

Ordinary Differential Equation Models in Population Ecology, with special reference to Deterrence

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Abstract

Nature consists of qualitatively different kinds of mutualistic systems. Different types of mutualistic interactions have different stability properties. The main important factors which contribute to this diversity are: the mechanism by which one species benefits the other and the number of species that must interact in order for there to be mutualism between two of them. In the second case, if the number of species is more than two, then the mutualism is called indirect mutualism and in this case the interactive dynamics is very complex. Thus the models, we shall consider in this paper will be at least three dimensional. We shall present a mutualist prey-predator model, modeling facultative mutualism with the prey species and the existence of periodic solution will be discussed. We shall also consider a model when a mutualist can modify a competitive outcome of the interaction, leading to coexistence in a system of competing species. Two four species models will also be presented.

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1 Introduction

Ecology is a branch of science, which deals with the interaction of organisms with one another and with the physical environment in which they live. Basic interactions, we are concerned with are: predator-prey interactions, competition for resources and the mutualistic interactions. Scientific curiosity and understanding of species relations and their mutual interactions are not just an academic exercise, but are related to the essential need of organisms. Every organism depends on some resource for its survival. The capacity to utilize the resource, which enabled the primitive man to survive, gradually attained multiple dimensions, which in modern times tends to threaten

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the life support systems. In the course of evolutionary history, humans and their activities were having significant impacts on natural dynamics of the earth system. However, the various human activities such as : food production, international trade and commerce, energy production etc. are transforming the earth system on various scales, ranging from local to global. Population explosion and the economic growth have drastically increased the degradation of natural resources. If we draw our attention to contemporary situations of the ecosystem, a very critical situation of our ecosystem appears, alarming the future prospective. Although mutualistic interactions are very much important for conservation of biodiversity, yet mathematical models are rare in literature. The purpose of this paper is to highlight the importance of mutualistic interactions on the crucial ecological issue of extinction/persistence , through some mathematical models, governed by system of autonomous ordinary differential equations.

The occurrence of mutualism can arise in a great variety of ways in nature (cf. [24, 1]). Some of the mutualistic benefits may be listed as; deterring predation, increasing prey availability, feeding on a predator, increasing or decreasing competitive outcomes, competing with a predator etc. All of these types of mutualistic benefits are well known to occur in nature. Early models of mutualism were two dimensional (cf. [3], [6]). Three dimensional mutualistic models, where the mutualism arise due to presence of a third population, were first analyzed in Rai, et al. (cf.[18]). Since then, until recently, there has been a fair amount of work, on three dimensional mutualistic models, (cf. [13, 14, 15, 18]). There is very little work on four dimensional mutualistic models. Freedman and Rai (cf. [12]) and Kumar and Freedman (cf. [16]), did some work to analyse four dimensional mutualistic models, throwing some light into the complex mutualistic interactions. Different types of mutualistic interactions have different stability properties (cf. [2]). Therefore, a diverse set of models of mutualism should be retained because conclusions based upon one type of mutualism need not apply to the other. We refer (cf. [21, 22, 23]) for mathematical analysis of recent four dimensional mathematical models of mutualism.

In any mutualistic system there may be more species involved in the interaction, because a mutualist could simultaneously benefit its partners in more than one ways (cf. [2], [3]). Ants as mutualist decrease predation on treehoppers, due to deterrence mechanism. Mutualism may arise indirectly where there is no contact between the species (cf. [23]). Some systems may involve interactions of at least five species in order for there to be mutualism between two of them. For example, consider a plant- herbivores aphids which attract ants, which in turn deter both the herbivores of the plant and the predators of the aphids. Other types of mutualisms involving beneficial interactions among two-species may still be very complex if there is multiple form of benefit involved in the system. For example, in the Acacia system described by Addicott and Freedman (cf. [2]), at least five benefits are involved in the interaction between ants and acacias, including deterring predation and competition, ameliorating abiotic mortality, providing habitat and food. Among much qualitatively different type of mutualisms, we refer (cf. [7, 9, 10, 11, 14, 15, 18]) for detailed analysis of three dimensional mathematical models, involving mutualistic interactions in different aspects, and (cf.[21, 22, 23, 16, 12, 19]) for four dimensional mathematical models.

A mutualist of prey may decrease the predation of its predators, or compete with its predators. A mutualist of a prey may help it to out compete its predators by aiding it directly, competing with competitors or preying on its predators. Ecologically, this could involve a variety of different mechanisms, but all would have the effect of decreasing the rate at which prey are captured by the predators (cf.[17]). For example a mutualist might camouflage the prey making it less apparent to the predators, or the mutualist might make the prey harder to be captured, or it might directly deter the predators from feeding upon the prey.

