

Lecture 4

Interacting population models

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1 A predator-prey model: plankton

Predator-prey interaction are ubiquitous in nature often leading to complex food chains. Considering a 2-species predator-prey interaction in isolation is simplistic, but in itself can lead to complex results.

We will focus on the interaction of **zooplankton** (microscopic sea animals = predator) and **phytoplankton** (microscopic sea plants = prey) (see plankton presentation slide).

Model assumptions:

1. Let

$P(t)$ = population density of phytoplankton (prey)

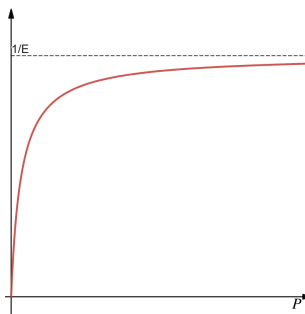
$Z(t)$ = population density of zooplankton (predator)

2. Prey population grows logistically in the absence of predators.

3. Phytoplankton is the only prey of zooplankton:

3.1 predation rate \propto predator density.

3.2 predators have limited appetite, assume predation rate $\propto \frac{P}{1 + EP}$



Combining assumptions 3.1 and 3.2 implies predation rate $\propto \frac{ZP}{1 + EP}$

4. Predator birth rate \propto predation rate.

5. Predators die “naturally” (e.g. disease, eaten by predatory zooplankton, fish, whales etc.).

Given these assumptions, a natural question is:

Question: predators convert food into offspring (assumption 4), how does the efficiency effect the dynamics of the interaction? Can it ever be too efficient to cause the prey to become extinct?

Applying assumptions 1 – 5, we obtain the system

$$\frac{dP}{dt} = rP \left(1 - \frac{P}{K}\right) - B \frac{ZP}{1 + EP} \quad (1)$$

$$\frac{dZ}{dt} = S \frac{BZP}{1 + EP} - cZ, \quad (2)$$

where r, K, B, E, S, c are all positive constants. Here, parameter S represents the mean number of new zooplankton per phytoplankton. Nondimensionalising the equations, via the 3-step process, using

$$P = K\hat{P}, \quad Z = \frac{EKr}{B}\hat{Z}, \quad t = \frac{\hat{t}}{r}$$

and define

$$\hat{d} = \frac{1}{EK}, \quad \hat{b} = \frac{SB}{Er}, \quad \hat{c} = \frac{c}{r}$$

leads to, on dropping the hats for clarity, to the non-dimensional version of the model

$$\frac{dP}{dt} = P(1 - P) - \frac{ZP}{d + P} \equiv f(P, Z) \quad (3)$$

$$\frac{dZ}{dt} = b \frac{ZP}{d + P} - cZ \equiv g(p, z), \quad (4)$$

which has the just three parameters b, c, d (+2 initial conditions).

Big Note 4A: The parameter that is central to this topic's question is b , as it is the only one that contains parameter S in its definition. We will thus focus most on this parameter in the analysis below.

As usual, we cannot solve the ODE system analytically, so start by applying the same analysis of Section 2.1.1 and 2.1.2, to see if the question can be answered.

1.1 Steady-state analysis

Using the approach of Section 3.1.1, the steady-states are found from the solutions of the equations

$$f(P^*, Z^*) = 0 \quad \Rightarrow \quad P^* \left(1 - P^* - \frac{Z^*}{d + P^*}\right) = 0 \quad (5)$$

$$g(P^*, Z^*) = 0 \quad \Rightarrow \quad Z^* \left(\frac{bP^*}{d + P^*} - c\right) = 0, \quad (6)$$

and are as follows

$$\begin{aligned} (P^*, Z^*) &= (0, 0) && : \quad \text{both species go extinct} \\ &= (1, 0) && : \quad \text{predators go extinct} \\ &= \left(\frac{cd}{b - c}, \frac{bd}{(b - c)^2} [b - c(1 + d)]\right) && : \quad \text{coexistent state.} \end{aligned}$$

For the coexistent state to be biologically relevant we need:

$$\begin{aligned} P^* > 0 &\Rightarrow b > c \\ Z^* > 0 &\Rightarrow b > c(1 + d) \end{aligned}$$

There are then 3 cases to consider

Case 1) $b < c$

Case 2) $c < b < c(1 + d)$

Case 3) $b > c(1 + d)$

The steady-state analysis provides a lower bound for the predators food-into-offspring efficiency parameter b . But we need to establish the stabilities of the steady-states to get a full picture.

