5. Competition models

[Case: Ch 14]

Exercise 5.1: Interpretation of a Lotka-Volterra model

Lotka-Volterra models for the interaction between two species are characterized by the fact that the *per capita* growth rate of each species is *linearly* related to the densities of the two species. Thus, a Lotka-Volterra model is of the general form:

$$\begin{cases} \dfrac{dN_1}{dt} = N_1\left(r_1 + a_{11}N_1 + a_{12}N_2 \right) \\ \dfrac{dN_2}{dt} = N_2\left(r_2 + a_{21}N_1 + a_{22}N_2 \right) \end{cases} \tag{1}$$

where N_1 and N_2 denote the densities of the two species; r_1 and r_2 denote their intrinsic growth rates (i.e. their *per capita* growth rates in isolation, where $N_1 = N_2 = 0$); a_{11} and a_{22} denote the effects of *intra*-specific interaction; and a_{12} and a_{21} denote the effects of *inter*-specific interaction. Since the members of the same species compete for the same limited resources, the terms a_{11} and a_{22} are usually assumed to be non-positive (i.e. negative or zero), i.e., it is assumed that the *per capita* growth rate of each species is negatively related to the density of the species. [This is not necessarily so: a_{11} and a_{22} might, for example, be positive if the members of a species co-operate with another.]

(a) Which signs of a_{12} and a_{21} would you expect in the following four scenarios:

(1) The two species compete with each other for the same resources.

(2) The two species are mutualists.

(3) Species 2 predates on species 1.

(4) Species 1 is a parasite of species 2.

Consider now the following four Lotka-Volterra systems:

$$\frac{dN_1}{dt} = N_1\left(1 - 2N_1 + N_2\right) \qquad \frac{dN_2}{dt} = N_2\left(1 + N_1 - N_2\right) \tag{2}$$

$$\frac{dN_1}{dt} = N_1\left(3 - N_1 - 2N_2\right) \qquad \frac{dN_2}{dt} = N_2\left(1 - 2N_1 - N_2\right) \tag{3}$$

$$\frac{dN_1}{dt} = N_1\left(3 - 2N_1 - N_2\right) \qquad \frac{dN_2}{dt} = N_2\left(3 - N_1 - 2N_2\right) \tag{4}$$

$$\frac{dN_1}{dt} = N_1\left(-1 - N_1 + 2N_2\right) \qquad \frac{dN_2}{dt} = N_2\left(3 - N_1 - N_2\right) \tag{5}$$

(b) Which type of interaction (competition, mutualism or predation) is modelled by the four systems, respectively?

(c) Calculate (with pen and paper) for at least one of the systems the equilibria and determine the stability of the interior equilibrium. Is the interior equilibrium a node, a spiral, or a saddle point?

(d) Sketch for the system in (c) the nullclines and indicate by arrows the dynamical behaviour of the system in the various regions separated by the isoclines [pen and paper!]. Try to sketch some typical solution curves.

(e) Check your calculations in (c) and (d) by numerically solving the Lotka-Volterra system in Excel.

Assume that (N_1^*, N_2^*) is an interior equilibrium of a Lotka-Volterra model (1) (i.e., both species have a *positive* density at equilibrium). In the lectures, we have seen that the "stability matrix" (i.e., the Jacobian at equilibrium) can be written in the form:

$$J = \begin{pmatrix} a_{11}N_1^* & a_{12}N_1^* \\ a_{21}N_2^* & a_{22}N_2^* \end{pmatrix} \tag{6}$$

As a consequence, trace and determinant of the stability matrix are given by:

$$\mathrm{tr}(J) = a_{11}N_1^* + a_{22}N_2^* \quad \text{and} \quad \det(J) = N_1^* N_2^* \cdot \left(a_{11}a_{22} - a_{12}a_{21}\right) \tag{7}$$

making it easy to check whether or not an interior equilibrium is stable. In fact, (7) implies that the trace is negative if the *intra*-specific competition terms a_{11} and a_{22} are negative, as is often the case. If the trace is negative, the equilibrium is stable if the determinant is positive. In view of (7), for this we only have to check whether $a_{11}a_{22} > a_{12}a_{21}$.

