Population Dynamics–Lotka-Volterra Model

Lotka-Volterra equations

The Lotka-Volterra equations are a pair of differential equations used to describe the (continuous time) two-population dynamics, such as the predator-prey system:

$$\frac{\mathrm{d}x}{\mathrm{d}t} = \alpha x - \beta x y$$
$$\frac{\mathrm{d}y}{\mathrm{d}t} = \delta x y - \gamma y$$

where

- x is the prey population
- y is the predator population
- $\mathrm{d}x/\mathrm{d}t$ and $\mathrm{d}y/\mathrm{d}t$ represent the growth rates
- t represents time
- $\alpha, \beta, \gamma, \delta$ are positive real parameters

Assumptions in the Lotka-Volterra equations

The Lotka-Volterra model makes a number of assumptions, not necessarily realizable in nature, about the environment and evolution of the predator and prey populations:

- The prey population finds ample food at all times
- The food supply of the predator population depends entirely on the size of the prey population
- The rate of change of population is proportional to its size
- During the process, the environment does not change in favor of one species, and genetic adaptation is inconsequential
- Predators have limitless appetite

No interaction between the two populations

First let us consider the evolution when both populations are not interacting: i.e. taking β and δ to be zero. In such a case, we have the following equations:

$$\frac{\mathrm{d}x}{\mathrm{d}t} = \alpha x, \quad \frac{\mathrm{d}y}{\mathrm{d}t} = -\gamma y$$

These can be solved exactly:

$$x(t) = Ae^{\alpha t}, \quad y(t) = Be^{-\gamma t}$$

where A and B are constants

- The prey population, $x(t)$, grows exponentially
- The predator population, $y(t)$, declines exponentially to extinction

Clearly, the exponential growth cannot continue indefinitely, as the environment can no longer support the growth after a while.

What are the possible long time scenarios when we take the full Lotka-Volterra equations?

Will there be constant coexistence populations as solutions to the LV equations?

Consider the full Lotka-Volterra equations:

$$\frac{\mathrm{d}x}{\mathrm{d}t} = \alpha x - \beta x y, \qquad \frac{\mathrm{d}y}{\mathrm{d}t} = \delta x y - \gamma y$$

Supposed after some time t, the two populations in the Lotka-Volterra equations become constant, and let us denote them by $x^\star$ and $y^\star$ respectively. This means that when these values are substituted into the right-hand side of the Lotka-Volterra equations, we get zero: the rates of change, i.e. derivatives, vanish – otherwise, the x and y populations will change in the next time step. We thus have

$$\frac{\mathrm{d}x}{\mathrm{d}t} = 0 = x^\star(\alpha - \beta y^\star)$$

$$\frac{\mathrm{d}y}{\mathrm{d}t} = 0 = y^\star(\delta x^\star - \gamma)$$

Will there be constant coexistence populations as solutions to the LV equations?

$$\frac{\mathrm{d}x}{\mathrm{d}t} = 0 = x^\star(\alpha - \beta y^\star), \quad \frac{\mathrm{d}y}{\mathrm{d}t} = 0 = y^\star(\delta x^\star - \gamma)$$

What are the possible value pairs $(x^\star, y^\star)$ that can satisfy these two conditions simultaneously?

- Clearly, $(0, 0)$ is one
- Can there be nonzero values?
  - Suppose $x^\star = 0$ but $y^\star \neq 0$. The first condition is satisfied, but if $x^\star = 0$, the second condition requires $y^\star\gamma = 0$. Since γ in general cannot be zero, this means we can only have $y^\star = 0$ also. The same argument also leads to the conclusion that we cannot have $(x^\star \neq 0, y^\star = 0)$.
  - That leaves us to explore the possibility of both $x^\star$ and $y^\star$ having nonzero values. The 2 conditions can only be satisfied if we have $(\alpha - \beta y^\star) = 0$ and $(\delta x^\star - \gamma) = 0$.

Will there be constant coexistence populations?

We are then led to the conclusion that

$$(x^\star, y^\star) = (0,0) \quad \text{or} \quad \left(\frac{\gamma}{\delta}, \frac{\alpha}{\beta}\right)$$

Note that the second possibility is only a valid one when the system parameter values are such that

$$0 < \gamma/\delta \leq 1, \;\; 0 < \alpha/\beta \leq 1$$

Note that we are dealing with normalized populations

Preparation for Numerical solution of ODE

$$\frac{\mathrm{d}x}{\mathrm{d}t} = \alpha x - \beta x y$$
$$\frac{\mathrm{d}y}{\mathrm{d}t} = \delta x y - \gamma y$$

This can also be expressed as:

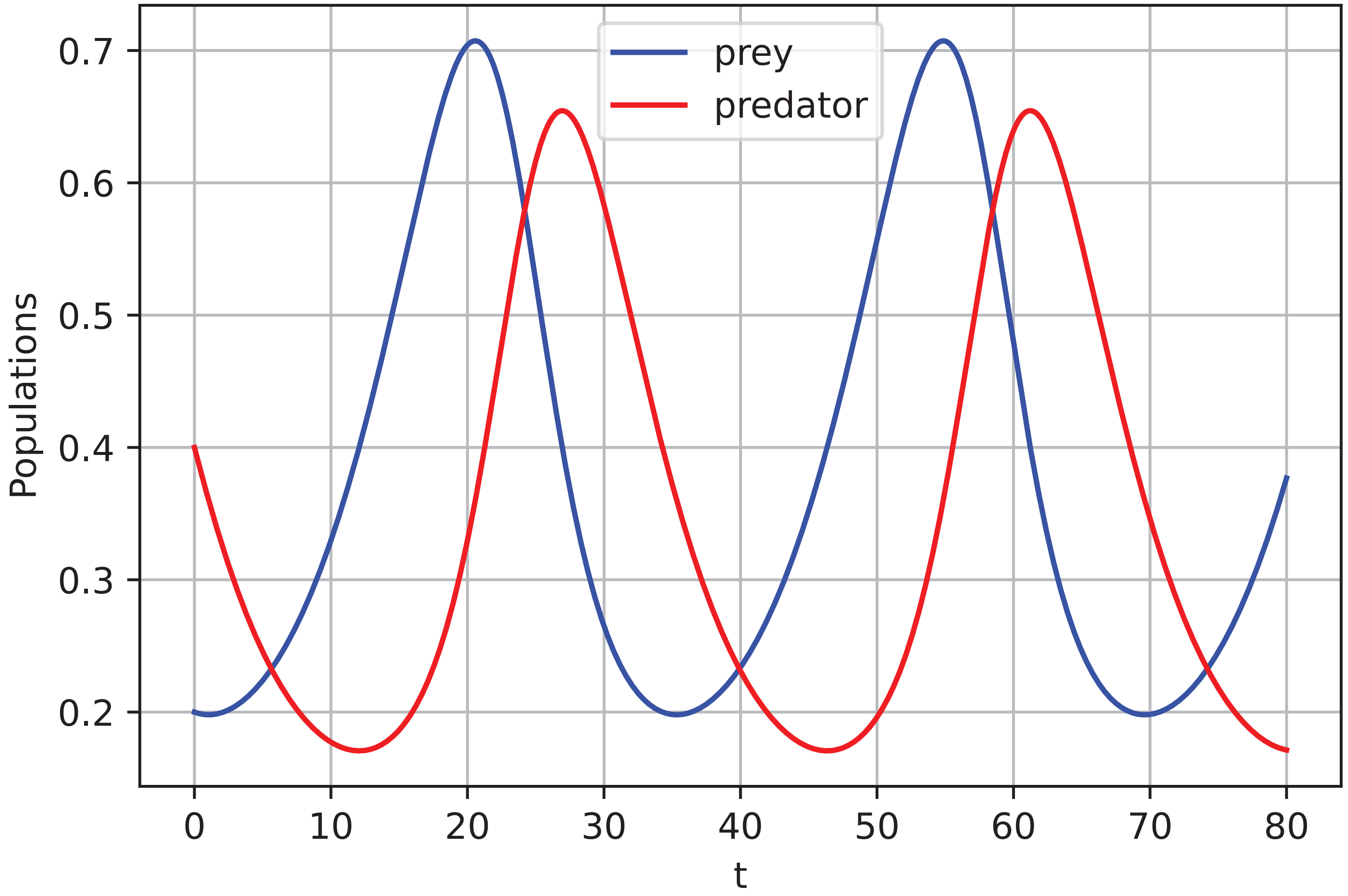
$$\frac{\mathrm{d}}{\mathrm{d}t}\begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} \alpha x - \beta x y \\ \delta x y - \gamma y \end{pmatrix}$$

$$\frac{\mathrm{d}\boldsymbol{Z}}{\mathrm{d}t} = \boldsymbol{G}, \quad \boldsymbol{Z} = \begin{pmatrix} x \\ y \end{pmatrix}$$

