VOLUME 2/NO.1/2014 ISN : 2337-392X

PROSIDING

SEMINAR NASIONAL MATEMATIKA, STATISTIKA, PENDIDIKAN MATEMATIKA, DAN KOMPUTASI

Peranan Matematika dan Statistika dalam Menyikapi Perubahan Iklim

http://seminar.mipa.uns.ac.id

Jurusan Matematika
Fakultas Matematika dan Ilmu Pengetahuan Alam
Universitas Sebelas Maret Surakarta
Jl. Ir. Sutami 36 A Solo - Jawa Tengah

ISSN: 2337-392X

Tim Prosiding

ISSN: 2337-392X

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ISSN: 2337-392X

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ISSN: 2337-392X

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Puji syukur dipanjatkan kepada Tuhan Yang Maha Esa sehingga prosiding seminar nasional Statistika, Pendidikan Matematika dan Komputasi ini dapat diselesaikan.

Prosiding ini bertujuan mendokumentasikan dan mengkomunikasikan hasil presentasi paper pada seminar nasional dan terdiri atas 95 *paper* dari para pemakalah yang berasal dari 30 perguruan tinggi/politeknik dan institusi terkait. Paper tersebut telah dipresentasikan di seminar nasional pada tanggal 18 Oktober 2014. Paper didistribusikan dalam 7 kategori yang meliputi kategori Aljabar 14%, Analisis 9%, Kombinatorik 8%, Matematika Terapan 14%, Komputasi 7%, Statistika Terapan 27%, dan Pendidikan Matematika 19%.

Terima kasih disampaikan kepada pemakalah yang telah berpartisipasi pada desiminasi hasil kajian/penelitian yang dimuat pada prosiding ini. Terimakasih juga disampaikan kepada tim *reviewer*, tim prosiding, dan *steering committee*.

Semoga prosiding ini bermanfaat.

Surakarta, 28 Oktober 2014

Ketua Panitia

Dr. Dewi Retno Sari Saputro, M.Kom

ISSN: 2337-392X

DAFTAR ISI

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ISSN: 2337-392X

HOW REALISTIC THE WELL-KNOWN LOTKA-VOLTERRA PREDATOR-PREY EQUATIONS ARE

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ABSTRACT. This paper gives assessment to the Lotka-Volterra predator-prey equations. A review of the mathematical model and solutions are presented. Our description is given with examples to help in understanding the behavior of the solution to the problem. The judgment on how realistic the model is given. This paper can be used as a reference for pedagogical purposes.

Keywords: *Lotka-Volterra, predator-prey, population growth, biological model, realistic model*

1. INTRODUCTION

An attempt to define mathematically the relationship between the population of a predator and that of its prey is the development of the Lotka-Volterra predator-prey equations. These equations were originally developed by Lotka (1925) and Volterra (1926) independently. This model can be found in some textbooks written such as by Chaston (1971), Cronin (1980), Grossman and Turner (1974). New developments of this model are done by some authors, such as Lin (2011), Liu, Ren, and Li (2011), Pang and Wang (2004), Shen and Li (2009).

In this paper, we investigate the behaviour of the solution to the Lotka-Volterra predator-prey equations by examples. We present the effects of increasing populations and the effects of the change of initial conditions. We discuss the existence of a stable configuration of the populations and the effects of the change of growth rate of the populations. How realistic the model is also discussed.

The remaining of this paper is organized as follows. Section 2 presents a review of the Lotka-Volterra predator-prey. Section 3 gives the assessment on how realistic the Lotka-Volterra model is. In Section 4 we wrap up the paper with some remarks.

2. A REVIEW OF THE LOTKA-VOLTERRA MODEL

In this section, we review the behavior of the solution to the Lotka-Volterra predator-prey equations. The effects of some changes are described by examples.

The Lotka-Volterra predator-prey equations

$$\frac{dN_1}{dt} = r\,N_1 - p\,N_1\,N_2\,, \tag{1}$$

$$\frac{dN_2}{dt} = p\,N_1\,N_2 - d\,N_2\,. \tag{2}$$

Here, N_1 is the population of a prey species (for example, rabbits), N_2 is the population of the predator species (for example, foxes), *r* is the doubling rate of the prey species, *p* is the rate of predation of the predator on the prey and *d* is the death rate of the predator.

