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Reproduction Rate Strategies in White-Footed Mice

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Reproduction Rate Strategies in White-Footed Mice

A thesis submitted in partial fulfillment of the requirement
for the degree of Bachelors of Science in Mathematics from
The College of William and Mary

by

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March 30, 2009

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Abstract

A photoperiod is the measure of the length of daylight each day. This value can potentially determine the behavior and/or biological processes of many species of animals and plants. *Peromyscus leucopus* (white-footed mouse) responds to changes in photoperiods by altering its reproductive strategies. White-footed mice adjust their reproduction rates because of the high cost of reproduction in the winter and in short photoperiods. In our research we have looked at two groups of mice: responsive mice which reproduce March through November and non-responsive mice which reproduce all year around. Interestingly, in Williamsburg, VA there exists a mixture of the responsive and non-responsive mice. The coexistence of these two types of mice suggests some kind of genetic variation. We have created nonlinear discrete population models to better understand the population dynamics of the two phenotypes of mice and whether coexistence over time is possible using our assumptions on environmental conditions and mice characteristics. Using one of our models, it seems that the coexistence of these mice is sensitive to the genetic inheritance of photoresponsiveness.

Chapter 1

Introduction

1.1 Summary

An interesting population of white-footed mice, *Peromyscus leucopus*, live around Williamsburg, VA. Here there exists a mixture of two phenotypes of mice; one that reproduces in warmer months or longer photoperiods and another that reproduces all year around including short photoperiods. These mice are called photoperiod responsive and non-responsive respectively. The difference between these two phenotypes has a genetic basis. [9].

The goal of this project is to understand the population dynamics of the two phenotypes of mice and whether coexistence over time is possible using our assumptions on environmental conditions and mice characteristics. We accomplish this goal by creating nonlinear discrete-time models to try and address the main complexities of the mouse population.

First we will introduce a basic phenotype and age class model (Chapter 2) that attempts to capture the critical characteristics of the mouse population while maintaining a lower dimension and complexity by defining only two age classes. One of our goals is to understand what conditions bring about coexistence of the two phe-

notypes of mice. Therefore, we normalize our basic phenotype and age class model so that we can track relative proportions of mice within the population. We also accomplish this goal by varying critical parameters, α and β . We use this model to study the dynamics of the *P. leucopus* population by using simulations and analytical techniques.

In Chapter 2 we show that coexistence seems to be extremely sensitive to two of our parameters α and β . By systematically checking various values of these parameters we have only found one set of values that shows coexistence of the two phenotypes, $\alpha = .29, \beta = .71$. When we change these values slightly, one of the phenotype populations goes extinct. The α and β values for coexistence suggest a male-dominant trait, meaning that the phenotype of a mouse depends more heavily on the father's phenotype than the mother's.

Next in Chapter 3 we will discuss our extended phenotype and stage class model. This model includes more age and stage classes of mice, but still describes similar interactions as seen in the basic model. Here we look at individual mice rather than proportions of mice. Using this extended model we vary parameters and conduct simulations to help get an intrinsic understanding of the population dynamics.

Finally we will conclude by describing the version of the extended model used in simulations in Chapter 4.

1.2 *Peromyscus leucopus*

Peromyscus leucopus, a nocturnal mammal, inhabits brushy areas and hardwood upland forests across North America and parts of Mexico. Depending on the location and season, *P.leucopus* consumes insects, green vegetation, starchy matter, seeds, nuts, and fruit [4].

These mice can be divided into three age classes: juveniles, weaned, and adults.

Juveniles or newborn mice cannot reproduce and depend on their mother for milk and protection. After about three weeks, mice are weaned; they no longer depend upon their mother and enter the weaned class. At around 40 days female mice experience their first estrus. Female and male mice become adults or sexually mature at around 42 days or six weeks of age, at which point they enter the Adult age class. Female mice will not mate unless they are ovulating, which occurs every four to five days, but this can shift due to fear, stress, pheromones, and food availability. The length of gestation lasts for 21-27 days or about 3 weeks; female mice will give birth to about 4 to 5 pups (or juveniles) at a time; each female will produce about 4 litters per year. *P.leucopus* are not monogamous; male mice provide little to no paternal care and instead seek additional mates [3]. The average lifespan of *P.leucopus* in the wild is about 3 months; this high mortality leads to essentially complete population turnover over the course of a year [4].

1.3 *Peromyscus leucopus* Responsive Behavior

A photoperiod is the measure of the length of daylight each day. This value can potentially determine the behavior and/or biological processes of many species of animals and plants. *P. leucopus* responds to changes in photoperiods by altering its reproductive strategies. Many small mammals experience a high cost of reproduction in the winter and in short photoperiods due to higher energy costs and less availability of nutrients. Populations of *P. leucopus* in the northern regions of the United States and Canada exhibit this responsive behavior and, therefore, reproduce only during the warmer months. However, populations of mice in areas with little to no fluctuations in seasonality do not display responsiveness and therefore their reproductive rates remain fairly constant throughout the year [8].

Complex genetic control controls the degree of responsiveness in *P. leucopus*. “One

or more variable locus may be responsible for much of the heritable variation present in this population.” This suggests that levels of responsiveness lie on a continuum; there exists intermediates between the responsive and non-responsive groups [2].

The main biological question underlying this research is whether, over time, these two phenotypes can coexist or whether one or both of these phenotypes eventually die out.

Chapter 2

Basic Phenotype and Age Class Model

Here we present a basic phenotype and age class model. This basic model consists of a system of nonlinear difference equations that preserve the fundamental characteristics of the white-footed mouse population while maintaining a low complexity. This basic model suggests that inheritance of photoresponsiveness is important.

In this model the mouse population is divided into two phenotypes: responsive and non-responsive. We further divide each group into two age classes: juvenile and adult. Seasonality plays a critical role in distinguishing between the two phenotypes of mice. Not only do the reproductive behaviors of the responsive mice depend on the season/photoperiod, the death rates of both phenotypes can also change according to the length of the photoperiod [8]. We incorporate seasonality by averaging the values of seasonal death and pregnancy rates over one year, and then track the population from year to year. Since our goal is to understand the conditions for the coexistence of the phenotypes we will track proportions of each class within the population. We do this by normalizing the size of each class by the size of the total population. Equivalently, the proportions of juvenile responsive, juvenile non-responsive, adult

responsive, and adult non-responsive mice must sum to one.

2.1 Assumptions

1. *The mouse population is divided into two phenotype groups: responsive and non-responsive and two age classes: juveniles and adults. These phenotypes interact with each other through mating.* While research suggests there exist mice that exhibit mating behavior which lies between these two extremes [9], we will make this simplifying assumption as a first approach to modeling the population. We also split the population into two age classes, we will call mice that are sufficiently mature to reproduce adults and all mice that cannot reproduce juveniles.
2. *Sex ratio is 1:1.* This 1:1 ratio has been documented in research in the wild [5]. Our model keeps track of the female mouse population and we assume that the number of males in each age/phenotype class is the same as the number of females in the corresponding classes.
3. *Reproductive photoresponsiveness is significantly heritable; we will assume a heritability of 1.* It has been cited that photoresponsiveness is significantly heritable. Heritability ranges anywhere from 0.54 to 0.74; this means, for example, that if we assume a heritability of .54, we would expect 54 percent of a mouse's phenotype to come from genes inherited from its parents, while 46 percent of its phenotype would be determined by the environment [9]. In our model we use a heritability of 1, which means that photoresponsiveness depends only on the phenotypes of the parents. For example, for a responsive juvenile to be born, at least one of the parents must also be responsive, therefore there are three types of couples that can give birth to responsive juveniles: responsive female/responsive male, responsive female/non-responsive male, and

non-responsive female/responsive male. This similarly holds for non-responsive juveniles.