In this paper, we are concerned with an important concept in theoretical ecology. Namely, does the introduction of a mutualist into an existing community of species serve to enhance the long term survival of the community? Here we address the question for the case in which existing community can be modeled by at least three autonomous differential equations. Often the consideration of a third species changes the commensal association into mutualism between the other two species. For example ants deter herbivores from feeding on plants (cf. [2]), and ants deter predators from feeding on aphids (cf. [1]). In the absence of herbivores and predators, the association between ants -plants and ants- aphids, respectively is surely commensal (cf. [20]).

The organization of this paper is as follows. In the next section, we will present two three-dimensional mutualistic models, each of them presenting a particular aspect of mutualistic interaction. Section 3 deals with a brief presentation of two four dimensional mathematical models, each of them possessing a rich wealth of ecological informations. Proper references have been given in

the end, with their citations in the text.

2 Three Species Models

In Addicott and Freedman (cf. [2]), the authors have considered the interactions of predator- prey populations in competitive environment with a slow-growing mutualist. Here we consider the general case where the dynamics of all the three species must be considered. Details and proofs of the results mentioned here are found in Rai, et.al.(cf. [18], [11]).

2.1 Predator-Prey-Mutualist Model

Here we propose a model of predator and prey populations interacting with a mutualist, to the prey species. Mathematically this model can be represented by the following system of autonomous differential equations

$$(2.1) \quad \begin{cases} \dot{u} = uh(u, x) \\ \dot{x} = \alpha x[g(u, x) - yp(u, x)], \\ \dot{y} = y[-s + cp(u, x)], \\ u(0) > 0, x(0) > 0, y(0) > 0. \end{cases}$$

where t represents time, $u(t)$ the population of mutualist at any time t , $x(t)$ population of prey at any time t , $y(t)$ population of predators at any time t , and $s > 0$, $c > 0$, $\alpha > 0$ are parameters of the system.

Functions $h(u, x)$, $g(u, x)$, $p(u, x)$, from $\mathbb{R}_+ \times \mathbb{R}_+ \rightarrow \mathbb{R}$ are continuous and sufficiently smooth to ensure the existence and uniqueness of solutions of initial value problem (1) with initial conditions in \mathbb{R}^+ and to allow the stability analysis of any solutions of (1). We also require the solutions to be defined on some interval $[0, T)$ where $0 \leq T < \infty$. we further make the following assumptions:

H1: The function $h(u, x)$ represents the specific growth rate of mutualist in the absence of prey and satisfies:

- (a) $h(0, x) > 0$,
- (b) $\exists L : \mathbb{R}_+ \rightarrow \mathbb{R}_+$ such that $h(L(x), x) = 0$ with $\frac{dL}{dx} \geq 0$,
- (c) $\frac{\partial h(u, x)}{\partial u} < 0$,
- (d) $\frac{\partial h(u, x)}{\partial x} > 0$.

Ecologically, the above assumptions impose the following conditions on mutualist population.

1. The mutualist can grow at low densities with or without the prey x . This indicates that mutualism is non-obligate for the mutualist.
2. The population of mutualist can not grow over a certain population size, which depends on population size of its partner prey; this means that it has carrying capacity L , which is a function of prey population.
3. The growth of population of mutualist is slowed by an increase in its own population, other populations remaining the same. This further implies that mutualist exhibits density dependent growth. Ecologically this is termed as "population effect".
4. Population of mutualist is enhanced by an increase in the prey population for any population of the mutualist.

H2: The function, $g(u, x)$ represents the specific growth rate of prey population. We propose the following hypotheses for this function:

- (a) $g(u, 0) > 0$,

- (b) $\frac{\partial g(u,x)}{\partial x} < 0$,
- (c) $\exists k : \mathbb{R}_+ \rightarrow \mathbb{R}$ such that $g(u, k(u)) = 0$, with $\frac{dk}{du} > 0$
- (d) $\frac{\partial g(u,x)}{\partial u} \leq 0$.

Ecologically the above assumptions, impose the following restrictions on specific growth rate of prey:

1. The prey can grow at low densities with or without the presence of mutualists, so the mutualism is also non-obligate for prey.
2. The population growth of prey is slowed by an increase in its own numbers, for a fixed population size of mutualist. In other words the prey exhibit density dependent growth pattern.
3. The population of prey can not grow over a certain size in any environment. In other words the environment has carrying capacity for prey, which depends on population size of the mutualist.
4. There may be a cost to prey associating with the mutualist. In other words the growth rate of prey is suppressed by an increase in the mutualist population.

H3: The function $p(u, x)$, represents the predator's response function. We propose the following hypotheses on this function:

- (a) $p(u, 0) = 0$,
- (b) $\frac{\partial p(u,x)}{\partial x} > 0$,
- (c) $\frac{\partial p(u,x)}{\partial u} \leq 0$,
- (d) $p(u, x) \geq 0$.

