



Monarch butterfly spatially discrete advection model

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Abstract

We study the population cycles of the Monarch butterfly using one of the simplest systems incorporating both migration and local dynamics. The annual migration of the Monarch involves four generations. Members of Generations 1–3 (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 Generation 3 and all members of the Generation 4 butterflies begin their return to the over-wintering grounds in August through October where they enter reproductive diapause for several months. We developed a simple discrete-time island chain model in which different fecundity functions are used to model the reproductive strategies of each generation. The fecundity functions are selected from broad classes of functions that capture the effects of either contest or scramble intraspecific competition in the Monarch population. 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 persistence of the overall butterfly populations. The stage structure used in modeling the 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 are explored.

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1. Introduction

The North American Monarch butterfly, *Danaus Plexippus* Lepidoptera, exhibits one of the most spectacular natural migration phenomena in the world. However, it is considered an *endangered phenomena* because scientists fear that the incredible Monarch migration pattern may not last beyond the next decade [6,43,44,50,53–55]. In this article, we use a simple mathematical model to study the effects of migration and intraspecific competition on the Monarch butterfly population dynamics. Our model, a spatially discrete advection model, tracks populations rather than probabilities of patch occupancy. The model does not assume stochastic extinctions, and in the model dispersal arises from deterministic directed motion rather than stochastic colonizations. Such models are sometimes called island chain models [2,13,18,22,28,39,40,52]. By their own nature, simple models cannot incorporate many of the complex biological factors. However, they often provide useful insights to help our understanding of complex processes.

Spatial heterogeneity is one of the most important factors influencing population dynamics, and our Monarch butterfly population model has a spatial structure [49]. Within the past three decades mathematical ecologists have had great success in showing how specific aspects of the spatial environment alters population and community environment [22,49]. Ecologists have often used spatial structure to explain the stable coexistence of species in a competitive environment [11,21,24,28,34], the persistence of predator–prey and host–parasite interactions [1,8,12,15,20,35,41,45,58], and the regional persistence of small populations subject to local stochastic extinction [9,10]. Spatial structure is also an important characteristic of metapopulation models [5,14,16,56].

Monarch butterfly population growth takes place at discrete-time intervals, and we use a system of non-linear difference equations rather than continuous-time differential equations to describe the growth process. Non-linear difference equations, even if simple and deterministic with respect to their characteristic parameters, are known to exhibit a remarkable spectrum of dynamic behavior including apparent random chaotic fluctuations [1,26,27,30–32,40,59]. Data collected from the 4th of July North American Monarch butterfly count indicates large population fluctuations from year to year with no apparent long-term trends [48]. Our model captures this observed annual fluctuations of the Monarch butterfly population, and for some choice of the model parameters, the dynamical fluctuations are in many respects indistinguishable from the sample realizations of a random process.

In this paper, we focus on *compensatory* (equilibrium) and *overcompensatory* (oscillatory) dynamics in the Monarch butterfly population, two types of density dependent intraspecific competition for resources. Compensatory dynamics is also referred to as pure *contest competition* because only a constant number of competitors survive in a single-habitat system. The term was initially proposed by Nicholson who contrasted it with *pure scramble competition*, the most extreme form of overcompensatory dynamics, where all the competitors may be so adversely affected by each other that none of them survive [4,36,56,60].

In Section 2, we develop the main model, a simple discrete-time Monarch butterfly population model that describes Monarch populations over four generations. Also in Section 2, we obtain the Monarch butterfly basic demographic reproductive number, $\mathcal{R}_d$, a threshold parameter for the persistence or extinction of the butterfly population. We consider different fecundity functions that depend on population densities and availability of resources. In Section 3, we focus on the effects of migration and contest (compensatory dynamics) intraspecific competition on Monarch

population dynamics. We prove that Monarch migrant populations under compensatory dynamics persist on a globally stable positive steady-state whenever $\mathfrak{R}_d > 1$, while $\mathfrak{R}_d < 1$ implies the global extinction of the Monarch butterfly. It is known that migration and overcompensatory dynamics can give rise to complex bifurcation patterns including multiple attractors with complex basins of attraction [7,17,56]. Section 4 is on the role of migration and scramble (overcompensatory dynamics) intraspecific competition on Monarch population dynamics. In Section 4, examples are used to demonstrate cyclic and chaotic attractors as well as coexisting ‘multiple’ attractors in the Monarch population model. Mixed contest and scramble competition models are studied in Section 5. When all the populations of the Monarch butterfly are under mixed compensatory–overcompensatory dynamics, we demonstrate population oscillations and explore how varying the migration and survival parameters affect the Monarch dynamics such as population abundance and the long-term steady-states (attractors) [4,5,36,40,56,60]. Our results are summarized in Section 6, and detailed proofs are collected in Appendix A.

2. The Monarch butterfly model

In this section, we construct a simple model that describes the life cycles of the Monarch butterfly. There are three to four generations of Monarchs within the expanse of one year, and the annual Monarch migration does not occur entirely within one generation. The initial Monarch clusters appear in trees near mountain tops of Mexico in early winter. Adult Monarchs travel southwest to the neovolcanic mountains of Central Mexico from their breeding grounds in Southern Canada and Northern United States. A proportion of the third generation,¹ 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 or Generation 4) that eclose (hatch) late in August and early fall [33]. 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 [3,5,19]. While remaining in Mexico from November through early February, the butterflies are in a physically dormant state and cluster in fir trees (see Fig. 1). 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. That is, the same migrating fall population returns to the northern breeding grounds in the spring [50]. Urquhart [50] 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 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

¹ We call this Generation 3 for modelling convenience.



Fig. 1. Monarch Butterfly (*Danaus Plexippus* Lepidoptera).

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 [50]. However, there have been other studies suggesting that the spring remigration does not occur in the manner described by Urquhart. In 1993, Malcolm 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 ubiquitous early spring milkweed, *A. viridis* [29]. Thus, Malcolm poses a successive brood remigration to the northern breeding grounds, while Urquhart essentially describes a single sweep migration.

Knight [25], in a study of spring remigration of the Gulf Coast states, 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 [25]. Thus, there is a three week critical time period to establish Generation 1 Monarchs. The population of Generation 1 and 2 that continue migrating northward and the majority of Generation 3 have a life-span of two to six weeks. The Generation 3 adults that emerge late in August undergo reproductive diapause and exhibit the extended life-span 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 within one migratory cycle.

