to grow at a rate of r_x until they reach their carrying capacity k_x. Thus we say that this fixed point is unstable against invasion by x. The same argument holds for invasion by z. If there is a small increase in the population of the predator y however, then they would not be able to survive due to lack of prey, and the system would return to the fixed point $(0, 0, 0)$. We say that the fixed point is stable against invasion by y. Since this equilibrium is stable in one direction, but unstable in others, we are dealing with a *saddle point*.

We can also show analytically that this fixed point is unstable, using the Jacobian. If we evaluate the Jacobian at the point $(0, 0, 0)$, we get:

$$\mathbf{J} = \begin{bmatrix} g_y & 0 & 0 \\ 0 & g_x & 0 \\ 0 & 0 & g_z \end{bmatrix}_{(0,0,0)} = \begin{bmatrix} -\mu & 0 & 0 \\ 0 & r_x & 0 \\ 0 & 0 & r_z \end{bmatrix}. \tag{5.83*}$$

The eigenvalues are $-\mu, r_x$ and r_z, two of which are positive, and one of which is negative. Thus this fixed point is a saddle point. Moreover, since this is a diagonal matrix, the eigenvectors are the standard basis vectors. This means that the eigenvalue in the y-direction is $-\mu$, and since this is always a negative number, we know that the fixed point is stable in the y-direction. In the same manner we conclude that the fixed point is unstable in the x- and z-directions, which confirms exactly what we deduced intuitively.

2). $(\hat{\mathbf{x}}, \hat{\mathbf{y}}, \hat{\mathbf{z}}) = (\mathbf{k_x}, \mathbf{0}, \mathbf{0})$
At this fixed point, both the predator and prey z have become extinct, which has allowed prey x to grow to its carrying capacity. We will again start by giving an intuitive argument for its stability. Say there is now a small increase in the population of z, since the two prey species do not interact, and there is no predator, the population of z can continue to grow until its carrying capacity is reached, which means the system will end up in the point $(k_x, 0, k_z)$. Thus we see that this fixed point is unstable against invastion by z. If there is a small change in the population of x, the system will return to the original fixed point, meaning that it is stable against changes in

x. If there is an increase in y however, they will start consuming the prey x, and if the mortality rate isn't higher than the rate at which they can produce offspring due to the consumption of x (i.e. if $\mu < \frac{\gamma_x}{h_x}$), then the predators are able to survive, and the system moves away from the fixed point.

We will now analytically show that our intuition is correct. The Jacobian at this point is given by:

$$\mathbf{J} = \begin{bmatrix} g_y & 0 & 0 \\ k_x \frac{dg_x}{dy} & k_x \frac{dg_x}{dx} + g_x & k_x \frac{dg_x}{dz} \\ 0 & 0 & g_z \end{bmatrix}_{(k_x,0,0)} = \begin{bmatrix} -\mu + \frac{a\gamma_x k_x}{1+ah_x k_x} & 0 & 0 \\ -\frac{ak_x}{1+ah_x k_x} & -r_x & 0 \\ 0 & 0 & r_z \end{bmatrix}. \tag{5.84*}$$

Since this matrix is triangular, the entries on the main diagonal are exactly the eigenvalues. From this we see that we have both positive eigenvalues ($\lambda = r_z$) and negative eigenvalues ($\lambda = -r_x$), which means that this fixed point is a saddle point, and therefore unstable. More specifically, we can see that this fixed point is unstable in the z-direction (the corresponding eigenvalue is r_z and always positive). In the x-direction, the eigenvalue is $-r_x$, and thus stable. The remaining eigenvalue is:

$$-\mu + \frac{a\gamma_x k_x}{1 + ah_x k_x} \tag{5.85}$$

The corresponding eigenvector is not a standard basis vector, it is nonzero in both the x and y directions, which tells us that an increase in y also induces a change in the population of x. This is what we would expect since the predator will start to consume prey x.

We can determine that this eigenvalue is positive (unstable) if

$$\mu < \frac{\gamma_x}{h_x} \qquad \text{and} \qquad k_x > \frac{\mu}{a(\gamma_x - \mu h_x)} \tag{5.86*}$$

This means that if the above conditions hold, then predator y is able to invade, and if the conditions do not hold, then the predators cannot survive, and the system will return to the equilibrium point.

3). $(\hat{\mathbf{x}}, \hat{\mathbf{y}}, \hat{\mathbf{z}}) = (\mathbf{0}, \mathbf{0}, \mathbf{k_z})$

This equilibrium describes the situation where both y and x have become extinct, and z has grown to carrying capacity. Note that since x is extinct, δ will be 1 around this point. Intuitively, we say that this point will be unstable against invasion by x, whose numbers would increase to k_x due to the absence of a predator. We also see that the fixed point is stable against changes in z. The predator is able to invade, only if the profitability of prey z is greater than the mortality rate, and if k_z is not too low.

The Jacobian at this point is:

$$\mathbf{J} = \begin{bmatrix} g_y & 0 & 0 \\ 0 & g_x & 0 \\ k_z \frac{dg_z}{dy} & k_z \frac{dg_z}{dx} & k_z \frac{dg_z}{dz} + g_z \end{bmatrix}_{(0,0,k_z)} = \begin{bmatrix} -\mu + \frac{a\gamma_z k_z}{1+ah_z k_z} & 0 & 0 \\ 0 & r_x & 0 \\ k_z \frac{dg_z}{dy} & 0 & -r_z \end{bmatrix}. \tag{5.87*}$$

The eigenvalues are again the entries on the main diagonal, and as in the previous situation, we have both a positive eigenvalue, ($\lambda = r_x$), and a negative one ($\lambda = -r_z$), which means this fixed point is a saddle point. More specifically, in the x-direction, the corresponding eigenvalue is r_x, and always positive, and thus unstable. In the z-direction, with corresponding eigenvalue r_z, the equilibrium is stable. The last eigenvalue, analogously to the previous fixed point, is:

$$-\mu + \frac{a\gamma_z k_z}{1 + a h_z k_z} \tag{5.88}$$

and is unstable if it holds that:

$$\mu < \frac{\gamma_z}{h_z} \qquad \text{and} \qquad k_z > \frac{\mu}{a(\gamma_z - \mu h_z)} \tag{5.89*}$$

So if the above conditions hold, then predator y is able to invade, and if the conditions do not hold, then the predators cannot survive, and the system will return to the equilibrium point.

4). $(\hat{\mathbf{x}}, \hat{\mathbf{y}}, \hat{\mathbf{z}}) = (\mathbf{k_x}, \mathbf{0}, \mathbf{k_z})$

This describes the situation in which the predator has become extinct, and both prey species were able to grow to their carrying capacities. Intuitively we find that any changes in the population of x or z will cause the system to return to the equilibrium, and predator y may be able to invade under certain conditions.

The Jacobian is given by:

$$\mathbf{J} = \begin{bmatrix} g_y & 0 & 0 \\ k_x \dfrac{dg_x}{dy} & k_x \dfrac{dg_x}{dx} + g_x & k_x \dfrac{dg_x}{d_z} \\ k_z \dfrac{dg_z}{dy} & k_z \dfrac{dg_z}{dx} & k_z \dfrac{dg_z}{dz} + g_z \end{bmatrix}_{(k_x,0,k_z)} = \begin{bmatrix} -\mu + \dfrac{a(\gamma_x k_x + \delta\gamma_z k_z)}{1 + a(h_x k_x + \delta h_z k_z)} & 0 & 0 \\ k_x \dfrac{dg_x}{dy} & -r_x & 0 \\ k_z \dfrac{dg_z}{dy} & 0 & -r_z \end{bmatrix}. \tag{5.90*}$$

The eigenvalues are again the entries on the diagonal. We see that this point is stable in both the x- and z-directions (eigenvalues $-r_x$ and $-r_z$ respectively). The remaining eigenvalue is

$$-\mu + \frac{a(\gamma_x k_x + \delta\gamma_z k_z)}{1 + a(h_x k_x + \delta h_z k_z)}. \tag{5.91}$$

If this is negative, then the fixed point is a stable attractor, otherwise it is a saddle point. The eigevalue is negative, and thus the fixed point stable, if the following holds:

$$\mu \geq \frac{\gamma_x}{h_x} \tag{5.92*}$$

or

$$\mu < \frac{\gamma_z}{h_z} \qquad \text{and} \qquad k_x < \frac{\mu}{a(\gamma_x - \mu h_x)} \qquad \text{and} \qquad k_z < \frac{\mu - a k_x(\gamma_x - \mu h_x)}{a(\gamma_z - \mu h_z)} \tag{5.93*}$$

or

$$\frac{\gamma_z}{h_z} \leq \mu < \frac{\gamma_x}{h_x} \qquad \text{and} \qquad k_x < \frac{\mu}{a(\gamma_x - \mu h_x)} \tag{5.94*}$$

If the above conditions do not hold, then the fixed point is a saddle point, and unstable against invasion by y.

Nontrivial Fixed Points

5). $(\hat{\mathbf{x}}, \hat{\mathbf{y}}, \hat{\mathbf{z}}) = (\mathbf{0}, \hat{\mathbf{y}}, \hat{\mathbf{z}})$

This describes the situation where the primary prey has become extinct, and the predator and secondary prey are at equilibrium. This means $\delta = 1$ near this fixed point. This fixed point is located at

$$(0, \hat{y}, \hat{z}) \qquad \text{with} \tag{5.95}$$

$$\hat{y} = \frac{r_z}{a}\left(1 - \frac{\mu}{a k_z(\gamma_z - \mu h_z)}\right)\left(1 + \frac{\mu h_z}{\gamma_z - \mu h_z}\right) \tag{5.96}$$

$$\hat{z} = \frac{\mu}{a(\gamma_z - \mu h_z)} \tag{5.97}$$

and is only feasible if it holds that

$$\mu < \frac{\gamma_z}{h_z} \qquad \text{and} \qquad k_z > \frac{\mu}{a\,(\gamma_z - \mu h_z)}. \tag{5.98}$$

In order to determine the stability of this fixed point, we look at the Jacobian at this point. We can say that $g_y = g_z = 0$ and we know that $x = 0$ at this point. This leads to the following Jacobian

$$\mathbf{J} = \begin{bmatrix} y\frac{dg_y}{dy} + g_y & y\frac{dg_y}{dx} & y\frac{dg_y}{dz} \\ x\frac{dg_x}{dy} & x\frac{dg_x}{dx} + g_x & x\frac{dg_x}{dz} \\ z\frac{dg_z}{dy} & z\frac{dg_z}{dx} & z\frac{dg_z}{dz} + g_z \end{bmatrix}_{(0,\hat{y},\hat{z})} = \begin{bmatrix} 0 & y\frac{dg_y}{dx} & y\frac{dg_y}{dz} \\ 0 & g_x & 0 \\ z\frac{dg_z}{dy} & z\frac{dg_z}{dx} & z\frac{dg_z}{dz} \end{bmatrix}_{(0,\hat{y},\hat{z})} \tag{5.99}$$

We can show that this fixed point is an *attractor* (stable) if it holds that:

$$\mu < \frac{\gamma_z}{h_z} \quad , \quad VI < k_z < VIII \qquad r_z \geq X \quad , \quad r_x < XII, \tag{5.100*}$$

and a *repeller* (unstable) if:

$$\mu < \frac{\gamma_z}{h_z} \quad , \quad k_z > VIII \quad , \quad r_z \geq X \quad , \quad r_x > XII, \tag{5.101*}$$

And a *saddle point* otherwise. Here we have

$$VI = \frac{\mu}{a(\gamma_z - \mu h_z)} \tag{5.102}$$

$$VII = \frac{\gamma_x + \mu h_x}{a h_x(\gamma_x - \mu h_x)} \tag{5.103}$$

$$VIII = \frac{\gamma_z + \mu h_z}{a h_z(\gamma_z - \mu h_z)} \tag{5.104}$$

$$IX = \frac{4a\gamma_x k_x(\gamma_x - \mu h_x)^2(-\mu + a k_x(\gamma_x - \mu h_x))}{\mu(\gamma_x - a\gamma_x h_x k_x + \mu h_x(1 + a h_x k_x))^2} \tag{5.105}$$

$$X = \frac{4a\gamma_z k_z(\gamma_z - \mu h_z)^2(-\mu + a k_z(\gamma_z - \mu h_z))}{\mu(\gamma_z - a\gamma_z h_z k_z + \mu h_z(1 + a h_z k_z))^2} \tag{5.106}$$

$$XI = r_x \frac{-\mu + a k_x(\gamma_x - \mu h_x)}{a k_x(\gamma_x - \mu h_x)} \tag{5.107}$$

$$XII = r_z \frac{-\mu + a k_z(\gamma_z - \mu h_z)}{a k_z(\gamma_z - \mu h_z)} \tag{5.108}$$

6). $(\hat{\mathbf{x}}, \hat{\mathbf{y}}, \hat{\mathbf{z}}) = (\hat{\mathbf{x}}, \hat{\mathbf{y}}, \mathbf{0})$
This fixed point describes the situation in which the alternative prey is extinct, and predator y and prey x are in equilibrium. The values for y and x at this point are given by:

$$\hat{x} = \frac{\mu}{a(\gamma_x - \mu h_x)} \tag{5.109}$$

$$\hat{y} = \frac{r_x}{a}\left(1 - \frac{\mu}{a k_x(\gamma_x - \mu h_x)}\right)\left(1 + \frac{\mu h_x}{\gamma_x - \mu h_x}\right) \tag{5.110}$$

and is only feasible if it holds that

$$\mu < \frac{\gamma_x}{h_x} \qquad \text{and} \qquad k_x > \frac{\mu}{a\,(\gamma_x - \mu h_x)}. \tag{5.111}$$

Recall from 5.72 that the Jacobian for the 3-species system is given by:

$$\mathbf{J} = \begin{bmatrix} y\frac{dg_y}{dy} + g_y & y\frac{dg_y}{dx} & y\frac{dg_y}{dz} \\ x\frac{dg_x}{dy} & x\frac{dg_x}{dx} + g_x & x\frac{dg_x}{dz} \\ z\frac{dg_z}{dy} & z\frac{dg_z}{dx} & z\frac{dg_z}{dz} + g_z \end{bmatrix}, \tag{5.112}$$

Since y and x are nonzero, we know g_y and g_x are zero. (Since equations 5.66 and 5.67 must be satisfied). Furthermore, we know that $z = 0$ at this fixed point.

We can show that this fixed point is an attractor if

$$\mu < \frac{\gamma_z}{h_z} \quad , \quad V < k_x < VII \quad , \quad r_x \geq IX \quad , \quad r_z < XI, \tag{5.113*}$$

and a repeller if

$$\mu < \frac{\gamma_x}{h_x} \quad , \quad k_x > VII \quad , \quad r_x \geq IX \quad , \text{ and } \quad \left[\mu > \frac{\gamma_z}{h_z} \quad \text{or} \quad r_z > XI\right]. \tag{5.114*}$$

In all other cases, this fixed point is a saddle point.

7). $(\hat{\mathbf{x}}, \hat{\mathbf{y}}, \hat{\mathbf{z}}) = (\hat{\mathbf{x}}, \hat{\mathbf{y}}, \mathbf{k_z})$

We have seen that this is a fixed point, only if

$$\frac{\gamma_z}{h_z} < \mu < \frac{\gamma_x}{h_x} \tag{5.115}$$

which also implies $\delta = 0$. Filling in the Jacobian gives us:

$$\mathbf{J} = \begin{bmatrix} y\frac{dg_y}{dy} + g_y & y\frac{dg_y}{dx} & 0 \\ x\frac{dg_x}{dy} & x\frac{dg_x}{dx} + g_x & 0 \\ 0 & 0 & -r_z \end{bmatrix}_{\delta=0} \tag{5.116}$$

Since $\delta = 0$, the upper-left portion of this Jacobian corresponds exactly to the system without z. The eigenvalues are $-r_z$ and the eigenvalues of the upper-left portion. Since $-r_z$ is always negative, this fixed point is stable if the system without z is stable, and a saddle point otherwise. This means that this fixed point, which is given by:

$$(\hat{x}, \hat{y}, k_z) \quad \text{with} \tag{5.117}$$

$$\hat{x} = \frac{\mu}{a(\gamma_x - \mu h_x)} \tag{5.118}$$

$$\hat{y} = \frac{r_x}{a}\left(1 - \frac{\mu}{ak_x(\gamma_x - \mu h_x)}\right)\left(1 + \frac{\mu h_x}{\gamma_x - \mu h_x}\right), \tag{5.119}$$

is only feasible if it holds that

$$\frac{\gamma_z}{h_z} < \mu < \frac{\gamma_x}{h_x} \quad \text{and} \quad k_x > \frac{\mu}{a\,(\gamma_x - \mu h_x)}, \tag{5.120}$$

and only is stable iff

$$k_x < \frac{\gamma_x + \mu h_x}{ah_x(\gamma_x - \mu h_x)}. \tag{5.121}$$

In summary, the stability of the fixed points 1-7 is given by:

trivial:

1). $(\hat{x}, \hat{y}, \hat{z}) = (0, 0, 0)$ *saddle point*

2). $(\hat{x}, \hat{y}, \hat{z}) = (k_x, 0, 0)$ *saddle point*

3). $(\hat{x}, \hat{y}, \hat{z}) = (0, 0, k_z)$ *saddle point*

4). $(\hat{x}, \hat{y}, \hat{z}) = (k_x, 0, k_z)$ *attractor* iff

$$\mu \geq \frac{\gamma_x}{h_x}$$

or

$$\mu < \frac{\gamma_z}{h_z} \quad \text{and} \quad k_x < V \quad \text{and} \quad k_z < III$$

or

$$\frac{\gamma_z}{h_z} \leq \mu < \frac{\gamma_x}{h_x} \quad \text{and} \quad k_x < V$$

saddle point otherwise

nontrivial:

5). $(\hat{x}, \hat{y}, \hat{z}) = (0, \hat{y}, \hat{z})$

attractor iff $\mu < \frac{\gamma_z}{h_z}$, $VI < k_z < VIII$, $r_z \geq X$, $r_x < XII$

repellor iff $\mu < \frac{\gamma_z}{h_z}$, $k_z > VIII$, $r_z \geq X$, $r_x > XII$

saddle point otherwise

6). $(\hat{x}, \hat{y}, \hat{z}) = (\hat{x}, \hat{y}, 0)$

attractor iff $\mu < \frac{\gamma_z}{h_z}$, $V < k_x < VII$, $r_x \geq IX$, $r_z < XI$

repellor iff $\mu < \frac{\gamma_x}{h_x}$, $k_x > VII$, $r_x \geq IX$, $\left[\mu > \frac{\gamma_z}{h_z} \quad \text{or} \quad r_z > XI\right]$

saddle point otherwise

7). $(\hat{x}, \hat{y}, \hat{z}) = (\hat{x}, \hat{y}, k_z)$

attractor iff $\frac{\gamma_z}{h_z} < \mu < \frac{\gamma_x}{h_x}$, $V < k_x < VII$

saddle point otherwise

The following table shows which of the fixed points 1-7 exist for different parameter ranges, and what their stability is. Fixed points 1-3 always exist, and are always saddle points. Any of the other fixed points not mentioned do not exits for that parameter range.

$\mu \geq \frac{\gamma_x}{h_x}$					*a: 4*
$\frac{\gamma_z}{h_z} \leq \mu < \frac{\gamma_x}{h_x}$	$k_x < V$				*a: 4*
	$V < k_x < VII$				*a: 7 , s: 4, 6*
	$k_x > VII$	$r_x < IX$			*s: 4,6,7*
		$r_x > IX$			*r: 6 , s: 4,7*
$\mu < \frac{\gamma_z}{h_z}$	$k_x < V$	$k_z < III$			*a: 4*
		$III < k_z < VI$			*s: 4*
		$VI < k_z < VIII$	$r_z \geq X$ and $r_x < XII$		*a: 5, s: 4*
			$r_z < X$ or $r_x \geq XII$		*s: 4,5*
		$k_z > VIII$	$r_z \geq X$ and $r_x < XII$		*r: 5, s: 4*
			$r_z < X$ or $r_x \geq XII$		*s: 4,5*
	$V < k_x < VII$	$k_z < VI$	$r_x \geq IX$ and $r_z < XI$		*a: 6, s: 4*
			$r_x < IX$ or $r_z \geq XI$		*s: 4,6*
		$k_z > VI$	$r_x \geq IX$ and $r_z < XI$		*a: 6 s: 4*
			$r_x < IX$ or $r_z \geq XI$	$r_z \geq X$ and $r_x < XII$	*a: 5 s: 4,6*
				$r_z < X$ or $r_x \geq XII$	*s: 4,5,6*
	$k_x > VII$	$k_z < VI$	$r_x < IX$ or $r_z \leq XI$		*s: 4,6*
			$r_x \geq IX$ and $r_z > XI$		*r: 6 s: 4*
		$VI < k_z < VIII$	$r_x < IX$ or $r_z \leq XI$	$r_z \geq X$ and $r_x < XII$	*a: 5 s: 4,6*
				$r_z < X$ or $r_x \geq XII$	*s: 4,5,6*
			$r_x \geq IX$ and $r_z > XI$	$r_z \geq X$ and $r_x < XII$	*r: 6 a: 5, s:4*
				$r_z < X$ or $r_x \geq XII$	*r: 6, s: 4,5*
		$k_z > VIII$	$r_x < IX$ or $r_z \leq XI$	$r_z \geq X$ and $r_x > XII$	*r: 5 s: 4,6*
				$r_z < X$ or $r_x \leq XII$	*s: 4,5,6*
			$r_x \geq IX$ and $r_z > XI$	$r_z \geq X$ and $r_x > XII$	*r: 5,6, s:4*
				$r_z < X$ or $r_x \leq XII$	*r: 6, s: 4,5*

Table 5.2: *Existence and stability of fixed points 4-7 for various parameter ranges. Fixed points 1-3 always exist and are always saddle points. a = attractor, r = repeller, s=saddle.*

Here we have that:

$$I = \frac{\mu r_x}{a(\gamma_x - \mu h_x)(r_x - r_z)}$$
$$II = \frac{-\mu r_z}{a(\gamma_z - \mu h_z)(r_x - r_z)}$$
$$III = \frac{\mu - ak_x(\gamma_x - \mu h_x)}{a(\gamma_z - \mu h_z)}$$
$$IV = \frac{\mu - ak_z(\gamma_z - \mu h_z)}{a(\gamma_x - \mu h_x)}$$
$$V = \frac{\mu}{a(\gamma_x - \mu h_x)}$$
$$VI = \frac{\mu}{a(\gamma_z - \mu h_z)}$$
$$VII = \frac{\gamma_x + \mu h_x}{ah_x(\gamma_x - \mu h_x)}$$
$$VIII = \frac{\gamma_z + \mu h_z}{ah_z(\gamma_z - \mu h_z)}$$
$$IX = \frac{4a\gamma_x k_x(\gamma_x - \mu h_x)^2(-\mu + ak_x(\gamma_x - \mu h_x))}{\mu(\gamma_x - a\gamma_x h_x k_x + \mu h_x(1 + ah_x k_x))^2}$$
$$X = \frac{4a\gamma_z k_z(\gamma_z - \mu h_z)^2(-\mu + ak_z(\gamma_z - \mu h_z))}{\mu(\gamma_z - a\gamma_z h_z k_z + \mu h_z(1 + ah_z k_z))^2}$$
$$XI = r_x\frac{-\mu + ak_x(\gamma_x - \mu h_x)}{ak_x(\gamma_x - \mu h_x)}$$
$$XII = r_z\frac{-\mu + ak_z(\gamma_z - \mu h_z)}{ak_z(\gamma_z - \mu h_z)}$$

6 Methods for Numerical Analysis

Often it is not possible to find exact solutions to (sets of) differential equations. When this is the case, we will have to settle for an approximation to the solution. In this section we will discuss a few of the most commonly used numerical approaches.

Suppose we want to approximate the solution to the following differential equation and a given initial point:

$$\frac{dy}{dt} = f(y,t), \qquad y(t_0) = y_0 \tag{6.1}$$

Euler Method
One of the simplest approximation methods is the Euler method. It is computationally cheap, but since it is only a first order approximation, the error term is second order in the time step and thus not accurate enough for most purposes. Given a value at time t, we approximate the solution at time $t+h$ by taking a step of size h along the tangent at point t:

$$y_{t+h} = y_t + hf(y,t) \tag{6.2}$$

A graphical representation of this approach is given in figure 6.1

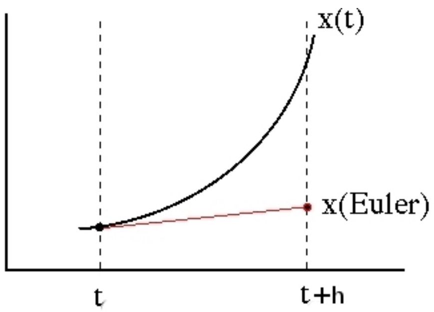


Figure 6.1: *The Euler method*

As mentioned earlier, the error in this approach is $O(h^2)$.

Midpoint Method
The midpoint method is computationally more expensive than the Euler method, but its error is $O(h^3)$. The name of this method comes from the fact that it employs a Euler *trial step* to the midpoint of the interval, $t + \frac{1}{2}h$, and evaluates the function f at that that halfway point, and uses that value to jump from t to $t+h$:

$$y_{t+h} = y_t + hf(y + \frac{h}{2}f(y,t), t + \frac{h}{2}) \tag{6.3}$$

A graphical representation of this method is given in the figure 6.2.

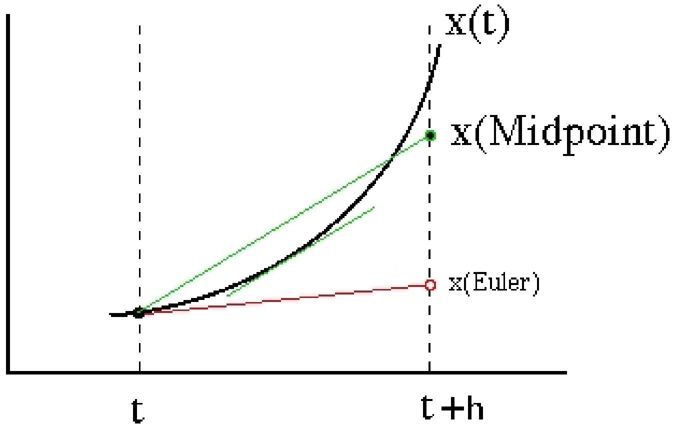


Figure 6.2: *The midpoint method. Given the value at point t, the midpoint method approximates the value at $t + h$ by taking a Euler step towards the midpoint of the interval and evaluating f(y,t) at that point.*

4th order Runge-Kutta Method
The fourth-order Runge-Kutta method is the most widely used integration method. It more computationally intensive than the method discussed previously, but also more accurate, the error term being $O(h^5)$. This method is similar to the midpoint method, but instead of taking a single *trial step*, it takes four, and uses their weighted average to approximate the value at time $t + h$:

$$
\begin{aligned}
k_1 &= hf(y,t) \\
k_2 &= hf(y + \frac{h}{2}k_1, t + \frac{h}{2}) \\
k_2 &= hf(y + \frac{h}{2}k_2, t + \frac{h}{2}) \\
k_4 &= hf(y + hk_3, t + h)
\end{aligned}
$$

$$y_{t+h} = y_t + \frac{1}{6}(k_1 + 2k_2 + 2k_3 + k_4)$$

The graphical representation is given in figure 6.3.

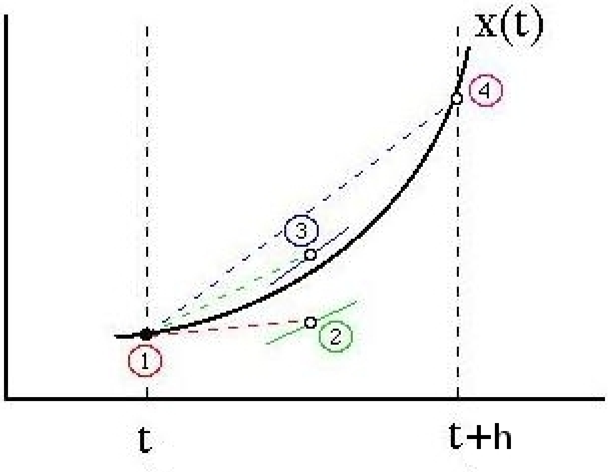


Figure 6.3: *The fourth order Runge-Kutta method (RK4). Given the value at time t, a weighted average of four trial steps is used to approximate the value at time $t + h$*

6.1 Finding Cycles

We can also look for orbits (cycles) in the system using numerical methods. An orbit must always have a fixed point in its interior. This fixed point may be attracting or repelling. Figure 6.4 shows phase portraits for three different kinds of orbits in a 2-dimensional system.

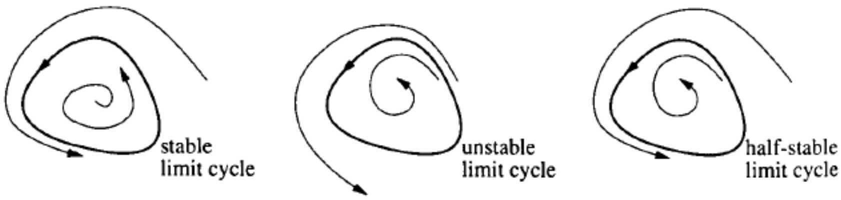


Figure 6.4: *Orbits can be stable, unstable or half-stable.*

A stable orbit attracts nearby points both in its interior and it exterior. Unstable orbits repel all nearby points, and half-stable orbits attract nearby points from one side, and repel nearby points from the other.

We can now look for orbits by starting from a point nearby a fixed point and iterating the system until we reach a cycle. If the fixed point is repelling, we start at a nearby point, and iterate forward in time. This will cause the system to end up in the orbit, if it exists. If the fixed point is attracting however, starting from a point nearby the fixed point will cause the system to end up in the fixed point. In order to find an orbit surrounding a stable fixed point, we start from a nearby point and iterate the system *backward* in time.

7 Single Patch Numerical Analysis

In this section we will look more closely at the dynamics of the predator prey system. We have already determined the various fixed points and their stability. We will now analyze the system further through numerical simulations.

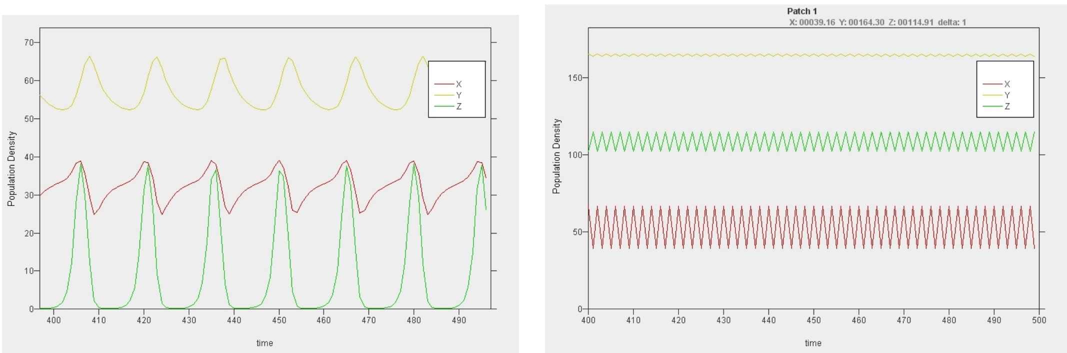
Even though we have not analytically shown the conditions for stability of fixed point 8, we can still determine a number of other things about this fixed point. For example we determine that the following statement holds:

If fixed point 8 exists, no other fixed point is stable. (7.1*)

Furthermore, we can see from table 5.2, that if there is a stable fixed point, it is the only fixed point which is stable.