<u>Exercise 5.2:</u> Stability of an interior equilibrium

Determine with the help of the above stability criterion whether for the systems (2) to (5) the interior equilibrium is stable or not. Check whether your results confirm those obtained earlier in Exercise 5.1.

<u>Exercise 5.3:</u> Lotka-Volterra competition models

Classical competition theory is based on Lotka-Volterra models of the form (1), where all interaction terms a_{ij} are negative. Consider the special case $r_1 = r_2 = 1$, $a_{11} = a_{22} = -1$ and the following three scenarios:

(1) $a_{12} = -2, \quad a_{21} = -0.25$
(2) $a_{12} = -2, \quad a_{21} = -4$
(3) $a_{12} = -0.5, \quad a_{21} = -0.25$

Answer of each of these scenarios the following questions:

(a) Sketch the phase space of the system with the nullclines of the two species and indicate the "phase portrait" (i.e., sketch some typical trajectories). Try to conclude from this graph alone (i.e., without performing any calculations) how the system will develop in time. Which species will win the competition? Is stable coexistence possible?

(b) Calculate now the equilibrium points of the system and determine the stability of the interior equilibrium (if it exists). Is the qualitative analysis in (b) in line with your graphical analysis in (a)? [Hint: You may use the simplified stability criterion derived above.]

(c) Now use Excel to plot some characteristic solution curves of the three systems. Check whether the plot confirms your earlier conclusions in (a) and (b).

(d) Is your analysis in line with the general principle that "stable coexistence is only possible if *intra*-specific competition is more intense than *inter*-specific competition"?

Lotka-Volterra models are useful first steps towards an understanding of biological interactions. However, these models are purely ‘phenomenological’ (i.e., they are based on simple assumptions concerning the shape of a relationship), without specifying the underlying mechanisms. For example, a Lotka-Volterra competition model reflects the assumption that the *per capita* growth rates of both species decrease *linearly* with the abundance of both species. The model does, however, not specify where the species are competing for. Do they compete for space, do they compete for the same prey, do they compete for nutrients, or do they compete for light? Doesn’t it matter at all *what* the species are competing for?

We will see later that for biological populations it matters quite a lot whether competition is for space, for biotic resources (prey), or for abiotic resources (nutrients or light). Accordingly, Lotka-Volterra models are much too limited for adequately understanding competition. Modern competition models are therefore ‘mechanistic’ in the sense that they explicitly incorporate what the species are competing for. Let us here consider competition for abiotic resources, i.e., for nutrients like nitrogen or phosphate.

The competition between several species i = 1, 2, 3, … for one limiting (abiotic) resource R is usually modelled by the following system of differential equations:

$$\begin{cases} \dfrac{dN_i}{dt} = N_i\left(\mu_i(R) - m_i\right) \\ \dfrac{dR}{dt} = D\cdot(S-R) - \sum\limits_i c_i N_i \mu_i(R) \end{cases} \tag{8}$$

Let us first try to understand this system. The first equation becomes more transparent if we write it in the form:

$$\frac{1}{N_i}\frac{dN_i}{dt} = \mu_i(R) - m_i \tag{9}$$

In words, this equation states that the *per capita* growth rate of species i is given by the difference between growth, $\mu_i(R)$, and losses, m_i. The growth and loss terms are species-specific. Moreover, growth depends on the availability of the resource, while the losses (which are caused by death, respiration, etc.) are assumed to be constant. For many micro-organisms, the growth term $\mu_i(R)$ is well described by the so-called ‘Monod equation’, which corresponds to a functional response curve of type 2:

$$\mu_i(R) = r_i \cdot \frac{R}{R+K_i} \tag{10}$$

The second equation in (8), describes the resource dynamics. In case of an abiotic nutrient, the change in resource availability is governed by two factors. The first term, $D\cdot(S-R)$, should be familiar from the chemostat equation: it corresponds to the difference between resource inflow and resource outflow. The parameter D describes the ‘turnover rate’ of the system, i.e., the velocity by which new resources enter the system and by which old resources are washed out of the system. The parameter S corresponds to the ‘resource supply rate’, i.e. the concentration of resources that become newly available, for example by mineralization. The second term in the resource dynamics corresponds to the consumption of resources by the consumer species i = 1, 2, 3,…

Exercise 5.4: Biotic versus abiotic resources

The resource dynamics in (8) is reasonable for a nutrient, i.e., for an *abiotic* resource. Indicate by means of an example how the resource dynamics would look like in case of a *biotic* resource, i.e., for the case that R denotes the density of a prey population.

