Intraspecific Competition in the Population of *Danaus plexippus*(L.)

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Abstract

We propose and analyze a model to describe the population cycles of the monarch butterfly. The annual migration of the monarch involves four generations with mixed reproductive strategies in each generation. Members of generations 1 through 3 (occasionally 4) migrate from the over-wintering site in central Mexico to breeding grounds that extend as far north as the northern United States and southern Canada. A portion of the third generation and all members of the fourth generation begin their return to the over-wintering grounds in August through October where they enter reproductive diapause for several months. We developed a discrete time model in which two different fecundity functions are used to model the reproductive strategies of each generation. The fecundity functions are selected from broad classes of functions used in ecology. The selection of the type of fecundity function used with each generation is based on biological observations. The objectives of our research are multiple and include the study of the generationally dependent intraspecific competition and its effect on the pool size of migrants as well as the persistance of the overall butterfly populations. The stage structure used in modeling the

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monarch butterfly dynamics and their generationally-dependent reproductive strategies naturally support fluctuating patterns and multiple attractors. The implications of these fluctuations and attractors on the long-term survival of the monarch butterfly population is explored analytically and through simulations.

1 Introduction

The monarch butterfly, *Danaus plexippus* L., exhibits complex migration that is seasonally driven and dependent on food quality [17]. Adult monarchs travel southwest to the neovolcanic mountains of central Mexico from their breeding grounds in southern Canada and the northern United States. The initial monarch clusters appear in trees near mountain tops of Mexico in early winter. The migration of the monarch does not occur entirely within one generation. There are three to four generations of monarchs within the expanse of one year. A proportion of the third generation[1], which is the generation that is born in the northern United States and southern Canada, reproduces in the northern breeding grounds. The rest of this generation migrates south with the fourth generation (offspring of generation 3) that eclose (hatch) late in August and early Fall [9]. These migrating individuals are in a reproductively dormant state. This reproductive diapause is triggered by changes in temperature and photoperiod, but on the whole is poorly understood. The migratory generations live approximately six to nine months [5], [1], [3]. While remaining in Mexico from November through early February, the butterflies are in a physically dormant state and cluster in fir trees. This period of time is commonly referred to as overwintering.

The third and fourth generations begin a northeasterly remigration in early spring and reproductive dormancy ends. The spring migration is an annual remigration, meaning that the same migrating fall population returns to the northern breeding grounds in the spring [17]. Urquhart (1987) denies the notion that spring remigrants travel northward for a short distance, deposit their eggs and then die. He states that only a few larvae are found in the southern United States in the spring and the female adults found in the northern breeding grounds in May and early June are greatly worn. Urquhart concludes that many of the overwintering females return to the breeding grounds of northern United States and southern Canada in spring and early summer producing the first generation along the way. The offspring of the migrating generation, generation 1, and the offspring of this first generation (generation 2) appear in the northern breeding areas in May through early July. The males of the migrating generation do not arrive in the northern breeding areas, as they will mate with the females in the early spring and die shortly after [17]. However, there have been other studies suggesting that the spring remigration does not occur in the manner described by Urquhart. Identifying differences in the cardenolide concentration of migrant adults found at the southern and northern locations, Malcolm (1993) determined that nearly all of the spring migrants found in northern breeding areas are the offspring of the Mexican overwintering generation. The monarchs remigrating from Mexico in the early spring lay most of their eggs in Texas and Louisiana on the

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[1]we call this generation 3 for modelling convenience

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ubiquitous early spring milkweed, *A. virdis*, which contains high cardenolide concentrations [8]. Thus, Malcolm poses a successive brood remigration to the northern breeding grounds, while Urquhart essentially describes a single sweep migration.

In a study of spring remigration of the Gulf Coast states, Knight (1998) emphasizes the critical time period in which remigrants must establish the new spring generation. If the overwintering monarchs arrive too early in March, there is a chance the milkweed where eggs are laid will be killed by frost, while if they arrive too late in the spring (mid to late April), then the milkweeds will have begun to senesce or wither [7]. Thus, there is a three week critical time period to establish the first generation monarchs. The first and second generations that continue migrating northward and the majority of the third generation have a lifespan of two to six weeks. The third generation adults that emerge late in August undergo reproductive diapause and exhibit the extended lifespan discussed previously. In the northern breeding areas during early summer, monarchs spend their energy in reproduction until the later summer generations appear. In essence, time is a crucial factor in determining the number of generations there will be within one migratory cycle. Rowe and Ludwig (1991) suggest that the nutritional and mass state of individuals approaching time-constrained reproductive events are possibly related to fitness.

In this paper, we develop a discrete time model that describes monarch populations over four generations. We consider different fecundity functions that depend on assumptions made about population densities and availability of resources. When all the monarch butterflies of the population are under *intraspecific contest competition* [2],[19] via the Beverton - Holt fecundity function, we obtain a threshold condition for the global persistance or extinction of the species. We provide conditions for global stability of various systems that are examined. When the monarch population is under *scramble intraspecific competition* [2], [19] or mixed scramble - contest competition, we find population oscillations and explore how varying certain parameters affects the monarch dynamics such as population abundance and attractors. Our paper is organized as follows: In Section 2 we introduce the general model. Section 3 consider the Beverton - Holt equation as the fecundity function; thresholds for stability are studied as well as population abundance. In Section 4 we study the cases where Ricker's equation represents the fecundity function of some generations and the the rest of the generations are modeled by a linear function or Beverton - Holt equation. Section 5 includes a discussion of our results.

2   The model

We develop a model describing the life cycles of monarchs, assuming four generations per year. Let $x_i(t)$ be the population size of generation i at time t, where t is a time period of one year. Note that by defining $x_i(t)$ in this form we are considering the total number of butterflies in each generation in the whole year, t, disregarding the fact that monarchs from different generations may have different life spans. The migratory proportion of the population of generation 3 is represented by $(1 - d)$, where $d < 1$. Thus d represents the proportion of nonmigratory individuals. The

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parameter γ_i denotes the survival probability of individuals producing generation i, so $0 < \gamma_i < 1$. Observe that the survival probability $\gamma_1 < \gamma_i$, (for $i = 2, 3, 4$) due to increased mortality of the migrating generations 3 and 4 while traveling from the northern breeding grounds to central Mexico. Additionally, overwintering in central Mexico decreases survival probability. The fecundity function for generation i, f_i describes how new individuals of generation i are born. The fecundity functions to be considered include Ricker's and Beverton-Holt equations since these models have density dependent properties that capture the two extreme forms of intraspecific competition, scramble and contest [13], [2]. Each generation is a function of the individuals in previous generations that reproduce successfully. The first generation includes the migrating proportion of generation 3 and the fourth generation depends on the nonmigratory proportion of generation 3. The following system of equations describes the monarch population dynamics:

$$
\begin{aligned}
x_1(t+1) &= f_1(\gamma_1[x_4(t) + (1-d)x_3(t)]) \\
x_2(t+1) &= f_2(\gamma_2 x_1(t+1)) \\
x_3(t+1) &= f_3(\gamma_3 x_2(t+1)) \\
x_4(t+1) &= f_4(d\gamma_4 x_3(t+1))
\end{aligned}
\tag{1}
$$

where x_i, $i \in \{1, ..., 4\}$, describe generations 1 through 4. In our model, generations 2, 3, and 4 in time $t+1$ depend on generations 1, 2, and 3 in time $t+1$, respectively because they are produced within the same year. However, because generation 1 is the first generation considered within a year then it depends on generations 3 and 4 from the previous year t. Using this model, we will describe changes in population abundance and compensatory mechanisms sufficient to ensure regeneration after population crash, evaluate the effects of variation in the parameter d (or the proportion of generation 3 that does not migrate), and look for periodic oscillations and presence of multiple attractors.

