

Evolution of parasites

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Year 2022-2023

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1. Research topic

In an isolated environment, we study the relation between a certain type of parasites and their host and how these evolve with time t (continuous or discrete). In our model, parasites deposit eggs on their hosts and when the eggs hatch, the host dies. Denote by H and P the number of hosts and parasites respectively (these can be modelled as a function of t). At each step (unit time), the number

of eggs deposited depend on the probability that a parasite and a host meet. One can assume that this probability is proportional to the product $H \times P$ of the populations.

We are given fixed values b and d - the birth and death rate of hosts when no parasites are present. Moreover, we let d_p be the death rate of the parasites.

Run simulations for given values of b , d and d_p and try to determine what happens with the populations H and P in time.

2. Experimental approach

For the experiment, 3 identical but individual hosts were studied in a laboratory of the Agricultural Sciences and Veterinary Medicine University in Cluj-Napoca. The hosts were 3 Petri vessels, and the 310 parasite eggs implanted/inserted in them were part of the parasitic species named *Strongylus equinus*. The evolution of the eggs was studied for ten days.



a) stage 1

b) stage 2

c) stage 3

Figure 1: Different stages of evolution as observed through microscope

At the beginning, all the eggs were in the first stage (see Figure 1 a)), during which the parasite cells started forming. In three days, the number of eggs decreased by 122 (40%). Subsequent to this, the 188 remaining eggs reached the second stage (Figure 1 b)). The larvae grew inside the egg, developing parasite characteristics. In the next week (seven days), the number of parasitic cells reduced again, this time by 30 (15%). Therefore, only 158 ova attained the third stage (Figure 1 c)), in the course of which the eggs hatched.

Supposing that the host is a living animal, after the third stage (prior explained) the health condition of the being would aggravate. However, the presence of this type of parasites could not cause the death of the animal.

The formula showing the parasite population depending on time, that was deduced from the data, is

$$P(t) = k(e^{-d_p \cdot t} + c)$$

where $P(t)$ is the parasite population at time t , k and c are constants, $e^{-d_p} = 0.8$ and $d_p = -\ln 0.8$ is the parasite death rate (1).

Obviously, this method is a very modified version of the problem, since there is a constant number of hosts: 3, coefficients b and d being zero. However, it provided us some information about the practical utility of the problem.

3. Analytical approach

3.1. Evolution of hosts

3.1.1 In the absence of parasites

When no parasites are present, the hosts population is influenced only by the b and d parameters, the natural birth and death rate (2). Because such *rates* show the number of newly born or dead individuals *with respect to the current population* it is straightforward to say that the difference between two populations within a certain (very short) time interval dt (that is, the derivative of the hosts population) equals the difference between the two rates times the current population

$$\frac{dH}{dt} = (b - d)H \quad (1)$$

b has the (+) sign because it contributes to the increase in population, while d has the (-) sign because it contributes to the decrease in population; b and d are both positive constants.

Rearranging equation (1)

$$\frac{dH}{H} = (b - d)dt \quad (2)$$

Integrating equation (2) from time 0 to t we obtain

$$\int_{H_0}^H \frac{dH}{H} = \int_0^t (b - d)dt$$

We therefore obtain the population size at time t when no parasites are present

$$\ln H - \ln H_0 = (b - d)t \iff \ln \frac{H}{H_0} = (b - d)t \iff \frac{H}{H_0} = e^{(b-d)t}$$

and the final form

$$H(t) = H_0 e^{(b-d)t}$$

where H_0 is constant and represents the initial population size and e is Euler's number.

Figure 2 shows different curves that the hosts population can follow depending on the relationship between the two parameters b and d .

3.1.2 In the presence of parasites

Since now parasites are present, a new term will appear in the expression of the derivative of the population of hosts. This term shows the number of hosts infested by parasites. As of the hypothesis, the number of eggs is proportional to the product $H \times P$. Therefore, the number of eggs layed over that period of time is rHP , where r is a constant. Since multiple eggs can be layed on the same host, and that host has to be counted only once, another constant has to be multiplied with the expression above, a constant that shows the average number of eggs/host. The final form of the new term, after combining the two constants is kHP .