Determining the conditions for stability for fixed point 8 analytically proved too involved, but we can determine some properties of this fixed point numerically. For instance, we find that this fixed point can be stable (see save file `fp8attractor.params`). A small perturbation from the equilibrium will cause the system to eventually end up back in the fixed point. This return can be swift (`fp8swiftreturn.params`), or may be preceded by damped oscillations, which may persist for many iterations before the system returns to the equilibrium. (`fp8oscillations.params`).

Fixed point 8 can also be repelling (`fp8repeller.params`). The repelling fixed point may also be surrounded by a stable orbit (`fp8orbit.params`, `fp8orbit2.params`). These orbits are also shown in figure 7.1.



(a) (b)

Figure 7.1: *Fixed point 8 can be surrounded by a stable orbit.*

From this figure, you can see that the shape of the orbits may differ significantly. In figure 1(a) we see that prey z undergoes enormous fluctuations during the cycle, reaching levels of almost zero and then shooting up again. In the second example (1(b)), we see that the cycle has a shorter period, and that the species' densities do not fluctuate as heavily.

We would like to find cycles in this system. A limit cycle must always surround a fixed point.

This fixed point must either be an attractor or a repeller. To find an orbit (cycle) around a repelling fixed point, we start from a point nearby the fixed point, and iterate forward in time until we reach the orbit. To find an orbit around an attractive fixed point, we also start from a point nearby the fixed point, but now we go backward in time from this point, to see if we end up in an orbit.

Since we have a discontinuity in our system due to the variable δ, it is also possible in our system that an orbit surrounds a saddle point. For instance consider fixed point 6, $(\hat{x}, \hat{y}, 0)$. If this occurs at a point where $\delta = 0$, then z is able to invade, making the fixed point unstable. But since z is not included in the diet, it is not really part of the system, and the increase in z will not influence the dynamics of the predator and the primary prey at all. So if the saddle point is stable in both the x and y directions, it may still be surrounded by an orbit. prey z will just not be part of this cycle. An example of this is stored in the save file `2speciesorbit.params`. A screen shot can be seen in figure 7.2. Starting from either fixed point 6 or fixed point 7, a small perturbation will lead to a cycle involving x and y, while z is either extinct or at carrying capacity. But since z is not involved in the dynamics, this is really just a 2-species system.

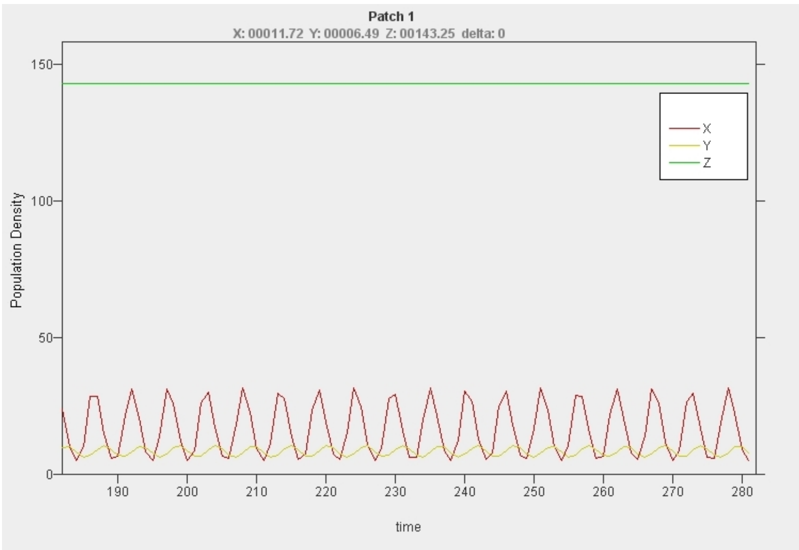


Figure 7.2: *Predator and primary prey are locked in a cycle, while alternative prey z does not influence the dynamics*

Because of this discontinuity in our system, we can also get unusual cycles. An example of such a cycle is stored in save file `interestingcycle.params`. This cycle was found by starting either in fixed point 6 ($(\hat{x}, \hat{y}, 0)$), or fixed point 7 ($(\hat{x}, \hat{y}, k_z)$) and perturbing the system (by hitting the *perturb* button). The resulting cycle is one in which the alternative prey z is at first not included in the predators' diet, but after a while the density of prey x decreases so much that prey z is included, which allows the density of prey x to increase again, up to a point where prey z is no longer hunted by the predator. This causes the density of prey x to decrease again, and so on. Screen shots of this cycle can be found in figure 7.3.

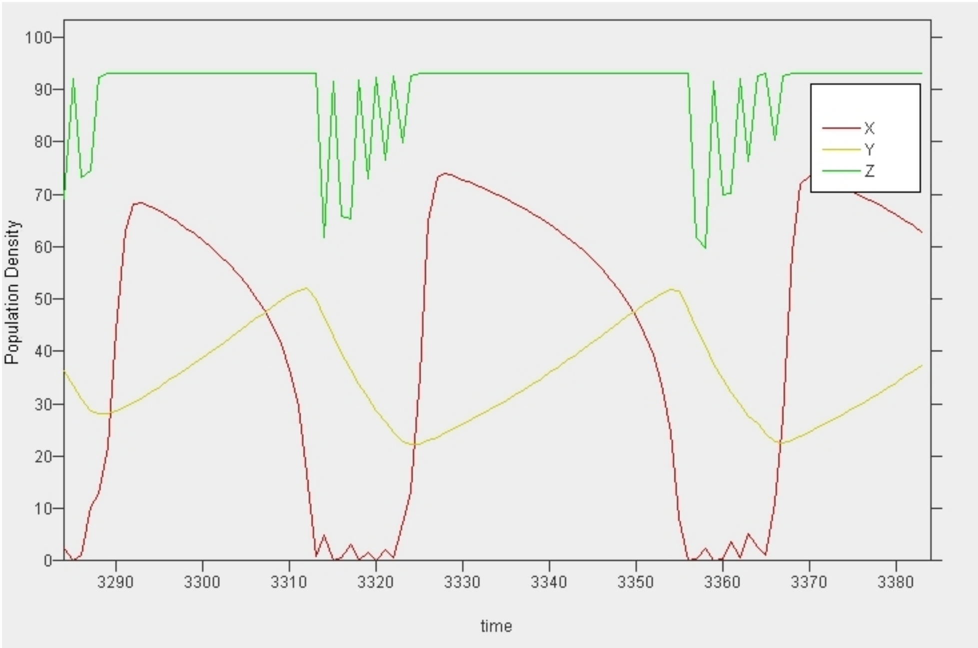


Figure 7.3: *A cycle in which alternative prey z is alternately included and not included in the predators diet.*

8 Landscape Model

To model a landscape, we construct a network of habitat patches, each with its own predator-prey system, which are connected through migration. The parameters of the predator-prey system can differ from one patch to another. For example, the attack rate a may be high in one patch, but low in another, as some patches may provide better hiding places for prey, which makes them harder to find for the predator. Mortality rate μ of the predator may also differ between patches indicating some habitats may constitute a more hospitable environment for the predator than other patches. The carrying capacity k can also vary between patches, indicating different sizes of the habitat patches. In this way we introduce spatial heterogeneity into our model.

Patches are connected to each other by migration channels, which are modelled as intermediate patches. In these intermediate patches, no interaction occurs between predator and prey. Using these intermediate patches enables us to simulate the delay involved in migration.

Figure 8.1 below shows the general form of such a system for three patches:

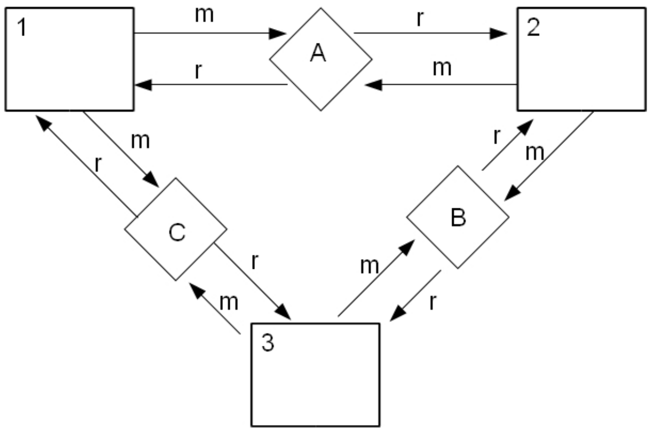


Figure 8.1: *The general form of the landscape model*

Predator y and/or prey x migrate according to a migration rate m and proportional to some migration function $E_i(x, y, z)$. For now we will assume this migration function is simply a proportion of the population. In other words, at any given time, a certain proportion of the population spontaneously decides to migrate, $E_x(x, y, z) = mx$. Note that prey z does not migrate in this model.

In each intermediate patch, there is a mortality rate which models the probability of dying during migration. This can also be used to indicate the danger of the landscape between patches. For instance, if there were a highway between two patches, the mortality rate may be very high. Species residing in the intermediate patch leave it at a rate of r, either back to where they came from, or on to the other patch.

We now distinguish three different cases, namely the one in which only the predator migrates, the case in which only prey x migrates, and the case where they both migrate. We will now give the full set of differential equations describing the system for each of these cases.

Let

$$Sx(x,y,z) = \frac{dy}{dt} = y\left[-\mu + \frac{a(\gamma_x x + \delta\gamma_z z)}{1 + a(h_x x + \delta h_z z)}\right] \tag{8.1}$$

$$Sy(x,y,z) = \frac{dx}{dt} = x\left[r_x(1 - \frac{x}{k_x}) - \frac{ay}{1 + a(h_x x + \delta h_z z)}\right] \tag{8.2}$$

$$Sz(x,y,z) = \frac{dz}{dt} = z\left[r_z(1 - \frac{z}{k_z}) - \frac{\delta ay}{1 + a(h_x x + \delta h_z z)}\right] \tag{8.3}$$

$$\delta = \begin{cases} 1 & \text{if} \quad x \le \dfrac{1}{a\left(h_z \dfrac{\gamma_x}{\gamma_z} - h_x\right)} \\ \\ 0 & \text{otherwise} \end{cases} \tag{8.4}$$

denote the single-patch dynamics.

8.1 Only Predator Migrates

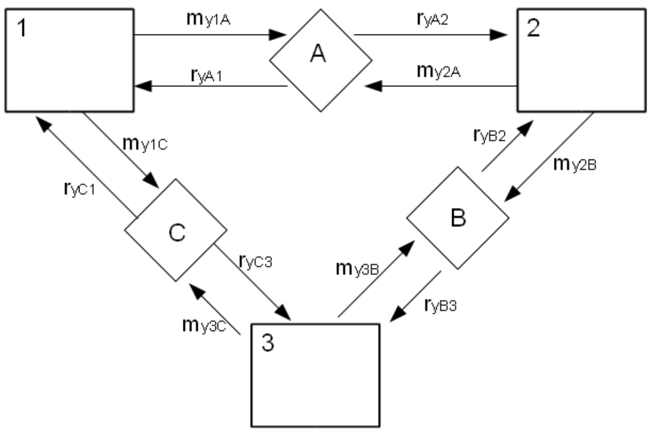


Figure 8.2: *The landscape model when only the predator migrates.*

patch 1:

$$\begin{aligned} \frac{dx_1}{dt} &= Sx_1(x_1, y_1, z_1) \\ \frac{dy_1}{dt} &= Sy_1(x_1, y_1, z_1) - y_1(m_{y12} + m_{y13}) + r_{y_{A1}}\ y_A + r_{y_{C1}}\ y_C \\ \frac{dz_1}{dt} &= Sz_1(x_1, y_1, z_1) \end{aligned}$$

patch 2:

$$\begin{aligned}
\frac{dx_2}{dt} &= Sx_2(x_2, y_2, z_2) \\
\frac{dy_2}{dt} &= Sy_2(x_2, y_2, z_2) - y_2(m_{y21} + m_{y23}) + r_{y_{A2}}\ y_A + r_{y_{B2}}\ y_B \\
\frac{dz_2}{dt} &= Sz_2(x_2, y_2, z_2)
\end{aligned}$$

patch 3:

$$\begin{aligned}
\frac{dx_3}{dt} &= Sx_3(x_3, y_3, z_3) \\
\frac{dy_3}{dt} &= Sy_3(x_3, y_3, z_3) - y_3(m_{y31} + m_{y32}) + r_{y_{B3}}\ y_B + r_{y_{C3}}\ y_C \\
\frac{dz_3}{dt} &= Sz_3(x_3, y_3, z_3)
\end{aligned}$$

intermediate patches:

$$\begin{aligned}
\frac{dy_A}{dt} &= -\mu_{y_A} y_A + m_{y12} y_1 + m_{y21} y_2 - y_A(r_{y_{A1}} + r_{y_{A2}}) \\
\frac{dy_B}{dt} &= -\mu_{y_B} y_B + m_{y23} y_2 + m_{y32} y_3 - y_B(r_{y_{B2}} + r_{y_{B3}}) \\
\frac{dy_C}{dt} &= -\mu_{y_C} y_C + m_{y13} y_1 + m_{y31} y_3 - y_C(r_{y_{C1}} + r_{y_{C3}})
\end{aligned}$$

8.2 Only Prey Migrates

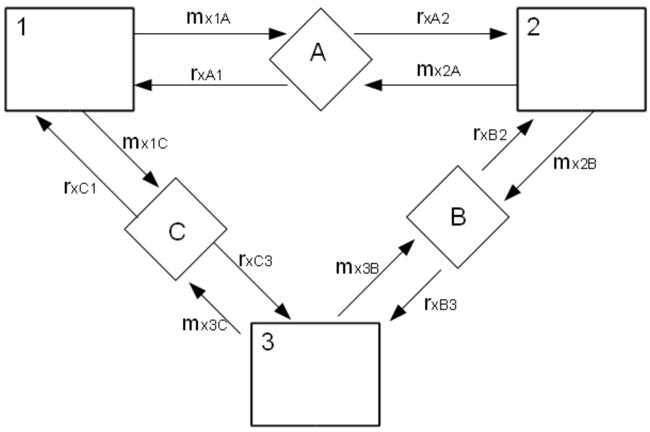


Figure 8.3: *The landscape model when only the prey migrates.*

patch 1:

$$\frac{dx_1}{dt} = Sx_1(x_1, y_1, z_1) - x_1(m_{x12} + m_{x13}) + r_{x_{A1}}\ x_A + r_{x_{C1}}\ x_C$$

$$\frac{dy_1}{dt} = Sy_1(x_1, y_1, z_1)$$

$$\frac{dz_1}{dt} = Sz_1(x_1, y_1, z_1)$$

patch 2:

$$\frac{dx_2}{dt} = Sx_2(x_2, y_2, z_2) - x_2(m_{x21} + m_{x23}) + r_{x_{A2}}\ x_A + r_{x_{B2}}\ x_B$$

$$\frac{dy_2}{dt} = Sy_2(x_2, y_2, z_2)$$

$$\frac{dz_2}{dt} = Sz_2(x_2, y_2, z_2)$$

patch 3:

$$\frac{dx_3}{dt} = Sx_3(x_3, y_3, z_3) - x_3(m_{x31} + m_{x32}) + r_{x_{B3}}\ x_B + r_{x_{C3}}\ x_C$$

$$\frac{dy_3}{dt} = Sy_3(x_3, y_3, z_3)$$

$$\frac{dz_3}{dt} = Sz_3(x_3, y_3, z_3)$$

intermediate patches:

$$
\begin{aligned}
\frac{dx_A}{dt} &= -\mu_{x_A} x_A + m_{x12} x_1 + m_{x21} x_2 - x_A(r_{x_{A1}} + r_{x_{A2}}) \\
\frac{dx_B}{dt} &= -\mu_{x_B} x_B + m_{x23} x_2 + m_{x32} x_3 - x_B(r_{x_{B2}} + r_{x_{B3}}) \\
\frac{dx_C}{dt} &= -\mu_{x_C} x_C + m_{x13} x_1 + m_{x31} x_3 - x_C(r_{x_{C1}} + r_{x_{C3}})
\end{aligned}
\tag{8.5}
$$

8.3 Predator and Prey Both Migrate

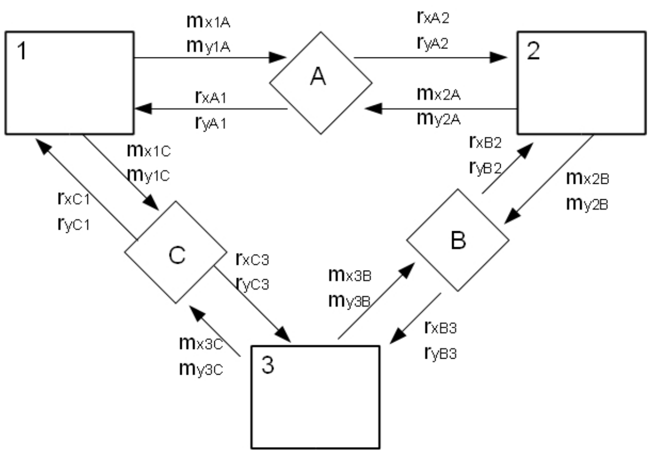


Figure 8.4: *The landscape model when both predator and prey migrate.*

The 3-patch system in which both the predator and the prey migrate can be described by the following set of differential equations:

patch 1:

$$
\begin{aligned}
\frac{dx_1}{dt} &= Sx_1(x_1, y_1, z_1) - x_1(m_{x12} + m_{x13}) + r_{x_{A1}}\ x_A + r_{x_{C1}}\ x_C \\
\frac{dy_1}{dt} &= Sy_1(x_1, y_1, z_1) - y_1(m_{y12} + m_{y13}) + r_{y_{A1}}\ y_A + r_{y_{C1}}\ y_C \\
\frac{dz_1}{dt} &= Sz_1(x_1, y_1, z_1)
\end{aligned}
$$

patch 2:

$$
\begin{aligned}
\frac{dx_2}{dt} &= Sx_2(x_2, y_2, z_2) - x_2(m_{x21} + m_{x23}) + r_{x_{A2}}\ x_A + r_{x_{B2}}\ x_B \\
\frac{dy_2}{dt} &= Sy_2(x_2, y_2, z_2) - y_2(m_{y21} + m_{y23}) + r_{y_{A2}}\ y_A + r_{y_{B2}}\ y_B \\
\frac{dz_2}{dt} &= Sz_2(x_2, y_2, z_2)
\end{aligned}
$$

patch 3:

$$\begin{aligned}
\frac{dx_3}{dt} &= Sx_3(x_3, y_3, z_3) - x_3(m_{x31} + m_{x32}) + r_{x_{B3}}\ x_B + r_{x_{C3}}\ x_C \\
\frac{dy_3}{dt} &= Sy_3(x_3, y_3, z_3) - y_3(m_{y31} + m_{y32}) + r_{y_{B3}}\ y_B + r_{y_{C3}}\ y_C \\
\frac{dz_3}{dt} &= Sz_3(x_3, y_3, z_3)
\end{aligned}$$

intermediate patches:

$$\begin{aligned}
\frac{dx_A}{dt} &= -\mu_{x_A} x_A + m_{x12} x_1 + m_{x21} x_2 - x_A(r_{x_{A1}} + r_{x_{A2}}) \\
\frac{dy_A}{dt} &= -\mu_{y_A} y_A + m_{y12} y_1 + m_{y21} y_2 - y_A(r_{y_{A1}} + r_{y_{A2}}) \\
\frac{dx_B}{dt} &= -\mu_{x_B} x_B + m_{x23} x_2 + m_{x32} x_3 - x_B(r_{x_{B2}} + r_{x_{B3}}) \\
\frac{dy_B}{dt} &= -\mu_{y_B} y_B + m_{y23} y_2 + m_{y32} y_3 - y_B(r_{y_{B2}} + r_{y_{B3}}) \\
\frac{dx_C}{dt} &= -\mu_{x_C} x_C + m_{x13} x_1 + m_{x31} x_3 - x_C(r_{x_{C1}} + r_{x_{C3}}) \\
\frac{dy_C}{dt} &= -\mu_{y_C} y_C + m_{y13} y_1 + m_{y31} y_3 - y_C(r_{y_{C1}} + r_{y_{C3}})
\end{aligned}$$

9 Multi-Patch Numerical Analysis

In order to study the effect migration has on this system, we conducted a series of numerical simulations. We started by looking at networks of identical patches, and investigated the effect of the migration parameters (m, r and μ), on the system. We did this for the two-patch system and the 3-patch system. The results are described in section 9.1. We then constructed a number of situations with some biological relevance. We looked at situations in which the predator or the prey is unable to survive in a single-patch system, and looked whether the creation of a *sanctuary patch* could be beneficial to the survival of the species. The results are described in section 9.2.

9.1 Identical Patches

We divided the predator prey system into a number of classes based on the parameter values. Which class a certain set of parameters falls into is determined by which fixed points exist and what their stabilities are. From table 5.2 we can determine that we can distinguish 17 different classes in this manner. These classes are listed below:

	attracting	repelling	saddle
1	4		
2	5		4
3	5		4,6
4	5	6	4
5	6		4
6	7		4,6
7		6	4
8		6	4,5
9		6	4,7
10		5	4
11		5	4,6
12		5,6	4
13			4
14			4,5
15			4,6
16			4,5,6
17			4,6,7

Note that we have no information about the stability of fixed point 8, but we do know something about when fixed point 8 exists. Each of the above can be split into two, one where fixed point 8 exists, and one where it does not, yielding a maximum of 34 cases. However, fixed point 8 may never exist for some of the above cases, or may always exist, so this number may turn out lower. For example, we know that we never have have that both fixed point 7 and fixed point 8 exist.

We then started each of the patches in one of the fixed points, and ran simulations for different values of the migration and return rates, and the mortality rate in the intermediate patches. We did this for the situation where only the prey migrates, only the predator, and both. We repeated this for each of the fixed points which exist as the starting point. When starting from a fixed point in which one of the species is extinct, we perturbed the starting point slightly, to ensure all three species are present initially.

This approach yields a great number of situations, in order reduce the number of simulations, we used a single migration rate per species, and set the return rate equal to this. In other words, for the 3-patch system we have $m_{x1A}, m_{x2A}, m_{x1C}, m_{x3C}, m_{x1B}, m_{x2B}, r_{xA1}, r_{xA2}, r_{xB2}, r_{xB3}, r_{xC1}, r_{xC3}$ all equal. The migration and return rates of predator y are also all equal to each other, though possibly different to the rates of prey x. Furthermore, we decided only to consider situations in which fixed point 8 exists, because all other fixed points are essentially 2-species systems. We let the simulations run until an equilibrium was reached, either a stable state or a cycle. Because we have identical patches and symmetric migration, each of the patches will have the same population levels in this equilibrium.

Below are the results of these simulations. We first looked at the situations in which a 3-species equilibrium exists in which the alternative prey z participates in the dynamics. In other words, we looked at cases in which fixed point 8, $(\hat{x}, \hat{y}, \hat{z})$, exists. Next we looked at situations in which we know that a stable cycle exists in the single patch case. Then we give an example of cycles induced by migration. In these situations no cycles exist in the single patch system, but when migration is present, cycles can appear. And finally we looked at situations in which the prey is unable to survive, and investigated the idea of having a *sanctuary patch*, a patch where predators are kept out.

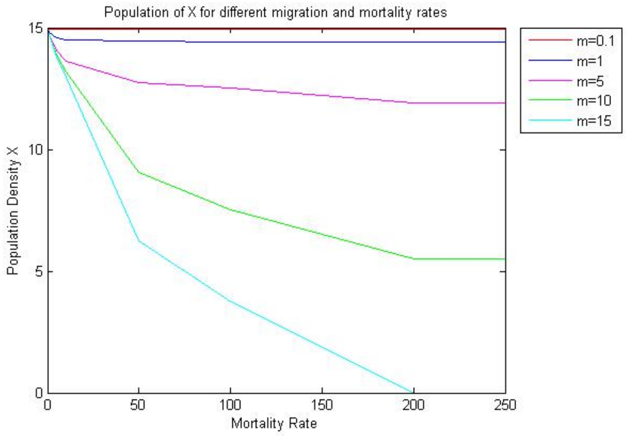
9.1.1 Fixed Point 8 Exists

We found that whenever fixed point 8 is attracting, qualitatively the same dynamics always occur. Here we describe these dynamics for one example situation.

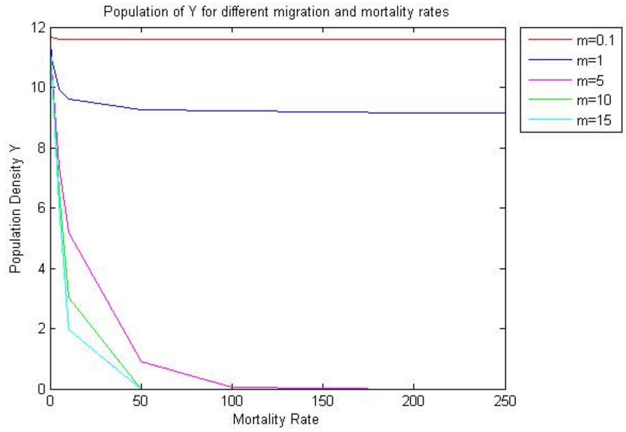
In the example we examine the situation in which fixed points 1-4 are saddle points, and fixed point 8 is the only other fixed point which exists. Starting both patches in fixed point 8, we examine the effect migration has on the system. The parameters of this situation are stored in the file `efp4s8_IFP8.params`. Without migration, both patches would remain in this fixed point, which is located at $(14.98, 11.87, 64.52)$.

Only the prey migrates

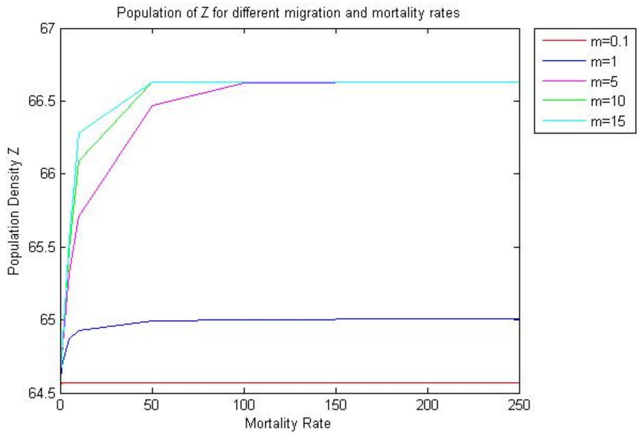
We ran the simulation for different migration rates and for each of these migration rates, we looked at different values for the mortality rate during migration. The results of these simulations are plotted in figure 9.0.



(a) *Primary Prey X*



(b) *Predator Y*



(c) *Secondary Prey Z*

Figure 9.0: *Effect of migration on population levels when only the primary prey migrates.*

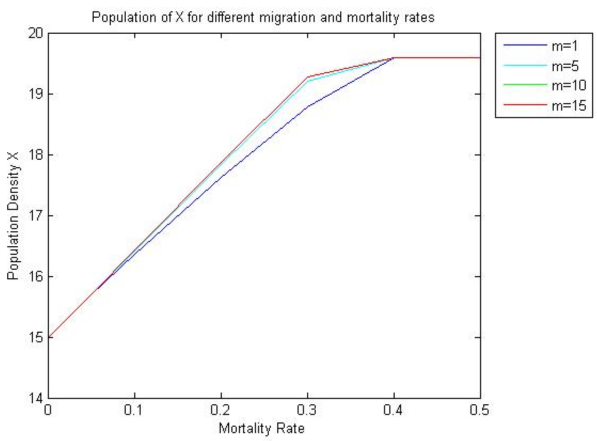
From these results we can tell that, as we would expect, the higher the migration rate is, the greater the effect the mortality rate during migration has. The higher the mortality rate, the lower the population density of x and y. The population density of z, however, increases with higher mortality of prey x. This may seem counterintuitive since one may expect that the less of prey x is available to the predator, the more it would hunt prey z. But it turns out that, for the situations in which fixed point 8 is attracting, it holds that if there is less of prey x, fewer predators are able to survive, which results in a lower predation pressure on alternative prey z, which means the population of z becomes higher.

For $m_x = 5$ we see that if the mortality rate is higher than 100, the predator goes extinct, but both the prey species survive. Only if the migration rate is even higher, $m_x = 15$, we get a situation in which the primary prey may also go extinct if the mortality is higher than some value.

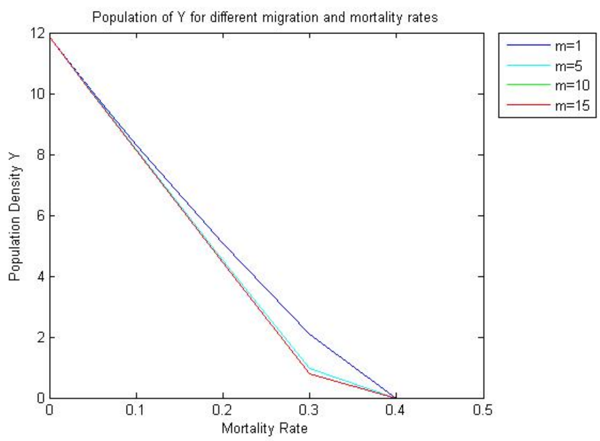
In summary, we can end up in a situation in which all three species coexist, or a situation in which only the two prey species survive, or a situation in which only the secondary prey survives.

Only the predator migrates

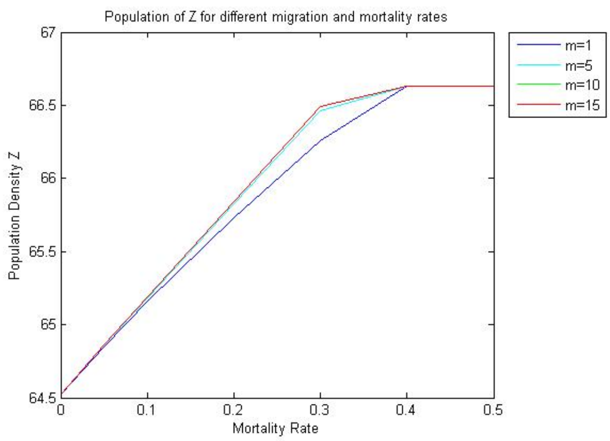
Next we looked at the situation in which only the predator migrates. The mortality rate of the predator within the patches is 1.826.



