Chapter 7. Stability and Steady State

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The ‘Steady-State’ Solution

The conditions under which the system does not change anymore.

Two techniques for finding these conditions:
1) Running the model for a long time
2) Setting the rate of change equal to zero and solving the resulting equations
The Steady-State

Stability of an equilibrium relates to the tendency of the system to return to its position when slightly disturbed.

- If stable, the system will return to its point when slightly disturbed
- If unstable, the system will move away from its point when slightly disturbed

Graphically Investigating the Steady-State

- Models with one differential equation, plot the rate of change as a function of the value of the state variable. Where \( \frac{dy}{dx} = 0 \), the system is at equilibrium.

- Models with two differential equations, plot the lines where the rate of change of each of the state variables is zero as a function of their values. Where \( \frac{dy}{dx_1} = \frac{dy}{dx_2} = 0 \), the system is at equilibrium.

- Models with more than two, mathematical methods might be more appropriate.
Population Dynamics Model

\[
\frac{dN}{dt} = r_i \cdot N \cdot \left(1 - \frac{N}{K}\right) - q \cdot \frac{N}{N + k_s}
\]

One first-order differential equation

- N – species density
- \(r_i\) – growth rate
- K – carrying capacity
- q – harvesting rate
- \(k_s\) – half-saturation density

Graphically Investigating the Steady-State
Graphically Investigating the Steady-State

Steady State Conditions
\[ \frac{dN}{dt} = 0 \]

Graphically Investigating the Steady-State

Positive Rate of Change

Negative Rate of Change
Graphically Investigating the Steady-State

- Domains of Attraction
- Separatrix

Graphically Investigating the Steady-State

- Domains of Attraction
- Separatrix
Solving the Steady-State

\[ 0 = N^* \cdot r_i \cdot \left( 1 - \frac{N^*}{K} \right) - q \cdot \frac{1}{N^* + k_s} \]

Steady state is reached when either:

\[ N^* = 0 \]

or

\[ r_i \cdot \left( 1 - \frac{N^*}{K} \right) - q \cdot \frac{1}{N^* + k_s} = 0 \]

Rearrange the terms:

\[ a x^2 + b x + c = 0 \]

\[ N^{*2} + (k_s - K) \cdot N^* + \frac{qK}{r_i} - k_s \cdot K = 0 \]
Solving the Steady-State

\[ x = \frac{-b \pm \sqrt{b^2 - 4ac}}{2a} \]

\[ N^* = \frac{-(k_s - K) \pm \sqrt{D}}{2} \]

Where:

\[ D = (k_s + K)^2 - \frac{4qK}{r_i} - k_s \cdot K \]

Parameter Values:

- \( K = 10 \)
- \( q = 0.1 \)
- \( k_s = 1 \)
- \( r_i = \text{variable} \)
The Spruce Budworm Model

\[
\frac{dB}{dt} = r_i \cdot B \cdot \left(1 - \frac{B}{K}\right) - \beta \cdot \frac{B^2}{B^2 + ks^2}
\]

- The spruce budworm is a very destructive insect that feeds on coniferous trees, particularly the balsam fir.
- Limiting features are the food supply and the effects of parasites and predators.

The Spruce Budworm Model

\[
\frac{dB}{dt} = r_i \cdot B \cdot \left(1 - \frac{B}{K}\right)
\]

- Carrying capacity depends upon the amount of foliage that is available (food supply).
The Spruce Budworm Model

\[ g(b) = \beta \cdot \frac{B^2}{B^2 + kS^2} \]

- Upper limit to the rate of budworm mortality due to predation (consumption by birds and parasites is limited).
- Impact by predators does not substantially increase with increasing budworm density.

---

```r
# load necessary packages
require(rootSolve)
require(shape)
require(rootSolve)

# define parameter values
r1 <- 0.05 # population growth rate
K <- 10 # carrying capacity
beta <- 0.1 # mortality rate
k3 <- 1 # half-saturation density at which mortality is half of the maximal rate

# calculates the rate of change (dN/dt) for a certain value of B and r1
rate <- function(B, r1, r1r=0.09)
B1^n(1-r1)
rate(B, r1, r1r)

B <- seq(10, length=500) # vector of population density with 500 values from 0-10 (rows)
rsq <- seq(0.05, 0.07, by=0.02) # vector of population growth rate
# increasing from 0.05 to 0.07 in steps of 0.02 (columns)
mat <- outer(B, rsq, function(X,Y) rate(B, X, r1, Y)) # generates a matrix
# for all combinations of B and rsq
```
The Spruce Budworm Model

```r
# plots all the columns of the above matrix at once
matplot(xs, matrix(xlab="t", ylab="d/dt", type="l", lty=1:4, col=1)
abline(h=0, lty=2) # adds axis
legend("bottomleft", legend = "rt", col=1, lty=1:4) # creates a legend in the bottom left corner
```