4. *The size of a litter that an adult female gives birth to, does not depend on her phenotype.* We assume that both responsive and non-responsive females give birth to an average of four juveniles [5].
5. *Seasonality is incorporated into phenotypic pregnancy and death rate parameters.* The average yearly pregnancy and death rates incorporate the following assumptions. Assuming fully responsive and non-responsive mice, we know that pregnancy rates during all seasons remain the same for non-responsive mice, while responsive mice do not mate during cold months or short photoperiods [9]. We also know that short photoperiods and reproduction increase death rate due to harsh conditions and the requirement of more nutrients respectively [8] [7]. This leads to average yearly pregnancy and death rates that are higher for the non-responsive population.
6. *Spatial structure is not explicitly modeled.* We assume that the groups of mice are sufficiently well mixed in the environment so that spatial interaction effects are negligible.
7. *Time is measured in units of weeks. The affect of various seasons on pregnancy and death rates is incorporated into the average weekly rates.*

2.2 The Model

We are now going to build a difference equation model based on Figure 2.1. We will use the variables given in Table 2.1 in the equations for the basic model.

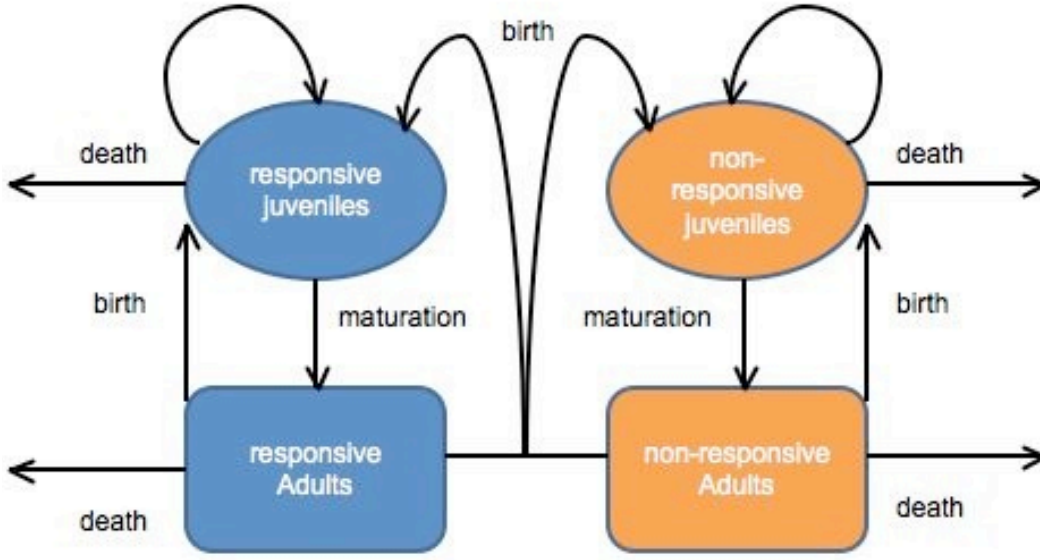


Figure 2.1: The flow chart for the basic model representing the age class structure for both phenotypes. For the accompanying equations, see Section 2.3.

Table 2.1: Table of Variables for Basic Model

Names	Variables	Description/Units
responsive juveniles	J_r	number of responsive juveniles
non-responsive juveniles	J_{nr}	number of non-responsive juveniles
responsive adults	A_r	number of responsive adults
non-responsive adults	A_{nr}	number of non-responsive adults

We begin by constructing a map

$$\Phi : \Omega \rightarrow \Omega \tag{2.1}$$

where

$$\Omega = \{ \underline{P} = (J_r, J_{nr}, A_r, A_{nr}) \in \mathbb{R}^4 \mid J_r, J_{nr}, A_r, A_{nr} \geq 0 \}. \tag{2.2}$$

This difference equation model describes the population of mice at discrete time steps. Here, we assume time is measured in weeks. For example, given a population $\underline{P} = (J_r, J_{nr}, A_r, A_{nr})$, the population after one week will be $\Phi(\underline{P})$. More specifically, $J'_r = \Phi_1(\underline{P})$ is size of the resulting responsive juvenile population after one week.

We will now describe the parameters and functions used in the construction of Φ . Look at Table 2.3 for more information.

To describe the maturation of juveniles to adults, we assume a constant *maturation rate/probability* $0 \leq m \leq 1$. More specifically, mJ_r responsive juveniles mature to responsive adults in one time step. The maturation process for non-responsive juveniles has the same form. Similarly, we assume a constant *juvenile death rate/probability* $0 \leq d \leq 1$ for juveniles. For example, dJ_r responsive juveniles die after one time step; this is similar for non-responsive juveniles. To describe the death of adults we assume a constant *adult death rate/probability* $0 \leq r_r \leq 1$ and $0 \leq r_{nr} \leq 1$ for responsive and non-responsive adults respectively. Unlike juveniles, the death rate of adults depends on phenotype, due to the higher risk of death in reproductive mice (Assumption 5).

The birth terms will be constructed from the product of a contact rate function with constant parameters: pregnancy rates and average litter size. Since the phenotype of a mouse depends on inheritance, we will consider the phenotype of the parents in determining the phenotypes of the resulting juveniles.

We model the *contact probability* by $0 \leq c(x, A) \leq 1$, where $c(x, A) = \frac{x}{A_r + A_{nr}}$, and x is either A_r or A_{nr} (depending on the phenotype of the male). This function changes with every time step and describes the probability of a responsive or non-responsive adult female coming into contact with either a responsive or non-responsive male. More specifically, $c(A_{nr}, A)A_r$ describes the *contact rate* between a responsive adult female and a non-responsive adult male.

The *average litter size*, $\ell > 0$, is the typical litter size of mice born from an adult female. We assume that this does not depend on phenotype (Assumption 4).

The *pregnancy rates* for responsive adult females and non-responsive adult females respectively are $0 \leq p_r \leq 1$ and $0 \leq p_{nr} \leq 1$. The product of the average litter size, ℓ , with the appropriate pregnancy rate, p_r or p_{nr} , gives the corresponding *birth rate* b_r or b_{nr} . Therefore the birth rate gives the number of juveniles born from a pregnant female. For example, $b_r A_r$, where $b_r = \ell \cdot p_r$, gives the number of juveniles born from a pregnant responsive adult female.

α and β describe the proportion of responsive juveniles born from either a responsive adult female and non-responsive adult male or of a non-responsive adult female and responsive adult male respectively. Using this logic, $(1 - \alpha)$ and $(1 - \beta)$ would describe the proportion of non-responsive juveniles born from the same couples described previously. In addition we assume that responsive couples only produce responsive juveniles and non-responsive couples only produce non-responsive juveniles (Assumption 3).