(a) *Primary Prey X*



(b) *Predator Y*



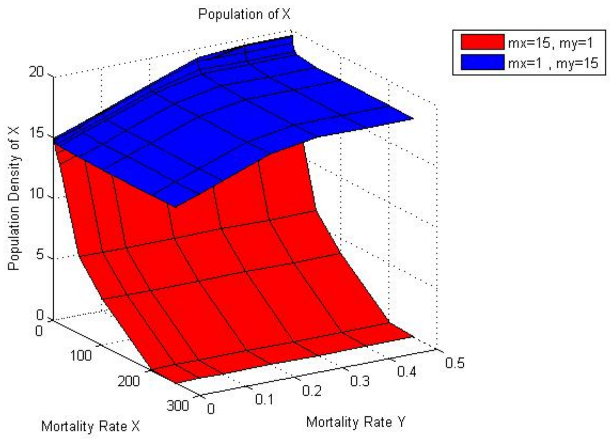
(c) *Secondary Prey Z*

Figure 9.0: *Effect of migration on population levels when only the predator migrates.*

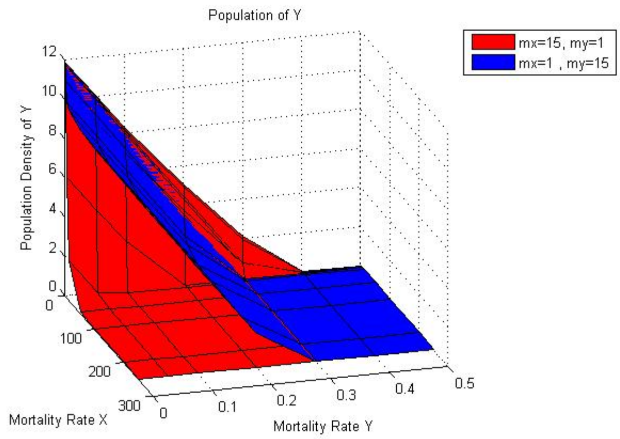
Here we see that the predator can go extinct even if the mortality rate during migration is lower than that within the patches. This is due to the fact that the predators do not produce offspring during migration like they do in the patches. We see that populations of both the prey species increase with more and more dangerous migration of the predator. The population of the predator decreases in those cases.

Both predator and prey migrate

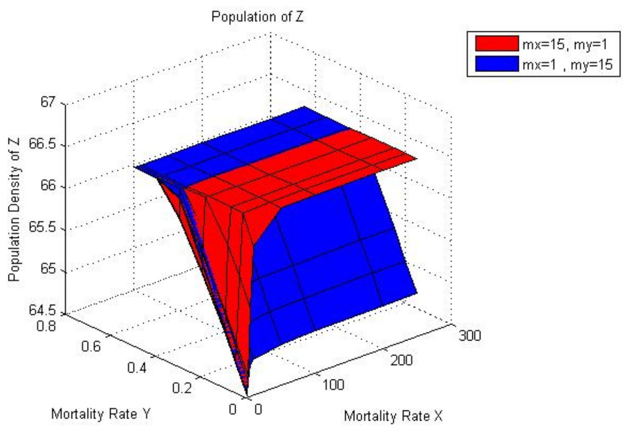
And lastly we look at the situation in which both the predator and the prey migrate. Here we looked at two different situations, one for which the predator has a higher migration rate than than the predator, and the reverse situation. We then looked at the different combinations of mortality rates for prey and predator. The results are shown in the 3D plots below.



(a) *Primary Prey X*



(b) *Predator Y*



(c) *Secondary Prey Z*

Figure 9.0: *Effect of migration on population levels when both the predator and the prey migrate.*

First consider prey x, figure 9.0a. We see that the higher the migration rate of x i, the more sensitive the population levels of x are to the mortality rate during migration. We see that the prey can go extinct when the migration and mortality rates are both high, but will not die out of either of these rates are low.

Now we look at the predator, figure 9.0b. Here we again observe that the population of y is more sensitive to the mortality of y during migration than that of prey x. Furthermore we again have that the higher the migration rate of y, the more sensitive the population is to changes in the mortality rate of y. Here we see that in both cases, it is possible for y to go extinct. Though for even lower migration rates of y, not depicted in the figures, we can get situations in which y does not go extinct, regardless of the mortality rate.

And last we consider the secondary prey z (figure 9.0c). Here we see that the population of z is most sensitive to changes in mortality rate of y. This is not surprising since z only interacts with the predator, not with the prey x. We see that if the mortality rate of y is high, the population of z will reach its carrying capacity.

It appears that whenever fixed point 8 is attracting, and we start each patch from this point, we get behaviour qualitatively similar to this example. This holds for both the 2-patch system and the 3-patch system. If fixed point 8 is repelling, then one of two things will happen:

1. One or more of the species will go extinct. The effect of the migration parameters on the populations of the remaining species is qualitatively similar to the previous example. The only exception is when the predator has died out. Varying the migration parameters of prey x no longer affects the population of the alternative prey z. And obviously, the migration parameters of an extinct species no longer influence the system at all.

2. Cycles may appear. These cycles may have been present in the single patch case. The effect migration has on these cycles is discussed in the following section. But it is also possible for cycles to be induced when none existed in the individual patches. These induced cycles are discussed further in section 9.1.3.

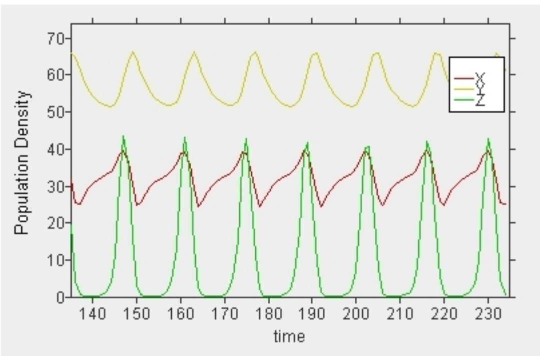
9.1.2 Effect of Migration on Cycles

After completing the systematic simulations above, we also looked at two special cases, in which we know stable cycles exist in the system, to see if this yields different behaviour. The two cases we considered were two of the 3-species cycles discussed in the single patch analysis (section 7). First we consider the system from figure 1(a).

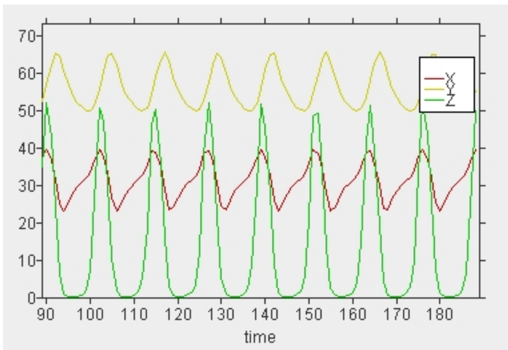
In the 2-patch system we start both patches in fixed point 8. This fixed point occurs at $(31.7, 57.7, 8.4)$. Without migration, a small perturbation from this stable state results in a cycle where the population densities of the three species vary between the following values:

$$\begin{aligned} 24.54 <&X < 39.63 \\ 51.60 <&Y < 66.17 \\ 0.20 <&Z < 43.30 \end{aligned}$$

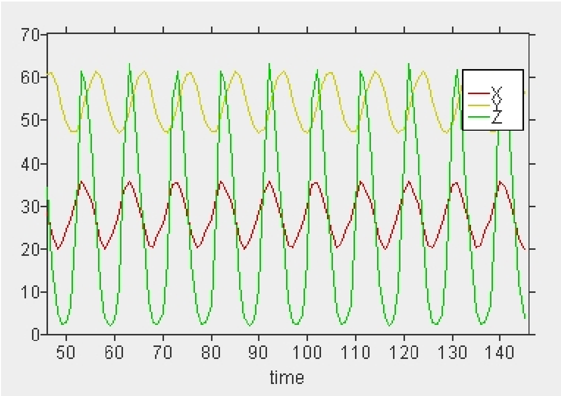
When the prey migrates at a rate of $m_x = 20$ we see that changing the mortality rate μ_x in the intermediate patch causes the cycles to changes in both amplitude and average value, or can cause them to disappear completely, with the system ending up in a stable state. It is also possible that the prey goes extinct and the system ends up in a stable state with only the predator and the alternative prey. The following figures depict the behaviour for these different values of μ_x.

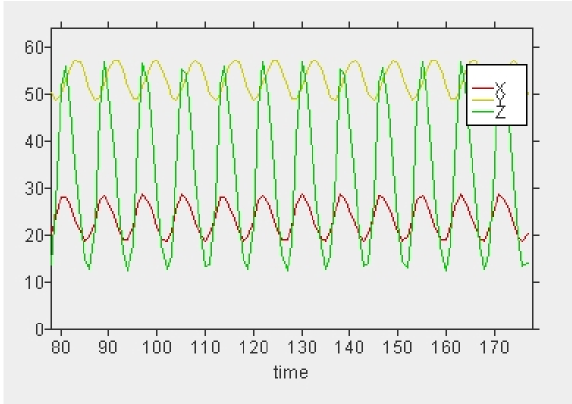


(a) *No Migration.*
$24.54 < X < 39.63$
$51.60.94 < Y < 66.17$
$0.20 \ < Z < 43.30$



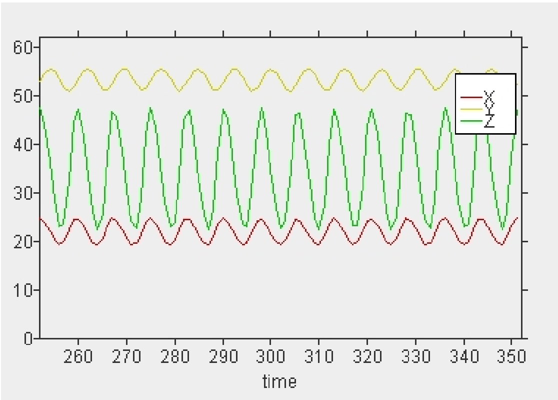
(b) $\mu_x = 1$.
$23.07 < X < 39.66$
$49.94 < Y < 65.59$
$0.31 \ < Z < 52.19$

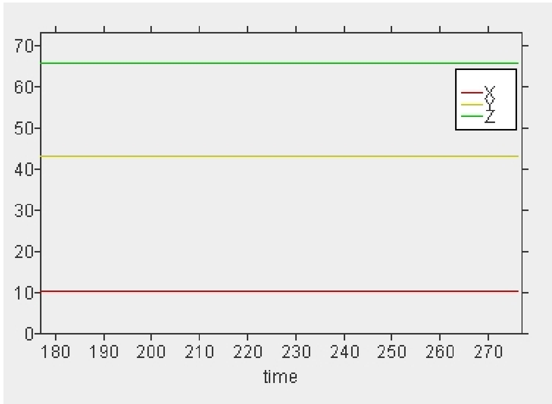




(c) $\mu_x = 5.$
$19.94 < X < 35.82$
$46.96 < Y < 61.50$
$2.22 \ < Z < 63.11$

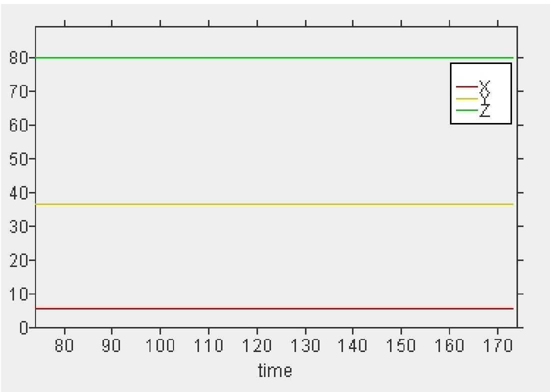
(d) $\mu_x = 10.$
$18.69 < X < 28.67$
$48.65 < Y < 57.33$
$12.59 < Z < 56.82$

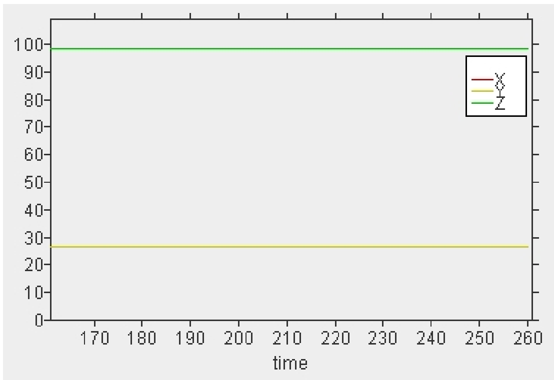




(e) $\mu_x = 12.$
$19.31 < X < 24.77$
$50.99 < Y < 55.54$
$22.44 < Z < 63.11$

(f) $\mu_x = 50.$
$X = 10.38$
$Y = 43.33$
$Z = 65.63$





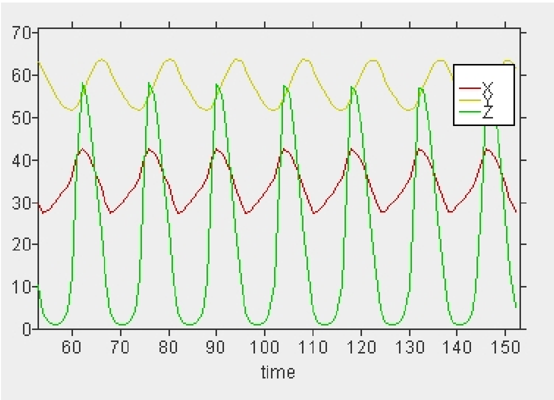
(g) $\mu_x = 100.$
$X = 5.63$
$Y = 36.65$
$Z = 80.06$

(h) $\mu_x = 150.X = 0 \qquad Y = 26.53 \qquad Z = 98.17$

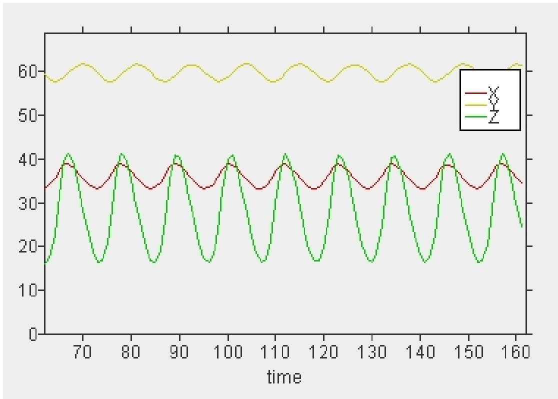
Figure 9.0

From the images we can see that the higher the mortality rate for the prey during migration, the less extreme the fluctuations in population levels of the three species become. If the mortality rate is higher than a certain value, the prey can even go extinct. For a migration rate of $m_x = 10$, we saw a qualitatively similar effect, though the prey never went extinct, even if no prey survived migration. If we lower the migration rate to $m_x = 1$, we see that the cycles do not disappear, no matter how high the mortality rate. Note that there are no parameter values for which the predator goes extinct. This is because in this situation fixed point 5, $(0, \hat{y}, \hat{z})$, also exist, which means the predator can also survive on a diet of strictly alternative prey z.

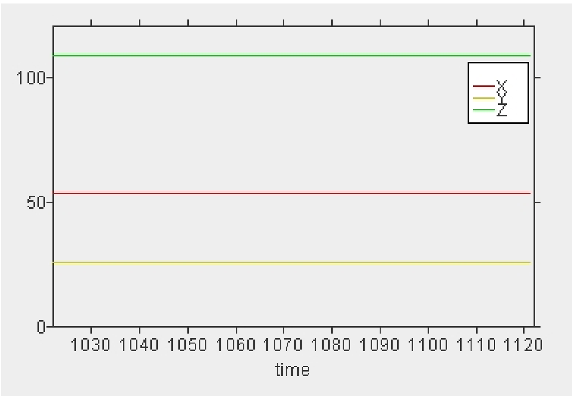
We do the same thing for the situation where the predator migrates. We get qualitatively similar behaviour, though at different parameter values. In the following we have again used a migration rate of $m_y = 20$.



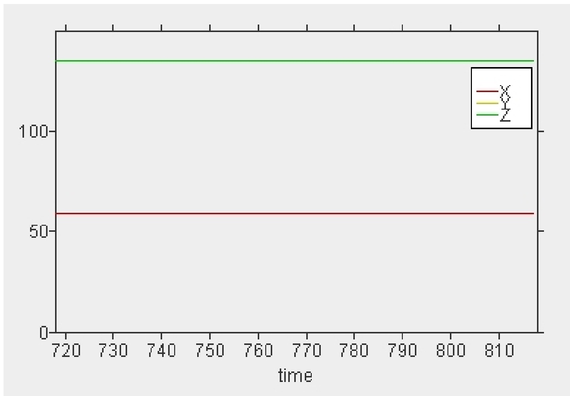
(a) $\mu_y = 0.05$.
$27.4 < X < 42.70$
$51.6 < Y < 63.70$
$1.07 < Z < 58.00$



(b) $\mu_y = 0.1$.
$33.23 < X < 38.88$
$57.78 < Y < 61.63$
$16.35 < Z < 41.23$



(c) $\mu_y = 0.3$.
$X = 53.39$
$Y = 26.11$
$Z = 108.99$



(d) $\mu_y = 0.5. X = 59 \quad Y = 0 \quad Z = 135$

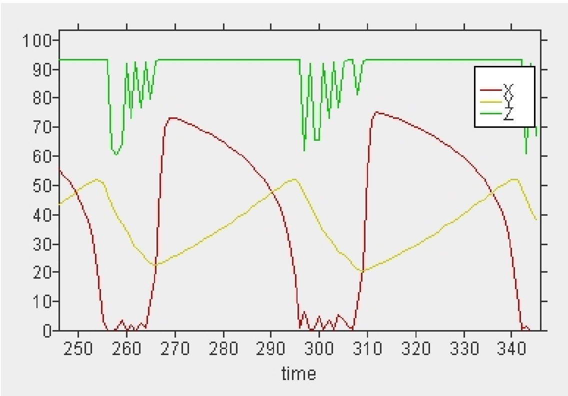
Figure 9.1

Notice that in this situation the predator can go extinct, but not the prey. We again have that if we use a low migration rate ($m_y < 0.1$), the predator will never go extinct, no matter how high the mortality rate during migration. And if we lower the migration even lower ($m_y < 0.05$), then the cycles will always remain.

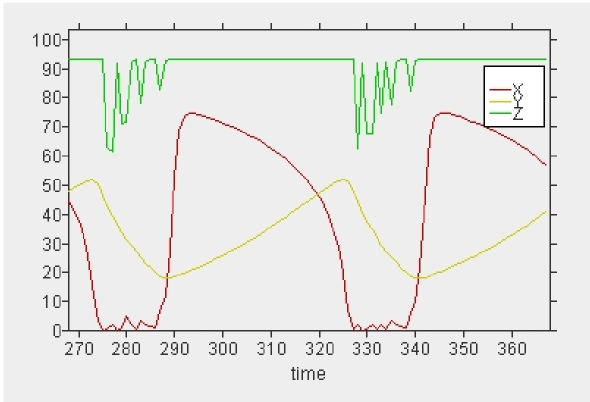
We ran the same simulations for the 3-patch case, and found qualitatively similar responses to changes in the migration parameters. The population levels were slightly lower in the 3-patch case, but this is also due to the fact that prey and/or predator migrate to two different intermediate patches from a habitat patch, and toward both at a rate of m, which means a larger proportion of the population will leave the patch than was the case in the 2-patch system for the same migration rate.

Interesting Cycle

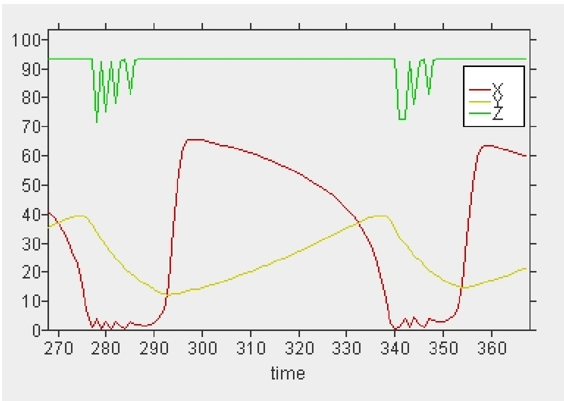
We now look at the situation leading to the dynamics depicted in figure 7.3. This is a 3-species cycle in which δ periodically switches value. We will now investigate how this system is affected by migration in the same way we did for the cycle in the previous section. The following figures show the dynamics for different values of μ_x and a migration rate of $m_x = 5$ for the prey. The predator does not migrate here.



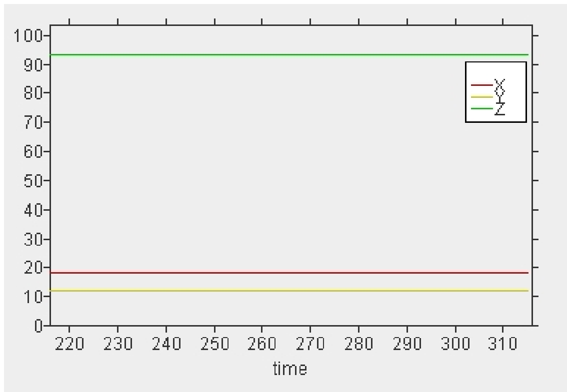
(a) *No Migration.*
$0.01 < X < 75.55$
$20.06 < Y < 52.02$
$60.04 < Z < 93.10 (k_z)$



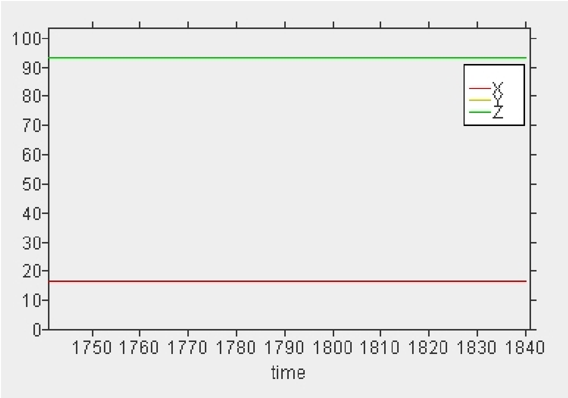
(b) $\mu_x = 0.1$.
$0.10 < X < 78.33$
$17.70 < Y < 51.88$
$61.66 < Z < 93.10$



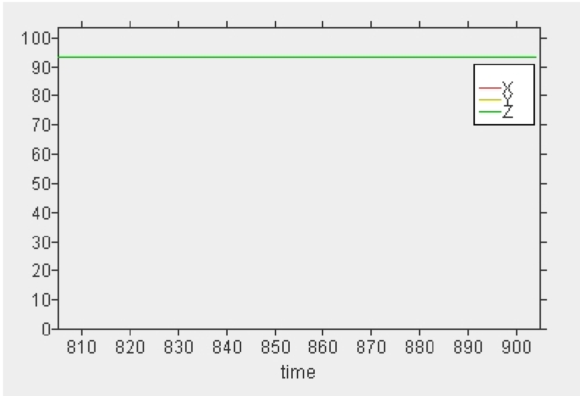
(c) $\mu_x = 1$.
$0.16 < X < 66.42$
$13.07 < Y < 39.47$
$71.85 < Z < 93.10$



(d) $\mu_x = 5 . X = 18.11$ $Y = 11.99$ $Z = 93.10$



(e) $\mu_x = 10.X = 16.62$ $Y = 0$ $Z = 93.10$

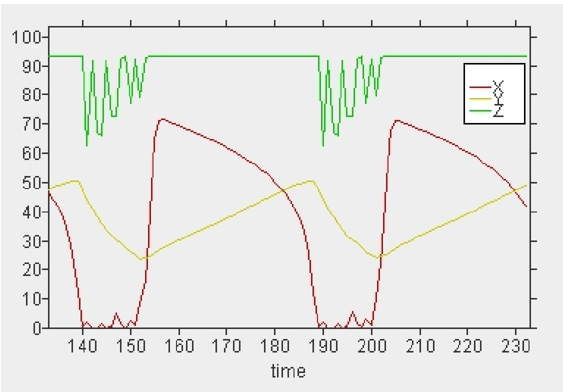


(f) $\mu_x = 20.X = 0$ $Y = 0$ $Z = 93.10$

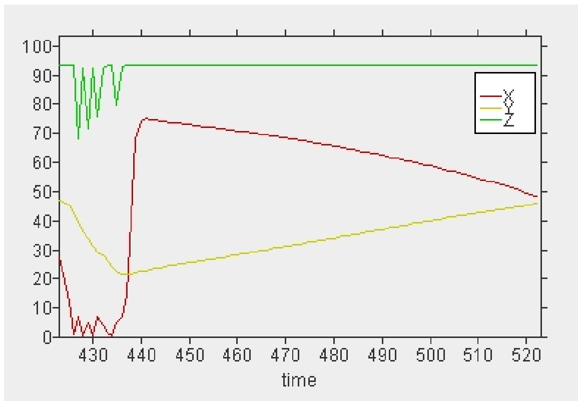
Figure 9.1

From these figures we see that increasing the mortality rate of the prey during migration again causes the fluctuations in population levels of all species to become less. What we also observe, is that the period of the cycle becomes longer. If the mortality rate becomes larger than a certain value, the cycles disappear, and give rise to a fixed point involving all three species. When we increase μ_x even further, the predator dies out, and only the two prey species remain in a stable state. If we increase the mortality rate further yet, prey x also dies out and only the alternative prey is left. Note that, unlike with the previous cycle, the predator can go extinct due to the migration of the prey. Note that in this situation fixed point 5 $(0, \hat{y}, \hat{z})$, does exist.

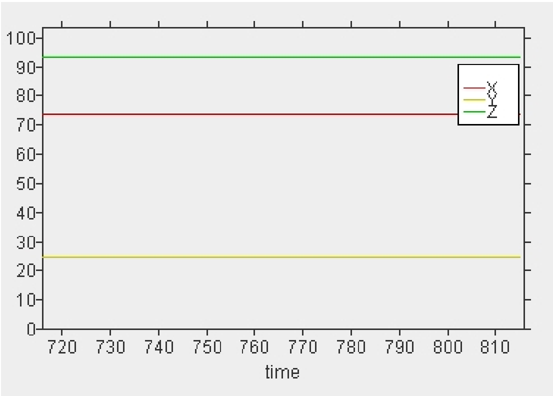
Now we look at the same cycle, but now let only the predator migrate.



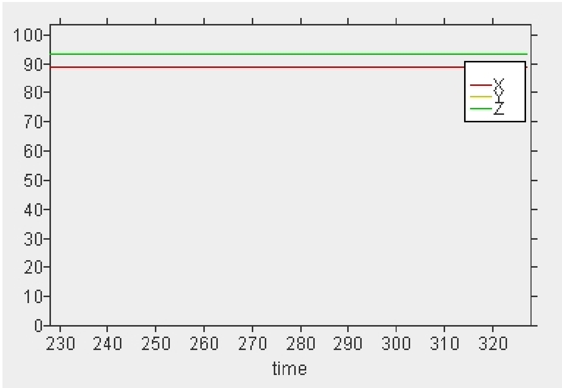
(a) $\mu_y = 0.01$.
$0.01 < X < 74.81$
$20.00 < Y < 49.97$
$62.60 < Z < 93.10$



(b) $\mu_y = 0.05$.
$0.02 < X < 77.09$
$16.84 < Y < 47.48$
$68.11 < Z < 93.10$



(c) $\mu_y = 0.1$.
$X = 73.73$
$Y = 24.51$
$Z = 93.10$



(d) $\mu_y \geq 0.5.X = 89.02$ $Y = 0$ $Z = 93.10$

Figure 9.1

For $\mu_y = 0.05$ we clearly see the period of the cycle getting longer. We again see that the cycle disappears and is replaced with an equilibrium (figure c), and if the mortality rate is very high, the predator dies out (figure d).

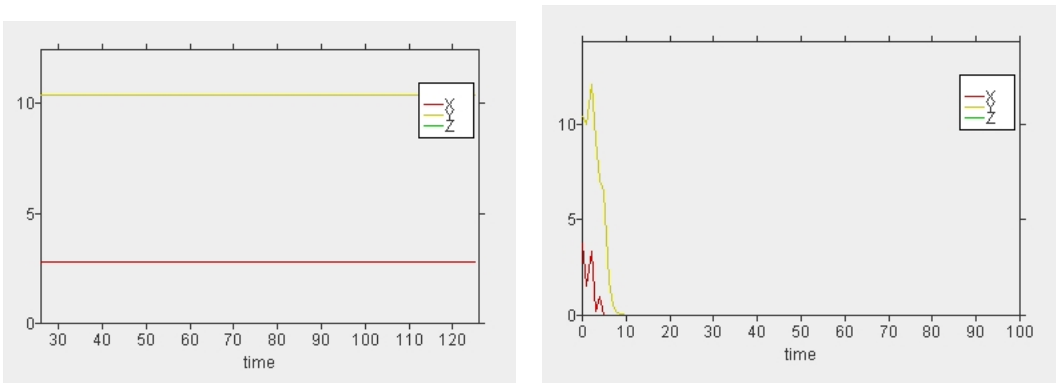
9.1.3 Cycles Induced By Migration

In this section we give an example of a situation in which no cycles exist in the single patch system, but when we connect 2 identical patches, the migration causes cycles to appear. The parameters of this example are stored in the file `migcyclefp7_2.params`.

The system we are examining in this cycle is one in which, if the patches were isolated, fixed points 6 and 7 exist and are both saddle points. We start each patch in fixed point 6 or 7 (both lead to the same results). For certain migration parameters, we get cyclic behaviour between predator and primary prey (z does not participate in the cycles).

Figures 9.2 and 9.3 show the resulting cycle for different values of the migration parameters. These result occur when we start the system either in fixed point 6 or fixed point 7. If we start in fixed point 7, the alternative prey z quickly goes extinct, leaving only predator and primary prey. In the following figures we used fixed point 6 as the initial point.