2.1. The effects of increasing population

Suppose that we have the growth rate of prey $r = 2$, the death rate of predator $d = 5$, the predation rate $p = 2$, the initial population of prey (rabbits) $N_1(0) = 0.5$, and the initial population of predators (foxes) $N_2(0) = 1$. When the population of rabbits increases, the population of foxes decreases slightly but then increases sharply. An increase of the population of foxes leads to a decrease of the population of rabbits. Figure 1 represents the fluctuation of the two species.

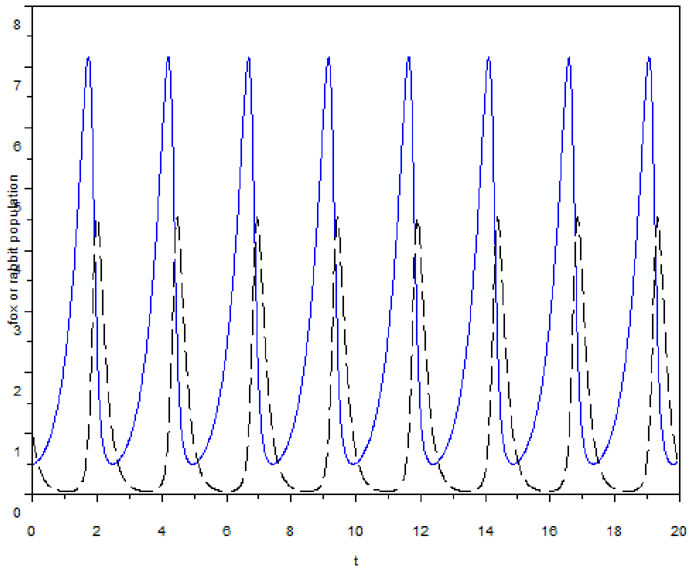


Figure 1: Graph for the population of rabbits (solid-line) and that of foxes (dash-line) where $r = 2$, $d = 5$, $p = 2$, $N_1(0) = 0.5$, and $N_2(0) = 1$.

Table 1: Experiment for various initial conditions for the populations.

$N_1(0)$	$N_2(0)$	Type of line in Figure 2
0.5	1.0	Solid line (-----)
1.0	0.5	Pluses (++++)
2.0	2.0	Triagles (ΔΔΔΔ)
5.0	5.0	Circles (oooo)

An interpretation is that when the fox population is at a maximum, the rabbit population is declining and that decline induces a drop in the number of foxes. The reduction of predators allows the rabbits to thrive followed by an increase in the number of foxes and the cycle repeats itself.

2.2. Change of the rates and that of initial conditions

Running the script with the growth rate of prey $r = 1$, the death rate of predator $d = 10$, and the predation rate $p = 1$ leads to a longer cycle-period than that presented in Subsection 2.1. In this case, the population of foxes sometimes 'disappears'. In other words, in some specific time the population of foxes is very close to zero, but it is not zero theoretically. The population of foxes increases dramatically when the population of rabbits is about maximum. The increase of the population of foxes affects the population of rabbits to go down sharply, and then it is followed by a very sharp decrease of the number of foxes.

If the initial conditions are changed, the ranges of populations change. From Figure 2, the maximum number of rabbits and foxes changes, but the trends are the same. In this experiment, we take the initial conditions as shown in Table 1.