code

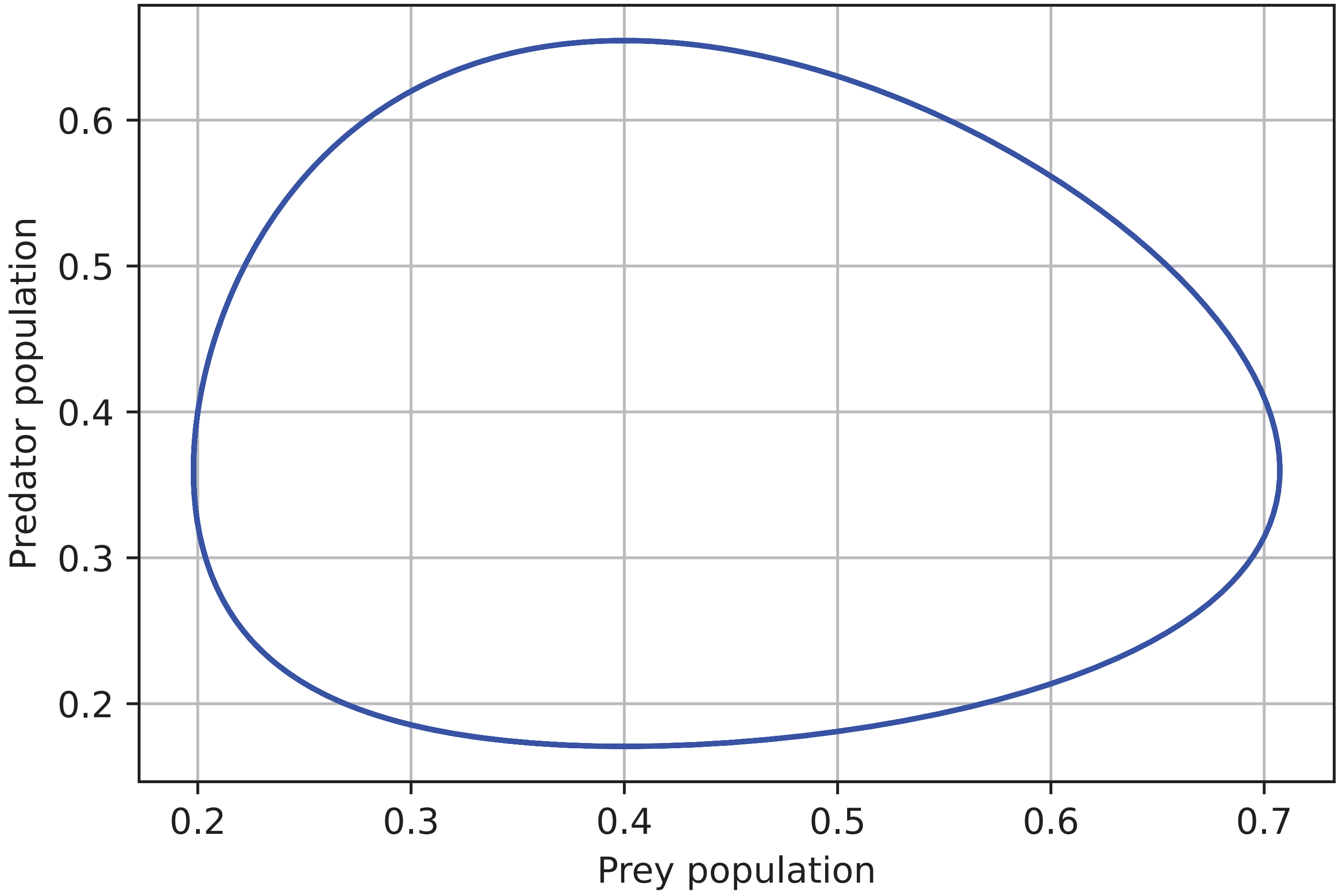

```
import matplotlib.pyplot as plt
import numpy as np
from scipy.integrate import odeint

# Lotka-Volterra
def LV(z, t):
    # z is a vector such that x=z[0] and y=z[1]. This function return [dx/dt, dy/dt]
    return [ a*z[0] - b*z[0]*z[1], d*z[0]*z[1]- c*z[1]  ]

tmax = 10  # for a short time to begin with
ticks = 20*tmax  # the total number of time points we want solutions at.
ts = np.linspace(0, tmax, ticks)

a=0.3; b=0.0; c=0.2; d=0.0;  #no interaction between the two populations.

# Now the initial conditions.
x0=0.1; y0=0.3; z0 = [x0, y0]

zs = odeint(LV, z0, ts) # Then call odeint module to generate a numerical solution

plt.plot(ts, zs[:,0], label='prey')  # plot prey population
plt.plot(ts, zs[:,1], label='predator')  # plot predator population
plt.legend(loc='upper left')
```

Some plots



$$\alpha = 0.180,\ \beta = 0.50,\ \gamma = 0.20,\ \delta = 0.50,\ (x_0, y_0) = (0.20, 0.40)$$

Some plots cont'd



$$\alpha = 0.180,\ \beta = 0.50,\ \gamma = 0.20,\ \delta = 0.50,\ (x_0, y_0) = (0.20, 0.40)$$

Equilibrium constant populations

Somehow, from our computational plots, we don't seem to see the population settling down to any constant population

The reason: the constant equilibrium populations are not stable populations

What this means is that for the parameters chosen, with almost all initial conditions, the populations would tend to behave in an oscillatory manner, rather than settling down to the constant equilibrium populations, unless the initial conditions are the constant equilibrium populations

Equilibrium constant populations cont'd

From our previous derivation, we have determined that the fixed equilibrium populations are

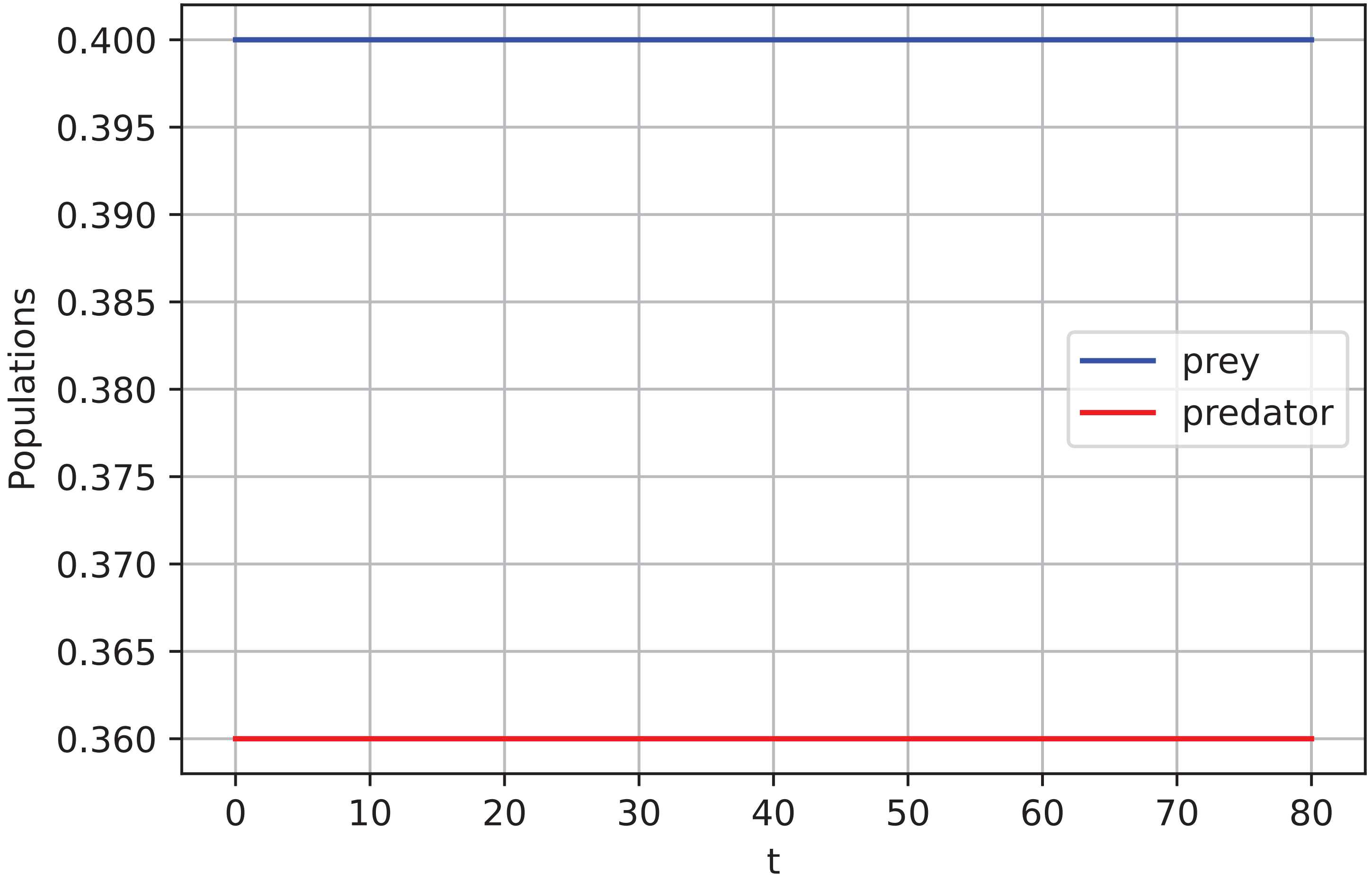
$$(x^\star, y^\star) = (0, 0) \quad \text{or} \quad \left(\frac{\gamma}{\delta}, \frac{\alpha}{\beta}\right)$$