Ecologically, these hypotheses impose the following restrictions on the predators response function:

1. The predator's response to the prey density, which refers to change in the density of prey per unit of time per predator as the prey density changes, is assumed always to be non-negative. Also there can not be any predation in the absence of prey.
2. For fixed population of other species, the predation is enhanced with the increase in the number of prey species.
3. The mutualist cuts down the effectiveness of predation on the prey. This may be termed as "Mutualist effect". This is the main effect incorporated in the model.

The death rate incorporated in the model is a combination of natural death and harvesting of predator by other enemies. Obviously our model is valid if a predator is harvested by other predators or they die a natural death. The above assumptions are ecologically reasonable and exemplified in nature as discussed in the introduction.

It is easy to show that our system is well behaved in the sense that all the solutions of the system (1) remain positive and bounded, with initial positive conditions(cf. [18]).

2.1.1 Main Results

Various equilibrium points of the system are : $E_1(0, 0, 0)$, $E_2(0, k(0), 0)$, $E_3(L(0), 0, 0)$, $E_4(0, \hat{x}, \hat{y})$, $E_5(\bar{u}, \bar{x}, 0)$, $E_6(u^*, x^*, y^*)$. The conditions for their existence have been given in detail in (cf. [18]). The main results are:

Theorem 2.1. *If the following conditions hold*

1. $\frac{s}{c} \in \text{Range } p(L(x), x)$,

2. $-s + cp(L(x), x) = 0$ and
3. $x < K(L(x))$,

then there exists a unique interior equilibrium.

Theorem 2.2. Let (u^*, x^*, y^*) be the interior equilibrium state of the system. Further let the following two conditions hold

1. $a_1, a_2, a_3 > 0$,
2. $b_1, b_2 < 0$,

then as the value of α (the bifurcation parameter) passes through $\alpha_0 (= -\frac{b_2}{b_1})$, small amplitude periodic solutions of the system appear, which bifurcate from the equilibrium state (u^*, x^*, y^*) .

(see (cf. [18]) for the values of a_1, a_2, a_3, b_1, b_2 and other details and proofs)

2.1.2 A Specific Example

Here we analyze a special case of the general model, incorporating all its important features, as mentioned in the model. We consider the following model

$$(2.2) \quad \begin{cases} \dot{u} = \gamma u \left[1 - \frac{u}{L_0 + lx} \right], \\ \dot{x} = \alpha x \left[1 - \frac{x}{K} \right] - \frac{\beta xy}{1 + mu}, \\ \dot{y} = y \left[-s + \frac{c\beta x}{1 + mu} \right]. \end{cases}$$

where the parameters $\alpha, \beta, \gamma, l, L_0, K, m, c, s$ all are positive. This particular model refers to the case, where in the absence of the predator y , the association between u and x is not mutualistic, but commensal. The mutualism occurs when we introduce the predator into the system. Possible equilibrium states are: $E_1(0, 0, 0)$, $E_2(0, K, 0)$, $E_3(L_0, 0, 0)$, $E_4(0, \frac{s}{c\beta}, \frac{\alpha}{\beta} [1 - \frac{s}{Kc\beta}])$, $E_5(L_0 + lK, K, 0)$. For the specific values of the parameters taken as $c = l = m = s = L_0 = 1, \beta = 2, \gamma = 4, K = 8$, all the restrictions of the assumptions are satisfied. With these values, conditions of the mathematical results are also satisfied and the value of α_0 comes out to be 8. Hence if 8 is in the range of the values of α , the equilibrium state $(3, 2, \frac{3}{2}\alpha)$ bifurcates into periodic orbits.

2.1.3 Discussions

In this model a predator-prey-mutualist system has been modeled and mathematically analyzed. Conditions for equilibria were given, and the stability of these equilibria were determined. Conditions were also given for the existence of three-dimensional periodic solutions. A specific example was given.

It was found that by adding a mutualist to the system, the prey equilibrium value is increased. This was the effect in the case of a stable interaction of increasing the effective carrying capacity for the prey species. Further the carrying capacity of the mutualist is also increased. However, as expected, all populations remain bounded. Depending upon the parameters, adding a mutualist to the system could be either stabilizing or destabilizing, and therefore limit cycles could appear, where they were not before, or disappear.

Finally, adding a mutualist to a predator-prey system could cause the predator to go extinct, in which case the prey and mutualist population numbers approach equilibrium values.