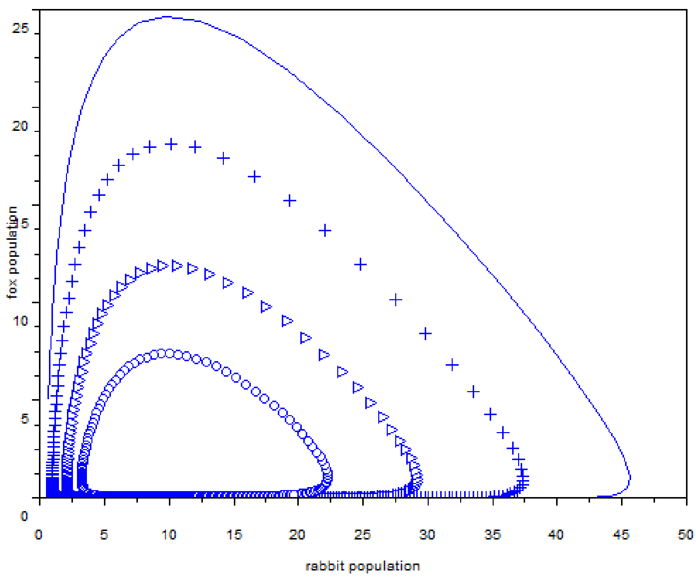


Figure 2: Phase portraits for various initial conditions of the populations of rabbits and foxes with $r = 1$, $d = 10$, $p = 1$ based on Table 1.

2.3. Existence of stable configuration

A stable configuration exists for every set of parameters *r*, *d*, and *p* constants where *p* non-zero (for Lotka-Volterra equations the parameters are all positive). In addition, we have to notice that only $N_1 \geq 0$ and $N_2 \geq 0$ are feasible since negative values of the populations are not realistic. Furthermore, the populations are stable if there are no changes of the populations over time. This means

$$\frac{dN_1}{dt} = \frac{dN_2}{dt} = 0, \tag{3}$$

Consequently, we have $r N_1 - p N_1 N_2 = 0$, and $p N_1 N_2 - d N_2 = 0$. By solving these two equations, we find stationary populations of rabbits and foxes

$$N_1 = 0 \text{ and } N_2 = 0; \quad (4)$$

$$N_1 = \frac{d}{p} \text{ and } N_2 = \frac{r}{p}. \quad (5)$$

If the initial conditions is $N_1(t) = 0$ and $N_2(t) = 0$ for $t = 0$, then the population of rabbits is always 0, and the population of foxes is also always 0. Assuming that the initial conditions are non-zero populations, $N_1(t) \neq 0$ and $N_2(t) \neq 0$ for $t = 0$, then the stable configuration for every set of parameters *r*, *d*, and *p* is that

$$N_1 = \frac{d}{p}, \quad N_2 = \frac{r}{p}, \quad (6)$$

where *p* is non-zero. Therefore, for $r = 1$, $d = 10$, $p = 1$, the stable population for rabbits is $N_1 = 10$ and the stable population for foxes is $N_2 = 1$.

Two remarks that should be noted are:

Remark A If the initial conditions is $N_1 \neq 0$ and $N_2 = 0$ then equations (1), (2) becomes

$$\frac{dN_1}{dt} = r\,N_1. \quad (7)$$

The solution for this equation is $N_1 = k\exp(r\,t)$ for some *k*, where *k* is positive to be realistic. In this case, the population of rabbits grows exponentially, while the population of foxes is always 0.

Remark B If the initial conditions is $N_1 = 0$ and $N_2 \neq 0$ then equations (1), (2) becomes

$$\frac{dN_2}{dt} = -d\;N_2. \quad (8)$$

The solution for this equation is $N_2 = \kappa\exp(-d\,t)$ for some κ, where κ is positive to be realistic. In this case, the population of foxes drops exponentially and asymptotically towards 0, while the population of rabbits is always 0.

2.4. Effects of increasing growth rate of the prey and that of increasing predation

The higher the growth rate of rabbits leads to the more periodic cycles of both populations, unless the populations are stable. Furthermore, the range of rabbit population is larger when the growth rate of rabbits is higher. Figure 3 represents rabbit population with various growth rates of rabbits related to the experiment in Table 2. Note that, in this experiment, we take four different growth rates of rabbits, other parameters are fixed and the initial conditions are also fixed as shown in Table 2.

Again, the higher the growth rate of rabbits leads to the more periodic of the cycle of fox population, unless the population is stable; and the range of the population is also larger when the growth rate of rabbits is higher. It is interesting that the stable level of fox population may be either the maximum level or the minimum level of fox population given different growth rates of rabbits as shown in Figure 4.