Consider the following parameter values:

$(\alpha, \beta, \gamma, \delta)$	γ/δ	α/β
(0.18, 0.5, 0.2, 0.5)	0.40	0.36
(0.20, 0.8, 0.2, 0.8)	0.25	0.25
(0.22, 0.6, 0.2, 0.6)	0.33	0.37
(0.27, 0.5, 0.2, 0.5)	0.40	0.54

If we start the solution with any of these values as the initial conditions, then we should not get any change at all from the ODE integrator.

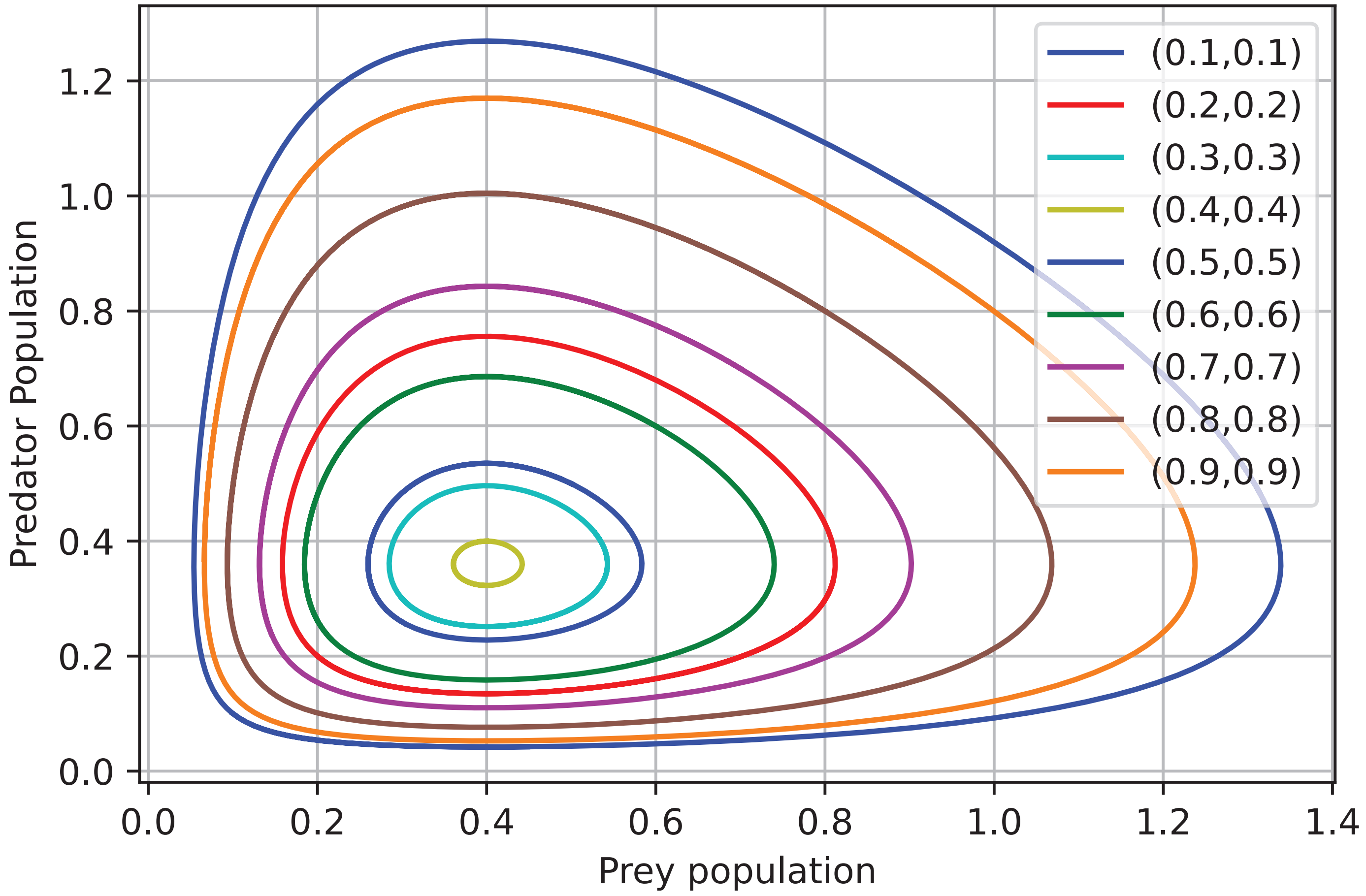
Equilibrium constant populations cont'd



$$\alpha = 0.180,\ \beta = 0.50,\ \gamma = 0.20,\ \delta = 0.50,\ (x_0, y_0) = (0.40, 0.36)$$