We let $x_i(t)$ denote the population size of Generation $i \in \{1, 2, 3, 4\}$ 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 Generation 3 population is represented by $(1 - d)$, where $d < 1$. Thus d represents the proportion of non-migratory individuals. The 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 each $i \in \{2, 3, 4\}$) 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 (see Fig. 2). The

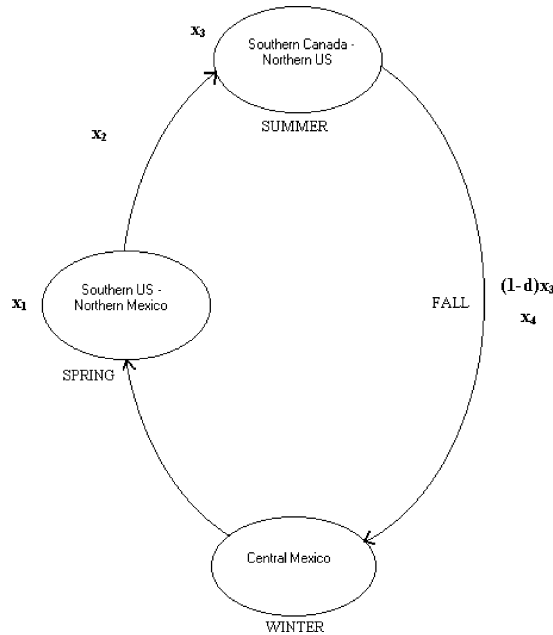


Fig. 2. Migration pattern of the Monarch butterfly.

fecundity function for each Generation i , f_i , describes how new individuals of Generation i are born. For each Generation $i \in \{1, 2, 3, 4\}$, unless declared otherwise, we assume that f_i takes on the form $f_i(x_i) = x_i g_i(x_i)$, where the per-capita growth function, $g_i : [0, \infty) \rightarrow (0, \infty)$, is assumed to be strictly decreasing positive and twice differentiable (C^2 on $[0, \infty)$) with $\lim_{x_i \rightarrow \infty} g_i(x_i) < 1$, and where x_i is the measure of the size of the population.

Definition 1. Generation $i \in \{1, 2, 3, 4\}$ Monarchs are governed by *compensatory* dynamics whenever $f_i(x_i) = x_i g_i(x_i)$ has a positive fixed point X_i and all positive densities approach the positive equilibrium at X_i monotonically under f_i iterations [36,56].

If f_i increases monotonically from zero with the rate of increase slowing down as x_i gets large then Generation i are under compensatory dynamics. The Beverton–Holt stock recruitment model, $f_i(x_i) = \frac{a_i x_i}{1 + b_i x_i}$, portrays compensatory dynamics where the positive constant $a_i > 1$ is the maximal per capita intrinsic growth rate of the population and the positive constant b_i scales the carrying capacity of the population. The map f_i has a global attractor at $X_i = \frac{a_i - 1}{b_i}$, and no initial condition overshoots X_i [56].

Definition 2. Generation $i \in \{1, 2, 3, 4\}$ Monarchs are governed by *overcompensatory* dynamics whenever $f_i(x_i) = x_i g_i(x_i)$ has a positive fixed point X_i and some positive population sizes ‘overshoot’ the positive equilibrium at X_i under f_i iterations [36,56].

Data collected from the 4th of July Monarch Butterfly Count, a one-day annual census of butterflies at selected sites, indicates that the North American Monarch butterflies fluctuate in

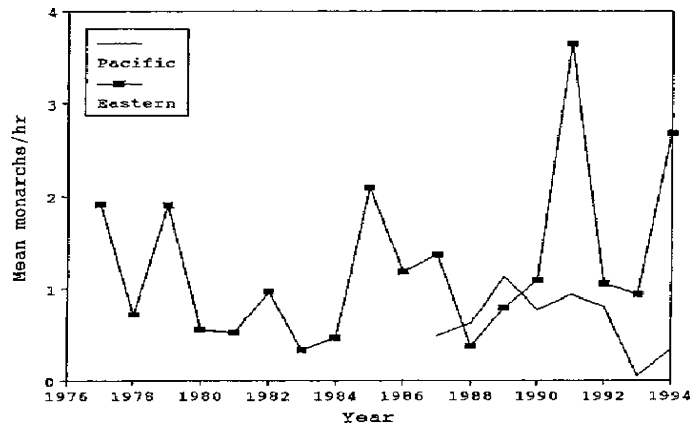


Fig. 3. Mean Monarch butterfly population per party hour in the 4th of July count for Eastern and Pacific areas from 1976 to 1994 [48].

abundance annually. However, no long-term trends were apparent from the data (see Fig. 3) [48]. In Sections 4 and 5, we use overcompensatory dynamics to understand long-term trends in the Monarch butterfly population whenever the Monarch population fluctuates in abundance annually.

If f_i is a one hump map with a stable (respectively, an unstable) positive fixed point, then the return to the stable fixed point takes the form of damped oscillations (respectively, the local behavior near the unstable fixed point takes the form of divergent oscillations), and the dynamics is overcompensatory. Whenever the carrying capacity of the population $r_i > 1$ and f_i is given by Ricker's model, $f_i(x_i) = x_i \exp(r_i - x_i)$, then Generation i Monarchs are governed by overcompensatory dynamics [42].

Definition 3. Generation $i \in \{1, 2, 3, 4\}$ fecundity function, f_i , is an α -monotone concave map if $f'_i(x_i) > 0$ and $f''_i(x_i) < 0$ for each $x_i \in [0, \alpha]$ [56].

Generation i Monarchs are under compensatory dynamics at population sizes in the closed interval $[0, \alpha]$ whenever f_i is an α -monotone concave map with a unique positive fixed point in the open interval $(0, \alpha)$. The Beverton–Holt model is an ∞ -monotone concave map (compensatory dynamics). When Generation i fecundity function, f_i , is an α -monotone concave map and some initial populations in the interval (α, ∞) overshoot the positive fixed point in the closed interval $[0, \alpha]$, then f_i describes situations in which there is compensatory and overcompensatory dynamics at lower densities and higher densities, respectively. Ricker's model $f_i(x_i) = x_i \exp(r_i - x_i)$ with $0 < r_i < 1$ is a 1-monotone concave map since all positive initial populations with densities in the interval $[0, 1]$ approach the unique positive fixed point $X_i = r_i$ monotonically but initial populations in $(1, \infty)$ overshoot the positive fixed point. That is, there is compensatory and overcompensatory dynamics in $[0, 1]$ and $(1, \infty)$, respectively [7,57].

