Lotka Volterra Model for Prey - Predator dynamics

Abstract

As the world population exceeds the seven billion mark, the question, " How many people can earth support and under what conditions ?" becomes at least as pressing as it was when Malthus (1798) posed it at the end of the eighteenth century in ' An Essay on the Principle of Population '. The ability to support growing populations within existing economic systems and environments has been one of the main concerns of societies throughout history.

Historically, the solutions to the question of overpopulation have had their basis in two underlying assumptions : first, that under constant positive per capita rates of population growth a population increases exponentially, that is, population " explosion" is observed; second, that resource limitations necessarily limit or control the magnitude of such an explosion. One of the simplified models for answering these questions based on the above assumptions can be given by the Predator - Prey models.

Predator - Prey models are arguably the building blocks of the bio and ecosystems as biomasses are grown out of their resources masses. Species compete, evolve and disperse simply for the purpose of seeking resources to sustain their struggle for their very existence. Now, depending on the specific settings of the application, these models can take the form of resource-consumer, plant-herbivore, parasite-host, tumor cells - immune system, etc. They deal with the general loss-win interactions and hence may have applications outside the ecosystem.

In 1926, the famous Italian mathematician Vito Volterra proposed a differential equation model to explain the observed increase in predator fish (and corresponding decrease in prey fish) in the Adriatic Sea during the Ist World War. These equations were also derived independently by the US mathematician Alfred Lotka (1925) to describe the hypothetical chemical reaction in which the chemical concentrations oscillate. Hence they are also called as the Lotka-Volterra Model.

Using this we try to solve the problem that is it possible to use a small number of predators to control a prey population so that the prey population remains approximately constant. We will try to solve the problem analytically as well as numerically.

Lotka- Volterra Model

Let,

$p(t)$ = prey density,
$$(1)$$
$P(t)$ = predator density

In the absence of interactions between the species, we assume that the prey population p breeds at a per-capita rate of a, which would lead to exponential growth.

i.e. $$\frac{dp}{dt} = ap \implies p(t) = p(0)\, e^{at} \qquad (2)$$

Yet exponential growth does not occur because the predators P eat more prey as the prey numbers increase. The interaction rate between predator and prey requires both to be present, with the simplest assumption being that it is proportional to their joint probability:

Interaction rate $= bpP$.

This leads to a prey growth rate including both predation and breeding

$$\boxed{\frac{dp}{dt} = ap - bpP} \qquad (3)$$

(LVM-I for prey)

If left to themselves, predators P will also breed and increase their population. Yet predators need animals to eat, and if there are no other populations to prey upon, they will eat each other (or their young) at a per-capita mortality rate m:

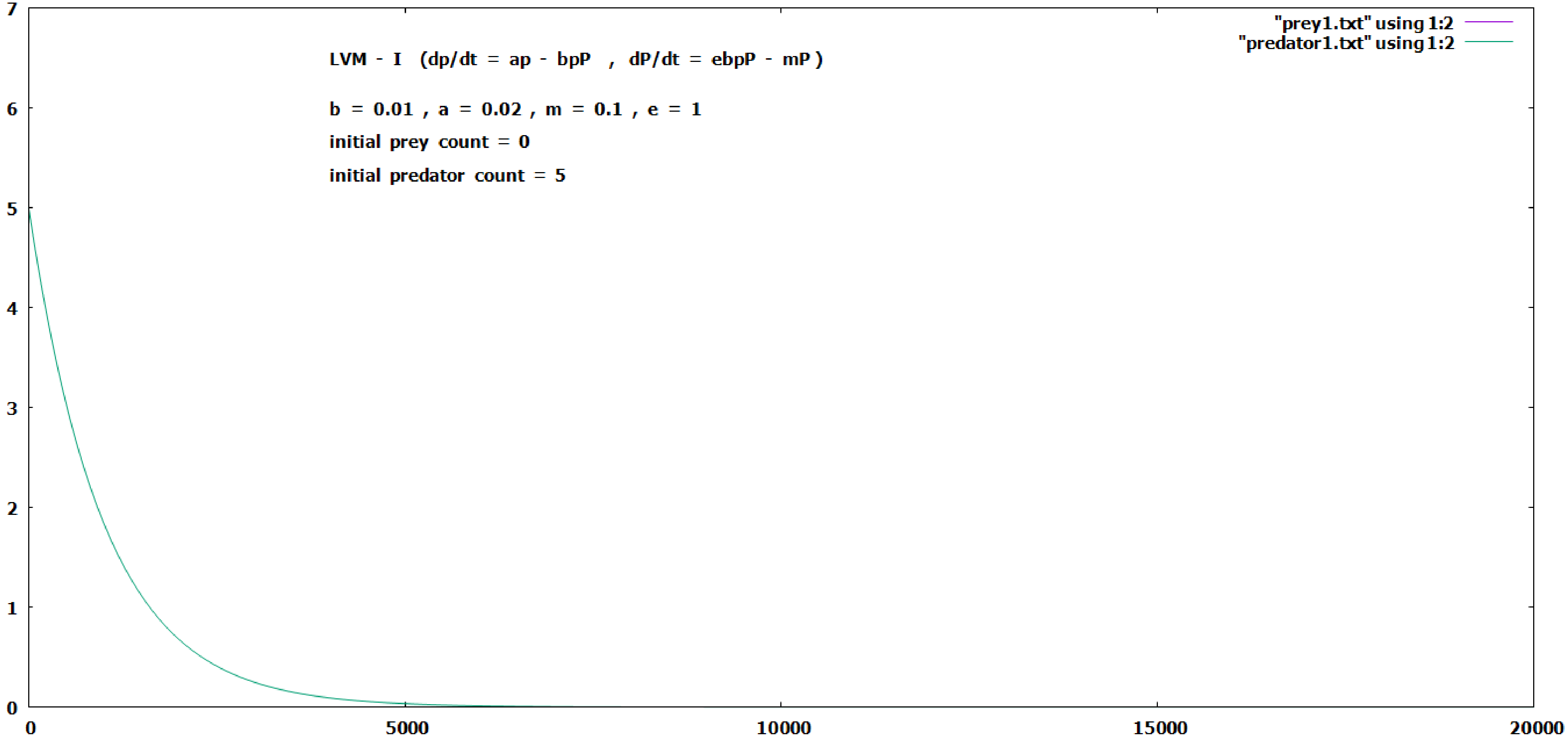
i.e. $$\left.\frac{dP}{dt}\right|_{\text{competition}} = -mP \Rightarrow P(t) = P(0)\,e^{-mt} \qquad (4)$$

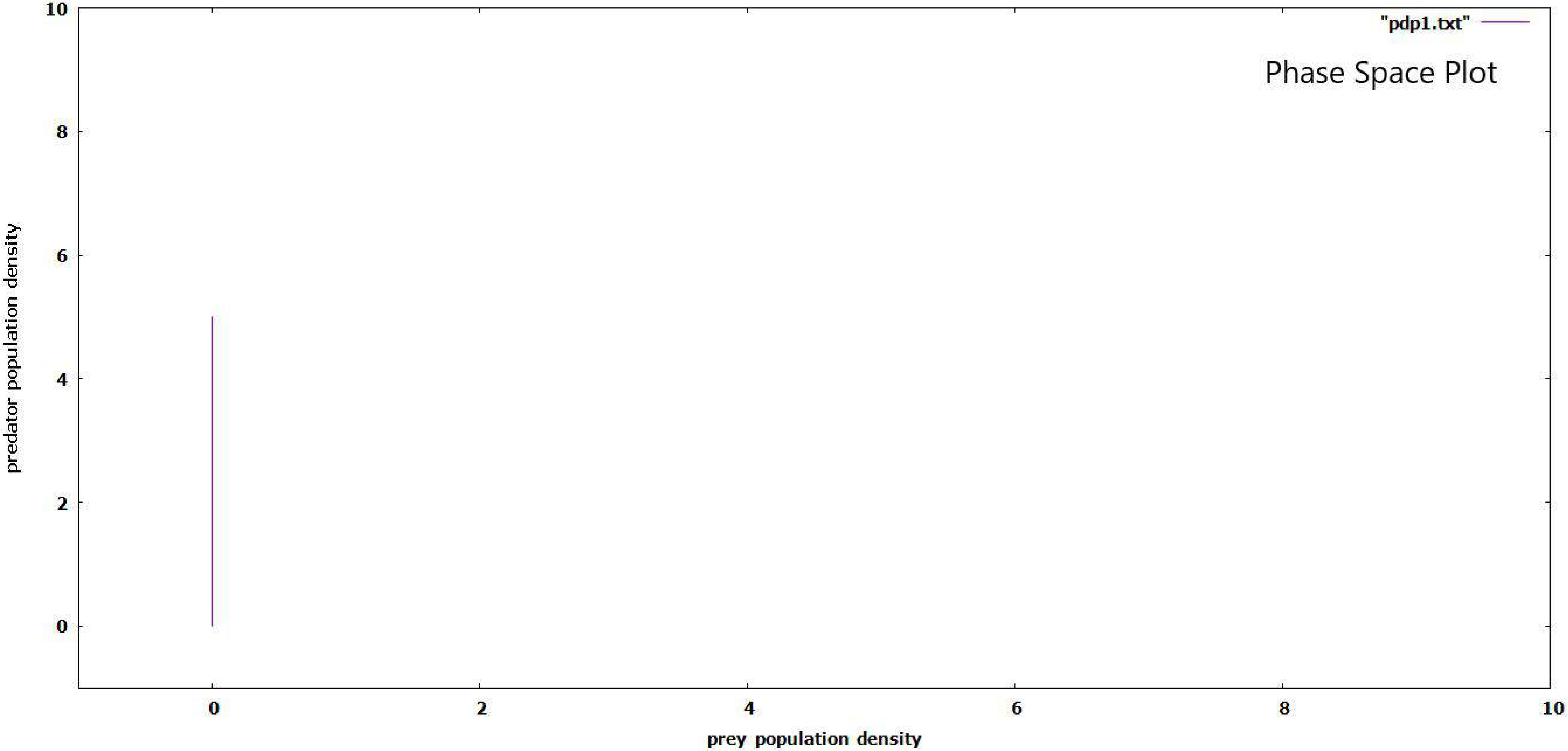
However, once there are prey to interact with ('eat') at the rate bpP, the predator population will grow at the rate.