The Beverton - Holt and Ricker's equations are utilized in our model because they provide density dependent fecundity functions. Monarch population growth in summer breeding areas has been modeled as density dependent [12]. These equations model two drastically different types of intraspecific competition. The Beverton-Holt equation takes the form, $f_i(x) = \frac{a_i x}{1+b_i x}$. The term a_i describes the per capita growth rate of the population and is assumed to be linear, while b_i acts as a scaling parameter. When $a_i > 1$, a globally asymptotically stable positive equilibrium exists and all positive population sizes limit on it monotonically (see Figure ??) [2]. The Beverton-Holt equation describes intraspecific *contest* competition, meaning that stronger individuals or competitors monopolize the resources [4]. Here, the superior individuals always survive, even when density is high. In contrast to the Beverton - Holt model, the Ricker's model describes *scramble* competition, where resources are divided equally among all competeing individuals [4]. The Ricker's model takes the form, $f_i(x) = xe^{r_i - x}$. The parameter r_i acts as the carrying capacity, while x is the population density. Here, the population increases while the population density x is lower than the carrying capacity of the environment, but once the density of the

population surpasses the carrying capacity, then the population decreases in the next year (figure 1).
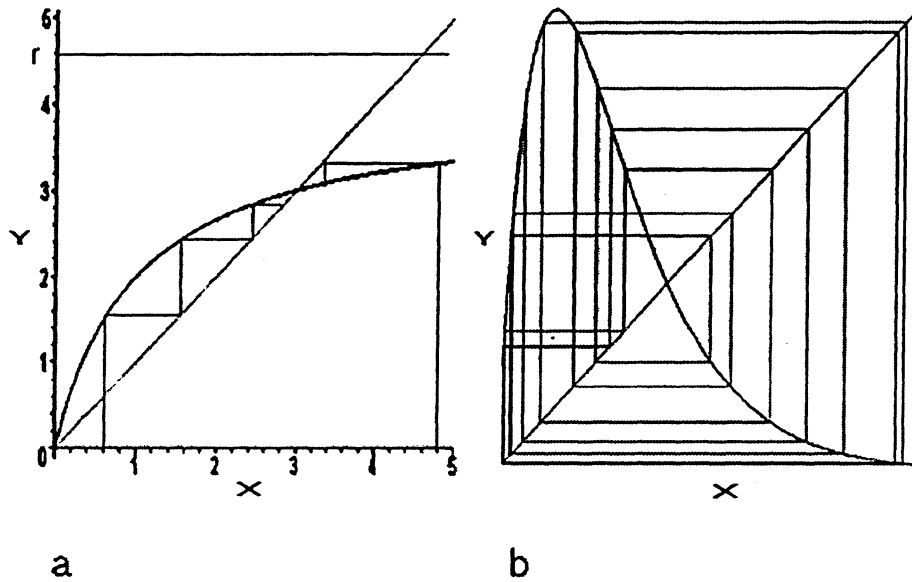

Figure 1: (a) The Beverton - Holt equation: in this case every solution tends toward the fixed point, where the reproduction curve and $y = x$ intersects (b) In contrast, the Ricker equation is able to support periodic cycles as well as chaotic dynamics.

3 The Beverton-Holt equation as the fecundity function for all generations

We describe the fecundity function for each generation with the Beverton-Holt equation, assuming that in each generation contest competition exists in the population. Then System (1) assumes the form:

$$x_1(t+1) = \frac{a_1\gamma_1[x_4(t)+(1-d)x_3(t)]}{1+b_1\gamma_1[x_4(t)+(1-d)x_3(t)]},$$

$$x_2(t+1) = \frac{a_2\gamma_2 x_1(t+1)}{1+b_2\gamma_2 x_1(t+1)},$$

$$x_3(t+1) = \frac{a_3\gamma_3 x_2(t+1)}{1+b_3\gamma_3 x_2(t+1)},$$ (2)

$$x_4(t+1) = \frac{da_4\gamma_4 x_3(t+1)}{1+db_4\gamma_4 x_3(t+1)},$$

but it can be reduced to the following system of two equations:

$$x_3(t+1) = \frac{a_3 a_2 a_1 \gamma_3 \gamma_2 \gamma_1[x_4(t)+(1-d)x_3(t)]}{1+[b_3 a_2 a_1 \gamma_3 \gamma_2 \gamma_1 + b_2 a_1 \gamma_2 \gamma_1 + b_1 \gamma_1][x_4(t)+(1-d)x_3(t)]}$$

$$x_4(t+1) = \frac{da_4 a_3 a_2 a_1 \gamma_4 \gamma_3 \gamma_2 \gamma_1[x_4(t)+(1-d)x_3(t)]}{1+[db_4 a_3 a_2 a_1 \gamma_4 \gamma_3 \gamma_2 \gamma_1 + b_3 a_2 a_1 \gamma_3 \gamma_2 \gamma_1 + b_2 a_1 \gamma_2 \gamma_1 + b_1 \gamma_1][x_4(t)+(1-d)x_3(t)]}$$ (3)

The next theorem shows conditions for the stability of equilibria of System (3). We prove that if each net per capita growth rate a_i is small, then the butterfly population will go extinct, that is, the equilibrium $(0,0)$ is globally stable. However, if the net per capita growth rate is large enough, then the population will persist to a nonzero stable equilibrium.

Theorem 3.1. *Let* $\lambda = a_3 a_2 a_1 \gamma_3 \gamma_2 \gamma_1((1-d)+a_4\gamma_4 d)$. *If* $\lambda \le 1$, *then* $(0,0)$ *is globally stable. If* $\lambda > 1$, *then System (3) has a unique nonzero fixed point that is globally attracting in* $(0,\infty) \times (0,\infty)$.

See appendix for proof.

The value of λ is highly dependent on the intrinsic per capita growth rates, the survival probabilities γ_i of all generations, as well as the migration rate d. These parameters are the most critical in determining the long term behavior of the population, either extinction or persistance. Small values of these parameters lead to extinction while large values lead to the persistance of the monarch butterflies.