---

The Spruce Budworm Model

```r
equilibrium <- function(r1)
{
  eq <- unroot.all(f-rate, interval=c(0, 10), r1=r1) # finds all the equilibrium points
  # for a growth rate of 0.05
  # for population densities 0-10
  # and creates a vector of these values
  etype <- vector(length=length(eq)) # creates an empty vector with the length of Eq
  for (i in 1:length(eq)) { # loops over all values of (x) in the vector Eq
    jac <- gradient(f-rate, x.eq[i], r1=r1) # estimates gradient matrix given Eq
    # and the rate function
    etype[i] <- sign(jac) * 2 # fills in etype vector with the sign (+1, -1, or 0) of the gradient matrix values
  }
  return(list(x=eq, type=etype)) # returns a list of the equilibrium points and the types of equilibrium points
}
```
The Spruce Budworm Model

```r
# plots ri = 0.05 only to inspect equilibrium points
curve(rate(x, 0.05), xlab = "n", ylab = "ds/dt", main = "ri=0.05",
from = 0, to = 10)
abline(h = 0)
# brings back equilibrium points for ri=0.05
eq <- equilibrium (ri=0.05)
# plots those points on the second graph from above
points(x = eq$x, y = eq(0, length(eq$x)), pch = 21, cex = 2,
bg = c("grey", "black", "white") [eq$type ])
# plots different colored circles for the eqtype
# grey stable, black saddle, white unstable
```

![Graph showing the Spruce Budworm Model with equilibrium points and stability analysis.](image)

The Spruce Budworm Model

```r
# make empty bifurcation plot
rseq <- seq(0.01, 0.07, by = 0.0001) # creates a vector from 0.01 to 0.07 in steps of 0.0001
plot(0, xlim = range(rseq), ylim = c(0, 10), type = "n", # type n creates an empty plot
xlab = "r", ylab = "n", main = "Spruce Budworm Model")
```

![Bifurcation plot showing the Spruce Budworm model.](image)
The Spruce Budworm Model

7.3 Stability of Two Differential Equations – Phase-Plane Analysis

Phase-plane analysis allows us to investigate the behavior of two coupled (first-order) differential equations graphically.

We do this by inspecting the phase plane graphs, and then drawing general conclusions concerning the dynamics of the model from them.

- **Phase Plane Graph** - an X-Y graph with the values of the first and second state variables plotted on the X and Y-axis respectively.
  - As the state variables are generally positive numbers, the phase plane is restricted to the part of the graph where \(x>0, y>0\).

- Information about the rate of change of the two state variables can then be added to the graph
1. **Zero Isocline** (of a state variable): A curve or line, depicting where the rate of change of one of the state variables is 0.
   - The point where they intersect is the Equilibrium Point.
   - There are generally multiple equilibrium points. Analysis allows us to make inferences about the nature of each of these.

2. Arrows are added into each divided section of the phase plane.
   - The direction indicates the sign of the rate of change of the two state variables at a particular point.
   - Arrows pointing at an Equilibrium Point indicate it is stable, if all point away, it is unstable. If neither, the stability properties need to be assessed in different ways.

3. We can run the model with different parameters and plot the trajectories on the phase plane.
   - Trajectories will converge to stable equilibria and diverge from unstable ones.
   - If initiated in the vicinity of a saddle point, they will first approach it and then move away from it.

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7.3.1 The Lotka-Volterra Predator-Prey Equation

\[
\begin{align*}
\frac{d\text{PREY}}{dt} &= r_t \cdot \text{PREY} \cdot \left(1 - \frac{\text{PREY}}{K}\right) - \alpha \cdot \text{PREDATOR} \cdot \text{PREY} \\
\frac{d\text{PREDATOR}}{dt} &= \gamma \cdot \text{PREDATOR} \cdot \text{PREY} - m \cdot \text{PREDATOR} 
\end{align*}
\]

- \( r_t \) = the rate of increase of prey
- \( K \) = carrying capacity
- \( \alpha \) = the ingestion rate of the predator
- \( \gamma \) = the assimilation efficiency
- \( m \) = the mortality rate

In the absence of predators, the prey density increases exponentially at low prey density, moving towards \( K \). In the presence of predation, the prey density is reduced proportionally to predator and prey density. Predator growth is stimulated by the presence of prey and experiences a first-order mortality.
7.3.1.1 The Phase Plane

First we draw our predator and prey zero isoclines.