Exercise 5.5: Competition for one limiting nutrient

Consider model (8) for the competition between three species for one limiting nutrient. Let us, for simplicity, assume that the turnover rate of the system is $D = 1$, that the resource supply rate is $S = 10$, and that the 'consumption rates' of all species are $c_i = 1$. The remaining parameters of the model are species-specific:

species 1: $r_1 = 5, \quad K_1 = 6, \quad m_1 = 1$
species 2: $r_2 = 6, \quad K_2 = 2, \quad m_2 = 3$
species 3: $r_3 = 4, \quad K_3 = 1, \quad m_3 = 2$

(a) Which species has the highest net growth rate $[\mu_i(R) - m_i]$ when the resource is abundant, i.e., for large values of R?

(b) Determine for each species the "minimal resource requirement" R_i^*. Based on the three R^*-values, determine the "competitive hierarchy" among the three species: Which species is the best, which is the intermediate, and which is the worst competitor for the limiting resource?

(c) Based on (a) and (b), indicate with a sketch the outcome of competition. Is it possible that two or more of the species can stably coexist with one another?

(d) Use Excel to run computer simulations of the system with varying initial conditions. Do the simulations confirm your previous conclusions?

Exercise 5.6: Competition for two limiting resources

The system of differential equations (8) considered above can easily be extended to describe competition between several species i = 1,2,… for *several* limiting resources j = 1,2,…:

$$\begin{cases} \dfrac{dN_i}{dt} = N_i\left(\mu_i(R_1,R_2,...) - m_i\right) \\ \dfrac{dR_j}{dt} = D\cdot(S-R_j) - \sum_i c_{ij} N_i \mu_i(R_1,R_2,...) \end{cases} \tag{11}$$

The main difference with (8) is that the growth of species i, μ_i, now depends on the availability of *all* the resources. We shall from now on focus on the special case where resource dependent growth is governed by "Liebig's Law of the Minimum":

$$\mu_i(R_1,R_2,...) = \min_j \left\{ r_i \cdot \frac{R_j}{R_j + K_{ij}} \right\} \tag{12}$$

where the minimum is taken over j = 1,2,…

(a) What is the biological interpretation of (11) and (12)? In particular, what is the interpretation of the parameters c_{ij} and K_{ij}?

We will now consider the competition between two species (i = 1,2) for two limiting resources (j = 1,2). Let us, for simplicity, assume that the turnover rate of the system is D = 1, that all species have the same loss rates $m_i = 1$, and that the maximal per capita growth rates of all the species are the same: $r_i = 4$. The consumption rates c_{ij} and the values K_{ij} specifying the growth rates are given by the matrices:

$$\mathbf{C} = \begin{pmatrix} c_{11} & c_{12} \\ c_{21} & c_{22} \end{pmatrix} = \begin{pmatrix} 2 & 1 \\ 1 & 2 \end{pmatrix} \quad \text{and} \quad \mathbf{K} = \begin{pmatrix} K_{11} & K_{12} \\ K_{21} & K_{22} \end{pmatrix} = \begin{pmatrix} 6 & 3 \\ 3 & 9 \end{pmatrix}$$

(b) In the lectures, we have seen how the system can be analyzed in 'resource space', i.e., in the space where the coordinates correspond to the concentrations (R_1, R_2) of the two resources. Plot the nullclines for both species. Where do the nullclines intersect? Attach the consumption vectors of the two species to this intersection point.

(c) Is coexistence of both species possible?

(d) Assume that the supply rate of resource 1 is $S_1 = 3$ and consider subsequently the following values for the supply rate of resource 2:

$$S_2 = 3.25, \quad S_2 = 4.00, \quad S_2 = 5.25$$

Plot for each of these cases the supply point (S_1, S_2) in resource space and predict the outcome of competition.