2.3 Difference Equations for the Basic Model

For $\underline{P} = (J_r, J_{nr}, A_r, A_{nr}) \in \Omega$, we define $\Phi(\underline{P})$ component-wise as follows:

$$\Phi_1(\underline{P}) = J'_r = \underbrace{b_r \cdot c(A_r, A)A_r + \alpha b_r \cdot c(A_{nr}, A)A_r + \beta b_{nr} \cdot c(A_r, A)A_{nr}}_{\text{births of responsive juveniles}} + \underbrace{(1 - m - d)J_r}_{\text{returning responsive juveniles}}$$

$$\Phi_2(\underline{P}) = J'_{nr} = b_{nr} \cdot c(A_{nr}, A)A_{nr} + (1 - \alpha)b_r \cdot c(A_{nr}, A)A_r + (1 - \beta)b_{nr} \cdot c(A_r, A)A_{nr} + (1 - m - d)J_{nr}$$

$$\Phi_3(\underline{P}) = A'_r = mJ_r + (1 - r_r)A_r$$

$$\Phi_4(\underline{P}) = A'_{nr} = mJ_{nr} + (1 - r_{nr})A_{nr}$$

$$0 \leq b_r, b_{nr}m, d, r_r, r_{nr} \leq 1, 0 \leq m + d \leq 1, 0 \leq \alpha, \beta \leq 1$$

Where

$$c(x, A) = \frac{x}{A_r + A_{nr}}, x = A_r, A_{nr}$$

Note that, for example, $\Phi_1(\underline{P})$ gives the number of responsive juveniles resulting from \underline{P} after one time step.

The following describes the equations of the responsive phenotype population. The equations for the non-responsive phenotype population are similar. The youngest stage class will be the responsive juvenile class J_r . These mice are either born from a responsive adult female, A_r , who has mated with a responsive or non-responsive male, or from a non-responsive adult female who has mated with a responsive male. The responsive juveniles can die at rate d , mature to the responsive adult class at a rate m , or remain in the responsive juvenile class at a rate $(1 - m - d)$.

The oldest stage class will be the responsive adults A_r . This stage class can either die at rate r_r or remain in the responsive adult class at a rate $(1 - r_r)$.

Proposition 1. $\Phi(\Omega) \subseteq \Omega$, where Φ is given on page 12 and

$$\Omega = \{\underline{P} = (J_r, J_{nr}, A_r, A_{nr}) \in \mathbb{R}^4 \mid J_r, J_{nr}, A_r, A_{nr} \geq 0\}.$$

Proof. Consider the equation describing the responsive juvenile population after one time step as given in Section 2.3

$$\Phi_1(\underline{P}) = J'_r = b \cdot c(A_r, A)p_1 \cdot A_r + \alpha b \cdot c(A_{nr}, A)p_1 \cdot A_r + \beta b \cdot c(A_r, A)p_2 \cdot A_{nr} + (1 - m - d)J_r.$$

Since by construction, the coefficients multiplying A_r , A_{nr} , and J_r are nonnegative, and each of these three variables is assumed to be nonnegative, $J'_r \geq 0$.

Similarly, $J'_{nr} \geq 0$.

Now consider the equation describing the responsive adult population after one time step from Section 2.3

$$\Phi_3(\underline{P}) = A'_r = mJ_r + (1 - r_1)A_r.$$

Again, all coefficients are positive and $A'_r \geq 0$. $A'_{nr} \geq 0$ follows similarly. Therefore, $\underline{P}' = \Phi(\underline{P}) \in \Omega$. □

We will now look at the map that describes our normalized basic model

$$\bar{\Phi} : \Omega \cap S^4 \rightarrow \Omega \cap S^4 \tag{2.3}$$

Where

$$S^4 = \{\underline{P} \in \mathbb{R}^4 \mid \|\underline{P}\| = |J_r| + |J_{nr}| + |A_r| + |A_{nr}| = 1\} \tag{2.4}$$

$$\bar{\Phi}(\underline{P}) = \frac{\Phi(\underline{P})}{\|\Phi(\underline{P})\|}. \tag{2.5}$$

Here $\bar{\Phi}_i(\underline{P})$ gives us the proportion of the population in class i after one time step.

This is the map we use to conduct simulations and analyze.

Claim.

$$\Phi^{-1}(\underline{0}) = \underline{0} \tag{2.6}$$

Proof. According to the following equations on page 12,

$$\Phi_3(\underline{P}) = A'_r = mJ_r + (1 - r_r)A_r$$

and

$$\Phi_4(\underline{P}) = A'_{nr} = mJ_{nr} + (1 - r_{nr})A_{nr}$$

we see that $A'_r = 0$, only when $J_r = A_r = 0$ and $A'_{nr} = 0$, only when $J_{nr} = A_{nr} = 0$. □

Proposition 2. $\bar{\Phi} : \Omega \cap S^4 \rightarrow \Omega \cap S^4$, where $\bar{\Phi}$ is given by Equation 2.5 and

$$S^4 = \{\underline{P} \in \mathbb{R}^4 \mid \|\underline{P}\| = |J_r| + |J_{nr}| + |A_r| + |A_{nr}| = 1\}.$$

Proof. Since $\underline{0} \notin \Omega \cap S^4$, according to Equation 2.6, clearly $\bar{\Phi}(\Omega \cap S^4) \subseteq \Omega \cap S^4$. □

2.4 Simulations

MATLAB was used to produce these simulations and the code used can be found online.

First we look at when the two phenotypes of mice coexist. Here we plot the phase portrait of responsive mice vs. nonresponsive mice.

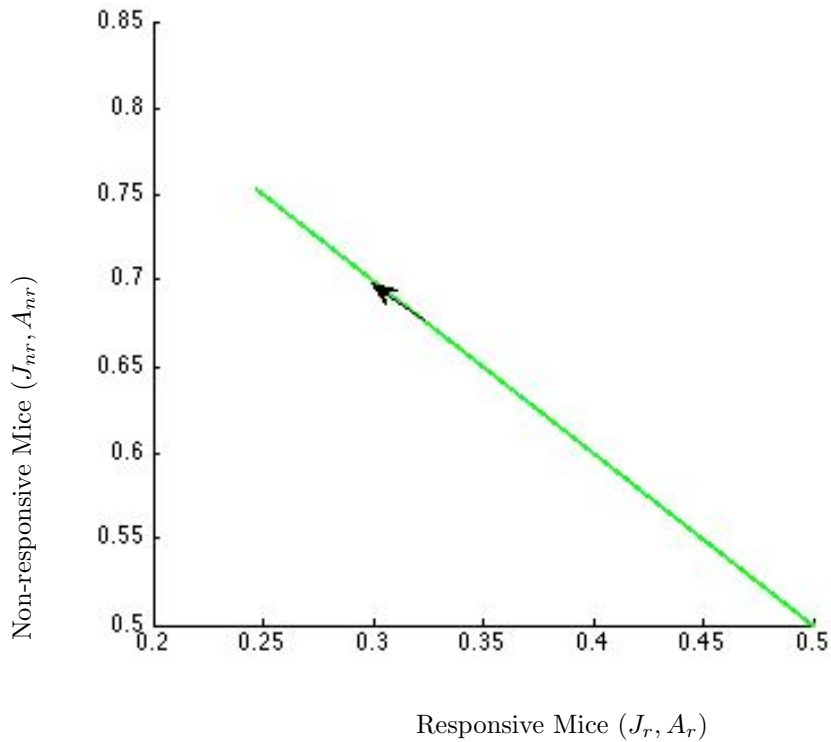


Figure 2.2: The following initial condition: $J_r = .25, J_{nr} = .25, A_r = .25, A_{nr} = .25$. We plotted 100,000 iterates and used $\alpha = .29, \beta = .71$. We can see by looking at this phase portrait that by starting out with equal proportions of responsive and non-responsive mice, we observe that this proportion shifts such that the non-responsive mice to responsive mice ratio increases. Look at Table 2.2 for values of the parameters used.

