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Population Dynamics Model for Coexistence of Three Interacting Species

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Abstract: Over the years applications of mathematics in the form of mathematical modeling in a whole range of different fields including physical, social, management, biological, and medical sciences have broken all bounds. In particular, the mathematical models to study population dynamics of various interacting species in an isolated environment have attracted the attention of mathematical biologists. In nature, there may be two, three, or more species interacting within themselves giving rise to the corresponding predator-prey models. In each case, both predator and prey evolve their own strategies to deal with the situation. The parameters which influence both the predator and the pry to evoke strategies for their survival include environmental conditions, predator's appetite, aggressiveness, liking for some particular prey, its physical fitness versus that of the prey, prey's agility, active prudence to run away or hide, etc. In the literature interactions between, two, three or more species, sharing the same habitat have been discussed in detail. In this paper we present a model pertaining to the interaction between three species. It is a realistic model in which three species, x, y and z, interact within themselves in such a way that species y (predator) preys on species x (prey), while the species z preys on both the species x and y. Accordingly, the resulting situation has been analyzed. The objective of this paper is to analyze the possibility for three interacting species to live in an isolated environment harmoniously. The model presented here has three equilibrium points, however, only one of them has been ascertained to be locally stable. The existence of this equilibrium point signifies amicable coexistence of the three species, if no outside intervention accrues any destabilization to the existing environment.

Keywords: Malthusian Growth Model, Carrying Capacity of Environment, Logistic Equation, Malthus-Verhulst Equation, Lotka-Volterra Equations, Equilibrium Point, Jacobian Matrix

1. Introduction

A population tends to grow over time if sufficient resources of food and space are available and there is no threat from predators. In such a case, the growth rate is proportional to the size of the population itself, so that in each unit of time, a certain percentage of the population gives birth to new offsprings. If the reproduction of the new individuals takes place just about continuously, the growth rate is given by,

$$\frac{dP}{dt} = \alpha P, \tag{1.1}$$

where, P is the population, t is the time and α is the constant of proportionality. Its solution is given as,

$$P = P_0 e^{\alpha t}, \tag{1.2}$$

where, P_0 is the population at time t = 0. In other words, the population grows exponentially. It is depicted in Fig. 1.1(a). Basically it is Malthusian Growth Model[1], named after an English cleric and scholar Thomas Robert Malthus (1766 – 1834), who discussed it in an essay in 1798. In the field of population ecology, this model is generally regarded as the first principle of population dynamics. He observed that, if not checked, the human population would grow exponentially while the production of food items grows arithmetically. Accordingly, he warned that at some point in time in the future, the continued population growth would exceed food growth resources, leading to naturally occurring catastrophic checks on population growth like famine, disease, war, etc.

The formula (1.2) may work for a short while but not for a long duration. As such, the exponential growth model of a population is unrealistic as it does not incorporate limitations due to food shortage, predation, disease, etc.

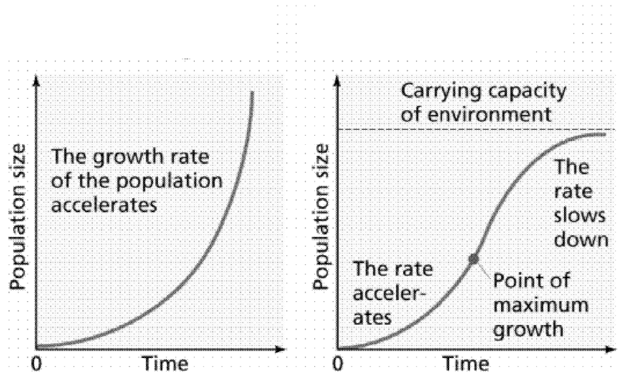

Fig. 1.1. *(a) Exponential Growth of Population (b) The S-shaped Curve of Logistic Growth.*

The environment imposes restrictions to the population growth, and most of the populations cannot grow continuously because during the process of their growth, a stage would reach when they would run short of food, water, sunlight, space, or other resources, required for their survival. At that stage the growth rate would begin to slow down, and tend to a *stable level* known as *carrying capacity of environment*. It is denoted by K, and we see that K >> P(t) at time t = 0. The carrying capacity of population is the maximum number of its individuals, which the existing resources can support in an environment. Thus, the function of carrying capacity is to act as a moderator in the growth process to slow down the growth rate to a stable level when resources become limited and stop growth once population size has reached this stage (see Fig 1.1 (b)). At that stage intraspecific competition evolves so that individuals within a population who are better adapted to the environment survive while others fade away.