An interesting biological question that we can ask is, how can we increase the population size of a specific generation of butterflies? In other words, what ecological conditions have more impact on monarchs? In order to answer these questions, we run several simulations varying different parameters and we study the effects that these changes have in each generation. We observe that parameters such as the intrinsic per capita growth rates or survival probabilities, directly affect the size of the population that they produce. That is, the population size in generation i increases as the intrinsic per capita growth rate a_i or the survival rate γ_i increases. This result is what we should expect. However, a variation in each of these parameters that produce generation i also has an effect in the other generations. Moreover, as the parameter increases, the population in the corresponding generation increases at a faster rate. Now, when we consider the proportion d of individuals in generation 3 that reproduce in Northern US as the parameter to be varied, we observe that as d increases from 0 to 1, the population of generation 4 increases starting from 0, while the rest of the generations exhibit small changes in abundance. It is apparent that parameter d can have a stronger impact on generation 4 than on any other generation and that generation 4 is increasing as a function of d (figure 2).
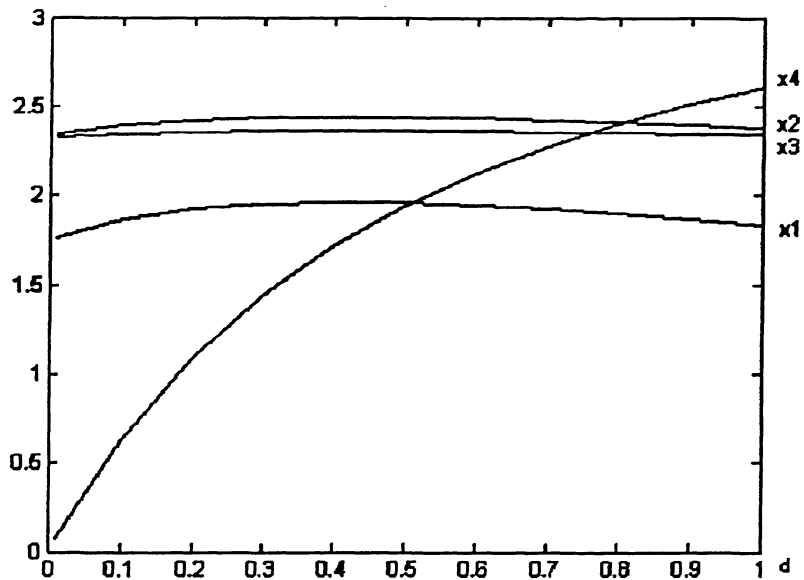
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Figure 2: The population of generation 4 increases as a function of d, which is the proportion of members in generation 3 that reproduce in summer breeding grounds.

4 The Ricker's equation as the fecundity function for two generations

We consider cases when the fecundity functions of two generations are given by the Ricker's model, while the remaining two are given by the linear function $f_i(x) = \sigma_i x$, where σ_i represents the proportion of new individuals in generation i with respect to the number of surviving individuals of the previous generation. Then $\sigma_i = \alpha_i \gamma_i$ where α_i is the per capita growth rate and γ_i is the survival probability of individuals producing generation i. By using the linear fecundity function, we simplify the system of equations. The simplification does not seem to deminish the "realism" of the model, as small larval densities will exist when there are concentrated abundant plant communities. We then assume that density dependent competition does not play a significant role consistently within all generations.

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4.1 Ricker's equation in generations 2 and 3

We examine the case when the first and fourth generations maintain linear fecundity functions, while the second and third generations are represented by the Ricker's model. System 1 then becomes:

$$
\begin{aligned}
x_1(t+1) &= \sigma_1[x_4(t) + (1-d)x_3(t)] \\
x_2(t+1) &= \gamma_2 x_1(t+1)e^{r_2 - \gamma_2 x_1(t+1)} \\
x_3(t+1) &= \gamma_3 x_2(t+1)e^{r_3 - \gamma_3 x_2(t+1)} \\
x_4(t+1) &= d\sigma_4 x_3(t+1).
\end{aligned}
\tag{4}
$$

System 4 reduces to the following two dimensional system

$$
\begin{aligned}
x_3(t+1) &= \gamma_3\gamma_2\sigma_1[x_4(t) + (1-d)x_3(t)]\cdot \\
&\quad e^{r_2+r_3-\gamma_2\sigma_1[x_4(t)+(1-d)x_3(t)][1+\gamma_3 e^{r_2-\gamma_2\sigma_1[x_4(t)+(1-d)x_3(t)]}]} \\
x_4(t+1) &= d\sigma_4\gamma_3\gamma_2\sigma_1[x_4(t) + (1-d)x_3(t)]\cdot \\
&\quad e^{r_2+r_3-\gamma_2\sigma_1[x_4(t)+(1-d)x_3(t)][1+\gamma_3 e^{r_2-\gamma_2\sigma_1[x_4(t)+(1-d)x_3(t)]}]}
\end{aligned}
\tag{5}
$$

4.2 Analysis of the Ricker's equation in generations 2 and 3

With the two dimensional system (5), we are able to determine conditions for stability of System 4. These conditions are established in the next theorem[2].

Theorem 4.1. *Suppose that* $\ln(\frac{1}{\gamma_3}) > r_2$. *Let* $p = \left(\frac{1}{2\gamma_2\sigma_1}, \frac{1}{2\gamma_2\sigma_1(1-d)}\right) \in R_+^2$ *and* $\lambda = \gamma_3\gamma_2\sigma_1((1-d) + \sigma_4 d)e^{r_2+r_3}$. *If* $\lambda \leq 1$, *then* $(0,0)$ *is globally stable in* $[0,p]$. *If* $\lambda > 1$, *then System 5 has a unique nonzero fixed point* $q \in (0,p)$ *that is attracting in* $[0,p] - \{0\}$.

See Appendix for a proof of this theorem.

Therefore, when survival probabilities γ_2 and γ_3 are sufficiently small, then λ can be less than one and the monarch population will go to extinction. If survival probabilities and d, the proportion individuals of generation 3 that reproduce to yield generation 4, are sufficiently large, then λ will be greater than one and the population will tend towards a nonzero stable population level.

In figure 3, we plotted the trajectory for x_3 versus x_4 and found it to be an invariant attracting line.

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[2]For $u = (u_1, \ldots, u_n), v = (v_1, \ldots, v_n) \in R^n$ we denote $[u, v] = [u_1, v_1] \times \cdots \times [u_n, v_n]$, where $[u_i, v_i]$ is a closed interval in R, for $i = 1, \ldots, n$.
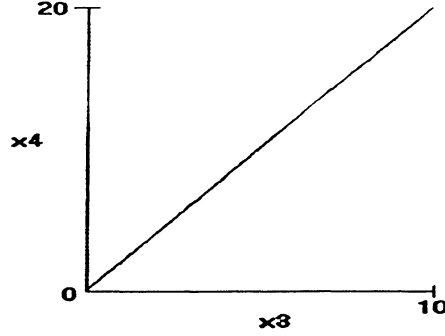
Figure 3: The line A is invariant, which implies that a point on A remains on line A after successive iterations. Parameter values: $x_3 = 10, x_4 = 10, r_2 = 0.7, r_3 = 4.5, \sigma_1 = 1.3, \gamma_2 = 0.7, \gamma_3 = 0.8, \sigma_4 = 2.6, d = 0.8$ The y axis is x_4 from 0 to 20 and the x axis is x_3 from 0 to 10.

