

EXTINCTION IN A GENERALIZED LOTKA-VOLTERRA PREDATOR-PREY MODEL

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In this paper we discuss the asymptotic behavior of a predator-prey model with distributed growth and mortality rates. We exhibit simple criteria on the parameters which guarantee that all subpopulations but one predator-prey pair are driven to extinction as $t \rightarrow \infty$. Finally, we present numerical simulations to illustrate the theoretical results.

Key words: A Generalized Lotka-Volterra Model, Predator-Prey, Asymptotic Behavior, Extinction.

AMS subject classifications: 34C35, 92D25.

1. Introduction

In recent years, several researchers have investigated the dynamics of the following multispecies Lotka-Volterra competition models:

$$\begin{cases} \frac{dx_i(t)}{dt} = x_i(t) \left(a_i - \sum_{j=1}^N b_{ij} x_j(t) \right), \\ x_i(0) = x_i^0, \quad i = 1, \dots, N. \end{cases} \quad (1.1)$$

In [4], Ahmad and Lazer gave conditions under which the N th component of the solution of (1.1) approaches zero, while the other components approach a certain solution of a lower dimensional system. In [5], Montes de Oca extends this result to the nonautonomous case where the a_i and b_{ij} are functions of t . In [8], Zeeman gives conditions under which all but one of the species is driven to extinction, while the remaining species approaches the carrying capacity determined by its growth and mortality parameters. Montes de Oca and Zeeman generalize this result to the nonautonomous case in [7]. In [6], these same authors consider the nonautonomous case where there is a balance between extinction and survival of different species. For a system with N populations, and for each $r < N$, they give conditions under which r of the populations survive while the remaining $N - r$ populations are driven to extinction.

A generalization of the logistic model is developed by Ackleh et al. [2]. In this generalization, the growth and mortality parameters are chosen as elements of continuous intervals rather than from discrete sets of numbers. That is, the population is divided into subpopulations having growth and mortality parameters $q = (q_1, q_2)$ lying in the set $Q = [a_1, b_1] \times [a_2, b_2]$, where $a_1, a_2, b_1, b_2 \in \mathbb{R}^+$. The point $q^* = (b_1, a_2)$ locates the subpopulation with the highest growth to mortality ratio. It is assumed that the growth part of the interaction function is subpopulation specific while mortality is driven by interaction with the entire population. Subpopulation densities replace subpopulation sizes as the state variables, and $x(t, q)$ denotes the density of individuals having parameter q at time t . The resulting model,

$$\begin{cases} \frac{dx(t, q)}{dt} = x(t, q) \left[q_1 - q_2 \int_Q x(t, q) dq \right], \\ x(0, q) = x^0(q), \end{cases} \quad (1.2)$$

is an integro-differential equation that can intuitively be thought of as a Lotka-Volterra model of type (1.1) with “infinitely many” competing subpopulations. In [2] the authors show that at each time t , the solution of system (1.2) induces a measure on the growth-mortality parameter space. All subpopulations, but the one with the highest growth to mortality ratio, become extinct as $t \rightarrow \infty$. The surviving subpopulation then stabilizes at the level determined by the carrying capacity of a classical logistic model specified by the growth and mortality parameters of q^* . This implies the measure induced by the limit of $x(t, q)$ as $t \rightarrow \infty$ is a delta measure of weight $\frac{b_1}{a_2}$ centered at q^* .

In the present paper, we consider a generalization of the predator-prey Lotka-Volterra model. Because of the different structures of the interaction functions for the predator-prey models considered here, we cannot employ the same techniques as those used in [2, 4-8] to establish the boundedness and strict positivity of the total predator and prey populations (these bounds are crucial in proving extinction). Instead, we construct an auxiliary function which will be used to establish such bounds.

This paper is organized as follows. In Section 2, we review the basic facts about the classical Lotka-Volterra predator-prey model. Then we discuss the structure of the generalized model and what is meant by *dominance* and by the *extinction of non-dominant subpopulations*. In Section 3, we state and prove the theorems that make precise those ideas discussed previously. Section 4 is devoted to the numerical illustration of the theory. In Section 5, we summarize the main results and indicate possible directions for future research.