Each generation of the Monarch butterfly is a function of the individuals in previous generations that are alive and reproduce successfully. Recall that all the four generations considered are born within a year. Therefore, at time $t + 1$, the fecundity functions of Generations 2, 3 and 4

depend on Generations 1, 2 and 3 populations at the same time $t + 1$, respectively. However, Generation 1, the first generation considered within a year, has a fecundity function that depends on Generations 3 and 4 from the previous year. The following system of non-linear difference equations describes the Monarch population dynamics:

$$\left. \begin{aligned} x_1(t+1) &= f_1(\gamma_1[x_4(t) + (1-d)x_3(t)]), \\ x_2(t+1) &= f_2(\gamma_2x_1(t+1)), \\ x_3(t+1) &= f_3(\gamma_3x_2(t+1)), \\ x_4(t+1) &= f_4(d\gamma_4x_3(t+1)), \end{aligned} \right\} \quad (1)$$

where $x_i(t)$, $i \in \{1, \dots, 4\}$, describe Generations 1–4 population size at time t . Using this island chain 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 population that does not migrate), and look for periodic oscillations and presence of multiple attractors.

System (1) can be written as the following system of first-order difference equations:

$$\left. \begin{aligned} x_1(t+1) &= f_1(\gamma_1[x_4(t) + (1-d)x_3(t)]), \\ x_2(t+1) &= f_2 \circ \gamma_2 f_1(\gamma_1[x_4(t) + (1-d)x_3(t)]), \\ x_3(t+1) &= f_3 \circ \gamma_3 f_2 \circ \gamma_2 f_1(\gamma_1[x_4(t) + (1-d)x_3(t)]), \\ x_4(t+1) &= f_4 \circ d\gamma_4 f_3 \circ \gamma_3 f_2 \circ \gamma_2 f_1(\gamma_1[x_4(t) + (1-d)x_3(t)]), \end{aligned} \right\} \quad (2)$$

where $f_i \circ f_j$ is f_i composed with f_j . Clearly, the dynamics of the 4-dimensional model can be completely determined from the last two equations in System (2), and henceforth we study the following 2-dimensional model:

$$\left. \begin{aligned} x(t+1) &= h_1(\gamma_1[y(t) + (1-d)x(t)]), \\ y(t+1) &= h_2(\gamma_1[y(t) + (1-d)x(t)]), \end{aligned} \right\} \quad (3)$$

where $x_3 = x$, $y = x_4$, $h_1 = f_3 \circ \gamma_3 f_2 \circ \gamma_2 f_1$ and $h_2 = f_4 \circ d\gamma_4 f_3 \circ \gamma_3 f_2 \circ \gamma_2 f_1$ (that is, $h_2 = f_4 \circ d\gamma_4 h_1$).

To write System (3) in a compact form, the vector of population sizes $(x(t), y(t))$ is written as (x, y) so that the *Monarch model* reproduction function $F : \mathbb{R}_+^2 \rightarrow \mathbb{R}_+^2$ may be written as

$$F(x, y) = (h_1(\gamma_1[y + (1-d)x]), h_2(\gamma_1[y + (1-d)x])).$$

F^t is F composed with itself t times. $F_i^t(x)$ is the i th component of F^t evaluated at the point (x, y) in $\mathbb{R}_+^2$. The set of iterates of the map F is equivalent to the set of all density sequences generated by System (3). Therefore, F^t gives the population densities in generation t .

Lemma 1. *The positive cone is invariant, and no non-negative orbit is unbounded in System (3).*

The proof of Lemma 1 is in Appendix A.

The basic demographic reproductive number is

$$\mathfrak{R}_d = \gamma_1 \gamma_2 \gamma_3 g_1(0) g_2(0) g_3(0) ((1-d) + \gamma_4 d g_4(0)).$$

$\mathfrak{R}_d < 1$ when the maximal value of each per capita growth rate $g_i(0) < 1$. In Theorem 1, we prove that $\mathfrak{R}_d < 1$ implies extinction of the Monarch butterflies in all generations, while $\mathfrak{R}_d > 1$ implies its persistence.

3. Monarch butterfly under compensatory dynamics

Here, we study the effects of migration and compensatory dynamics on the persistence of the Monarch butterfly. The dynamics of each Generation $i \in \{1, 2, 3, 4\}$ are assumed to be compensatory. That is, each fecundity function, f_i , is an α -monotone concave map with a unique positive fixed point in the open interval $(0, \alpha)$. Independent of initial Monarch population sizes, we prove that migration and $\mathfrak{R}_d > 1$ lead to an overall globally stable positive steady-state and the Monarch population persists, while migration and $\mathfrak{R}_d < 1$ lead to an overall global extinction. Consequently, if each net per capita growth rate $\gamma_i g_i(0)$ is small, then the butterfly population will go extinct in System (3), 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 on a positive stable equilibrium whenever the dynamics of each Generation $i \in \{1, 2, 3, 4\}$ are compensatory. We collect these results in the following theorem.

Theorem 1. *In System (3), for each Generation $i \in \{1, 2, 3, 4\}$ let each fecundity function be modeled by f_i , an α -monotone concave map with $X_i \in (0, \alpha)$. Then the Monarch population persists on a globally attracting positive fixed point $q = (q_1, q_2) \in R_+^2$ such that $F^t(x) \rightarrow q$ as $t \rightarrow \infty$ for every point $x \in [0, p] - \{0\}$, provided that $\mathfrak{R}_d > 1$ and $p = (\alpha, \alpha) \in \text{int}(R_+^2)$. However, if $\mathfrak{R}_d \leq 1$, then for every $x \in [0, p]$, $F^t(x) \rightarrow 0$ as $t \rightarrow \infty$, and the Monarch population goes extinct.*

The proof of Theorem 1 is in Appendix A.