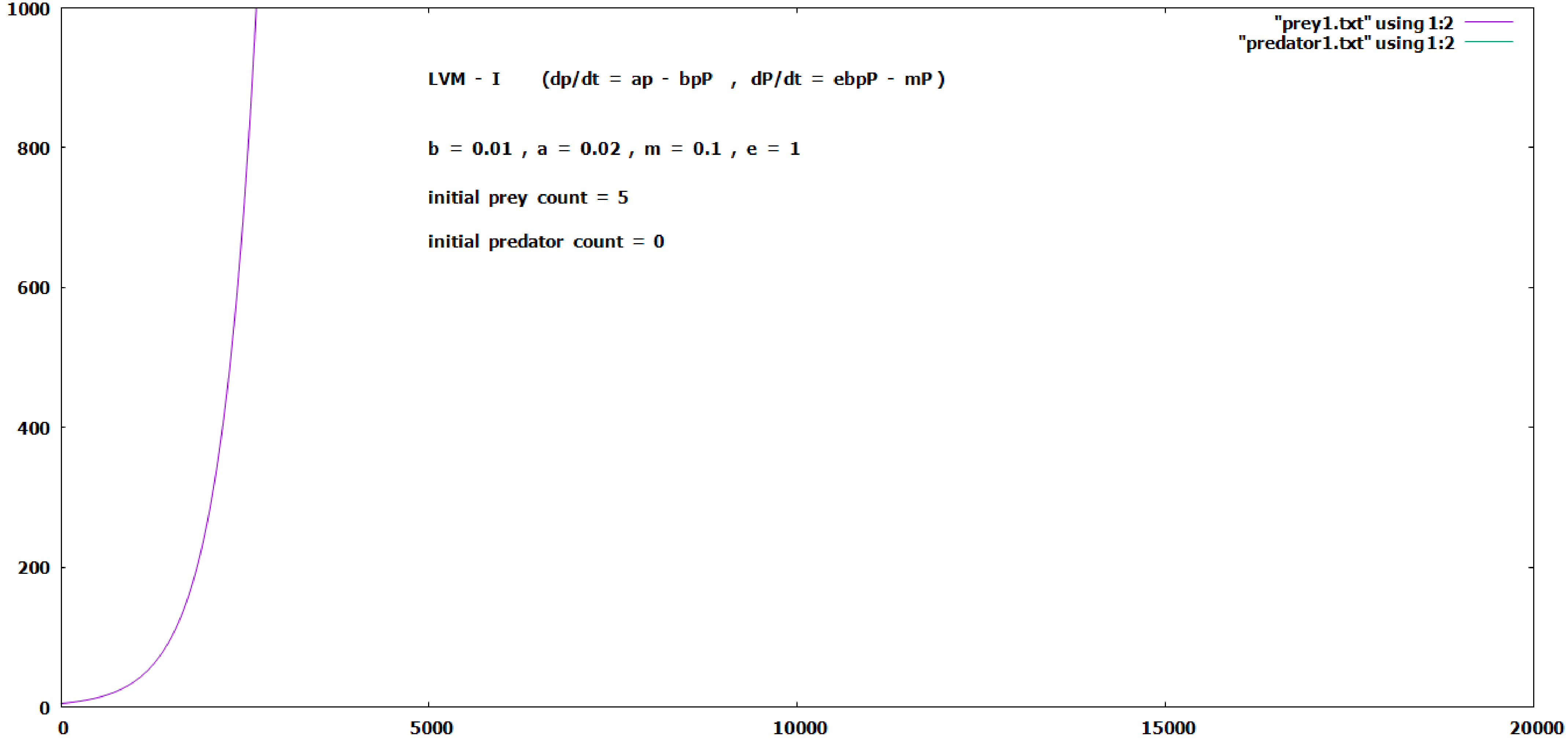
$$\boxed{\frac{dP}{dt} = \varepsilon bpP - mP} \qquad (5)$$

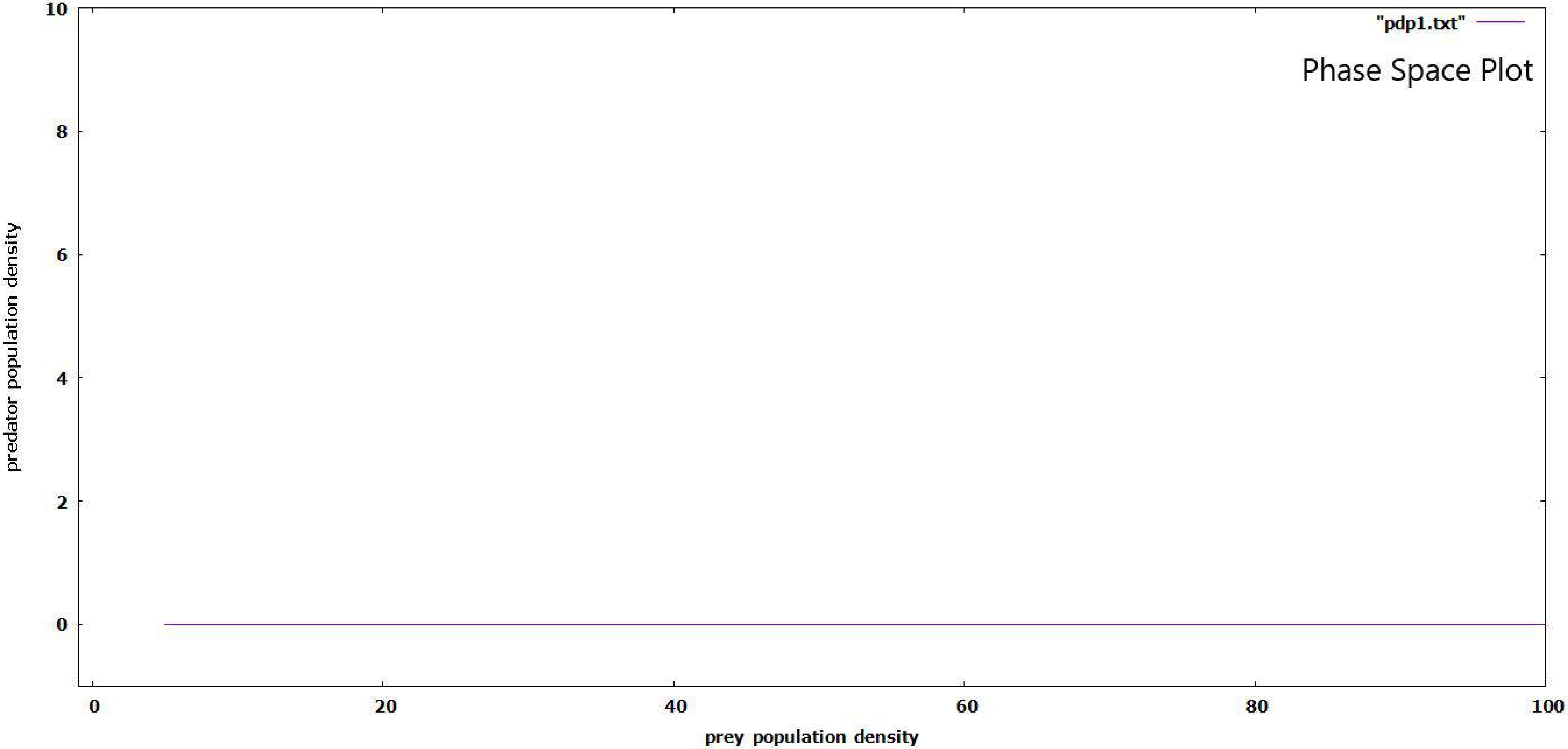
(LVM-I for predators)

where ε is a constant that measures the efficiency with which predators convert prey interaction into food.

