Math4You

2023–2025

Trophic functions in predator-prey models

Mathematical models play an important role in the study of nature. These models open the possbilities to predict future development, but they also have other important roles.

The use of ecological models is sometimes referred to as physical approach in ecology because they study the ecosystem in terms of the evolution of populations and using mathematical methods originally derived to solve physical problems. The outputs of the models include the following information.

- **Predictions** Ability to work with mathematical models of ecosystems allows to predict future ecosystem development. This may include the evolution of population in static environment as well as an evolution in an environment in which the parameters are changing. Knowledge of the model will then reveals how the parameters change the ecosystem.
- **Understanding the principles** Mathematical models allow ecologists and scientists to examine the interactions between different components of ecosystems and understand the dynamics of these systems. They help to identify factors that influence the structure and function of these ecosystems.
- **Optimising decision making** Mathematical modelling of ecosystems can can be used to optimize decision-making in areas such as biodiversity conservation or forest and fisheries management. It helps to identify the best strategies for to achieve desired objectives.

  One of the fundamental relationships in ecosystems is the relationship between *predator and prey*. This relationship can be the only interaction in an ecosystem or it can be complemented by other interactions. The importance of predator-prey models will be illustrated with the following historically significant examples.

Lotka-Volterra model

In 1926, one of the first predator-prey models was published by the Italian mathematician Vito Voterra. The motivation to build this model was the fact that during the fishing restrictions of World War I in the percentage of predatory fish in the catch increased. The marine biologist Umberto D'Ancona noticed this phenomenon and was not able to find an explanation. He even expected the opposite: with the

Co-funded by the Erasmus+ Programme of the European Union.

restrictions on fishing he expected an increase in the percentage of smaller fish species that are food for predators. D'Ancona introduced this problem to his father-in-law Volterra. Volterra's model explains this behaviour as as a result of the simple idea of predator-prey interaction.

The model contains two equations. The first equation describing the prey population contains the assumption that the population grows naturally, but the growth is slowed down by predation. More predators lead to a slower growth of the prey. Too many predators can even lead to the fact that the size of the prey population will decline and the prey will die out. The second equation (for predator population) contains the assumption that without the presence of prey, the predator population dies out. However, the more prey is available to predators, the more likely this extinction turns into an increase in the predator population.

In the system described above, cycles occur naturally. Enough prey allows the predator population to increase. Many predators then act on the prey population negatively and the prey population begins to die off. This extinction results in a lack of food for the predators and and the predators also begin to die out. Over time, the predator population is reduced to the point where the prey feels the presence of the predator little. Therefore, the prey population can grow again and multiply to its original state. However, the increase in prey population allows the predator population to grow again, closing the cycle. These periodic changes in the size of both populations can be seen in the records of fur buying of snowshoe hare and lynx furs in the Hudson Bay area.

Volterra's model explains not only the origin of the cycles, but also that by decreasing the hunting rate, the equilibrium position around which the predator and prey oscillate shifts in favour of the predator and not the prey. This phenomenon observed by D'Ancona is called the *Volterra effect*.

The same model as Volterra's has been proposed in 1910 by the American mathematician Alfred J. Lotka. For this reason is the model called the Lotka-Volterra model.

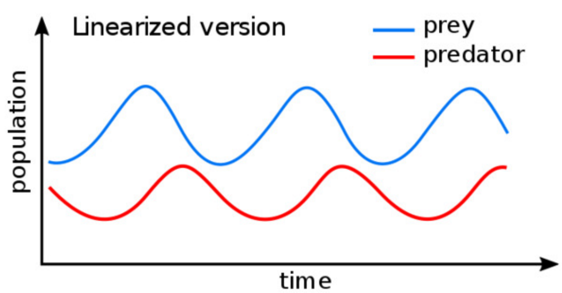

Figure 1: On the left, a typical pattern of predator and prey population sizes. A maximum of prey is followed by a maximum of predator and then a decline in both populations. On the right, the island fox, which has gone from being a top predator on its island to a prey endangered by extinction

Spruce budworm model

Similar periodic fluctuations as in the Lotka-Volterra model can also be observed in Canadian forests. Here, after approximately 30 to 40 years mass outbreak of the spruce budworm (*Choristoneura fumifer-*

ana) occurs. The population of this butterfly is relatively small most of the time, but some years it increases by a factor of thousands and its caterpillars can kill up to 80% of the trees in of the forest, virtually destroying it. One of the last mass occurrences was since 2006 in Quebec. Here, by 2019, about 9.6 million hectares of forest [^1], more than the size of Hungary.

See [^1]: source at `https://www.nrcan.gc.ca`.