We can hereby write the expression of the derivative of the hosts population size as

$$\frac{dH}{dt} = (b - d)H - kHP \quad (3)$$

The new term has been introduced with sign (-) because it contributes to the decrease of the population size.

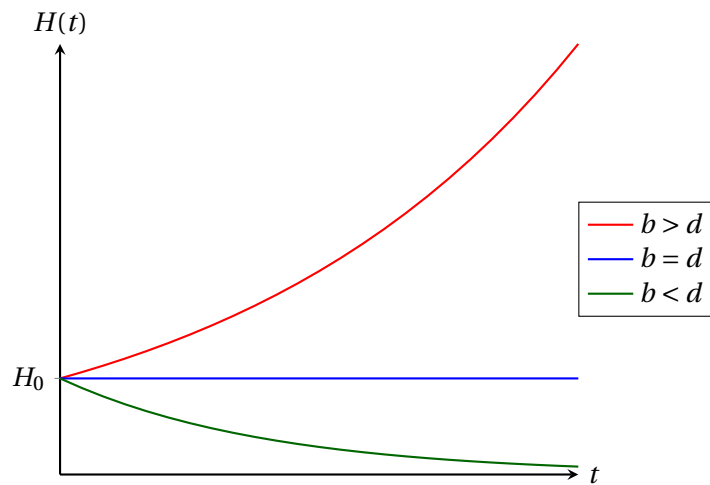


Figure 2: Evolution of hosts in the absence of parasites

3.2. Evolution of parasites

3.2.1 In the absence of hosts

When no hosts are present, the parasites only have a natural death rate d_p . Similarly as for the hosts, we can now write for parasites the differential equation that shows how their population evolves in time in the absence of hosts

$$\frac{dP}{dt} = -d_p P \quad (4)$$

Solving equation (4) similarly as for the hosts, yields the solution

$$P(t) = P_0 e^{-d_p t} \quad (5)$$

Figure 3 shows the evolution of the parasite population when no hosts are present. As we expected, the population always decreases asymptotically to 0 in this case because parasites need hosts in order to reproduce.

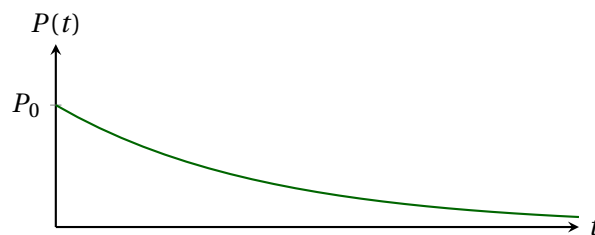


Figure 3: Evolution of parasites in the absence of hosts

3.2.2 In the presence of hosts

In section 3.1.2 we found that the number of eggs laid within a time interval dt is rHP . This is equal to the newly-born individuals that contribute to the parasite population in that time interval. Therefore,

this is the quantity that should be added to the derivative of the parasite population in equation (4). We obtain

$$\frac{dP}{dt} = -d_P P + rHP \quad (6)$$

3.3. The system of equations

Combining equations (3) and (6) altogether we obtain a non-linear coupled system of differential equations known in mathematics as the *Lotka-Volterra system*. It is nonlinear, because it contains unknowns to the power of 2 (in the products HP) and it is coupled, because both derivatives depend on both populations.

Renaming the two populations as x (hosts) and y (parasites) and the constants conveniently, the system can be written as

$$\begin{cases} \frac{dx}{dt} = \alpha x - \beta xy \\ \frac{dy}{dt} = -\gamma y + \delta xy \end{cases} \quad (7)$$

where

$$\begin{cases} x = H \\ y = P \\ \alpha = b - d \\ \beta = k \\ \gamma = d_P \\ \delta = r \end{cases}$$

In the current section we will discuss a series of mathematical methods that allow us to visualise the evolution of the two populations in time, as described by the Lotka-Volterra system of equations.

3.3.1 Vector fields

Since the evolution of the two populations is described by equations depending only on their sizes at a certain moment in time, and *not* on the time moment, we can conclude that being given a pair of population sizes (x, y) , from then on, they will always evolve in the same manner, no matter *when* that pair of populations happens to exist. Therefore, instead of representing the two populations against time separately, we can eliminate time and represent the two populations against each other.