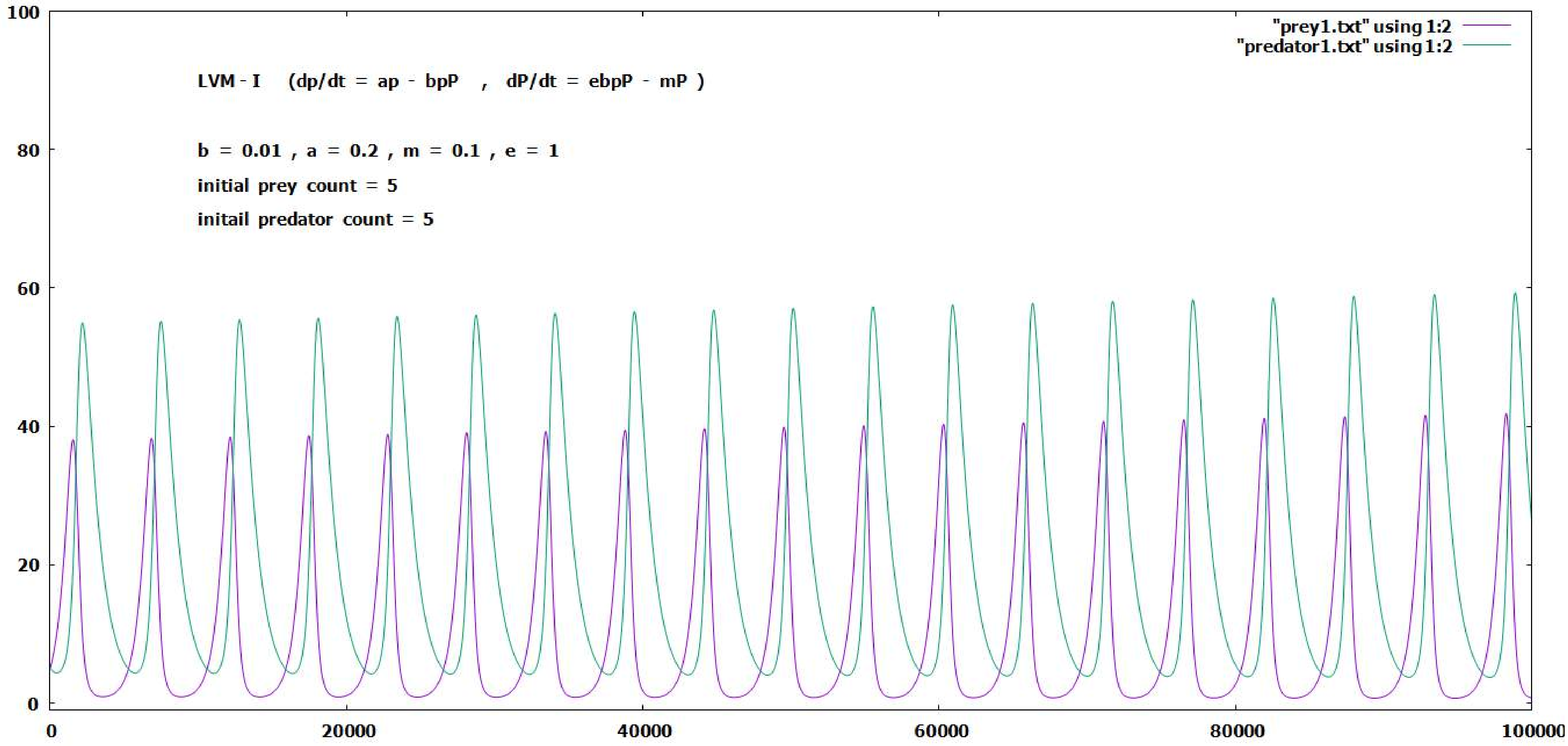

"prey1.txt" using 1:2
"predator1.txt" using 1:2
LVM - I (dp/dt = ap - bpP , dP/dt = ebpP - mP)
b = 0.01 , a = 0.02 , m = 0.1 , e = 1
initial prey count = 0
initial predator count = 5
0
1
2
3
4
5
6
7
0
5000
10000
15000
20000

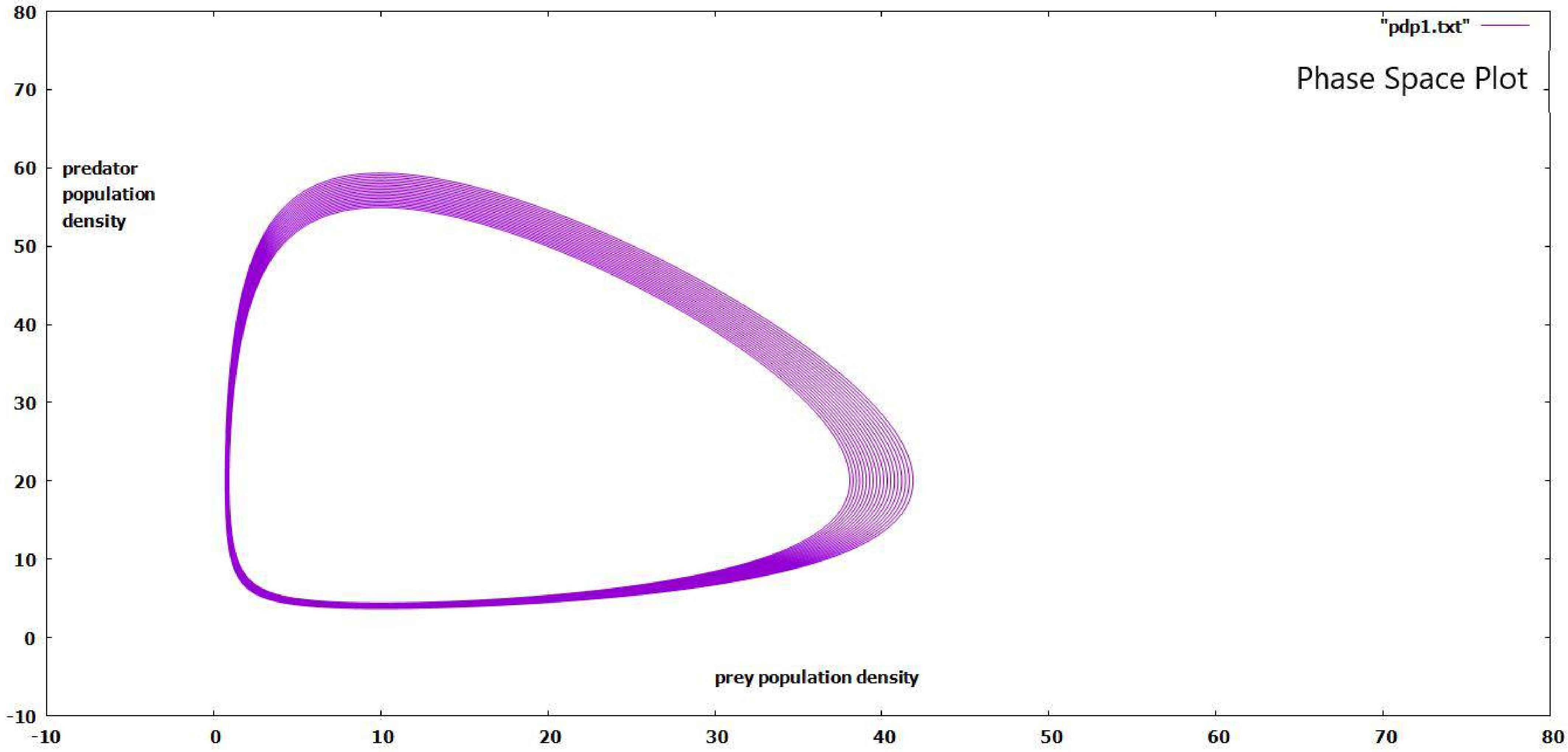

"pdp1.txt"
Phase Space Plot
predator population density
prey population density
0
2
4
6
8
10


"prey1.txt" using 1:2
"predator1.txt" using 1:2
LVM - I (dp/dt = ap - bpP , dP/dt = ebpP - mP)
b = 0.01 , a = 0.02 , m = 0.1 , e = 1
initial prey count = 5
initial predator count = 0
1000
800
600
400
200
0
0
5000
10000
15000
20000