In 1978, scientists D. Ludwig, D. D. Jones and C. S. Holling proposed a model that was not only able to model the evolution of the spruce budworm population, but helped to clarify the reasons why the described outbreaks occur. The reason is predation. In this case, it is the consumption of caterpillars by birds. Birds served as a limiting factor in nature for caterpillar numbers, but only up to a certain limit. When the forest grows large enough, it provides enough food for the caterpillar population. The caterpillar population then grows to to such an extent that the birds reach saturation in their food consumption and they are no more able to reduce the caterpillar population. Thus, the role of birds as predators becomes less important and the caterpillar population can multiply rapidly and then devastate the forest.

In this case, predation is important to limit the population caterpillars. Because birds as predators have a much slower reproductive cycle than the insect, their population can be considered constant. Through saturation, birds can then limit the growth rate to a limited extent. However, this limitation from a certain size the spruce budworm population is no longer sufficient, and it becomes uncontrollably overpopulated.

Island fox model

The island fox (*Urocyon littoralis*) is a unique species, endemic only to the islands around California. It is as large as a cat and trusting due to the absence of natural enemies. As a species, it is sensitive and vulnerable due to low genetic variation and low resistance to diseases introduced from the mainland. It is one of the smallest canids. Unlike other canids, however, it can climb trees.

As a result of human activity, the population of the island fox was near to extinction at the end of the millennium. On San Miguel Island, the population has declined from 450 adults in 1994 to 15 in 1999[1]. A similar situation has been experienced also on the other islands, each of which is inhabited by a separate subspecies of the island fox. The cause of the mortality was a chain of events: The production of the insecticide DDT in the 1940s resulted in the extinction of the bald eagle (*Haliaeetus leucocephalus*) which has been replaced by the golden eagle (*Aquila chrysaetos*). A predator feeding fish-eating predator was replaced on the island by a mammal-preferring predator. This was fatal to the island fox. The foxes, formerly apex predators, suddenly became prey, and by the turn of the millennium they were close to extinction. Moreover, unlike the Lotka-Volterra model, there was no hope of a return foxes back to their original numbers through oscillations, because the eagles also had alternative food in the form of wild pigs and skunks.

Fortunately, with tremendous effort, the island fox as a species has been saved. First, the causes of their of the decline was identified. Then it was enough to replenish the fox population and ensure the conditions in which the population is stable. This involved excluding feral pigs, the relocation of golden eagles to mainland, the return of bald eagles, the artificial breeding of foxes, their return to the wild and their vaccination against introduced diseases. All of this was achieved in record time, in one decade. It was one of the most successful rescues mammal rescue programme.

[1] For source see `https://www.iucnredlist.org/species/22781/13985603`.

Trophic functions

An important component of predator-prey models, whether it be any of the above examples, is the *trophic function*. This function describes the effect of a single predator on a prey population. It is given by the rate at which the growth of prey is slowed by a single predator. If x is the size of the prey population and y is the rate at which one predator slows the growth of prey down (i.e., the amount of prey taken by a predator in unit time), we can write this function mathematically in the form

$$y = f(x).$$

We'll try to find natural assumptions that the trophic function must satisfy. Then we will try to find a suitable analytical form.

Exercise 1. Assumptions about the predator's effect on prey are reflected in the properties that a trophic function must have.

1. A predator in an environment with a poor food supply also has a poor catch. More prey means easier prey reach and thus more catch.
2. Without food, a predator will not catch anything. If the amount of prey is zero, the amount of prey a predator will catch per unit time is zero.
3. Predators consume food only until they are saturated. If food is is abundant, predators will not catch more food per unit time than their saturation.

Express these characteristics in terms that we use to describe properties of functions. What property of functions does each of the following correspond to points?

Solution.

1. The function $y = f(x)$ is increasing.
2. The function $y = f(x)$ goes through the origin, i.e., $f(0) = 0$.
3. The function $y = f(x)$ is bounded above. Since the function is increasing and is bounded above, its graph has a horizontal asymptote at infinity.

Holling's type II trophic function

The trophic function indicates how much prey one predator kills per unit time for a given prey population size. It must therefore be defined on set of non-negative numbers and the function values will be non-negative (this follows from points 1 and 2 in Exercise 1). In the previous section it was shown that the trophic function has to pass through the origin and grow to the horizontal asymptote (growth and boundedness from above). These properties will not be satisfied if we look for a trophic function in the set of linear functions. So we try the simplest nonlinear function, the inverse proportionality.

