13 A thousand and one population models

In Section I we analyzed the classical predator–prey Lotka–Volterra model that predicts periodic oscillations of the prey and predator population sizes. The model was written in a way to present the simplest possible mathematical expressions that describe the interactions between two populations. A very similar approach was used in the last lectures, when a predator–prey and competition models with intraspecific competition were analyzed. In these models all the interactions are described by linear function, which can be summarized in

Definition 1. *The Lotka–Volterra model for two interacting species is the model of the form*

$$\begin{aligned} \dot{x} &= x(b_1 + a_{11}x + a_{12}y), \\ \dot{y} &= y(b_2 + a_{21}x + a_{22}y), \end{aligned}$$

for some constants $b_1, b_2, a_{11}, a_{12}, a_{21}, a_{22}$.

In particular, for the classical predator–prey model I have $b_1 > 0, b_2 < 0, a_{11} = a_{22} = 0, a_{12} < 0, a_{21} > 0$:

$$\begin{aligned} \dot{N} &= aN - bNP, \\ \dot{P} &= cNP - dP. \end{aligned} \tag{1}$$

A next possible step in formulating mathematical models of two interacting populations is to consider *nonlinear* expressions for the description of intra- and interspecific interaction. Here, I will follow A.D. Bazykin's approach[1] and consider the example of the prey–predator model. I start with a generalization of (1):

$$\begin{aligned} \dot{N} &= A(N) - B(N, P), \\ \dot{P} &= C(N, P) - D(P), \end{aligned} \tag{2}$$

where N, P are the populations of prey and predator respectively, $A(N)$ is the function describing the prey dynamics when the predator is absent, $D(P)$ is the function describing the extinction of the predator when the prey is absent, function $B(N, P)$ gives the rate of consumption of the prey by the predator, and $C(N, P)$ is the effectiveness of consumption of prey. For $A(N)$ and $D(P)$ I used either the Malthus law of exponential growth or decay, or the logistic equation, which takes into account intraspecific competitions of the individuals in the population. Additionally, I can consider the case when the rate of growth of a population is low (or even negative), when the population size is small (think of a species where the individuals cannot find a mate), for example, I can take

$$A(N) = \frac{aN^2}{A + N}$$

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The title of this section is inspired by (or borrowed from) Hethcote, H. W. (1994). A thousand and one epidemic models. In Frontiers in mathematical biology (pp. 504-515). Springer Berlin Heidelberg, which I very much recommend for reading

[1]Bazykin, A. D. (1998). Nonlinear dynamics of interacting populations (Vol. 11). World Scientific

for some constants $a, A > 0$.

Next assumption is to consider

$$B(N,P) = B_1(N)B_2(P), \quad C(N,P) = C_1(N)C_2(P).$$

For instance, function $B_1(N)$ is called the *trophic predation function* or the functional reaction of the predator to the prey population density. In (2) I simply had linear function $B_1(N) = bN$, which is equivalent to the absence of any predation saturation as the prey population grows (I already used similar reasonings when discussing the model of the insect outbreak). In general, there are three most common trophic functions: linear function (or piecewise linear, as indicated in the figure, function I). The second type is a function that display the saturation effect: $\lim_{N\to\infty} B_1(N) = b > 0$. For example I can take (see curve II in the figure)

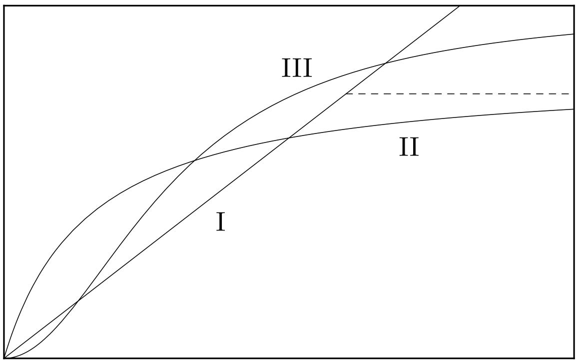

Figure 1: Three types of trophic functions

$$B_1(N) = \frac{bN}{1+\alpha N}\,.$$

A similar dependence is given by

$$B_1(N) = b(1 - e^{-\alpha N}).$$

The third type of the trophic predation function takes into account two elementary factors: the saturation effect of the predator, and nonlinear character of the prey consumption by the predator (the predator may look for another source of energy if the prey population is scares). In the figure you can see the qualitative character of this curve (III), analytical formula can be taken as

$$B_1(N) = \frac{bN^2}{1+\alpha N^2}\,,$$

or, even more generally,

$$B_1(N) = \frac{bN^2}{1+\alpha_1 N + \alpha_2 N^2}\,.$$

Now let me turn the attention to $B_2(P)$, which is $\propto P$ in (2) and in many other mathematical models, which can be interpreted as the absence of the competition among the predator individuals for prey. If I'd like to take this competition into account, I can take

$$B_2(P) = \frac{P}{1+\beta P}\,.$$

Therefore, I already have six choices for function $B(N,P)$.

A similar discussion can be made about $C(N,P)$, which often takes the form $C(N,P) = B_1(N)C_2(P)$. For instance, if one would like to take into account nonlinear predator birth at small population sizes, he or she can take

$$C(N,P) = C_1(N)\frac{cP}{C+P}\,,$$

for some constants $c, C > 0$.

Let me list the elementary factors that can be taken into account at generalizing (2):

- Nonlinear character of the prey growth rate for small N ($A(N) = aN^2/(A+N)$).
- Intraspecific prey competition ($A(n) = aN(1 - N/K_1)$).
- Predator saturation ($B_1(N) = bN/(1+\alpha N)$).
- Nonlinear character of the prey consumption by the predator ($B_1(N) = bN^2/(1+\alpha N)$).
- Predator competition for prey ($B_2(P) = P/(1+\beta P)$).
- Predator intraspecific competition $D(P) = P(1 + P/K_2)$.
- Nonlinear dependence of the predator birth rate at small P ($C_2(P) = dP/(C+P)$).

Now I can combine these elementary factors in different ways to obtain a particular example of the predator–prey model (1). For example, a model with prey competition, predator competition for prey, predator saturation takes the form

$$\begin{aligned}\dot{N} &= aN\left(1 - \frac{N}{K_1}\right) - \frac{bNP}{(1+\alpha N)(1+\beta P)}\,,\\ \dot{P} &= -dP + \frac{dNP}{1+\alpha N}\,.\end{aligned}$$

This model has 7 parameters. This number can be reduced to 4 by a change of the variables. Taking into account that each of the elementary factors given above means adding one more dimensionless parameter to (2), which in its turn has one dimensionless parameter. It is well known that analysis of the ODE systems with the number of parameters exceeding three is quite involved, and, more importantly, the results of such analysis are quite difficult to interpret. Therefore, it becomes crucial to be able to identify the key factors for each particular situation.

The same reasonings are applicable to other ecological interactions, including interspecies competition and mutualism.