A proof is given to show that the trajectory of generation 3 versus 4 is invariant, when $x_4 = d\sigma_4 x_3$ and generation 2 and 3 are represented by the Ricker's equation. Proving that invariance exists, allows us to conclude that the model is one dimensional, and the system can be analyzed using the one dimensional cobwebbing approach in order to examine attractors.

Proof of invariance of the trajectory Let $A = \left\{ (x, y) \in R_+^2 : y = d\sigma_4 x \right\}$ and let $F : R_+^2 \to R_+^2$ be given by:

$$F(x, y) = \left(\gamma_3 \gamma_2 \sigma_1 [y + (1 - d)x] e^{r_2 + r_3 - \gamma_2 \sigma_1 [y + (1-d)x][1 + \gamma_3 e^{r_2 - \gamma_2 \sigma_1 [y + (1-d)x]}]}, \right.$$

$$\left. d\sigma_4 \gamma_3 \gamma_2 \sigma_1 [y + (1 - d)x] e^{r_2 + r_3 - \gamma_2 \sigma_1 [y + (1-d)x][1 + \gamma_3 e^{r_2 - \gamma_2 \sigma_1 [y + (1-d)x]}]} \right)$$

$$= \left(F_1(x, y), F_2(x, y) \right)$$

Lemma 4.2. *The set A is invariant under F.*

Proof. Let $(u, v) \in A$, then $F_1(u, v) \geq 0$ and $F_2(u, v) = d\sigma_4 F_1(u, v)$. Hence $\left(F_1(u, v), F_2(u, v) \right) \in A$, so that $F(u, v) \in A$. Thus $F(A) \subset A$ and therefore, A is invariant under F. □

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The proof of invariance shows that the monarch population remains on the line A when the initial conditions begin on that line. The dynamics in the set A is governed by a Ricker's map which can support diverse dynamical behavior such as periodic doubling bifurcations and chaotic events.

The linear invariant trajectory for generations 3 and 4, when x_4 is a multiple of x_3, is also an attractor. Because it is shown that any point in A, (u, v), evaluated in the function F will yield a point belonging to the subset A, then any real positive point will immediately be attracted towards A, the chaotic trajectory. Running simulations indicates that an initial condition that does not lie on A will be immediately attracted to the set on the first iteration.

Because we have a linear invariant trajectory, the system is therefore one dimensional. Using this fact, we plot the one dimensional cobweb diagram in figure 4 to further examine the chaotic events present.
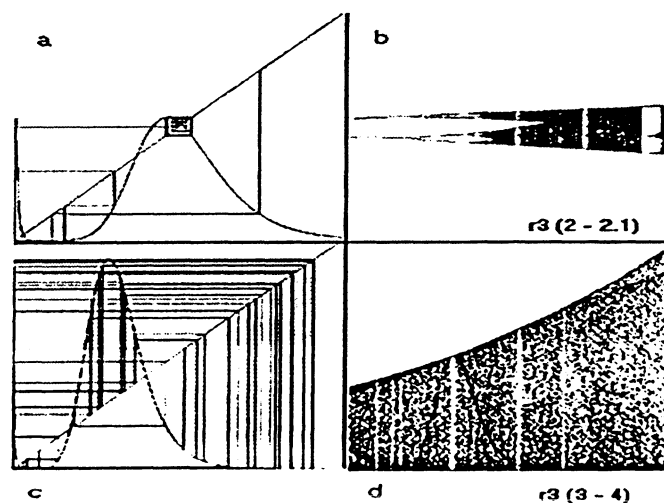

Figure 4: (a) Cobwebbing for $r_3 = 2.0$ in generation 3: a stable two cycle exists (b) When varying r_3 from 2.0 to 2.1 in generation 3 we observe a period doubling corresponding to (a). (c) Cobwebbing for $r_3 = 3.0$ in generation 3: chaotic cycling occurs. (d) Varying r_3 from 3 to 4 in generation 3, we observe chaotic cycling corresponding to (c). Parameter values: $x_3 = 3, x_4 = 2, r_2 = 3.5, \sigma_1 = 1.3, \gamma_2 = 0.7, \gamma_3 = 0.8, \sigma_4 = 2.6, d = 0.8$

We find that certain values of parameters within the system potentially maintain stable cyclic dynamics which are characteristic of monarch populations [18].

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4.3 Ricker's equations in generations 3 and 4

When generations 3 and 4 are represented by the Ricker's equations and the first and second generations maintain the linear fecundity function[3], the model system becomes:

$$
\begin{aligned}
x_1(t+1) &= \sigma_1[x_4(t) + (1-d)x_3(t)] \\
x_2(t+1) &= \sigma_2 x_1(t+1) \\
x_3(t+1) &= \gamma_3 x_2(t+1)]e^{r_3 - \gamma_3 x_2(t+1)} \\
x_4(t+1) &= d\gamma_4 x_3(t+1)e^{r_4 - d\gamma_4 x_3(t+1)}
\end{aligned}
\tag{6}
$$

System (6) can be reduced to a system of two equations given by

$$
\begin{aligned}
x_3(t+1) &= \gamma_3 \sigma_2 \sigma_1 [x_4(t) + (1-d)x_3(t)]e^{r_3 - \gamma_3 \sigma_2 \sigma_1 [x_4(t) + (1-d)x_3(t)]} \\
x_4(t+1) &= d\gamma_4 \gamma_3 \sigma_2 \sigma_1 [x_4(t) + (1-d)x_3(t)] \cdot \\
&\quad e^{r_3 + r_4 - \gamma_3 \sigma_2 \sigma_1 [x_4(t) + (1-d)x_3(t)]e^{r_3 - \gamma_3 \sigma_2 \sigma_1 [x_4(t) + (1-d)x_3(t)]}}
\end{aligned}
\tag{7}
$$

4.4 Analysis of the Ricker's equation in generations 3 and 4

To analyze dynamics of the system, we investigate the bifurcation diagrams of generations 3 and 4 when certain parameters are varied separately, and all other parameters are constant. Analyzing the system dynamics through varying different parameters enables us to qualitatively understand its sensitivity. Through bifurcation diagrams, we determine if parameter variation induces changes in dynamics between generations 3 and 4. Additionally, we characterize the types of bifurcations that occur. Lyapunov exponents are plotted against the parameter range to further expose the chaotic events or orbits within the system. Lyapunov exponents are indicators of chaotic events in dynamical systems, describing the average behavior of the derivative map on a trajectory [11]. Analyzing these components provides greater evidence that the apparent chaotic orbits present in the bifurcation diagrams are truly chaotic. An invariant trajectory is found and its proof is given.