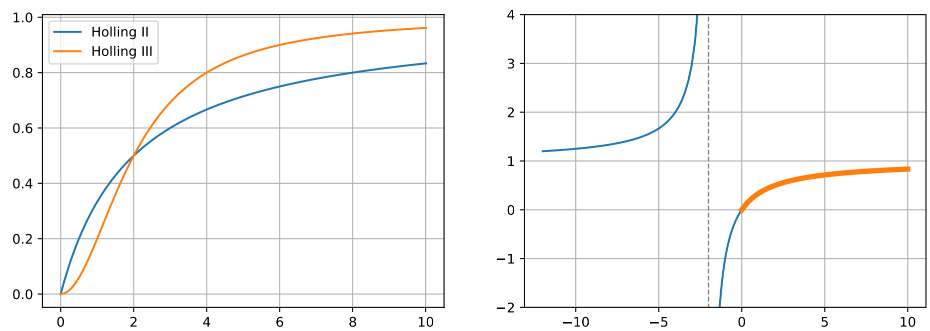

Figure 2: On the left, two typical trophic functions, called Holling's functions. The growth rate of the function of type II slows down. The type III function grows slowly at first, accelerates and then slows down again. On the right, the type II function as part of transformed graph of inverse proportionality. (own figure)

Exercise 2. Graph the function $y = \frac{1}{x}$. On this function perform transformations that change the graph as described below.

1. Scale the graph k times in the vertical direction. This does not change the monotonicity nor the position of the horizontal asymptote, but we can change the growth rate.
2. Flip the graph around the horizontal axis and move S units up. This produces a function which is positive and increasing for positive x and the function grows to the asymptote of S.
3. After the above transformations, the graph has a vertical asymptote at zero and one intersection with the horizontal axis to the right of the origin. Move the graph to the left so that the vertical asymptote is to the left of the vertical axis and the intersection with the x-axis is shifted to the origin.

Solution. A function whose graph is obtained by rescaling the graph of the function $y = \frac{1}{x}$ in the vertical direction k times is

$$y = \frac{k}{x}.$$

The inversion is achieved by multiplying the function by a factor of -1 and the shift is achieved by by adding the value of S. These adjustments give the function

$$y = S - \frac{k}{x}.$$

The shift to the left by b is achieved by substituting the expression $x+b$ for x. This gives us the function

$$y = S - \frac{k}{x+b}.$$

When converted to the common denominator the function takes the form

$$y = \frac{Sx + Sb}{x+b} - \frac{k}{x+b} = \frac{Sx + (Sb-k)}{x+b}.$$

To ensure $f(0) = 0$, the followin condition must be satisfied.

$$Sb - k = 0$$

This condition shows that the three constants are not independent, but there is a relationship between them.

Note. In the previous exercise we derived an analytical form for one of the basic trophic functions. This is an increasing function, which initially grows towards the horizontal asymptote and the rate of growth gradually decreases. Such a function is called the Holling's type II function. It is common to write it in the form

$$f(x) = \frac{Sx}{x+b}, \tag{1}$$

where S is the saturation level and b is a constant. The role of the constant b will be explained in the following exercise.

Exercise 3. Show that for a population size equal to b the value of the trophic function (1) is equal to half the value of saturation.

Solution. By setting $x = b$ in (1), we get

$$f(b) = \frac{Sb}{b+b} = \frac{Sb}{2b} = \frac{S}{2}.$$

This proves the statement.

The following exercise shows the reverse process, where from a trophic function of the form (1) we derive a form showing the successive transformations of the function $y = \frac{1}{x}$.

Exercise 4. Modify the formula for the function

$$y = \frac{6x}{x+2}$$

into its basic form, i.e. so that we can read the successive transformations of the function $y = \frac{1}{x}$$ on the graph of the given function.

Solution. We solve the problem by cleverly modifying the fraction. In the numerator, we create a multiple of the denominator, divide the fraction in two and truncate:

$$\frac{6x}{x+2} = \frac{6(x+2)-12}{x+2} = \frac{6(x+2)}{x+2} - \frac{12}{x+2} = 6 - 12\frac{1}{x+2}$$

This calculation shows that the graph of the above function is obtained by expanding the graph of the function $y = \frac{1}{x}$ in the vertical direction twelve times, by inverting it around the horizontal axis, shifting six units up and two units to the left.

The same result can be obtained by dividing the denominator by the numerator.

Exercise 5. Construct a trophic function if you know that the predator saturation is 6, and that the consumption rate is half of the saturation for a prey population of 210.

Solution. Thanks to the note before the Exercise 3 about the general form of the trophic function, we know that the prescription will be of the form

$$y = \frac{Sx}{x+b},$$

where S is the saturation value of the predator, i.e.

$$y = \frac{6x}{x+b}.$$

We can tell the value of the parameter b straight away as a resuls of Exercise 3, but we can also quickly compute it from the second condition in the problem. Really, we know that

$$3 = \frac{6 \cdot 210}{210 + b}$$

and from there, $b = 210$. So the final form of the function is

$$y = \frac{6x}{x + 210}.$$

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