

Prey-Predators Defensive Switching Model of Tanganyika Lake

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Abstract

We studied a mathematical model where two predators interact with one prey. The prey species is age structured having two life stages immature and mature. Predators consume both the young and adult of the prey individuals. The mature prey individuals guard itself more against the abundant predator individuals and the rare predator individuals gets greater hunting success. Interaction of both predator individuals with young prey will be more if young prey are in abundance because they have no defensive capability. Local and global stabilities of equilibrium sets are discussed.

Keywords: *predator, prey, stability, global stability, switching*

1 Introduction

A predator which feeds on more than one prey species does not attack all types of prey indiscriminately. When one type of prey becomes scarce in the environment, the predator may stop searching for this species entirely and begin to hunt instead another, more abundant prey type. This is found to be the case when prey species is relatively smaller in size with little or insignificant defense capability with respect to predator. This preferential phenomenon is called switching. If prey species is of large size and have the ability of group defense which will be effective in the habitat where the population of prey is large. The predator will be attracted towards that habitat where prey are less in number.

Hori [1] did field experiments from lake Tanganyika and found that two phenotypes dextral and sinistral attack the prey from two different directions. These species are unique because individuals mouth opens either rightward or leftward as a result of an asymmetrical joint of the jaw to the suspensorium. The

right-handed (dextral) individuals always attack the prey's left side, and left handed (sinistral) on the right side. The side of attack be a functional requisite for the success in feeding of these scale eaters. Each phenotype will be at an advantage when they are less numerically. If dextral individuals are more abundant in the population, prey fish will tend to guard more against attacks to their left side, which results in sinistral individuals gaining greater hunting success. When sinistral individuals were numerically dominant, the prey suffered scale-eating from dextral individuals more frequently than from sinistral individuals. This result clearly demonstrates that the prey fish focused their guard toward either right or left side, depending on which predators phenotype was most abundant. This is an example in which numerically less predator individuals get greater hunting success in a natural population.

Saleem et al. [2] studied a mathematical model of antipredator behaviour of lake Tanganyika where prey guards more against the more abundant phenotype (dextral or sinistral) and the rare type gains advantage. They considered the defense of the prey against the more abundant predator individuals through its defensive switching that results more hunting success to the numerically less predator species. They found that the system generally has a stable three species coexisting equilibrium state.

In the natural world, almost all animals have the age structure of immature and mature. There are two types of stage dependent predation in predator-prey interaction models. In the first of these the predators eat only adults. These are the cases where insects are preyed upon only in the adult stage (e.g. Lloyd and Dybas [3]). On the other hand, there are well documented cases where predators consume only immature prey Le Caven et al. [4] and Nielson [5] have described such cases. Several models have been proposed to account for the stage structure of immature and mature of the species. One can refer

[6-10].

In this paper we have looked at phenotype [dextral and sinistral], interaction with age structured prey species while Saleem et. al. assumed non-age structured prey species. In our model predators can feed on either stage of prey but instead of choosing individuals at random, predators will interact more with young prey if they are in abundance because they do not have defensive capability. The adult prey guards more against the more abundant phenotype (dextral or sinistral) and the rare type gains advantage, which shows a defensive switching behaviour. The predator individuals which are less numerically will get greater hunting success.

Tansky [11] investigated a mathematical model of two prey and one predator system which has the switching property of predation of the following form

$$\begin{aligned}\frac{dx}{dt} &= \left\{ b_1 - \frac{az}{1 + (y/x)^n} \right\} x, \\ \frac{dy}{dt} &= \left\{ b_2 - \frac{bz}{1 + (x/y)^n} \right\} y, \\ \frac{dz}{dt} &= -\mu + \frac{axz}{1 + (y/x)^n} + \frac{byz}{1 + (x/y)^n} \quad n = 1, 2, 3 \dots\end{aligned}$$

where x, y and z denote abundance of two kinds of the prey species and a predator species, respectively. b_1 and b_2 are the specific growth rates of the prey species in the absence of predation and μ is the per capita death rate of the predator. The functions $\frac{a}{1 + (y/x)^n}$ and $\frac{b}{1 + (x/y)^n}$ have a characteristic property of switching mechanism. The predatory rate that an individual of the prey species (small size) is attacked by a predator decreases when the population of that species becomes rare compared with population of another prey species. Switching of predator will be in opposite direction if the prey species is of large size having group defense capability. This property is much amplified for large value of n .