Theorem 1 is a generalization of a result of Sáenz and Stein [46]. For an application of Theorem 1, we describe the fecundity function for each Generation $i \in \{1, 2, 3, 4\}$ with the Beverton–Holt equation

$$f_i(x_i) = \frac{a_i x_i}{1 + b_i x_i},$$

where each $a_i > 1$. That is, each f_i is an α -monotone concave map with $X_i = \frac{a_i - 1}{b_i} \in (0, \alpha)$ and $g_i(0) = a_i$. Consequently, each f_i dynamics is compensatory and in each generation contest competition exists in the population. Then System (3) assumes the following form:

$$\left. \begin{aligned} x(t+1) &= \frac{a_3 a_2 a_1 \gamma_3 \gamma_2 \gamma_1 [y(t) + (1-d)x(t)]}{1 + [b_3 a_2 a_1 \gamma_3 \gamma_2 \gamma_1 + b_2 a_1 \gamma_2 \gamma_1 + b_1 \gamma_1] [y(t) + (1-d)x(t)]}, \\ y(t+1) &= \frac{d a_4 a_3 a_2 a_1 \gamma_4 \gamma_3 \gamma_2 \gamma_1 [y(t) + (1-d)x(t)]}{1 + [d b_4 a_3 a_2 a_1 \gamma_4 \gamma_3 \gamma_2 \gamma_1 + b_3 a_2 a_1 \gamma_3 \gamma_2 \gamma_1 + b_2 a_1 \gamma_2 \gamma_1 + b_1 \gamma_1] [y(t) + (1-d)x(t)]}. \end{aligned} \right\} \quad (4)$$

In System (4), the basic demographic reproductive number is

$$\mathfrak{R}_d = \gamma_1 \gamma_2 \gamma_3 a_1 a_2 a_3 ((1-d) + \gamma_4 d a_4).$$

The value of $\mathfrak{R}_d$ 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 persistence. Small values of these parameters lead to extinction while large values lead to the persistence of the Monarch butterflies (Theorem 1).

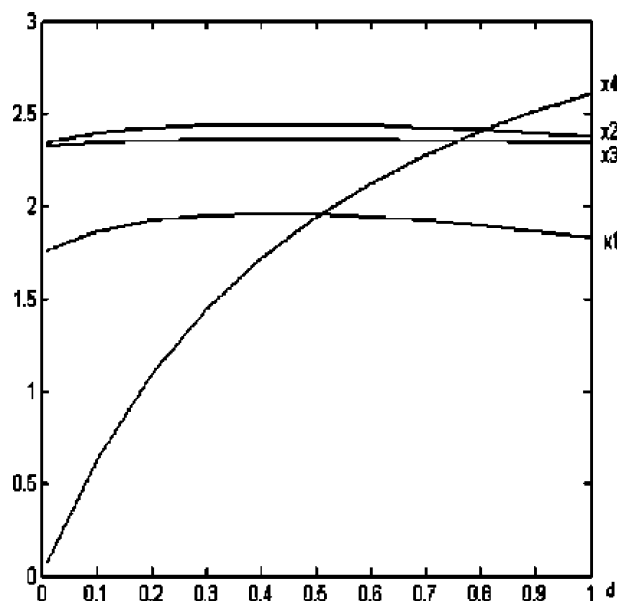


Fig. 4. The effects of migration on each generation of Monarch butterfly. On the horizontal axis, $0 \leq d \leq 1$.

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 Monarch butterflies? 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 one would expect. However, a variation in each of these parameters that produces 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. 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 only exhibit small changes in abundance. It is apparent that parameter d can have a stronger impact on Generation 4 than on any other generation; Generation 4 is an increasing function of d (Fig. 4).

4. Monarch butterfly under overcompensatory dynamics

We now study the effects of migration and overcompensatory dynamics on the persistence of the Monarch butterfly. Hence, we consider cases when the fecundity functions of two generations are under overcompensatory dynamics, while the remaining two are given by the linear function $f_i(x_i) = \sigma_i x_i$, 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. This simplification does not seem to diminish the ‘realism’ of the model, as small larval densities will exist when there are concentrated abundant plant communities. That is, we assume that density dependent competition does not play a consistent significant role within all generations.

First, we examine the case when Generation 1 and Generation 4 Monarch populations maintain linear fecundity functions, while the Generation 2 and Generation 3 populations are under overcompensatory dynamics. That is, $f_1(x_1) = \sigma_1 x_1$ and $f_4(x_4) = \sigma_4 x_4$. Then System (3) reduces to

$$\left. \begin{aligned} x(t+1) &= h_1(\gamma_1[y(t) + (1-d)x(t)]), \\ y(t+1) &= d\sigma_4 h_1(\gamma_1[y(t) + (1-d)x(t)]). \end{aligned} \right\} \quad (5)$$

In System (5), the invariant ‘diagonal’ line $L = \{(x, y) \in R_+^2 \mid y = d\sigma_4 x\}$ is globally attracting. That is, the Monarch population live on the diagonal line. On L , the dynamics of System (5) is given by the set of iterates of the 1-dimensional map, $H : [0, \infty) \rightarrow [0, \infty)$ defined by $H(x) = d\sigma_4 h_1(\gamma_1[(d\sigma_4 + (1-d))x])$. We summarize these in the following result.

Theorem 2. *In System (5), the invariant ‘diagonal’ line*

$$L = \{(x, y) \in R_+^2 \mid y = d\sigma_4 x\}$$

is globally attracting, and the dynamics on L are qualitatively equivalent to that of the 1-dimensional map, $H : [0, \infty) \rightarrow [0, \infty)$ defined by

$$H(x) = d\sigma_4 h_1(\gamma_1[(d\sigma_4 + (1-d))x]).$$

The proof of Theorem 2 is in Appendix A.

To explore the possible complex overcompensatory dynamics on L , we assume that Generation 2 and Generation 3 fecundity functions in System (5) are given by the Ricker models, $f_2(x_2) = x_2 e^{r_2 - x_2}$ and $f_3(x_3) = x_3 e^{r_3 - x_3}$, respectively. Then System (5) becomes

$$\left. \begin{aligned} x(t+1) &= \gamma_3 \gamma_2 \sigma_1 [y(t) + (1-d)x(t)] \cdot e^{r_2 + r_3 - \gamma_2 \sigma_1 [y(t) + (1-d)x(t)]} [1 + \gamma_3 e^{r_2 - \gamma_2 \sigma_1 [y(t) + (1-d)x(t)]}], \\ y(t+1) &= d\sigma_4 \gamma_3 \gamma_2 \sigma_1 [y(t) + (1-d)x(t)] \cdot e^{r_2 + r_3 - \gamma_2 \sigma_1 [y(t) + (1-d)x(t)]} [1 + \gamma_3 e^{r_2 - \gamma_2 \sigma_1 [y(t) + (1-d)x(t)]}]. \end{aligned} \right\} \quad (6)$$

In System (6), the dynamics on the globally attracting invariant line L are generated by the 1-dimensional map

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

For some values of the parameters, H supports stable cyclic overcompensatory dynamics via period-doubling bifurcations route to chaos which are characteristic of Monarch populations (see Fig. 5) [51].