2.2 Competitor-Competitor-Mutualist Model

We propose as a model, two competing species x_1, x_2 and a third species u , which acts as a mutualist to the species x_1 (cf. [11]). We shall assume that there is no direct interaction between u and x_2 . The dynamical behavior of a Competitor-Competitor-Mutualist community is represented by the following system of equations:

$$(2.3) \quad \begin{cases} \dot{u} = uh(u, x_1), \\ \dot{x}_1 = \alpha x_1 [g_1(u, x_1) - q_1(u, x_1, x_2)], \\ \dot{x}_2 = x_2 [g_2(x_2) - q_2(x_1, x_2)], \\ u(0) > 0, x_1(0) > 0, x_2(0) > 0, \end{cases}$$

where u, x_1 form a mutualist pair. The hypotheses implicit in the system (3) are that the rate of increase or decrease of the populations does not depend upon time and that the populations are so large as to be measurable with real numbers and not subject to the random fluctuations. The functions $h(u, x_1)$ and $g_i, i = 1, 2$ are as in system (1), and the competition functions $q_i, i = 1, 2$ are increasing functions of x_1 and x_2 , but in addition q_1 is a decreasing function of u , which is the mutualist of x_1 .

2.2.1 Main Results

In addition to local and global stability behavior (cf. [8, 5]), the following results have been proved.

Theorem 2.3. *Let the following conditions hold, in addition to those mentioned in the assumptions*

1. $\min \{[g_1(0, 0) - q_1(0, 0, K_2)], [g_1(0, L(0)) - q_1(0, L(0), K_2)]\} > 0$,
2. $\min \{[g_2(0) - q_2(K_1(0), 0)], [g_2(0) - q_2(\bar{x}_1, 0)]\} > 0$,
3. $\frac{\partial g_1(u, x_1)}{\partial u} > 0$,
4. $uh_u(u, x_1) + x_1 h_{x_1}(u, x_1) \leq -\alpha_1 < 0; u g_{1u}(u, x_1) + x_1 g_{1x_1}(u, x_1) \leq -\alpha_1 < 0$,

then the system (3) is persistent.

(see (cf. [11]) for other details)

Theorem 2.4. *Let $(\bar{u}, \bar{x}_1, \bar{x}_2)$ be an interior equilibrium state of the system (3), lying in positive octant of the phase space of the variables u, x_1, x_2 . Also, let the following conditions hold*

1. $a_1 > 0, a_2 > 0, a_3 > 0$,
2. there exist $\alpha_0 > 0$ such that $b_1 \alpha_0^2 + b_2 \alpha_0 + b_3 = 0$, and $b_2^2 > 4b_1 b_3$,

then as the value of α (the bifurcation parameter) passes through α_0 , there appear small amplitude periodic solution of the system (3), bifurcating from the equilibrium $(\bar{u}, \bar{x}_1, \bar{x}_2)$.

(see (cf. [11]) for the values of a_1, a_2, a_3, α and other details)

2.2.2 An Example

Here we give a numerical example to illustrate the appearance of small amplitude periodic solutions if the functions h, g_1, g_2, q_1 and q_2 are chosen properly. Consider the following system:

$$(2.4) \quad \begin{cases} \dot{u} = \frac{u}{10} [1 - u + x_1], \\ \dot{x}_1 = \alpha x_1 [1 - x_1 - \frac{572}{1155} \cdot \frac{u}{1+x_1}] - \frac{\alpha x_1 x_2}{1+u} \\ \dot{x}_2 = x_2 [1 - x_2] - \frac{3x_1 x_2}{2}. \end{cases}$$

We find that $\bar{u} = \frac{11}{10}, \bar{x}_1 = \frac{1}{10}, \bar{x}_2 = \frac{17}{20}$ is an equilibrium state. Calculations at $E^*(\frac{11}{10}, \frac{1}{10}, \frac{17}{20})$ show that

$a_1 = .0096 + 00549\alpha > 0, a_3 = .0008\alpha > 0, b_1 = -.0002, b_2 = -.0006, b_3 = .0897$ and the value of the parameter α comes out to be approximately 19.73. Thus all the hypotheses framed and the mathematical conditions are satisfied and we shall have perturbed periodic solutions in three dimensions (cf. [11]).

2.2.3 Discussions

In this model, a Competitor-Competitor-Mutualist system has been modeled and analyzed. Conditions for equilibria were given, and the stability of these equilibria were determined. Conditions were also given for the existence of three-dimensional periodic solutions. A specific numerical example was given to support the mathematical analysis.

It was found that the mutualist will play a very important role in such an ecosystem. For example, when the inhibitory effect of the species x_2 on the species x_1 is very high, the mutualist reduces the effectiveness of the competition coefficient and thereby could cause the reversal of stability of the interior equilibrium state in both the cases and reverse competitive outcome. Also, in the absence of the mutualist, the competitive sub community, does not admit any interior equilibrium, but the introduction of mutualist into the system always guarantees an equilibrium state. This shows that the mutualist could change competitive exclusion to coexistence.