To each pair of current population sizes (x, y) , a vector can be assigned, indicating the direction in which the populations will evolve from then on. The vector's horizontal and vertical components are equal to the derivatives of the two populations and can therefore be calculated using the Lotka-Volterra system. The vector's modulus, equal to $\sqrt{(dx/dt)^2 + (dy/dt)^2}$, shows how "fast" the population sizes are changing. Such a representation is called *vector field*.

Obviously, the shape of the vector field depends on the four parameters $\alpha, \beta, \gamma, \delta$. It does not depend, however, on the initial population sizes, since any point in the plane can play the role of a starting point.

Figure 4 shows the vector field for chosen parameters of $\alpha = 0.02, \beta = 0.004, \gamma = 0.06, \delta = 0.008$. The field looks as we expected: if we go on the horizontal axis, those are points that correspond to hosts in absence of parasites (case that has been studied in subsection 3.1.1). And because we chose $\alpha > 0 \iff b > d$, the hosts grow exponentially and parasites remain to 0 (all vectors are overlapped with the horizontal axis). Similarly, if we go on the vertical axis we are in the case of parasites in absence of hosts (subsection 3.2.1), with parasite population decreasing exponentially to 0.

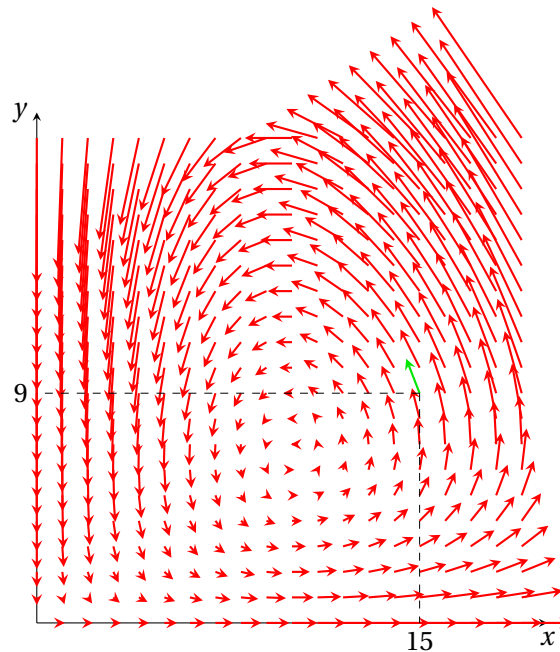


Figure 4: Vector field

As an example we chose the vector at point $(15, 9)$, meaning that we have current populations of 15 hosts and 9 parasites. The evolution of the populations one unit in time afterwards is described by the vector \vec{v} , drawn green here. Its horizontal component equals

$$|\vec{v}_x| = \frac{dx}{dt} = \alpha x - \beta xy = 0.02 \cdot 15 - 0.004 \cdot 15 \cdot 9 = -0.24$$

and its vertical component equals

$$|\vec{v}_y| = \frac{dy}{dt} = -\gamma y + \delta xy = -0.06 \cdot 9 + 0.008 \cdot 15 \cdot 9 = 0.54$$

This means that after a time unit dt , we will have 14.76 hosts and 9.54 parasites.

Observation The reader may be confused by the non-integer value of the number of individuals, but since it is mathematically correct, it does not matter. The values of $H(t)$ and $P(t)$ may represent, for instance, hundreds or thousand of individuals (3).

3.3.2 Stationary points

It would be interesting to find out whether there exist populations that can co-exist in such an equilibrium with each other that their sizes don't change in time at all, remaining constant. This would be such a state, so that the number of hosts infested by parasites compensates their natural growth and the parasites born equal their natural death rate.

Because once entering in such a state of equilibrium, the populations won't leave it, these points are called *stationary points*.