2 The Model

The two-predators and one prey interaction model with simple multiplicative effect where we only consider the stage structure of immature and mature of the prey species, and do not consider the stage struc-

ture of the both predators species is of the form:

$$\begin{aligned}\frac{dx_1}{dt} &= ax_2 - kx_1 - \beta x_1 - \frac{bx_1^2 y_1}{x_1 + x_2} - \frac{bx_1^2 y_2}{x_1 + x_2}, \\ \frac{dx_2}{dt} &= \beta x_1 - kx_2 - \frac{dy_1 y_2 x_2}{y_1 + y_2} - \frac{dy_1 y_2 x_2}{y_1 + y_2}, \\ \frac{dy_1}{dt} &= -\alpha y_1 + \frac{bx_1^2 y_1}{x_1 + x_2} + \frac{dy_1 y_2 x_2}{y_1 + y_2}, \\ \frac{dy_2}{dt} &= -\alpha y_2 + \frac{bx_1^2 y_2}{x_1 + x_2} + \frac{dy_1 y_2 x_2}{y_1 + y_2},\end{aligned}$$

with $x_i(0) > 0, y_i(0) > 0, i = 1, 2$.

The predatory rate that an individual of immature prey is attacked by a predator increases when the population of immature prey is in abundance because the immature prey individuals has no defensive capability. The predatory rate that an individual of the mature prey is attacked by a predator decreases when the population of that species become large compared with the population of another predator species. The reason behind the predatory rate diminishes at large densities is because when the population of a predator becomes large, the prey defends itself against it and switches to another predator species with a relatively smaller population in order to avoid too much predation of its individuals. Too much predation of prey species is likely because the large predator population may not leave enough safer places for the prey individuals to hide.

Our model has the following parameters:

- a - per capita birth rate of immature prey population; which is proportional to the existing mature prey population;
- k - per capita death rate of both stages of prey species;
- x_i - the population of the immature and mature prey species of stage i ;
- y_i - population of both predators species;
- β - maturation rate from immature stage to mature stage;
- α - per capita death rate of both predators;
- b - encounter rates of predators y_1 and y_2 with immature prey x_1 ;
- d - encounter rate of both predators y_1 and y_2 with mature prey x_2

In order to reduce the number of parameters, we

consider

$$\begin{aligned} at = \tau, \quad \frac{b}{a}x_1 = X_1, \quad \frac{b}{a}x_2 = X_2, \quad \frac{b}{a}y_1 = Y_1, \quad \frac{b}{a}y_2 = Y_2, \\ \frac{k}{a} = k_1, \quad \frac{\beta}{a} = \beta_1, \quad \frac{\alpha}{a} = \alpha_1, \quad \frac{d}{b} = d_1 \end{aligned} \quad (2.2)$$

the non-dimensionalized form of system (2.1) can be written as

$$\begin{aligned} \frac{dX_1}{d\tau} &= X_2 - (k_1 + \beta_1)X_1 - \frac{X_1^2 Y_1}{X_1 + X_2} - \frac{X_1^2 Y_2}{X_1 + X_2}, \\ \frac{dX_2}{d\tau} &= \beta_1 X_1 - k_1 X_2 - \frac{2d_1 Y_1 Y_2 X_2}{Y_1 + Y_2}, \\ \frac{dY_1}{d\tau} &= -\alpha_1 Y_1 + \frac{X_1^2 Y_1}{X_1 + X_2} + \frac{d_1 Y_1 Y_2 X_2}{Y_1 + Y_2}, \\ \frac{dY_2}{d\tau} &= -\alpha_1 Y_2 + \frac{X_1^2 Y_2}{X_1 + X_2} + \frac{d_1 Y_1 Y_2 X_2}{Y_1 + Y_2}. \end{aligned} \quad (2.3)$$

3 Steady States

We find the steady states of equations (2.3) by equating the derivatives on the left hand sides to zero and solving the resulting algebraic equations. This gives two possible steady states