3 Four Species Models

In this section, we consider two four dimensional mutualistic models, reflecting different aspects of complex mutualistic interactions and their dynamics. We refer Freedman and Rai, (cf. [12]) and Rai and Singh, (cf. [22]) for details and proofs of the results mentioned here.

3.1 Competitor-Mutualist Model

We consider as a model of two competitors interacting with two mutualists (cf. [12]). The dynamical behavior of the system under consideration is governed by the following system of autonomous differential equations:

$$(3.1) \quad \begin{cases} \dot{u}_1 = u_1 h_1(u_1, x_1), \\ \dot{x}_1 = x_1 g_1(u_1, x_1) - x_1 x_2 q_1(u_1), \\ \dot{u}_2 = u_2 h_2(u_2, x_2) \\ \dot{x}_2 = x_2 g_2(u_2, x_2) - x_1 x_2 q_2(u_2), \\ u_i(0) > 0, x_i(0). \end{cases}$$

where t represents time, $u_i(t)$ represent the mutualist population of $x_i(t)$ at any time t , $i = 1, 2$, and $x_i(t)$ is the corresponding competitor. Corresponding to these interactions, we propose the following hypotheses for the functions occurring in the model. H0: We assume that h_i, g_i, q_i are sufficiently smooth so that solutions to the initial value problem exist and are unique.

H1: $h_i(0, x_i) > 0$, $\frac{\partial h_i(u_i, x_i)}{\partial u_i} < 0$, $\frac{\partial h_i(u_i, x_i)}{\partial x_i} > 0$; there exists

$L_i(x_i), L_i(0) > 0$ such that $h_i(L_i(x_i), x_i) = 0, i = 1, 2$. The above hypotheses impose the following properties on the h_i , respectively. The mutualist population is capable of growing on its own, and hence the mutualism of x_i on u_i is facultative. The growth rate, however, is decelerated as its population numbers increase due to environmental limitations, x_i is the mutualist of u_i . There is a carrying capacity of the environment which limits the mutualist populations as a function of the number of x_i .

H2: $g_i(u_i, 0) > 0$; $g_{i,x_i}(u_i, x_i) < 0$; there exist $K_i(u_i), K_i(0) > 0$ such that $g_i(u_i, K_i(u_i)) = 0$ and such that $\lim_{u_i \rightarrow \infty} K_i(u_i) = \bar{K}_i < \infty$ as time tends to infinite. These hypotheses are described as follows. Each competitor is capable of growing on its own, but the growth rate decreases as the population increases, limited by its carrying capacity, which is a function of the mutualist population.

H3: $q_i(u_i) > 0$, $\frac{\partial q_i(u_i)}{\partial u_i} \leq 0, i = 1, 2$. It may be noted that the competition effect is reduced by the mutualist. In any case, competition is always increased by a rise in the either population. From the above hypotheses, it is straight forward to show that the system (5) is dissipative. In fact, we can describe a region A , which contains the region of attraction.

3.1.1 Main Results

There are a large number of possible equilibria for the system under consideration. First we note that $E_0(0, 0, 0, 0)$ always exist. As well, the following equilibria are obvious, $E_1(L_1(0), 0, 0, 0)$, $E_2(0, K_1(0), 0, 0)$, $E_3(0, 0, L_2(0), 0)$, $E_4(0, 0, 0, K_2(0))$, $E_5(L_1(0), 0, L_2(0), 0)$, $E_6(L_1(0), 0, 0, K_2(0))$, $E_7(0, K_1(0), L_2(0), 0)$, $\bar{E}(0, \frac{56500}{271}, 0, \frac{45000}{271})$, and $E^*(1200, \frac{2375}{2}, 2413, \frac{875}{4})$.

In addition to the assumptions, let the following conditions (From local stability analysis) also hold.

H4: $g_2(L_2(0), 0) - x_1 \hat{x}_1 q_2(L_2(0), \hat{x}_1, 0) > 0$.

H5: \tilde{M}_1 and \tilde{M}_2 (see (cf. [12])) have no eigen values with zero real parts, and

H6: \tilde{E}_i , if it exists, is globally asymptotically stable with respect to solutions initiating in the interior of the $u_i - x_1 - x_2$ space for $i = 1, 2$. The following result has been proved (see (cf. [12])).

Theorem 3.1. *Let H(0)–H(6) hold, then the system (5) persists.*

From the results in Butler et al. (cf. [4]), the following corollary is obvious.

