Fall 2014

A periodic matrix population model for monarch butterflies

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A Periodic Matrix Population Model for Monarch Butterflies

An Honors Program Project Presented to

the Faculty of the Undergraduate

College of Science and Mathematics

James Madison University

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in Partial Fulfillment of the Requirements

for the Degree of Bachelor of Science

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December 2014

Accepted by the faculty of the Department of Mathematics and Statistics, James Madison University, in partial fulfillment of the requirements for the Degree of Bachelor of Science.

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Acknowledgements

Special thanks to:

Dr. Anthony Tongen
Dr. D. Brian Walton
Dr. Patrice Ludwig

and

James Madison University, Harrisonburg, VA
Department of Mathematics and Statistics
Universidad de Colima, in Colima, Mexico
The Jeffery E. Tickle ‘90 Family Endowment Scholarship
NSF-DMS-0734284 at James Madison University

Abstract

The migration pattern of the monarch butterfly (*Danaus plexippus*) consists of a sequence of generations of butterflies that originate in Michoacán, Mexico each spring, travel as far north as Southern Canada, and ultimately return to the original location in Mexico the following fall. We use periodic population matrices to model the life cycle of the eastern monarch butterfly and find that, under this model, this migration is not currently at risk. We extend the model to address the three primary obstacles for the long-term survival of this migratory pattern: deforestation in Mexico, increased extreme weather patterns, and milkweed degradation.

1 Introduction

The population of monarch butterflies (*Danaus plexippus*) in the overwintering sanctuaries in the Mexican states of México and Mochoacán have declined over the past ten years [3]. This observable decline is suspected to be a result of three primary factors: deforestation of the overwintering habitat in Mexico, a decrease in available milkweed, and an increase in extreme inclement weather [2].

Although the monarch butterfly is common throughout North America, the unique migration pattern is only exhibited by those monarchs to the east of the Rocky Mountains [2]. Although this migration of the monarch butterfly was thought completely different from any other known animal migration throughout the world [2], it is still a rare phenomenon exhibited by few other species [19]. The ten cm wide butterflies travel over 1700 km to Canada [16], only to have their dependents return three months later to the same location in southern Mexico. Up to seven generations of butterflies are born throughout a single annual migration [12].

This unique phenomenon was first recorded in the late 1800s when land cultivation in the midwest led to an increase in milkweed plants, accentuating the monarch migration [3].The migration of the eastern monarch butterfly has become an endangered phenomenon meaning that rather than the species itself being in danger of extinction, it is the phenomenon of multi-generational migration that is in danger [2]. We focus on the eastern monarch butterfly population since they are the only faction of monarchs which exhibit multi generational migration.

Recently, the eastern monarch butterflies appear to have experienced particularly extreme population loss. In the Fall of 2013, newspapers and magazines throughout the United States published articles about these unique insects with titles such as "The Year the Monarch Didn't Appear" instilling worry and concern in the general population. This concern is certainly valid, since in this past year there was approximately a 43% decrease of the total land covered by overwintering monarchs in Mexico between 2012 and 2013 [18]. Such dramatic drops in the overall population of the butterfly is a concern for all those who wish to preserve this insect and its one-of-a-kind migration.

For over 60 years, the monarch butterfly has become a topic of increased research and study, even before the overwintering butterfly sanctuaries in the Mexican states of Michoacán and México were discovered in 1976 [6]. Soon after this monumental discovery, the importance of having the correct temperature in order to produce the optimal number of viable adult butterflies and eggs was discovered [1]. In 1993 it was determined that the spring migration of the butterflies occurred through several successive generations [5, 10]. The effects of photoperiod (day length), temperature, and host plant age on adult monarch butterflies were extensively studied, while other scientists focused on the potential deforestation problem [9, 20]. Recently, the scientific focus has shifted from individual butterflies to the migration process of the butterflies and whether or not the unique phenomenon is in danger of extinction [3, 6, 17].

In general, there has been limited mathematical work concerning the migration of the monarch butterfly. In 2004, Yakubu et al. focused on the theoretical aspect of the migration using differential equations to model the four distinct stages of the monarch life cycle. This paper also considered generationally dependent reproductive strategies and the implications of these on longterm survival [21]. Several years later a team of undergraduates and graduate students used difference equations to examine the effect of milkweed abundance on the migration using the seasons to divide the year into four distinct stages [12]. Most recently, the monarch butterfly is predicted to become extinct in the next hundred years using position-dependent matrices[8].

2 Annual Life Cycle of the Monarch Butterfly

A female monarch lays up to 700 eggs throughout her lifetime [16], and up to 55% of those eggs are infertile [14]. The eggs are laid on common milkweed, ideally one egg per plant [14], although higher densities of butterflies result in more eggs per milkweed plant [7]. When the caterpillars hatch after four days, they feed on the milkweed for the next two weeks [16]. Then, after spending about ten days in a chrysalis, an adult monarch butterfly emerges to spend two to six weeks reproducing before dying [16].

Eastern monarch butterflies begin the annual migratory cycle by leaving Mexico in groups, starting in mid-March, heading towards southern Canada. As the butterflies leave Mexico, the initial generation begins to lay eggs primarily on common milkweed throughout the southern United States [17]. As those eggs become larvae and then adults, a process which takes about 4 weeks total, the adults travel further north, continually laying eggs. Current research suggests three or four generations are necessary to complete the entire spring migration from Mexico to southern Canada [21]. However, reproduction occurs continuously from mid-March through September thereby creating indistinguishable generations.