"pdp1.txt"
Phase Space Plot
predator population density
prey population density
10
8
6
4
2
0
0
20
40
60
80
100


"prey1.txt" using 1:2
"predator1.txt" using 1:2
LVM - I (dp/dt = ap - bpP , dP/dt = ebpP - mP)
b = 0.01 , a = 0.2 , m = 0.1 , e = 1
initial prey count = 5
initail predator count = 5
100
80
60
40
20
0
0
20000
40000
60000
80000
100000


"pdp1.txt"
Phase Space Plot
predator population density
prey population density
80
70
60
50
40
30
20
10
0
-10
-10
0
10
20
30
40
50
60
70
80

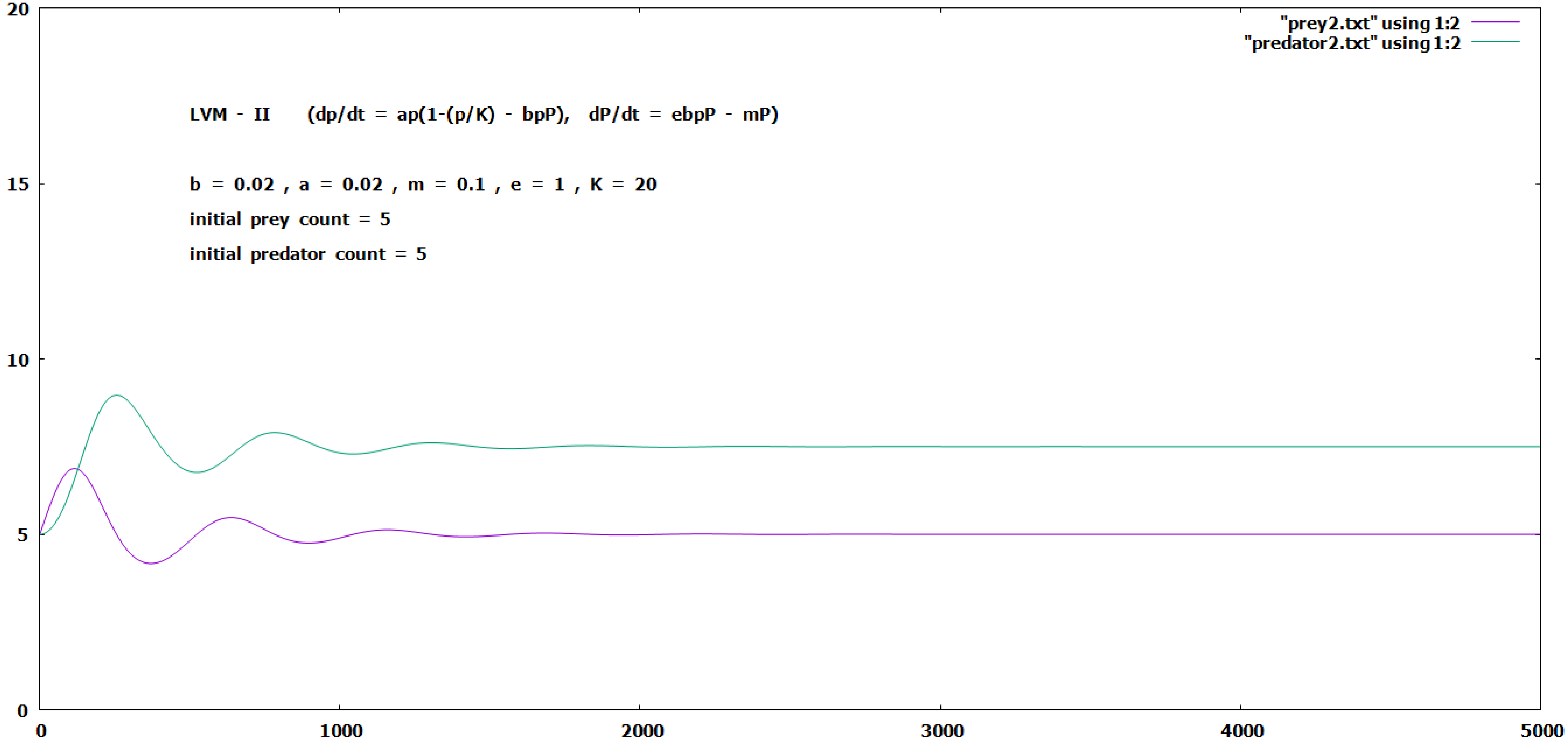
Including Prey Limit

The initial assumption in the LVM that prey grows without limit in the absence of predators in clearly unrealistic. Hence, we include a limit on prey numbers that accounts for depletion of the food supply as the prey population grows. Accordingly, we modify the constant growth rate i.e. $a \to a(1 - p/K)$ so that growth vanishes when the population reaches a limit K, i.e. the carrying capacity.

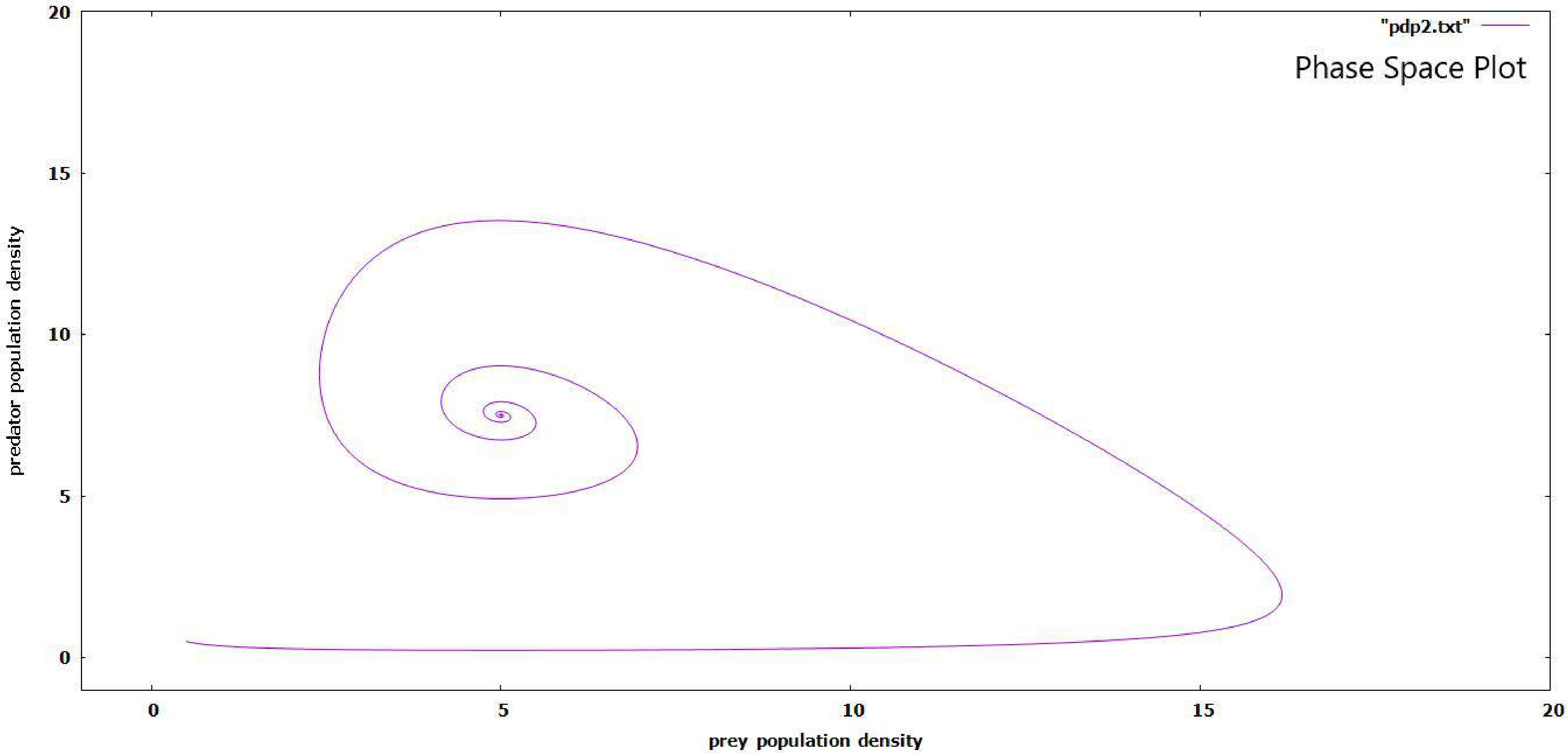
$$\therefore \quad \boxed{\frac{dp}{dt} = ap\left(1 - \frac{p}{K}\right) - bpP} \qquad (6)$$