- (i) $\bar{E}_0(0, 0, 0, 0)$ where the population is extinct
- (ii) Coexisting state where prey individuals and both predators individuals exist is

$$\bar{E}_1 = (\bar{X}_1, \bar{X}_2, \bar{Y}_1, \bar{Y}_2) = \left(\begin{array}{l} \frac{2\alpha_1(1+\bar{X})\bar{X}}{d_1(1+\bar{X})+2\bar{X}^2}, \\ \frac{2\alpha_1(1+\bar{X})}{d_1(1+\bar{X})+2\bar{X}^2}, \\ \frac{\beta_1\bar{X}-k_1}{d_1}, \frac{\beta_1\bar{X}-k_1}{d_1} \end{array} \right)$$

or equivalently

$$= \left(\begin{array}{l} \frac{2\alpha_1(1+\bar{X})\bar{X}}{d_1(1+\bar{X})+2\bar{X}^2}, \\ \frac{2\alpha_1(1+\bar{X})}{d_1(1+\bar{X})+2\bar{X}^2}, \\ \frac{(1+\bar{X})(1-(k_1+\beta_1)\bar{X})}{2\bar{X}^2}, \\ \frac{(1+\bar{X})(1-(k_1+\beta_1)\bar{X})}{2\bar{X}^2} \end{array} \right) \quad (3.1)$$

where

$$\bar{Y}_1 = \bar{Y}_2 = \frac{\beta_1\bar{X} - k_1}{d_1} = \frac{(1+\bar{X})(1-(k_1+\beta_1)\bar{X})}{2\bar{X}^2} \quad (3.2)$$

and $\bar{X} = \frac{\bar{X}_1}{\bar{X}_2}$ is a real positive root of the cubic equation,

$$L\bar{X}^3 + M\bar{X}^2 + N\bar{X} - d_1 = 0 \quad (3.3)$$

where $L = 2\beta_1$, $M = d_1(k_1 + \beta_1) - 2k_1$, $N = d_1(k_1 + \beta_1) - d_1$.

The cubic equation (3.3) is obtained from equation (3.2). Since the leading and absolute terms are positive and negative respectively, there is at least one positive root of (3.3).

This equilibrium (3.1) exists if $\frac{k_1}{\beta_1} < \bar{x} < \frac{1}{(k_1 + \beta_1)}$.

We find that the function $f(\bar{x})$ given by equation (3.3), will have only one positive root if one of the following conditions satisfies (i) $M > 0$ (ii) $M < 0$ and $N < 0$ or (iii) $M^2 < 3LN$ (see Appendix A).

Linearizing the system (2.3) about the trivial state \bar{E}_0 and using Routh-Hurwitz criteria, it can be shown that \bar{E}_0 will be stable if $k_1^2 > \beta_1(1 - k_1)$ (see Appendix B).

4 Stability of Coexisting State

An ecosystem model is globally stable if every trajectory of the model which begins at a positive octant state remains in the positive octant for all finite values of time and converges to positive equilibrium as $\tau \rightarrow \infty$. Let us consider the following function:

$$\begin{aligned} V(X_1, X_2, Y_1, Y_2) &= (X_1 - \bar{X}_1) + (X_2 - \bar{X}_2) \\ &+ \left[(Y_1 - \bar{Y}_1) - \bar{Y}_1 \ln \left(\frac{Y_1}{\bar{Y}_1} \right) \right] \\ &+ \left[(Y_2 - \bar{Y}_2) - \bar{Y}_2 \ln \left(\frac{Y_2}{\bar{Y}_2} \right) \right] \end{aligned} \quad (4.1)$$

Differentiating (4.1) with respect to τ and using (2.3) and (3.1), we have

$$\begin{aligned} \frac{dv}{d\tau} &= \left[X_2 - (k_1 + \beta_1)X_1 - \frac{X_1^2 Y_1}{X_1 + X_2} - \frac{X_1^2 Y_2}{X_1 + X_2} \right] \\ &+ \left[\beta_1 X_1 - k_1 X_2 - \frac{2d_1 Y_1 Y_2 X_2}{Y_1 + Y_2} \right] \\ &+ \left[-\alpha_1 Y_1 + \frac{X_1^2 Y_1}{X_1 + X_2} + \frac{d_1 Y_1 Y_2 X_2}{Y_1 + Y_2} \right] \left(\frac{Y_1 - \bar{Y}_1}{Y_1} \right) \\ &+ \left[-\alpha_1 Y_2 + \frac{X_1^2 Y_2}{X_1 + X_2} + \frac{d_1 Y_1 Y_2 X_2}{Y_1 + Y_2} \right] \left(\frac{Y_2 - \bar{Y}_2}{Y_2} \right) \end{aligned} \quad (4.2)$$