Once the butterflies arrive in southern Canada, they continue to reproduce, although they no longer move northward. Throughout the process, the generations overlap and cease to be well defined individual generations, eliminating the possibility of an accurate estimation of generations. However, by considering the amount of time spent during this stage, we can estimate two or three generations of butterflies in Canada.

As September approaches, the butterflies approaching sexually maturity enter reproductive diapause, when a butterfly freezes in its life cycle, postponing sexual maturity. Overwintering is a status which the monarchs maintain throughout the winter months in relative stillness. By entering reproductive diapause, the butterfly readies itself to begin the Fall migration back to the overwintering locations in Mexico, approximately 1700 km from their current location. Although monarchs occasionally overwinter in Florida or Cuba [6], these occurrences account for a small percentage of butterflies and have been neglected in this study. Only the eastern monarch butterfly annually travels from southern Mexico to southern Canada and back [16]. These butterflies travel from southern Canada to southern Mexico, within one single generation. By late October, all of the butterflies are resting in the Oyamel fir trees in the butterfly sanctuaries of southern Mexico [3], and remain relatively dormant until beginning the spring migration four months later [16].

3 Model Description

Population matrices are used to model the growth rate of a population over the course of an assigned time period, as well as other information to assess the growth of the population as a whole. Population matrices may also be used to predict future populations. Our population matrices model the growth of the monarch butterfly populations based on unlimited resources and ideal weather conditions.

The array P_t, given by

$$P_t = \begin{bmatrix} p_l \\ p_c \\ p_a \end{bmatrix}, \tag{3.1}$$

can be used to predict the i monarch population of larvae (p_l), chrysalis (p_c), and adult monarch butterflies (p_a) in a few year (t years in the future) given the current population. Since the monarch exhibits four distinct patterns annually, we used four distinct matrices multiplied together to determine an annual growth rate,

$$P_{t+1} = MP_t \tag{3.2}$$

$$M = M_4 M_3 M_2^y M_1^z \tag{3.3}$$

where P is total population, M_n is the matrix associated with each particular stage, y is the number of two week periods in the Sumer (Stage 2), and z is the number of two week periods in the Spring Migration (Stage 1). We combine the individual stages together in order to have a more complete understanding of the population growth in one year [4]. It is important to note that although the matrices associated with the overwintering stage (Stage 4) and Fall migration (Stage 3) each represent the entirety of the respective stage while the matrices of both the Spring migration and Summer only focus on two week periods. The butterfly life-cycle is divided into three separate stages, larval, chrysalis, and adult, each with complete metamorphasis. Since of these stages can be expressed easily as a product of one or more two week increments, each matrix for both of these stages represents two weeks. Since both of these stages last more than two weeks, we take the power of the matrices in order calculate the results from these stages.

Symbol	Description	Initial Parameter
A_1	Adult survival for a two week period (Stage 1).	.125
A_2	Adult survival for a two week period (Stage 2).	.333
A_3	Adult survival for the entire fall migration (Stage 3).	.6864
A_4	Adult survival for the entire winter(Stage 4).	.85
F	The fecundity of a single monarch butterfly	52.5
L	The survival rate of the eggs to the chrysalis stage	0.03426
C	The survival of the chrysalis into a butterfly	.85

Table 1: Original Matrix Parameters

For further explanation of parameters see Appendix A

After fully computing M (using MATLAB) we find the dominant eigenvalue. This predicts what the annual growth of the butterfly population should be, base on our parameters. Throughout the rest of this paper, we will use the dominant eigenvalue of M as well as the associated eigenvectors.

3.1 Spring Migration

Stage 1 models the Spring migration and includes the period when the butterflies leave the overwintering sanctuaries in southwestern Mexico and travel northward to southern Canada. The first butterflies leave Michoacán and México mid-March but the first butterflies in Canada are not reported until the end of May [16]. We use an average departure and arrival date and thus estimate that Stage 1 lasts 12 weeks. Since the number of weeks is variable, we also use the variable z to represent the number of two week periods in the Spring migration. We consider the Spring migration to be mid-March to mid-June.

M_1 describes a two-week period of time (the caterpillar from hatching to forming the chrysalis) so it follows that M_1^6 is the total 12 week spring migration, with

$$M_1 = \begin{bmatrix} 0 & 0 & F_1 \\ L_1 & 0 & 0 \\ 0 & C_1 & A_1 \end{bmatrix}, \tag{3.4}$$

where F_1 is adult fecundity (adult fertility), L_1 is the probability that a caterpillar survives to form a chrysalis, C_1 is the probability that a chrysalis hatches to become a butterfly, and A_1 is probability the adult survives past two weeks for Stage 1. Thus the two week Spring migration matrix used in our preliminary model is:

$$M_1 = \begin{bmatrix} 0 & 0 & 52.5 \\ 0.03426 & 0 & 0 \\ 0 & 0.85 & 0.125 \end{bmatrix}. \tag{3.5}$$

3.2 Summer

Stage 2 models the butterflies' behavior in the northern United States and southern Canada. This stage begins directly upon the termination of the Spring migration, mid-June, and lasts until mid-September, when the butterflies are reported in central North America. Again, the various generations of butterflies move continuously, so although these dates are not exact, they do describe the average annual dates of the Summer period for the butterflies. We define y as the number of two week increments in the Summer.