The above discussion leads us to replace Eqn.(1.1) by the following differential equation, called logistic equation, or Verhulst equation[2],[3],[4] (named after Belgian mathematician Pierre Francois Verhulst (1804-1849)). Generally it is called Malthus-Verhulst equation,

$$\frac{dP}{dt} = \alpha P(1 - \frac{P}{K}), \tag{1.3}$$

where, K is the carrying capacity of the environment, as described above. We see that if K > P, then $\frac{dP}{dt} > 0$, and the population growth rate increases, while for K < P, the above equation gives $\frac{dP}{dt} < 0$, i.e., the growth rate declines.

The equilibrium points of the logistic equation (1.3) are those where $\frac{dP}{dt} = 0$. They are, P(t) = 0, and P(t) = K

The logistic equation (1.3) can be solved by the method of separation of variables as,

$$\int \frac{dP}{P(1-\frac{P}{K})} = \int \alpha \, dt.$$

Resolving the integrand on the left hand side into partial fractions, and integrating both sides we obtain the solution to the logistic equation as,

$$P(t) = \frac{K}{1+Ae^{-\alpha t}}, \tag{1.4}$$

where, $P(0) = \frac{K}{1+A}$, so that, $A = \frac{K-P(0)}{P(0)}$.

In ecology, the predator-prey theory revolves around dynamical relationship between the predators and the prey. This theory has its origin in *Malthus-Verhulst logistic theory* given by Eqn.(1.3), which concerns single-species population dynamics. If we replace P by variable x and α by a, Eqn.(1.3) becomes,

$$\frac{dx}{dt} = ax(1 - \frac{x}{K}), \tag{1.5}$$

where, x is the present population size, t is the time, a is a constant defining the growth rate and K is the carrying capacity of the environment. Although this equation appears to be a simple one but it plays the main role in the population dynamics of single-species.

Alfred James Lotka[5],[11], [13] (1880–1949), a US bio-mathematician, bio-physicist and bio-statistician is the next to make significant contributions in the field of population dynamics. He derived the logistic equation using the first principles, and proposed the first model for predator-prey interactions (now called Lotka-Volterra equations) in 1925. Vito Volterra[6],[11] ,[13] (1860 – 1940), an Italian bio-mathematician and bio-physicist independently investigated these equations in 1926 while making statistical analysis of fish catches in the Adriatic sea during World War-I. The Lotka-Volterra equations (or predator-prey equations), which describe the growth rates of two interacting species[14] ,[15], are,

$$\left.\begin{aligned} \frac{dx}{dt} &= a_1x - b_1xy \\ \frac{dy}{dt} &= -a_2y + b_2xy \end{aligned}\right\}, \tag{1.6}$$

where,

(i) x is the population size of prey at time t,
(ii) y is the population size of predator,
(iii) All a_i's and b_i's are positive constants,
(iv) a_1 is the intrinsic growth rate of prey x,
(v) a_2 is the death rate of predator y in the absence of prey x,
(vi) b_1 is the death rate of prey x due to predation by predator y,
(vii) b_2 is the growth rate of predator y on predation of prey x.

In this model it is assumed that the two species interact only within themselves, and no outside factor has any effect on the system, like influence of some other species or the environment. Although this model makes unrealistic assumptions, nevertheless it provides a base for the researchers to refine and make it a tractable model.