To find these points, having in mind that the populations remain constant, it means that we should set both derivatives to zero

$$\begin{cases} \frac{dx}{dt} = 0 \\ \frac{dy}{dt} = 0 \end{cases} \stackrel{(7)}{\iff} \begin{cases} \alpha x - \beta xy = 0 \\ -\gamma y + \delta xy = 0 \end{cases}$$

The system has the solutions

$$(0, 0), \left(\frac{\gamma}{\delta}, \frac{\alpha}{\beta} \right)$$

which are represented in blue on the vector field in Figure 5.

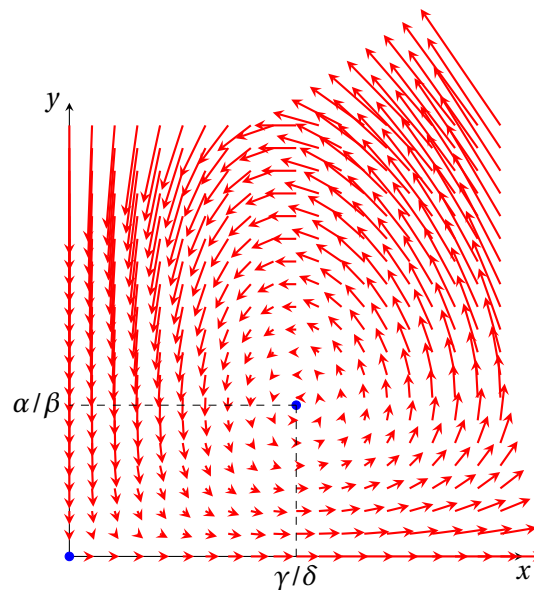


Figure 5: Stationary points

It is obvious that if both populations are zero they will remain zero. There is, however, the second point, which is of interest to us, a point with both populations non-zero. As of the definition of the vector field, to these points null vectors are assigned. As we can see, all other vectors rotate counter-clockwise around the second stationary point (4).

3.3.3 Discretisation

A method that can yield good numerical values, showing us how the populations evolve given an initial state (x, y) is the discretisation. We can turn the functions into sequences.

By doing that, the magnitude of a derivative becomes the difference between two consecutive terms. We can therefore calculate the populations step by step using the formula

$$(7) \implies \begin{cases} x_{n+1} - x_n = \alpha x_n - \beta x_n y_n \\ y_{n+1} - y_n = -\gamma y_n + \delta x_n y_n \end{cases} \iff \begin{cases} x_{n+1} = x_n(1 + \alpha - \beta y_n) \\ y_{n+1} = y_n(1 - \gamma + \delta x_n) \end{cases} \quad (8)$$

Writing a software that uses the discretisation formulas (8) we were able to see how the populations evolve in time, from a starting pair (x, y) . The software generates the population sizes within

timeInterval time units. If any of the two reach zero or exceed an upper limit of maxSize, the execution ends.

```

1 for i in range(timeInterval):
2     hnew = h * (1 + alpha - (beta * p))
3     pnew = p * (1 - gamma + (delta * h))
4     if(hnew > maxSize or pnew > maxSize):
5         outputFile.write('Value exceeding upper limit\n')
6         break
7     if(hnew <= 0):
8         outputFile.write('Hosts population died\n')
9         break
10    if(pnew <= 0):
11        outputFile.write('Parasite population died\n')
12        break
13    h = hnew
14    p = pnew
15    outputFile.write(str(h) + ', ' + str(p) + '\n')

```

The data that is generated by the code can be represented as a path directly on the vector field (Figure 6). As expected, the path obeys the vector field, being tangent to the vectors in all points it passes through.

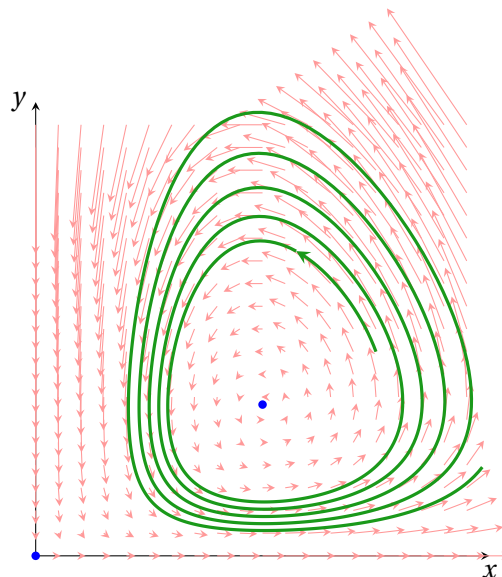


Figure 6: The path followed by the populations for initial pair (15,9) and parameters $\alpha = 0.02$, $\beta = 0.004$, $\gamma = 0.06$, $\delta = 0.008$