Similar to Stage 1, we use a two week matrix to simulate the distinct stages in the monarch life span. This matrix is very similar to our previous matrix (3.1), with slightly adjusted rates to reflect the improved survival when the adults are not migrating

$$M_2 = \begin{bmatrix} 0 & 0 & F_2 \\ L_2 & 0 & 0 \\ 0 & C_2 & A_2 \end{bmatrix}, \tag{3.6}$$

with F_2, L_2, C_2 and A_2 defined similarly to F_1, L_1, C_1, and A_1 in (3.1). The two week Summer matrix used in our preliminary model is:

$$M_2 = \begin{bmatrix} 0 & 0 & 52.5 \\ 0.03426 & 0 & 0 \\ 0 & 0.85 & .333 \end{bmatrix} \tag{3.7}$$

3.3 Fall migration

The fall migration to southwestern Mexico, Stage 3, begins mid-September and lasts until the end of October. During this time, butterflies that entered reproductive diapause in southern Canada make the return journey of over 1700 km, traveling down through Texas to arrive in the butterfly sanctuaries of México and Michoacán. Since the butterflies entered reproductive diapause, there is no reproduction, so the population only decreases during this stage.

Since there is no reproduction during the fall migration, we have a sparse matrix with a single entry, A_3, the survival rate of the adults throughout Stage 3, and describes the entire migration rather then two week increments. Thus

$$M_3 = \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & A_3 \end{bmatrix}, \tag{3.8}$$

such that A_3 is the survival of the butterfly during the migration from Canada to Mexico. The fall migration matrix used in our preliminary model is:

$$M_3 = \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & .6864 \end{bmatrix}. \tag{3.9}$$

3.4 Overwintering

Stage 4 represents the overwintering period in the sanctuaries in southwestern Mexico. The host Oyamel fir trees where the butterflies stay dormant throughout the winter are the exact same trees each year and are protected under Mexican law [14]. The butterflies stay there, protected by each other [11] and surrounding forests until mid-March when the Spring migration begins. Again, there is no breeding during this stage, so there is only one entry in the matrix, the adult survival rate. The adult survival rate is for the entire overwintering period, so

$$M_4 = \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & A_4 \end{bmatrix}, \tag{3.10}$$

reflects the monarch population from November to mid-March. The overwinding matrix used in our preliminary model is:

$$M_4 = \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & .85 \end{bmatrix}. \tag{3.11}$$

4 Results

The results below use parameter values a defined by 8 and further described in Appendix A.

4.1 Growth Rate

Based on data from JourneyNorth, Spring migration and Summer each last twelve weeks [16]. This is our standard division, used throughout as the expected length of time for each stage. However, since it is unknown precisely what prompts the initiation of the Spring migration each March, we consider several scenarios for the lengths of the Spring migration and Summer. Within these scenarios, we change the length of time spent migrating and in Canada.

	Stage 1 ($2z$)	Stage 2 ($2y$)	Stage 3	Stage 4	Stage 1 + Stage 2 ($2z + 2y$)	Annual Growth Rate
Standard division	12	12	10	18	24	3.7771
Stage 1 is two weeks shorter and Stage 2 is two weeks longer	10	14	10	18	24	3.7798
Spring migration is two weeks shorter	10	12	10	20	22	1.1607
Fall migration begins two weeks earlier	12	10	10	20	22	1.1562
Spring migration begins two weeks earlier	12	14	10	16	26	4.2418
Spring migration and summer are both two weeks shorter	10	10	10	22	20	1.9643

Table 2: The impact on the annual growth rate (the dominant eigenvalue) when the number of weeks in Stage 1 ($2z$) and Stage 2 ($2y$) are changed.

4.2 Sensitivity and Elasticity

We can rewrite both M_1 and M_2 in terms of their right and left eigenvectors, w and v, respectively. The sensitivity of a matrix gives a linear approximation to how a small change in a matrix entries impact the annual growth rate (the dominant eigenvalue), and is given by

$$S_i = \left(\frac{\bar{v} w^T}{v^* w} \right) \tag{4.1}$$

where v and w are the eigenvectors associated with the dominant eigenvalue and S_i refers to the sensitivity matrix of the i^{th} stage [4].

Since four stages combine to form one full cycle, one might expect a single sensitivity matrix. However, since matrix multiplication is intrinsically nonlinear, each entry of the final matrix is a complex sum of products [4]. For this reason, it is more helpful to examine the sensitivity matrix for each stage. Since both the spring and summer matrices have more than one entry, we calculated sensitivity matrices for a two week period.

Spring migraton:

$$S_1 = \begin{bmatrix} 0.3208 & 0.0092 & 0.0073 \\ 11.1931 & 0.3208 & 0.2548 \\ 15.7391 & 0.4511 & 0.3583 \end{bmatrix} \tag{4.2}$$

Summer:

$$S_2 = \begin{bmatrix} 0.2981 & 0.0080 & 0.0072 \\ 11.0911 & 0.2981 & 0.2693 \\ 16.6303 & 0.4470 & 0.4037 \end{bmatrix} \tag{4.3}$$

Elasticity is another important component to consider since it compares distinct parameters, examining the impact of proportional changes on the annual growth rate. Since the initial parameters of M_1 and M_2 have one entry on the order of 50 and all other nonzero entries less than one, elasticities allow for a comparison on a similar scale.