$$\boxed{\frac{dP}{dt} = \varepsilon bpP - mP}$$

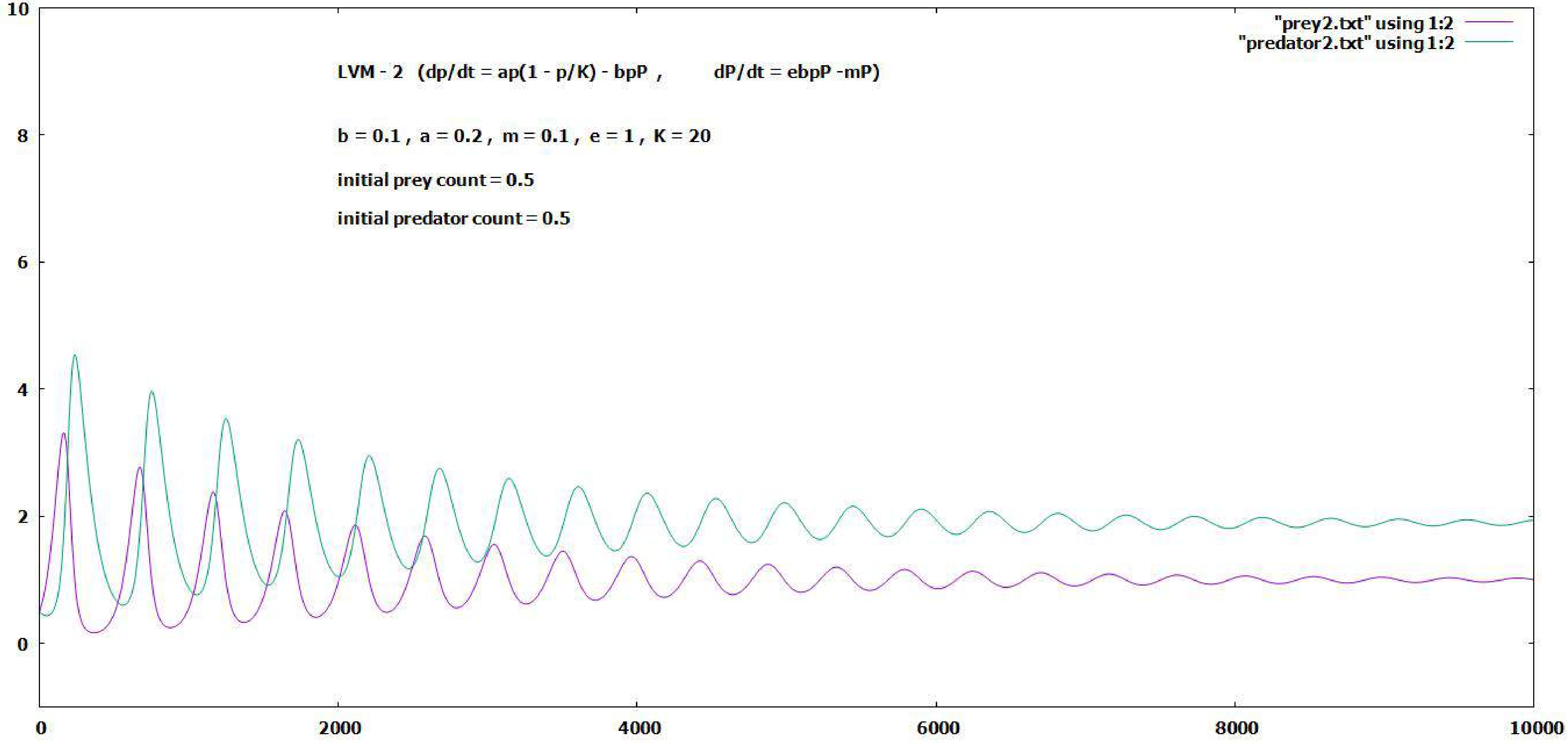
(LVM – II)