Corollary 3.1. *Let the assumptions (H0)–(H6) hold, then the interior equilibrium E^* exists.*

(see (cf. [12]) for proofs and other details)

3.1.2 An Example

Here we give an example to illustrate our results. The numerical coefficients are for illustrative purposes and do not necessarily represent any real system. Consider the following system

$$(3.2) \quad \begin{cases} \dot{u}_1 = 400u_1 \left[1 - \frac{u_1}{1150 + \frac{4x_1}{95}} \right], \\ \dot{x}_1 = 300x_1 \left[1 - \frac{x_1}{1500} \right] - \frac{14x_1x_2}{9(1 + \frac{u_1}{270})}, \\ \dot{u}_2 = 450u_2 \left[1 - \frac{u_2}{2394 + \frac{76x_2}{875}} \right], \\ \dot{x}_2 = 250x_2 \left[1 - \frac{x_2}{1000} \right] - \frac{x_1x_2}{1 + \frac{u_2}{475}}. \end{cases}$$

Various possible equilibrium points of the above system are $E_0(0, 0, 0, 0)$, $E_1(1150, 0, 0, 0)$, $E_2(0, 1500, 0, 0)$, $E_3(0, 0, 2394, 0)$, $E_4(0, 0, 0, 1000, 0)$, $E_5(1150, 0, 2394, 0)$, $E_6(1150, 0, 0, 1000)$, $E_7(0, 1150, 2394, 0)$, $\bar{E}(0, \frac{56500}{271}, 0, \frac{45000}{271})$, and $E^*(1200, \frac{2375}{2}, 2413, \frac{875}{4})$.

We observe that all the conditions framed in the hypothesis are satisfied and the other conditions of the results are also satisfied. Hence the system (6) persists.

3.1.3 Discussions

In this model we have considered a system of four autonomous ordinary differential equations as a model of four interacting populations, two species competing with each other and two mutualists, one for each competitor. Our main interest was to give criteria for the persistence of all the four populations. We have been able to investigate such criteria in terms of parameters of the system. It has been shown that in the absence of one of the mutualists the corresponding three dimensional subspace has no interior equilibrium state but if the mutualist is allowed to interact, then we do have an interior equilibrium state in the four dimensional state, establishing the fact that the mutualist has altered the competitive outcome, and as a result all the four species could persist.

3.2 Four Species Prey-Mutualist Model

We propose as a model, the interaction of two competing predators y, z for the same prey x , which is in mutualistic association with u . We refer Rai and Singh, (cf. [22]) for detail. The dynamical behavior of the system can be described by the following system of autonomous ordinary differential equations:

$$(3.3) \quad \begin{cases} \dot{u} = uh(u, x), \\ \dot{x} = \alpha xg(u, x) - yp_1(u, x) - zp_2(u, x), \\ \dot{y} = y[-s_1(y) - q_1(z) + c_1p_1(u, x)], \\ \dot{z} = z[-s_2(z) - q_2(y) + c_2p_2(u, x)], \\ u(0) > 0, x(0) > 0, y(0) > 0, z(0) > 0, \end{cases}$$

where t represents time, u the population of mutualist at any time t , x population of prey at any time t , y population of first predator at any time t , z population of second predator at any time t , $c_i > 0$, where $i = 1, 2$, $\alpha > 0$ are parameters and $s_1(y)$ and $s_2(z)$ are the specific growth rates of the predator species.

Functions h, g, p_i, q_i for $i = 1, 2$ from $\mathbb{R}_+ \times \mathbb{R}_+ \rightarrow \mathbb{R}$ are continuous and sufficiently smooth to ensure the existence and uniqueness of solutions of initial value problem (3.3) with initial conditions in \mathbb{R}^+ and to allow the stability analysis of any solutions of (3.3). Mathematical properties and their ecological implications of these functions are given in detail in assumptions. We also require the solutions to be defined on some interval $[0, T)$ where $0 \leq T < \infty$, we further frame the following assumptions on the functions appearing in the model:

H1: The function $h(u, x)$ represents the specific growth rate of the mutualist and satisfies:

- (a) $h(0, x) > 0$,
- (b) $\exists L : \mathbb{R}_+ \rightarrow \mathbb{R}$ such that $h(L(x), x) = 0$,
- (c) $\frac{\partial h(u, x)}{\partial u} < 0$,
- (d) $\frac{\partial h(u, x)}{\partial x} > 0$.

Ecologically, the above assumptions impose the following conditions on mutualist population:

1. The mutualist can grow at low densities with or without the prey x . This indicates that mutualism is non-obligate for mutualists.
2. The population of mutualists can not grow over a certain population size, which depends on population size of its partner prey; this means that it has a carrying capacity L , which is a function of prey population.
3. The growth of population of mutualist is slowed by an increase in its own population, other populations remaining the same. This further implies that mutualist exhibits density dependent growth. Ecologically this is termed as "population effect".
4. Population of mutualists is enhanced by an increase in the prey population for any population of the mutualist.