Since elasticity matrices are calculated by multiplying corresponding entries in two matrices rather than by normal matrix multiplication (or finding the Hadamard product), we have drastically different elasticities for the two and twelve week matrices for both the Spring migration and Summer stages. The Spring migration and Summer elasticity matrices are defined by the subscript clarifying for which stage it shows the elasticity, with a further clarification of 12 indicating that the matrix refers to the elasticity over the course of twelve weeks rather than two.

Elasticity of two weeks of Spring migration:

$$E_1 = \begin{bmatrix} 0 & 0 & 0.3208 \\ 0.3208 & 0 & 0 \\ 0 & 0.3208 & 0.0375 \end{bmatrix} \tag{4.4}$$

Elasticity of a twelve week Spring migration:

$$E_{1_12} = \begin{bmatrix} 0.2576 & 0.0538 & 0.0094 \\ 0.0031 & 0.2576 & 0.0601 \\ 0.0601 & 0.0094 & 0.2888 \end{bmatrix} \tag{4.5}$$

Elasticity of two weeks of Summer:

$$E_2 = \begin{bmatrix} 0 & 0 & 0.2981 \\ 0.2981 & 0 & 0 \\ 0 & 0.2981 & 0.1056 \end{bmatrix} \tag{4.6}$$

Elasticity of a twelve week Summer:

$$E_{2_12} = \begin{bmatrix} 0.1665 & 0.0861 & 0.0455 \\ 0.0151 & 0.1665 & 0.1166 \\ 0.1166 & 0.0455 & 0.2416 \end{bmatrix} \tag{4.7}$$

4.3 Impact of Deforestation in Overwintering Butterfly Sanctuaries

Currently, the overwintering location is at risk due to immense illegal deforestation [3]. Although the trees used annually by the butterflies generally remain untouched, the surrounding forests have decreased significantly in the last ten years, consequently diminishing the butterflies' protection from the natural elements. In recent years, extreme weather has become more common, so increasingly large amounts of butterflies are killed by winter weather. The butterflies also depend on the canopy level of the forest to protect them from sun overexposure. Warmth causes the butterflies to use their lipid energy reserves more quickly. With limited nectar sources, they are often unable to replenish these stores, increasing the overwintering death rate [2].

To model the effect of deforestation on the survival of the monarch butterfly we alter the adult survival rate A_4. It is this simple since A_4 describes the probability that an adult will survive from October to March, and thus we need only decrease the survival rate in order to illustrate increased deforestation.

Adult Survival (A_4)	Projected growth rate
.85	3.7771
.80	3.5364
.75	3.3154
.70	3.0944
.60	2.6523
.50	2.2103
.40	1.7682
.30	1.3262
.25	1.15051
.225	.9998
.20	0.8841

Table 3: Impact of changing adult survival, A_s, on the dominant eigenvalue of M.

We consider that regardless of arboreal protection there is some level of predation, approximately 13% death rate [8], as well as some degree of basic weather influences. Since there is always some death rate during the winter, we consider our model with a variety of adult survival rates from 20% to 85%, as seen in Table 3.

4.4 Impact of Inclement Weather

We also consider the effect of a serious environmental event on the monarch butterfly such as an unseasonably late or early frost and how it impacts the total population growth of the butterflies. Consider the possibility of such an event occurring two weeks into the Spring migration or alternatively two weeks before the Fall migration begins. There are two plausible scenarios: the butterflies are more susceptible to death due to the delicacy of the wing or the larva, chrysalis, and butterflies are equally susceptible to frost. A survival rate of 0.26 for all h is the highest survival rate which results in a growth rate lower then 1. As both the sensitivity and elasticity matrices indicate, the adult survival rate has minimal effect on the annual growth rate.

In order to determine the effect on the annual growth rate, we form a diagonal matrix H with the survival rates of the insects at each stage and insert this matrix in the appropriate location. To see the result of a late frost in spring, we use an annual cycle of

$$M = M_4 M_3 M_2^6 M_1^5 H M_1. \tag{4.8}$$

. To see the result of an early frost is fall, we use an annual cycle of

$$M = M_4 M_3 M_2 H M_2^5 M_1^6. \tag{4.9}$$

To see the result of both a late frost in the spring and an early frost in the fall, we use an annual cycle of

$$M = M_4 M_3 M_2 H_2 M_2^5 M_1^5 H_1 M_1, \tag{4.10}$$

where H is the diagonal matrix:

$$H = \begin{bmatrix} h_l & 0 & 0 \\ 0 & h_c & 0 \\ 0 & 0 & h_a \end{bmatrix} \tag{4.11}$$

where h_l in the survival rate of the larvae, h_c is the survival rate of the chrysalis, and h_a is the survival rate of the adults. We then insert this matrix after the first two week period, such that the two week Spring migration matrix is first multiplied by H, and then by the Spring migration matrix five more times.