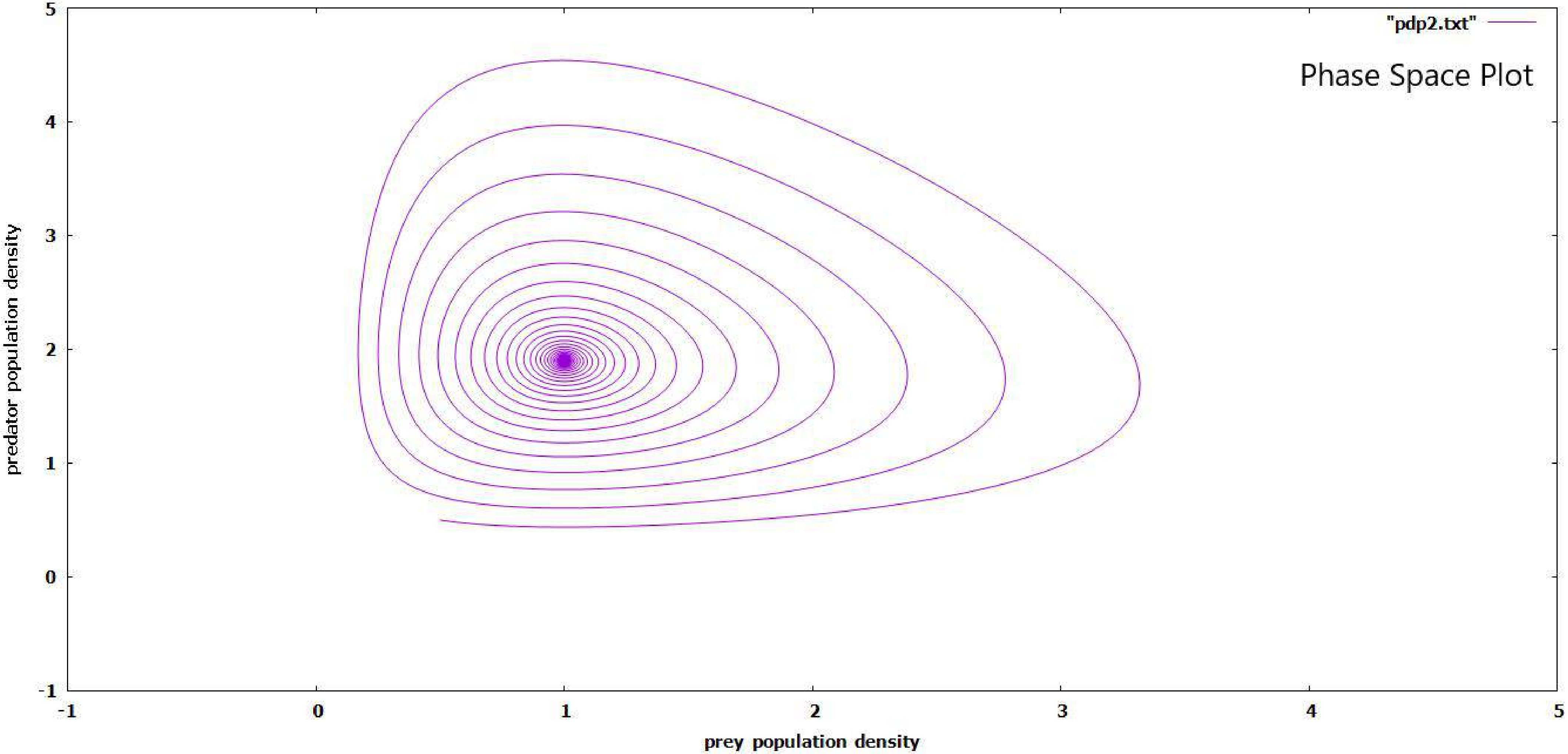


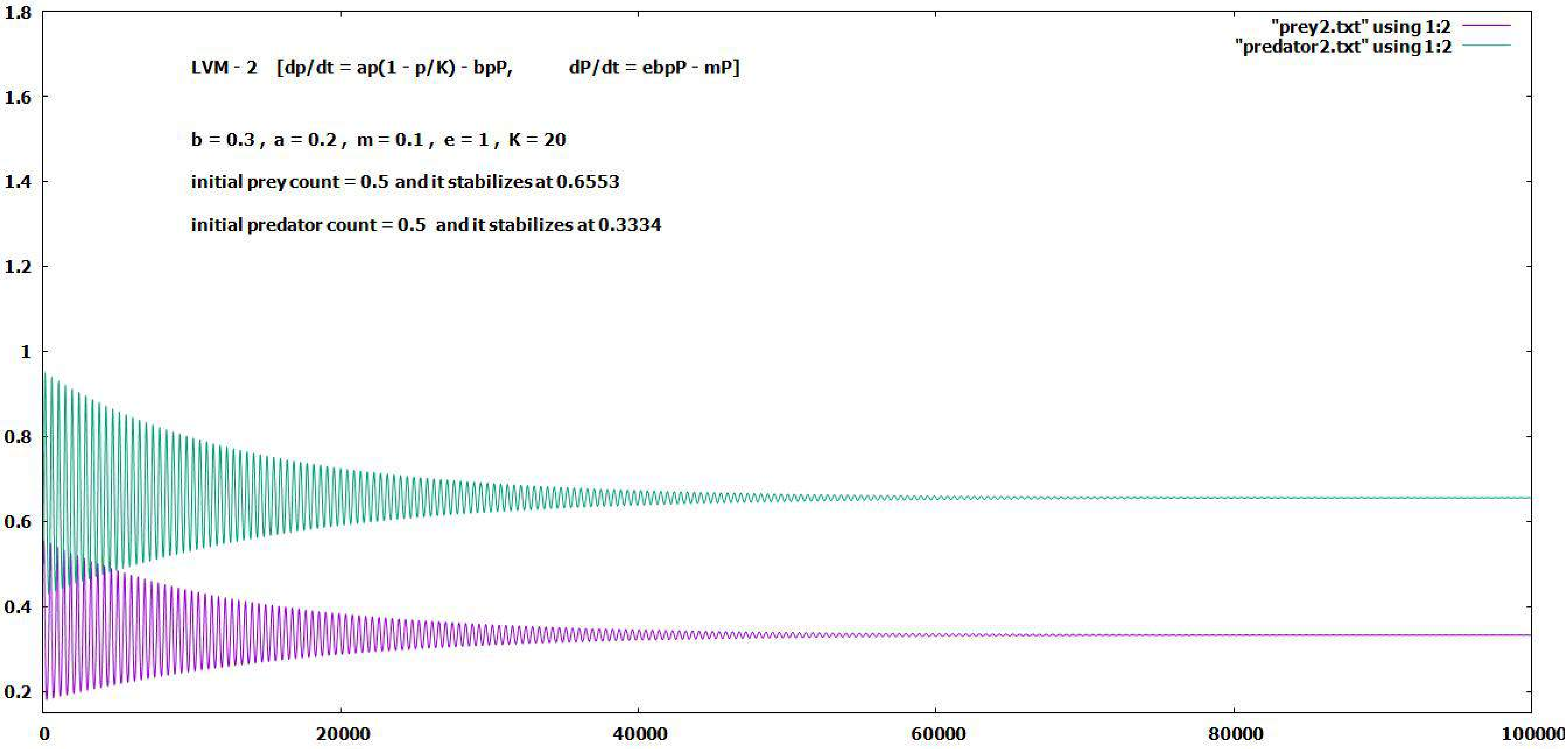
"prey2.txt" using 1:2
"predator2.txt" using 1:2
LVM - II (dp/dt = ap(1-(p/K) - bpP), dP/dt = ebpP - mP)
b = 0.02 , a = 0.02 , m = 0.1 , e = 1 , K = 20
initial prey count = 5
initial predator count = 5
0
5
10
15
20
0
1000
2000
3000
4000
5000



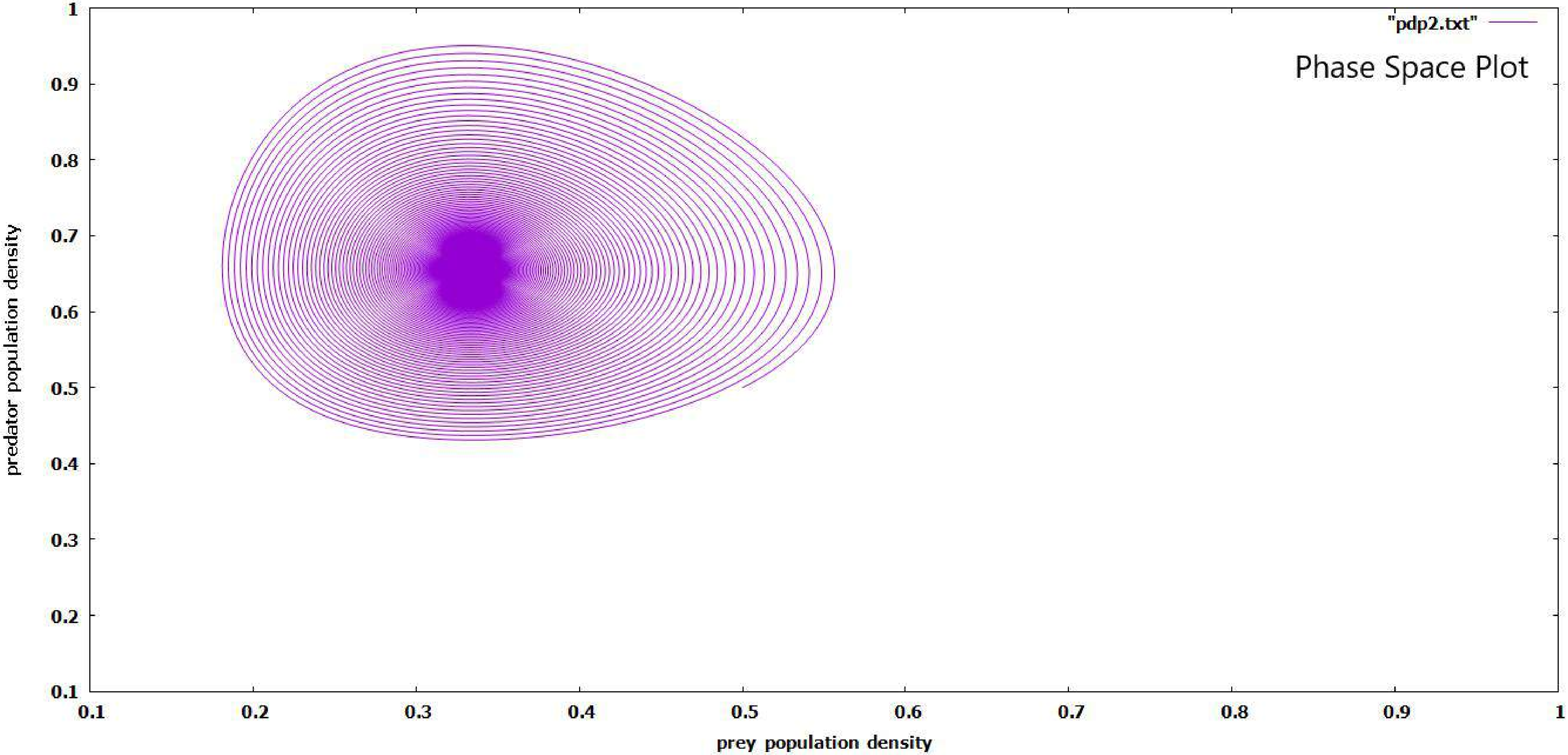
"pdp2.txt"
Phase Space Plot
predator population density
prey population density
0
5
10
15
20


"prey2.txt" using 1:2
"predator2.txt" using 1:2
LVM - 2 (dp/dt = ap(1 - p/K) - bpP , dP/dt = ebpP -mP)
b = 0.1 , a = 0.2 , m = 0.1 , e = 1 , K = 20
initial prey count = 0.5
initial predator count = 0.5
10
8
6
4
2
0
0
2000
4000
6000
8000
10000


"pdp2.txt"
Phase Space Plot
predator population density
prey population density
5
4
3
2
1
0
-1
-1
0
1
2
3
4
5



"prey2.txt" using 1:2
"predator2.txt" using 1:2
LVM - 2 [dp/dt = ap(1 - p/K) - bpP, dP/dt = ebpP - mP]
b = 0.3 , a = 0.2 , m = 0.1 , e = 1 , K = 20
initial prey count = 0.5 and it stabilizes at 0.6553
initial predator count = 0.5 and it stabilizes at 0.3334
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
20000
40000
60000
80000
100000



"pdp2.txt"
Phase Space Plot
predator population density
prey population density
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1

With Predation Efficiency

An additional unrealistic assumption in the original LVM is that the predators immediately eat all the prey with which they interact. As anyone who has watched a cat hunt a mouse knows, predators spend time finding prey and also chasing, killing, eating, and digesting it (all together called handling). This extra time decreases the rate bpP at which prey are eliminated. We define the functional response p_a as the probability of one predator finding one prey. If a single predator spends time t_{search} searching for prey, then.

$$p_a = bt_{search}\,p \implies t_{search} = \frac{p_a}{bp} \qquad (7)$$

If we take t_h 'the time a predator spends handling a single prey', then the effective time a predator spends handling a prey is $p_a t_h$. Such being the case, the total time T that a predator spends finding and handling a single prey is

$$T = t_{search} + t_{handling}$$

$$T = \frac{p_a}{bp} + p_a t_h$$

i.e.