Equilibrium constant populations cont'd

Various initial conditions:



$$\alpha = 0.180,\ \beta = 0.50,\ \gamma = 0.20,\ \delta = 0.50$$

Equilibrium constant populations cont'd

For the parameter values that we explore here, integrating the Lotka-Volterra equations yield stable periodic solutions – unless we start off with the initial conditions that are exactly the fixed equilibrium populations.

- The constant equilibrium populations are still valid solutions, but are just not found by the numerical integrator
- In fact, the actual variations ("trajectories") of the populations in time depend on the initial conditions

Logistic Lotka-Volterra

Logistic Lotka-Volterra

In our earlier encounter with population dynamics, we argued for a (prey) population growth that is limited by ecological resources, leading to the Logistic map

We now incorporate the Logistic term for the prey population:

$$\frac{\mathrm{d}x}{\mathrm{d}t} = \alpha x(1-x) - \beta xy$$

$$\frac{\mathrm{d}y}{\mathrm{d}t} = \delta xy - \gamma y$$

Note that the parameters α, β, γ, and δ here share the same interpretation as that of the original Lotka-Volterra equations, but their numerical values may be different

Constant coexistence populations $(x^\star, y^\star)$?

Will there be constant equilibrium populations?

Clearly, $x^\star$ and $y^\star$ must satisfy

$$\begin{aligned} x^\star(\alpha(1-x^\star) - \beta y^\star) &= 0 \\ y^\star(\delta x^\star - \gamma) &= 0 \end{aligned}$$

which allow for

$$(x^\star, y^\star) = (0,0) \quad \text{or} \quad \left(\frac{\gamma}{\delta}, \frac{\alpha}{\beta}\left(1 - \frac{\gamma}{\delta}\right)\right)$$

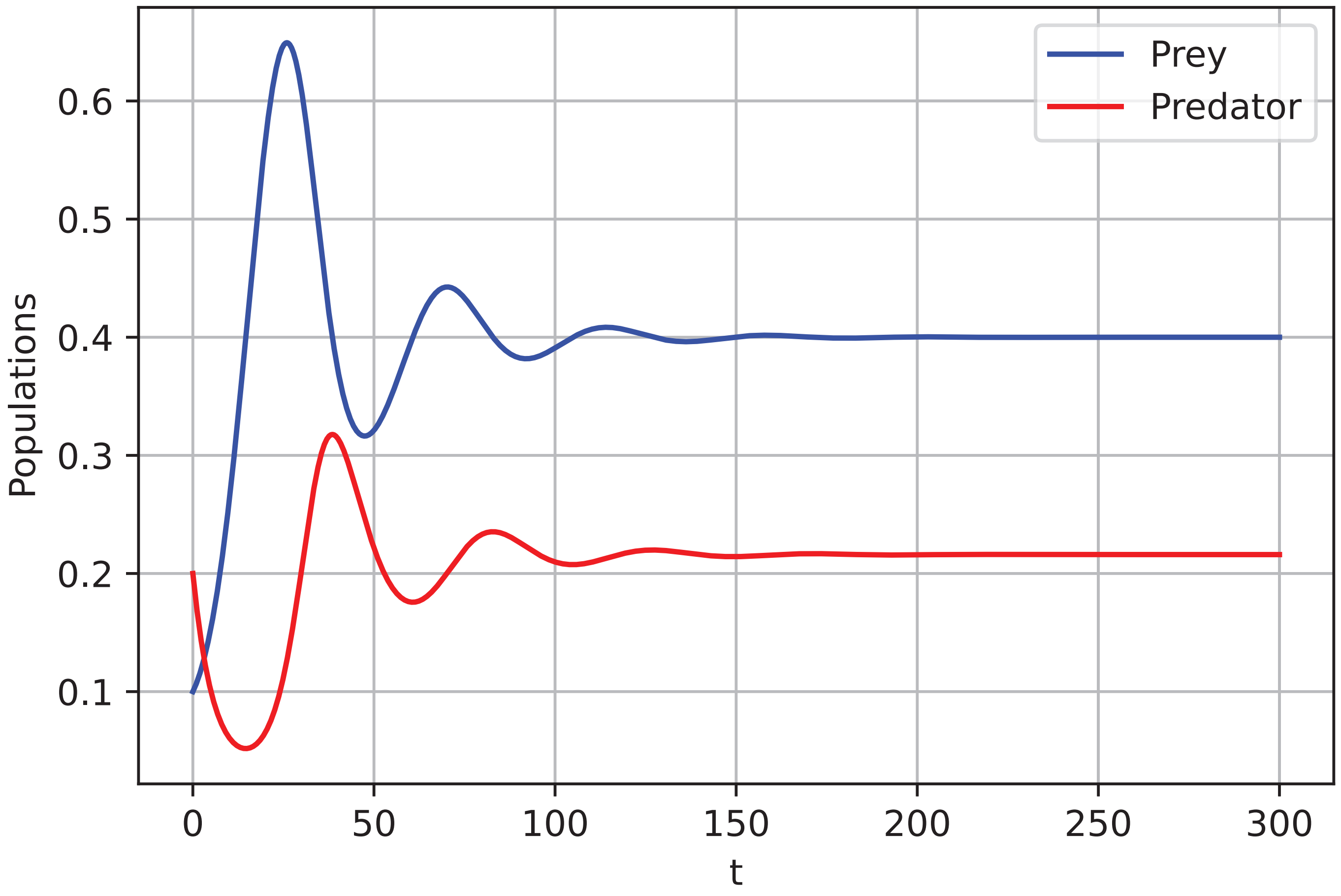
Some values of the coexistence populations