Models for three interacting species[7],[8] have been studied extensively since early seventies. In this regard a number of models have been discussed, the following being of interest to many of the researchers[9],[10],[11],[12],

$$\left.\begin{aligned}\frac{dx}{dt} &= a_1x - b_1xy \\ \frac{dy}{dt} &= -a_2y + b_2xy - c_1\, yz \\ \frac{dz}{dt} &= -a_3z + c_2\, yz\end{aligned}\right\}, \tag{1.7}$$

where, x, y and z are the population sizes of the three species. In this model,

(i) The species y preys on x,
(ii) The species z preys on y,
(iii) a_1 is the intrinsic growth rate of species x (prey),
(iv) a_2 is the death rate of species y (predator) in the absence of species x (prey),
(v) a_3 is the death rate of species z (predator) in the absence of species y (prey),
(vi) b_1 is the death rate of species x (prey) due to predation by species y (predator),
(vii) b_2 is the growth rate of species y (predator) on predation of species x (prey),
(viii) c_1 is the death rate of species y (prey) due to predation by species z (predator),
(ix) c_2 is the growth rate of species z (predator) on predation of species y (prey).

In what follows, we shall discuss two-dimensional and three-dimensional models that are available in the literature, before discussing our model.

2. Two Dimensional Model

As illustrated above, the model describing dynamical behaviour between two interacting species is given by the system (1.6) In this model, the population of the two species is in equilibrium when both $\frac{dx}{dt}$ and $\frac{dy}{dt}$ are zero, i.e., x and y do not change with time. Accordingly, Eqn.(1.6) gives, say, F(x, y) = 0, as

$$\left.\begin{aligned}x(a_1 - b_1\, y) &= 0 \\ y(-a_2 + b_2x) &= 0\end{aligned}\right\}. \tag{2.1}$$

This system has two solutions (i.e., stationery points or equilibrium points), the trivial solution, (0, 0) and $(\frac{a_2}{b_2}, \frac{a_1}{b_1})$. The first equilibrium point (0, 0) is of no interest because it implies non-existence of any organism in the system, however, the second equilibrium point needs to be analyzed to study the dynamics of the system. The dynamical behaviour (i.e., stability or otherwise) of an equilibrium point can be studied by computing the eigenvalues of the Jacobian matrix of the system (2.1). It amounts to linearization of this system (by taking partial derivatives) as,

$$\nabla F(x, y) = J(x, y) = \begin{bmatrix} a_1 - b_1\, y & -\, b_1\, x \\ b_2y & -a_2 + b_2x\end{bmatrix}. \tag{2.2}$$

The Jacobian matrix at the equilibrium point (0, 0) is given as,

$$J(0, 0) = \begin{bmatrix} a_1 & 0 \\ 0 & -a_2\end{bmatrix}. \tag{2.3}$$

Its eigenvalues are a_1, and $-a_2$. Since a_1 and a_2 are always greater than zero, both these eigenvalues have opposite signs. As such, the equilibrium point (0, 0) at the origin is a saddle point, i.e., an unstable equilibrium point. If it were a stable equilibrium point, the non-zero population of the two species would be attracted towards this point resulting in the extinction of both of them for any initial population sizes of the two species. Since it is an unstable equilibrium point so natural extinction of both the species would not be possible unless the prey were artificially eradicated leading to the death of predators due to starvation. On the other hand if the predators were artificially eradicated, the population of the prey would grow exponentially.

For the second equilibrium point $(\frac{a_2}{b_2}, \frac{a_1}{b_1})$, Eqn.(2.2) gives,

$$J(\frac{a_2}{b_2}, \frac{a_1}{b_1}) = \begin{bmatrix} 0 & -\frac{a_2b_1}{b_2} \\ \frac{a_1b_2}{b_1} & 0\end{bmatrix}. \tag{2.4}$$

Its eigenvalues are $\lambda_1 = i\sqrt{a_1\, a_2}$, and $\lambda_2 = -i\sqrt{a_1\, a_2}$. Thus $(\frac{a_2}{b_2}, \frac{a_1}{b_1})$ is a stable equilibrium point.