1.2 Phase-plane analysis

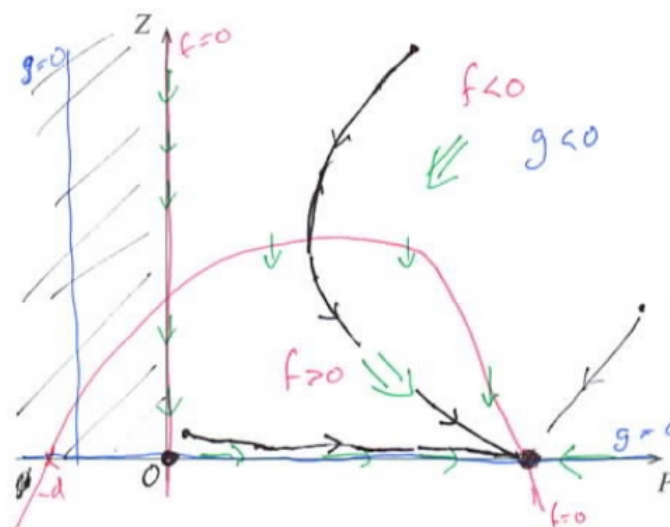
Proceeding the same way described in Section 3.2.1, the nullclines formula are

$$\begin{aligned} \frac{dP}{dt} = f(P, Z) = P \left(1 - P - \frac{Z}{d+P} \right) = 0 &\Rightarrow P = 0, \quad 1 - P - \frac{Z}{d+P} = 0 \\ &\Rightarrow Z = (1 - P)(d + P) \\ \frac{dZ}{dt} = g(P, Z) = Z \left(\frac{bP}{d+P} - c \right) = 0 &\Rightarrow Z = 0, \quad \frac{bP}{d+P} - c = 0 \\ &\Rightarrow P = \frac{cd}{b - c} \end{aligned}$$

from which we can construct the phase-planes for each of the three cases.

Case 1) $b < c$

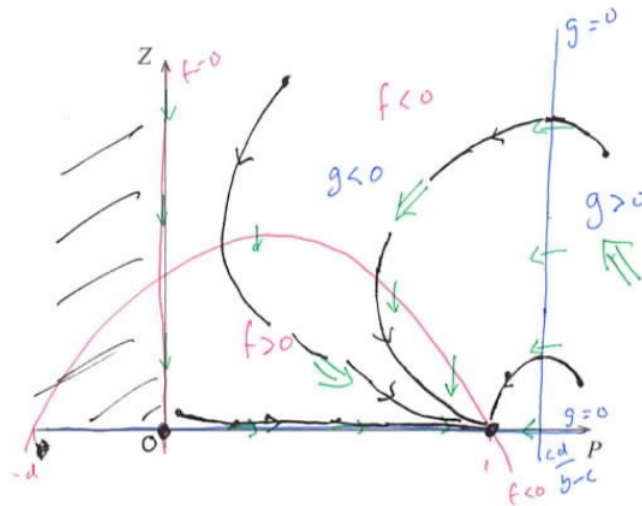
Because $b < c$, the g -nullcline $P = \frac{cd}{b - c}$ will be located in the negative P axis, which is not biologically relevant.



We have $(P, Z) \rightarrow (1, 0)$ as $t \rightarrow \infty$. So, $(1, 0)$ is a stable node, $(0, 0)$ is unstable (saddle).

Case 2) $c < b < c(1 + d)$

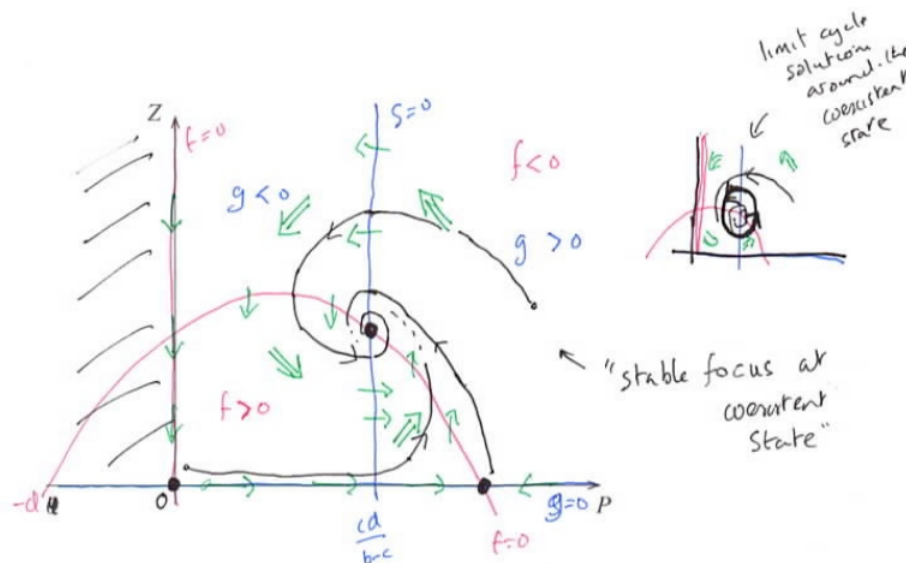
Because $b < c(1 + d)$, it follows that $b - c < cd$, and hence $\frac{cd}{b-c} > 1$. The g -nullcline $P = \frac{cd}{b-c}$ is thus located in the positive P axis, to the *right* of 1.