Larva Survival (h_l)	Chrysalis Survival (h_c)	Adult Survival (h_a)	Growth Rate
1	1	1	3.7574
.9	.9	.1	3.2656
.5	.5	.5	1.8787
.5	.5	.1	1.8207
0.26	0.26	0.26	0.9769

Table 4: The effect of a late frost at the beginning of the Spring migration: $M = M_4 M_3 M_2^6 M_1^5 H M_1$.

Similarly, to determine the effect of an early frost, we placed H two weeks before the Fall migration.

Larva Survival (h_l)	Chrysalis Survival (h_c)	Adult Survival (h_a)	Eigenvalue
1	1	1	3.7574
.9	.9	.1	3.0734
.5	.5	.5	1.8787
.5	.5	.1	1.7245
0.26	0.26	0.26	0.9769

Table 5: The effect of an early end to the Summer: $M = M_4M_3M_2HM_2^5M_1^6$.

We consider the scenario where there is an extreme storm on both ends of the reproductive stages.

Where

$$H_1 = \begin{bmatrix} h_1^1 \\ h_2^1 \\ h_3^1 \end{bmatrix} \tag{4.12}$$

and

$$H_2 = \begin{bmatrix} h_1^2 \\ h_2^2 \\ h_3^2 \end{bmatrix} \tag{4.13}$$

	$h_{1,2}^1 = 1$, $h_3^1 = 1$	$h_{1,2}^1 = .9$, $h_3^1 = .1$	$h_{1,2}^1 = .5$, $h_3^1 = .5$	$h_{1,2}^1 = .5$ $h_3^1 = .1$	$h_{1,2}^1 = .26$ $h_3^1 = .26$
$h_{1,2}^2 = 1$, $h_3^2 = 1$	3.7574	3.2656	1.8787	1.8207	0.9769
$h_{1,2}^2 = .9$, $h_3^2 = .1$	3.0734	2.7139	1.5367	1.5106	0.7991
$h_{1,2}^2 = .5$, $h_3^2 = .5$	1.8787	1.6328	0.9394	0.9103	0.4885
$h_{1,2}^2 = .5$, $h_3^2 = .1$	1.7245	1.5202	0.8623	0.8464	0.4484
$h_{1,2}^2 = .26$, $h_3^2 = .26$	0.9769	0.8491	0.4885	0.4734	0.2540

Table 6: The effect osf different mortality rates at the beginning and end of the reproductive months: $M = M_4M_3M_2H_2M_2^5M_1^5H_1M_1$.

Table 6 uses H_1 to indicate the change in mortality due to a late frost in the Summer migration and H_2 to similarly indicate the change in mortality due to a frost during the late Summer months. For this reason the first column should read the same as Table 5 since there is no increased mortality due to weather except for the early frost. Similarly, since the first row is only an increased mortality due to a late frost in the Spring migration, this row shows the same eigenvalues as Table 4. Notice that the diagonal shows the eigenvalue when the mortality rates are equal as a result of a late frost in the Spring migration and an early frost in the Summer.

4.5 Impact of Milkweed Availability

With a limited number of milkweed plants, the monarch butterfly lays several eggs per per plant though not on the same leaf. As the caterpillars become more densely populated, more leaves play host to monarch eggs. When several eggs are laid on a single leaf, often the first caterpillar to hatch will eat the other (unhatched) eggs [15] For this reason, it is important to consider the effects of high densities of larva especially due to the 60% decline in milkweed in the midwest [3].

To this end, we incorporate a nonlinearity based on statistical probabilities of milkweed availability throughout the continental United States [8]. It describes the density dependent survival of the monarch larva P_d as number of eggs per milkweed stalk d

$$P_d = \frac{1}{1 + \frac{1}{e^{1.0175 - 0.1972d}}}. \tag{4.14}$$

By varying d, we see a decreased larval survival rate dependent on milkweed availability.

Larval density (d)	Annual Growth Rate
1	3.7771
2	2.9325
3	2.2139
4	1.6145
5	1.1365
6	0.7763

Table 7: The impact of increasing the number of eggs per leaf, d, on the growth rate (or dominant eigenvalue) of the monarch population.

4.6 Effect of Deforestation, Milkweed Deficiencies, and Inclement Weather

Figure 1 shows the effect of increased deforestation on the overwintering rates (A_4), ranging from 0 to .85 and increased caterpillar densities (ranging from $1 - 9$ where 1 is the least densely populated option, and indicating one monarch egg per milkweed plant) on the dominant eigenvalue, or growth rate. The plane is a visual representation of where the dominant eigenvalue is equal to 1. Above this plane, the monarch population is increasing annually while below the plane the population is decreasing.

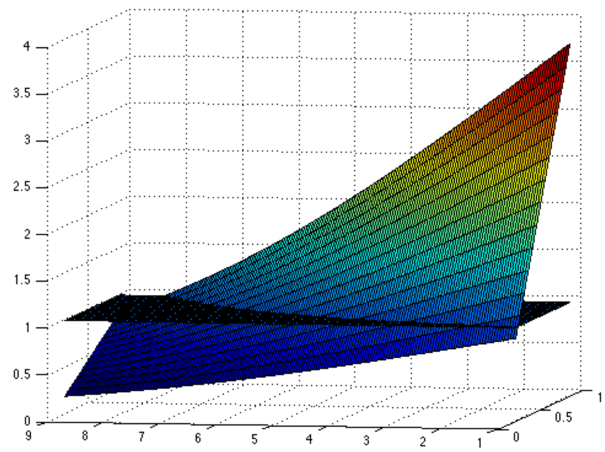

Figure 1: The annual eigenvalue after taking into account decreasing overwintering survival rates from 0 to .85 and milkweed densities (d) from 1 to 9. Graphic created using MATLAB.