Now, we examine the case when Generation 1 and Generation 2 Monarch populations maintain linear fecundity functions, while the Generation 3 and Generation 4 populations are under overcompensatory dynamics. That is, $f_1(x_1) = \sigma_1 x_1$ and $f_2(x_2) = \sigma_2 x_2$. Then System (3) reduces to

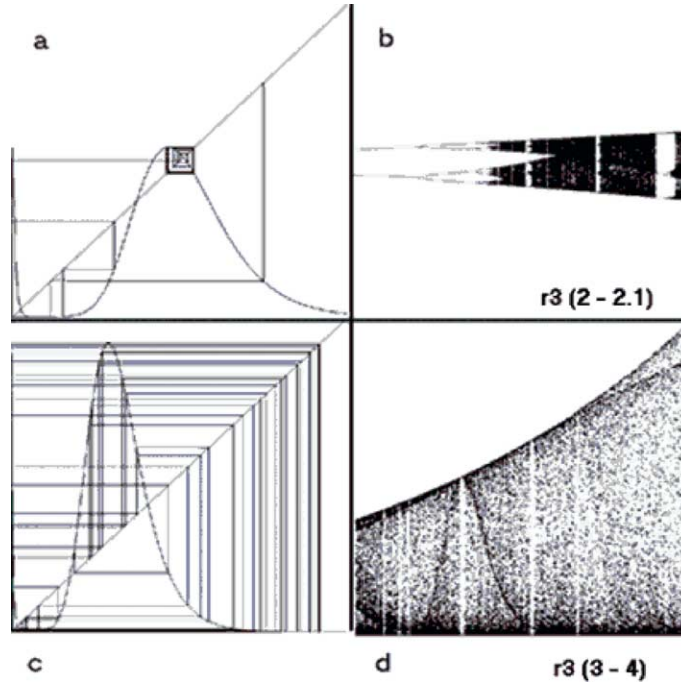


Fig. 5. Stable periodic attractors and unstable interval attractors in the Monarch population under overcompensatory dynamics.

$$\left. \begin{aligned} x(t+1) &= f_3(\gamma_3 \sigma_2 \sigma_1 [y(t) + (1-d)x(t)]), \\ y(t+1) &= f_4(d \sigma_4 f_3(\gamma_3 \sigma_2 \sigma_1 [y(t) + (1-d)x(t)])) \end{aligned} \right\} \quad (7)$$

System (7), a 2-dimensional model, is capable of supporting simple and complex (chaotic) dynamics including periodic attractors, chaotic attractors and multiple attractors with complex basins of attraction whenever f_3 and f_4 are governed by overcompensatory dynamics. To illustrate these dynamical structures in System (7), we let $f_3(x) = xe^{r_3-x}$ and $f_4(y) = ye^{r_4-y}$. Then System (7) becomes

$$\left. \begin{aligned} x(t+1) &= \gamma_3 \sigma_2 \sigma_1 [y(t) + (1-d)x(t)] e^{r_3 - \gamma_3 \sigma_2 \sigma_1 [y(t) + (1-d)x(t)]}, \\ y(t+1) &= d \gamma_4 \gamma_3 \sigma_2 \sigma_1 [y(t) + (1-d)x(t)] \cdot e^{r_3 + r_4 - \gamma_3 \sigma_2 \sigma_1 [y(t) + (1-d)x(t)] e^{r_3 - \gamma_3 \sigma_2 \sigma_1 [y(t) + (1-d)x(t)]}} \end{aligned} \right\} \quad (8)$$

We explore the dynamics of System (8) when certain parameters are varied separately, and all other parameters are kept fixed. Through bifurcation diagrams, we determine if parameter variation induces changes in dynamics between Generations 3 and 4. Also, 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.

The bifurcation diagrams in Fig. 6(a)–(d) compare the parameter γ_4 , the survival probability that individuals from Generation 2 survive to reproduce, with d , the parameter that describes the proportion of non-migratory reproducing members of Generation 3. By varying the same parameter over Generations 3 and 4, Fig. 6 shows that it is possible for the bifurcation from chaos to stable equilibria or periodic cycles to occur at the same values in Generations 3 and 4, but the

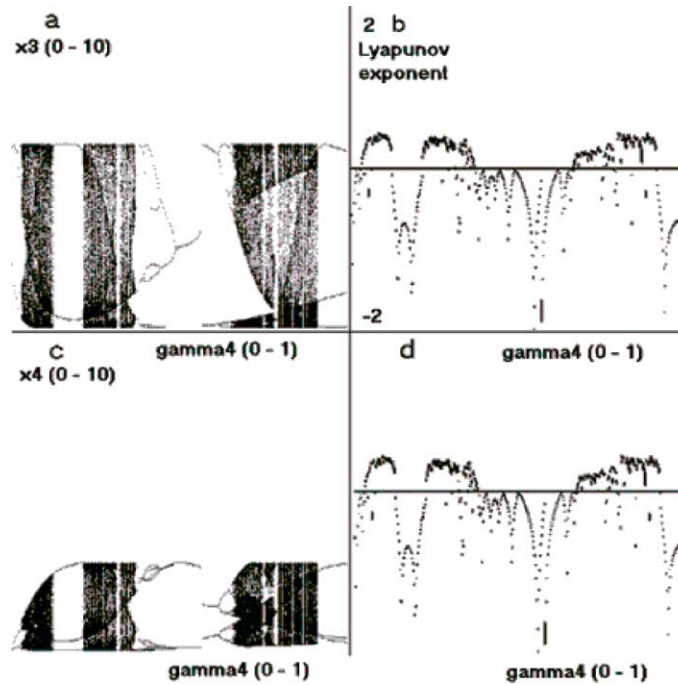


Fig. 6. Periodic and chaotic attractors in System (8).

scale of the vertical axis deviates between generations. 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, periodic cycles occur at different points between generations. These patterns occur 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 patterns are observed, as they play equal roles within the system.

The plots of Lyapunov exponents support the observation that dynamics across Generations 3 and 4 remained constant as the same parameters are varied [37]. In this case γ_4 is varied from 0 to 1. A region of positive Lyapunov exponents occur from $\gamma_4 = 0.7$ to $\gamma_4 = 0.8$. Accordingly, the bifurcations of diagrams (a) and (c) show that chaotic dynamics occur when γ_4 is 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 $r_4 = 2$ to $r_4 = 3$. Therefore, for this choice of parameters, it appears that differences in population size do not affect the system greatly.