H2: The function, $g(u, x)$ represents the specific growth rate of prey population. We propose the following hypotheses for this function:

- (a) $g(u, 0) > 0, \forall u$,
- (b) $\frac{\partial g(u, x)}{\partial x} < 0$,
- (c) $\exists k : \mathbb{R}_+ \rightarrow \mathbb{R}$ such that $g(k(u), u) = 0$,
- (d) $\frac{\partial g(u, x)}{\partial u} \leq 0$.

Ecologically the above assumptions, impose the following restrictions on specific growth rate of prey:

1. The prey can grow at low densities with or without the presence of mutualists, so the mutualism is also non-obligate for prey.
2. The population growth of prey is slowed by an increase in its own numbers, for a fixed population size of mutualist. In other words the prey exhibit density dependent growth pattern.
3. The population of prey can not grow over a certain size in any environment. In other words the environment has a carrying capacity for prey, which depends on population size of the mutualist.
4. There may be a cost to the prey associating with the mutualist. In other words the growth rate of prey is suppressed by an increase in the mutualist population.

H3: The functions $p_i(u, x)$, $i = 1, 2$ represent the predator's response functions. We propose the following hypotheses on these functions:

- (a) $p_i(u, 0) = 0, p_i(u, x) \geq 0, \forall x, u$ and $i = 1, 2$,
- (b) $\frac{\partial p_i(u, x)}{\partial x} \geq 0$,
- (c) $\frac{\partial p_i(u, x)}{\partial u} \leq 0$.

Ecologically, these hypotheses impose the following restrictions on the predators response function:

1. The predator's response to the prey density, which refers to change in the density of prey per unit of time per predator as the prey density changes, is assumed always to be non-negative. Also there can not be any predation in the absence of prey.
2. For fixed population of other species, the predation is enhanced with the increase in the number of prey species.
3. The mutualist cuts down the effectiveness of predation on the prey. This may be termed as "Mutualist effect". This is the main effect incorporated in the model.

H4: The functions $q_1(z)$ and $q_2(y)$ represent the intensity of competition between predators y and z . We propose the following hypotheses on these functions

- (a) $q_i(0) = 0, i = 1, 2$,
- (b) $\frac{\partial q_1}{\partial z} > 0$,
- (c) $\frac{\partial q_2}{\partial y} > 0$.

Ecologically, these hypotheses impose the following restrictions on the functions $q_i, i = 1, 2$:

1. In the absence of competing predators there is no competition.
2. Competition increases with the increase in rival densities.

Here, in the present formulation, the word competition stands for both intra specific and inter specific competitions. The terms $q_i, i = 1, 2$ incorporate only inter specific competition, while intra specific competitions have been incorporated with growth rate functions of all the species, in the absence of competition.

H5: The functions $s_1(y)$ and $s_2(z)$ are death rates of competing predators. We propose the following hypotheses on these functions:

- (a) $s_i(0) > 0, i = 1, 2$,
- (b) $\frac{\partial s_1(y)}{\partial y} > 0$,
- (c) $\frac{\partial s_2(z)}{\partial z} > 0$.

Ecologically, these hypotheses impose the following restrictions on the death rates.

1. Initially death rates are positive.
2. Death rates remain positive for all the time.

The death rates incorporated in the model are a combination of natural death and harvesting of predator by other predators. Obviously our model is valid if a predator is harvested by other predators or they die a natural death. The above assumptions are ecologically reasonable and exemplified in nature as discussed in the introduction.

3.2.1 Main Results

Here we mention only main results, and for details we refer to Rai and Singh, (cf. [22, 19]). First we observe that trivial equilibrium $E_1(0, 0, 0, 0)$ always exists. As well the following one-dimensional and concerned two-dimensional equilibria are obvious, $E_2(L(0), 0, 0, 0)$, $E_3(0, K(0), 0, 0)$, $E_4(0, x_1, y_1, 0)$, $E_5(\bar{u}, \bar{x}, 0, 0)$, $E_6(0, x_2, 0, z_2)$. On ecological point of view, there must exist equilibrium in $u-x$ plane, for otherwise one of the populations would become extinct contradicting the concept of mutualism. Hence, we assume that E_5 will always exist.

There are other possible equilibria, which are in relative three-dimensional subspaces. Criteria for existence may be found in (cf.[18, 23]). If they exist, we denote them by $E_7(u_3, x_3, y_3, 0)$, $E_8(u_4, x_4, 0, z_4)$, $E_9(0, x_5, y_5, z_5)$. Finally, there may be a positive interior equilibrium denoted by $E_{10}(u^*, x^*, y^*, z^*)$. Apart from the stability analysis, the following theorem for coexistence of all the species has been proved.