We found that while varying the same parameter over generations 3 and 4, the dynamics of the system remained the same between the generations, although the bifurcation diagrams do not appear identical in shape. That is, the change from chaos to stable equilibria or periodicity occurs at the same points in generations 3 and 4, but the scale of the y axis deviates between generations. The bifurcation diagrams in figure 5 (a - d) compare the parameter γ_3, the survival probability that individuals from generation 2 survive to reproduce, with d, the parameter that describes the proportion of nonmigratory reproducing members of generation 3.

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[3]Systems (4) and (6) include all mathematical possibilities for our system when two generations are given by $f_i(x) = \sigma_i x$ and the remaining two by the Ricker's equation.
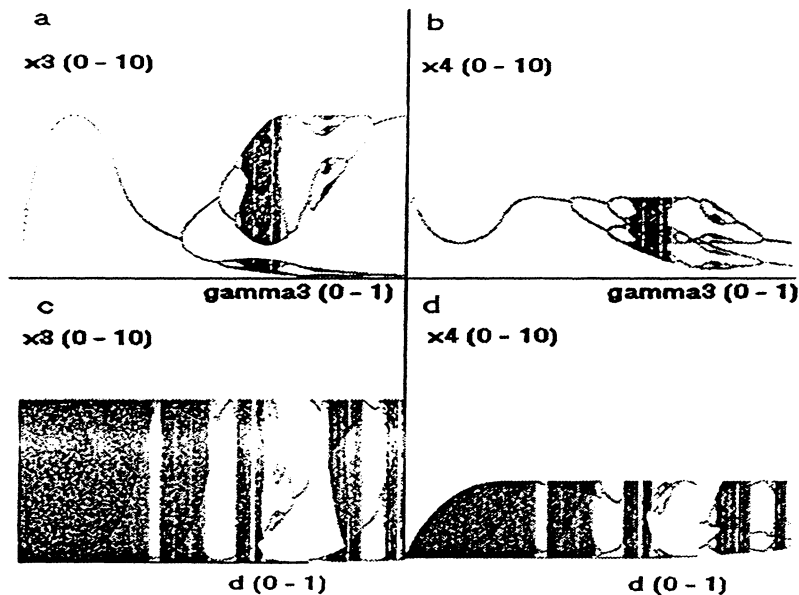
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Figure 5: Parameter values: $x_3 = 10, x_4 = 10, r_3 = 2.7423, r_4 = 2.0, \sigma_1 = 1.85, \sigma_2 = 1.7, \gamma_3 = 0.85, \gamma_4 = 0.65, d = 0.8$ The y axis is $x_i, i = (3, 4)$ from 0 to 10 and the x axis is the range of parameter values from 0 to 1. (a)Varying γ_3 from 0 to 1, in generation 3 (b)Varying γ_3 from 0 to 1, in generation 4 (c)Varying d from 0 to 1 in generation 3 (d)Varying d from 0 to 1 in generation 4

We are able to determine that the dynamics between generations 3 and 4 are static, but these dynamics are extremely sensitive to parameter values given. When γ_3 is varied from zero to one, the values at which chaos appears is approximately 0.6 in generations 3 and 4, but strikingly different patterns of chaos appear when d is the varying parameter. Likewise, the period cycles occur at different points between generations. We observe these results consistently when parameters other than σ_1 and σ_2 are varied. When σ_1 and σ_2 have the same range of values, identical dynamics result, as they play equal roles within the system.

The Lyapunov exponents were obtained and plotted against the parameter range. We confirmed that the positive and negative Lyapunov exponents corresponded directly to the dynamics observed in the bifurcation diagrams (figure 6).
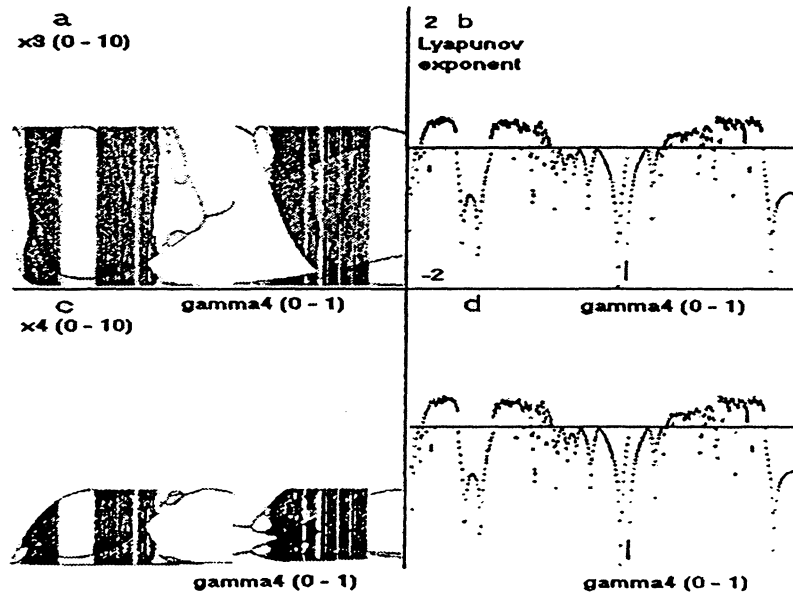

Figure 6: Bifurcations and corresponding Lyapunov exponents. (a)The y axis is x_3 from 0 to 10 and the x axis is γ_4 from 0 to 1 (b) On the y axis are Lyapunov exponent values from -2 to 2, on the x axis are values of γ_4 from 0 to 1 in x_3. (c) The y axis is x_4 from 0 to 10 and the x axis is γ_4 from 0 to 1. (d) On the y axis are Lyapunov exponent values from -2 to 2, on the x axis are values of γ_4 from 0 to 1 in x_4. Parameter values: $x_3 = 10, x_4 = 10, r_3 = 2.7423, r_4 = 2.0, \sigma_1 = 1.85, \sigma_2 = 1.7, \gamma_3 = 0.85, d = 0.8$

The plots of Lyapunov exponents support the observation that dynamics across generations 3 and 4 remained constant when the same parameters were varied. In this case γ_4 is varied from 0 to 1. We observe that a region of positive Lyapunov exponents occur from 0.7 to 0.8. Accordingly, the bifurcations of diagrams (a) and (b) show that chaotic events exist between 0.7 and 0.8. We varied the initial conditions of x_3 and x_4 to find if certain population sizes evoked different dynamics in the system. Lyapunov exponent diagrams showed identical dynamics between these variations in initial conditions when r_4 was the varying parameter from 2 to 3. Therefore, we