2. The Generalized Model

We establish some notation for the discussion that follows. In the space \mathbb{R}^N , we denote the closed positive cone by \mathbb{R}_+^N and the open positive cone by $int\mathbb{R}_+^N$.

Recall that the classical Lotka-Volterra predator-prey model is given by:

$$\left\{ \begin{array}{l} \frac{dX(t)}{dt} = X(t)[a - bY(t)], \\ \frac{dY(t)}{dt} = Y(t)[-c + dX(t)], \\ X(0) = X^0, \quad Y(0) = Y^0. \end{array} \right. \tag{2.1}$$

Here $X(t)$ and $Y(t)$ denote the prey and predator population size, respectively, at time $t \geq 0$. For the prey component, the parameters a and b are the fixed growth and mortality rates, respectively. For the predator component, the parameters d and c are the fixed growth and mortality rates, respectively. Note that these four parameters are meant to represent these rates for all individuals in the population. It is well known that for system (2.1) with fixed point $(\frac{c}{d}, \frac{a}{b}) \in \text{int}\mathbb{R}^2_+$, the solution is a closed curve in $\text{int}\mathbb{R}^2_+$ satisfying $dX + bY - c \ln X - a \ln Y = k$, where k is a constant depending upon initial conditions and the point $(\frac{c}{d}, \frac{a}{b})$ is interior to the curve.

In order to incorporate differences among individual growth and mortality, we must alter the model. We follow the approach given by Ackleh in [1]. We assume the prey and predator populations are divided into M and N subpopulations, respectively. We assume that growth for the prey is subpopulation specific, while mortality is driven by interaction with the entire predator population. Similarly, the mortality for the predator is subpopulation specific, while growth is driven by interaction with the entire prey population. Let $x_i(t)$ and $y_j(t)$ be the sizes of the i th prey subpopulation and the j th predator subpopulation, respectively, at time $t \geq 0$, where $i = 1, \dots, M$; $j = 1, \dots, N$. Let $x(t) = (x_1(t), \dots, x_M(t))$, and $y(t) = (y_1(t), \dots, y_N(t))$. We use $X(t) = \sum_{i=1}^M x_i(t)$ and $Y(t) = \sum_{j=1}^N y_j(t)$ for the total prey and predator population sizes, respectively. Then the *generalized predator-prey model* is:

$$\left\{ \begin{array}{l} \frac{dx_i(t)}{dt} = x_i(t)[a_i - b_i Y(t)], \quad i = 1, \dots, M, \\ \frac{dy_j(t)}{dt} = y_j(t)[-c_j + d_j X(t)], \quad j = 1, \dots, N, \\ x(0) = (x_1(0), \dots, x_M(0)), \quad y(0) = (y_1(0), \dots, y_N(0)). \end{array} \right. \tag{2.2}$$

Given any $(x(0), y(0)) \in \text{int}\mathbb{R}^{M+N}_+$, the existence and uniqueness of global solutions $(x, y) \in C^1([0, \infty); \text{int}\mathbb{R}^{M+N}_+)$ follow from standard results in the theory of systems of ordinary differential equations.

In system (2.2), suppose the subpopulations are ordered such that $\frac{a_1}{b_1} > \frac{a_k}{b_k}$, $k = 2, \dots, M$, and $\frac{d_1}{c_1} > \frac{d_k}{c_k}$, $k = 2, \dots, N$. With this specification, we say that subpopulations x_1 and y_1 are *dominant* in the sense that they have the highest growth to mortality ratios within the prey and predator classes, respectively. We will show that for such a system, $x_k(t) \rightarrow 0$, as $t \rightarrow \infty$, $k = 2, \dots, M$ and $y_k(t) \rightarrow 0$, as $t \rightarrow \infty$, $k = 2, \dots, N$. Meanwhile x_1 and y_1 remain bounded and strictly positive and as $t \rightarrow \infty$, this dominant pair of subpopulations traces a trajectory in $\text{int}\mathbb{R}^2_+$ such that it becomes increasingly close to a classical Lotka-Volterra orbit.