In order to analyze the system (1.6) further we divide the second equation by the first to get,

$$\frac{dy}{dx} = \frac{-a_2y + b_2xy}{a_1x - b_1xy} = \frac{y(-a_2 + b_2x)}{x(a_1 - b_1\, y)}.$$

It is a first order *separation of variables* type differential equation. On solving this equation we obtain,

$$a_1 \ln y - b_1 \ln y + a_2 \ln x - b_2 \ln x = \ln K,$$

where, K is the constant of integration. On further simplification it yields,

$$K = y^{a_1}\, e^{-b_1y} x^{a_2}\, e^{-b_2x} = \frac{x^{a_2}\, y^{a_1}}{e^{\,b_2x + b_1y}}, \tag{2.5}$$

where e is the Euler number. This quantity approaches its maximal value for x > 0, y > 0, at the equilibrium point $(\frac{a_2}{b_2}, \frac{a_1}{b_1})$, which is,

$$K_{max} = [\frac{a_2}{b_2\, e}]^{a_2}\, [\frac{a_1}{b_1\, e}]^{a_1}$$

3. Three Dimensional Model

We shall discuss the model (1.7) concerning three interacting species. We know that at the equilibrium points, $\frac{dx}{dt}$, $\frac{dy}{dt}$, and $\frac{dz}{dt}$ are zero. Therefore, the system (1.7) gives,

$$\left.\begin{aligned}x(a_1 - b_1\, y) &= 0 \\ y(-a_2 + b_2x - c_1\, z) &= 0 \\ z(-a_3 + c_2\, y) &= 0\end{aligned}\right\} \tag{3.1}$$

This system has two equilibrium points, (0, 0, 0) and $(\frac{a_2}{b_2}, \frac{a_1}{b_1}, 0)$. We shall discuss both of them separately as the stability of the system depends on these points.

As describes above, the dynamical behaviour (i.e., stability or otherwise) of an equilibrium point can be studied by computing the eigenvalues of the Jacobian matrix of the system (3.1). It amounts to linearization of this system (by taking partial derivatives) as,

$$J(x,y,z) = \begin{bmatrix} a_1 - b_1 y & -b_1 x & 0 \\ b_2 y & -a_2 + b_2 x - c_1 z & -c_1 y \\ 0 & c_2 z & -a_3 + c_2 y \end{bmatrix}. \tag{3.2}$$

Therefore, the Jacobian matrix at the equilibrium point (0, 0, 0) is given as,

$$J(0,0,0) = \begin{bmatrix} a_1 & 0 & 0 \\ 0 & -a_2 & 0 \\ 0 & 0 & -a_3 \end{bmatrix}. \tag{3.3}$$

The eigenvalues of this Jacobian matrix are: $\lambda_1 = a_1$, $\lambda_2 = -a_2$, and $\lambda_3 = -a_3$. Thus, we see that the equilibrium point (0, 0, 0) is a saddle point.

For the equilibrium point $(\frac{a_2}{b_2}, \frac{a_1}{b_1}, 0)$, the Jacobian matrix (3.2) becomes,

$$J(\frac{a_2}{b_2}, \frac{a_1}{b_1}, 0) = \begin{bmatrix} 0 & -\frac{a_2 b_1}{b_2} & 0 \\ \frac{a_1 b_2}{b_1} & 0 & -\frac{a_1 c_1}{b_1} \\ 0 & 0 & -a_3 + \frac{a_1 c_2}{b_1} \end{bmatrix}. \tag{3.4}$$

The eigenvalues of this Jacobian matrix are: $\lambda_1 = i\sqrt{a_1 a_2}$, $\lambda_2 = -i\sqrt{a_1 a_2}$, and $\lambda_3 = \frac{a_1 c_2 - a_3 b_1}{b_1}$. Thus we see that the equilibrium point $(\frac{a_2}{b_2}, \frac{a_1}{b_1}, 0)$ is locally stable if the eigenvalue λ_3 is negative, i.e., $a_3 b_1 > a1c_2$. As such, the equilibrium point $(\frac{a_2}{b_2}, \frac{a_1}{b_1}, 0)$ provides a possible equilibrium state in Lotka-Volterra model.