On the contrary, the higher the predation rate affects the longer period for a cycle of the system unless the populations are stable. In other words, the cycles of both populations are less periodic when the predation rate is higher as shown in Figures 5 and 6. Note that, now, we take four different predation rates, other parameters are fixed and the initial conditions are also fixed as in Table 3.

2.5. A case regarding the doubling rate of the prey species

Given that rabbits breed once every 15 days with an average litter size of three, that male and female rabbits are born in equal proportions, and that rabbits are always eaten by foxes before they die of other causes. We can find the correct value of *r* as follows.

Let the initial population of rabbits is $N_1(0)$, that is $\frac{1}{2}N_1(0)$ males and $\frac{1}{2}N_1(0)$ females. After 15 days all females breed with an average litter size of three so that the new population of rabbits is

$$N_1(15) = N_1(0) + 3 \cdot \tfrac{1}{2} N_1(0) = \tfrac{5}{2} N_1(0). \tag{9}$$

If there is no foxes in the system, then $p = 0$ and the equation for the population of rabbits is

$$\frac{dN_1}{dt} = r\,N_1. \tag{10}$$

Table 2: Setting parameter values with various growth rates of rabbits.

r	p	d	$N_1(0)$	$N_2(0)$	Type of line in Figures 3-4
0.5	1.0	1.0	1.0	1.0	Solid line (-----)
1.0	1.0	1.0	1.0	1.0	Pluses (++++)
2.0	1.0	1.0	1.0	1.0	Triagles (ΔΔΔΔ)
4.0	1.0	1.0	1.0	1.0	Circles (oooo)

Table 3: Setting parameter values with various predation rates.

r	p	d	$N_1(0)$	$N_2(0)$	Type of line in Figures 5-6
1.0	0.5	1.0	1.0	1.0	Solid line (-----)
1.0	1.0	1.0	1.0	1.0	Pluses (++++)
1.0	2.0	1.0	1.0	1.0	Triagles (ΔΔΔΔ)
1.0	4.0	1.0	1.0	1.0	Circles (oooo)

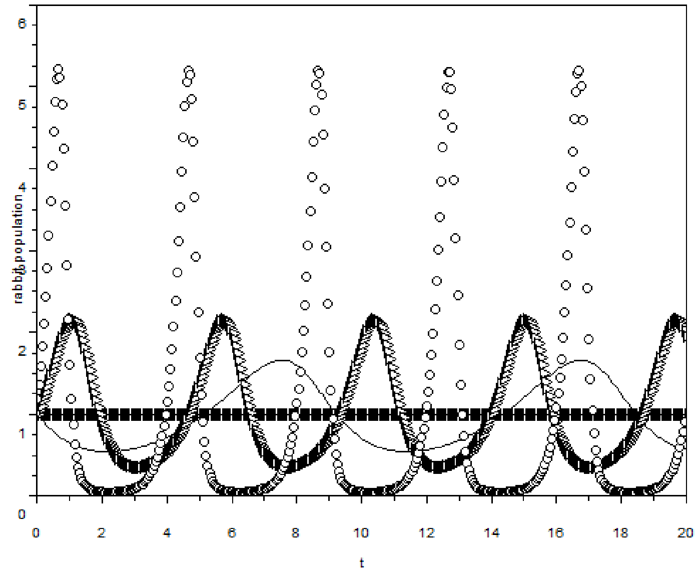


Figure 3: Rabbit population with various growth rates of rabbits based Table 2.