3. Extinction of Nondominant Subpopulations

We begin by outlining our strategy. We define a scalar valued auxiliary function H and show that H' , the total derivative of H along solutions of system (2.2), is negative. So H is bounded above by $H(0)$. From the boundedness of H along solutions of (2.2) and from the formula for H , we deduce that all of the components x_i , $i = 1, \dots, M$, and y_j , $j = 1, \dots, N$, of a solution of (2.2) are bounded above and that the dominant subpopulation components x_1 and y_1 are strictly positive. Using these facts, we show that all non-dominant subpopulations approach zero in the limit as $t \rightarrow \infty$.

Throughout the discussion, $(x(t), y(t))$ denotes the solution of (2.2) corresponding to given initial conditions $(x(0), y(0)) \in \text{int}\mathbb{R}_+^{M+N}$. For any $t \geq 0$, define $H(t) = \Gamma(t) + \Lambda(t) + \Phi(t) + \Psi(t)$, where

$$\begin{aligned} \Gamma(t) &= \frac{d_1}{b_1} \left(x_1(t) - \frac{c_1}{d_1} - \frac{c_1}{d_1} \ln \left(\frac{d_1 x_1(t)}{c_1} \right) \right), \\ \Lambda(t) &= \left(y_1(t) - \frac{a_1}{b_1} - \frac{a_1}{b_1} \ln \left(\frac{b_1 y_1(t)}{a_1} \right) \right), \\ \Phi(t) &= \sum_{i=2}^M \frac{d_1}{b_i} x_i(t), \end{aligned}$$

and

$$\Psi(t) = \sum_{j=2}^N \frac{c_1}{c_j} y_j(t).$$

Observe that $H \in C^1([0, \infty); \mathbb{R}_+)$.

Lemma 3.1: *The total derivative of H along any solution of system (2.2) is negative. That is,*

$$H'(t) = \frac{\partial H}{\partial x_1} \frac{dx_1}{dt} + \dots + \frac{\partial H}{\partial x_M} \frac{dx_M}{dt} + \frac{\partial H}{\partial y_1} \frac{dy_1}{dt} + \dots + \frac{\partial H}{\partial y_N} \frac{dy_N}{dt} < 0$$

for all $t \geq 0$. Hence, the auxiliary function H is bounded above on $[0, \infty)$.

Proof: For convenience, we suppress the explicit dependence on t . Let $\tilde{X} = \sum_{i=2}^M x_i$ and $\tilde{Y} = \sum_{j=2}^N y_j$. Then $H' = \Gamma' + \Lambda' + \Phi' + \Psi'$, where

$$\begin{aligned} \Gamma' &= \frac{d_1}{b_1} \left(x_1' - \frac{c_1}{d_1} \frac{x_1'}{x_1} \right) = \frac{d_1}{b_1} x_1' \left((a_1 - b_1 Y) - \frac{c_1(a_1 - b_1 Y)}{d_1 x_1} \right) \\ &= \frac{d_1}{b_1} x_1' (a_1 - b_1 Y) \left(\frac{d_1 x_1 - c_1}{d_1 x_1} \right) = \frac{1}{b_1} (a_1 - b_1 Y) (d_1 x_1 - c_1) \\ &= \left(\frac{a_1}{b_1} - y_1 \right) (d_1 x_1 - c_1) - (d_1 x_1 - c_1) \tilde{Y}; \\ \Lambda' &= y_1' - \frac{a_1}{b_1} \frac{y_1'}{y_1} = y_1' \left(1 - \frac{a_1}{b_1} \frac{1}{y_1} \right) \end{aligned}$$