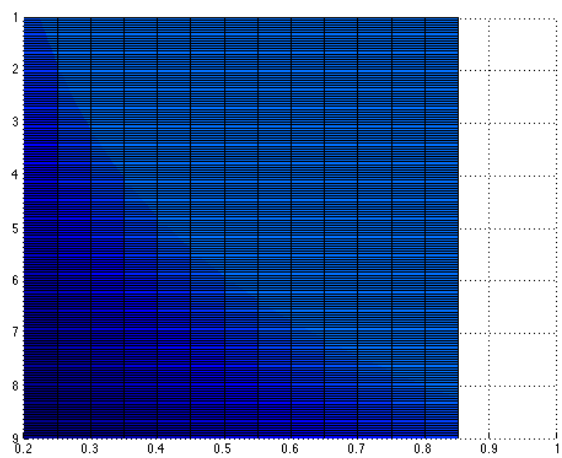

Figure 2: Using increasing deforestation rates and increasing milkweed densities, consider where the annual eigenvalue drops below 1. Graphic created using MATLAB.

Figure 2 shows Figure 1 from below. The gradients of colors indicate where the annual eigenvalue is less than 1 which occurs when increased deforestation in Mexico and increased caterpillar density.

5 Discussion

5.1 Growth Rate

The total number of weeks in Stage 1 and Stage 2 significantly impacts the annual growth rate, as seen in Table 2. Notice that although there is very little difference in the dominant eigenvalues (less then .01) when the same number of weeks in both Stage 1 and Stage 2 sum to be the same value, there is a large difference between the eigenvalues when the sum is different. The significant difference is expected, since the eigenvalue of one two week period is 1.2313 for the Spring migration and 1.3103 for the Summer. Although this is not a description of annual growth rate, it shows how quickly the population grows during the breeding seasons. Thus it seems clear that when the total number of weeks for the breeding season is equal, the division into spring and summer has minimal difference, while completely removing two (or more) weeks of the breeding season significantly changes the annual growth rate. Regardless, even when the breeding season short, the annual growth rate is 2.0085, well above one.Therefore, although the exact lengths of the Spring migration and Summer are not completely necessary, the total time for both changes the annual growth rate quite significantly.

The larger growth rate for twenty total weeks is surprising. However, since the Fall and Overwintering matrices have only one value–the adult survival rate during the two stages–the eigenvalue of the final matrix depends heavily on the value in the bottom right corner. During just the Spring migration and Summer stages, the eigenvalue is significantly larger. However, there is a large population of larvae and pupae which do not survive since they are not able to enter reproductive diapause in time for fall migration, and thus are no longer counted in the total population.

5.2 Sensitivity and Elasticity

The sensitivity matrices imply that the larval survival stage is the most critical parameter value, as the values are greater than 11 for both matrices. The other three entries (chrysalis survival, adult survival and fecundity) are all below 1. The higher the sensitivity, the more the dominant eigenvalue changes as a result of a small change in the parameter. Thus a small change in the larval survival will result in a large change in the annual growth rate, while a small change in the other three parameters would be less noticeable over the course of a year. This suggests that although each parameter is important to the longevity of the species and this unique migratory phenomenon, it would be most effective to attempt to improve the survival rate of the larva in order to improve the annual population survival rates.

Here it is important to notice that in both of the two week matrices, we have equivalent values in our adult fecundity, larva survival, and chrysalis survival while the adult survival is much smaller than these elasticities (see Appendix B for further explanation). This implies that the importance of offspring is greater than that of adult survival. This is slightly different from what was suggested by the sensitivity matrices, as here the suggestion is that fecundity, larval survival and chrysalis survival are equally important–to improve one would have the same effect as improving another. Recall that the elasticity results are demonstrating the impact of proportional changes and therefore neglect the large initial difference in the parameter values.

5.3 Impact of Deforestation in Overwintering Butterfly Sanctuaries.

Since the butterflies overwinter in some of the poorest states in Mexico, the sanctuaries are often at risk due to deforestation. However, in the past 10 years, the Mexican government has formed programs to create incentives for the locals to cease all illegal logging, which have been surprisingly effective. Illegal logging has decreased to under 1%, and it is unrealistic that logging will decrease any further [6, 8].

Since deforestation has been a problem in the past, and is one of the three primary concerns for the butterfly population, we consider the effect of increased deforestation. From Table 3 it is clear that deforestation would have to increase significantly in order to make a significant impact on the butterfly population. This result indicates that although illegal deforestation could have a large impact on the monarch survival, it is not a primary concern with regard to maintaining this migration phenomenon.

5.4 Impact of Inclement Weather

Inclement weather is something over which the human population has very little control excluding global climate change due to anthropogenic effects. Tables 4-6 imply that a series of minor storms would be insufficient to severely impact the annual survival of the species (note that when 90% survive two separate storms the annual eigenvalue is well above 1.) However, if there are just two semi-major storms throughout the breeding season which kill half of the total monarch population, we find an annual growth rate below 1. Thus we can conclude that the increasing extreme weather has a major impact on the longevity of the species and migration phenomenon.