4. Model Formulation

It is felt that the three dimensional model (1.7) does not represent the real picture of an isolated ecological environment. In this model the species z prey on the species y only, which is contrary to reality. In fact, the species z would prey both on species y as well species x. Keeping the same in view we present our model as under,

$$\left.\begin{aligned} \frac{dx}{dt} &= a_1 x - b_1 xy - c_1 xz \\ \frac{dy}{dt} &= -a_2 y + b_2 xy - c_2 yz \\ \frac{dz}{dt} &= -a_3 z + b_3 xz + c_3 yz \end{aligned}\right\}, \tag{4.1}$$

where, all a_i, b_i, and c_i, (i = 1, 2, 3), are positive constants giving intrinsic rates as under,

(i) a_1 = Intrinsic growth rate of species x (prey) in the absence of species y and z (predators),
(ii) a_2 = Death rate of species y (predator) in the absence of species x (prey),
(iii) a_3 = Death rate of species z (predator) in the absence of species x, and y (preys),
(iv) b_1 = Death rate of species x (prey) due to predation by species y (predator),
(v) b_2 = Growth rate of species y (predator) on predation of species x (prey),
(vi) b_3 = Growth rate of species z (predator) on predation of species x (prey),
(vii) c_1 = Death rate of species x (prey) due to predation by species z (predator),
(viii) c_2 = Death rate of species y (prey) due to predation by species z (predator),
(ix) c_3 = Growth rate of species z (predator) on predation of species y (prey),

4.1. Equilibria and Linear Analysis

While analyzing systems of differential equations it is often useful to consider the solutions that do not change with time, i.e., solutions for which, $\frac{dx}{dt}$, $\frac{dy}{dt}$, and $\frac{dz}{dt}$ are zero. Such solutions are called *equilibria, steady states* or *fixed points*. Accordingly, system (4.1) becomes,

$$\left.\begin{aligned} x(a_1 - b_1 y - c_1 z) &= 0 \\ y(-a_2 + b_2 x - c_2 z) &= 0 \\ z(-a_3 + b_3 x + c_3 y) &= 0 \end{aligned}\right\}. \tag{4.2}$$

The solutions or equilibrium points of this system are: the trivial solution (0, 0, 0), and $(0, \frac{a_3}{c_3}, \frac{-a_2}{c_2})$, $(\frac{a_3}{b_3}, 0, \frac{a_1}{c_1})$, $(\frac{a_2}{b_2}, \frac{a_1}{b_1}, 0)$. Thus, we see that at the most, there exist three non-negative equilibrium points of the system (4.1).

4.2. Stability of Equilibrium Points

The stability of the equilibrium points can be analyzed by computing the eigenvalues of the Jacobian matrix of system (4.2) at these points. The Jacobian matrix of this system is given as

$$J(x,y,z) = \begin{bmatrix} a_1 - b_1 y - c_1 z & -b_1 x & -c_1 x \\ b_2 y & -a_2 + b_2 x - c_2 z & -c_2 y \\ b_3 z & c_3 z & -a_3 + b_3 x - c_3 y \end{bmatrix}. \tag{4.3}$$

We shall transcribe the Jacobian matrix at the equilibrium points and then compute the eigenvalues to examine the stability of these equilibrium points.

4.2.1. Equilibrium Point: (0, 0, 0)

Corresponding to the equilibrium point (0, 0, 0), the

Jacobian matrix (4.3) becomes,

$$J(0, 0, 0) = \begin{bmatrix} a_1 & 0 & 0 \\ 0 & -a_2 & 0 \\ 0 & 0 & -a_3 \end{bmatrix}. \quad (4.4)$$

The eigenvalues of this matrix are given as, $\lambda_1 = a_1$, $\lambda_2 = -a_2$, and $\lambda_3 = -a_3$. This shows that the equilibrium point (0, 0, 0) is a saddle point. Thus (0, 0, 0) is an unstable equilibrium point, and of no interest to us.