$$\begin{aligned}
 &= y_1' \left(\frac{b_1 y_1 - a_1}{b_1 y_1} \right) = y_1 (-c_1 + d_1 X) \left(\frac{b_1 y_1 - a_1}{b_1 y_1} \right) \\
 &= (-c_1 + d_1 x_1) \left(y_1 - \frac{a_1}{b_1} \right) + d_1 \left(y_1 - \frac{a_1}{b_1} \right) \tilde{X}; \\
 \Phi' &= \sum_{i=2}^M \frac{d_1}{b_i} x_i' = \sum_{i=2}^M \frac{d_1}{b_i} x_i (a_i - b_i Y) = \sum_{i=2}^M \frac{d_1}{b_i} x_i (a_i - b_i y_1) + \sum_{i=2}^M \frac{d_1}{b_i} x_i (-b_i \tilde{Y}) \\
 &= \sum_{i=2}^M d_1 x_i \left(\frac{a_i}{b_i} - y_1 \right) - \tilde{Y} \sum_{i=2}^M d_1 x_i = \sum_{i=2}^M d_1 x_i \left(\frac{a_i}{b_i} - y_1 \right) - d_1 \tilde{X} \tilde{Y} \\
 &< \sum_{i=2}^M d_1 x_i \left(\frac{a_1}{b_1} - y_1 \right) - d_1 \tilde{X} \tilde{Y} = \left(\frac{a_1}{b_1} - y_1 \right) d_1 \tilde{X} - d_1 \tilde{X} \tilde{Y};
 \end{aligned}$$

and

$$\begin{aligned}
 \Psi' &= \sum_{j=2}^N \frac{c_1}{c_j} y_j' = \sum_{j=2}^N \frac{c_1}{c_j} y_j (-c_j + d_j X) \\
 &= c_1 \sum_{j=2}^N y_j \left(-1 + \frac{d_j}{c_j} x_1 + \frac{d_j}{c_j} \tilde{X} \right) = c_1 \sum_{j=2}^N y_j \left(\frac{d_j}{c_j} x_1 - 1 \right) + c_1 \sum_{j=2}^N y_j \frac{d_j}{c_j} \tilde{X} \\
 &< c_1 \sum_{j=2}^N y_j \left(\frac{d_1}{c_1} x_1 - 1 \right) + c_1 \sum_{j=2}^N y_j \frac{d_1}{c_1} \tilde{X} = (d_1 x_1 - c_1) \tilde{Y} + d_1 \tilde{X} \tilde{Y}.
 \end{aligned}$$

Combining these results, we have

$$\begin{aligned}
 H' &< \left(\frac{a_1}{b_1} - y_1 \right) (d_1 x_1 - c_1) - (d_1 x_1 - c_1) \tilde{Y} \\
 &+ (-c_1 + d_1 x_1) \left(y_1 - \frac{a_1}{b_1} \right) + d_1 \left(y_1 - \frac{a_1}{b_1} \right) \tilde{X} \\
 &+ \left(\frac{a_1}{b_1} - y_1 \right) d_1 \tilde{X} - d_1 \tilde{X} \tilde{Y} + (d_1 x_1 - c_1) \tilde{Y} + d_1 \tilde{X} \tilde{Y} = 0.
 \end{aligned}$$

That is, $H'(t) < 0$ along solutions of system (2.2). So $H(t) \leq H(0)$ for each $t \geq 0$. \square

From Lemma 3.1 we obtain the following corollary.

Corollary 3.2: *There exists a positive constant U such that $0 \leq x_i(t) \leq U$, $i = 1, \dots, M$, $0 \leq y_j(t) \leq U$, $j = 1, \dots, N$, $\forall t \geq 0$. Furthermore, there exists a positive constant δ such that $0 < \delta \leq x_1(t)$, $0 < \delta \leq y_1(t)$, $\forall t \geq 0$.*

Proof: The results follows immediately from H being bounded on $[0, \infty)$. \square

Remark: We point out that U and δ depend on the initial conditions and the growth and mortality parameters.

In the next theorem, we show that all nondominant subpopulations are driven to

extinction.

Theorem 3.3: For system (2.2), $x_k(t) \rightarrow 0$ and $y_k(t) \rightarrow 0$ as $t \rightarrow \infty$, for $k \neq 1$.