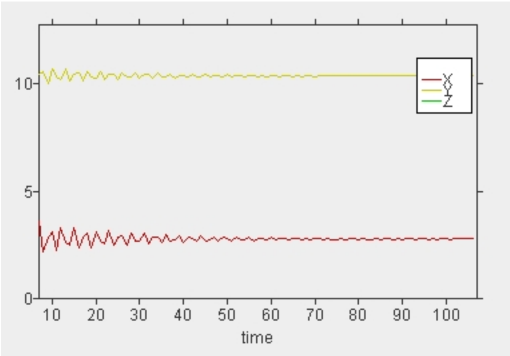
Without migration, both species remain in equilibrium, but a small equilibrium will cause them to go extinct:



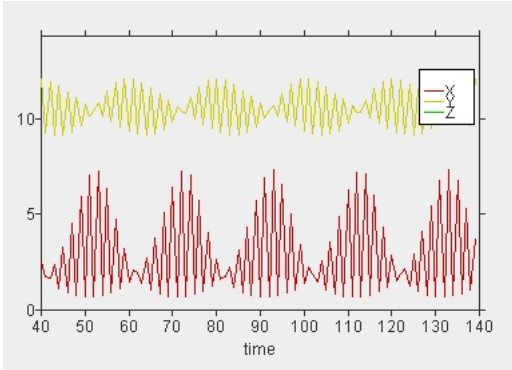
(a) *No migration* (b) *No migration after perturbation*

Figure 9.2

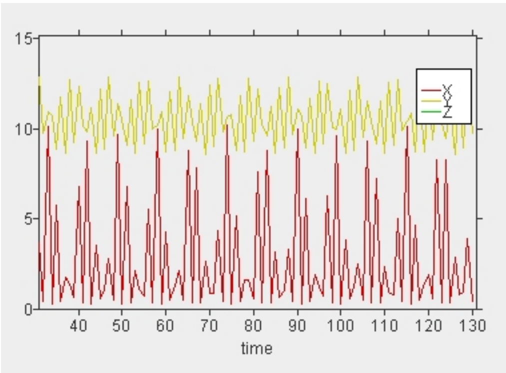
Next we allow the prey to migrate. In this case it is possible that cycles are induced that do not occur in the single-patch situation. Figure 9.3 shows an example for the cycles that occur when we set the migration and return rates to 1.0 and several different values for the mortality rate of prey x during migration.



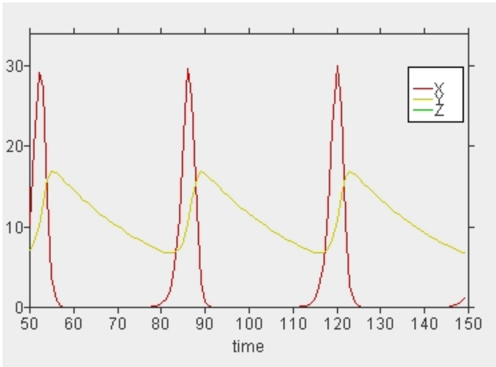
(a) $m_x = 1,\ \mu_x = 0.01$



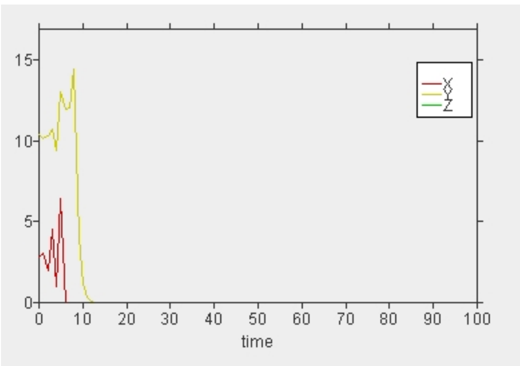
(b) $m_x = 1,\ \mu_x = 0.1$



(c) $m_x = 1,\ \mu_x = 1$



(d) $m_x = 1,\ \mu_x = 10$



(e) $m_x = 1,\ \mu_x = 20$

Figure 9.3

We see that for low mortality rates, the system undergoes some damped oscillations and settles into a stable state. When we raise the mortality rate, the cycles appear, and when the mortality rate becomes too high, the prey dies out, and as a consequence so does the predator (and the alternative prey z if they were still present). In figure 9.3d, we see that these cycles can take the form of a *cycle within a cycle*, that is, the population levels continually cycle between a minimum or maximum value, but these minimum and maximum values also vary periodically.

If we let only the predator migrate, these cycles do not appear, regardless of the parameter values used, and all species eventually go extinct:

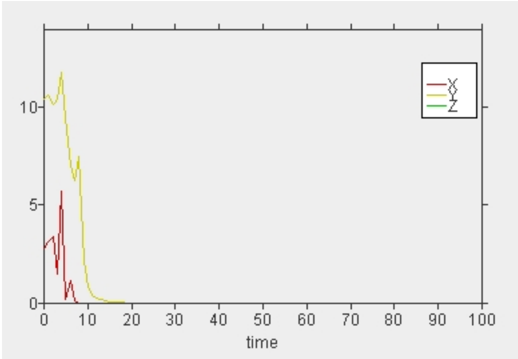


Figure 9.4: $m_y = 0.1 \mu_y = 0.1$. *All values of migration parameters yield this behaviour*

If we let both the predator and the prey migrate, the cycles show up again, and the progression of behaviour for different mortality rates is similar to the case where only the prey migrates. The migration of the predator does not affect the behaviour greatly.

9.2 Sanctuary Patch

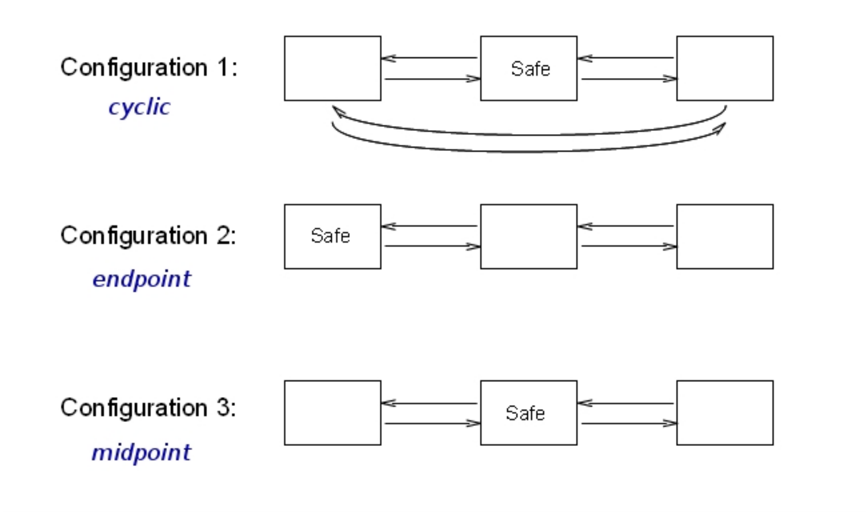
In this section we will investigate the idea of having one patch in a network which acts as a sanctuary for either the predator or the prey species. The hope is that this will allow the species to survive where it could not otherwise. In our simulations we looked at situations in which the predator or prey are unable to survive in any of the patches. We then transformed one of the patches into a sanctuary patch, and ran the simulation to see if the presence of the safe patch could increase the chances of survival for the predator or prey.

We looked at two different situations:

1. Prey migrates
   In this situation the prey is unable to survive anywhere in the network. For this case we create a safe patch by removing all predators from this patch.

2. Predator migrates
   In this situation the predator is unable to survive anywhere in the network. We create a sanctuary patch for the predator by increasing the carrying capacity of the primary prey, k_x. If there are more prey, then the predators may also be able to survive more easily.

For each of these situations, we also considered three different configurations of the (3-patch) network:



In the cyclic configuration, every patch is connected to every other patch in the network. This means that every patch is directly connected to the sanctuary patch. In the endpoint configuration, one of the patches is not directly connected to the safe patch, but only indirectly, through another patch. In the midpoint configuration, two patches are directly connected to the safe patch, but not to each other.

We will now discuss the results of these simulations for the three different situations.

Prey migrates

In this situation, we started with a network in which the prey cannot survive. We used parameters such that in every individual patch the only non-trivial fixed point which exists is fixed point 5, $(0, \hat{y}, \hat{z})$, and this fixed point is attracting. This means that there are no initial conditions for which the prey does not eventually go extinct (except when no predators are present). We connected three such patches in the three different configurations mentioned above. We converted patch 1 into a sanctuary patch by removing all the predators from the system. In the single patch case, introducing a small number of prey would now cause the system to reach fixed point 4, $(k_x, 0, k_z)$. The other two patches remain unchanged. We allow the prey to migrate and determine whether the presence of the sanctuary has an effect on the overall survival of the prey. Below the results are listed for each of the three configurations. The parameter settings used in this example can be found in the file `sanctuary1.params`

- No migration
  $x_1 = 200$ $\quad$ $x_2 = x_3 = 0$
  $y_1 = 0$ $\quad$ $y_2 = y_3 = 20.94$
  $z_1 = 900$ $\quad$ $z_2 = z_3 = 300.04$
  $x_{migrating} = 0$
  $x_{total} = 200$
- Configuration 1 (Cyclic)

$x_1 = 191.28$ $\quad$ $x_2 = x_3 = 4.24$
$y_1 = 0$ $\quad$ $y_2 = y_3 = 26.21$
$z_1 = 900$ $\quad$ $z_2 = z_3 = 101.92$
$x_{migrating} = 133.17$
$x_{total} = 332.93$

- Configuration 2 (Endpoint)
  $x_1 = 195.54$ $\quad$ $x_2 = 4.24$ $\quad$ $x_3 = 0.45$
  $y_1 = 0$ $\quad$ $y_2 = 26.21$ $\quad$ $y_3 = 21.62$
  $z_1 = 900$ $\quad$ $z_2 = 101.92$ $\quad$ $z_3 = 275.91$
  $x_{migrating} = 68.16$
  $x_{total} = 268.39$

- Configuration 3 (Midpoint)
  $x_1 = 191.28$ $\quad$ $x_2 = x_3 = 4.32$
  $y_1 = 0$ $\quad$ $y_2 = y_3 = 26.29$
  $z_1 = 900$ $\quad$ $z_2 = z_3 = 98.60$
  $x_{migrating} = 131$
  $x_{total} = 330.92$

The first thing we observe is that the prey is now indeed able to survive, even in patches other than the sanctuary patch. We can conclude that the presence of a sanctuary patch in a network may be beneficial to the survival of the prey in all patches in the network. When we determine the total population in the network, we see that there is a real increase in population levels, not simply a redistribution of prey over the various patches. When we look at configuration 2, we see that the patch which is connected to the sanctuary patch benefits from it more than the patch indirectly connected. Furthermore, when we compare configuration 1 to configuration 3, we see that the in configuration 3, in which the two unsafe patches are not connected to each other, the population density of the prey is slightly higher. This would indicate that a connection to a bad patch may be detrimental. Thus increased connectivity may not always be a positive thing. Also note that in our attempts to protect the prey species, we have also increased the population of the predator (at least in the non-sanctuary patches).

Predator migrates

Here we look at the situation in which the predator cannot survive. This happens if the parameters are such that in each patch only the non-trivial fixed points exist (these are the fixed points in which there are no predators). The parameters used in this example can be found in the file `sanctuary2.params`. We start patches from fixed point 4, $(k_x, 0, k_z)$, which is attracting in this example. This means if we introduce predators into the system, they will always go extinct. We again turn patch 1 into a sanctuary patch. We do this by increasing the carrying capacity of the primary prey x. In natural systems this could be accomplished by increasing the resources or the number of nesting places for the prey. Note that this may lead to additional fixed points appearing in the single-patch system of the sanctuary patch.

We start the patches in fixed point 4, and then introduce a small number of predators to the system. We found that it does not matter in which patch the predators are released, the following results were obtained. Though in practice it would make sense to release the predators into the sanctuary patch and letting them migrate to the other patches from there. We have take the mortality rate of the predators during migration to be equal to the mortality rate within the patches, to avoid any effects from the migration itself acting as a sanctuary.

- No migration
  $x_1 = 200$ $\quad x_2 = x_3 = 50$
  $y_1 = 0$ $\quad y_2 = y_3 = 0$
  $z_1 = 900$ $\quad z_2 = z_3 = 900$
  $y_{migrating} = 0$
  $y_{total} = 0$
- Configuration 1 (Cyclic)
  $x_1 = 191.22$ $\quad x_2 = x_3 = 49.61$
  $y_1 = 30.21$ $\quad y_2 = y_3 = 5.52$
  $z_1 = 516.08$ $\quad z_2 = z_3 = 831.10$
  $y_{migrating} = 21.91$
  $y_{total} = 63.16$
- Configuration 2 (Endpoint)
  $x_1 = 179.67$ $\quad x_2 = 49.23$ $\quad x_3 = 49.79$
  $y_1 = 70.31$ $\quad y_2 = 10.88$ $\quad y_3 = 3.05$
  $z_1 = 5.76$ $\quad z_2 = 764.17$ $\quad z_3 = 861.99$
  $y_{migrating} = 25.26$
  $y_{total} = 109.5$
- Configuration 3 (Midpoint)
  $x_1 = 190.51$ $\quad x_2 = x_3 = 49.40$
  $y_1 = 32.67$ $\quad y_2 = y_3 = 8.50$
  $z_1 = 484.80$ $\quad z_2 = z_3 = 793.90$
  $y_{migrating} = 21.86$
  $y_{total} = 71.53$

From these result we again see that the predator is now able to survive in every patch of the system. The result are similar to those of the situation in which the prey migrates. When we look at configuration 2, we see that the patch directly connected to the sanctuary patch has higher population levels than the patch indirectly connected to the sanctuary patch. And when we compare configuration 1 to configuration 3 we see that the added connection between unsafe patches which is present in configuration 1, leads to lower predator populations. Note that the total population is highest for the endpoint configuration in this example. This is not true in general, but interesting nevertheless. This shows that the predator population may suffer from added connections between patches. Another interesting observation is that the population of the alternative prey z in the sanctuary patch drops significantly for configuration 2 as compared to the other patches. If we lower the mortality rate of the predators during migration, it can happen that the alternative prey will go extinct altogether. What we learn from this is that our attempts to rescue the predator, may be at the expense of losing another species.

Both predator and prey migrate

When both the predator and the prey migrate, and we wish to protect the prey, we cannot create a safe patch by removing all predators from one of the patches, they would be able to simply migrate back to the sanctuary patch from the other patches. What we could do in this case, is restrict the ease of migration of the predator to the sanctuary patch. In real systems this could be accomplished by placing fences or water barriers around a patch for example. We will show that this approach can lead to the survival of the prey in all patches of the system.

We again consider a network of identical patches, in which, if isolated, the prey is unable to survive. We then connect the patches and set the migration parameter setting such that one of the patches is largely (but not necessarily completely) shielded from predators.

The situation we studied in this example is stored in the file `sanctuary.params`. In this situation fixed point 5, $(0, \hat{y}, \hat{z})$ is an attractor, which means that if we introduce a small population of prey x into this system, it will go extinct. This can be seen in figure 9.5.

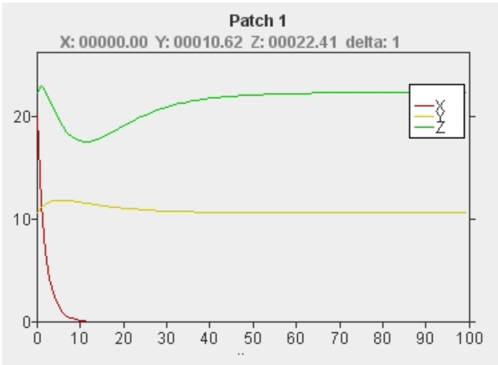


Figure 9.5: *The primary prey cannot survive in an isolated patch*

Now we connect 3 of these (identical) patches. We set all migration rates, return rates, and mortality rates to a value of 1.0. We observe that the prey is still unable to survive (figure 9.6)

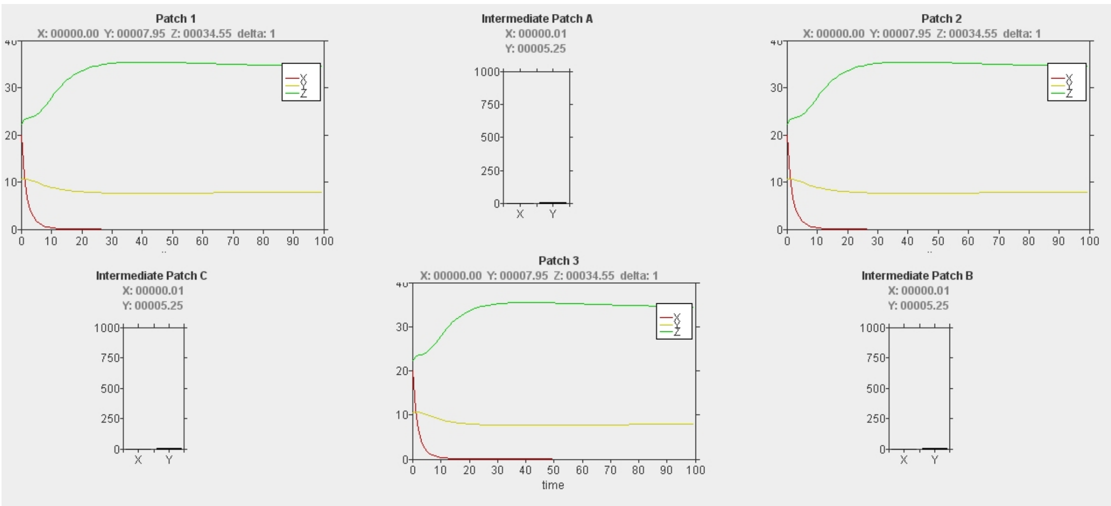


Figure 9.6: *The primary prey cannot survive in a connected system with symmetric migration parameters*

Now we change two parameters, namely the return rates of the predator to patch one. We set those to 0.1. Thus we have shielded patch one from predators. What we observe is that it is now possible for the primary prey x to survive, not only in the safe patch, but in all three patches (figure 9.7)

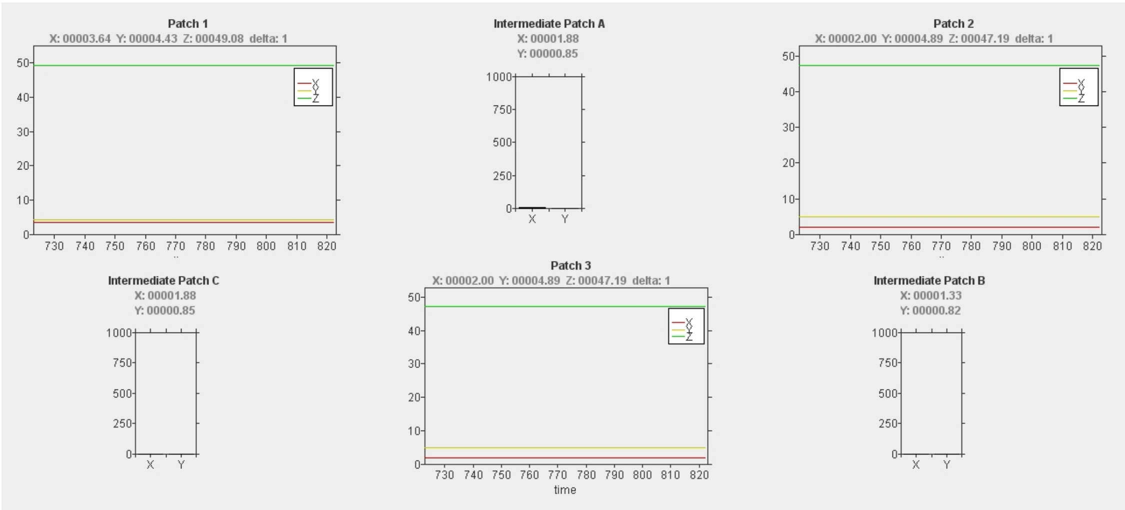


Figure 9.7: *If we shield one of the patches from predators, prey x is able to survive in all patches.*

Even if we release a small population of prey x into one of the unshielded patches, the presence of the sanctuary patch is enough to ensure the survival of the prey in the system. This example again illustrates that it does not always hold that greater connectivity is always better. In this case it was beneficial for the prey to restrict the connectivity between patches for the predator.

References

[1] C.S. Holling. The components of predation as revealed by a study of small mammal predation of the european pine sawfly. *The Canadian Entomologist*, 91:293–320, 1959.

[2] C.S. Holling. Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist*, 91:385–398, 1959.

[3] A.J. Lotka. *Elements of Physical Biology.* Williams and Wilkins, 1925.

[4] V. Volterra. *Variations and fluctuations of the number of individuals in animal species living together.* Animal Ecology, 1926.

[5] V. Volterra. Variazioni e fluttuazioni del numero dindividui in specie animali conviventi. *Mem. Acad. Lineci Roma*, 2:31–113, 1926.

10 Appendix A: Full Derivations

Here we give full derivations and calculations per section:

4.1 Optimal Foraging

Equation 4.5*

The predator will only include prey z in its diet if this leads to an increase in the energy intake rate. This means that, in order for the predator to include prey z in its diet, the following inequality must hold:

$$\begin{aligned}
\textit{Energy intake rate without } z &< \textit{Energy intake rate when } z \textit{ is included} \\
\Rightarrow \frac{\lambda_x E_x}{1+\lambda_x h_x} &< \frac{\lambda_x E_x + \lambda_z E_z}{1+\lambda_x h_x + \lambda_z h_z} \\
\Rightarrow \lambda_x E_x (1+\lambda_x h_x + \lambda_z h_z) &< (1+\lambda_x h_x)(\lambda_x E_x + \lambda_z E_z) \qquad \text{(cross-multiplication)} \\
\Rightarrow \lambda_x E_x + \lambda_x^2 h_x E_x + \lambda_x \lambda_z E_x h_z &< \lambda_x E_x + \lambda_z E_z + \lambda_x^2 h_x E_x + \lambda_x \lambda_z E_z h_x \\
\Rightarrow \lambda_x \lambda_z E_x h_z &< \lambda_z E_z + \lambda_x \lambda_z E_z z h_x \qquad \text{(eliminating the common terms)} \\
\Rightarrow \lambda_x E_x h_z &< E_z + \lambda_x E_z h_x \qquad \text{(eliminating the factor } \lambda_z\text{)} \\
\Rightarrow \lambda_x E_x h_z &< E_z (1+\lambda_x h_x).
\end{aligned}$$

Gathering all the terms pertaining to prey x on one side, and prey z on the other, this results in the requirement that:

$$\frac{\lambda_x E_x}{1+\lambda_x h_x} < \frac{E_z}{h_z}. \tag{10.1}$$

If this requirement holds, prey z is included in the diet, and otherwise it is not. Notice that whether or not z is included depends only on the encounter rate of the primary prey x, not on the encounter rate of prey z itself.

4.4 Change in diet

Equation 4.20*

Given the definition of δ:

$$\delta = \begin{cases} 1 & \text{if} \quad \dfrac{a\gamma_x x}{1+ah_x x} < \dfrac{\gamma_z}{h_z} \\ \\ 0 & \text{otherwise} \end{cases},$$

we can see that it depends only on the abundance of prey x, not on the abundance of prey z. We can then calculate the threshold for the abundance of prey x for which δ becomes 1:

$$\begin{aligned}
\frac{a\gamma_x x}{1+ah_x x} &< \frac{\gamma_z}{h_z} \\
ah_z\gamma_x x &< \gamma_z + ah_x\gamma_z x \\
(ah_z\gamma_x - ah_x\gamma_z)x &< \gamma_z \\
x &< \frac{\gamma_z}{a(h_z\gamma_x - h_x\gamma_z)} \\
x &< \frac{1}{a(h_z\frac{\gamma_x}{\gamma_z} - h_x)}.
\end{aligned}$$

If the density of x is greater than this threshold, δ will be zero.

5 Analysis

5.1 System without x

The derivation of the zero isoclines of predator and prey goes as follows:

Equation 5.2*a and 5.2*b

The prey zero-isocline is obtained by setting $\frac{dz}{dt} = 0$:

$$\begin{aligned}
\frac{dz}{dt} &= 0 \\
z\left[r_z\left(1-\frac{z}{k_z}\right) - \frac{ay}{1+ah_z z}\right] &= 0 \\
r_z\left(1-\frac{z}{k_z}\right) - \frac{ay}{1+ah_z z} = 0 &\quad \vee \quad z = 0 \\
\frac{ay}{1+ah_z z} = r_z\left(1-\frac{z}{k_z}\right) &\quad \vee \quad z = 0 \\
y = \frac{r_z}{a}\left(1-\frac{z}{k_z}\right)(1+ah_z z) &\quad \vee \quad z = 0
\end{aligned}$$

Equation 5.2*c and 5.2*d

The predator zero-isoclines are found by setting $\frac{dy}{dt} = 0$:

$$\begin{aligned}
\frac{dy}{dt} &= 0 \\
y\left[-\mu + \frac{a\gamma_z z}{1+ah_z z}\right] &= 0
\end{aligned} \tag{10.2}$$

$$
\begin{aligned}
-\mu + \frac{a\gamma_z z}{1 + ah_z z} &= 0 \quad \vee \quad y = 0 \\
\frac{a\gamma_z z}{1 + ah_z z} &= \mu \quad \vee \quad y = 0 \\
a\gamma_z z &= \mu + \mu a h_z z \quad \vee \quad y = 0 \\
z(a\gamma_z - \mu a h_z) &= \mu \quad \vee \quad y = 0 \\
z &= \frac{\mu}{a\left(\gamma_z - h_z\right)} \quad \vee \quad y = 0
\end{aligned}
$$

5.1 Equilibria

Equations 5.3* and 5.4*

These equilibrium point are found by determining the intersections isoclines a and d:

$$
\begin{aligned}
y &= \frac{r_z}{a}(1 - \frac{z}{k_z})(1 + ah_z z) \\
0 &= \frac{r_z}{a}(1 - \frac{z}{k_z})(1 + ah_z z) \\
1 - \frac{z}{k_z} = 0 \quad &\vee \quad 1 + ah_z z = 0 \\
\frac{z}{k_z} = 1 \quad &\vee \quad z = \frac{-1}{ah_z} \\
z = k_z &
\end{aligned}
$$

Stability of fixed points

5.1.1 Graphical Approach

Equation 5.9

Here we determine the are of positive growth for the prey species z. There is positive growth if:

$$
\begin{aligned}
\frac{dz}{dt} &> 0 \\
z\left[r_z(1 - \frac{z}{k_z}) - \frac{ay}{1 + ah_z z}\right] &> 0 \\
r_z(1 - \frac{z}{k_z}) - \frac{ay}{1 + ah_z z} &> 0
\end{aligned}
$$

$$
\begin{aligned}
r_z(1-\frac{z}{k_z}) &> \frac{ay}{1+ah_z z} \\
y &< r_z(1-\frac{z}{k_z})(\frac{1+ah_z z}{a}) \\
y &< \frac{r_z}{a}(1-\frac{z}{k_z})(1+ah_z z).
\end{aligned}
$$

Here we have used the fact that z and all the parameters are nonnegative numbers in our system.

Equation 5.10*

The peak of the isocline can be found by setting its derivative (with respect to z) to zero:

$$
\begin{aligned}
\frac{d}{dz}\left[\frac{r_z}{a}(1-\frac{z}{k_z})(1+ah_z z)\right] &= 0 \\
\frac{d}{dz}\left[(\frac{r_z}{a}-\frac{r_z}{ak_z}z)(1+ah_z z)\right] &= 0 \\
\frac{d}{dz}\left[\frac{r_z}{a}-\frac{r_z}{ak_z}z+\frac{r_z ah_z}{a}z-\frac{r_z ah_z}{ak_z}z^2)\right] &= 0 \\
\frac{d}{dz}\left[\frac{r_z}{a}+(r_z h_z-\frac{r_z}{ak_z})z-\frac{r_z h_z}{k_z}z^2)\right] &= 0 \\
r_z h_z-\frac{r_z}{ak_z}-2\frac{r_z h_z}{k_z}z &= 0 \\
2\frac{r_z h_z}{k_z}z &= r_z h_z-\frac{r_z}{ak_z} \\
z &= \frac{r_z h_z k_z}{2r_z h_z}-\frac{r_z k_z}{2ak_z r_z h_z} \\
z &= \frac{k_z}{2}-\frac{1}{2ah_z} \\
z &= \frac{1}{2}(k_z-\frac{1}{ah_z})
\end{aligned}
$$

Equation 5.11

The predators undergo a positive growth if it holds that:

$$
\begin{aligned}
\frac{dy}{dt} &> 0 \\
y\left[-\mu+\frac{a\gamma_z z}{1+ah_z z}\right] &> 0 \\
-\mu+\frac{a\gamma_z z}{1+ah_z z} &> 0 \\
\frac{a\gamma_z z}{1+ah_z z} &> \mu
\end{aligned}
$$

$$
\begin{aligned}
a\gamma_z z &> \mu(1 + ah_z z) \\
a\gamma_z z &> \mu + \mu ah_z z) \\
z(a\gamma_z - \mu ah_z) &> \mu \\
z &> \frac{\mu}{a(\gamma_z - \mu h_z)} && \text{(since } \mu < \tfrac{\gamma_z}{h_z}\text{)}
\end{aligned}
$$

5.1.1 Analytical Approach

Equation 5.18*

We have

$$
\begin{aligned}
\frac{dy}{dt} &= yg_y \\
\frac{dy}{dt} &= zg_z
\end{aligned}
$$

where

$$
\begin{aligned}
g_y &= -\mu + \frac{a\gamma_z z}{1 + ah_z z} \\
g_z &= r_z(1 - \frac{z}{k_z}) - \frac{ay}{1 + ah_z z}.
\end{aligned}
$$

We will now derive the four entries of the Jacobian:

$$
\begin{aligned}
&y\frac{dg_y}{dy} = \\
&y\frac{d}{dy}(-\mu + \frac{a\gamma_z z}{1 + ah_z z}) = \\
&0.
\end{aligned}
$$

$$
\begin{aligned}
&y\frac{dg_y}{dz} = \\
&y\left[\frac{d}{dz}(-\mu + \frac{a\gamma_z z}{1 + ah_z z})\right] = \\
&y\left[z\frac{d}{dz}(\frac{a\gamma_z}{1 + ah_z z}) + \frac{a\gamma_z}{1 + ah_z z}\frac{d}{dz}(z)\right] = && \text{(product rule)} \\
&y\left[z\frac{d}{du}(\frac{a\gamma_z}{u})\frac{du}{dz} + \frac{a\gamma_z}{1 + ah_z z}\frac{d}{dz}(z)\right] = && \text{(substitute } u = 1 + ah_z z\text{)}
\end{aligned}
$$

$$
\begin{aligned}
&y\left[z(\frac{-a\gamma_z}{u^2})ah_z + \frac{a\gamma_z}{1+ah_zz}\right] = \\
&y\left[\frac{a\gamma_z}{1+ah_zz} - \frac{a^2\gamma_zh_zz}{(1+ah_zz)^2}\right]
\end{aligned}
$$

$$
\begin{aligned}
&z\frac{dg_z}{dy} = \\
&z\frac{d}{dy}(r_z(1-\frac{z}{k_z}) - \frac{ay}{1+ah_zz}) = \\
&-\frac{az}{1+ah_zz}
\end{aligned}
$$

$$
\begin{aligned}
&z\frac{dg_z}{dz} = \\
&z\frac{d}{dz}(r_z(1-\frac{z}{k_z}) - \frac{ay}{1+ah_zz}) = \\
&z\left[\frac{d}{dz}(r_z(1-\frac{z}{k_z})) - \frac{d}{dz}(\frac{ay}{1+ah_zz})\right] = \\
&z\left[-\frac{r_z}{k_z} - \frac{d}{du}(\frac{ay}{u})\frac{du}{dz}\right] = \qquad\qquad \text{(substitute } u = 1+ah_zz\text{)} \\
&z\left[-\frac{r_z}{k_z} - \frac{d}{du}(\frac{ay}{u})\frac{d}{dz}(1+ah_zz)\right] = \\
&z\left[-\frac{r_z}{k_z} + \frac{ay}{u^2}ah_z\right] = \\
&z\left[-\frac{r_z}{k_z} + \frac{a^2h_zy}{(1+ah_zz)^2}\right]
\end{aligned}
$$