Let us explore whether we get coexistence populations for some selected parameter values:

$(\alpha, \beta, \gamma, \delta)$	α/β	γ/δ	$(\alpha/\beta)(1-\gamma/\delta)$
(0.18, 0.50, 0.20, 0.50)	0.36	0.40	0.22
(0.20, 0.40, 0.20, 0.40)	0.50	0.50	0.25
(0.25, 0.50, 0.20, 0.50)	0.50	0.40	0.30

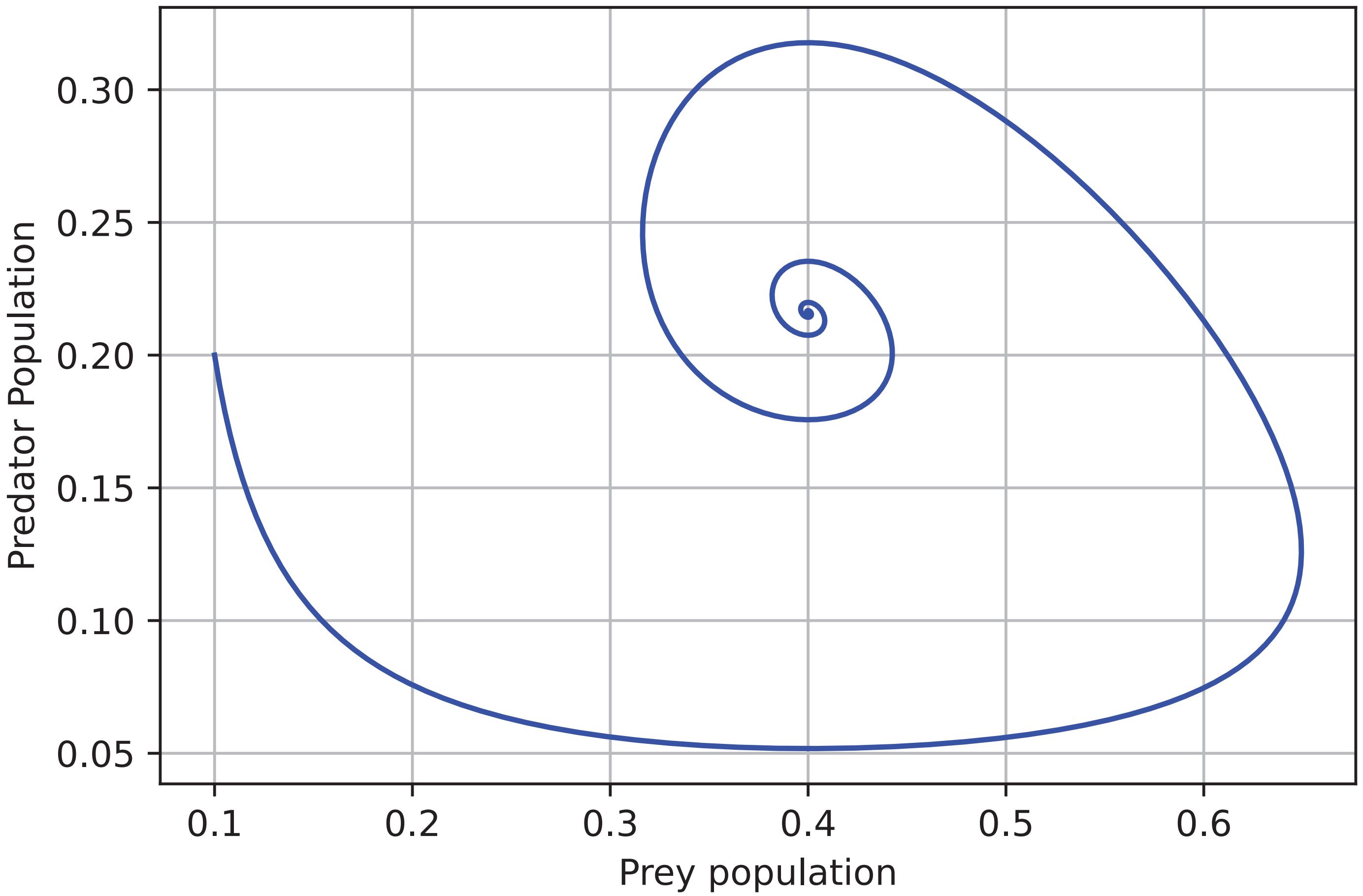
The following plots, especially the predator-prey plots, show that the system evolves towards the fixed points (0.40, 0.22), (0.50, 0.25) and (0.40, 0.30) respectively