Proof: We begin by considering the prey case. Use the ratio $r(t) = \frac{\frac{1}{b_k} x_k(t)}{\frac{1}{b_1} x_1(t)}$ to establish a comparison between $x_1(t)$ and $x_k(t)$ and then use the fact that $x_1(t)$ is bounded on $[0, \infty)$, along with the comparison result, to conclude that $x_k(t) \rightarrow 0$ as $t \rightarrow \infty$. If $k \in \{2, \dots, M\}$, then

$$\begin{aligned} \frac{d}{dt} \begin{bmatrix} \frac{1}{b_k} x_k \\ \frac{1}{b_1} x_1 \end{bmatrix} &= \begin{bmatrix} \frac{1}{b_k} x_k^{b_k} (a_k - b_k Y) - \frac{1}{b_1} x_k^{b_k} (a_1 - b_1 Y) \end{bmatrix} \begin{pmatrix} \frac{1}{b_k} \\ \frac{1}{b_1} \end{pmatrix} \\ &= \begin{bmatrix} \frac{1}{b_k} x_k \\ \frac{1}{b_1} x_1 \end{bmatrix} \left(\frac{a_k}{b_k} - \frac{a_1}{b_1} \right). \end{aligned}$$

By the dominance of x_1 , we have $\frac{a_k}{b_k} - \frac{a_1}{b_1} = -\lambda_k$, where λ_k is a positive constant. So we have a first order differential equation of the form $r'(t) = -\lambda_k r(t)$, whose solution is $r(t) = r(0)e^{-\lambda_k t}$. In terms of x , we have

$$\frac{\frac{1}{b_k} x_k(t)}{\frac{1}{b_1} x_1(t)} = \left[\frac{\frac{1}{b_k} x_k(0)}{\frac{1}{b_1} x_1(0)} \right] e^{-\lambda_k t}.$$

Solving for x_k , we obtain

$$x_k(t) = \left[\frac{x_k(0)}{\frac{b_k}{b_1} x_1(0)} \right] e^{-\lambda_k b_k t} \frac{b_k}{b_1} x_1(t).$$

Since $x_1(t)$ is bounded on $[0, \infty)$, there exists a positive constant A such that $x_k(t) \leq A e^{-\lambda_k b_k t}$, for $t \geq 0$. So $x_k(t) \rightarrow 0$ as $t \rightarrow \infty$, for $k \neq 1$.

An analogous argument for the predator case yields $y_k(t) \rightarrow 0$ as $t \rightarrow \infty$, for $k \neq 1$. \square

4. Numerical Results

We present an example to illustrate the behavior of the model (2.2). In this simulation, there are ten predator and ten prey subpopulations. For the dominant prey subpopulation, the growth parameter is $a_1 = 1$ and the mortality parameter is $b_1 = 0.8$. For the dominant predator subpopulation, the mortality parameter is $c_1 = 0.6$ and the growth parameter is $d_1 = 1.2$. Using these parameters a, b, c and d in the setting

of the classical model (2.1), the equilibrium value for the prey population is $\frac{c}{d} = 0.5$, while the equilibrium value for the predator population is $\frac{a}{b} = 1.25$.

Each $x_i(0)$, $i = 1, \dots, M$, and $y_j(0)$, $j = 1, \dots, N$, is set equal to 0.1. The growth and mortality parameters for the nondominant subpopulations are set as follows:

$$a_n = a_{n-1} - 0.020(n - 1),$$

$$b_n = b_{n-1} + 0.016(n - 1)$$

$$c_n = c_{n-1} + 0.012(n - 1)$$

and

$$d_n = d_{n-1} - 0.024(n - 1), \quad n = 2, \dots, 10.$$

With these initial conditions and parameters, we solve system (2.2) for $t \in [0, 250]$.