It is worth noting, however, that this is only an approximate method, and the path generated is close but not identical with the real path, because it is calculated discretely, with evaluation of the derivatives at certain time intervals. For the real path to be generated, the derivatives would need to be calculated at infinitesimally small time intervals.

To check that, we can adapt the discretisation method to reduce the time interval between two calculations (let's say, not every day of our ecosystem, but every hour or minute). What needs to be changed in our calculation method to provide that?

We will take the Lotka-Volterra system again, but this time we will consider a time interval of fdt

instead of dt , with $f \in (0, 1)$. The rewritten Lotka-Volterra system is equivalent with (5)

$$\left\{ \begin{array}{l} \frac{dx}{f dt} = \alpha x - \beta xy \\ \frac{dy}{f dt} = -\gamma y + \delta xy \end{array} \right. \iff \left\{ \begin{array}{l} \frac{dx}{dt} = f\alpha x - f\beta xy \\ \frac{dy}{dt} = -f\gamma y + f\delta xy \end{array} \right. \iff \left\{ \begin{array}{l} \frac{dx}{dt} = (f\alpha)x - (f\beta)xy \\ \frac{dy}{dt} = -(f\gamma)y + (f\delta)xy \end{array} \right. \quad (9)$$

System (9) indicates that if we want to calculate the populations f^{-1} times more often we have to multiply each parameter α , β , γ , δ by our chosen factor f . Figure 7 shows the path obtained using our software for factors 0.5 and 0.2. As we can see, as f decreases, the path approaches a closed path.

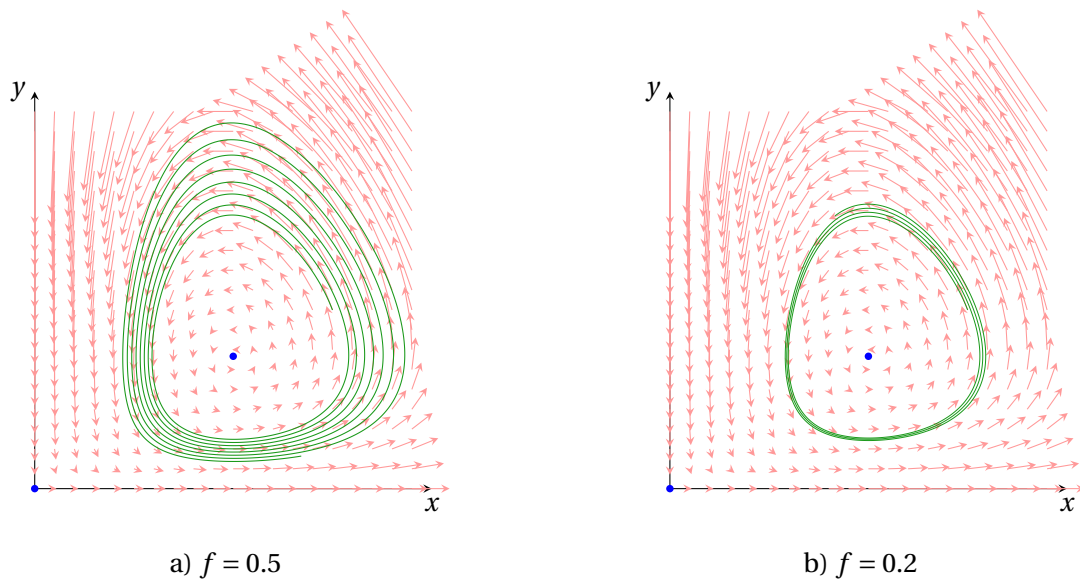


Figure 7: Making discretisation at smaller time intervals

Is it possible that, at the limit for $f \rightarrow 0$ (the real case), this path is a closed path? This observation is discussed in the next subsection.