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expect that differences in population size do not affect the system greatly. Multiple attractors were found for the case when generations 3 and 4 are characterized by Ricker's fecundity equations (figure 7). Therefore, long term behavior of the monarch population is influenced by initial conditions.
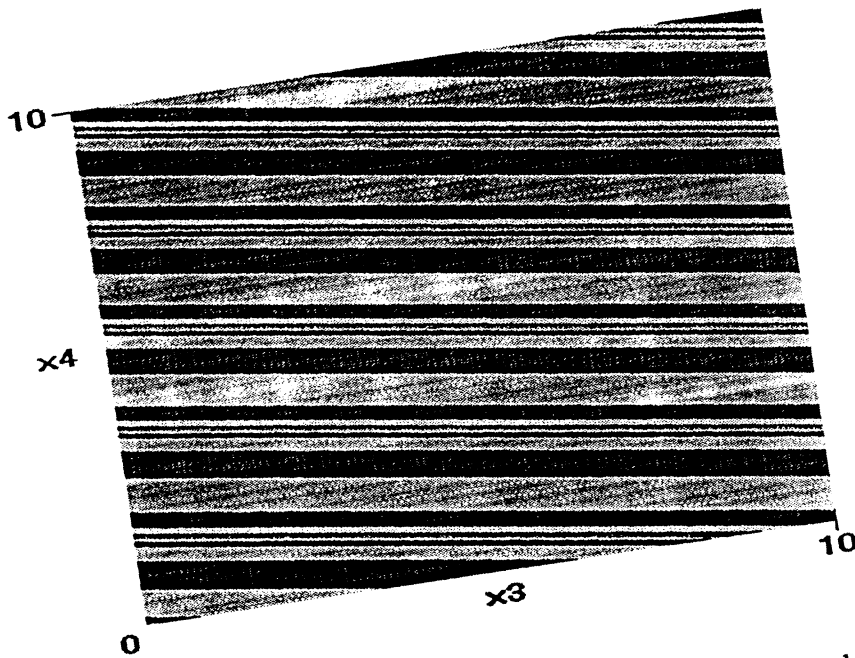

Figure 7: Mulitple attractors shown for Ricker's in generation III and IV. Parameter values: $r_3 = 2.5$, $r_4 = 2.0$, $\sigma_1 = 1.85$, $\sigma_2 = 1.7$, $\gamma_3 = 0.85$, $\gamma_4 = 0.65$, $d = 0.8$

The graph of x_4 versus x_3 was plotted with parameter values shown to yield chaos and the trajectory is shown to be invariant via simulations. Additionally, the trajectory is thought to be an attractor, through shown invariance, simulations, and basin of attraction. Figure 8 (a) gives the basin of attraction, providing evidence that invariant curves of the type shown in the trajectory of figure 8 (b) is attracting. When the trajectory was plotted using other parameter values, a deviation of the curve in figure 8 was obtained. All initial conditions that do not lie on the curve immediately travel to it on the first iteration. We cannot conclude that the attracting curve is a Ricker's curve, as multiple attractors exist in the system.
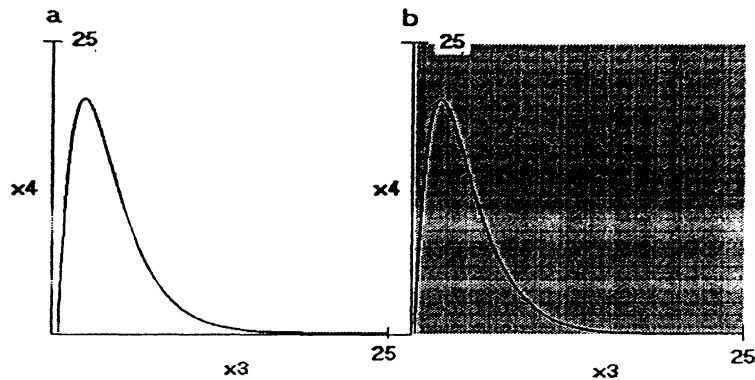
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Figure 8: (a) Shows the basin of attraction curve, with the following parameter values: $x_3 = 3$, $x_4 = 2$, $\sigma_1 = 1.85$, $\sigma_2 = 1.7$, $\gamma_3 = 0.85$, $\gamma_4 = 0.65$, $d = 0.8$, $r_3 = 4.5$, $r_4 = 4.0$ The grey area is the region that is attracted to the curve shown. The curve acts as the basin. (b) The trajectory of x_3 v. x_4 with the following parameter values yielding chaos: $x_3 = 10, x_4 = 10, r_3 = 2.7423, r_4 = 2.0, \sigma_1 = 1.85, \sigma_2 = 1.7, \gamma_3 = 0.85, \gamma_4 = 0.8, d = 0.8$ The y axis is x_4 from $(0 - 4)$ and the x axis is x_3 from 0 to 6.

We can conclude that the monarch population exhibiting initial conditions that place the population on the invariant curve will yield a subsequent population that will remain on the invariant curve. We found the same results when the fecundity of generations 2 and 3 were represented by the Ricker's equations, while 1 and 4 were linear fecundity functions. We observe the pattern that the dynamics on both the invariant curve trajectory and the invariant linear trajectory are dominated by the Ricker's map. That is, both simple oscillations, such as period doubling, and chaotic events occur, dependent on the parameter values given.

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4.5 A mixed system: the Ricker's and Beverton-Holt equations as fecundity functions of separate generations

Because there is little field data on fecundity available, we do not have a precise understanding of which factors affect fecundity the most. It is possible that the fecundity of different generations are formed through varying biological factors. We coupled the Ricker's and Beverton-Holt equations within our model system, analyzing the parameter variation with the Ricker's equation in generation 2 and Beverton-Holt in generation 3. For simplicity, we use linear fecundity function to describe generations 1 and 4 in the system. In utilizing the coupled equations, we examine the conditions driving the dynamics when pure contest competition and pure scramble competition are in place. The equations take the form:

$$x_1(t+1) = \sigma_1[d\sigma_4 + (1-d)]x_3(t)$$

$$x_2(t+1) = \gamma_2\sigma_1[d\sigma_4 + (1-d)]x_3(t)e^{r_2 - \sigma_1[d\sigma_4 + (1-d)]x_3(t)}$$

$$x_3(t+1) = \frac{\gamma_3 a_3 \gamma_2 \sigma_1[d\sigma_4 + (1-d)]x_3(t)e^{r_2 - \sigma_1[d\sigma_4 + (1-d)]x_3(t)}}{1 + b_3 \gamma_2 \sigma_1[d\sigma_4 + (1-d)]x_3(t)e^{r_2 - \sigma_1[d\sigma_4 + (1-d)]x_3(t)}}$$

$$x_4(t+1) = d\sigma_4 x_3(t+1)$$

Fascinating behavior arises when the Beverton-Holt and Ricker's equations are used within the same model system. Essentially, the fecundity functions compete for dominance in driving the behavior of the population. The resulting bifurcations are highly unusual when a single parameter value is perturbed while holding the bifurcation range of the varying parameter constant (figure 9).