• The rate of change of the predator is zero, so predator density will remain constant, when:

\[
\frac{d\text{PREDATOR}}{dt} = 0 = \alpha \cdot \gamma \cdot \text{PREDATOR} \cdot \text{PREY} - m \cdot \text{PREDATOR} \quad (7.9)
\]

\[
\text{PREDATOR} = 0 
\]

\[
\text{PREY} = \frac{m}{\alpha \cdot \gamma} 
\]

\[
A \text{ constant horizontal line} \quad (7.10)(7.11)
\]

• Prey density is constant (rate of change=0) when:

\[
\frac{d\text{PREY}}{dt} = 0 = r_l \cdot \text{PREY} \cdot \left(1 - \frac{\text{PREY}}{K}\right) - \alpha \cdot \text{PREDATOR} \cdot \text{PREY} \quad (7.12)
\]

Crosses Y-axis at:

\[
\text{PREY} = 0 \quad (7.13)
\]

PREDATOR = \frac{r_l}{\alpha} \quad (7.14)

Crosses X-axis at:

\[
\text{PREY} = K
\]

When we consider only the isoclines that differ from the X and Y axes, there are 2 different outcomes, depending on the relative position of the intersection of the isoclines with X.

\[
(1) \quad \frac{m}{\alpha \cdot \gamma} < K \quad (7.15)
\]

\[
(2) \quad \frac{m}{\alpha \cdot \gamma} > K \quad (7.16)
\]

1. The two isoclines intersect and both populations can coexist in a stable equilibrium.

2. If the prey food supply is not sufficient (\(\alpha \gamma\)), or mortality (m) is too high, the predator goes extinct.
Case 1. Stable coexistence
- 1st scenario from the previous slide
- 3 equilibrium points
- To determine stability, integrate the equation for a sufficiently long time and see where the predator/prey couple ends up.
- We see that the central point is stable but what of the other two points?
- If we perturb the other equilibrium points by running models with very small initial values \((0.001, 0.001)\) and \((0.001, K+0.001)\) we can note the trajectory of the predator/prey couples.
  - They do not return to the original equilibrium point but converge to the central equilibrium point, demonstrating them unstable.

Parameter Values:
- \(r_i = 1\)
- \(\alpha = 0.2\)
- \(\gamma = 0.5\)
- \(m = 0.2\)
- \(K = 10\)

Case 2. Predator Extinction
- 2nd scenario from the previous slide
- If \(K\) is lower than the predator isocline, the two isoclines will not intersect.
- 2 equilibrium points, 1 unstable \((0,0)\) & 1 stable \((0,K)\)
- The carrying capacity of the prey is insufficient to withstand the feeding need of the predator, and the predator is driven to extinction.

Parameter Values:
- \(r_i = 1\)
- \(\alpha = 0.2\)
- \(\gamma = 0.5\)
- \(m = 0.2\)
- \(K = 1\)
Case 3. Neutral Stability

- Now we reconsider the original L-V model where prey is not limited \( (K = \infty) \)
  \[
  \frac{d\text{prey}}{dt} = r_i \cdot \text{prey} - \alpha \cdot \text{predator} \cdot \text{prey}
  \]
  \[
  \frac{d\text{predator}}{dt} = \gamma \cdot \text{predator} \cdot \text{prey} - m \cdot \text{predator} \quad (2.17)
  \]

- The predator/prey trajectory follows an elliptical path, coming back to where it started, but not on an equilibrium point.
  - This = neutral stability

- The trajectory will be different when started with different initial conditions.

- Pushing the system will start a new type of oscillation, that will bring it back to the point to which it has been pushed.

Parameter Values:

\[ ri = 1 \]
\[ \alpha = 0.2 \]
\[ \gamma = 0.5 \]
\[ m = 0.2 \]
\[ K = \infty \]

7.4 Multiple Equations

- Phase-plane analysis is very well suited for analyzing the behavior of two coupled differential equations.

- Adding more equations will increase the dimensions of the graph which is generally beyond the scope of most people’s ability to understand visually.

- Modelers instead resort to mathematical methods for finding the equilibrium conditions and apply formal tests of stability.
How to interpret the eigenvalues of the Jacobian matrix

<table>
<thead>
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<th>Imaginary Part</th>
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<tr>
<td>+</td>
<td>zero Real</td>
</tr>
<tr>
<td></td>
<td>Non-zero Complex</td>
</tr>
<tr>
<td>-</td>
<td>zero Real</td>
</tr>
<tr>
<td></td>
<td>Non-zero Complex</td>
</tr>
</tbody>
</table>

Opposite signs → saddle point

A case study in R

7.8.2 Phase-Plane Analysis: The Lotka-Volterra Competition Equations