System (8) is capable of supporting multiple attractors with fractal basin boundaries (see Fig. 7) [37]. In this situation, long term behavior of the Monarch population is influenced by initial conditions. Hanski et al. [17] have observed multiple steady-states in field data on the butterfly *Melitaea cinxia*. For some parameter values, System (8) supports an invariant curve that is attracting. Fig. 8 shows the invariant curve and its basin of attraction. We cannot conclude that the attracting curve is a Ricker's curve, as multiple attractors exist in the system. Monarch populations

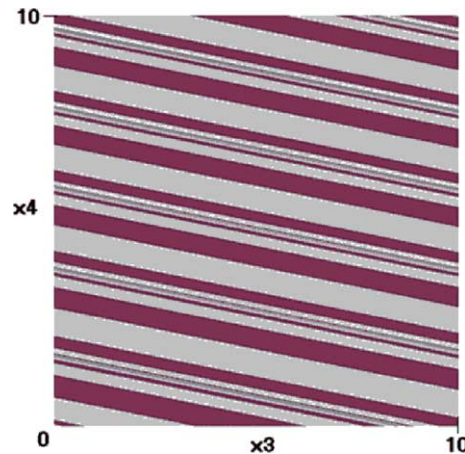


Fig. 7. Basins of attraction of two coexisting 2-cycle attractors at $\{(0.0845, 0.3107), (4.44, 1.69)\}$ and $\{(0.0238, 0.0905), (2.405, 2.6457)\}$; in System (8).

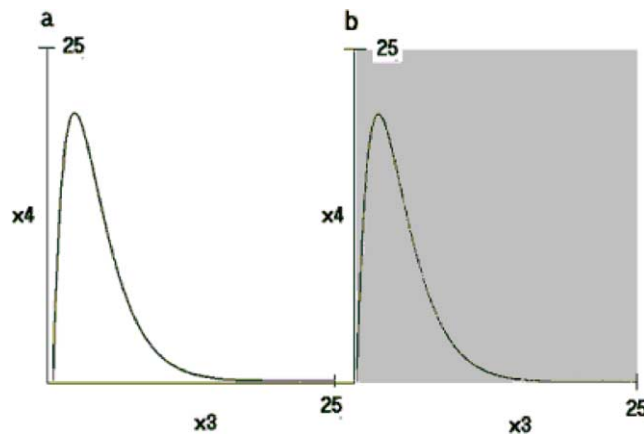


Fig. 8. System (8) supports an attracting invariant curve.

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 functions of Generations 2 and 3 were represented by Ricker's model (overcompensatory dynamics), while 1 and 4 were linear fecundity functions. In that case, the invariant set is a line (see Theorem 2). The dynamics on both the invariant curve and the invariant line are similar to the dynamics generated by the Ricker's map. That is, simple cyclic oscillations, period-doubling bifurcations and chaotic events occur on the invariant sets; dependent on the parameter values.

5. Monarch butterfly under mixed dynamics

Due to the lack of ample data on fecundity functions of the Monarch butterfly it is difficult to precisely understand which factors affect fecundity the most. It is possible that fecundity functions

of the different generations are formed through varying biological factors [23]. For simplicity, we use linear fecundity functions to describe Generations 1 and 4 in the system. System (1) takes the form

$$\left. \begin{aligned} x_1(t+1) &= \sigma_1[d\sigma_4 + (1-d)]x_3(t), \\ x_2(t+1) &= f_2(\gamma_2\sigma_1[d\sigma_4 + (1-d)]x_3(t)), \\ x_3(t+1) &= f_3(\gamma_3f_2(\gamma_2\sigma_1[d\sigma_4 + (1-d)]x_3(t))), \\ x_4(t+1) &= d\sigma_4f_3(\gamma_3f_2(\gamma_2\sigma_1[d\sigma_4 + (1-d)]x_3(t))). \end{aligned} \right\} \quad (9)$$

Clearly, the dynamics of the 4-dimensional model can be completely determined from the third equation in System (9), and hence we study the 1-dimensional model,

$$x_3(t+1) = f_3(\gamma_3f_2(\gamma_2\sigma_1[d\sigma_4 + (1-d)]x_3(t))). \quad (10)$$

In Eq. (10), we examine the conditions that drive the dynamics when pure contest competition (compensatory dynamics) and pure scramble competition (overcompensatory dynamics) are in place.

First, we assume that Generation 2 dynamics is governed by compensatory dynamics while that of Generation 3 is overcompensatory. In this situation, it is possible for the simple Generation 2 compensatory dynamics to ‘drive’ the mixed Monarch population dynamics. For example, if Generation 2 is under the Beverton–Holt equation (compensatory dynamics) and Generation 3 is under the Ricker equation, then System (10) reduces to

$$x_3(t+1) = \frac{\gamma_3a_2\gamma_2\sigma_1[d\sigma_4 + (1-d)]x_3(t)}{1 + b_2\gamma_2\sigma_1[d\sigma_4 + (1-d)]x_3(t)} e^{\left(r_3 - \frac{\gamma_3a_2\gamma_2\sigma_1[d\sigma_4 + (1-d)]x_3(t)}{1 + b_2\gamma_2\sigma_1[d\sigma_4 + (1-d)]x_3(t)}\right)}. \quad (11)$$

If $\gamma_3a_2 > r_3b_2$, then Eq. (11) supports a positive steady-state at

$$x_{3\infty} = \frac{r_3}{\gamma_2\sigma_1[d\sigma_4 + (1-d)](\gamma_3a_2 - r_3b_2)}.$$

When $r_3 = 2.1$, $\sigma_1 = \sigma_4 = 0.9$, $\gamma_2 = \gamma_3 = 0.9$, $a_2 = 4$, $b_2 = 1$ and $d = 0.5$, System (11) supports a stable fixed point at $x_{3\infty} = 2.007$ (compensatory dynamics, see Fig. 9). In Fig. 9, we explore the effects of increasing different parameters on the equilibrium population. If the parameters r_3 , σ_1 , σ_4 , γ_2 , γ_3 , a_2 and b_2 are kept fixed at their current values while the migration rate d is varied between 0 and 1, Fig. 9 shows that $x_{3\infty}$ increases monotonically. A similar monotonic increase seem to occur with increasing values of either r_3 or γ_3 . However, increasing values of a_2 can lead to a monotonic increase in $x_{3\infty}$ (up to a maximum value) followed by a monotonic decrease (see Fig. 9).