When the parameter $b_3 > a_3$, then we find that no bifurcations exist on the diagram as the figure for generation 2 is a curve increasing to infinity on the y axis and the graph of generation 3 is linear. Under the condition $b_3 > a_3$, we conclude that the Beverton - Holt equation in generation 3 is the dominant function of the system. However, when a_3 is sufficiently larger than b_3, then complex dynamics emerge and the Ricker's equation is the more dominant function. In figure 9(a) and 9(c), an interesting phenomenon occurs, as a simple behavior bifurcates to a more complex one with period doubling, but then reverts back to the simple form, creating a bubble effect. The same event occurs in figure 9(b) and (d), but the interior complex behavior becomes chaotic.

5 Discussion

In developing a reasonable model, functions that reflect aspects of monarch fecundity must be developed. Currently, however, information on generational fecundity in breeding areas is scarce. In laboratory research Oberhauser has found that larval reserves do not affect fecundity, but do have an effect on reproductive success. In the laboratory, the time that a female has to lay previously produced eggs is the limiting
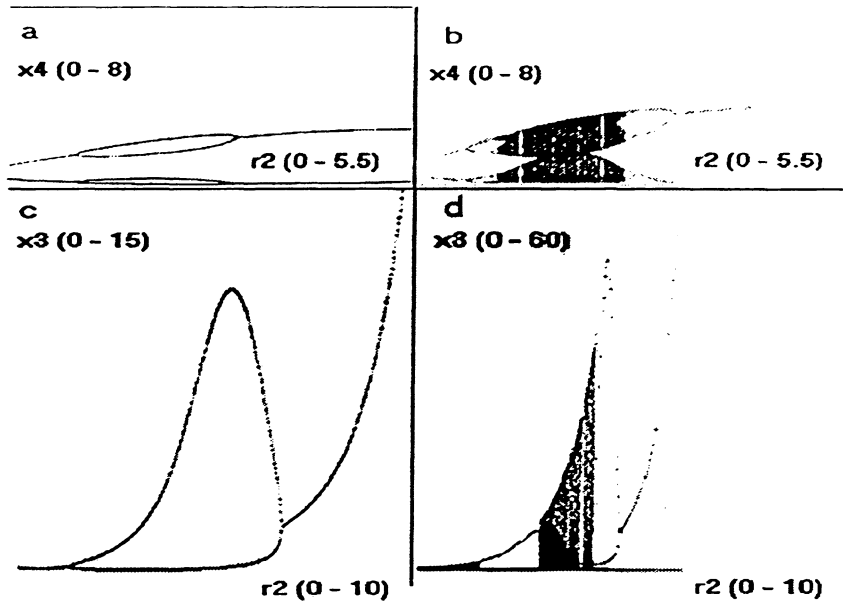
Figure 9: (a),(b) Bifurcation in generation 4, with b_3 as the altered parameter. In (a), $b_3 = 2.5$. In (b), $b_3 = 2.2$. (c),(d) Bifurcation in generation 3, with γ_3 as the altered parameter. In (c), $\gamma_3 = 0.4$. In (d), $\gamma_3 = 0.8$. Parameter values: $x_3 = 3$, $x_4 = 5$, $\sigma_1 = 3$, $\sigma_4 = 2$, $\gamma_2 = 0.5$, $\gamma_3 = 0.7$, $d = 0.8$, $a_3 = 9.0$, $b_3 = 2.0$

factor on realized fecundity. The production of eggs itself is not the limiting factor. Oberhauser (1997) explains that larval reserves should not be a significant limitation on fecundity when enough adult resources have been accumulated in the form of spermatophores and nectar. She concludes that females use the spermatophores or male derived nutrients to increase egg production, while more quantities of larval reserves will increase egg laying lifespan [10]. Thus important elements to the fecundity function are total adult resources and the time in which the female has to lay eggs (dependent on larval reserves). Time-constraint is a relevant issue to migration as well as fecundity. In addition to these aspects, temperature and aging also affect the fecundity of insects in general [6]. During the reproductive period, Roff (1992) describes the iteroparous insect fecundity function as triangular, having a large increase of fecundity directly after the onset of reproduction, then a slow decline follows as the insect ages. The model developed by Kindlmann (2001), predicts differing effects of temperature and food quality on adult size as a function of senescence.

Throughout this paper, we analyze different discrete time models for the population cycles of monarch butterflies, utilizing two types of intraspecific density dependent fecundity functions. Beverton - Holt and Ricker's model were chosen for their characteristic behavior describing contest and scramble competition respectively. Each model system considers four generations during a time period of one year. The impact of each parameter on population size was studied for each generation. We determined the importance of the proportion of nonmigratory reproducing individuals in generation 3 to the population size in generation 4. Such importance includes the possibilities of persistance or extinction in generation 4. Survival probabilities and per capita growth rates can drive the system to persistance and extinction as well. Specific relations of these parameters were found as thresholds for population continuation. Carrying capacity can also play an essential role in determining long-term behavior.

As the ecological conditions change, similar repercussions are observed in all generations. The dynamics of each generation maintain similar behavior for some cases when factors such as survival probabilities are varied. Changing conditions will produce periodic lifecycles to chaotic behaviors. Interesting dynamics are observed where simple behavior fluctuates to more complex dynamics, and even more interesting are the cases where complex dynamics stabilize to simpler behavior. Multiple attractors exist in model systems that we investigated, showing that long term behavior is greatly affected by initial conditions. Additionally, we found invariant trajectories that act as attractors under certain conditions. Chaotic trajectories are identified via Lyapunov exponents.

6 Appendix

To prove Theorem 3.1 and Theorem 4.1 we need the following results from Smith (1986)

Theorem 6.1. *Let $T : R_+^n \to R_+^n$ be continuous, C^1 in R_+^n and suppose $DT(0)$ exists with $\lim_{x \to 0^+} DT(x) = DT(0)$. In addition, assume[4]*

$$(i):\ DT(x) > 0 \ if \ x > 0,$$

and

$$(ii):\ DT(y) < DT(x) \ if \ 0 < x < y.$$

If $T(0) = 0$, let $\lambda = \rho(DT(0))$. If $\lambda \leq 1$, then for every $x \geq 0$, $T^n(x) \to 0$ as $n \to \infty$. If $\lambda > 1$ then either $T^n(x) \to \infty$ as $n \to \infty$ for every $x > 0$ or there exists a unique nonzero fixed point q of T. In the later case, $q > 0$ and for every $x > 0$, $T^n(x) \to q$ as $n \to \infty$.
If $T(0) \neq 0$, then either $T^n(x) \to \infty$ as $n \to \infty$ for every $x \geq 0$ or there exists a unique fixed point q of T. In the later case, $q > 0$ and for every $x \geq 0$, $T^n(x) \to q$ as $n \to \infty$.

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[4]Matrices' inequalities are considered componentwise

Theorem 6.2. *Let $p \in R^n_+$ and $T : [0,p] \to [0,p]$ be continuous, C^1 in $(0,p)$ and suppose $DT(0)$ exists with $\lim_{x\to 0^+} DT(x) = DT(0)$. In addition, assume (i) and (ii) of theorem 6.1 hold for $0 < x < y < p$ and that $T(p) < p$.*

If $T(0) = 0$, let $\lambda = \rho(DT(0))$. If $\lambda \leq 1$, then for every $x \in [0,p]$, $T^n(x) \to 0$ as $n \to \infty$. If $\lambda > 1$ then T has a unique nonzero fixed point q. Moreover, $q \in (0,p)$ and $T^n(x) \to q$ as $n \to \infty$ for every $x \in [0,p] - \{0\}$.