This result is concerning, because an increase in extreme weather (i.e. storms, high temperatures, and low temperatures) can affect the overall survival of the larva, chrysalis, and adults. The onset of more extreme weather results in annual eigenvalues which are below 1 regularly, indicating a decline in the species. This concern is more evident when considering Table 6. It is evident that as long as more than half of the population survives each incident of inclement weather, the overall annual survival rate is above one.

5.5 Impact of Milkweed Availability

The milkweed plant has seen a decrease by 60% surrounding the cultivated fields in the midwest in the past 10 years [3]. Since milkweed in the only viable food source for the Monarch caterpillar, this decline should impact the butterfly population.

In an ideal world, only one egg would be laid per milkweed plant. However, butterflies are not able to be so conscientious. In fact, if the butterfly cannot find a new milkweed plant, she will resort to laying multiple eggs per plant. The results of these types of overcrowding are quite straight forward: the eggs not laid on milkweed will die quickly; multiple eggs on the same leaf will result in whichever caterpillar hatches first to eat the other eggs; and finally, less milkweed for all of the caterpillars will result in smaller caterpillars, then smaller butterflies will reduce the life span of the butterflies [14].

Since milkweed availability so strongly impacts longevity of the species, and since it is one of the only three parameters we can conceivably improve, it was vital for us to assess the effects of milkweed availability. Table 4.5 shows the impact of increasing egg density on the dominant eigenvalue. Notice that as the density of caterpillars per milkweed plant (d) increases, the dominant eigenvalue is severely impacted. Only 6 caterpillars per plant results in an eigenvalue below 1 indicating a state of equilibrium somewhere between 5 and 6 eggs per plant.

Although our annual growth rate is quite large, this does not take into account the deforestation of the butterfly overwintering sanctuaries in Mexico, increasing extreme weather nor restricted milkweed availability. Based on the three potential problems, our primary focus should be on increasing the number of viable milkweed plants throughout the breeding grounds of the monarch butterfly. This is particularly true of the land where the butterflies spend the summer months, the northern midwest and southern Canada.The midwest particularly has experienced extensive decline in the past ten years [3]

5.6 Impact of Deforestation, Inclement Weather, and Milkweed Availability

Since weather patterns are difficult to control, we focus the analysis on the impact of more easily controlled variables, namely deforestation and caterpillar density on milkweed plants. In Figure 1 we see a clear curve of where the eigenvalue dips below one, a sign of eventual extinction of the species. This indicates that as long as milkweed density stays low and deforestation remains minimal, the monarch population ought to be increasing annually.

From Figure 2 as well as previous work, it is evident that if either deforestation rates or milkweed densities become extremely high, then the entire monarch population is greatly at risk of extinction. It is important to note that deforestation would have to increase as well and having consistently high densities of each milkweed plant in order for these parameters to severely impact the overall longevity of the butterfly. Should deforestation increase to about 10% while density increased to about eight caterpillars per plant, the eigenvalue then becomes less than 1. As previously mentioned, illegal deforestation has decreased to less than 1%. For this reason it seems unlikely that the deforestation rate will increase rapidly, but high density of caterpillars per milkweed plant is an ever prevalent concern. Since biologists have reported signs of decreasing monarch populations, our largest concern should be planting more milkweed throughout the United States and Canada.

5.7 Future work

Although our model suggests high annual growth for the monarch butterfly, we are not seeing an increase in the total population of butterflies each winter. Our model works to explain this difference in our speculation and actuality by addressing the three major concerns of leading experts. In order to further improve our model, we would like to investigate further into inclement weather, including but not limited to more information about the survival of the species after a variety of types of weather, how often inclement weather hits throughout the annual cycle of the Monarch Butterfly, and the extent of the damage of typical spring and summer weather patterns in North America. We would also like to further investigate the true density of the monarch butterfly per milkweed plant and consider how citizen efforts could potentially combat this issue.

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Appendix A: Initial Parameters

Although monarchs have been studied, it is very difficult to find reliable data about numbers and life cycles, since observation is difficult to accurately complete in nature. This is, in part, due to the relatively short life span of the butterfly, as well as the huge distance that these unique insects cover in a short amount of time.

Symbol	Description	Assigned Value
A_1	The survival rate of adult monarch butterflies during the spring migration for a two week period (Stage 1).	$.125$
A_2	The survival rate of adult monarch butterflies during the summer in Canada for a two week period (Stage 2).	$.333$
A_3	The survival rate of adult monarch butterflies during the entire migration from Canada to Mexico (Stage 3).	$.6864$
A_4	The survival rate of adult monarch butterflies while over-wintering in southern Mexico (Stage 4).	$.85$
F	The fecundity of a single monarch butterfly in terms of the amount of fertile female eggs she can be expected to lay two week period. This value depends on the stage, so is denoted as either stage 1 or 2 by a subscript.	52.5
L	The survival rate of the eggs to the chrysalis stage. This value depends on the stage, so is denoted as either stage 1 or 2 by a subscript.	0.03426
C	The survival of the chrysalis into a butterfly. This value depends on the stage, so is denoted as either stage 1 or 2 by a subscript.	$.85$

Table 8: Original Matrix Parameters

Monarch butterflies are expected to live between 2 and 6 weeks, we decided that a life span of 3 weeks would be most appropriate since 6 weeks is an outlier However, we considered that the survival rate of adults migrating to be slightly smaller than average due to the challenges of migration, decreased time to find and consume food, and wear on their bodies from traveling. For this reason we suggested that only $.125$ of the monarchs survive each two week period during the migration, while $.333$ of the population survives each two week period during the summer months. This means that each butterfly lives an average of 16 days or 21 days, respectively.