Figure 1 represents the predator population vs. prey population for $t \in [0, 50]$. The solid curve is the trajectory for the total populations, while the dashed curve is the trajectory for the dominant subpopulations. When $t = 0$, the total population trajectory starts at the point $(X(0), Y(0)) = (1, 1)$ and moves in a counterclockwise fashion. The trajectory for the dominant subpopulations begins at the point $(x_1(0), y_1(0)) = (0.1, 0.1)$ and moves in a counterclockwise fashion as it approaches the total population trajectory. The behavior discussed in the previous sections is already becoming clear. Since every prey subpopulation other than the dominant one approaches zero as $t \rightarrow \infty$, the dominant prey subpopulation must approach the total prey population as $t \rightarrow \infty$. The predator case is strictly analogous. So the trajectories must approach one another. Figure 2 shows the same trajectories for $t \in [0, 250]$. In the later portion of this time interval, the trajectories are indistinguishable.

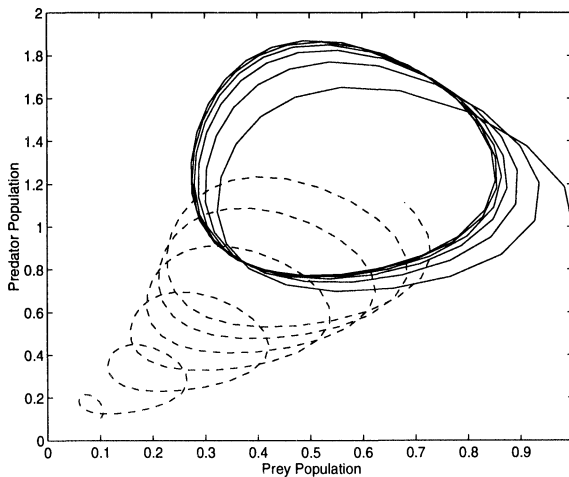


Figure 1: Total and dominant population trajectories for $t \in [0, 50]$.

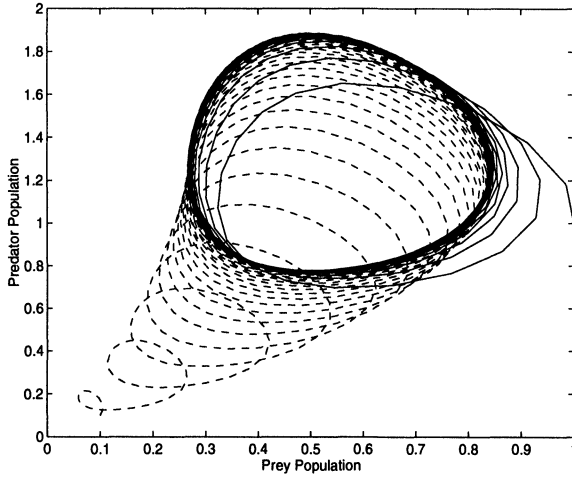


Figure 2: Total and dominant population trajectories for $t \in [0, 250]$.

Figure 3 is a plot of total population minus dominant subpopulation vs. time. The upper (lower) curve is the difference of the total and dominant predator (prey) populations. This plot clearly indicates that the dominant subpopulations of predator and prey cease to differ from the corresponding total populations by any appreciable amount after a sufficient amount of time has elapsed.

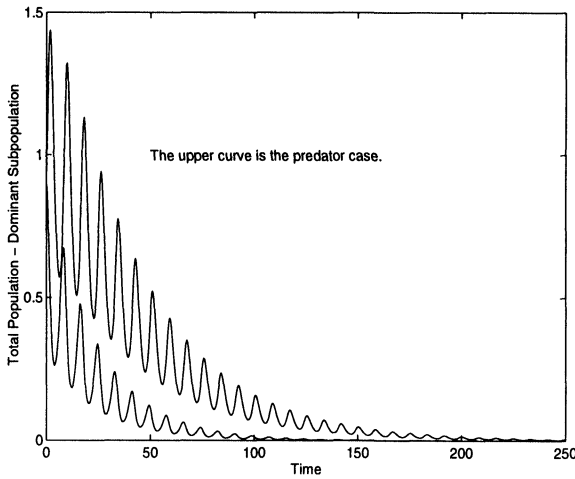


Figure 3: Population differences vs. time.