Equation 5.20*

We know that at the equilibrium point

$$y = \frac{r_z}{a}\left(1-\frac{z}{k_z}\right)(1+ah_zz)\,.$$

We can use this to simplify two of the entries of the Jacobian:

$$
\begin{aligned}
&y\left[\frac{a\gamma_z}{1+ah_zz} - \frac{a^2\gamma_zh_zz}{(1+ah_zz)^2}\right] = \\
&\frac{r_z}{a}\left(1-\frac{z}{k_z}\right)(1+ah_zz)\left[\frac{a\gamma_z}{1+ah_zz} - \frac{a^2\gamma_zh_zz}{(1+ah_zz)^2}\right] =
\end{aligned}
$$

$$\frac{a\gamma_z r_z(1-\frac{z}{k_z})(1+ah_z z)}{a(1+ah_z z)} - \frac{a^2\gamma_z h_z r_z z(1-\frac{z}{k_z})(1+ah_z z)}{a(1+ah_z z)^2} =$$
$$\gamma_z r_z(1-\frac{z}{k_z}) - \frac{a\gamma_z h_z r_z z(1-\frac{z}{k_z})}{1+ah_z z}$$

$$z\left[-\frac{r_z}{k_z} + \frac{a^2 h_z y}{(1+ah_z z)^2}\right] =$$
$$z\left[-\frac{r_z}{k_z} + \frac{a^2 h_z r_z(1-\frac{z}{k_z})(1+ah_z z)}{a(1+ah_z z)^2}\right] =$$
$$z\left[-\frac{r_z}{k_z} + \frac{ah_z r_z(1-\frac{z}{k_z})}{1+ah_z z}\right]$$

Stability of the nontrivial fixed point
Below is the Jacobian at the nontrivial fixed point:

$$\mathbf{J} = \begin{bmatrix} 0 & \gamma_z r_z(1-\frac{\hat{z}}{k_z}) - \frac{\gamma_z a h_z r_z \hat{z}(1-\frac{\hat{z}}{k_z})}{1+ah_z\hat{z}} \\ -\frac{a\hat{z}}{1+ah_z\hat{z}} & \hat{z}\left(-\frac{r_z}{k_z} + \frac{ah_z r_z(1-\frac{\hat{z}}{k_z})}{1+ah_z\hat{z}}\right) \end{bmatrix}.$$

Equation 5.22*

In order to determine the stability of the nontrivial fixed point, we require that the determinant be positive:

$$\det(\mathbf{J}) > 0$$
$$\left[-\gamma_z r_z(1-\frac{\hat{z}}{k_z}) + \gamma_z r_z\frac{ah_z\hat{z}(1-\frac{\hat{z}}{k_z})}{1+ah_z\hat{z}}\right]\left[-\frac{a\hat{z}}{1+ah_z\hat{z}}\right] > 0$$
$$\frac{a\gamma_z r_z\hat{z}\left[(1-\frac{\hat{z}}{k_z}) - \frac{ah_z\hat{z}(1-\frac{\hat{z}}{k_z})}{1+ah_z\hat{z}}\right]}{1+ah_z\hat{z}} > 0$$
$$a\gamma_z r_z\hat{z}\left[(1-\frac{\hat{z}}{k_z}) - \frac{ah_z\hat{z}(1-\frac{\hat{z}}{k_z})}{1+ah_z\hat{z}}\right] > 0 \qquad \text{(denominator is always positive)}$$
$$\hat{z}(1-\frac{\hat{z}}{k_z}) - \frac{ah_z\hat{z}^2(1-\frac{\hat{z}}{k_z})}{1+ah_z\hat{z}} > 0$$
$$\hat{z}(1-\frac{\hat{z}}{k_z})(1+ah_z\hat{z}) - ah_z\hat{z}^2(1-\frac{\hat{z}}{k_z}) > 0 \qquad \text{(next we will divide by } (1-\tfrac{\hat{z}}{k_z})\text{)}$$
$$(1-\frac{\hat{z}}{k_z}) > 0 \;\wedge\; \hat{z}+ah_z\hat{z}^2-ah_z\hat{z}^2 > 0 \qquad \vee \qquad (1-\frac{z}{k_z}) < 0 \;\wedge\; z+ah_z z^2-ah_z\hat{z}^2 < 0$$
$$\hat{z} < k_z \;\wedge\; \hat{z} > 0 \qquad \vee \qquad \hat{z} > k_z \;\wedge\; \hat{z} < 0$$

Since k_z is nonnegative, the second option is not possible, leaving us with $0 < \hat{z} < k_z$.

Equation 5.23*

We know that the determinant is positive if it holds that

$$0 < \hat{z} < k_z.$$

Where $\hat{z}$ is the value of z at the equilibrium point. We know that

$$\hat{z} = \frac{\mu}{a(\gamma_z - \mu h_z)}$$

This means that the requirements for the determinant being positive are met if:

$$\begin{array}{rcl}
\hat{z} > 0 & \text{and} & \hat{z} < k_z \\
\dfrac{\mu}{a(\gamma_z - \mu h_z)} > 0 & \text{and} & \dfrac{\mu}{a(\gamma_z - \mu h_z)} < k_z \\
a(\gamma_z - \mu h_z) > 0 & \text{and} & k_z > \dfrac{\mu}{a(\gamma_z - \mu h_z)} \\
\gamma_z > \mu h_z & & \\
\mu < \dfrac{\gamma_z}{h_z} & &
\end{array}$$

Equation 5.24*

Requiring that the trace be negative gives us:

$$\begin{aligned}
\mathrm{Tr}(\mathbf{J}) &< 0 \\
\hat{z}\left[-\frac{r_z}{k_z} + \frac{ah_z r_z(1-\frac{\hat{z}}{k_z})}{1+ah_z\hat{z}}\right] &< 0 \\
-\frac{r_z}{k_z} + \frac{ah_z r_z(1-\frac{\hat{z}}{k_z})}{1+ah_z\hat{z}} &< 0 \qquad\qquad (\ z \text{ is positive}) \\
\frac{r_z}{k_z} &> \frac{ah_z r_z(1-\frac{\hat{z}}{k_z})}{1+ah_z\hat{z}} \\
r_z(1+ah_z\hat{z}) &> ah_z k_z r_z(1-\frac{\hat{z}}{k_z}) \\
1+ah_z\hat{z} &> ah_z k_z - \frac{ah_z k_z\hat{z}}{k_z} \\
2ah_z\hat{z} &> ah_z k_z - 1 \\
\hat{z} &> \frac{1}{2}\left(k_z - \frac{1}{ah_z}\right)
\end{aligned}$$

Equation 5.25*

We know that in order for the trace to be negative, it must hold that:

$$\hat{z} \;>\; \frac{1}{2}\left(k_z - \frac{1}{ah_z}\right)$$

We also have an expression for $\hat{z}$, the value of z at the equilibrium point:

$$\hat{z} = \frac{\mu}{a(\gamma_z - \mu h_z)}.$$

Combining these two expressions gives us the conditions for which the trace will be negative:

$$\begin{aligned}
\hat{z} &> \frac{1}{2}\left(k_z - \frac{1}{ah_z}\right)\\
\frac{\mu}{a(\gamma_z - \mu h_z)} &> \frac{1}{2}\left(k_z - \frac{1}{ah_z}\right)\\
\frac{2\mu}{a(\gamma_z - \mu h_z)} &> k_z - \frac{1}{ah_z}\\
k_z &< \frac{2\mu}{a(\gamma_z - \mu h_z)} + \frac{1}{ah_z}\\
k_z &< \frac{2a\mu h_z}{a^2h_z(\gamma_z - \mu h_z)} + \frac{a(\gamma_z - \mu hz)}{a^2h_z(\gamma_z - \mu h_z)}\\
k_z &< \frac{2a\mu h_z + a(\gamma_z - \mu h_z)}{a^2h_z(\gamma_z - \mu h_z)}\\
k_z &< \frac{2\mu h_z + \gamma_z - \mu h_z}{ah_z(\gamma_z - \mu h_z)}\\
k_z &< \frac{\gamma_z + \mu h_z}{ah_z(\gamma_z - \mu h_z)}
\end{aligned}$$

Stability of the trivial fixed points

Equations 5.31* and 5.32*

The trivial fixed point $(y, z) = (0, k_z)$ is a stable attractor iff:

$$\begin{aligned}
-\mu + \frac{a\gamma_z k_z}{1 + ah_z k_z} &< 0\\
\mu &> \frac{a\gamma_z k_z}{1 + ah_z k_z}\\
\mu(1 + ah_z k_z) &> a\gamma_z k_z\\
\mu + \mu a h_z k_z &> a\gamma_z k_z\\
a\gamma_z k_z - \mu a h_z k_z &< \mu\\
k_z a(\gamma_z - \mu h_z) &< \mu\\
\gamma_z - \mu h_z < 0 \quad &\vee \quad \left[k_z < \frac{\mu}{a(\gamma_z - \mu k_z)} \quad \text{and} \quad \gamma_z - \mu h_z > 0\right]\\
\mu > \frac{\gamma_z}{h_z} \quad &\vee \quad \left[k_z < \frac{\mu}{a(\gamma_z - \mu k_z)} \quad \text{and} \quad \mu < \frac{\gamma_z}{h_z}\right]
\end{aligned}$$

5.2 System including primary prey

5.2.1 Equilibria

Equation 5.38*a,b

The predator zero-isoclines are found by setting $\dfrac{dy}{dt} = 0$:

$$\begin{aligned}
y\left[-\mu + \frac{a(\gamma_x x + \delta\gamma_z z)}{1 + a(h_x x + \delta h_z z)}\right] &= 0 \\
-\mu + \frac{a(\gamma_x x + \delta\gamma_z z)}{1 + a(h_x x + \delta h_z z)} &= 0 \quad \vee \quad y = 0 \\
\frac{a(\gamma_x x + \delta\gamma_z z)}{1 + a(h_x x + \delta h_z z)} &= \mu \\
a\gamma_x x + \delta a\gamma_z z &= \mu + a\mu h_x x + \delta a\mu h_z z \\
x(a\gamma_x - a\mu h_x) &= \mu + \delta a\mu h_z z - \delta a\gamma_z z \\
x &= \frac{\mu + \delta a\mu h_z z - \delta a\gamma_z z}{(a\gamma_x - a\mu h_x)} \\
x &= \frac{\mu + \delta a z(\mu h_z - \gamma_z)}{a(\gamma_x - \mu h_x)} \\
x &= \frac{\mu - \delta a z(\gamma_z - \mu h_z)}{a(\gamma_x - \mu h_x)} \qquad (10.3)
\end{aligned}$$

Equation 5.38*c,d

The zero-isoclines of prey x are found by setting $\dfrac{dx}{dt} = 0$:

$$\begin{aligned}
x\left[r_x(1 - \frac{x}{k_x}) - \frac{ay}{1 + a(h_x x + \delta h_z z)}\right] &= 0 \\
x = 0 \qquad \vee \qquad r_x(1 - \frac{x}{k_x}) - \frac{ay}{1 + a(h_x x + \delta h_z z)} &= 0 \\
\frac{ay}{1 + a(h_x x + \delta h_z z)} &= r_x(1 - \frac{x}{k_x}) \\
y &= \frac{r_x}{a}(1 - \frac{x}{k_x})(1 + ah_x x + \delta a h_z z) \qquad (10.4)
\end{aligned}$$

Equation 5.38*e,f,g

The zero-isoclines of prey z are found by setting $\dfrac{dz}{dt} = 0$:

$$
\begin{aligned}
& & & z\left[r_z(1-\frac{z}{k_z})-\frac{\delta a y}{1+a(h_x x+\delta h_z z)}\right] &= 0\\
z=0 & \quad\vee & & r_z(1-\frac{z}{k_z})-\frac{\delta a y}{1+a(h_x x+\delta h_z z)} &= 0\\
z=0 & \quad\vee & (\delta=0\wedge z=k_z) \quad\vee & \frac{\delta a y}{1+a(h_x x+\delta h_z z)} &= r_z(1-\frac{z}{k_z})\\
& & & y &= \frac{r_z}{\delta a}(1-\frac{z}{k_z})(1+ah_x x+\delta a h_z z)
\end{aligned} \tag{10.5}
$$

Equation 5.39*

Intersection of isoclines (b),(d) and (e):
Here $x = y = 0$. Filling this in in (e) gives:

$$
\begin{aligned}
y &= \frac{r_z}{\delta a}(1-\frac{z}{k_z})(1+ah_x x+\delta a h_z z)\\
0 &= \frac{r_z}{\delta a}(1-\frac{z}{k_z})(1+\delta a h_z z)\\
0 &= (1-\frac{z}{k_z}) \qquad \vee \qquad 1+\delta a h_z z = 0\\
\frac{z}{k_z} &= 1 \qquad\qquad \vee \qquad z = -\frac{1}{\delta a h_z}\\
z &= k_z \qquad\qquad \vee \qquad \rightarrow \textit{always negative, infeasible}
\end{aligned}
$$

This means this intersection gives us the fixed point $(x, y, z) = (0, 0, k_z)$

Equation 5.40*

Intersection of isoclines (b),(c) and (f):
Here $y = z = 0$. Filling this in in (c) gives:

$$
\begin{aligned}
y &= \frac{r_x}{a}(1-\frac{x}{k_x})(1+ah_x x+\delta a h_z z)\\
0 &= \frac{r_x}{a}(1-\frac{x}{k_x})(1+ah_x x)\\
0 &= (1-\frac{x}{k_x}) \qquad \vee \qquad 1+ah_x x = 0\\
\frac{x}{k_x} &= 1 \qquad\qquad \vee \qquad x = -\frac{1}{ah_x}\\
x &= k_x \qquad\qquad \vee \qquad \rightarrow \textit{always negative, infeasible}
\end{aligned}
$$

Thus this leads to the fixed point $(x, y, z) = (k_x, 0, 0)$

Equation 5.41*

The intersection of isoclines (b),(c), and (e): Here $y = 0$. Filling this in in (c) gives:

$$\begin{aligned}
y &= \frac{r_x}{a}(1 - \frac{x}{k_x})(1 + ah_x x + \delta ah_z z) \\
0 &= \frac{r_x}{a}(1 - \frac{x}{k_x})(1 + ah_x x + \delta ah_z z) \\
0 &= (1 - \frac{x}{k_x}) \\
\frac{x}{k_x} &= 1 \\
x &= k_x
\end{aligned}$$

And filling $y = 0$ in in (e) gives:

$$\begin{aligned}
y &= \frac{r_z}{\delta a}(1 - \frac{z}{k_z})(1 + ah_x x + \delta ah_z z) \\
0 &= \frac{r_z}{\delta a}(1 - \frac{z}{k_z})(1 + ah_x x + \delta ah_z z) \\
0 &= (1 - \frac{z}{k_z}) \\
\frac{z}{k_z} &= 1 \\
z &= k_z
\end{aligned}$$

Thus we see that these isoclines intersect at the point $(x, y, z) = (k_x, 0, k_z)$

Equations 5.42* and 5.43*

The intersection of isoclines (a), (d) and (e): Here $x = 0$. This means $\delta = 1$. Filling this in in (a) gives:

$$\begin{aligned}
x &= \frac{\mu - \delta az(\gamma_z - \mu h_z)}{a(\gamma_x - \mu h_x)} \\
x &= \frac{\mu - az(\gamma_z - \mu h_z)}{a(\gamma_x - \mu h_x)} \\
\mu - az(\gamma_z - \mu h_z) &= 0 \qquad\qquad (\text{and} \gamma_x \neq \mu h_x) \\
az(\gamma_z - \mu h_z) &= \mu \\
z &= \frac{\mu}{a(\gamma_z - \mu h_z)}
\end{aligned}$$

Using this result in equation (e) we determine y to be:

$$\begin{aligned}
y &= \frac{r_z}{\delta a}(1 - \frac{z}{k_z})(1 + ah_x x + \delta ah_z z) \\
y &= \frac{r_z}{a}(1 - \frac{z}{k_z})(1 + ah_z z)
\end{aligned}$$

$$
\begin{aligned}
y &= \frac{r_z}{a}\left(1 - \frac{1}{ak_z(\frac{\gamma_x}{\mu} - h_x)}\right)\left(1 + \frac{ah_z}{a(\frac{\gamma_z}{\mu} - h_z)}\right) \\
y &= \frac{r_z}{a}\left(1 - \frac{\mu}{ak_z(\gamma_x - \mu h_x)}\right)\left(1 + \frac{\mu h_z}{(\gamma_z - \mu h_z)}\right)
\end{aligned}
$$

Equation 5.44*

We can see that y is only positive (feasible) if

$$h_z < \frac{\gamma_z}{\mu},$$

which ensures the last term is positive, and if

$$k_z > \frac{\mu}{a\,(\gamma_z - \mu h_z)},$$

which ensures the second term is positive.

Equation 5.45*

$\delta = 1$ at this point if:

$$
\begin{aligned}
\frac{1}{a(h_z\frac{\gamma_x}{\gamma_z} - h_x)} &> 0 \\
a(h_z\frac{\gamma_x}{\gamma_z} - h_x) &> 0 \\
h_z\frac{\gamma_x}{\gamma_z} &> h_x \\
\frac{\gamma_x}{h_x} &> \frac{\gamma_z}{h_z},
\end{aligned}
$$

which is always true in our system.

Equations 5.46* and 5.47*

The intersection of isoclines (a), (c) and (f): At this point, $z = 0$. Plugging this into (a) gives:

$$
\begin{aligned}
x &= \frac{\mu - \delta az(\gamma_z - \mu h_z)}{a(\gamma_x - \mu h_x)} \\
x &= \frac{\mu}{a(\gamma_x - \mu h_x)},
\end{aligned}
$$

Entering the above into (c) we get the expression for y:

$$
\begin{aligned}
y &= \frac{r_z}{a}(1-\frac{x}{k_x})(1+ah_xx+\delta ah_zz) \\
y &= \frac{r_z}{a}(1-\frac{\mu}{ak_x(\gamma_x-\mu h_x)})(1+\frac{a\mu h_x}{a(\gamma_x-\mu h_x)}) \\
y &= \frac{r_z}{a}(1-\frac{\mu}{ak_x(\gamma_x-\mu h_x)})(1+\frac{\mu h_x}{\gamma_x-\mu h_x})
\end{aligned}
$$

Equation 5.48*

In order for this fixed point to be biologically realistic, the values of x and y at this equillibrium point must be positive. x is positive if:

$$
\begin{aligned}
x &= \frac{\mu}{a(\gamma_x-\mu h_x)} > 0 \\
& a(\gamma_x-\mu h_x) > 0 \\
& \gamma_x > \mu h_x \\
& \mu < \frac{\gamma_x}{h_x}.(*)
\end{aligned}
$$

y is positive if:

$$
y = \frac{r_z}{a}(1-\frac{\mu}{ak_x(\gamma_x-\mu h_x)})(1+\frac{\mu h_x}{\gamma_x-\mu h_x}) > 0
$$

Because of requirement $(*)$, we know that the third term in the above inequality is positive. This means that y is only positive if the second term is also positive:

$$
\begin{aligned}
& 1-\frac{\mu}{ak_x(\gamma_x-\mu h_x)} > 0 \\
& 1 > \frac{\mu}{ak_x(\gamma_x-\mu h_x)} \\
& k_x > \frac{\mu}{a(\gamma_x-\mu h_x)}
\end{aligned}
$$

Equations 5.49* and 5.50*

The intersection of isoclines (a), (c) and (g): Here $z = k_z$ and $\delta = 0$ (from (g)). Filling this in in (a) gives:

$$
\begin{aligned}
x &= \frac{\mu-\delta az(\gamma_z-\mu h_z)}{a(\gamma_x-\mu h_x)} \\
x &= \frac{\mu}{a(\gamma_x-\mu h_x)} \\
x &= \frac{\mu}{a(\gamma_x-\mu h_x)},
\end{aligned}
$$

Entering the above into (c) we get the expression for y:

$$
\begin{aligned}
y &= \frac{r_z}{a}(1 - \frac{x}{k_x})(1 + ah_x x + \delta a h_z z) \\
y &= \frac{r_z}{a}(1 - \frac{1}{ak_x(\frac{\gamma_x}{\mu} - h_x)})(1 + \frac{ah_x}{a(\frac{\gamma_x}{\mu} - h_x)}) \\
y &= \frac{r_z}{a}(1 - \frac{\mu}{ak_x(\gamma_x - \mu h_x)})(1 + \frac{\mu h_x}{\gamma_x - \mu h_x})
\end{aligned}
$$

Equation 5.49* and 5.50*

In order for this fixed point to be biologically realistic, the values of x and y at this equillibrium point must be positive. x is positive if:

$$
\begin{aligned}
x &= \frac{\mu}{a(\gamma_x - \mu h_x)} > 0 \\
& a(\gamma_x - \mu h_x) > 0 \\
& \gamma_x > \mu h_x \\
& \mu < \frac{\gamma_x}{h_x}.(*)
\end{aligned}
$$

y is positive if:

$$
y = \frac{r_z}{a}(1 - \frac{\mu}{ak_x(\gamma_x - \mu h_x)})(1 + \frac{\mu h_x}{\gamma_x - \mu h_x}) > 0
$$

Because of requirement $(*)$, we know that the third term in the above inequality is positive. This means that y is only positive if the second term is also positive:

$$
\begin{aligned}
1 - \frac{\mu}{ak_x(\gamma_x - \mu h_x)} &> 0 \\
1 &> \frac{\mu}{ak_x(\gamma_x - \mu h_x)} \\
k_x &> \frac{\mu}{a(\gamma_x - \mu h_x)}
\end{aligned}
$$

Equation 5.52*

The requirement that $\delta = 0$ can be expressed as:

$$
\begin{aligned}
\hat{x} &> \frac{1}{h_z(\frac{\gamma_x}{\gamma_z} - h_x)} \\
\frac{\mu}{a(\gamma_x - \mu h_x)} &> \frac{1}{a(h_z \frac{\gamma_x}{\gamma_z} - h_x)}
\end{aligned}
$$

$$
\begin{aligned}
\frac{1}{a(\frac{\gamma_x}{\mu}-h_x)} &> \frac{1}{a(h_z\frac{\gamma_x}{\gamma_z}-h_x)} \\
a(\frac{\gamma_x}{\mu}-h_x) &< a(h_z\frac{\gamma_x}{\gamma_z}-h_x) \\
\frac{\gamma_x}{\mu}-h_x &< h_z\frac{\gamma_x}{\gamma_z}-h_x \\
\frac{\gamma_x}{h_x} > \frac{\gamma_z}{h_z} &\wedge \frac{\gamma_z}{h_z} < \mu < \frac{\gamma_x}{h_x}.
\end{aligned}
$$

The first part is always true in our system.

Equation 5.54*,5.55*, and 5.56*

Intersection of isoclines (a), (c) and (e): The nontrivial equilibrium is found by determining the intersection between the following isoclines:

$$
x = \frac{1+\delta az(h_z-\frac{\gamma_z}{\mu})}{a(\frac{\gamma_x}{\mu}-h_x)} = \frac{\mu-\delta az(\gamma_z-\mu h_z)}{a(\gamma_x-\mu h_x)} \tag{10.6}
$$

$$
y = \frac{rx}{a}(1-\frac{x}{k_x})(1+ah_xx+\delta ah_zz) \tag{10.7}
$$

$$
y = \frac{rz}{\delta a}(1-\frac{z}{k_z})(1+ah_xx+\delta ah_zz) \tag{10.8}
$$

Equating 10.7 and 10.8 gives us an expression for x:

$$
\begin{aligned}
\frac{r_x}{a}(1-\frac{x}{k_x})(1+ah_xx+\delta ah_zz) &= \frac{r_z}{\delta a}(1-\frac{z}{k_z})(1+ah_xx+\delta ah_zz) \\
\frac{r_x}{a}(1-\frac{x}{k_x}) = \frac{r_z}{\delta a}(1-\frac{z}{k_z}) \quad &\vee \quad (1+ah_xx+\delta ah_zz) = 0 \\
\frac{r_x}{a}-\frac{r_x}{ak_x}x = \frac{r_z}{\delta a}-\frac{r_z}{\delta ak_z}z \quad &\vee \quad x = -\frac{1+\delta ah_zz}{ah_x} \\
\frac{r_x}{ak_x}x = \frac{r_x}{a}-\frac{r_z}{\delta a}+\frac{r_z}{\delta ak_z}z \quad &\vee \quad \rightarrow \textit{always negative, infeasible} \\
x &= \frac{ar_xk_x}{ar_x}-\frac{ar_zk_x}{\delta ar_x}+\frac{ar_zk_x}{\delta ar_xk_z}z \\
x &= k_x-\frac{r_zk_x}{\delta r_x}+\frac{r_zk_x}{\delta r_xk_z}z \\
x &= k_x(1-\frac{r_z}{\delta r_x}+\frac{r_z}{\delta r_xk_z}z) \\
x &= \frac{k_x(\delta r_xk_z-r_zk_z+r_zz)}{\delta r_xk_z}
\end{aligned} \tag{10.9}
$$

Next we combine result 10.9 with the isocline 10.6 to obtain an expression for z:

$$
\begin{aligned}
\frac{k_x(\delta r_x k_z - r_z k_z + r_z z)}{\delta r_x k_z} &= \frac{\mu - \delta a z(\gamma_z - \mu h_z)}{a(\gamma_x - \mu h_x)} \\
a k_x(\delta r_x k_z - r_z k_z + r_z z)(\gamma_x - \mu h_x) &= \delta \mu r_x k_z - \delta^2 a r_x k_z(\gamma_z - \mu h_z) z \\
a r_z k_x(\gamma_x - \mu h_x) z + a k_x(\delta r_x k_z - r_z k_z)(\gamma_x - \mu h_x) &= \delta \mu r_x k_z - \delta a r_x k_z(\gamma_z - \mu h_z) z \qquad (\delta^2 = \delta) \\
z\left(a r_z k_x(\gamma_x - \mu h_x) + \delta a r_x k_z(\gamma_z - \mu h_z)\right) &= \delta \mu r_x k_z - a k_x(\delta r_x k_z - r_z k_z)(\gamma_x - \mu h_x) \\
z &= \frac{\delta \mu r_x k_z - a k_x(\delta r_x k_z - r_z k_z)(\gamma_x - \mu h_x)}{a r_z k_x(\gamma_x - \mu h_x) + \delta a r_x k_z(\gamma_z - \mu h_z)} \\
z &= \frac{k_z}{a}\left[\frac{\delta r_x - a k_x(\delta r_x - r_z)(\gamma_x - \mu h_x)}{r_z k_x(\gamma_x - \mu h_x) + \delta r_x k_z(\gamma_z - \mu h_z)}\right] \\
z &= -\frac{k_z}{a}\left[\frac{a k_x(\delta r_x - r_z)(\gamma_x - \mu h_x) - \delta \mu r_x}{r_z k_x(\gamma_x - \mu h_x) + \delta r_x k_z(\gamma_z - \mu h_z)}\right] \qquad (10.10)
\end{aligned}
$$

Equating 10.7 and 10.8 can also give us an expression for z:

$$
\begin{aligned}
\frac{r_x}{a}(1 - \frac{x}{k_x})(1 + a h_x x + \delta a h_z z) &= \frac{r_z}{\delta a}(1 - \frac{z}{k_z})(1 + a h_x x + \delta a h_z z) \\
\frac{r_x}{a}(1 - \frac{x}{k_x}) = \frac{r_z}{\delta a}(1 - \frac{z}{k_z}) \quad &\vee \quad (1 + a h_x x + \delta a h_z z) = 0 \\
\frac{r_x}{a} - \frac{r_x}{a k_x} x = \frac{r_z}{\delta a} - \frac{r_z}{\delta a k_z} z \quad &\vee \quad x = -\frac{1 + \delta a h_z z}{a h_x} \\
\frac{r_z}{\delta a k_z} z = \frac{r_z}{\delta a} - \frac{r_x}{a} + \frac{r_x}{a k_x} x \quad &\vee \quad \rightarrow \textit{always negative, infeasible} \\
z &= \frac{\delta a r_z k_z}{\delta a r_z} - \frac{\delta a r_x k_z}{a r_z} + \frac{\delta a r_x k_z}{a r_z k_x} x \\
z &= k_z - \frac{\delta r_x k_z}{r_z} + \frac{\delta r_x k_z}{r_z k_x} x \\
z &= k_z(1 - \frac{\delta r_x}{r_z} + \frac{\delta r_x}{r_z k_x} x) \\
z &= \frac{k_x(r_z k_x - \delta r_x k_x + \delta r_x x)}{r_z k_x} \qquad (10.11)
\end{aligned}
$$

If we now fill in 10.11 into equation 10.6 and solve for x, we get:

$$
\begin{aligned}
x &= \frac{\mu - \delta a z(\gamma_z - \mu h_z)}{a(\gamma_x - \mu h_x)} \\
x &= \frac{\mu - \delta a \frac{k_z(r_z k_x - \delta r_x k_x + \delta r_x x)}{r_z k_x}(\gamma_z - \mu h_z)}{a(\gamma_x - \mu h_x)} \\
a(\gamma_x - \mu h_x)x &= \mu - \delta a \frac{k_z(r_z k_x - \delta r_x k_x + \delta r_x x)}{r_z k_x}(\gamma_z - \mu h_z) \\
a r_z k_x(\gamma_x - \mu h_x)x &= \mu r_z k_x - \delta a k_z(r_z k_x - \delta r_x k_x + \delta r_x x)(\gamma_z - \mu h_z) \\
a r_z k_x(\gamma_x - \mu h_x)x &= \mu r_z k_x - \delta a k_z(r_z k_x - \delta r_x k_x)(\gamma_z - \mu h_z) - \delta^2 a r_x k_z(\gamma_z - \mu h_z)x \\
a r_z k_x(\gamma_x - \mu h_x)x + \delta a r_x k_z(\gamma_z - \mu h_z)x &= \mu r_z k_x - \delta a k_z(r_z k_x - \delta r_x k_x)(\gamma_z - \mu h_z) \\
x(a r_z k_x(\gamma_x - \mu h_x) + \delta a r_x k_z(\gamma_z - \mu h_z)) &= \mu r_z k_x - \delta a k_z(r_z k_x - \delta r_x k_x)(\gamma_z - \mu h_z) \\
x &= \frac{\mu r_z k_x - \delta a k_z(r_z k_x - \delta r_x k_x)(\gamma_z - \mu h_z)}{a r_z k_x(\gamma_x - \mu h_x) + \delta a r_x k_z(\gamma_z - \mu h_z)} \\
x &= \frac{k_x}{a}\left[\frac{\mu r_z - \delta a k_z(r_z - \delta r_x)(\gamma_z - \mu h_z)}{r_z k_x(\gamma_x - \mu h_x) + \delta r_x k_z(\gamma_z - \mu h_z)}\right] \\
x &= \frac{k_x}{a}\left[\frac{\delta a k_z(\delta r_x - r_z)(\gamma_z - \mu h_z) + \mu r_z}{r_z k_x(\gamma_x - \mu h_x) + \delta r_x k_z(\gamma_z - \mu h_z)}\right] \qquad (10.12)
\end{aligned}
$$

Now that we have expressions for x and z, it remains to find an expression for y. We do this by filling in our expressions for x and z into one of the expressions for y (10.7 or 10.8).