Next we look at the responsive and non-responsive mice over time.

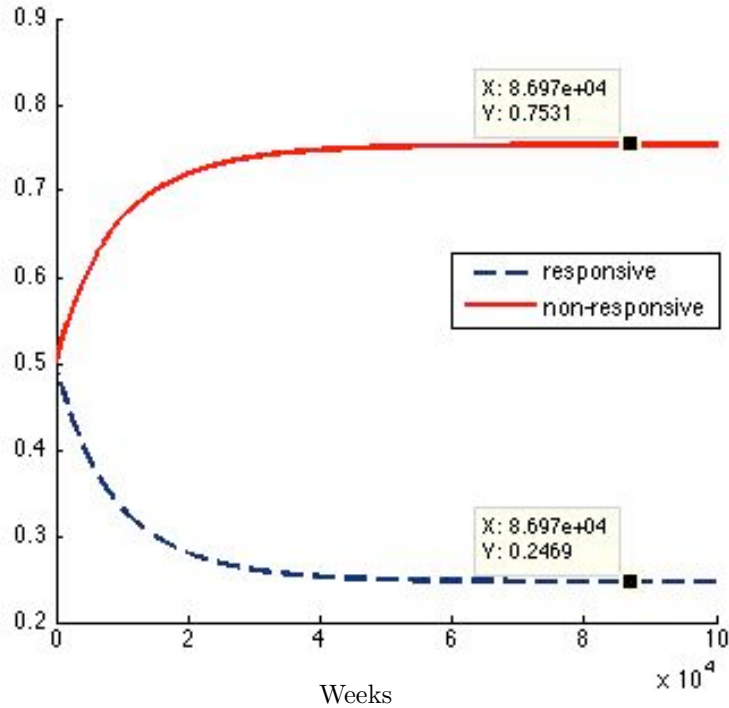


Figure 2.3: As the initial condition we used $J_r = .25, J_{nr} = .25, A_r = .25, A_{nr} = .25$, and plotted 100,000 iterates. We see that both populations coexist over time. Both populations stabilize at 86,970 weeks (look at data points shown). The proportion of responsive mice in the population is .2469 and the proportion of non-responsive mice is .7531. The α and β strongly affect whether the two phenotypes will coexist. At this $\alpha = .29, \beta = .71$ it seems that we will only observe coexistence. This α indicates that when a responsive adult female mates with a non-responsive adult male, only 29% of her babies will be responsive juveniles. This β indicates that when a non-responsive adult female mates with a responsive male, 79% of her babies will be responsive juveniles. These values demonstrate that photosensitivity is a male dominant trait. In addition changing initial conditions do not seem to affect this equilibrium. Look at Table 2.2 for the values of the parameters used.

However, by just changing the coexisting values of $\alpha = .29$ and $\beta = .71$ each by one one hundredth, we do not see coexistence.

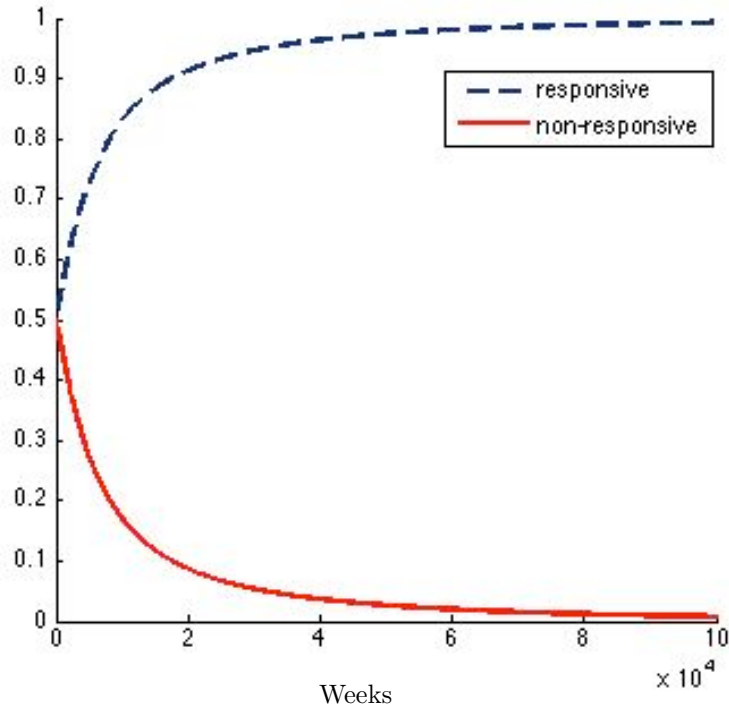


Figure 2.4: Using the same initial condition as before, here we plotted 100,000 iterates and used $\alpha = .28$ and $\beta = .72$. We see that over time the total mouse population seems to be only comprised of responsive mice; the non-responsive population is approaching 0 or becoming extinct. These values demonstrate that the genetic component of photosensitivity is extremely sensitive in this model. Look at Table 2.2 for the values of the parameters used.

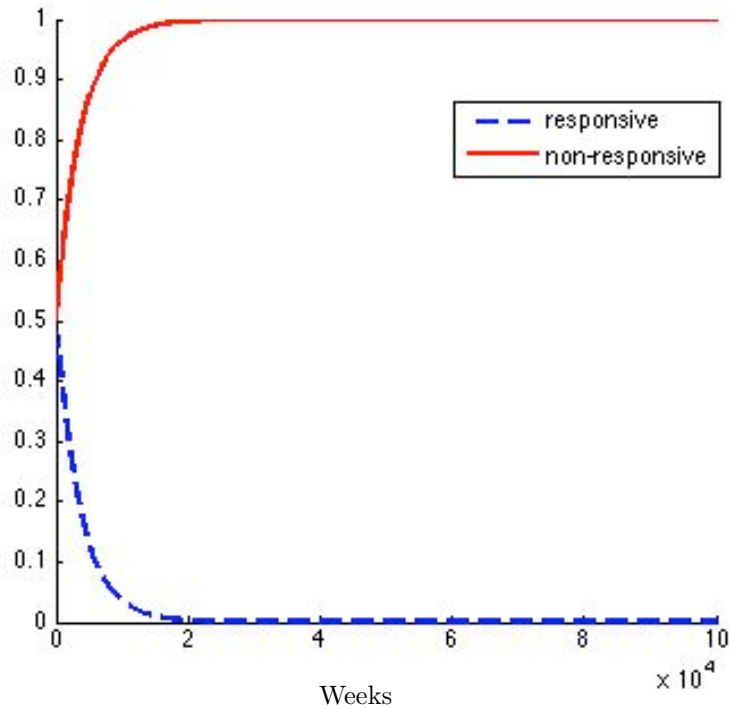


Figure 2.5: Again using the same initial condition as before, here we plotted 100,000 iterates and used $\alpha = .30$ and $\beta = .70$. We see that over time the total mouse population seems to be only comprised of non-responsive mice; the responsive population is approaching 0 or becoming extinct. This scenario is reversed from the previous Figure 2.4. Look at Table 2.2 for the values of the parameters used.