We have $(P, Z) \rightarrow (1, 0)$ as $t \rightarrow \infty$. So, $(1, 0)$ is a stable node, $(0, 0)$ is unstable (saddle).

Case 3) $b > c(1 + d)$

In this case, $\frac{cd}{b-c} < 1$. The g -nullcline $P = \frac{cd}{b-c}$ is thus located to the *left* of 1.



The states $(0, 0)$ $(1, 0)$ are unstable saddles. We need more information.

Although the stability and type is established for two of the steady-states from the diagram, it cannot be established for the coexistent state.

- it is clearly not a saddle point from the general direction arrows (the arrows are looping round, not pointing towards it in one direction and away from it in the other).
- however, the general direction arrows do not preclude the possibility of it being a node or focus or whether it is stable or unstable.

Here, the phase-plane approach is too crude a tool to deduce whether the coexistent state is a stable or unstable node or focus. We need another approach to analyze this case.

1.2.1 Linear stability analysis for case 3: $b > c(1 + d)$

Using the ideas of the **Lecture 3 Appendix** the stability matrix (or Jacobian) A for the predator-prey model is

$$A = \left(\begin{array}{cc} \frac{\partial f}{\partial P} & \frac{\partial f}{\partial Z} \\ \frac{\partial g}{\partial P} & \frac{\partial g}{\partial Z} \end{array} \right) \bigg|_{(P^*, Z^*)} = \left(\begin{array}{cc} 1 - 2P - \frac{dZ}{(P+d)^2} & -\frac{P}{P+d} \\ \frac{2bdZ}{(P+d)^2} & \frac{bP}{d+P} - c \end{array} \right) \bigg|_{(P^*, Z^*)} \quad (7)$$

and we seek the eigenvalues for each of the steady-states (P^*, Z^*) ,

- $(P^*, Z^*) = (0, 0)$

$$A(0, 0) = \begin{pmatrix} 1 & 0 \\ 0 & -c \end{pmatrix}$$

The eigenvalues are the diagonal elements, $\lambda_1 = 1 > 0$, $\lambda_2 = -c < 0 \Rightarrow (0, 0)$ is an unstable saddle point.

- $(P^*, Z^*) = (1, 0)$

$$A(1, 0) = \begin{pmatrix} -1 & \frac{-1}{1+d} \\ 0 & \frac{b}{1+d} - c \end{pmatrix}$$

The eigenvalues are the diagonal elements, $\lambda_1 = -1 < 0$, $\lambda_2 = \frac{b}{1+d} - c = \frac{1}{1+d}[b - c(1 + d)]$, which is positive for case 3 (unstable saddle), and negative for cases 1&2 (stable node).

- $(P^*, Z^*) = \left(\frac{cd}{b-c}, \frac{bd}{(b-c)^2}[b - c(1 + d)] \right)$

$$A_{\text{coex}} = \begin{pmatrix} \frac{[b(1-d) - c(1+d)]c}{b(b-c)} & \frac{-c}{b} \\ b - c(1+d) & 0 \end{pmatrix}$$

The eigenvalues of A_{coex} are rather cumbersome to compute.

Eigenvalues that are intractably complicated is a typical situation in two-variable systems. When we can't deduce the eigenvalues instantly as with the first two cases above, we can often get the information we need from the trace and determinant of matrix $A(P^*, Z^*)$, see **Appendix**.