i.e. $\frac{p_a}{T} = \frac{bp}{1+bpt_h}$

where p_a/T is the effective rate of eating prey. We see that as the number of prey $p \to \infty$, the efficiency in eating them $\to 1$. We include the efficiency in (6) by modifying the rate b at which a predator eliminates prey to $b/(1+bpt_h)$

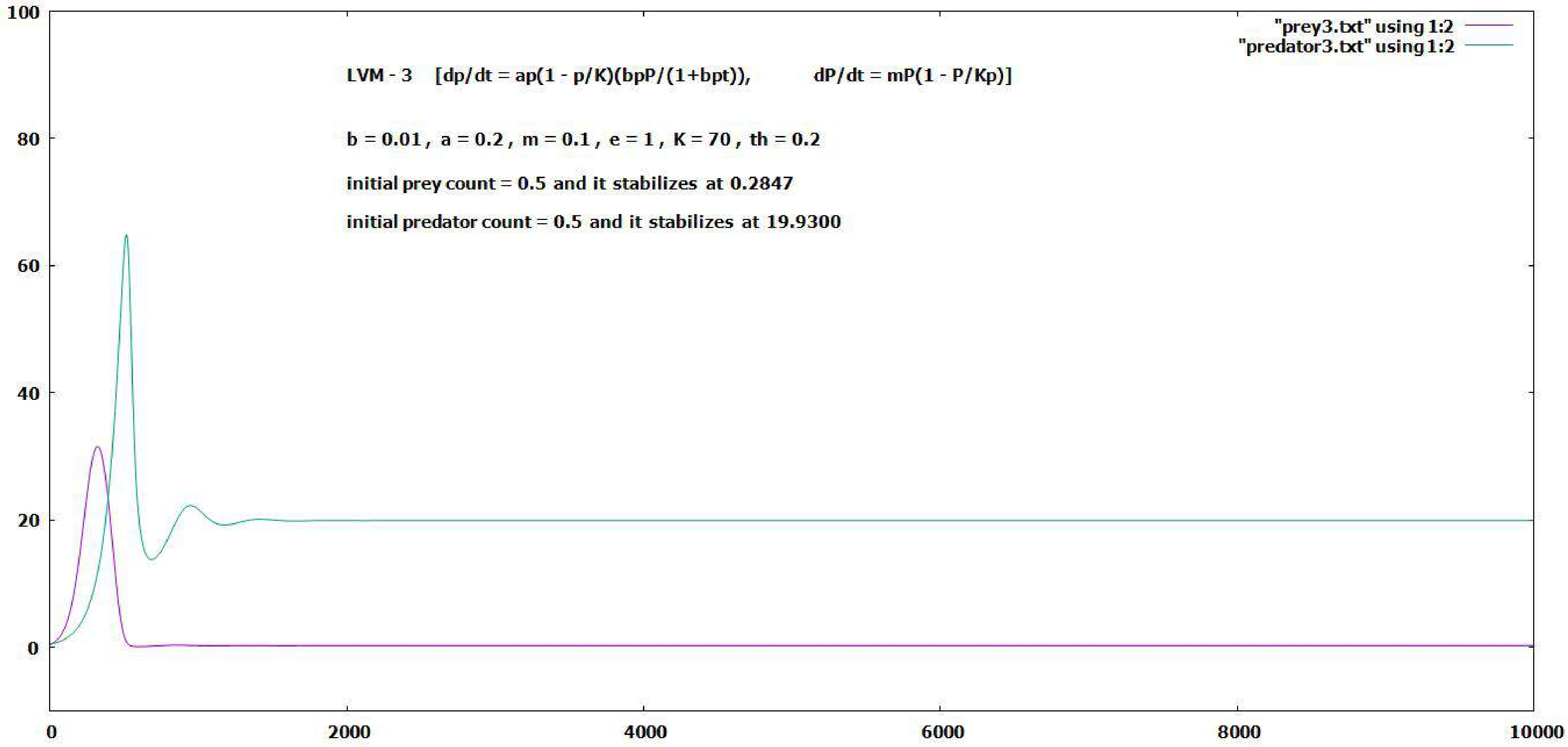
$$\boxed{\frac{dp}{dt} = ap\left(1-\frac{p}{K}\right) - \frac{bpP}{1+bpt_h}} \qquad (8)$$

(LVM - III for prey)

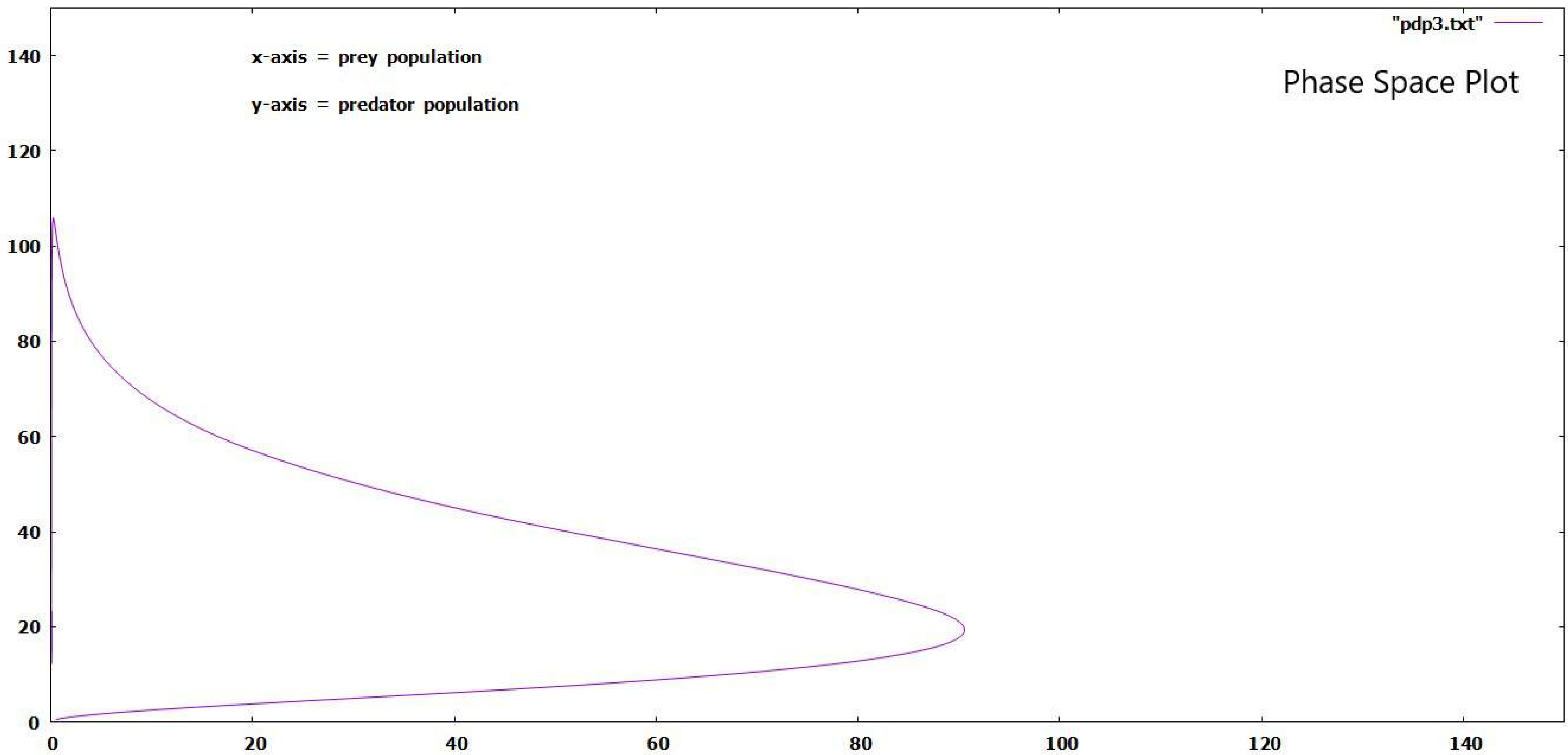
To be more realistic about the predator growth, we also place a limit on the predator carrying capacity but make it proportional to the number of prey:

$$\boxed{\frac{dP}{dt} = mP\left(1-\frac{P}{kp}\right)} \qquad (9)$$

(LVM - III for predator)



"prey3.txt" using 1:2
"predator3.txt" using 1:2
LVM - 3 [dp/dt = ap(1 - p/K)(bpP/(1+bpt)), dP/dt = mP(1 - P/Kp)]
b = 0.01 , a = 0.2 , m = 0.1 , e = 1 , K = 70 , th = 0.2
initial prey count = 0.5 and it stabilizes at 0.2847
initial predator count = 0.5 and it stabilizes at 19.9300
100
80
60
40
20
0
0
2000
4000
6000
8000
10000


"pdp3.txt"
x-axis = prey population
y-axis = predator population
Phase Space Plot
140
120
100
80
60
40
20
0
0
20
40
60
80
100
120
140

Analytical Method

We try to find whether the models that we have considered have a steady state solution or not analytically. And further we will check the stability of those fixed points.