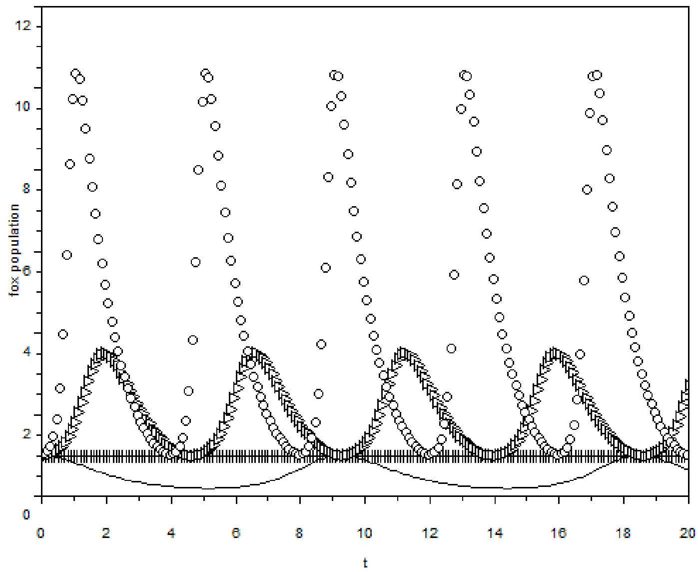


Figure 4: Fox population with various growth rates of rabbits based on Table 2.

Integrating the previous equation, we obtain

$$\int \frac{dN_1}{N_1} = \int r\, dt \,. \tag{11}$$

that is $N_1(t) = k\,e^{rt}$, k is constant.

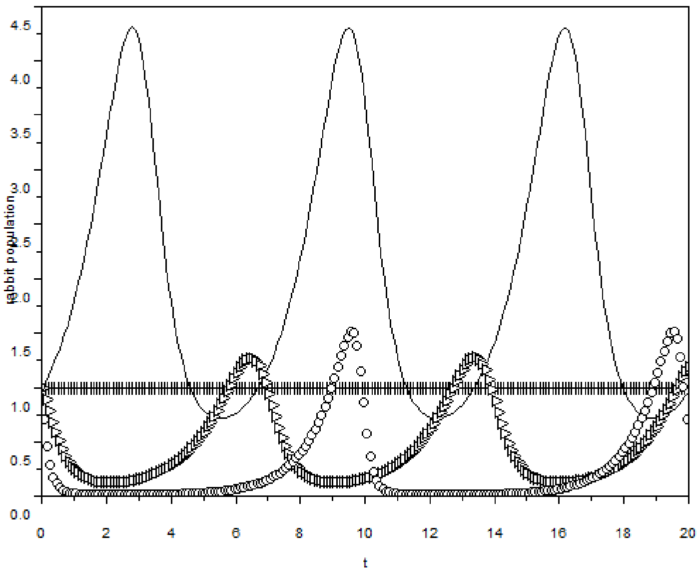


Figure 5: Rabbit population with various predation rate based on Table 3.

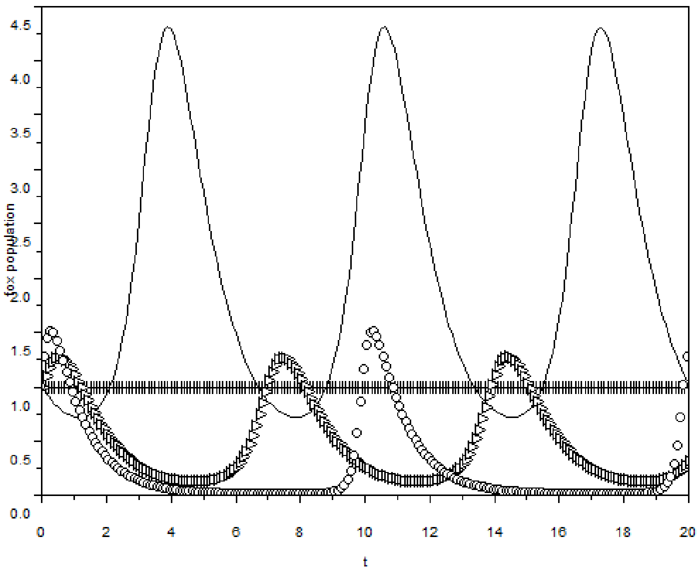


Figure 6: Fox population with various predation rate based on Table 3.