Using the ideas in the **Appendix** below, we have for the coexistent state

$$\begin{aligned}\det(A_{\text{coex}}) &= 0 - \left[-\frac{c}{b}(b - c(1 + d)) \right] = \frac{c}{b}[b - c(1 + d)] > 0 \\ \text{Tr}(A_{\text{coex}}) &= \frac{c}{b(b - c)}[b(1 - d) - c(1 + d)]\end{aligned}\tag{8}$$

Given b, c, d , the stability and type here depends on the sign of $\text{Tr}(A_{\text{coex}})$ and the discriminant $\text{Disc}(A_{\text{coex}}) = \text{Tr}(A_{\text{coex}})^2 - 4 \det(A_{\text{coex}})$. In fact all four combinations are possible for this Case-3 system,

(b, c, d)	$\text{Tr}(A_{\text{coex}})$	$\text{Disc}(A_{\text{coex}})$	coexistent st-st type/stability
$(\frac{11}{5}, 1, 1)$	< 0	> 0	stable node
$(3, 1, 1)$	< 0	< 0	stable focus
$(3, 1, \frac{1}{3})$	> 0	< 0	unstable focus
$(\frac{11}{10}, 1, \frac{1}{100})$	> 0	> 0	unstable node

All these listed possibilities are demonstrated in **Maple file 2.2**.

What we have learnt:

- When the coexistent state is stable, then we expect $(P, Z) \rightarrow$ the coexistent state as $t \rightarrow \infty$ (the analysis is complete in this case).
- The coexistent state being unstable when $\text{Tr}(A_{\text{coex}}) = b(1 - d) - c(1 + d) > 0$, implies
 - 1) $d < 1$, i.e., predators are 'greedy' (necessary condition);
 - 2) $b > b_c \equiv \frac{c(1 + d)}{1 - d}$, high efficiency in turning food into offspring.

The only question that remains is where do the solutions (P, Z) go as $t \rightarrow \infty$, when there are no stable steady states? There are two possibilities:

1. $(P, Z) \rightarrow$ periodic solution, also called *limit cycle*, as $t \rightarrow \infty$.
2. $P \rightarrow \infty$ and/or $Z \rightarrow \infty$ as $t \rightarrow \infty$.

It turns out the first scenario is relevant here, but this needs proving, which we will do in the next chapter.

Appendix

A Linear stability analysis of two ODEs: Part 2

Note: You will not be required to derive the theory below in the exam, but proficiency in its application is expected.

A.1 The trace and determinant method

Often evaluating eigenvalues for general parameters in a stability matrix \mathbf{A} can lead to messy, unwieldy expressions that indicate little about the stability or type of steady-state. In these cases, **evaluating the trace and determinant of \mathbf{A} often helps**. Consider a general 2×2 matrix with *real* elements

$$\mathbf{A} = \begin{pmatrix} a & b \\ c & d \end{pmatrix},$$

then the eigenvalues λ satisfy

$$\det(\mathbf{A} - \lambda \mathbf{I}) = \begin{vmatrix} a - \lambda & b \\ c & d - \lambda \end{vmatrix} = \lambda^2 - (a + d)\lambda + ad - bc = 0.$$

Noting that $\text{Tr}(\mathbf{A}) = a + d$ and $\det(\mathbf{A}) = ad - bc$, then the eigenvalues satisfy

$$\lambda^2 - \text{Tr}(\mathbf{A})\lambda + \det(\mathbf{A}) = 0, \quad \text{i.e.} \quad \lambda_{1,2} = \frac{\text{Tr}(\mathbf{A}) \pm \sqrt{\text{Tr}(\mathbf{A})^2 - 4\det(\mathbf{A})}}{2}.$$

Moreover, $\lambda_1 \lambda_2 = \det(\mathbf{A})$ and $\lambda_1 + \lambda_2 = \text{Tr}(\mathbf{A})$. The trace and determinant of \mathbf{A} can thus be used to determine the **stability** of the steady-state:

- $\text{Tr}(\mathbf{A}) < 0$ **and** $\det(\mathbf{A}) > 0 \Leftrightarrow \Re(\lambda_1), \Re(\lambda_2) < 0 \Rightarrow$ steady-state is **stable**.
- $\text{Tr}(\mathbf{A}) > 0$ **or** $\det(\mathbf{A}) < 0 \Leftrightarrow \exists \Re(\lambda) > 0 \Rightarrow$ steady-state is **unstable**.

as well as the steady-state **types** (see Appendix Lecture 3):

- If $0 < \det(\mathbf{A}) < \text{Tr}(\mathbf{A})^2/4 \Leftrightarrow \lambda_1, \lambda_2$ are real \Rightarrow **node**.
- If $\det(\mathbf{A}) > \text{Tr}(\mathbf{A})^2/4 \Leftrightarrow \lambda_1$ and λ_2 are complex conjugates \Rightarrow **focus**.
- If $\det(\mathbf{A}) < 0 \Leftrightarrow \lambda_1, \lambda_2 \in \mathbb{R}$ with different signs \Rightarrow **saddle node**.

All this can be summarised by the diagram below in $\text{Tr}(\mathbf{A}) - \det(\mathbf{A})$ space.