To see that the expression for y is correct, please refer to the Mathematica notebook entitled *Fixed point 8* in Appendix B. Below is an excerpt of this notebook.

```
xd[x_, y_, z_] := x * (rx * (1 - x / kx) - a * y / (1 + a * hx * x + a * hz * z))

yd[x_, y_, z_] := y * (-m + a * (gx * x + gz * z) / (1 + a * hx * x + a * hz * z))

zd[x_, y_, z_] := z * (rz * (1 - z / kz) - a * y / (1 + a * hx * x + a * hz * z))

Simplify[Solve[{xd[x, y, z] == 0, yd[x, y, z] == 0, zd[x, y, z] == 0}, {x, y, z}]]
```

$$
\begin{aligned}
&\Big\{\{x \to 0,\ y \to 0,\ z \to 0\},\ \{y \to 0,\ x \to 0,\ z \to kz\},\ \{y \to 0,\ x \to kx,\ z \to kz\},\\
&\{y \to 0,\ z \to 0,\ x \to kx\},\ \Big\{y \to \frac{gx\,(-m + a\,kx\,(gx - hx\,m))\,rx}{a^2\,kx\,(gx - hx\,m)^2},\ z \to 0,\ x \to \frac{m}{a\,gx - a\,hx\,m}\Big\},\\
&\Big\{y \to \frac{gz\,(-m + a\,kz\,(gz - hz\,m))\,rz}{a^2\,kz\,(gz - hz\,m)^2},\ x \to 0,\ z \to \frac{m}{a\,gz - a\,hz\,m}\Big\},\\
&\Big\{y \to ((m + a\,(-gx\,kx - gz\,kz + hx\,kx\,m + hz\,kz\,m))\,rx\,rz\,(-gz\,kz\,(rx + a\,hx\,kx\,rx - a\,hx\,kx\,rz) -\\
&\quad gx\,kx\,(rz + a\,hz\,kz\,(-rx + rz))))\Big/\big(a^2\,(gz\,kz\,rx - hz\,kz\,m\,rx + kx\,(gx - hx\,m)\,rz)^2\big),\\
&x \to \frac{kx\,(a\,kz\,(gz - hz\,m)\,(rx - rz) + m\,rz)}{a\,(gz\,kz\,rx - hz\,kz\,m\,rx + kx\,(gx - hx\,m)\,rz)},\ z \to \frac{kz\,(m\,rx - a\,kx\,(gx - hx\,m)\,(rx - rz))}{a\,(gz\,kz\,rx - hz\,kz\,m\,rx + kx\,(gx - hx\,m)\,rz)}\Big\}\Big\}
\end{aligned}
$$

Other isocline intersections

There are four other intersections of isoclines we have not yet discussed. We will show that these intersections either yield either duplicate fixed points or biologically infeasible ones.

The intersection of isoclines (a), (d) and (f):

Here we have

$$
\begin{aligned}
x &= 0 \\
z &= 0 \\
x &= \frac{\mu - \delta a z(\gamma_x - \mu h_x)}{a(\gamma_x - \mu h_x)},
\end{aligned}
$$

which leads to:

$$0 = \frac{\mu}{a(\gamma_x - \mu h_x)}$$

And since this requires that $\mu = 0$, which is generally not the case in our system, this intersection does not lead to an equilibrium point.

The intersection of isoclines (a), (d) and (g):
Here we have

$$
\begin{aligned}
x &= 0 \\
z &= k_z, \delta = 0 \\
x &= \frac{\mu - \delta a z(\gamma_x - \mu h_x)}{a(\gamma_x - \mu h_x)},
\end{aligned}
$$

which leads to:

$$0 = \frac{\mu}{a(\gamma_x - \mu h_x)}$$

And since this requires that $\mu = 0$, which is generally not the case in our system, this intersection does not lead to an equilibrium point.

The intersection of isoclines (b), (c) and (g):
Here we have

$$
\begin{aligned}
y &= 0 \\
z &= k_z, \delta = 0 \\
y &= \frac{r_x}{a}(1 - \frac{x}{k_x})(1 + a h_x x),
\end{aligned}
$$

which leads to:

$$
\begin{aligned}
0 &= \frac{r_x}{a}(1 - \frac{x}{k_x})(1 + ah_x x) \\
1 - \frac{x}{k_x} = 0 \qquad &\vee \qquad 1 + ah_x x = 0 \\
x = k_x \qquad &\vee \qquad x = -\frac{1}{ah_x}
\end{aligned}
$$

This second value for x is infeasible since it is negative, and the first would lead to fixed point $(k_x, 0, k_z)$, which we had already found.

The intersection of isoclines (b), (d) and (g):
Here we have

$$
\begin{aligned}
&y = 0 \\
&x = 0 \\
&z = 0, delta = 0
\end{aligned}
$$

which leads to the fixed point $(0, 0, k_z)$, which we had already found.

Table 5.1*

The derivation of the conditions for existence of fixed point 8 is rather involved, and was done using Mathematica. See also the notebook entitled *fp8.nb* and Appendix B.

Let fixed point 8 be denoted by $(\hat{x}, \hat{y}, \hat{z})$. For this fixed point to exist, all population densities must be positive. Furthermore, we know that at this point δ must be 1, which means the density of x must be lower than the threshold where δ flips values.

We let mathematica calculate under what conditions the following requirements are satisfied:

$$
\begin{aligned}
&0 < \hat{x} < \text{deltaThreshold} \\
&\hat{y} > 0 \\
&\hat{z} > 0,
\end{aligned}
$$

Where

$$
\text{deltaThreshold} = \frac{1}{a(h_z \frac{\gamma_x}{\gamma_z} - h_x)}
$$

When we enter this in Mathematica, we get the following output:

```
Simplify[Reduce[{xfp8 < deltaThreshold, a > 0, m > 0, kx > 0, kz > 0, hx > 0, hz > 0,
   gx > 0, gz > 0, rx > 0, rz > 0, gx / hx > gz / hz, zfp8 > 0, yfp8 > 0, xfp8 > 0}]]
```

$$\text{hz} > 0 \,\&\&\, \text{hx} > 0 \,\&\&\, \text{gz} > 0 \,\&\&\, \text{gx} > \frac{\text{gz hx}}{\text{hz}} \,\&\&\, 0 < \text{m} < \frac{\text{gz}}{\text{hz}} \,\&\&\, \text{kz} > 0 \,\&\&$$
$$\text{kx} > 0 \,\&\&\, \text{rz} > 0 \,\&\&\, \text{a} > \frac{\text{m}}{\text{gx kx} + \text{gz kz} - (\text{hx kx} + \text{hz kz})\ \text{m}} \,\&\&\, \Bigg(\text{rx} == \text{rz} \,||$$
$$\left(\text{rx} > 0 \,\&\&\, \text{rx} < \text{rz} \,\&\&\, \text{a} + \frac{\text{m rz}}{\text{kz}\ (\text{gz} - \text{hz m})\ (\text{rx} - \text{rz})} < 0\right) \,||\, \left(\text{a} < \frac{\text{m rx}}{\text{kx}\ (\text{gx} - \text{hx m})\ (\text{rx} - \text{rz})} \,\&\&\, \text{rx} > \text{rz}\right)\Bigg)$$

Here we see that we must have that $\mu < \frac{\gamma_z}{h_z}$. We also see that we can separate 3 subcases, namely $r_x < r_z$, $r_x = r_z$, and $r_x > r_z$. We next ask Mathematica again, for each of these three subcases, and ask Mathematica to give us the conditions in terms of k_x and/or k_z. First we look at the case $r_x < r_z$:

```
Simplify[Reduce[{xfp8 < deltaThreshold, a > 0, m > 0, kx > 0, kz > 0, hx > 0, hz > 0, gx > 0,
   gz > 0, rx > 0, rz > 0, gx / hx > gz / hz, zfp8 > 0, yfp8 > 0, xfp8 > 0, rx < rz}, kz]]
```

$$\text{hz} > 0 \,\&\&\, \text{hx} > 0 \,\&\&\, \text{gz} > 0 \,\&\&\, \text{gx} > \frac{\text{gz hx}}{\text{hz}} \,\&\&\, 0 < \text{m} < \frac{\text{gz}}{\text{hz}} \,\&\&$$
$$\text{kx} > 0 \,\&\&\, \text{rz} > 0 \,\&\&\, 0 < \text{rx} \,\&\&\, \text{kz} + \frac{\text{m rz}}{\text{a}\ (\text{gz} - \text{hz m})\ (\text{rx} - \text{rz})} < 0 \,\&\&\, \text{rx} < \text{rz} \,\&\&$$
$$\left(\left(0 < \text{a} \,\&\&\, \text{a} < \frac{\text{m}}{\text{gx kx} - \text{hx kx m}} \,\&\&\, \frac{-\text{a gx kx} + \text{m} + \text{a hx kx m}}{\text{a}\ (\text{gz} - \text{hz m})} < \text{kz}\right) \,||\, \left(\text{a} \geq \frac{\text{m}}{\text{gx kx} - \text{hx kx m}} \,\&\&\, 0 < \text{kz}\right)\right)$$

This tells us that we must have:

$$k_z < \frac{-\mu r_z}{a(\gamma_z - \mu h_z)(r_x - r_z)}, \qquad (k_z < II)$$

and either

$$k_x \geq \frac{\mu}{a(\gamma_x - \mu h_x)}, \qquad (k_x \geq V)$$

or

$$k_x < \frac{\mu}{a(\gamma_x - \mu h_x)}\ , \quad k_z > \frac{\mu - a k_x(\gamma_x - \mu h_x)}{a(\gamma_z - \mu h_z)} \qquad (k_x < V \quad \text{and} \quad k_z > III)$$

Next we look at the situation $r_x = r_z$:

```
Simplify[Reduce[{xfp8 < deltaThreshold, a > 0, m > 0, kx > 0, kz > 0, hx > 0, hz > 0, gx > 0, gz > 0,
   rx > 0, rz > 0, gx / hx > gz / hz, zfp8 > 0, yfp8 > 0, xfp8 > 0, rx == rz}, {kx, kz}]]
```

$$hz > 0 \;\&\&\; hx > 0 \;\&\&\; gz > 0 \;\&\&\; gx > \frac{gz\,hx}{hz} \;\&\&\; 0 < m < \frac{gz}{hz} \;\&\&\; rz > 0 \;\&\&\; a > 0 \;\&\&\; rx == rz \;\&\&$$
$$\left(\left(0 < kx \le \frac{m}{a\,gx - a\,hx\,m} \;\&\&\; kz > \frac{-a\,gx\,kx + m + a\,hx\,kx\,m}{a\,(gz - hz\,m)}\right) \;||\; \left(kx > \frac{m}{a\,gx - a\,hx\,m} \;\&\&\; kz > 0\right)\right)$$

Here we see that we must have

$$k_x > \frac{\mu}{a(\gamma_x - \mu h_x)}, \qquad\qquad (k_x > V)$$

Or,

$$k_x \le \frac{\mu}{a(\gamma_x - \mu h_x)}\ ,\quad k_z > \frac{\mu - ak_x(\gamma_x - \mu h_x)}{a(\gamma_z - \mu h_z)} \qquad\qquad (k_x \le V \quad \text{and} \quad k_z > III).$$

And finally, we look at the situation $r_x > r_z$:

```
Simplify[Reduce[{xfp8 < deltaThreshold, a > 0, m > 0, kx > 0, kz > 0, hx > 0, hz > 0, gx > 0,
   gz > 0, rx > 0, rz > 0, gx / hx > gz / hz, zfp8 > 0, yfp8 > 0, xfp8 > 0, rx > rz}, kx]]
```

$$hz > 0 \;\&\&\; hx > 0 \;\&\&\; gz > 0 \;\&\&\; gx > \frac{gz\,hx}{hz} \;\&\&\; 0 < m < \frac{gz}{hz} \;\&\&$$
$$kz > 0 \;\&\&\; rx > rz \;\&\&\; rz > 0 \;\&\&\; kx < \frac{m\,rx}{a\,(gx - hx\,m)\,(rx - rz)} \;\&\&$$
$$\left(\left(0 < a \;\&\&\; a < \frac{m}{gz\,kz - hz\,kz\,m} \;\&\&\; \frac{-a\,gz\,kz + m + a\,hz\,kz\,m}{a\,(gx - hx\,m)} < kx\right) \;||\; \left(a \ge \frac{m}{gz\,kz - hz\,kz\,m} \;\&\&\; 0 < kx\right)\right)$$

Here we see that we must have

$$k_x < \frac{\mu r_x}{a(\gamma_x - \mu h_x)(r_x - r_z)}, \qquad\qquad (k_x < I)$$

And either

$$k_z \ge \frac{\mu}{a(\gamma_z - \mu h_z)}, \qquad\qquad (k_z \ge VI)$$

or

$$k_z < \frac{\mu}{a(\gamma_z - \mu h_z)}\ ,\quad k_x > \frac{\mu - ak_z(\gamma_z - \mu h_z)}{a(\gamma_x - \mu h_x)} \qquad\qquad (k_z < VI \quad \text{and} \quad k_x > IV)$$

If we put this all into a table, we get:

<table>
<tr><td rowspan="6">$\mu < \frac{\gamma_z}{h_z}$</td><td rowspan="2">$r_x < r_z$</td><td>$k_x < V$</td><td>$III < k_z < II$</td></tr>
<tr><td>$k_x \geq V$</td><td>$k_z < II$</td></tr>
<tr><td rowspan="2">$r_x = r_z$</td><td>$k_x \leq V$</td><td>$k_z > III$</td></tr>
<tr><td colspan="2">$k_x > V$</td></tr>
<tr><td rowspan="2">$r_x > r_z$</td><td>$k_z < VI$</td><td>$IV < k_x < I$</td></tr>
<tr><td>$k_z \geq VI$</td><td>$k_x < I$</td></tr>
</table>

5.2.2 Stability Analysis

Equation 5.73*

$$
\begin{aligned}
&\frac{dg_y}{dy} = \\
&\frac{d}{dy}\left[-\mu + \frac{a\gamma_x x + \delta a \gamma_z z}{1 + ah_x x + \delta a h_z z}\right] = \\
&0
\end{aligned}
$$

Equation 5.74*

$$
\begin{aligned}
&\frac{dg_y}{dx} = \\
&\frac{d}{dx}\left[-\mu + \frac{a\gamma_x x + \delta a \gamma_z z}{1 + ah_x x + \delta a h_z z}\right] = \\
&\frac{d}{dx}\left[-\mu\right] + \frac{d}{dx}\left[\frac{a\gamma_x x}{1 + ah_x x + \delta a h_z z}\right] + \frac{d}{dx}\left[\frac{\delta a \gamma_z z}{1 + ah_x x + \delta a h_z z}\right] = \\
&x\frac{d}{dx}\left[\frac{a\gamma_x}{1 + ah_x x + \delta a h_z z}\right] + \frac{a\gamma_x}{1 + ah_x x + \delta a h_z z}\frac{d}{dx}\left[x\right] + \frac{d}{dx}\left[\frac{\delta a \gamma_z z}{1 + ah_x x + \delta a h_z z}\right] = \qquad \text{(product rule)} \\
&x\frac{d}{du}\left[\frac{a\gamma_x}{u}\right]\frac{du}{dx} + \frac{a\gamma_x}{1 + ah_x x + \delta a h_z z} + \frac{d}{du}\left[\frac{\delta a \gamma_z z}{u}\right]\frac{du}{dx} = \qquad \text{(substitute } u = 1 + ah_x + \delta a h_z z\text{)}
\end{aligned}
$$

$$x\frac{d}{du}\left[\frac{a\gamma_x}{u}\right]\frac{d}{dx}\left[1+ah_xx+\delta ah_zz\right]+\frac{a\gamma_x}{1+ah_xx+\delta ah_zz}+\frac{d}{du}\left[\frac{\delta a\gamma_zz}{1+ah_xx\delta ah_zz}\right]\frac{d}{dx}\left[1+ah_xx+\delta ah_zz\right]=$$
$$x\frac{-a\gamma_x}{u^2}ah_x+\frac{a\gamma_x}{1+ah_xx+\delta ah_zz}-\frac{\delta a\gamma_zz}{u^2}ah_xx=$$
$$\frac{-a^2h_x\gamma_xx}{(1+ah_xx+\delta ah_zz)^2}+\frac{a\gamma_x}{1+ah_xx+\delta ah_zz}-\frac{\delta a^2h_x\gamma_zz}{(1+ah_xx+\delta ah_zz)^2}=$$
$$\frac{a\gamma_x}{1+ah_xx+\delta ah_zz}-\frac{a^2h_x(\gamma_xx+\delta\gamma_zz)}{(1+ah_xx+\delta ah_zz)^2}.$$

Equation 5.75*

$$\frac{dg_y}{dz}=$$
$$\frac{d}{dz}\left[-\mu+\frac{a\gamma_xx+\delta a\gamma_zz}{1+ah_xx+\delta ah_zz}\right]=$$
$$\frac{d}{dz}\left[-\mu\right]+\frac{d}{dz}\left[\frac{a\gamma_xx}{1+ah_xx+\delta ah_zz}\right]+\frac{d}{dz}\left[\frac{\delta a\gamma_zz}{1+ah_xx+\delta ah_zz}\right]=$$
$$\frac{d}{dz}\left[\frac{a\gamma_xx}{1+ah_xx+\delta ah_zz}\right]+\frac{\delta a\gamma_z}{1+ah_xx+\delta ah_zz}\frac{d}{dz}\left[z\right]+z\frac{d}{dz}\left[\frac{\delta a\gamma_z}{1+ah_xx+\delta ah_zz}\right]=\qquad\text{(product rule)}$$
$$\frac{d}{du}\left[\frac{a\gamma_xx}{u}\right]\frac{du}{dz}+\frac{\delta a\gamma_z}{1+ah_xx+\delta ah_zz}+z\frac{d}{du}\left[\frac{\delta a\gamma_z}{u}\right]\frac{du}{dz}=\qquad\text{(substitute } u=1+ah_x+\delta ah_zz\text{)}$$
$$\frac{d}{du}\left[\frac{a\gamma_xx}{u}\right]\frac{d}{dz}\left[1+ah_xx+\delta ah_zz\right]+\frac{\delta a\gamma_z}{1+ah_xx+\delta ah_zz}+z\frac{d}{du}\left[\frac{\delta a\gamma_z}{u}\right]\frac{d}{dz}\left[1+ah_xx+\delta ah_zz\right]=$$
$$\frac{-a\gamma_xx}{u^2}\delta ah_z+\frac{\delta a\gamma_z}{1+ah_xx+\delta ah_zz}-z\frac{\delta a\gamma_z}{u^2}\delta ah_z=$$
$$\frac{-\delta a^2h_z\gamma_xx}{(1+ah_xx+\delta ah_zz)^2}+\frac{\delta a\gamma_z}{1+ah_xx+\delta ah_zz}-\frac{\delta^2a^2h_z\gamma_zz}{(1+ah_xx+\delta ah_zz)^2}=$$
$$\frac{\delta a\gamma_z}{1+ah_xx+\delta ah_zz}-\frac{\delta a^2h_z(\gamma_xx+\gamma_zz)}{(1+ah_xx+\delta ah_zz)^2}$$

Equation 5.76*

$$\frac{dg_x}{dy}=$$
$$\frac{d}{dy}\left[r_x(1-\frac{x}{k_x})-\frac{ay}{1+ah_xx+\delta ah_zz}\right]=$$
$$-\frac{a}{1+ah_xx+\delta ah_zz}.$$

Equation 5.77*

$$\frac{dg_x}{dx} =$$
$$\frac{d}{dx}\left[r_x(1-\frac{x}{k_x})-\frac{ay}{1+ah_xx+\delta ah_zz}\right] =$$
$$\frac{d}{dx}\left[r_x(1-\frac{x}{k_x})\right]-\frac{d}{dx}\left[\frac{ay}{1+ah_xx+\delta ah_zz}\right] =$$
$$-\frac{r_x}{k_x}-\frac{d}{du}\left[\frac{ay}{u}\right]\frac{du}{dx} =$$
$$-\frac{r_x}{k_x}-\frac{d}{du}\left[\frac{ay}{u}\right]\frac{d}{dx}\left[1+ah_xx+\delta ah_zz\right] =$$
$$-\frac{r_x}{k_x}+\frac{ay}{u^2}ah_x =$$
$$-\frac{r_x}{k_x}+\frac{a^2h_xy}{(1+ah_xx+\delta ah_zz)^2}.$$

Equation 5.78*

$$\frac{dg_x}{dz} =$$
$$\frac{d}{dz}\left[r_x(1-\frac{x}{k_x})-\frac{ay}{1+ah_xx+\delta ah_zz}\right] =$$
$$\frac{d}{dz}\left[r_x(1-\frac{x}{k_x})\right]-\frac{d}{dz}\left[\frac{ay}{1+ah_xx+\delta ah_zz}\right] =$$
$$-\frac{d}{du}\left[\frac{ay}{u}\right]\frac{du}{dx} =$$
$$-\frac{d}{du}\left[\frac{ay}{u}\right]\frac{d}{dx}\left[1+ah_xx+\delta ah_zz\right] =$$
$$\frac{ay}{u^2}\delta ah_z =$$
$$\frac{\delta a^2h_zy}{(1+ah_xx+\delta ah_zz)^2}.$$

Equation 5.80*

$$\frac{dg_z}{dy} =$$
$$\frac{d}{dy}\left[r_z(1-\frac{z}{k_z})-\frac{\delta ay}{1+ah_xx+\delta ah_zz}\right] =$$

$$- \frac{\delta a}{1 + ah_x x + \delta a h_z z}$$

Equation 5.81*

$$\frac{dg_z}{dx} =$$
$$\frac{d}{dx}\left[r_z(1 - \frac{z}{k_z}) - \frac{\delta a y}{1 + ah_x x + \delta a h_z z}\right] =$$
$$\frac{d}{dx}\left[r_z(1 - \frac{z}{k_z})\right] - \frac{d}{dx}\left[\frac{\delta a y}{1 + ah_x x + \delta a h_z z}\right] =$$
$$- \frac{d}{du}\left[\frac{\delta a y}{u}\right]\frac{du}{dx} =$$
$$- \frac{d}{du}\left[\frac{\delta a y}{u}\right]\frac{d}{dx}\left[1 + ah_x x + \delta a h_z z\right] =$$
$$\frac{\delta a y}{u^2} a h_x =$$
$$\frac{\delta a^2 h_x y}{(1 + ah_x x + \delta a h_z z)^2}.$$

Equation 5.82*

$$\frac{dg_z}{dz} =$$
$$\frac{d}{dz}\left[r_z(1 - \frac{z}{k_z}) - \frac{\delta a y}{1 + ah_x x + \delta a h_z z}\right] =$$
$$\frac{d}{dz}\left[r_z(1 - \frac{z}{k_z})\right] - \frac{d}{dz}\left[\frac{\delta a y}{1 + ah_x x + \delta a h_z z}\right] =$$
$$- \frac{r_z}{k_z} - \frac{d}{du}\left[\frac{\delta a y}{u}\right]\frac{du}{dz} =$$
$$- \frac{r_z}{k_z} - \frac{d}{du}\left[\frac{\delta a y}{u}\right]\frac{d}{dz}\left[1 + ah_x x + \delta a h_z z\right] =$$
$$- \frac{r_z}{k_z} + \frac{\delta a y}{u^2}\delta a h_z =$$
$$- \frac{r_z}{k_z} + \frac{\delta^2 a^2 h_x y}{(1 + ah_x x + \delta a h_z z)^2} =$$
$$- \frac{r_z}{k_z} + \frac{\delta a^2 h_x y}{(1 + ah_x x + \delta a h_z z)^2}. \qquad \text{(since } \delta^2 = \delta\text{)}$$

5.2.2 Stability Analysis

Trivial fixed points

Equation 5.83*

The Jacobian of the system is given by:

$$\mathbf{J} = \begin{bmatrix} y\frac{dg_y}{dy} + g_y & y\frac{dg_y}{dx} & y\frac{dg_y}{dz} \\ x\frac{dg_x}{dy} & x\frac{dg_x}{dx} + g_x & x\frac{dg_x}{dz} \\ z\frac{dg_z}{dy} & z\frac{dg_z}{dx} & z\frac{dg_z}{dz} + g_z \end{bmatrix},$$

We now evaluate the Jacobian at the point $(x, y, z) = (0, 0, 0)$:

$$\begin{bmatrix} y\frac{dg_y}{dy} + g_y & y\frac{dg_y}{dx} & y\frac{dg_y}{dz} \\ x\frac{dg_x}{dy} & x\frac{dg_x}{dx} + g_x & x\frac{dg_x}{dz} \\ z\frac{dg_z}{dy} & z\frac{dg_z}{dx} & z\frac{dg_z}{dz} + g_z \end{bmatrix}_{(0,0,0)} = \begin{bmatrix} g_y & 0 & 0 \\ 0 & g_x & 0 \\ 0 & 0 & g_z \end{bmatrix}_{(0,0,0)} =$$

$$\begin{bmatrix} -\mu + \frac{a(\gamma_x x+\delta\gamma_z z)}{1+ah_x x+\delta ah_z z} & 0 & 0 \\ 0 & r_x(1-\frac{x}{k_x}) - \frac{ay}{1+ah_x x+\delta ah_z z} & 0 \\ 0 & 0 & r_z(1-\frac{z}{k_z}) - \frac{\delta ay}{1+ah_x x+\delta ah_z z} \end{bmatrix}_{(0,0,0)} = \begin{bmatrix} -\mu & 0 & 0 \\ 0 & r_x & 0 \\ 0 & 0 & r_z \end{bmatrix}.$$

Equation 5.84*

The Jacobian of the system is given by:

$$\mathbf{J} = \begin{bmatrix} y\frac{dg_y}{dy} + g_y & y\frac{dg_y}{dx} & y\frac{dg_y}{dz} \\ x\frac{dg_x}{dy} & x\frac{dg_x}{dx} + g_x & x\frac{dg_x}{dz} \\ z\frac{dg_z}{dy} & z\frac{dg_z}{dx} & z\frac{dg_z}{dz} + g_z \end{bmatrix},$$

We now evaluate the Jacobian at the point $(x, y, z) = (k_x, 0, 0)$:

$$\begin{bmatrix} y\frac{dg_y}{dy} + g_y & y\frac{dg_y}{dx} & y\frac{dg_y}{dz} \\ x\frac{dg_x}{dy} & x\frac{dg_x}{dx} + g_x & x\frac{dg_x}{dz} \\ z\frac{dg_z}{dy} & z\frac{dg_z}{dx} & z\frac{dg_z}{dz} + g_z \end{bmatrix}_{(k_x,0,0)} = \begin{bmatrix} g_y & 0 & 0 \\ k_x\frac{dg_x}{dy} & k_x\frac{dg_x}{dx} + g_x & k_x\frac{dg_x}{dz} \\ 0 & 0 & g_z \end{bmatrix}_{(k_x,0,0)} =$$

$$\begin{bmatrix} -\mu + \frac{a(\gamma_x x+\delta\gamma_z z)}{1+ah_x x+\delta ah_z z} & 0 & 0 \\ \frac{ak_x}{1+ah_x x+\delta ah_z z} & -r_x + \frac{a^2h_xk_xy}{1+ah_x x+\delta ah_z z} + r_x(1-\frac{x}{k_x}) - \frac{ay}{1+ah_x x+\delta ah_z z} & \frac{\delta a^2h_zk_xy}{1+ah_x x+\delta ah_z z} \\ 0 & 0 & r_z(1-\frac{z}{k_z}) - \frac{\delta ay}{1+ah_x x+\delta ah_z z} \end{bmatrix}_{(k_x,0,0)} =$$

$$\begin{bmatrix} -\mu + \frac{a\gamma_x k_x}{1+ah_xk_x} & 0 & 0 \\ -\frac{ak_x}{1+ah_xk_x} & -r_x & 0 \\ 0 & 0 & r_z \end{bmatrix}$$

Equation 5.86*

The predator can invade if

$$\begin{aligned}
-\mu + \frac{a\gamma_x k_x}{1 + ah_x k_x} &> 0 \\
\frac{a\gamma_x k_x}{1 + ah_x k_x} &> \mu \\
a\gamma_x k_x &> \mu(1 + ah_x k_x) \\
a\gamma_x k_x - a\mu h_x k_x &> \mu \\
ak_x(\gamma_x - \mu h_x) &> \mu
\end{aligned}$$

$$k_x > \frac{\mu}{a(\gamma_x - \mu h_x)} \quad \text{and} \quad \gamma_x - \mu h_x > 0 \qquad \vee \qquad k_x < \frac{\mu}{a(\gamma_x - \mu h_x)} \quad \text{and} \quad \gamma_x - \mu h_x < 0 k_x > \frac{\mu}{a(\gamma_x - \mu h_x)} \quad \text{ar}$$

Since this second case requires k_z to be negative, we are left with just the first case:

$$k_x > \frac{\mu}{a(\gamma_x - \mu h_x)} \quad \text{and} \quad \mu > \frac{\gamma_x}{h_x}$$

Equation 5.87*

The Jacobian of the system is given by:

$$\mathbf{J} = \begin{bmatrix} y\frac{dg_y}{dy} + g_y & y\frac{dg_y}{dx} & y\frac{dg_y}{dz} \\ x\frac{dg_x}{dy} & x\frac{dg_x}{dx} + g_x & x\frac{dg_x}{dz} \\ z\frac{dg_z}{dy} & z\frac{dg_z}{dx} & z\frac{dg_z}{dz} + g_z \end{bmatrix},$$