Now, we analyze the parameter variation with the Ricker equation in Generation 2 and the Beverton–Holt equation in Generation 3. In this situation, System (10) reduces to

$$x_3(t+1) = \frac{\gamma_3a_3\gamma_2\sigma_1[d\sigma_4 + (1-d)]x_3(t)e^{r_2 - \sigma_1[d\sigma_4 + (1-d)]x_3(t)}}{1 + b_3\gamma_2\sigma_1[d\sigma_4 + (1-d)]x_3(t)e^{r_2 - \sigma_1[d\sigma_4 + (1-d)]x_3(t)}}. \quad (12)$$

Fascinating dynamical behavior arises in mixed compensatory–overcompensatory systems. Essentially, the fecundity functions compete for dominance in driving the model dynamics. The resulting bifurcations are unusual when a single parameter value is perturbed while holding the other parameters fixed. When the parameter $b_3 > a_3$, then we found no interesting bifurcations and we conclude that the Beverton–Holt equation in Generation 3 (compensatory dynamics) is the dominant function of the system. However, when a_3 is sufficiently larger than b_3 , then complex

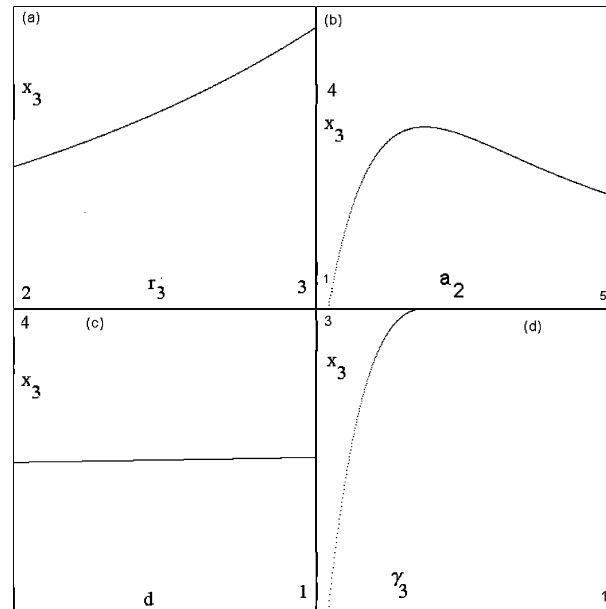


Fig. 9. For most parameter values, the mixed System (11) supports compensatory dynamics when Generation 2 is under compensatory dynamics while Generation 3 is under overcompensatory dynamics.

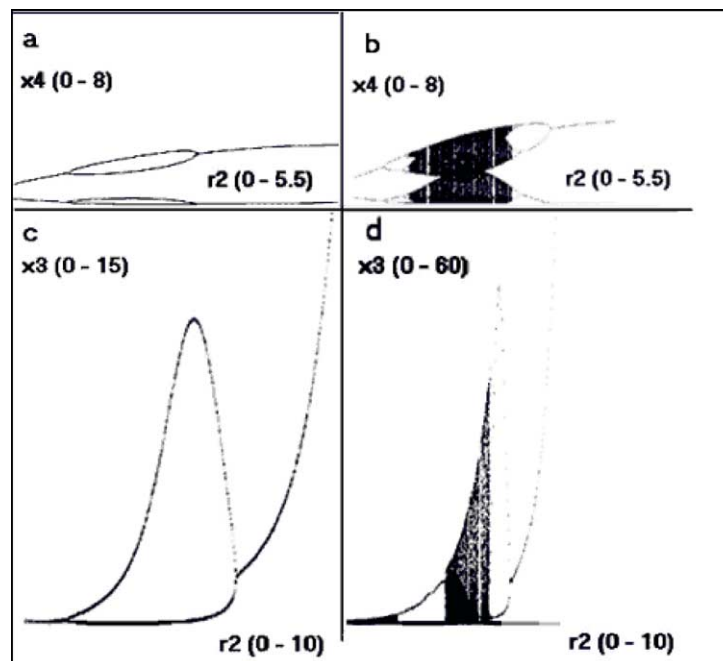


Fig. 10. In mixed systems, the dominant dynamics depends on parameter values.

overcompensatory dynamics emerge and the Ricker's equation is the more dominant function. In Fig. 10(a) and (c), an interesting phenomenon occurs, a simple equilibrium dynamics bifurcates to a cyclic one (period-doubling bifurcation), but then reverts back to the simple form (period-doubling reversal), creating a *bubble effect*. The same event occurs in Fig. 10(b) and (d), but the interior dynamics becomes chaotic. Clearly, these examples have only highlighted few possible dynamical outcomes in the Monarch butterfly model under mixed scramble-contest competition.

6. Conclusion

In constructing valuable Monarch models, functions that reflect aspects of Monarch fecundity must be developed. Currently, however, information on generational fecundity in breeding areas is scarce. Our Monarch butterfly island chain model, a starting point in the study of Monarch population dynamics, utilizes two extreme types of intraspecific density dependent fecundity functions. One general class of the fecundity functions supports compensatory dynamics and the other class supports overcompensatory dynamics. This paper focuses on the effects of compensatory, overcompensatory and mixed compensatory–overcompensatory generational dynamics on the Monarch migration pattern. Beverton–Holt's and Ricker's parametric models were chosen as examples of contest (compensatory dynamics) and scramble (overcompensatory dynamics) intraspecific 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 non-migratory reproducing individuals in Generation 3 to the population size in Generation 4. Such importance includes the possibilities of persistence or extinction in Generation 4. Survival probabilities and per capita growth rates can drive the Monarch population to either persistence or extinction. Specific relations of these parameters were found as thresholds for population continuation. The Monarch carrying capacity can also play an essential role in determining long-term behavior.

Our Monarch model supports a unique stable equilibrium population when all generational dynamics are compensatory. Generational populations under compensatory or overcompensatory dynamics support single attractors. However, migration and overcompensatory generational dynamics fracture basins of attraction through their support of multiple attractors. Our model supports multiple attractors, showing that it is possible for long-term Monarch dynamics to depend on initial conditions whenever generational populations are under overcompensatory dynamics. Additionally, the Monarch model under overcompensatory dynamics supports invariant trajectories that can act as cyclic or chaotic attractors. Thus, the model under overcompensatory dynamics captures the observed population fluctuations of the Monarch butterfly [48].