The parameter values in Table 2.2 match our intuition regarding phenotypic and mouse behavior.

We see that the pregnancy rate for non-responsive adult mice p_2 is larger than the pregnancy rate for responsive adult mice p_1 , this matches the notion that non-responsive mice mate year around, while responsive mice only mate in warmer months (Assumption 5).

We also observe a higher death rate in the juveniles, due to the fact that these mice are more vulnerable. The non-responsive adult death rate r_2 is larger than the responsive adult death rate r_1 , because reproduction increases death rate (due to foraging and nutrient requirements), therefore the more reproductive non-responsive mice have a higher chance of dying (Assumption 5).

Table 2.2: Table of Parameters

Parameters	value
ℓ	4
p_r	.1875/3
p_{nr}	.25/3
m	.4
d	.1563
r_r	.082875
r_{nr}	.0975

The following table will describe more in depth about the parameters used in this basic model:

Table 2.3: Table of Parameters for Basic Model

Parameters/Functions	Description	units	references
α	proportion of responsive juveniles born from responsive adult females impregnated by a non-responsive adult male	none	
β	proportion of responsive juveniles born from non-responsive adult females impregnated by a responsive adult male	none	
$c(x, A)$	probability an adult female will come into contact with a responsive or non-responsive adult male	none	
ℓ	number of Juveniles born from an Adult female (litter size)	$\frac{J}{\text{Adults}}$	[5]
p_r	pregnancy rate of responsive adult females	$\frac{1}{\text{week}}$	[1]
p_r	pregnancy rate of non-responsive adult females	$\frac{1}{\text{week}}$	[1]
m	maturation rate of juveniles	$\frac{1}{\text{week}}$	[6]
d	death rate of juveniles	$\frac{1}{\text{week}}$	[6]
r_r	death rate of responsive adults	$\frac{1}{\text{week}}$	[7]
r_{nr}	death rate of non-responsive adults	$\frac{1}{\text{week}}$	[7]

Chapter 3

Extended Phenotype and Stage Class Model

This extended phenotype and stage class model, like the basic model, tries to capture the overall dynamics of the two phenotypes of the white-footed mouse population by using a system of nonlinear difference equations. Also like the basic model, we only look at the female mouse population. Here we include the full spectrum of age and stage classes that naturally seem to occur [5]. We incorporate a weaned age class, after the juvenile class, and split the adult class into three stages: breeding, gestating, and lactating. In total we consider five classes of female mice: juvenile, weaned, breeding, gestating, and lactating.

The juvenile and weaned mice lack reproductive capabilities and the breeding mice are the only group of mice able to reproduce, under Assumption 8. Each of the five classes are divided into a responsive or non-responsive group. In addition, the gestating and lactating stage classes are divided by the type of male, responsive or non-responsive, they mated with. By keeping track of the male's phenotype we can identify the phenotype of a juvenile born from a gestating mouse, since we assume that the heritability of photoresponsiveness of mice depend only on the genetics of

the parents, under Assumption 3.

We incorporate seasonality by rotating seasonal death and pregnancy rates every season, or thirteen weeks; so these parameters depend on time. Additionally, we track the number of mice in the population, instead of a proportion of mice.

3.1 Assumptions

1. *The mouse population is divided into responsive and non-responsive groups. These two phenotypes interact with each other by means of mating.* While research suggests there exists mice between these two extreme behaviors [9], our model will first look at this scenario in order to reduce dimensions and complexity.
2. *Sex ratio is 1:1.* This 1:1 ratio has been documented in research in the wild [5]. Our model keeps track of the female mouse population and we assume that the number of responsive and non-responsive males is the same as the number of responsive and non-responsive females.
3. *Reproductive photoresponsiveness is significantly heritable; we will assume a heritability of 1.* It has been cited that photoresponsiveness is significantly heritable. Heritability ranges anywhere from 0.54 to 0.74; this means, for example, that if we assume a heritability of .54, we would expect 54 percent of a mouse's genetics to come from its parents, while 46 percent of its genetics would be determined by the environment [9]. In our model we use a heritability of 1, which means that photoresponsiveness depends only on the phenotypes of the parents. This means that for a responsive juvenile to be born, one of the parents must also be responsive, therefore there are three types of couples that can give birth to responsive juveniles: responsive female/male, responsive female/non-responsive

male, and non-responsive female/responsive male.

4. *The size of a litter that an adult female gives birth to, does not depend on her phenotype or the phenotype of the male.* We assume that both responsive and non-responsive gestating females give birth to an average of four juveniles [5].
5. *Seasonality is incorporated into phenotypic pregnancy and death rate parameters*
We rotate our pregnancy and death rate parameters every 13 weeks or every season. We do this because of the following facts. Assuming fully responsive and non-responsive mice, we know that pregnancy rates during all seasons remain the same for non-responsive mice, while responsive mice do not mate during cold months or short photoperiods [9]. We also know that short photoperiods and reproduction increase death rate due to harsh conditions and the requirement of more nutrients respectively [8] [7]. Since in our model only breeding adults reproduce, the death rate of a responsive breeding adult will differ from the death rate of a non-responsive adult, whereas for all other stage classes of mice, the death rate does not differ between the two phenotypes.
6. *Spatial structure is not explicitly modeled.* We assume that the groups of mice are sufficiently well mixed in the environment so that spatial interaction effects are negligible.
7. *Time is measured in units of weeks.*
8. *Gestating and lactating mice cannot mate.* While pregnant mice cannot mate, lactating mice can mate and become pregnant, but the probability of this occurring is small, so for the moment this possibility is not taken into account [5].
9. *All birth rates remain unchanged in non-responsive, while in the winter all birth*

rates equal zero for responsive mice. This assumption holds since we are assuming fully responsive and non-responsive mice [9].

10. *Reproduction increases death rate.* Reproductive mice require more nutrients, and therefore must increase foraging time/frequency, which in turn increases the risk of dying due to predation [7].
11. *Winter increases death rate.* Winter brings harsher conditions for mice, when less vegetation and colder temperatures increase the likelihood of death [8].

3.2 The Model

We are now going to build a difference equation model based on Figure 3.1. We will use the variables given in Table 3.1 in the equations for the extended model.

We began by constructing a map

$$\Psi : \Lambda \rightarrow \Lambda$$

where

$$\Lambda = \{ \underline{P} = (J_r, J_{nr}, W_r, W_{nr}, B_r, B_{nr}, G_{r,r}, G_{r,nr}, G_{nr,r}, G_{nr,nr}, L_{r,r}, L_{r,nr}, L_{nr,r}, L_{nr,nr}) \in \mathbb{R}^{14} \mid$$

$$J_r, J_{nr}, W_r, W_{nr}, B_r, B_{nr}, G_{r,r}, G_{r,nr}, G_{nr,r}, G_{nr,nr}, L_{r,r}, L_{r,nr}, L_{nr,r}, L_{nr,nr} \geq 0 \}.$$

This difference equation model describes the population of mice at discrete time steps. Here, we assume time is measured in weeks. For example, given a population \underline{P} , the population after one week will be $\Psi(\underline{P})$. More specifically, $J'_r = \Psi_1(\underline{P})$ is the size of the resulting responsive juvenile population after one week.