Model - I

$$f(x,y) = \frac{dx}{dt} = ax - bxy \quad \text{—— (1)}$$

$$g(x,y) = \frac{dy}{dt} = ebxy - my \quad \text{—— (2)}$$

where x = prey population density

y = predator population density.

Let x_{ss} and y_{ss} be the steady state solutions of the above equations. Consider a point x very close to x_{ss}, such that

$$x - x_{ss} = \delta x$$

Similarly $y - y_{ss} = \delta y$

Now, lets check the stability of the solutions due to this disturbance.

To see if the disturbance grows or decays, we need to derive a differential equation for δx.

$$\therefore \frac{d}{dt}(\delta x) = \frac{d}{dt}(x - x_{ss})$$

$$= \dot{x} \qquad \left\{ \frac{dx_{ss}}{dt} = 0 \right\}$$

$$= f(x_{ss} + \delta x, \; y_{ss} + \delta y)$$

Now using Taylor series expansion

$$= f(x_{ss}, y_{ss}) + \left(\frac{\partial f}{\partial x}\right)(\delta x) + \frac{\partial f}{\partial y}(\delta y)$$

$$+ \frac{\partial^2 f}{\partial x^2}\frac{\delta x^2}{2!} + \frac{\partial^2 f}{\partial y^2}\frac{\delta y^2}{2!} + \cdots$$

$$= f(x_{ss}, y_{ss}) + \frac{\partial f}{\partial x}(\delta x) + \frac{\partial f}{\partial y}(\delta y) + O(\cancel{\delta x^2, \delta y^2}\, \delta x)$$

$$+ O(\delta x^2, \delta y^2, \delta x\, \delta y)$$

where $O(\delta x^2, \delta y^2, \delta x\, \delta y)$ is the group of all the higher order terms and combination (quadratic) terms of δx & δy.

Now, since we chose the disturbance $(\delta x, \delta y)$ to be very small, these higher order terms and quadratic terms can be neglected, as they will come out to be extremely small.

Thus we get

$$\frac{d}{dt}(\delta x) = \left(\frac{\partial f}{\partial x}\right)(\delta x) + \left(\frac{\partial f}{\partial y}\right)(\delta y) \qquad \{f(x_{ss}, y_{ss}) = 0\}$$

Similarly for the predator equation, we get

$$\frac{d}{dt}(\delta y) = \left(\frac{\partial g}{\partial x}\right)(\delta x) + \left(\frac{\partial g}{\partial y}\right)(\delta y).$$

These two equations can be represented in an easier way

$$\frac{d}{dt}\begin{bmatrix} \delta x \\ \delta y \end{bmatrix} = \begin{bmatrix} f_x' & f_y' \\ g_x' & g_y' \end{bmatrix} \begin{bmatrix} \delta x \\ \delta y \end{bmatrix}$$

where $f_x' = \frac{\partial f}{\partial x}$ and so on.

$$\therefore \quad \frac{d}{dt}\begin{bmatrix} \delta x \\ \delta y \end{bmatrix} = \begin{bmatrix} a - by & -bx \\ eby & ebx - m \end{bmatrix} \begin{bmatrix} \delta x \\ \delta y \end{bmatrix} \qquad (3)$$

[From (1) & (2)]

where $J = \begin{bmatrix} a - by & -bx \\ eby & ebx - m \end{bmatrix}$ is the Jacobian matrix for the fixed point (x_{ss}, y_{ss}).

Now for finding the steady state, we simply take

$$\frac{dx}{dt} = 0 \quad \& \quad \frac{dy}{dt} = 0$$

From (1) $\quad 0 = a\cancel{x} - b\cancel{x}y$

$$\boxed{\therefore \quad y_{ss} = a/b}$$

From (2) $\quad 0 = eb x\cancel{y} - m\cancel{y}$ $\quad \left\{ \text{For } x, y \neq 0 \right\}$

$$\boxed{\therefore \quad x_{ss} = m/be}$$

Using this in the Jacobian matrix,

$$J = \begin{bmatrix} 0 & -m/e \\ ae & 0 \end{bmatrix}$$

From (3), we get

$$\frac{d}{dt}(\delta x) = -m/e \, \delta y$$

$$\frac{d}{dt}(\delta y) = ae \, \delta x$$

Here solution of the second equation will diverge. Hence the steady state solutions that we have chosen are not stable.

Model – II

$$f(x,y) = \frac{dx}{dt} = ax\left(1 - \frac{x}{K}\right) - bxy \quad \text{—— (1)}$$

$$g(x,y) = \frac{dy}{dt} = ebxy - my \quad \text{—— (2)}$$

As we found earlier, the Jacobian of the matrix of steady state solution is

$$J = \begin{bmatrix} f_x' & f_y' \\ g_x' & g_y' \end{bmatrix}$$

$$J = \begin{bmatrix} a - 2ax/K - by & -bx \\ eby & ebx - m \end{bmatrix}$$

∴ We get

$$\frac{d}{dt}\begin{bmatrix} \delta x \\ \delta y \end{bmatrix} = \begin{bmatrix} a - 2ax/K - by & -bx \\ eby & ebx - m \end{bmatrix}\begin{bmatrix} \delta x \\ \delta y \end{bmatrix} \quad \text{—— (3)}$$

Now, for steady state solutions

$$\frac{dx}{dt} = 0 \quad \& \quad \frac{dy}{dt} = 0$$

$$0 = ax\left(1 - \frac{x}{K}\right) - bxy = 0$$

$$0 = ebxy - my = 0$$

$$x_{ss} = m/be$$

$$y_{ss} = \left[\frac{a}{b}\left(1 - \frac{m}{bek}\right)\right]$$

$$\therefore \quad J = \begin{bmatrix} a - \frac{2a}{k}\left(\frac{m}{be}\right) - \cancel{b}\left(\frac{a}{\cancel{b}}\right)\left[1 - \frac{m}{bek}\right] & -\cancel{b}\left(\frac{m}{\cancel{b}e}\right) \\ e\cancel{b}\left(\frac{a}{\cancel{b}}\right)\left(1 - \frac{m}{bek}\right) & \cancel{e}\cancel{b}\left(\frac{m}{\cancel{b}\cancel{e}}\right) - m \end{bmatrix}$$

$$= \begin{bmatrix} \cancel{a} - \frac{2am}{kbe} - \cancel{a} + \frac{am}{bek} & -\frac{m}{e} \\ ae - \frac{am}{bk} & 0 \end{bmatrix}$$

$$J = \begin{bmatrix} \frac{-am}{bek} & -\frac{m}{e} \\ ae - \frac{am}{bk} & 0 \end{bmatrix}$$

From (3)

$$\frac{d}{dt}\begin{bmatrix} \delta x \\ \delta y \end{bmatrix} = \begin{bmatrix} \frac{-am}{bek} & \frac{-m}{e} \\ a\left(e - \frac{m}{bk}\right) & 0 \end{bmatrix}\begin{bmatrix} \delta x \\ \delta y \end{bmatrix}$$

$$\frac{d}{dt}(\delta x) = \left(\frac{-am}{bek}\right)\delta x - \left(\frac{m}{e}\right)\delta y$$

$$\frac{d}{dt}(\delta y) = \left(ae - \frac{ma}{bk}\right)\delta x$$

The solution can be stable only if the coefficient of the second equation is negative.

i.e. $ae - \frac{ma}{bk} < 0$

i.e. $e < \frac{m}{bk}$

If this condition is satisfied, then the steady state solution will be stable.

Reference :

Books

(i) Mathematical Models in Population Biology and Epidemiology
— Fred Brauer & Carlos Castillo - Chavez

(ii) Non-linear Dynamics and Chaos
— Steven H. Strogatz

(iii) A Survey of Computational Physics
— Rubin H. Landau, Manuel José Paez & Christian C. Bordeianu.

(iv) Computer Oriented Numerical Methods
— V. Raja Raman

Conclusion

We see that for the first model, we do not obtain a steady state for which the solutions are stable. For a finite initial prey and predator population densities we get an oscillating values for their population number for any values of the variables present. This is also matched by the result found analytically as well as numerically. Now for the second model, we do find a somewhat stable steady state. After solving the problem numerically we see that the system reaches equilibrium after a certain time. And the time required to reach this state is directly proportional to the interaction rate between them. Analytically too we get a condition, following which we get a stable steady state solution.

As for the third model, we found the steady state solution changes for different values of interaction rate constant. Analytically we could not simplify the solution to deduce whether the system will reach steady state or not and in what condition.

So overall, as we made the problem more and more realistic it got harder to predict but we could get could get a rough idea of the movement of the population system using the Lotka Voltera model.