Theorem 3.2. *Let the following conditions hold, in addition to those mentioned in the assumptions*

1. $s_i(0) < c_i p_i(0, K(0))$, $i = 1, 2$,
2. $s_2(0) < c_2 p_2(0, x_1)$,
3. $s_i(0) < c_i p_i(\bar{u}, \bar{x})$, $i = 1, 2$,
4. $s_1(0) < c_1 p_1(0, x_2) - q_1(z_2)$,
5. $s_2(0) < c_2 p_2(u_3, x_3) - q_2(y_3)$,
6. $s_1(0) < c_1 p_1(u_4, x_4) - q_1(z_4)$,

then the system (3.3) is uniformly persistent.

(see (cf. [22]) for other details)

From the results in Butler et al. (cf. [4]), the following corollary is obvious.

Corollary 3.2. *Let the assumptions (H1)–(H5) hold and conditions of theorem 3.2 are satisfied, then the interior equilibrium $E_{10}(u^*, x^*, y^*, z^*)$ exists.*

3.2.2 An Example

In order to illustrate the above we consider the following example. All coefficients and functions are taken for mathematical convenience, not exactly from a real ecological system. In this illustration the occurrence of all the boundary equilibrium points for a particular system is shown. Also uniform persistence is demonstrated by the use of the theorem. For this purpose we consider the following system

$$(3.4) \quad \begin{cases} \dot{u} = u \left[1 - \frac{u}{3+x} \right] \\ \dot{x} = 4x \left(1 - \frac{x}{1+4u} \right) - \frac{x}{1+4u} y - \frac{x}{1+4u} z \\ \dot{y} = y \left[-\frac{1}{3} - z + \frac{3x}{1+4u} \right] \\ \dot{z} = z \left[-\frac{1}{3} - y + \frac{5x}{1+4u} \right] \end{cases}$$

Various possible equilibrium points of the above system are listed as follows:

$$E_0(0, 0, 0, 0), E_1(3, 0, 0, 0), E_2(0, 4, 0, 0), E_3(7, 4, 0, 0), E_4(0, \frac{1}{9}, \frac{35}{9}, 0), E_5(0, \frac{1}{9}, 0, \frac{35}{9}), E_6(\frac{28}{5}, \frac{13}{5}, \frac{7}{5}, 0),$$

$E_7(\frac{28}{5}, \frac{28}{5}, 0, \frac{7}{5}), E_8(0, \frac{2}{3}, \frac{5}{3}, \frac{5}{3}), E^*(6.8529, 3.8529, 0.0735, 0.0735)$.

We obtain for the system (3.4)

$$H_1(x) = -\frac{79}{9} < 0, H_2(x) = \frac{35}{81} > 0, H_3(x) = \frac{1}{28} > 0, H_4(x) = -\frac{149}{9} < 0.$$

We also observe that conditions (H1) – (H5), framed in the assumptions are satisfied and all the conditions of results are satisfied, and thus the system (3.4) persists uniformly.

(see (cf. [22]) for the definition of $H_i(x), i = 1, 2, 3, 4$.)

3.2.3 Discussions

In this model, we have proposed and analyzed a system of four autonomous differential equations as a model of four interacting populations, two species competing with each other for a single prey species which is in beneficial interaction with a mutualist. Our main aim was to obtain criteria for the persistence of all the four species. We have been able to obtain such criteria in terms of parameters of the system and have illustrated the results with a numerical example. It has been established that if death rates of the predator are less than a certain threshold value depending upon conversion efficiency of the individual predator and the intensity of competition of the competitor, then the coexistence is possible.

4 Conclusion

In this paper, we are concerned with an important concept in theoretical ecology. Namely, does the introduction of a mutualist into an existing community of species serve to enhance the long term survival of the community? Here we address the question for the case in which existing community can be modeled by at least three autonomous differential equations. Often the consideration of a third species changes the commensal association into mutualism between the other two species. For this purpose, we have modeled four ecological interactions governed by system of autonomous differential equations: two three dimensional and two four dimensional, arising due to interactions of species exploring different aspects of complex ecological interactions. Main mathematical results, followed by a brief discussion, exploring their ecological implications, has been given in respective sections. Numerical examples supporting the analysis has also been given for each model.

After analysis, it was found that by adding a mutualist to the system, to interact, the prey equilibrium value is increased. This establishes the effect in the case of a stable interaction of increasing the effective carrying capacity to the prey species. Further the carrying capacity of the mutualist is also increased, due to positive interaction with the prey. Finally, if the death rates of the predators are less than a certain threshold value, depending upon conversion efficiency and the competition by the rivals, the uniform persistence of all the interacting species takes place.

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