Some plots



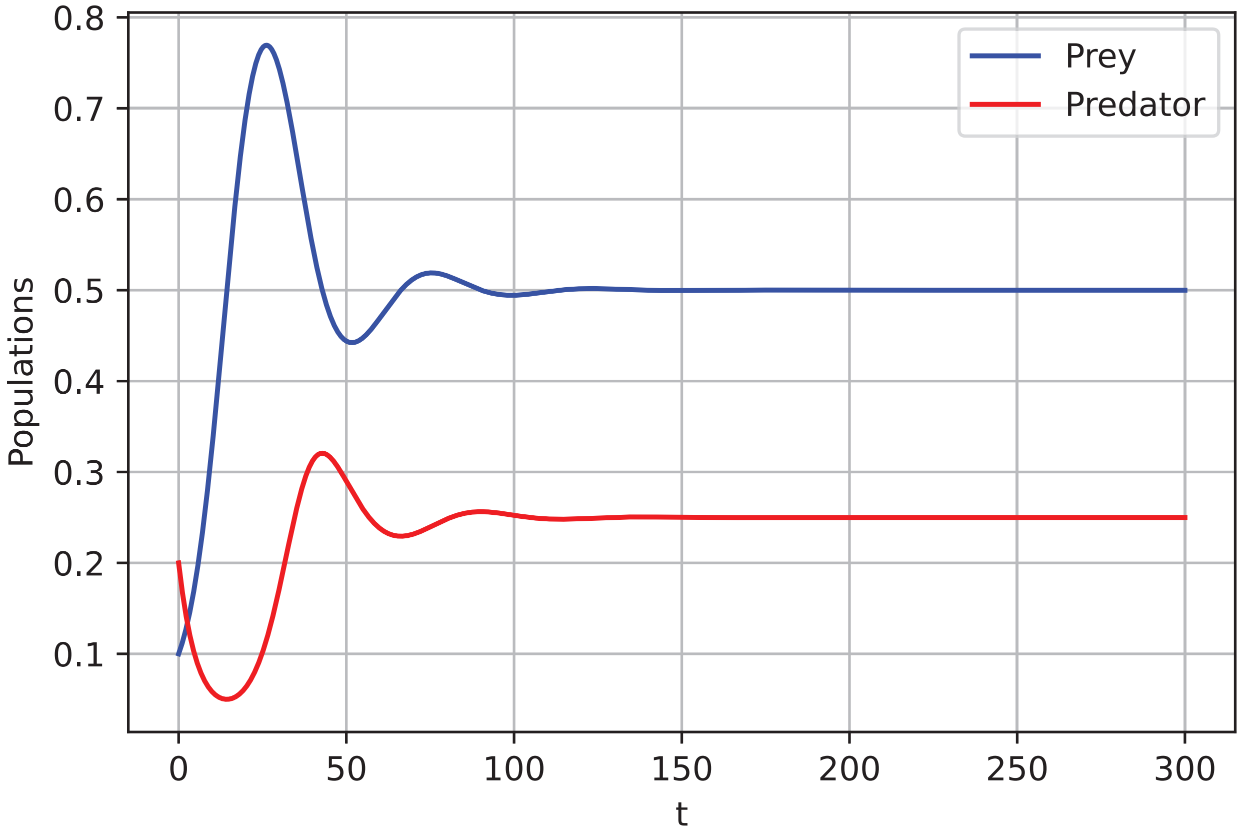
$$\alpha = 0.180,\ \beta = 0.50,\ \gamma = 0.20,\ \delta = 0.50,\ (x_0, y_0) = (0.10, 0.20)$$