Since we have the value of $N_1(t)$ for $t=0$, then $k=N_1(0)$. Consequently, the population of rabbits in the time-step *t* is

$$N_1(t)=N_1(0)e^{rt}. \quad (12)$$

Substituting $N_1(t) = \frac{5}{2} N_1(0)$ for $t = 15$ in the above equation, we get

$$r = \frac{1}{15} \cdot \ln\left(5/2\right). \quad (13)$$

2.6. A case regarding the death rate of the predator and the rate of predation

Foxes live an average of three years in the wild but survive only three days without food. We can find the correct values of *p* and *d* as follows. Let the initial population of foxes is $N_2(0)$. If there is no food, i.e. there is no rabbits, then one third of the foxes die and only two thirds of foxes are still alive in the following day. This means that

$$N_2(1) = \frac{2}{3} N_2(0). \quad (14)$$

If there is no rabbits in the system, then $p = 0$ and the equation for the population of foxes is

$$\frac{dN_2}{dt} = -d\, N_2 \,. \quad (15)$$

Solving it in a similar way to that in Subsection 2.5., we get $N_2(t) = \kappa e^{-dt}$, κ is constant. Since we have the value of $N_2(t)$ for $t = 0$, then $\kappa = N_2(0)$. Consequently, the population of foxes in the time-step *t* is

$$N_2(t) = N_2(0) e^{-dt} \,. \quad (16)$$

Substituting $N_2(t) = \frac{2}{3} N_2(0)$ for $t = 1$ in the above equation, we get

$$d = -\ln\left(2/3\right) = \ln(3/2)\,. \quad (17)$$

Given that each fox eats one rabbit per day. It means that the rate of predation of the predator on prey is one, and we write $p = 1$. If these conditions together with those in Subsection 2.5 are correct, foxes can still survive, but the period of the cycle is becoming much larger. When we look at the time from 0 to 20 unit-time, it seems that foxes cannot survive. Figure 7 represents this phenomenon.

However, if we look at a longer duration, say between 0 and 200 unit-time, it is clear that the foxes can survive still as well as the rabbits. Figure 8 represents the cycle for both populations for the time between 0 and 200 unit-time. The solid-line is the population of rabbits and the dash-line is the population of foxes.

3. HOW REALISTIC THE LOTKA-VOLTERRA MODEL

These Lotka-Volterra equations are not very realistic in terms of explaining the interaction between predators and preys, and are limited under conditions that are used to build the model, but qualitatively we can say that this model is fair-realistic. It is understandable that there is no such model that is really perfect to explain the real system.

Recall the statement in Subsection 2.1.: "when the fox population is at a maximum, the rabbit population is declining and that decline induces a drop in the number of foxes; the reduction of predators allows the rabbits to thrive followed by an increase in the number of foxes and the cycle repeats itself." If we look only at that statement, it seems that the equations are realistic. However, once again we should be aware that these equations are just a simplification of the real system. These equations are limited to the assumptions that are used to build the model. There are many other facets which are not included in the equations to describe the interaction between the two populations, for example the ability of the preys to find a refuge which makes it impossible for them to be caught, and changes in the environment conditions.

One of the weaknesses of these equations is that there is an unbounded exponential growth for the rabbit population when there are no predators (see Remark A in Subsection 2.3.). If we consider this weakness in the real world, those equations are not realistic. In the real world, the population of rabbits is not only influenced by the population of foxes. Both populations may be affected by space, climate, pollution, diseases, etc. The unbounded exponential growth of the population is one of the reasons which makes that the model is not realistic.

In addition, in place of exponential growth for the rabbits when there are no predators, it can be supposed that the growth is logistic so that

$$\frac{dN_1}{dt} = r\,N_1 - g\,N_1^2 - p\,N_1\,N_2 \quad (18)$$

$$\frac{dN_2}{dt} = p\,N_1\,N_2 - d\,N_2 \quad (19)$$

which includes equations (1), (2) as a special case with $g = 0$. Furthermore, if we suppose that A_o of rabbits can find a refuge, the model becomes