We now evaluate the Jacobian at the point $(x, y, z) = (0, 0, k_z)$:

$$\begin{bmatrix} y\frac{dg_y}{dy} + g_y & y\frac{dg_y}{dx} & y\frac{dg_y}{dz} \\ x\frac{dg_x}{dy} & x\frac{dg_x}{dx} + g_x & x\frac{dg_x}{dz} \\ z\frac{dg_z}{dy} & z\frac{dg_z}{dx} & z\frac{dg_z}{dz} + g_z \end{bmatrix}_{(0,0,k_z)} = \begin{bmatrix} g_y & 0 & 0 \\ 0 & g_x & 0 \\ k_z\frac{dg_z}{dy} & k_z\frac{dg_z}{dx} & k_z\frac{dg_z}{dz} + g_z \end{bmatrix}_{(0,0,k_z)} =$$

$$\begin{bmatrix} -\mu + \frac{a(\gamma_x x + \delta\gamma_z z)}{1 + ah_x x + \delta a h_z z} & 0 & 0 \\ 0 & r_x(1 - \frac{x}{k_x}) - \frac{ay}{1 + ah_x x + \delta a h_z z} & 0 \\ -\frac{\delta a k_z}{1 + ah_x x + \delta a h_z z} & \frac{\delta a^2 h_x k_x y}{1 + ah_x x + \delta a h_z z} & -r_z + \frac{\delta a^2 h_x k_z y}{(1 + ah_x x + \delta a h_z z)^2} + r_z(1 - \frac{z}{k_z}) - \frac{\delta a y}{1 + ah_x x + \delta a h_z z} \end{bmatrix}_{(0,0,k_z)} =$$

$$\begin{bmatrix} -\mu + \frac{\delta a \gamma_z k_z}{1 + ah_z k_z} & 0 & 0 \\ 0 & r_x & 0 \\ -\frac{\delta a k_z}{1 + ah_z k_z} & 0 & -r_z \end{bmatrix}$$

Equation 5.90*

The Jacobian of the system is given by:

$$\mathbf{J} = \begin{bmatrix} y\frac{dg_y}{dy} + g_y & y\frac{dg_y}{dx} & y\frac{dg_y}{dz} \\ x\frac{dg_x}{dy} & x\frac{dg_x}{dx} + g_x & x\frac{dg_x}{dz} \\ z\frac{dg_z}{dy} & z\frac{dg_z}{dx} & z\frac{dg_z}{dz} + g_z \end{bmatrix},$$

We now evaluate the Jacobian at the point $(x, y, z) = (k_x, 0, k_z)$:

$$\begin{bmatrix} y\frac{dg_y}{dy} + g_y & y\frac{dg_y}{dx} & y\frac{dg_y}{dz} \\ x\frac{dg_x}{dy} & x\frac{dg_x}{dx} + g_x & x\frac{dg_x}{dz} \\ z\frac{dg_z}{dy} & z\frac{dg_z}{dx} & z\frac{dg_z}{dz} + g_z \end{bmatrix}_{(k_x,0,k_z)} = \begin{bmatrix} g_y & 0 & 0 \\ k_x\frac{dg_x}{dy} & k_x\frac{dg_x}{dx} + g_x & k_x\frac{dg_x}{dz} \\ k_z\frac{dg_z}{dy} & k_z\frac{dg_z}{dx} & k_z\frac{dg_z}{dz} + g_z \end{bmatrix}_{(k_x,0,k_z)} =$$

$$\begin{bmatrix} -\mu + \frac{a(\gamma_x x + \delta\gamma_z z)}{1+ah_x x+\delta ah_z z} & 0 & 0 \\ \frac{-ak_x}{1+ah_x x+\delta ah_z z} & -r_x + \frac{a^2 h_x k_x y}{1+ah_x x+\delta ah_z z} + g_x & \frac{\delta a^2 h_z k_x y}{1+ah_x x+\delta ah_z z} \\ -\frac{\delta ak_z}{1+ah_x x+\delta ah_z z} & \frac{\delta a^2 h_x k_x y}{1+ah_x x+\delta ah_z z} & -r_z + \frac{\delta a^2 h_x k_z y}{(1+ah_x x+\delta ah_z z)^2} + g_z \end{bmatrix}_{(k_x,0,k_z)} =$$

$$\begin{bmatrix} -\mu + \frac{\delta a\gamma_z k_z}{1+ah_z k_z} & 0 & 0 \\ \frac{-ak_x}{1+ah_x x+\delta ah_z z} & -r_x + r_x(1-\frac{x}{k_x}) - \frac{ay}{1+ah_x x+\delta ah_z z} & 0 \\ -\frac{\delta ak_z}{1+ah_z k_z} & 0 & -r_z + r_z(1-\frac{z}{k_z}) - \frac{\delta ay}{1+ah_x x+\delta ah_z z} \end{bmatrix}_{(k_x,0,k_z)} =$$

$$\begin{bmatrix} -\mu + \frac{\delta a\gamma_z k_z}{1+ah_z k_z} & 0 & 0 \\ \frac{-ak_x}{1+ah_x x+\delta ah_z z} & r_x & 0 \\ -\frac{\delta ak_z}{1+ah_z k_z} & 0 & -r_z \end{bmatrix}$$

Equations 5.92* - 5.94*

Here we determine when fixed point 4 is stable. This is the case iff:

$$\mu > \frac{a\gamma_x k_x + \delta a\gamma_z k_z}{1 + ah_x k_x + \delta ah_z k_z}.$$

First we look at the situation where $\delta = 0$.

$$\begin{aligned} &\mu > \frac{a\gamma_x k_x}{1 + ah_x k_x} \\ &\mu(1 + ah_x k_x) > a\gamma_x k_x \\ &\mu > ak_x(\gamma_x - \mu h_x) \end{aligned}$$

We see that this holds in the following cases:

$$\begin{aligned} &\text{case 1:} \quad && \mu < \frac{\gamma_x}{h_x} \quad \text{and} \quad k_x < \frac{\mu}{a(\gamma_x - \mu h_x)} \\ &\text{case 2:} && \mu > \frac{\gamma_x}{h_x} \quad \text{and} \quad k_x > \frac{\mu}{a(\gamma_x - \mu h_x)} \\ &\text{case 3:} && \mu = \frac{\gamma_x}{h_x} \end{aligned}$$

Since we have said that $\delta = 0$, we also know that:

$$k_x > \frac{1}{a(h_z\frac{\gamma_x}{\gamma_z} - h_x)}.$$

Letting $(A) = \frac{\mu}{a(\gamma_x - \mu h_x)}$, and $(B) = \frac{1}{a(h_z\frac{\gamma_x}{\gamma_z} - h_x)}$, we determine that

$$(A) < (B) \quad \text{if} \quad \mu < \frac{\gamma_z}{h_z} \quad \vee \quad \mu > \frac{\gamma_x}{h_x}$$
$$(B) < (A) \quad \text{if} \quad \frac{\gamma_z}{h_z} < \mu < \frac{\gamma_x}{h_x}$$

Which means that for case 1, where we require $(B) < k_x < (A)$, we also know that $(B) < (A)$ must hold, and so is only possible if $\frac{\gamma_z}{h_z} < \mu < \frac{\gamma_x}{h_x}$.

For case 2 we have that both $k_x > (A)$ and $k_x > (B)$ must hold, and since $\mu > \frac{\gamma_x}{h_x}$, we know that $(A) < (B)$, and therefore it suffices to require only $k_x > (B)$ since this implies $k_x > (A)$.

Thus we are left with the following two requirements:

$$\text{case 1:} \qquad \frac{\gamma_x}{h_z} < \mu < \frac{\gamma_x}{h_x} \quad \text{and} \quad k_x < (A)$$
$$\text{case 2:} \qquad \mu > \frac{\gamma_x}{h_x} \quad \text{and} \quad k_x > (B).$$

Next we consider the case where $\delta = 1$.

$$\mu > \frac{a\gamma_x k_x + \delta a\gamma_z k_z}{1 + ah_x k_x + \delta ah_z k_z}$$
$$\mu > \frac{a\gamma_x k_x + a\gamma_z k_z}{1 + ah_x k_x + ah_z k_z}$$
$$\mu + a\mu h_x k_x + a\mu h_z k_z > a\gamma_x k_x + a\gamma_z k_z$$
$$\mu + ak_z(\mu h_z - \gamma_z) > ak_x(\gamma_x - \mu h_x)$$

We see that this holds in the following two cases:

$$\text{case 1:} \qquad \mu < \frac{\gamma_z}{h_z} \quad \text{and} \quad k_z < (C)$$
$$\text{case 2:} \qquad \mu > \frac{\gamma_z}{h_z} \quad \text{and} \quad k_z > (C)$$
$$\text{case 3:} \qquad \mu = \frac{\gamma_z}{h_z} \quad \text{and} \quad k_x < (A)$$

Where $(C) = \frac{\mu - ak_x(\gamma_x - \mu h_x)}{a(\gamma_z - \mu h_z)}$

For our further analysis, we need to know when (C) is positive and when it is negative. To that end, we determine when the numerator and denominator are positive and when they are negative. It is easily shown that

$$\text{denominator negative:} \qquad \mu > \frac{\gamma_z}{h_z}$$
$$\text{denominator positive:} \qquad \mu < \frac{\gamma_z}{h_z}$$
$$\text{numerator negative:} \qquad k_x > (A)$$
$$\text{numerator positive:} \qquad k_x < (A)$$

First let us consider case 1. The denominator of (C) is positive since we have $\mu < \frac{\gamma_z}{h_z}$. We have determined that the numerator is negative (and thus (C) negative) if $k_x > (A)$. If this holds, then $k_z < (C)$ is impossible. Note that since we require $\delta = 1$, we also have $k_x < (B)$. But since $\mu < \frac{\gamma_z}{h_z}$ we have $(A) < (B)$, so this does not change the conditions.

Next we consider case 2. We will split this case into two subcases:

$$\begin{aligned} &\text{case 2a:} \qquad \frac{\gamma_z}{h_z} < \mu <= \frac{\gamma_x}{h_x} \quad \text{and} \quad k_z > (C) \\ &\text{case 2b:} \qquad \mu > \frac{\gamma_x}{h_x} \quad \text{and} \quad k_z > (C). \end{aligned}$$

Let us consider case 2a. Here we have that the denominator of (C) is negative. If we also have that $k_x < (A)$, then the numerator is positive, and (C) negative, which means that the requirement $k_z > (C)$ always holds. If, on the other hand $k_x > (A)$, then (C) is positive. But since we say that $\delta = 1$ here, which means $k_x < (B)$, and we have that $(A) > (B)$ here, it cannot hold that both $k_x > (A)$ and $k_x < (B)$. This means case 2a is reduced to $\frac{\gamma_z}{h_z} < \mu < \frac{\gamma_x}{h_x}$ and $k_x < (A)$
Now let us look at case 2b. Here we have that the denominator is negative, and the numerator positive, which means (C) is negative and the requirement $k_z > (C)$ always holds.

All this leads to the following cases:

$$\begin{aligned} &\text{case 1:} \qquad \mu < \frac{\gamma_z}{h_z} \quad \text{and} \quad k_x < (A) \quad \text{and} \quad k_z < (C) \\ &\text{case 2a:} \qquad \frac{\gamma_z}{h_z} <= \mu < \frac{\gamma_x}{h_x} \quad \text{and} \quad k_x < (A) \\ &\text{case 2b:} \qquad \mu >= \frac{\gamma_x}{h_x} \quad (\text{and} \quad k_x < (B) \quad \text{since } \delta = 1 \text{ here}). \end{aligned}$$

Now what remains to be done is to combine the cases for $\delta = 0$ and $\delta = 1$. We see that case 1 in the situation $\delta = 0$ is identical to case 2b. And case 2 of the situation $\delta = 0$ can be combined with case 2b. This leads to the following final set of conditions:

$$\begin{aligned} &\mu < \frac{\gamma_z}{h_z} \quad \text{and} \quad k_x < \frac{\mu}{a(\gamma_x - \mu h_x)} \quad \text{and} \quad k_z < \frac{\mu - a k_x(\gamma_x - \mu h_x)}{a(\gamma_z - \mu h_z)}, \qquad \text{or} \\ &\frac{\gamma_z}{h_z} <= \mu < \frac{\gamma_x}{h_x} \quad \text{and} \quad k_x < \frac{\mu}{a(\gamma_x - \mu h_x)}, \quad \text{or} \\ &\mu >= \frac{\gamma_x}{h_x}. \end{aligned}$$

Equations 5.100* and 5.101*

See also the Mathematica Notebook in Appendix B entitled *Stability of fixed points 5 and 6.*

First we determine when this fixed point is an attractor:

```
In[14]:= Simplify[Reduce[{EV1[yfp, zfp] < 0, EV2[yfp, zfp] < 0, EV3[yfp, zfp] < 0, a > 0,
    m > 0, hx > 0, hz > 0, kx > 0, kz > 0, rx > 0, rz > 0, gx > 0, gz > 0, gx / hx > gz / hz}]]
```

Out[14]= $m > 0 \;\&\&\; gz > 0 \;\&\&\; 0 < hz < \frac{gz}{m} \;\&\&\; kz > 0 \;\&\&\; \frac{m}{gz\,kz - hz\,kz\,m} < a < \frac{gz + hz\,m}{gz\,hz\,kz - hz^2\,kz\,m} \;\&\&$

$rz \geq \frac{4\,a\,gz\,kz\,(gz - hz\,m)^2\,(-m + a\,kz\,(gz - hz\,m))}{m\,(gz - a\,gz\,hz\,kz + hz\,(1 + a\,hz\,kz)\,m)^2} \;\&\&$

$0 < rx < \frac{a\,gz\,kz\,rz - m\,rz - a\,hz\,kz\,m\,rz}{a\,gz\,kz - a\,hz\,kz\,m} \;\&\&\; hx > 0 \;\&\&\; gx > \frac{gz\,hx}{hz} \;\&\&\; kx > 0$

This gives us

$$\mu < \frac{\gamma_z}{h_z} \quad , \quad VI < k_z < VIII \qquad r_z \geq X \quad , \quad r_x < XII,$$

And second we determine when this fixed point is a repeller:

```
In[15]:= Simplify[Reduce[{EV1[yfp, zfp] > 0, EV2[yfp, zfp] > 0, EV3[yfp, zfp] > 0, a > 0,
    m > 0, hx > 0, hz > 0, kx > 0, kz > 0, rx > 0, rz > 0, gx > 0, gz > 0, gx / hx > gz / hz}]]
```

Out[15]= $m > 0 \;\&\&\; gz > 0 \;\&\&\; 0 < hz < \frac{gz}{m} \;\&\&\; kz > 0 \;\&\&$

$a > \frac{gz + hz\,m}{gz\,hz\,kz - hz^2\,kz\,m} \;\&\&\; rz \geq \frac{4\,a\,gz\,kz\,(gz - hz\,m)^2\,(-m + a\,kz\,(gz - hz\,m))}{m\,(gz - a\,gz\,hz\,kz + hz\,(1 + a\,hz\,kz)\,m)^2} \;\&\&$

$rx > \frac{a\,gz\,kz\,rz - m\,rz - a\,hz\,kz\,m\,rz}{a\,gz\,kz - a\,hz\,kz\,m} \;\&\&\; hx > 0 \;\&\&\; gx > \frac{gz\,hx}{hz} \;\&\&\; kx > 0$

which gives us:

$$\mu < \frac{\gamma_z}{h_z} \quad , \quad k_z > VIII \quad , \quad r_z \geq X \quad , \quad r_x > XII,$$

Equations 5.113* - 5.114*

See also the Mathematica Notebook in Appendix B entitled *Stability of fixed points 5 and 6.* At this point, δ can be both zero or one. First we will consider the case where $\delta = 0$, then the case where $\delta = 1$, and then we will combine the results. If this equilibrium occurs at a point where z is not included in the diet ($\delta = 0$), then this equilibrium is never an attractor:

```
In[29]:= Simplify[Reduce[{EV61[xfp, yfp6] < 0, EV62[xfp, yfp6] < 0,
    EV63[xfp, yfp6] < 0, a > 0, m > 0, hx > 0, hz > 0, kx > 0, kz > 0, rx > 0, rz > 0,
    gx > 0, gz > 0, d == 0, gx / hx > gz / hz, xfp > 1 / (a * (hz * gx / gz - hx))}]]

Out[29]= False
```

It can, however, be a repeller:

```
In[30]:= Simplify[Reduce[{EV61[xfp, yfp6] > 0, EV62[xfp, yfp6] > 0,
    EV63[xfp, yfp6] > 0, a > 0, m > 0, hx > 0, hz > 0, kx > 0, kz > 0, rx > 0, rz > 0,
    gx > 0, gz > 0, d == 0, gx / hx > gz / hz, xfp > 1 / (a * (hz * gx / gz - hx))}]]
```

Out[30]= $m > 0 \,\&\&\, gx > 0 \,\&\&\, 0 < hx < \frac{gx}{m} \,\&\&\, gz > 0 \,\&\&\, hz > \frac{gz}{m} \,\&\&\, kx > 0 \,\&\&\, a > \frac{gx + hx\,m}{gx\,hx\,kx - hx^2\,kx\,m} \,\&\&$
$rx \geq \frac{4\,a\,gx\,kx\,(gx - hx\,m)^2\,(-m + a\,kx\,(gx - hx\,m))}{m\,(gx - a\,gx\,hx\,kx + hx\,(1 + a\,hx\,kx)\,m)^2} \,\&\&\, rz > 0 \,\&\&\, kz > 0 \,\&\&\, d == 0$

Here we see that it is a repeller if:

$$\frac{\gamma_z}{h_z} < \mu < \frac{\gamma_x}{h_x} \quad , \quad k_x > VII \quad , \quad r_x \geq IX$$

If, however, this equilibrium occurs at a point where z is included in the diet, ($\delta = 1$), then it is possible for this fixed point to be an attractor:

```
In[27]:= Simplify[Reduce[{EV61[xfp, yfp6] < 0, EV62[xfp, yfp6] < 0,
    EV63[xfp, yfp6] < 0, a > 0, m > 0, hx > 0, hz > 0, kx > 0, kz > 0, rx > 0, rz > 0,
    gx > 0, gz > 0, d == 1, gx / hx > gz / hz, xfp < 1 / (a * (hz * gx / gz - hx))}]]
```

Out[27]= $m > 0 \,\&\&\, gx > 0 \,\&\&\, 0 < hx < \frac{gx}{m} \,\&\&\, gz > 0 \,\&\&\, \frac{gz\,hx}{gx} < hz < \frac{gz}{m} \,\&\&\, kx > 0 \,\&\&$
$\frac{m}{gx\,kx - hx\,kx\,m} < a < \frac{gx + hx\,m}{gx\,hx\,kx - hx^2\,kx\,m} \,\&\&\, rx \geq \frac{4\,a\,gx\,kx\,(gx - hx\,m)^2\,(-m + a\,kx\,(gx - hx\,m))}{m\,(gx - a\,gx\,hx\,kx + hx\,(1 + a\,hx\,kx)\,m)^2} \,\&\&$
$0 < rz < \frac{a\,gx\,kx\,rx - m\,rx - a\,hx\,kx\,m\,rx}{a\,gx\,kx - a\,hx\,kx\,m} \,\&\&\, kz > 0 \,\&\&\, d == 1$

Here we see that we have

$$\mu < \frac{\gamma_z}{h_z} \quad , \quad V < k_x < VII \quad , \quad r_x \geq IX \quad , \quad r_z < XI$$

For $\delta = 1$, this fixed point can also be a repeller:

```
In[28]:= Simplify[Reduce[{EV61[xfp, yfp6] > 0, EV62[xfp, yfp6] > 0,
    EV63[xfp, yfp6] > 0, a > 0, m > 0, hx > 0, hz > 0, kx > 0, kz > 0, rx > 0, rz > 0,
    gx > 0, gz > 0, d == 1, gx / hx > gz / hz, xfp < 1 / (a * (hz * gx / gz - hx))}]]
```

Out[28]= $m > 0 \,\&\&\, gx > 0 \,\&\&\, 0 < hx < \frac{gx}{m} \,\&\&\, gz > 0 \,\&\&\, \frac{gz\,hx}{gx} < hz < \frac{gz}{m} \,\&\&\, kx > 0 \,\&\&$
$a > \frac{gx + hx\,m}{gx\,hx\,kx - hx^2\,kx\,m} \,\&\&\, rx \geq \frac{4\,a\,gx\,kx\,(gx - hx\,m)^2\,(-m + a\,kx\,(gx - hx\,m))}{m\,(gx - a\,gx\,hx\,kx + hx\,(1 + a\,hx\,kx)\,m)^2} \,\&\&$
$rz > \frac{a\,gx\,kx\,rx - m\,rx - a\,hx\,kx\,m\,rx}{a\,gx\,kx - a\,hx\,kx\,m} \,\&\&\, kz > 0 \,\&\&\, d == 1$

This gives us:

$$\mu < \frac{\gamma_z}{h_z} \quad , \quad k_x > VII \quad , \quad r_x \geq IX \quad , \quad r_z > XI$$

We can combine the above conditions for stability. The fixed point is an attractor if

$$\mu < \frac{\gamma_z}{h_z} \quad , \quad V < k_x < VII \quad , \quad r_x \geq IX \quad , \quad r_z < XI,$$

and it is a repeller if

$$\mu < \frac{\gamma_x}{h_x} \quad , \quad k_x > VII \quad , \quad r_x \geq IX \quad , \text{and} \quad \left[\mu > \frac{\gamma_z}{h_z} \quad \text{or} \quad r_z > XI\right]$$

In all other cases, this fixed point is a saddle point.

Table 5.2

Here we will derive the table for the existences and stabilities of fixed points 1-7.
First we list all the conditions for stability and existence of the different fixed points:

- Fixed points 1-3 always exist and are always saddle points.
- Fixed point 4 always exists and is stable if

$$\begin{aligned} &\mu \geq \frac{\gamma_x}{h_x}, \\ &\frac{\gamma_z}{h_z} \leq \mu < \frac{\gamma_x}{h_x} \; , \;\; k_x < V, \text{ or,} \\ &\mu < \frac{\gamma_z}{h_z} \; , \;\; k_x < V, \;\; k_z < III \end{aligned}$$

- Fixed point 5 exists if $\mu < \frac{\gamma_z}{h_z}$ and $k_z > VI$. It is stable if

$$\mu < \frac{\gamma_z}{h_z} \quad VI < k_z < VIII \; , \;\; r_z \geq X \; , \;\; r_x < XII.$$

  It is a repeller if

$$\mu < \frac{\gamma_z}{h_z} \quad k_z > VIII \; , \;\; r_z \geq X \; , \;\; r_x > XII.$$

  And a saddle point otherwise.

- Fixed point 6 exists if $\mu < \frac{\gamma_x}{h_x}$ and $k_x > V$. It is stable if

$$\mu < \frac{\gamma_z}{h_z} \quad V < k_x < VII \; , \;\; r_x \geq IX \; , \;\; r_z < XI.$$

It is a repeller if

$$\mu < \frac{\gamma_x}{h_x} \quad k_x > VII \ , \quad r_x \geq IX \ , \quad \left[\mu > \frac{\gamma_z}{h_z} \quad \text{or} \quad r_z > XI\right].$$

And a saddle point otherwise.

- Fixed point 7 exists if $\frac{\gamma_z}{h_z} \leq \mu < \frac{\gamma_x}{h_x}$ and $k_x > V$. It is stable if also $k_x < VII$.

We will first divide the parameter space into three situations, based on the value of μ:

$$\begin{aligned} &1). \quad \mu \geq \frac{\gamma_x}{h_x} \\ &2). \quad \frac{\gamma_z}{h_z} \leq \mu < \frac{\gamma_x}{h_x} \\ &3). \quad \mu < \frac{\gamma_z}{h_z} \end{aligned}$$

Let us consider the first situation. We see that for this parameter range, fixed points 5,6,7, and 8 do not exist, and fixed point 4 is always stable. This leads us to the sub-table:

$\mu \geq \frac{\gamma_x}{h_x}$	attractor: 4

Next we look at situation 2, $\frac{\gamma_z}{h_z} \leq \mu < \frac{\gamma_x}{h_x}$. We now look at each fixed point individually to see when, if ever, they exist and what their stability is in this situation:

- fixed point 4 exists, and is stable if it also holds that $k_x < V$. If $k_x \geq V$, then fixed point 4 is a saddle point.
- fixed point 5 does not exist for these values of μ
- fixed point 6 exists, and it is a repeller if it also holds that $k_x > VII$ and $r_x \geq IX$. If these two conditions do not hold, then fixed point 6 is a saddle point.
- fixed point 7 exists if we also have that $k_x > V$ is stable if it also holds that $k_x < VII$.
- fixed point 8 does not exist for this parameter range.

We see that we have conditions in terms of k_x compared to both V and VII. We can determine that $V < VII$ iff $\mu < \frac{\gamma_x}{h_x}$. Since this is always true for this parameter range, we can now subdivide this situation into the following 3 cases, based on the value of k_x:

$$\begin{aligned} k_x &< V, \\ V < k_x &< VII, \\ k_x &> VII. \end{aligned}$$

And this last case can be further subdivided based on the value of r_x. This leads to the following sub-table:

$\frac{\gamma_z}{h_z} \leq \mu < \frac{\gamma_x}{h_x}$	$k_x < V$		*attractor: 4*
	$V < k_x < VII$		*attractor: 7 , saddle: 4, 6*
	$k_x > VII$	$r_x < IX$	*saddle: 4,6,7*
		$r_x \geq IX$	*repeller: 6 , saddle: 4,7*

Finally, we look at situation 3, $\mu < \frac{\gamma_z}{h_z}$. We again look at each fixed point individually to see what their conditions for existence and stability are in this situation:

- fixed point 4 exists, and is stable if it also holds that $k_x < V$ and $k_z < III$.
- fixed point 5 exists if $k_z > VI$.
  It is an attractor if $VI < k_z < VIII$, $r_z \geq X$, and $r_x < XII$
  It is a repeller if $k_z > VIII$, $r_z \geq X$, and $r_x > XII$
- fixed point 6 exists if $k_x > V$.
  It is an attractor if $V < k_x < VII$, $r_x \geq IX$, and $r_z < XI$
  It is a repeller if $k_x > VII$, $r_x \geq IX$, $r_z > XI$
- fixed point 7 does not exist.
- fixed point 8 may exist in this parameter range.

We determine that in this range, the following holds:

$$\begin{aligned} V &< VII \\ III < VI &< VIII. \end{aligned}$$

We also see that $r_x < XII$ implies that $r_x < r_z$:

$$\begin{aligned} r_x &< XII \\ r_x < r_z &\left[\frac{-\mu + ak_z(\gamma_z - \mu h_z)}{ak_z(\gamma_z - \mu h_z)}\right] \end{aligned}$$

And since the expression in the square brackets is always smaller than 1, this means that r_x is smaller than r_z. In a similar fashion we determine that $r_z < XI$ implies that $r_x > r_z$. Thus we see that we can never have both $r_x < XII$ and $r_z < XI$, which also means we never have that both fixed point 5 and fixed point 6 stable. Using these facts, we can now construct the last part of the table:

$\mu < \frac{\gamma_z}{h_z}$	$k_x < V$	$k_z < III$	*attractor: 4*		
		$III < k_z < VI$	*saddle: 4*		
		$VI < k_z < VIII$	$r_z \geq X$ and $r_x < XII$	*attractor: 5, saddle: 4*	
			$r_z < X$ or $r_x \geq XII$	*saddle: 4,5*	
		$k_z > VIII$	$r_z \geq X$ and $r_x < XII$	*repeller: 5, saddle: 4*	
			$r_z < X$ or $r_x \geq XII$	*saddle: 4,5*	
	$V < k_x < VII$	$k_z < VI$	$r_x \geq IX$ and $r_z < XI$	*attr: 6, saddle: 4*	
			$r_x < IX$ or $r_z \geq XI$	*saddle: 4,6*	
		$k_z > VI$	$r_x \geq IX$ and $r_z < XI$	*attr: 6 saddle: 4*	
			$r_x < IX$ or $r_z \leq XI$	$r_z \geq X$ and $r_x < XII$	*attr: 5 saddle: 4,6*
				$r_z < X$ or $r_x \geq XII$	*saddle: 4,5,6*
	$k_x > VII$	$k_z < VI$	$r_x < IX$ or $r_z \leq XI$	*saddle: 4,6*	
			$r_x \geq IX$ and $r_z > XI$	*repeller: 6 saddle: 4*	
		$VI < k_z < VIII$	$r_x < IX$ or $r_z \leq XI$	$r_z \geq X$ and $r_x < XII$	*attr: 5 saddle: 4,6*
				$r_z < X$ or $r_x \geq XII$	*saddle: 4,5,6*
			$r_x \geq IX$ and $r_z > XI$	$r_z \geq X$ and $r_x < XII$	*repeller: 6 attr: 5, saddle:4*
				$r_z < X$ or $r_x \geq XII$	*repeller: 6, saddle: 4,5*
		$k_z > VIII$	$r_x < IX$ or $r_z \leq XI$	$r_z \geq X$ and $r_x > XII$	*repeller: 5 saddle: 4,6*
				$r_z < X$ or $r_x \leq XII$	*saddle: 4,5,6*
			$r_x \geq IX$ and $r_z > XI$	$r_z \geq X$ and $r_x > XII$	*repeller: 5,6, saddle:4*
				$r_z < X$ or $r_x \leq XII$	*repeller: 6, saddle: 4,5*

If we put all these sub-tables together, we get table 5.2.

7 Single Patch Analysis

*Statement 7.1**

Here we will show that whenever fixed point 8 exists, none of the other fixed points are stable. See also Mathematia notebook entitled *Conditions* for some of the following derivations. Below is the table for existence for fixed point 8:

<table>
<tr><td rowspan="6">$\mu < \frac{\gamma_z}{h_z}$</td><td rowspan="2">$r_x < r_z$</td><td>$k_x < V$</td><td>$III < k_z < II$</td></tr>
<tr><td>$k_x \geq V$</td><td>$k_z < II$</td></tr>
<tr><td rowspan="2">$r_x = r_z$</td><td>$k_x \leq V$</td><td>$k_z > III$</td></tr>
<tr><td colspan="2">$k_x > V$</td></tr>
<tr><td rowspan="2">$r_x > r_z$</td><td>$k_z < VI$</td><td>$IV < k_x < I$</td></tr>
<tr><td>$k_z \geq VI$</td><td>$k_x < I$</td></tr>
</table>

We enter the various conditions into Mathematica:

```
In[1]:= RI := m * rx / (a * (gx - m * hx) * (rx - rz))

In[2]:= RII := -m * rz / (a * (gz - m * hz) * (rx - rz))

In[3]:= RIII := (m - a * kx * (gx - m * hx)) / (a * (gz - m * hz))

        RIV := (m - a * kz * (gz - m * hz)) / (a * (gx - m * hx))

In[5]:= RV := m / (a * (gx - m * hx))

In[6]:= RVI := m / (a * (gz - m * hz))

In[7]:= RVII := (gx + m * hx) / (a * hx * (gx - m * hx))

In[8]:= RVIII := (gz + m * hz) / (a * hz * (gz - m * hz))

In[9]:= RIX := (4 * a * gx * kx * (gx - m * hx) ^ 2 * (-m + a * kx * (gx - m * hx))) /
           (m * (gx - a * gx * hx * kx + m * hx * (1 + a * hx * kx)) ^ 2)

In[10]:= RX := (4 * a * gz * kz * (gz - m * hz) ^ 2 * (-m + a * kz * (gz - m * hz))) /
           (m * (gz - a * gz * hz * kz + m * hz * (1 + a * hz * kz)) ^ 2)

In[11]:= RXI := rx * (-m + a * kx * (gx - m * hx)) / (a * kx * (gx - m * hx))

In[12]:= RXII := rz * (-m + a * kz * (gz - m * hz)) / (a * kz * (gz - m * hz))
```

First we consider fixed point 4. This fixed point is stable if one of the three following conditions hold:

$$\begin{aligned}
&1). \quad \mu \geq \frac{\gamma_x}{h_x}, \\
&2). \quad \frac{\gamma_z}{h_z} \leq \mu < \frac{\gamma_x}{h_x} \ , \quad k_x < V, \ \text{or}, \\
&3). \quad \mu < \frac{\gamma_z}{h_z} \ , \quad k_x < V, \quad k_z < III
\end{aligned}$$

We immediately see that if we require that fixed point 8 exist, we are left with only situation 3. Next we look at the situation $r_x < r_z$ and $k_x < V$ in the conditions for existence of fixed point 8. We see that for existence, it is also required that $k_z > III$, but the stability of fixed point 4 requires $k_z < III$, so for $r_x < r_z$ we see that we never have that both fixed point 8 exists and fixed point 4 is stable.