To find adult fecundity of two weeks, consider that a female butterfly lays up to 700 eggs in her life span. Since this is an upper limit and the maximum life span is six weeks, we divide 700 by three to find the number of eggs laid in a two week time period [12]. The infertility rate of the Monarch is quite high, at a maximum of 55% infertile [14]. To account for this, we multiplied $\frac{700}{3}$ by $.45$ (the proportion of fertile eggs) and found $F = 52.5$. We could also potentially find the adult fecundity by using an average number of eggs laid, which we found to be between 400 and 500 eggs in her lifetime [13]. Using a similar process to find the number of fertile female eggs that an adult female would be expected to lay in two weeks, we found that she would lay between 45 and 56.25. Since these are close to our previous estimate, we use the maximum in our simulations.

The larvae have an incredibly small survival rate due to predators and food shortages. However, in this model we assume sufficient milkweed for the larva to feed and the adult monarchs to lay their eggs. We found that the lowest survival rate of the larvae against predators in one week in a lab study to be 18% [14]. Since lab studies are considered to be ideal circumstances, we felt this estimate to most likely be a realistic representation of the true survival rate of the larvae. Since the experiment only lasted one week, we squared this value in order to find a survival rate of the larva after two weeks and found the rate to be 0.0326, which is similar to the 95%-98% death rates projected by Messan et al. [12].

The final component, survival of the chrysalis to adulthood, was much more challenging to assign, as no real data has been gathered. It seems unlikely that the death rate will be particularly large, since they are no longer foraging for food, and thus no deaths due to lack of resources, and they are relatively sheltered from their surroundings, we use on a rather large survival rate of 85%.

Until recently there was little comparable work done considering the monarch migration. We have compared our base parameters to the only known similar model, and found them to be sufficiently close [8].

Appendix B: Generalizing the Matrix

Since we estimated many of the parameters, it would be helpful to have a general form for the dominant eigenvalue and eigenvector for further analysis. To this end, we calculated the dominant eigenvalue of matrix M found in equation (3.3), which is given by

$$det \begin{bmatrix} -\lambda & 0 & F \\ L & -\lambda & 0 \\ 0 & C & A-\lambda \end{bmatrix} = 0 \tag{5.1}$$

where λ is the dominant eigenvalue. We find

$$\lambda^3 - A\lambda^2 + FCL = 0. \tag{5.2}$$

When factoring, we noticed that each λ looked similar, so we found a common factor to make each λ more manageable to write, which we call N, such that

$$N = \left(108CLF + 8A^3 + 12\sqrt{81L^2C^2F^2 + 12CLFA^3}\right)^{1/3}. \tag{5.3}$$

Now we have:

$$\lambda_1 = \frac{N}{6} + \frac{2A^2}{3N} + \frac{A}{3}, \tag{5.4}$$

$$\lambda_2 = \frac{-N}{12} - \frac{A^2}{3N} + \frac{A}{3} + \frac{\sqrt{3}i}{i}\left(\frac{N}{6} - \frac{2A^2}{3N}\right), \tag{5.5}$$

$$\lambda_3 = \frac{-N}{12} - \frac{A^2}{3N} + \frac{A}{3} - \frac{\sqrt{3}i}{i}\left(\frac{N}{6} - \frac{2A^2}{3N}\right), \tag{5.6}$$

where λ_1 is the dominant eigenvalue of matrix (5.1).

Thus we now have the general form for all eigenvalues for this population matrix of monarch butterflies. We then need the general form for the eigenvector of the dominant eigenvalue, which in this case, will always be λ_1. Rather then assigning $x_1 = 1$, as is common, we chose to normalize the sum to give the stable stage distribution:

$$x_1 + x_2 + x_3 = 1 \tag{5.7}$$

to give us the population percentage at each stage of the Monarch lifespan. With this in mind, we found that the eigenvector is

$$x = \begin{bmatrix} w \\ \\ \frac{wL}{\lambda_1} \\ \\ \frac{w\lambda_1}{F} \\ \\ \end{bmatrix}, \tag{5.8}$$

where

$$w = (1 + \frac{L}{\lambda} + \frac{\lambda}{F})^{-1}. \tag{5.9}$$

Thus

$$x = \begin{bmatrix} (1 + \frac{L}{\lambda} + \frac{\lambda}{F})^{-1} \\ \frac{L}{(1+\frac{L}{\lambda}+\frac{\lambda}{F})\lambda_1} \\ \frac{\lambda}{(1+\frac{L}{\lambda}+\frac{\lambda}{F})F} \end{bmatrix} \tag{5.10}$$

With this, we have a general dominant eigenvalue and eigenvector, which can be used to better understand the relationship of each parameter.