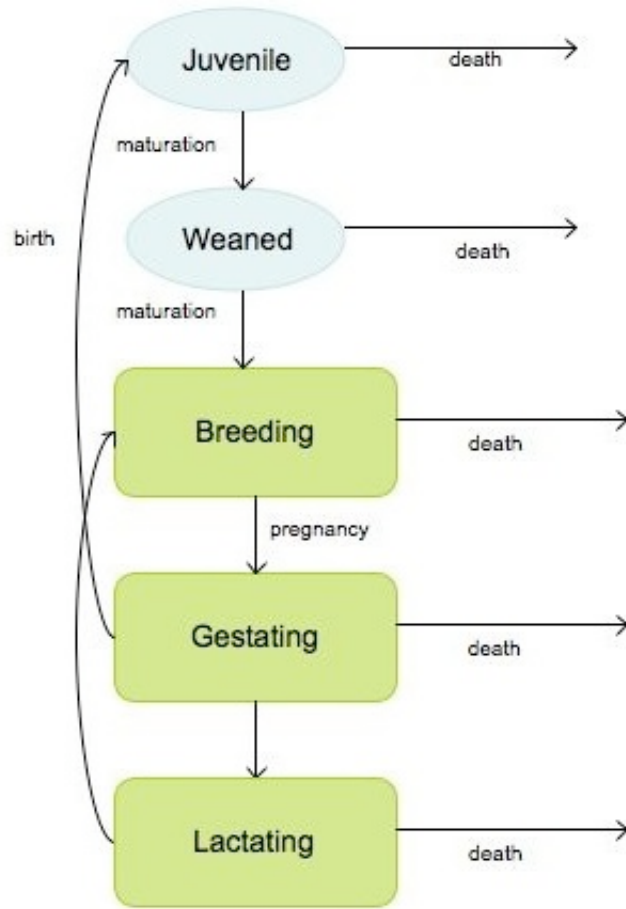


Figure 3.1: The flow chart for the extended model representing the stage class structure for both phenotypes. For the accompanying equations, see Section 3.3.

Table 3.1: Table of Variables for Extended Model

Names	Variables	Description
r juveniles	J_r	responsive juveniles
nr juveniles	J_{nr}	non-responsive juveniles
r weaned	W_r	responsive weaned
nr weaned	W_{nr}	non-responsive weaned
r breeding	B_r	responsive breeding adults
nr breeding	B_{nr}	non-responsive breeding adults
r,r gestating	$G_{r,r}$	responsive gestating (impregnated by a responsive male)
r,nr gestating	$G_{r,nr}$	responsive gestating (impregnated by a non-responsive male)
r gestating	G_r	total responsive gestating, $G_r = G_{r,r} + G_{r,nr}$
nr,r gestating	$G_{nr,r}$	non-responsive gestating (impregnated by a responsive male)
nr,nr gestating	$G_{nr,nr}$	non-responsive gestating (impregnated by a non-responsive male)
nr gestating	G_{nr}	total non-responsive gestating, $G_{nr} = G_{nr,r} + G_{nr,nr}$
r,r lactating	$L_{r,r}$	responsive lactating (impregnated by a responsive male)
r,nr lactating	$L_{r,nr}$	responsive lactating (impregnated by a non-responsive male)
r lactating	L_r	total responsive lactating, $L_r = L_{r,r} + L_{r,nr}$
nr,r lactating	$L_{nr,r}$	non-responsive lactating (impregnated by a responsive male)
nr,nr lactating	$L_{nr,nr}$	non-responsive lactating (impregnated by a non-responsive male)
nr lactating	L_{nr}	total non-responsive lactating, $L_{nr} = L_{nr,r} + L_{nr,nr}$
r adults	A_r	responsive adults, $A_r = B_r + G_r + L_r$
nr adults	A_{nr}	non-responsive adults, $A_{nr} = B_{nr} + G_{nr} + L_{nr}$

We will now describe the parameters and functions used in the construction of Ψ . Look at Table 3.4 for more information.

To describe the maturation of juveniles to weaned mice, we assume a constant *juvenile maturation rate* $0 \leq m \leq 1$. More specifically, mJ_r responsive juveniles mature to responsive weaned mice in one time step. This similar maturation process holds for non-responsive juveniles. Weaned mice mature to breeding adult mice at a constant *weaned maturation rate* $0 \leq f \leq 1$. Gestating adult mice mature to lactating adult mice once they give birth, we assume a constant *gestating maturation rate* $0 \leq k_g \leq 1$. We also assume a constant *lactating maturation rate* $0 \leq k_l \leq 1$, that describes the maturation of lactating adult mice to breeding adult mice.

We model the *juvenile and weaned death rate* using $0 \leq d(t), q(t) \leq 1$ for juveniles and weaned respectively. For example, $d(t)J_r$ responsive juveniles and $q(t)W_r$ responsive weaned mice die after one time step; this is similar for non-responsive juveniles and weaned mice. To describe the *breeding adult death rate* we assume the following respective rates: $0 \leq r_{br}(t), r_{bnr}(t) \leq 1$ for responsive and non-responsive breeding adults respectively. Unlike breeding adults, the death rate of gestating and lactating adults does not depend on phenotype, according to Assumption 5. *Gestating and lactating adult death rate* will be $0 \leq r_g(t), r_l(t) \leq 1$ respectively.

The birth terms will consist of a contact rate function and constant parameters: pregnancy rates and average litter size. Since the phenotype of a mouse depends on inheritance, we will consider the phenotype of the parents in determining the phenotypes of the resulting juveniles.

We model the *contact probability* by $0 \leq c(x, A) \leq 1$, where $c(x, A) = \frac{x}{A_r + A_{nr}}$, and x is either A_r or A_{nr} (depending on the phenotype of the male). This function, changes with every time step, and describes the probability of a responsive or non-responsive breeding adult female coming into contact with either a responsive or non-responsive adult male. For example, $c(A_{nr}, A)B_r$ describes the *contact rate* between a responsive

breeding adult female and a non-responsive adult male.

The *pregnancy rate per contact* for responsive and non-responsive breeding adult females are $0 \leq p_r \leq 1$ and $0 \leq p_{nr}(t) \leq 1$ respectively. Here $c(A_r, A)p_r(t)B_r$ gives the number of responsive breeding adult females (B_r) that came into contact with responsive adult males (A_r) and become pregnant; these mice now become responsive gestating mice ($G_{r,r}$). The *average litter size*, $\ell > 0$, is the typical litter size of mice born from a gestating adult female. We assume that this does not depend on phenotype [5]. Therefore the $\ell k_g G_{r,r}$ gives the number of responsive juveniles born from a responsive gestating adult (impregnated by a responsive male).

Most importantly, α and β describe the proportion of responsive juveniles born from either an responsive adult female and non-responsive adult male or of a non-responsive adult female and responsive adult male respectively. Using this logic, $(1-\alpha)$ and $(1-\beta)$ would describe the proportion of non-responsive juveniles born from the same couples described above. In addition we assume that responsive couples only produce responsive juveniles and non-responsive couples only produce non-responsive juveniles (Assumption 3).