In mixed systems, the dynamics are as complex as those under overcompensatory generational dynamics. Any one of the two different dynamics is capable of driving the mixed system. Changing conditions can produce periodic life cycles and chaotic behaviors. Interesting dynamics are observed where simple cyclic behaviors shift to more complex chaotic dynamics, and even more interesting are the cases where complex chaotic dynamics stabilize to simpler cyclic behavior. Studies on testing these model predictions with field data on the North American Monarch butterfly would be welcome [38].

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Appendix A

Proof of Lemma 1. Recall that $F_1(x, y) = f_3 \circ \gamma_3 f_2 \circ \gamma_2 f_1(\gamma_1(y + (1 - d)x))$ and $F_2(x, y) = f_4 \circ d\gamma_4 f_3 \circ \gamma_3 f_2 \circ \gamma_2 f_1(\gamma_1(y + (1 - d)x))$, where $f_i(x_i) = x_i g_i(x_i)$. Therefore, $F_1(x, y) > 0$ and $F_2(x, y) > 0$ whenever $x, y > 0$. That is, the positive cone is invariant.

To prove that no non-negative orbit is unbounded, we need to show that for each $i \in \{1, 2\}$ the sequence $\{F_i^t(x, y)\}_{t \geq 0}$ is bounded, where $(x, y) \in \mathbb{R}_+^2$ is an arbitrary point. Recall that, if $z \leq \max I_i$ then $f_i(z) = z g_i(z) \leq \max I_i$ but if $z > \max I_i$ then $f_i(z) = z g_i(z) < z$, where $I_i \equiv f_i([0, X_i])$ and X_i is the unique positive fixed point of f_i . Let $\max I = \max_{i \in \{1, 2, 3, 4\}}(\max I_i)$. Then

$$F_1(x, y) \leq \max\{\max I, \gamma_1(y + (1 - d)x)\}$$

and

$$F_2(x, y) \leq \max\{\max I, \gamma_1(y + (1 - d)x)\}.$$

Recall that each $\gamma_i \in (0, 1)$. Thus, each $\{F_i^t(x, y)\}_{t \geq 0}$ is a bounded sequence, and every point in System (3) has a bounded orbit.

The following result of Hal Smith [47] for monotone systems will be useful in proof of Theorem 1.

Theorem A.1 ([47]) *Let $p \in \text{int}(\mathbb{R}_+^N)$ and $T : [0, p] \rightarrow [0, p]$ be continuous, C^1 in $(0, p)$ and suppose $DT(0)$ exists with $\lim_{x \rightarrow 0, x > 0} DT(x) = DT(0)$. In addition, assume $DT(x) > 0$ and $DT(y) \leq DT(x)$ for $0 < x < y < p$ and that $Tp < p$.*

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

If $T(0) \not\geq 0$, then T has a unique fixed point $q \in [0, p]$. Moreover, $q \in (0, p)$ and $T^n(x) \rightarrow q$ as $n \rightarrow \infty$ for every $x \in [0, p]$.

Proof of Theorem 1. The proof uses Theorem A.1 of Hal Smith. To establish the proof we show with a sequence of lemmas that all the hypotheses of Theorem A.1 are satisfied. $\square$

Lemma A.1. *In System (3), for each Generation $i \in \{1, 2, 3, 4\}$, let each fecundity function be modeled by f_i , an α -monotone concave map. Then for each $i \in \{1, 2\}$, $h'_i > 0$ and $h''_i < 0$.*

Proof of Lemma A.1. Recall that $h_1 = f_3 \circ \gamma_3 f_2 \circ \gamma_2 f_1$ and $h_2 = f_4 \circ d\gamma_4 f_3 \circ \gamma_3 f_2 \circ \gamma_2 f_1$, where each $f'_i > 0$ and $f''_i < 0$. By the chain rule,

$$h'_1 = f'_3(\gamma_3 f_2 \circ \gamma_2 f_1) \gamma_3 f'_2(\gamma_2 f_1) \gamma_2 f'_1 > 0$$

and

$$h''_1 = f''_3(\gamma_3 f_2 \circ \gamma_2 f_1) (\gamma_3 f'_2(\gamma_2 f_1))^2 (\gamma_2 f'_1)^2 + \gamma_3 f'_3(\gamma_3 f_2 \circ \gamma_2 f_1) (f''_2(\gamma_2 f_1) (\gamma_2 f'_1)^2 + f'_2(\gamma_2 f_1) \gamma_2 f''_1) < 0.$$

Proceed exactly as above to establish that $h'_2 > 0$ and $h''_2 < 0$.

Lemma A.2.

- (i) $DF(x, y) > 0$ if $(x, y) > (0, 0)$.
- (ii) $DF(0, 0)$ exists with $\lim_{(x,y) \rightarrow (0^+, 0^+)} DF(x, y) = DF(0, 0)$.
- (iii) $DF(u, v) < DF(x, y)$ if $0 < (x, y) < (u, v) < (\alpha, \alpha)$.
- (iv) The spectral radius of $DF(0, 0)$ is $\gamma_1 \gamma_2 \gamma_3 g_1(0) g_2(0) g_3(0) ((1-d) + \gamma_4 d g_4(0))$.

Proof of Lemma A.2.

$$DF(x, y) = \begin{bmatrix} \gamma_1(1-d)h'_1(\gamma_1(y + (1-d)x)) & \gamma_1 h'_1(\gamma_1(y + (1-d)x)) \\ \gamma_1(1-d)h'_2(\gamma_1(y + (1-d)x)) & \gamma_1 h'_2(\gamma_1(y + (1-d)x)) \end{bmatrix}$$

By Lemma A.1, we have (i) and (iii). Continuity of $DF(x, y)$ guarantees (ii). To obtain (iv) notice that the eigenvalues of $DF(0, 0)$ are $\lambda_1 = 0$ and $\lambda_2 = \gamma_1 \gamma_2 \gamma_3 g_1(0) g_2(0) g_3(0) ((1-d) + \gamma_4 d g_4(0))$.

By Lemmas 1 and A.2, all the hypotheses of Theorem A.1 of Hal Smith are satisfied, and this proves Theorem A.1.

Proof of Theorem 2. In System (5), $F_2(x, y) = d\sigma_4 F_1(x, y)$. Hence, the line

$$L = \{(x, y) \in R_+^2 \mid y = d\sigma_4 x\}$$

is invariant and every point not on it gets mapped to it in one iteration. On the line L , $F_2(x, y) = d\sigma_4 h_1(\gamma_1(d\sigma_4 + (1-d)x))$, a one-variable function. $\square$

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