3.4. The prime integral of the system

In order to obtain the mathematical expression of the path we observe that we can apply the separation of variables method in the Lotka-Volterra system (6).

$$\frac{dy}{dx} = \frac{dy}{dt} \cdot \frac{dt}{dx} = \frac{y'}{x'} \stackrel{(7)}{=} \frac{-\gamma y + \delta xy}{\alpha x - \beta xy} = \frac{y(-\gamma + \delta x)}{x(\alpha - \beta y)} \iff \frac{\alpha - \beta y}{y} dy = \frac{-\gamma + \delta x}{x} dx \quad (10)$$

Integrating expression (10) gives

$$\begin{aligned} \alpha \int \frac{dy}{y} - \beta \int dy &= -\gamma \int \frac{dx}{x} + \delta \int dx \\ \alpha \ln y - \beta y &= -\gamma \ln x + \delta x + C \\ \alpha \ln y - \beta y + \gamma \ln x - \delta x - C &= 0 \end{aligned} \quad (11)$$

Equation (11) represents the mathematical equation of the path the two populations follow in time, where C is a constant that depends on the initial conditions. Since the equality is obeyed at any moment, even at the initial one, C can be written depending on H_0 and P_0 as

$$C = \alpha \ln P_0 - \beta P_0 + \gamma \ln H_0 - \delta H_0$$

Figure 8 illustrates the characteristic path the two populations follow in time depending on their initial sizes.

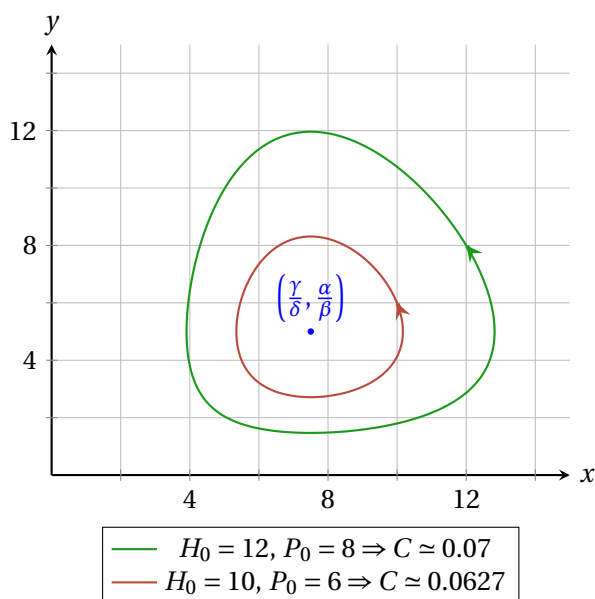


Figure 8: Curves describing the evolution of hosts and parasites in time using the prime integral of the system

4. Conclusion

We are aware of the fact that the field of differential equations is a fairly vast field, our research topic approaching only a narrow part of it. Although our high-school knowledge did not enable us to give a complete and comprehensive solution to the problem of competing species, we hope that our work represents a satisfying insight into this field, especially for the younger ones.

References

- [1] James C. Robinson, *An introduction to ordinary differential equations*, Cambridge University Press, 2004
- [2] Desmos, *Graphing calculator*, <https://www.desmos.com/calculator>, accessed on 1st June 2023

Editing Notes

- (1) This can be compared with the formula (5) found for the evolution of parasites in the absence of hosts. Here, the mortality rate is equal to d_p only if $c = 0$.
- (2) This is the simplest model. There are more complex models that take into account resource limitations.
- (3) We can say that if H and P are large enough, treating them as derivable functions is a mathematically correct approximation.
- (4) There is a big difference between these two stationary points. A point close to $(0, 0)$ will move far away (unless it is on the y -axis), so there is no stability, while on the contrary a point close to the other stationary point stays close to it.
- (5) Formally, in the equations below, x and y are replaced by the functions $t \mapsto x(f t)$ and $y \mapsto y(f t)$.
- (6) A first observation is that eliminating time from equations (7) yields a differential equation linking x and y as the system evolves, so that each trajectory $\{(x(t), y(t)); t \geq 0\}$ remains on some given solution of this equation.