$$\begin{aligned} \frac{dv}{d\tau} = & X_2 - k_1 (X_1 + X_2) + \frac{d_1 Y_1 Y_2 X_2}{Y_1 + Y_2} \\ & \left[\left(-1 + \frac{Y_1 - \bar{Y}_1}{Y_1} \right) + \left(\frac{Y_2 - \bar{Y}_2}{Y_2} - 1 \right) \right] \\ & + \frac{X_1^2 Y_1}{X_1 + X_2} \left[\frac{Y_1 - \bar{Y}_1}{Y_1} - 1 \right] + \frac{X_1^2 Y_2}{X_1 + X_2} \left[\frac{Y_2 - \bar{Y}_2}{Y_2} - 1 \right] \\ & + \alpha_1 \bar{Y}_1 + \alpha_1 \bar{Y}_2 - \alpha_1 Y_1 - \alpha_1 Y_2 \end{aligned}$$

Since $\bar{Y}_1 = \bar{Y}_2$

$$\begin{aligned} \frac{dv}{d\tau} = & X_2 - k_1 (X_1 + X_2) + \bar{Y}_1 \left[\alpha_1 - \frac{d_1 Y_2 X_2}{Y_1 + Y_2} - \frac{X_1^2}{X_1 + X_2} \right] \\ & + \bar{Y}_1 \left[\alpha_1 - \frac{d_1 Y_1 X_2}{Y_1 + Y_2} - \frac{X_1^2}{X_1 + X_2} \right] - \alpha_1 Y_1 - \alpha_1 Y_2 \end{aligned} \quad (4.3)$$

$$\frac{dY_1}{d\tau} > 0 \text{ leads to } \alpha_1 - \frac{X_1^2}{X_1 + X_2} - \frac{d_1 Y_2 X_2}{Y_1 + Y_2} < 0 \quad (4.4)$$

and

$$\frac{dY_2}{d\tau} > 0 \text{ gives } \alpha_1 - \frac{X_1^2}{X_1 + X_2} - \frac{d_1 Y_1 X_2}{Y_1 + Y_2} < 0 \quad (4.5)$$

Hence

$$\frac{dv}{d\tau} \leq 0 \text{ if } k_1 > \frac{1}{1 + \left(\frac{X_1}{X_2} \right)} \text{ for all } \tau \geq 0 \quad (4.6)$$

where X_1 is the population of immature individuals and naturally their population will be much higher than mature individuals X_2 . So k_1 will satisfy the following inequality

$$\frac{1}{1 + \frac{X_1}{X_2}} < k_1 < 1 \quad (4.7)$$

Hence $\frac{dv}{d\tau} \leq 0$

Here the equality holds of $X_1 = \bar{X}_1, \bar{X}_2 = \bar{X}_2$, and $Y_1 = \bar{Y}_1$

We summarize the preceding details in the following theorem.

Theorem 1 Suppose $\bar{E}_1 = (\bar{X}_1, \bar{X}_2, \bar{Y}_1, \bar{Y}_2)$ exists, the condition (4.7) is satisfied and \bar{X} is the real positive root of equation (3.3), then the system (2.1) has a globally stable coexisting state \bar{E}_1 .

5 Summary and Conclusions

In this paper we have studied one prey and two predators model for the fish population of Tanganyika lake. The prey population was divided into two classes; those who cannot defend themselves (immature) and

those have defensive capability (mature). Mature prey individuals guards more against the abundant predator individuals and the rare predator individuals gains advantage. There are two possible equilibria: one where the population is extinct; one where population coexist. Saleem et al. [21] examined the similar model but they did not consider age structured prey population. We concentrated mainly on the stability of equilibrium points. Here we showed that the population extinct equilibrium was locally stable if $k_1^2 \geq \beta_1 (1 - k_1)$ and unstable if $k_1^2 < \beta_1 (1 - k_1)$. We also showed that the coexisting state will be globally stable by considering natural fact that mature prey population will always be less numerically than immature prey population. We gave the detailed proof for global stability.