$$\frac{dN_1}{dt} = r\,N_1 - g\,N_1^2 - p\,(N_1 - A_o)N_2 \quad (20)$$

$$\frac{dN_2}{dt} = p(N_1 - A_o)\,N_2 - d\,N_2 \quad (21)$$

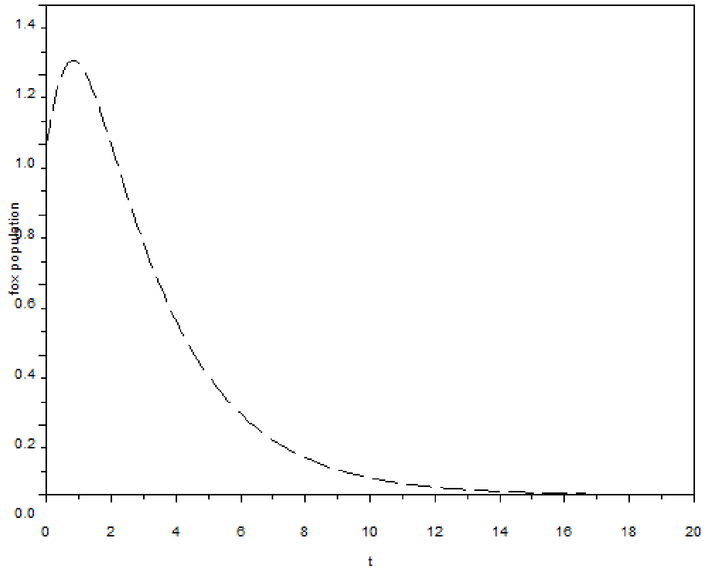
We can still generalise Lotka-Volterra equations with more general assumptions to make the model more realistic. One of the more general forms is that so called Rosenzweig-MacArthur model (Jones and Sleeman, 1983).

4. CONCLUSION

We have investigated the Lotka-Volterra predator-prey equations. Our presentation yields nice pedagogical materials. This paper can be extended to the use of a computer software for the investigation of the considered model.

ACKNOWLEDGEMENT

The author thanks Dr. B. Robson at the CSIRO Land and Water as well as Prof. A. J. Jakeman at the Integrated Catchment Assessment and Management Centre, The Fenner School of Environment and Society, The Australian National University for some discussions.



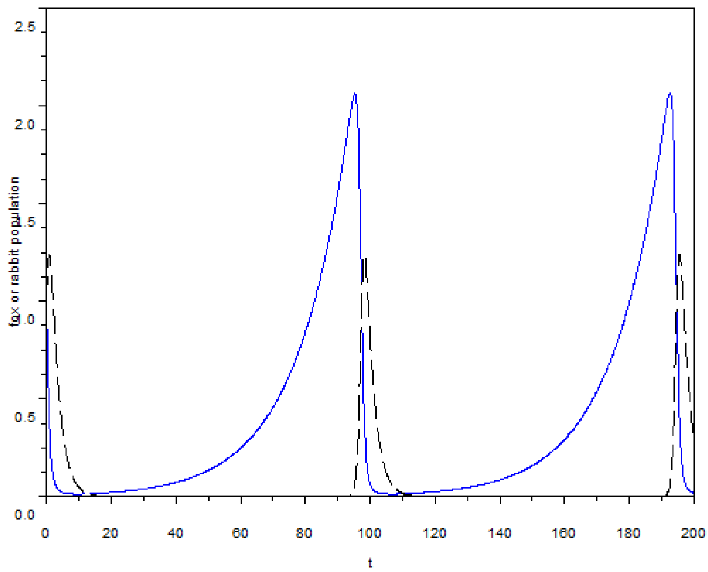


Figure 7: Population of foxes $r = (1/15)\cdot\ln(5/2)$, $d = \ln(3/2)$, $p = 1$ with initial conditions $N_1(0) = 1$ and $N_2(0) = 1$ from 0 to 20 unit-time.

Figure 8: Population of rabbits (solid line) and foxes (dashes) where $r = (1/15)\cdot\ln(5/2)$, $d = \ln(3/2)$, $p = 1$ with $N_1(0) = 1$ and $N_2(0) = 1$ from 0 to 200 unit-time.

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