Consider the classical predator-prey system (2.1) with $a = a_1$, $b = b_1$, $c = c_1$ and

$d = d_1$. Solving this system for the initial conditions $(X(0), Y(0)) = (x_1(250), y_1(250))$, we obtain the solution curve illustrated in Figure 4. The small circle in the middle of the figure marks the equilibrium point for the system. Figure 5 is an overlay of the dominant subpopulation trajectory from Figure 3 and the classical solution curve from Figure 4. The generalized system evolves in such a way as to “become classical.” That is, after enough time has passed, the trajectory for the dominant predator-prey pair from the generalized system closely approximates the solution curve of a classical predator-prey system whose initial conditions are taken to be the values of the dominant pair at a late enough time.

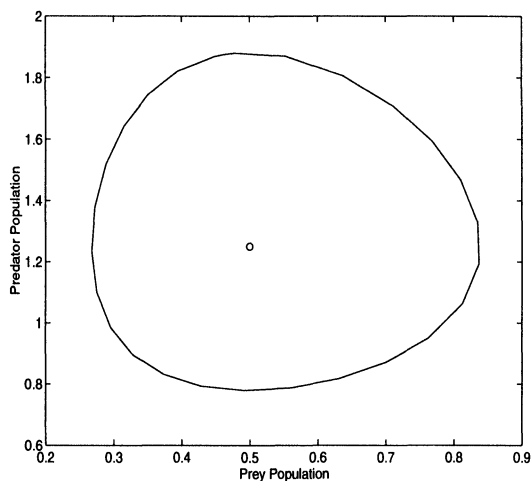


Figure 4: Classical population trajectory.

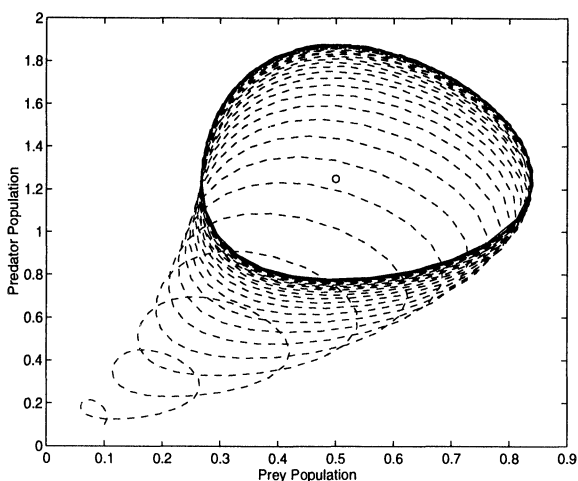


Figure 5: Overlay of classical and dominant population trajectories.

5. Conclusions

As we have seen from both the theoretical and numerical results, all nondominant subpopulations in system (2.2) are forced to extinction as $t \rightarrow \infty$. This is due to the fact that in the development of the model (2.2), we have assumed that reproduction is closed, that is, those individuals with the highest growth to mortality ratio only produce more of themselves. We believe that this conclusion changes with open reproduction, where individuals in one subpopulation have a positive probability of producing individuals with different characteristics (i.e., belong to a different subpopulation). In this case, the dominant subpopulation produces individuals that belong to nondominant subpopulations. Hence, survival of the dominant species implies the survival of some of the others. In fact, initial numerical results corroborate this idea and furthermore, they indicate that surviving subpopulations have an oscillatory behavior. We remark that the assumption of open reproduction is studied in [3] for a special case of the finite dimensional generalized logistic model, where individuals of one subpopulation have an equal probability of producing individuals that belong to any other subpopulation. Therein, the survival of all subpopulations is established.

Another system we plan to investigate is the continuum version of the predator-prey model, as is done in [2] for the generalized logistic model. In the continuum case, subpopulation numbers are replaced by subpopulation densities, and solutions of the system induce time dependent measures on the growth-mortality parameter space. Hence, using convergence of measures as in [2], we expect to extend the results in this paper to analogous results in the continuum case.

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