Next look at the situation $r_x == r_z$ and again the requirement $k_x < V$. We see that the existence of 8 again requires $k_z > III$, while the stability of fixed point 4 requires $k_z < III$.

Last we look at $r_x > r_z$. Here we have that $k_x > IV$ must hold for existence of fixed point 8, and $k_z < III$ and $\mu < \frac{\gamma_z}{h_z}$ must hold for stability of fixed point 4. These conditions are never all true:

```
In[52]:= Simplify[Reduce[{kx > RIV, kz < RIII, a > 0, m > 0, kx > 0, kz > 0,
    hx > 0, hz > 0, gx > 0, gz > 0, rx > 0, rz > 0, gx / hx > gz / hz, m < gz / hz}]]

Out[52]= False
```

Thus we can conclude that if fixed point 8 exists, fixed point 4 is not stable.

Next we look at fixed point 5. This fixed point is stable if

$$\mu < \frac{\gamma_z}{h_z} \quad VI < k_z < VIII \ , \quad r_z \geq X \ , \quad r_x < XII.$$

The condition $r_x < XII$ implies that $r_x < r_z$. From the table for existence of fixed point 8, we see that we would then also need $k_z < II$. We can see that we will never have both $r_x < XII$ (required for stability of fixed point 5) and $\mu < \frac{\gamma_z}{h_z}, k_z < II$ (requirement for existence fixed point 8):

```
In[51]:= Simplify[Reduce[{rx < RXII, kz < RII, a > 0, m > 0, kx > 0, kz > 0,
    hx > 0, hz > 0, gx > 0, gz > 0, rx > 0, rz > 0, gx / hx > gz / hz, m < gz / hz}]]

Out[51]= False
```

Next we look at fixed point 6. This fixed point is stable if

$$\mu < \frac{\gamma_z}{h_z} \quad V < k_x < VII \ , \quad r_x \geq IX \ , \quad r_z < XI.$$

The condition $r_z < XI$ implies that $r_z < r_x$. We can see that we will never have both $r_z < XI$ (required for stability of fp5) and $\mu < \frac{\gamma_z}{h_z}$ and $k_z < II$ (requirements for existence fixed point 8):

```
In[54]:= Simplify[Reduce[{rz < RXI, kx < RI, a > 0, m > 0, kx > 0, kz > 0,
            hx > 0, hz > 0, gx > 0, gz > 0, rx > 0, rz > 0, gx / hx > gz / hz, m < gz / hz}]]
Out[54]= False
```

Fixed point 7 does not exist for the parameter range $\mu < \frac{\gamma_z}{h_z}$. So fixed point 7 and fixed point 8 never both exist.

Thus we can say that if fixed point 8 exists, there will not be another fixed point which is stable.

11 Appendix B: Mathematica Notebooks

This appendix contains the code used in Mathematica to perform several of the more involved calculations. The following notebooks can be found here:

11.1 Fixed point 8

In this notebook, the location of fixed point 8 is determined, as well as the conditions for its existence. The notebook file is named `fixedpoint8.nb`.

11.2 Stability of fixed points 5 and 6

As the title indicates, this notebook contains calculations of the conditions for stability of fixed points 5 and 6. The notebook file is named `fp56.nb`.

11.3 Conditions

This notebook contains the conditions I-XII and was used to show that if fixed point 8 exists, none of the other fixed points are ever stable. The file containing this notebook is named `conditions.nb`.

Fixed Point 8

First we determine the location of the fixed points:

```
xd[x_, y_, z_] := x * (rx * (1 - x / kx) - a * y / (1 + a * hx * x + a * hz * z))

yd[x_, y_, z_] := y * (-m + a * (gx * x + gz * z) / (1 + a * hx * x + a * hz * z))

zd[x_, y_, z_] := z * (rz * (1 - z / kz) - a * y / (1 + a * hx * x + a * hz * z))

Simplify[Solve[{xd[x, y, z] == 0, yd[x, y, z] == 0, zd[x, y, z] == 0}, {x, y, z}]]
```

$$\Big\{\{x\to 0,\ y\to 0,\ z\to 0\},\ \{y\to 0,\ x\to 0,\ z\to kz\},\ \{y\to 0,\ x\to kx,\ z\to kz\},$$
$$\{y\to 0,\ z\to 0,\ x\to kx\},\ \Big\{y\to \frac{gx\,(-m+a\,kx\,(gx-hx\,m))\,rx}{a^2\,kx\,(gx-hx\,m)^2},\ z\to 0,\ x\to \frac{m}{a\,gx-a\,hx\,m}\Big\},$$
$$\Big\{y\to \frac{gz\,(-m+a\,kz\,(gz-hz\,m))\,rz}{a^2\,kz\,(gz-hz\,m)^2},\ x\to 0,\ z\to \frac{m}{a\,gz-a\,hz\,m}\Big\},$$
$$\Big\{y\to ((m+a\,(-gx\,kx-gz\,kz+hx\,kx\,m+hz\,kz\,m))\,rx\,rz\,(-gz\,kz\,(rx+a\,hx\,kx\,rx-a\,hx\,kx\,rz)-$$
$$gx\,kx\,(rz+a\,hz\,kz\,(-rx+rz))))\Big/\left(a^2\,(gz\,kz\,rx-hz\,kz\,m\,rx+kx\,(gx-hx\,m)\,rz)^2\right),$$
$$x\to \frac{kx\,(a\,kz\,(gz-hz\,m)\,(rx-rz)+m\,rz)}{a\,(gz\,kz\,rx-hz\,kz\,m\,rx+kx\,(gx-hx\,m)\,rz)},\ z\to \frac{kz\,(m\,rx-a\,kx\,(gx-hx\,m)\,(rx-rz))}{a\,(gz\,kz\,rx-hz\,kz\,m\,rx+kx\,(gx-hx\,m)\,rz)}\Big\}\Big\}$$

The last of these is the 3-species fixed point, fixed point 8, the one we are interested in. We now determine when this fixed point exists, by requiring that x,y and z all be nonnegative numbers, and that delta be 1 at the intersection:

```
xfp8 :=
  (kx / a) * ((a * kz * (gz - m * hz) * (rx - rz) + m * rz) / (rz * kx * (gx - m * hx) + rx * kz * (gz - m * hz)))

zfp8 :=
  -(kz / a) * ((a * kx * (gx - m * hx) * (rx - rz) - m * rx) / (rz * kx * (gx - m * hx) + rx * kz * (gz - m * hz)))

yfp8 := (rx * rz / a^2) * (((m + a * (-gx * kx - gz * kz + hx * kx * m + hz * kz * m)) *
        (-gz * kz * (rx + a * hx * kx * rx - a * hx * kx * rz) - gx * kx * (rz + a * hz * kz * (-rx + rz)))) /
     (rz * kx * (gx - m * hx) + rx * kz * (gz - m * hz)) ^2 )

deltaThreshold := 1 / (a * (hz * gx / gz - hx))

Simplify[Reduce[{xfp8 < deltaThreshold, a > 0, m > 0, kx > 0, kz > 0, hx > 0, hz > 0,
    gx > 0, gz > 0, rx > 0, rz > 0, gx / hx > gz / hz, zfp8 > 0, yfp8 > 0, xfp8 > 0}]]
```

$$hz>0\ \&\&\ hx>0\ \&\&\ gz>0\ \&\&\ gx>\frac{gz\,hx}{hz}\ \&\&\ 0<m<\frac{gz}{hz}\ \&\&\ kz>0\ \&\&$$
$$kx>0\ \&\&\ rz>0\ \&\&\ a>\frac{m}{gx\,kx+gz\,kz-(hx\,kx+hz\,kz)\,m}\ \&\&\ \Bigg(rx==rz\ ||$$
$$\left(rx>0\ \&\&\ rx<rz\ \&\&\ a+\frac{m\,rz}{kz\,(gz-hz\,m)\,(rx-rz)}<0\right)\ ||\ \left(a<\frac{m\,rx}{kx\,(gx-hx\,m)\,(rx-rz)}\ \&\&\ rx>rz\right)\Bigg)$$

To simplify matters, we will look at three cases separately, namely rx < rz, rx == rz and rx > rz :

First the case rx < rz:

```
Simplify[Reduce[{xfp8 < deltaThreshold, a > 0, m > 0, kx > 0, kz > 0, hx > 0, hz > 0, gx > 0,
    gz > 0, rx > 0, rz > 0, gx / hx > gz / hz, zfp8 > 0, yfp8 > 0, xfp8 > 0, rx < rz}, kz]]
```

$$hz > 0 \,\&\&\, hx > 0 \,\&\&\, gz > 0 \,\&\&\, gx > \frac{gz\,hx}{hz} \,\&\&\, 0 < m < \frac{gz}{hz} \,\&\&$$
$$kx > 0 \,\&\&\, rz > 0 \,\&\&\, 0 < rx \,\&\&\, kz + \frac{m\,rz}{a\,(gz - hz\,m)\,(rx - rz)} < 0 \,\&\&\, rx < rz \,\&\&$$
$$\left(\left(0 < a \,\&\&\, a < \frac{m}{gx\,kx - hx\,kx\,m} \,\&\&\, \frac{-a\,gx\,kx + m + a\,hx\,kx\,m}{a\,(gz - hz\,m)} < kz\right) \,||\, \left(a \geq \frac{m}{gx\,kx - hx\,kx\,m} \,\&\&\, 0 < kz\right)\right)$$

Now for the case rx == rz:

```
Simplify[Reduce[{xfp8 < deltaThreshold, a > 0, m > 0, kx > 0, kz > 0, hx > 0, hz > 0, gx > 0, gz > 0,
    rx > 0, rz > 0, gx / hx > gz / hz, zfp8 > 0, yfp8 > 0, xfp8 > 0, rx == rz}, {kx, kz}]]
```

$$hz > 0 \,\&\&\, hx > 0 \,\&\&\, gz > 0 \,\&\&\, gx > \frac{gz\,hx}{hz} \,\&\&\, 0 < m < \frac{gz}{hz} \,\&\&\, rz > 0 \,\&\&\, a > 0 \,\&\&\, rx == rz \,\&\&$$
$$\left(\left(0 < kx \leq \frac{m}{a\,gx - a\,hx\,m} \,\&\&\, kz > \frac{-a\,gx\,kx + m + a\,hx\,kx\,m}{a\,(gz - hz\,m)}\right) \,||\, \left(kx > \frac{m}{a\,gx - a\,hx\,m} \,\&\&\, kz > 0\right)\right)$$

And finally the case rx > rz:

```
Simplify[Reduce[{xfp8 < deltaThreshold, a > 0, m > 0, kx > 0, kz > 0, hx > 0, hz > 0, gx > 0,
    gz > 0, rx > 0, rz > 0, gx / hx > gz / hz, zfp8 > 0, yfp8 > 0, xfp8 > 0, rx > rz}, kx]]
```

$$hz > 0 \,\&\&\, hx > 0 \,\&\&\, gz > 0 \,\&\&\, gx > \frac{gz\,hx}{hz} \,\&\&\, 0 < m < \frac{gz}{hz} \,\&\&$$
$$kz > 0 \,\&\&\, rx > rz \,\&\&\, rz > 0 \,\&\&\, kx < \frac{m\,rx}{a\,(gx - hx\,m)\,(rx - rz)} \,\&\&$$
$$\left(\left(0 < a \,\&\&\, a < \frac{m}{gz\,kz - hz\,kz\,m} \,\&\&\, \frac{-a\,gz\,kz + m + a\,hz\,kz\,m}{a\,(gx - hx\,m)} < kx\right) \,||\, \left(a \geq \frac{m}{gz\,kz - hz\,kz\,m} \,\&\&\, 0 < kx\right)\right)$$

Stability of fixed points 5 and 6

- **Here we show that fixed points 5 and 6 of our predator-prey system are always unstable. At these fixed points, one of the two prey species is extinct, while the other is in equilibrium with the predator. Fixed point 5 is (0,y,z) and fixed point 6 is (x,y,0).**

First we will consider fixed point 5. Since x=0 here, we know that delta=1. The value of y and z at equilibrium is:

```
yfp := (rz / a ) * (1 - 1 / (a * kz * (gz / m - hz))) * (1 + hz / (gz / m - hz))

zfp := 1 / (a * (gz / m - hz))
```

The Jacobian at this point is of the form

```
0 b c
0 e 0
g h j
```

and it has the following eigenvalues :

```
Eigenvalues[{{0, b, c}, {0, e, 0}, {g, h, j}}]
```

$$\left\{e,\ \frac{1}{2}\left(j-\sqrt{4\,c\,g+j^2}\right),\ \frac{1}{2}\left(j+\sqrt{4\,c\,g+j^2}\right)\right\}$$

Here e,j, c and g are given by:

```
b[y_, z_] := y * (a * gx / (1 + a * hz * z) - a * a * hx * gz * z / (1 + a * hz * z) ^2)

c[y_, z_] := y * (a * gz / (1 + a * hz * z) - a * a * hz * gz * z / (1 + a * hz * z) ^2)

e[y_, z_] := rx - a * y / (1 + a * hz * z)

g[y_, z_] := -a * z / (1 + a * hz * z)

h[y_, z_] := z * (a^2 * hx * y / (1 + a * hz * z))

j[y_, z_] := z * (- (rz / kz) + a^2 * hz * y / (1 + a * hz * z) ^2)
```

Thus, the eigenvalues are given by:

```
EV1[y_, z_] := e[y, z]

EV2[y_, z_] := (1 / 2) * (j[y, z] - Sqrt[4 * c[y, z] * g[y, z] + j[y, z] ^2])

EV3[y_, z_] := (1 / 2) * (j[y, z] + Sqrt[4 * c[y, z] * g[y, z] + j[y, z] ^2])
```

Now we require all three eigenvalues to be negative, to find the conditions for which this fixed point is an attractor:

```
Simplify[Reduce[{EV1[yfp, zfp] < 0, EV2[yfp, zfp] < 0, EV3[yfp, zfp] < 0, a > 0,
   m > 0, hx > 0, hz > 0, kx > 0, kz > 0, rx > 0, rz > 0, gx > 0, gz > 0, gx / hx > gz / hz}]]
```

$$m > 0 \,\&\&\, gz > 0 \,\&\&\, 0 < hz < \frac{gz}{m} \,\&\&\, kz > 0 \,\&\&\, \frac{m}{gz\,kz - hz\,kz\,m} < a < \frac{gz + hz\,m}{gz\,hz\,kz - hz^2\,kz\,m} \,\&\&$$
$$rz \geq \frac{4\,a\,gz\,kz\,(gz - hz\,m)^2\,(-m + a\,kz\,(gz - hz\,m))}{m\,(gz - a\,gz\,hz\,kz + hz\,(1 + a\,hz\,kz)\,m)^2} \,\&\&$$
$$0 < rx < \frac{a\,gz\,kz\,rz - m\,rz - a\,hz\,kz\,m\,rz}{a\,gz\,kz - a\,hz\,kz\,m} \,\&\&\, hx > 0 \,\&\&\, gx > \frac{gz\,hx}{hz} \,\&\&\, kx > 0$$

Or, to see when (if ever) it is a repeller, we require that all eigenvalues be positive:

```
Simplify[Reduce[{EV1[yfp, zfp] > 0, EV2[yfp, zfp] > 0, EV3[yfp, zfp] > 0, a > 0,
   m > 0, hx > 0, hz > 0, kx > 0, kz > 0, rx > 0, rz > 0, gx > 0, gz > 0, gx / hx > gz / hz}]]
```

$$m > 0 \,\&\&\, gz > 0 \,\&\&\, 0 < hz < \frac{gz}{m} \,\&\&\, kz > 0 \,\&\&$$
$$a > \frac{gz + hz\,m}{gz\,hz\,kz - hz^2\,kz\,m} \,\&\&\, rz \geq \frac{4\,a\,gz\,kz\,(gz - hz\,m)^2\,(-m + a\,kz\,(gz - hz\,m))}{m\,(gz - a\,gz\,hz\,kz + hz\,(1 + a\,hz\,kz)\,m)^2} \,\&\&$$
$$rx > \frac{a\,gz\,kz\,rz - m\,rz - a\,hz\,kz\,m\,rz}{a\,gz\,kz - a\,hz\,kz\,m} \,\&\&\, hx > 0 \,\&\&\, gx > \frac{gz\,hx}{hz} \,\&\&\, kx > 0$$

In all other cases, this point is a saddle point.

Next we look at fixed point 6. The derivation is very similar to that of fixed point 5. First we set the values for x and y at equilibrium:

```
yfp6 := (rx / a ) * (1 - 1 / (a * kx * (gx / m - hx))) * (1 + hx / (gx / m - hx))
```

```
xfp := 1 / (a * (gx / m - hx))
```

The Jacobian at this point is of the form

0 b c
d e f
0 0 j

Which has the following eigenvalues:

```
Eigenvalues[{{0, b, c}, {d, e, f}, {0, 0, j}}]
```

$$\left\{\frac{1}{2}\left(e - \sqrt{4\,b\,d + e^2}\right),\ \frac{1}{2}\left(e + \sqrt{4\,b\,d + e^2}\right),\ j\right\}$$

The values of e, b, d and j are given by:

```
b6[x_, y_] := y * (a * gx / (1 + a * hx * x) - a^2 * hx * gx * x / (1 + a * hx * x) ^2)
```

```
d6[x_, y_] := -a * x / (1 + a * hx * x)
```

```
e6[x_, y_] := x * (-rx / kx + a^2 * hx * y / (1 + a * hx * x) ^2)
```

```
j6[x_, y_] := rz - d * a * y / (1 + a * hx * x)
```

And the eigenvalues are:

```
EV61 [x_, y_] := j6[x, y]

EV62[x_, y_] := (1 / 2) * (e6[x, y] - Sqrt[4 * b6[x, y] * d6[x, y] + e6[x, y] ^2])

EV63[x_, y_] := (1 / 2) * (e6[x, y] + Sqrt[4 * b6[x, y] * d6[x, y] + e6[x, y] ^2])
```

We again require that all three eigenvalues are negative:

```
Simplify[Reduce[{EV61[xfp, yfp6] > 0, EV62[xfp, yfp6] > 0,
   EV63[xfp, yfp6] < 0, a > 0, m > 0, hx > 0, hz > 0, kx > 0, kz > 0, rx > 0, rz > 0,
   gx > 0, gz > 0, d == 1, gx / hx > gz / hz, xfp < 1 / (a * (hz * gx / gz - hx))}]]
```

```
False
```

in these cases the fixed point is an attractor. To determine under which conditions it is a repeller, we require all eigenvalues to be positive.

```
Simplify[Reduce[{EV61[xfp, yfp6] > 0, EV62[xfp, yfp6] > 0,
   EV63[xfp, yfp6] > 0, a > 0, m > 0, hx > 0, hz > 0, kx > 0, kz > 0, rx > 0, rz > 0,
   gx > 0, gz > 0, d == 1, gx / hx > gz / hz, xfp < 1 / (a * (hz * gx / gz - hx))}]]
```

$$m > 0 \,\&\&\, gx > 0 \,\&\&\, 0 < hx < \frac{gx}{m} \,\&\&\, gz > 0 \,\&\&\, \frac{gz\,hx}{gx} < hz < \frac{gz}{m} \,\&\&\, kx > 0 \,\&\&$$
$$a > \frac{gx + hx\,m}{gx\,hx\,kx - hx^2\,kx\,m} \,\&\&\, rx \geq \frac{4\,a\,gx\,kx\,(gx - hx\,m)^2\,(-m + a\,kx\,(gx - hx\,m))}{m\,(gx - a\,gx\,hx\,kx + hx\,(1 + a\,hx\,kx)\,m)^2} \,\&\&$$
$$rz > \frac{a\,gx\,kx\,rx - m\,rx - a\,hx\,kx\,m\,rx}{a\,gx\,kx - a\,hx\,kx\,m} \,\&\&\, kz > 0 \,\&\&\, d == 1$$

In all other cases the fixed point is a saddle point.

Until now we have looked at the situation where delta=1. We will now consider the situation where delta=0:

```
Simplify[Reduce[{EV61[xfp, yfp6] < 0, EV62[xfp, yfp6] < 0,
   EV63[xfp, yfp6] < 0, a > 0, m > 0, hx > 0, hz > 0, kx > 0, kz > 0, rx > 0, rz > 0,
   gx > 0, gz > 0, d == 0, gx / hx > gz / hz, xfp > 1 / (a * (hz * gx / gz - hx))}]]
```

```
False
```

Thus we see that it is never an attractor when delta is zero. It can, however, be a repeller:

```
Simplify[Reduce[{EV61[xfp, yfp6] > 0, EV62[xfp, yfp6] > 0,
   EV63[xfp, yfp6] > 0, a > 0, m > 0, hx > 0, hz > 0, kx > 0, kz > 0, rx > 0, rz > 0,
   gx > 0, gz > 0, d == 0, gx / hx > gz / hz, xfp > 1 / (a * (hz * gx / gz - hx))}]]
```

$$m > 0 \,\&\&\, gx > 0 \,\&\&\, 0 < hx < \frac{gx}{m} \,\&\&\, gz > 0 \,\&\&\, hz > \frac{gz}{m} \,\&\&\, kx > 0 \,\&\&\, a > \frac{gx + hx\,m}{gx\,hx\,kx - hx^2\,kx\,m} \,\&\&$$
$$rx \geq \frac{4\,a\,gx\,kx\,(gx - hx\,m)^2\,(-m + a\,kx\,(gx - hx\,m))}{m\,(gx - a\,gx\,hx\,kx + hx\,(1 + a\,hx\,kx)\,m)^2} \,\&\&\, rz > 0 \,\&\&\, kz > 0 \,\&\&\, d == 0$$

In all other cases it is a saddle point.

Fixed Point 8

First we determine the location of the fixed points:

```
xd[x_, y_, z_] := x * (rx * (1 - x / kx) - a * y / (1 + a * hx * x + a * hz * z))

yd[x_, y_, z_] := y * (-m + a * (gx * x + gz * z) / (1 + a * hx * x + a * hz * z))

zd[x_, y_, z_] := z * (rz * (1 - z / kz) - a * y / (1 + a * hx * x + a * hz * z))

Simplify[Solve[{xd[x, y, z] == 0, yd[x, y, z] == 0, zd[x, y, z] == 0}, {x, y, z}]]
```

$$\Big\{\{x \to 0,\ y \to 0,\ z \to 0\},\ \{y \to 0,\ x \to 0,\ z \to kz\},\ \{y \to 0,\ x \to kx,\ z \to kz\},$$
$$\{y \to 0,\ z \to 0,\ x \to kx\},\ \Big\{y \to \frac{gx\,(-m + a\,kx\,(gx - hx\,m))\,rx}{a^2\,kx\,(gx - hx\,m)^2},\ z \to 0,\ x \to \frac{m}{a\,gx - a\,hx\,m}\Big\},$$
$$\Big\{y \to \frac{gz\,(-m + a\,kz\,(gz - hz\,m))\,rz}{a^2\,kz\,(gz - hz\,m)^2},\ x \to 0,\ z \to \frac{m}{a\,gz - a\,hz\,m}\Big\},$$
$$\Big\{y \to ((m + a\,(-gx\,kx - gz\,kz + hx\,kx\,m + hz\,kz\,m))\,rx\,rz\,(-gz\,kz\,(rx + a\,hx\,kx\,rx - a\,hx\,kx\,rz) -$$
$$gx\,kx\,(rz + a\,hz\,kz\,(-rx + rz)))) \Big/ \left(a^2\,(gz\,kz\,rx - hz\,kz\,m\,rx + kx\,(gx - hx\,m)\,rz)^2\right),$$
$$x \to \frac{kx\,(a\,kz\,(gz - hz\,m)\,(rx - rz) + m\,rz)}{a\,(gz\,kz\,rx - hz\,kz\,m\,rx + kx\,(gx - hx\,m)\,rz)},\ z \to \frac{kz\,(m\,rx - a\,kx\,(gx - hx\,m)\,(rx - rz))}{a\,(gz\,kz\,rx - hz\,kz\,m\,rx + kx\,(gx - hx\,m)\,rz)}\Big\}\Big\}$$

The last of these is the 3-species fixed point, fixed point 8, the one we are interested in. We now determine when this fixed point exists, by requiring that x,y and z all be nonnegative numbers, and that delta be 1 at the intersection:

```
xfp8 :=
  (kx / a) * ((a * kz * (gz - m * hz) * (rx - rz) + m * rz) / (rz * kx * (gx - m * hx) + rx * kz * (gz - m * hz)))

zfp8 :=
  -(kz / a) * ((a * kx * (gx - m * hx) * (rx - rz) - m * rx) / (rz * kx * (gx - m * hx) + rx * kz * (gz - m * hz)))

yfp8 := (rx * rz / a^2) * (((m + a * (-gx * kx - gz * kz + hx * kx * m + hz * kz * m)) *
        (-gz * kz * (rx + a * hx * kx * rx - a * hx * kx * rz) - gx * kx * (rz + a * hz * kz * (-rx + rz)))) /
     (rz * kx * (gx - m * hx) + rx * kz * (gz - m * hz))^2 )

deltaThreshold := 1 / (a * (hz * gx / gz - hx))

Simplify[Reduce[{xfp8 < deltaThreshold, a > 0, m > 0, kx > 0, kz > 0, hx > 0, hz > 0,
    gx > 0, gz > 0, rx > 0, rz > 0, gx / hx > gz / hz, zfp8 > 0, yfp8 > 0, xfp8 > 0}]]
```

$$hz > 0\ \&\&\ hx > 0\ \&\&\ gz > 0\ \&\&\ gx > \frac{gz\,hx}{hz}\ \&\&\ 0 < m < \frac{gz}{hz}\ \&\&\ kz > 0\ \&\&$$
$$kx > 0\ \&\&\ rz > 0\ \&\&\ a > \frac{m}{gx\,kx + gz\,kz - (hx\,kx + hz\,kz)\,m}\ \&\&\ \Big(rx == rz\ ||$$
$$\left(rx > 0\ \&\&\ rx < rz\ \&\&\ a + \frac{m\,rz}{kz\,(gz - hz\,m)\,(rx - rz)} < 0\right)\ ||\ \left(a < \frac{m\,rx}{kx\,(gx - hx\,m)\,(rx - rz)}\ \&\&\ rx > rz\right)\Big)$$

To simplify matters, we will look at three cases separately, namely rx < rz, rx == rz and rx > rz :

First the case rx < rz:

```
Simplify[Reduce[{xfp8 < deltaThreshold, a > 0, m > 0, kx > 0, kz > 0, hx > 0, hz > 0, gx > 0,
   gz > 0, rx > 0, rz > 0, gx / hx > gz / hz, zfp8 > 0, yfp8 > 0, xfp8 > 0, rx < rz}, kz]]
```

$$hz > 0 \,\&\&\, hx > 0 \,\&\&\, gz > 0 \,\&\&\, gx > \frac{gz\,hx}{hz} \,\&\&\, 0 < m < \frac{gz}{hz} \,\&\&$$
$$kx > 0 \,\&\&\, rz > 0 \,\&\&\, 0 < rx \,\&\&\, kz + \frac{m\,rz}{a\,(gz - hz\,m)\,(rx - rz)} < 0 \,\&\&\, rx < rz \,\&\&$$
$$\left(\left(0 < a \,\&\&\, a < \frac{m}{gx\,kx - hx\,kx\,m} \,\&\&\, \frac{-a\,gx\,kx + m + a\,hx\,kx\,m}{a\,(gz - hz\,m)} < kz\right) \,||\, \left(a \geq \frac{m}{gx\,kx - hx\,kx\,m} \,\&\&\, 0 < kz\right)\right)$$

Now for the case rx == rz:

```
Simplify[Reduce[{xfp8 < deltaThreshold, a > 0, m > 0, kx > 0, kz > 0, hx > 0, hz > 0, gx > 0, gz > 0,
   rx > 0, rz > 0, gx / hx > gz / hz, zfp8 > 0, yfp8 > 0, xfp8 > 0, rx == rz}, {kx, kz}]]
```

$$hz > 0 \,\&\&\, hx > 0 \,\&\&\, gz > 0 \,\&\&\, gx > \frac{gz\,hx}{hz} \,\&\&\, 0 < m < \frac{gz}{hz} \,\&\&\, rz > 0 \,\&\&\, a > 0 \,\&\&\, rx == rz \,\&\&$$
$$\left(\left(0 < kx \leq \frac{m}{a\,gx - a\,hx\,m} \,\&\&\, kz > \frac{-a\,gx\,kx + m + a\,hx\,kx\,m}{a\,(gz - hz\,m)}\right) \,||\, \left(kx > \frac{m}{a\,gx - a\,hx\,m} \,\&\&\, kz > 0\right)\right)$$

And finally the case rx > rz:

```
Simplify[Reduce[{xfp8 < deltaThreshold, a > 0, m > 0, kx > 0, kz > 0, hx > 0, hz > 0, gx > 0,
   gz > 0, rx > 0, rz > 0, gx / hx > gz / hz, zfp8 > 0, yfp8 > 0, xfp8 > 0, rx > rz}, kx]]
```

$$hz > 0 \,\&\&\, hx > 0 \,\&\&\, gz > 0 \,\&\&\, gx > \frac{gz\,hx}{hz} \,\&\&\, 0 < m < \frac{gz}{hz} \,\&\&$$
$$kz > 0 \,\&\&\, rx > rz \,\&\&\, rz > 0 \,\&\&\, kx < \frac{m\,rx}{a\,(gx - hx\,m)\,(rx - rz)} \,\&\&$$
$$\left(\left(0 < a \,\&\&\, a < \frac{m}{gz\,kz - hz\,kz\,m} \,\&\&\, \frac{-a\,gz\,kz + m + a\,hz\,kz\,m}{a\,(gx - hx\,m)} < kx\right) \,||\, \left(a \geq \frac{m}{gz\,kz - hz\,kz\,m} \,\&\&\, 0 < kx\right)\right)$$