4.2.2. Equilibrium Point: $(\frac{a_3}{b_3}, 0, \frac{a_1}{c_1})$

With regard to the equilibrium point $(\frac{a_3}{b_3}, 0, \frac{a_1}{c_1})$, the Jacobian matrix (4.3) becomes,

$$J(\frac{a_3}{b_3}, 0, \frac{a_1}{c_1}) = \begin{bmatrix} 0 & -\frac{a_3 b_1}{b_3} & -\frac{a_3 c_1}{b_3} \\ 0 & -a_2 + \frac{a_3 b_2}{b_3} - \frac{a_1 c_2}{c_3} & 0 \\ \frac{a_1 b_3}{c_1} & \frac{a_1 c_3}{c_1} & 0 \end{bmatrix}. \quad (4.5)$$

The eigenvalues of this matrix are computed as: $\lambda_1 = i\sqrt{a_1 a_3}$, $\lambda_2 = -i\sqrt{a_1 a_3}$, and $\lambda_3 = [\frac{a_3 b_2}{b_3} - (a_2 + \frac{a_1 c_2}{c_3})]$. Therefore, the equilibrium point $(\frac{a_3}{b_3}, 0, \frac{a_1}{c_1})$ is locally stable if the eigenvalue λ_3 is negative, i.e., if $(a2 + \frac{a_1 c_2}{c_3}) > \frac{a_3 b_2}{b_3}$.

4.2.3. Equilibrium Point: $(\frac{a_2}{b_2}, \frac{a_1}{b_1}, 0)$

In respect of the equilibrium point $(\frac{a_2}{b_2}, \frac{a_1}{b_1}, 0)$, the Jacobian matrix (4.3) yields,

$$J(\frac{a_2}{b_2}, \frac{a_1}{b_1}, 0) = \begin{bmatrix} 0 & -\frac{a_2 b_1}{b_2} & -\frac{a_2 c_1}{b_2} \\ \frac{a_1 b_2}{b_1} & 0 & -\frac{a_1 c_2}{b_1} \\ 0 & 0 & -a_3 + \frac{a_2 b_3}{b_2} + \frac{a_1 c_3}{b_1} \end{bmatrix}. \quad (4.6)$$

The eigenvalues of this matrix are: $\lambda_1 = i\sqrt{a_1 a_2}$, $\lambda_2 = -i\sqrt{a_1 a_2}$, and $\lambda_3 = \left[-a_3 + (\frac{a_2 b_3}{b_2} + \frac{a_1 c_3}{b_1})\right]$. We see that the equilibrium point $(\frac{a_2}{b_2}, \frac{a_1}{b_1}, 0)$ is locally stable only if $a_3 > (\frac{a_2 b_3}{b_2} + \frac{a_1 c_3}{b_1})$, which is not likely. Therefore, it is an unstable equilibrium point.

5. Discussion about the Results

We have seen that there are three non-negative equilibrium points of the system (4.1): (0, 0, 0), $(\frac{a_3}{b_3}, 0, \frac{a_1}{c_1})$, and $(\frac{a_2}{b_2}, \frac{a_1}{b_1}, 0)$. We have analyzed each one of them separately and have found that,

(i) (0, 0, 0) is a saddle point, therefore, it is an unstable equilibrium point.

(ii) $(\frac{a_3}{b_3}, 0, \frac{a_1}{c_1})$ is locally stable equilibrium point if $(a_2 + \frac{a_1 c_2}{c_3}) > \frac{a_3 b_2}{b_3}$

(iii) $(\frac{a_2}{b_2}, \frac{a_1}{b_1}, 0)$ is an unstable equilibrium point.

From the above discussion we deduce that the system (4.1) has only one locally stable equilibrium point.

6. Conclusion

The predator-prey interactions between various kinds of species living in an isolated environment and sharing the same habitat manifest very perplexing phenomena. The proverb "survival of the fittest" applies to such a situation in letter and spirit. The preys design their deceptive strategies for their survival while the predators evolve aggressive as well as delusive lines of action to capture the preys. In this paper we have discussed the case of three species x, y and . It conforms to the nature wherein the species y preys upon species x, while the species z preys on both x and y species. Accordingly, we have found an equilibrium point for coexistence of the three species in a particular isolated environment.

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