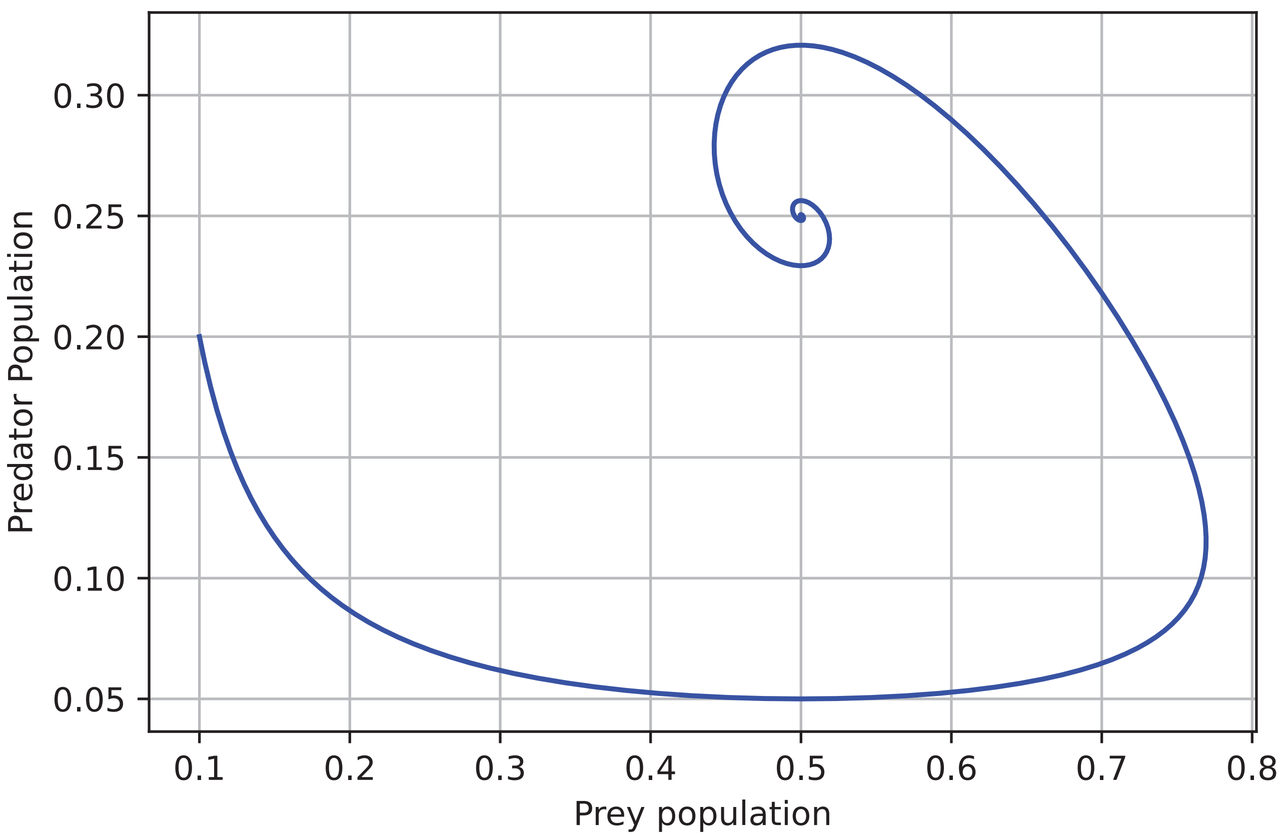
Some plots



$$\alpha = 0.180,\ \beta = 0.50,\ \gamma = 0.20,\ \delta = 0.50,\ (x_0, y_0) = (0.10, 0.20)$$

Some plots: $\alpha = 0.20$, $\beta = 0.40$, $\gamma = 0.20$, $\delta = 0.40$, $(x_0, y_0) = (0.10, 0.20)$





What's the difference?

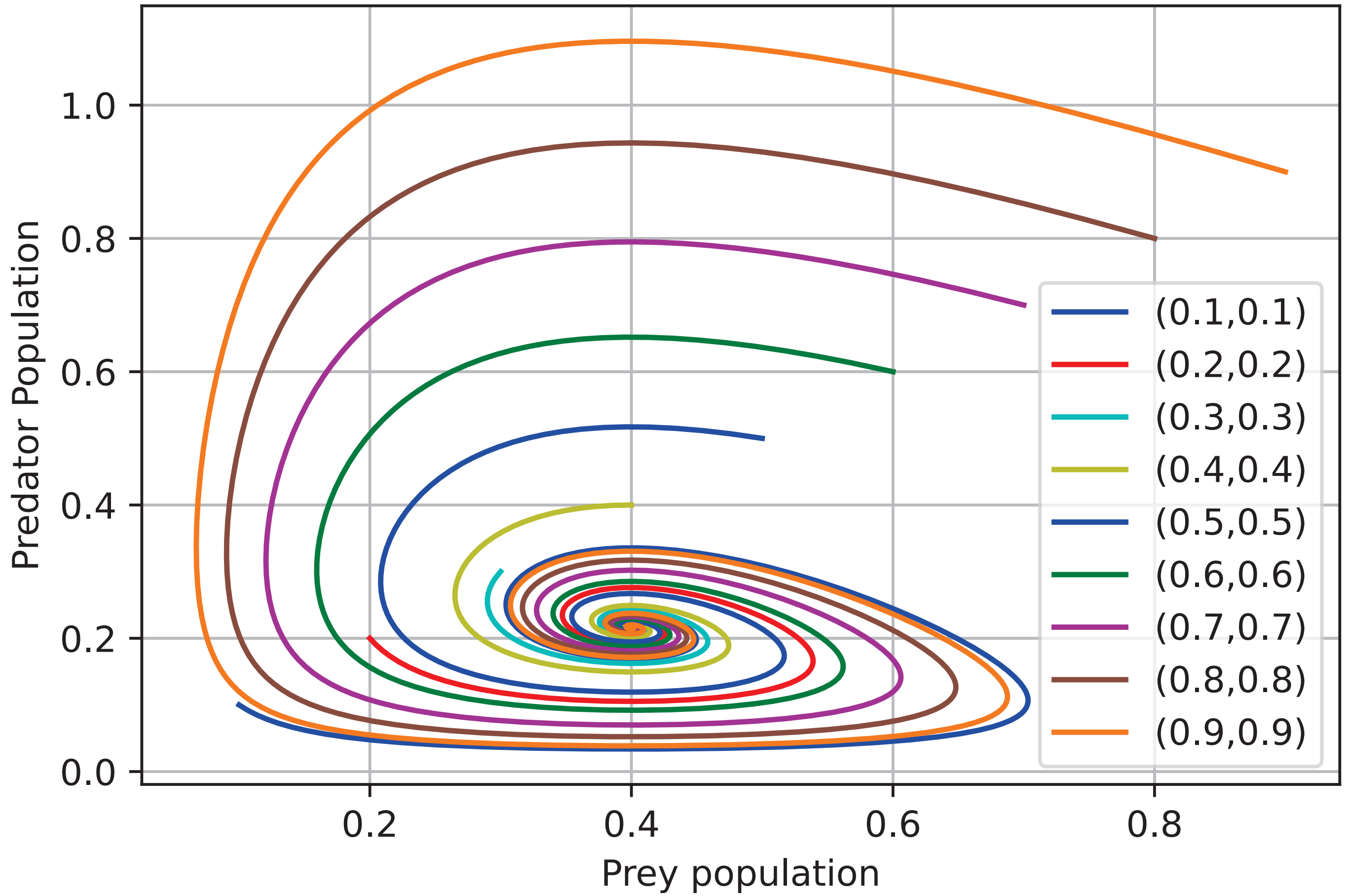
Unlike the original Lotka-Volterra equations, the system with the Logistic term seems to prefer settling onto the constant coexistence populations.

This is evident from the computational plots. For the values of the parameters that we explored, the constant coexistence populations are stable configurations, and they are reached regardless of the starting populations.

This convergence is illustrated in the following plots.

Convergence to constant populations

Various initial conditions:



$$\alpha = 0.180, \ \beta = 0.50, \ \gamma = 0.20, \ \delta = 0.50$$