If $T(0) > 0$, then T has a unique fixed point $q \in [0,p]$. Moreover, $q \in (0,p)$ and $T^n(x) \to q$ as $n \to \infty$ for every $x \in [0,p]$.

Proof of Theorem 3.1

Let $F : R^2_+ \to R^2_+$ be given by

$$F(x,y) = \left(\frac{\mu(y + (1-d)x)}{1 + \rho(y + (1-d)x)}, \frac{da\mu(y + (1-d)x)}{1 + (db + \rho)(y + (1-d)x)} \right) \tag{8}$$

where μ, ρ, a, $b > 0$ and $0 \leq d \leq 1$. Observe that this function F is equivalent to System (3). Then, the jacobian matrix for F is

$$DF(x,y) = \begin{pmatrix} \frac{\mu(1-d)}{[1+\rho(y+(1-d)x)]^2} & \frac{\mu}{[1+\rho(y+(1-d)x)]^2} \\ \frac{ad\mu(1-d)}{[1+(\rho+bd\mu)(y+(1-d)x)]^2} & \frac{ad\mu}{[1+(\rho+bd\mu)(y+(1-d)x)]^2} \end{pmatrix}$$

and since $(1 - d) \geq 0$ then $DF(x,y) > 0$ for $x > 0$, $y > 0$. Moreover, the components of $DF(x,y)$ are continuous functions whenever $x \geq 0$, $y \geq 0$. Hence, $\lim_{x,y\to 0^+} DF(x,y) = DF(0,0)$. Now, consider the function $h : R^2_+ \to R^2_+$, defined by

$$h(x,y) = \frac{a}{(b + cx + y)^2} \tag{9}$$

where $a,b,c > 0$. Suppose $0 < (x,y) < (u,v)$, *i.e.*, $x < u$ and $y < v$. Then

$$0 < b + cx + y < b + cu + v$$
$$0 < (b + cx + y)^2 < (b + cu + v)^2$$
$$\frac{a}{(b + cu + v)^2} < \frac{a}{(b + cx + y)^2}$$
$$h(u,v) < h(x,y).$$

Therefore, the function h is decreasing. But, each component of $DF(x,y)$ is equivalent to $h(x,y)$ for specific values of a, b and c. So that, each of these components is decreasing. Therefore, $DF(u,v) < DF(x,y)$, if $(x,y) < (u,v)$. Now, let $\lambda = \rho(DF(0,0))$ be the spectral radius of the Jacobian matrix $DF(0,0)$. Then λ is equal to the largest eigenvalue of $DF(0,0)$. So that, $\lambda = a_3 a_2 a_1 \gamma_3 \gamma_2 \gamma_1((1 - d) + a_4 \gamma_4 d)$. In addition, $F(0,0) = (0,0)$. Hence by theorem 6.1, if $\lambda \leq 1$, then $(0,0)$ is globally stable and if $\lambda > 1$, then System (3) has a unique nonzero fixed point that is globally attracting in $(0,\infty) \times (0,\infty)$.

Proof of Theorem 4.1

Let $p = \left(\frac{1}{2\gamma_2\sigma_1}, \frac{1}{2\gamma_2\sigma_1(1-d)}\right) \in R_+^2$ and let $F : [0,p] \to [0,p]$ be defined as

$$F(x,y) = \left(\gamma_3\gamma_2\sigma_1[y + (1-d)x]e^{r_2+r_3-\gamma_2\sigma_1[y+(1-d)x][1+\gamma_3e^{r_2-\gamma_2\sigma_1[y+(1-d)x]}]},\right.$$
$$\left.\sigma_4 d\gamma_3\gamma_2\sigma_1[y + (1-d)x]e^{r_2+r_3-\gamma_2\sigma_1[y+(1-d)x][1+\gamma_3e^{r_2-\gamma_2\sigma_1[y+(1-d)x]}]}\right)$$

which represents System (5). The Jacobian matrix for this function is given by

$$DF(x,y) = \begin{pmatrix} (1-d)f(x,y) & f(x,y) \\ \sigma_4 d(1-d)f(x,y) & \sigma_4 df(x,y) \end{pmatrix}$$

where

$$f(x,y) = \gamma_3\gamma_2\sigma_1\left(1 - \gamma_2\sigma_1\big(y + (1-d)x\big)\right)\left(e^{r_2+r_3-\gamma_2\sigma_1\big(y+(1-d)x\big)}\big(1+\gamma_3e^{r_2-\gamma_2\sigma_1(y+(1-d)x)}\big)\right)$$
$$-\gamma_3\gamma_2\sigma_1\big(y + (1-d)x\big)e^{2r_2+r_3-\gamma_2\sigma_1\big(y+(1-d)x\big)}\big(2+\gamma_3e^{r_2-\gamma_2\sigma_1(y+(1-d)x)}\big)\right).$$

Suppose $\ln(\frac{1}{\gamma_3}) > r_2$, then for $(x,y) \in (0,p)$ we have that $f(x,y) > 0$. Therefore, $DF(x,y) > 0$ for $(x,y) \in (0,p)$.

Now, consider the function

$$g(z) = (1-z)\left(e^{b-z(1+e^{c-z})} - ze^{d-z(2+e^{c-z})}\right)$$

which is equivalent to $f(x,y)$ for $z = y + (1-d)x$. Observe that the function $g(z)$ satisfies $g'(z) < 0$, so that is decreasing. Let $(x,y),(u,v) \in (0,p)$ be such that $(x,y) < (u,v)$ and define $z_1 = y + (1-d)x$, $z_2 = v + (1-d)u$. Then $z_1 < z_2$, and since g is decreasing then $g(z_2) < g(z_1)$. Hence, $f(u,v) < f(x,y)$. Therefore, $DF(u,v) < DF(x,y)$ if $(0,0) < (x,y) < (u,v) < p$. Now, let $\lambda = \rho(DF(0,0))$ be the spectral radius of the Jacobian matrix $DF(0,0)$. Then λ is equal to the largest eigenvalue of $DF(0,0)$. So that, $\lambda = \gamma_3\gamma_2\sigma_1((1-d) + \sigma_4 d)e^{r_2+r_3}$. In addition, $F(0,0) = (0,0)$. Hence by Theorem 6.2, if $\lambda \leq 1$, then for every $x \in [0,p]$, $F^n x \to 0$ as $n \to \infty$, and if $\lambda > 1$ then System (5) has a unique nonzero fixed point $q \in (0,p)$ and $F^n x \to q$ as $n \to \infty$ for every $x \in [0,p] - \{0\}$.

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