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Appendix: At equilibrium from equations (2.3)₃ and (2.3)₄, we get

$$\frac{\bar{X}_1^2}{\bar{X} + \bar{X}_2} + \frac{d_1 \bar{Y}_2 \bar{X}_2}{\bar{Y}_1 + \bar{Y}_2} = \frac{\bar{X}_1^2}{\bar{X}_1 + \bar{X}_2} + \frac{d_1 \bar{Y}_1 \bar{X}_2}{\bar{Y}_1 + \bar{Y}_2} \quad (\text{A.1})$$

equation (A.1) clearly shows that

$$\bar{Y}_1 = \bar{Y}_2 \quad (\text{A.2})$$

using equation (2.3)₁ at equilibrium, we get

$$\bar{Y}_1 = \frac{\bar{X}_1 + \bar{X}_2}{2\bar{X}_1^2} [\bar{X}_2 - (k_1 + \beta_1) \bar{X}_1] \quad (\text{A.3})$$

similarly from equation (2.3)₂ at equilibrium, we get

$$\bar{Y}_1 = \frac{1}{d_1 \bar{X}_2} [\beta_1 \bar{X}_1 - k_1 \bar{X}_2] \quad (\text{A.4})$$

using equation (A.3), and (A.4) we obtain

$$\frac{1}{d_1 \bar{X}_2} [\beta_1 \bar{X}_1 - k_1 \bar{X}_2] = \frac{\bar{X}_1 + \bar{X}_2}{2\bar{X}_1^2} [\bar{X}_2 - (k_1 + \beta_1) \bar{X}_1]$$

this leads to

$$L\bar{X}^3 + M\bar{X}^2 + N\bar{X} - d_1 = 0 \quad (\text{A.5})$$

where $L = 2\beta_1, d_1(k_1 + \beta_1) - 2k_1 = M$, and $d_1(k_1 + \beta_1) - d_1 = N$

Cubic equation is positive for large values of \bar{X} and negative at $\bar{X} = 0$. So it will have either one or three positive real roots.

Let $f(\bar{x}) = L\bar{X}^3 + M\bar{X}^2 + N\bar{X} - d_1$
so $f'(\bar{x}) = 3L\bar{X}^2 + 2M\bar{X} + N$

$$f'(\bar{x}) = 0 \text{ if } \bar{X} = \frac{-M + \sqrt{M^2 - 3LN}}{3L} \quad (\text{A.6})$$

There are three possible cases under which $f'(\bar{x}) \neq$

(i) If $M^2 < 3LN$ both roots of (A.6) will be complex

(ii) If $M > 0$ both roots of (A.6) will be negative

(iii) If $M < 0$ and $N < 0$ then there will be only one positive root of (A.6)

Hence if any of the above three inequalities satisfies then equation (3.3) will have only one positive root.

Appendix B: Consider a small perturbation about the equilibrium level $X_1 = \bar{X}_1 + u, \bar{X}_2 = \bar{X}_2 + v, Y_1 = \bar{Y}_1 + w, Y_2 = \bar{Y}_2 + s$. Substituting these into the differential equations (2.3) and neglecting products of small quantities, we obtain stability matrix

$$\begin{pmatrix} -(k_1 + \beta_1) - \lambda & 1 & 0 & 0 \\ \beta_1 & -k_1 - \lambda & 0 & 0 \\ 0 & 0 & -\alpha_1 - \lambda & 0 \\ 0 & 0 & 0 & -\alpha_1 - \lambda \end{pmatrix} \quad (\text{B.1})$$

The characteristic equation of this matrix is

$$(\alpha_1 + \lambda)^2 [(k_1 + \alpha)(k_1 + \beta_1 + \alpha) - \beta_1] = 0 \quad (\text{B.2})$$

If $k_1^2 > \beta_1(1 - k_1)$, the equilibrium $\bar{E}_0 = (0, 0, 0, 0)$ is locally stable otherwise unstable.