(e) Is it, in principle, possible that a third species can coexist with the two species described above? Why/why not?

(f) Run for all scenarios in (d) computer simulations with Excel and check whether your predictions in (d) were correct.

6. Competitive coexistence

Exercise 6.1: Two predators on a single prey

As a general rule, it is very difficult to achieve coexistence of predators and prey in a lab environment. Utida (1957), however, achieved coexistence of a host species (H), the bean weevil *Callosobruchus chinensis*, with two of its parasites, the wasp species *Heterospilus prosopidis* [P1] and *Neocatolaccus mamezophagus* [P2]. Interestingly, coexistence strongly depended on the death rates of the two wasp species that was manipulated during the experiment. It is your task in this exercise to model this situation and to explain the outcome of Utida's experiments on the basis of this model. You should take the Rosenzweig-MacArthur model as your point of departure:

$$\begin{cases} \dfrac{dN}{dt} = r\,N \cdot \left(1 - \dfrac{N}{K}\right) - P \cdot \Phi(N) \\ \dfrac{dP}{dt} = P\left(-d + b \cdot \Phi(N)\right) \end{cases} \tag{1}$$

with

$$\Phi(N) = E\frac{N}{N+H} \qquad \text{or} \qquad \Phi(N) = E\frac{N^2}{N^2+H^2} \tag{2}$$

(a) Extend the Rosenzweig-McArthur model by introducing a second predator (or parasite) species. Assume that the parameter b in (1) is equal to one for both wasp species.

To arrive at a more specific version of the model, which is applicable to Utida's system, the following facts have to be taken into account:

- The bean weevils have an intrinsic growth rate of 0.1 per time unit [= 5 weeks], and, in the absence of wasps, the bean weevils reach an equilibrium density of 200 individuals per unit area [= 1 petri dish].
- The functional response curve of both parasites is approximated well by Holling's disk equation. However, the two wasp species differ significantly with respect to the parameters specifying the disk equation. In fact, Utida obtained for the two species the following estimates of the host encounter rate and the handling time:

$$P_1:\ a = 0.04,\ T_h = 1.2 \qquad P_2:\ a = 0.02,\ T_h = 0.9$$

- In two separate experiments, the following death rates were imposed upon the two parasites:

$$\text{experiment 1: } d_1 = d_2 = 0.75 \qquad \text{experiment 2: } d_1 = d_2 = 0.65$$

(b) Use the above information to write down a concrete version of your general model in (a) for each of the two experimental setups.

(c) Plot the functional response curves of the two wasp species in a single graph. Which species is more efficient at high prey density, and which species is more efficient at low density? Use this information to speculate what the effects might be of a higher or lower parasite death rate: A higher value of d_i (as in experiment 1) will remove some of the predation pressure and, hence, lead to higher prey densities. Which of the two parasites profits from higher prey densities? Which parasite profits from an increased death rate of the parasites?

(d) Before analysing the whole three-species system, consider first the special case where one wasp species is absent. [set P_1 or P_2 equal to zero.] For each of the two experimental setups, you get two Rosenzweig-McArthur models for the interaction of one wasp species with its prey. Plot for all four scenarios the nullclines of the system, and determine on the basis of this graph whether the interior equilibrium is stable or not. Check for each of the four scenarios whether the prey density at equilibrium is in the range where – according to your results in (c) – the absent wasp species is more efficient than the one that is present. Use the result to predict whether or not the absent wasp species would be able to invade into the system when rare.

(e) The invasion analysis of the two-species systems in (d) gives us an important clue of the behaviour of the full three-species system. For example, one might expect coexistence of both wasp species if each of the species can invade when rare. Without performing any simulations and solely based on your results in (d), predict the outcome of the three-species interaction in both experimental setups. Do you think that all three species can stably coexist?

(f) Now run simulations with Excel where all three species are present. Under which conditions does coexistence of all three species occur? Are the simulation results in line with your expectation in (e)?

(g) Doesn't coexistence of *two* consumer species on *one* resource contradict the "Principle of Competitive Exclusion"? Explain your answer.