3.3 Difference Equations for the Extended Model

For $\underline{P} = (J_r, J_{nr}, W_r, W_{nr}, B_r, B_{nr}, G_{r,r}, G_{r,nr}, G_{nr,r}, G_{nr,nr}, L_{r,r}, L_{r,nr}, L_{nr,r}, L_{nr,nr}) \in \Lambda$, we define $\Psi(\underline{P})$ component-wise as follows:

$$J'_r = \ell k_g G_{r,r} + \alpha \ell k_g G_{r,nr} + \beta \ell k_g G_{nr,r} - m J_r - d(t) J_r + J_r$$

$$J'_{nr} = \ell k_g G_{nr,nr} + (1 - \alpha) \ell k_g G_{r,nr} + (1 - \beta) \ell k_g G_{nr,r} - m J_{nr} - d(t) J_{nr} + J_{nr}$$

$$W'_r = m J_r - f W_r - q(t) W_r + W_r$$

$$W'_{nr} = m J_{nr} - f W_{nr} - q(t) W_{nr} + W_{nr}$$

$$B'_r = f W_r + k_l L_{r,r} + k_l L_{r,nr} - c(A_r, A) p_r(t) B_r - c(A_{nr}, A) p_r(t) B_r - r_{br}(t) B_r + B_r$$

$$B'_{nr} = f W_{nr} + k_l L_{nr,nr} + k_l L_{nr,r} - c(A_r, A) p_{nr}(t) B_{nr} - c(A_{nr}, A) p_{nr}(t) B_{nr} - r_{bnr}(t) B_{nr} + B_{nr}$$

$$G'_{r,r} = c(A_r, A) p_r(t) B_r - k_g G_{r,r} - r_g(t) G_{r,r} + G_{r,r}$$

$$G'_{r,nr} = c(A_{nr}, A) p_r(t) B_r - k_g G_{r,nr} - r_g(t) G_{r,nr} + G_{r,nr}$$

$$G'_r = G_{r,r} + G_{r,nr}$$

$$G'_{nr,r} = c(A_r, A) p_{nr}(t) B_{nr} - k_g G_{nr,r} - r_g(t) G_{nr,r} + G_{nr,r}$$

$$G'_{nr,nr} = c(A_{nr}, A) p_{nr}(t) B_{nr} - k_g G_{nr,nr} - r_g(t) G_{nr,nr} + G_{nr,nr}$$

$$G'_{nr} = G_{nr,r} + G_{nr,nr}$$

$$\begin{aligned}
L'_{r,r} &= k_g G_{r,r} - k_l L_{r,r} - r_l(t) L_{r,r} + L_{r,r} \\
L'_{r,nr} &= k_g G_{r,nr} - k_l L_{r,nr} - r_l(t) L_{r,nr} + L_{r,nr} \\
L'_r &= L_{r,r} + L_{r,nr} \\
L'_{nr,r} &= k_g G_{nr,r} - k_l L_{nr,r} - r_l(t) L_{nr,r} + L_{nr,r} \\
L'_{nr,nr} &= k_g G_{nr,nr} - k_l L_{nr,nr} - r_l(t) L_{nr,nr} + L_{nr,nr} \\
L'_{nr} &= L_{nr,r} + L_{nr,nr} \\
\\
A'_r &= B_r + G_r + L_r \\
A'_{nr} &= B_{nr} + G_{nr} + L_{nr} \\
A' &= A_r + A_{nr}
\end{aligned}$$

$$0 \leq l, p_r(t), p_{nr}(t), m, f, k_g, k_l, d(t), q(t)r_{br}(t), r_{bnr}(t), r_g(t), r_l(t) \leq 1, 0 \leq \alpha, \beta \leq 1$$

Where

$$c(x, A) = \frac{x}{A_r + A_{nr}}, x = A_r, A_{nr}$$

The following describes the equations of the responsive phenotype population. The equations for the non-responsive phenotype population are similar. The youngest stage class will be the responsive juvenile class J_r . These mice are either born from an responsive gestating female who has mated with a responsive or non-responsive adult male, or from a non-responsive gestating female who has mated with a responsive adult male. The responsive juveniles can die at a rate $d(t)$, mature to the responsive

weaned class at a rate m , or remain in the responsive juvenile class at a rate $(1 - m - d(t))$. The next stage class will be the responsive weaned mice W_r . They can die at a rate $q(t)$, mature to the responsive breeding adult class at a rate f , or remain in the responsive weaned class at a rate $(1 - f - q(t))$.

The oldest stage class will be the responsive adults. This age class will be further divided into breeding, gestating, and lactating stages. The responsive breeding adults B_r can either die at a rate $r_{br}(t)$, come in contact with a male and get pregnant at a rate $c(x, A)p_r(t)$, or remain in the responsive breeding class at a rate $(1 - c(x, A)p_r(t) - r_{br}(t))$. Once a responsive breeding adult becomes pregnant she becomes a responsive gestating adult.

The responsive gestating class G_r is further divided into two groups, representing responsive gestating females that have become pregnant by responsive males ($G_{r,r}$) or non-responsive males ($G_{r,nr}$). Mice within this class can die at a rate $r_g(t)$, give birth and become lactating adults at a rate k_g , or remain within the responsive gestating class at a rate $(1 - k_g - r_g(t))$.

The responsive lactating class L_r is further divided into two groups, representing R lactating females that have become pregnant by responsive males ($L_{r,r}$) or non-responsive males ($L_{r,nr}$). The responsive lactating adults can either die at a rate $r_l(t)$, become responsive breeding adults once they have completed lactating at a rate k_l , or remain in the responsive lactating class at a rate $(1 - k_l - r_l(t))$.

3.4 Simulations

MATLAB was used to produce the following simulations of the extended model (see Chapter 4)

Here we will look at the responsive and non-responsive mouse population over time.

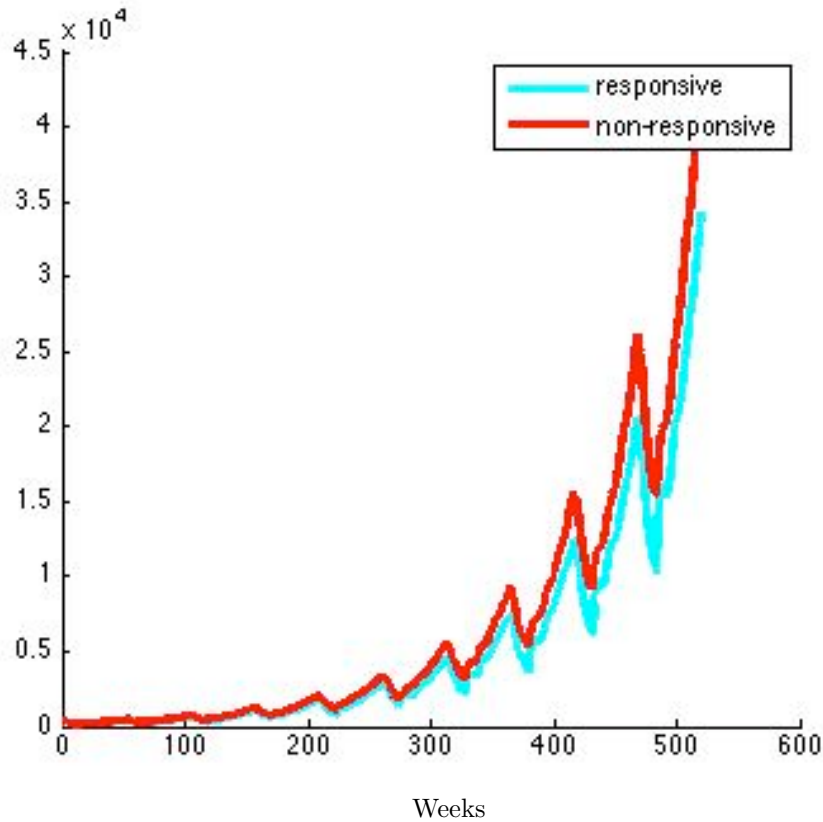


Figure 3.2: We use the following initial conditions: $J_r = 30, J_{nr} = 30, W_r = 30, W_{nr} = 30, B_r = 20, B_{nr} = 20, G_{r,r} = 30, G_{r,nr} = 30, G_{nr,r} = 30, G_{nr,nr} = 30, L_{r,r} = 30, L_{r,nr} = 30, L_{nr,r} = 30, L_{nr,nr} = 30$. We plotted the two phenotype populations over 5 years or 260 weeks. Both phenotype populations seem to be coexisting, with the non-responsive population increasing quicker than the responsive population. However, both populations seem to be growing to infinity. In this model we do not include a carrying capacity, which is probably the cause of this total population explosion. In our future work we will incorporate a carrying capacity term. In addition, we see both populations decreasing and increasing in a regular pattern; this seems to occur because of the time dependent death and pregnancy rate parameters. In this model, reproduction and winter increase death rate, look at assumptions 10 and 11 respectively. For particular values of parameters look at Tables 3.2 and 3.3.

Table 3.2: Table of Parameters

Parameters	value
ℓ	4
α	.29
β	.71

Table 3.3: Table of Parameters Dependent on Time

Parameters	Winter value	Spring value	Summer value	Fall value
$p_r(t)$	0	.25	.25	.25
$p_{nr}(t)$.25	.25	.25	.25
$d(t)$.195	.156	.156	.156
$q(t)$.195	.156	.156	.156
$r_{br}(t)$.0975	.078	.078	.078
$r_{bnr}(t)$.156	.078	.078	.078
$r_g(t)$.0975	.078	.078	.078
$r_l(t)$.0975	.078	.078	.078

Table 3.4: Table of Parameters for Extended Model

Parameters/Functions	Description	units	reference
ℓ	number of juveniles born from a gestating female (litter size)	$\frac{J}{\text{gestating}}$	[5]
α	proportion of responsive juveniles born from responsive gestating females impregnated by a non-responsive male	none	
β	proportion of responsive juveniles born from non-responsive gestating females impregnated by a responsive male	none	
$c(x, A)$	probability a adult female will come into contact with a responsive or non-responsive male	none	
$p_r(t)$	pregnancy rate of responsive breeding females	$\frac{1}{\text{week}}$	[1]
$p_{nr}(t)$	pregnancy rate of non-responsive breeding females	$\frac{1}{\text{week}}$	[1]
m	maturation rate of juveniles	$\frac{1}{\text{week}}$	[6]
f	maturation rate of weaned	$\frac{1}{\text{week}}$	[6]
k_g	maturation rate of gestating adults	$\frac{1}{\text{week}}$	[6]
k_l	maturation rate of lactating adults	$\frac{1}{\text{week}}$	[6]
$d(t)$	death rate of juveniles	$\frac{1}{\text{week}}$	[6]
$q(t)$	death rate of weaned	$\frac{1}{\text{week}}$	[6]
$r_{br}(t)$	death rate of responsive breeding adults	$\frac{1}{\text{week}}$	[7]
$r_{bnr}(t)$	death rate of non-responsive breeding adults	$\frac{1}{\text{week}}$	[7]
$r_g(t)$	death rate of gestating adults	$\frac{1}{\text{week}}$	[7]
$r_l(t)$	death rate of lactating adults	$\frac{1}{\text{week}}$	[7]

Chapter 4

Extended Model without Maturation Rates

This section describes the method in which we conducted MATLAB simulations of the extended model. We slightly modified the equations in the extend model to conduct simulations. We preserved the parameters and structure of the equations discussed previously, however we no longer include any maturation rates.

Previously the juvenile, weaned, gestating, and lactating classes all required maturation rates, now instead of including these rates we divide each stage class into age classes. Because we use a time step of a week and the juvenile, weaned, gestating, and lactating classes each require three weeks to mature, we have broken down each of these stage classes into three age classes, week 1, week 2, and week 3 [5]. Therefore for each time step a mouse will move to the next age class and after the the last age class, week 3, the mouse will mature or leave its respective class. Using this model in MATLAB allows us to ensure that mice are moving from one group to the next at the appropriate times.

4.1 The Model

Here we will only describe the changes made to the previous extended model difference equations. We will use slightly different notation than the extended model, for example $r1, nr$ lactating mice refers to week 1 responsive lactating mice (that have mated with a non-responsive male). The following describes the equations for the responsive phenotype, these are similar to the non-responsive equations.

The youngest stage class will be the $r1$ juvenile class, mice born will come into this class. These mice will either die or survive and mature to the $r2$ juveniles. $r2$ juveniles can either die or mature to the $r3$ juvenile class. The $r3$ juveniles will either die or mature into the $r1$ weaned mice.

The next stage class will be the $r1$ weaned class, these mice will either die or survive and mature to the $r2$ weaned class. $r2$ weaned mice can either die or mature to the $r3$ weaned class. The $r3$ weaned mice will either die or mature into the r breeding adults.

The r breeding class can either die, remain in the r breeding class, or become pregnant. This class is not broken down into age classes. This is the only class that can become pregnant; once an r breeding adult female is pregnant she becomes a r gestating adult.

The r gestating class is further divided into two groups, representing r gestating females that have become pregnant by r males (r, r gestating) or nr males (r, nr gestating). Both types of r gestating mice will each be broken down into three age classes and mice will either die or mature during each age class/time step. At the third age class, both $r3, r$ and $r3, nr$ gestating mice will either die or give birth and become either $r1, r$ or $r1, nr$ lactating mice respectively.

Both r, r and r, nr lactating mice are broken down into three age classes, and mice will either die or mature during each age class/time step. At the third age class, $r3, r$ and $r3, nr$, lactating mice will either die or return to a r breeding adults.

In this model, like the extended model, the second argument of the subscript displays the phenotype of the male that has mated with the female adult. In addition, a 1, 2, or 3 will appear for the juvenile, weaned, gestating, and lactating classes after the first argument of the subscript (the female phenotype). For example $G_{r1,r}$ denotes a week 1 responsive gestating female, which has mated with a male.

For our model we let J_r denote the responsive juvenile population and W_r denote the responsive weaned population. A_r denotes the responsive adult population which consists of: B_r , the responsive breeding population, $G_{r,r}$ and $G_{r,nr}$, the responsive gestating population, and $L_{r,r}$ and $L_{r,nr}$, the responsive lactating population. All other parameters remain the same except there are no longer any maturation rates. Refer to Tables 3.1 and 3.4 more detailed information on the variables and parameters.

4.2 Difference Equations for Extended Model without Maturation Rates

$$J_{r1} = \ell(1 - r_g(t))G_{r3,r} + \alpha\ell(1 - r_g(t))G_{r3,nr} + \beta\ell(1 - r_g(t))G_{nr3,r}$$

$$J_{r2} = (1 - d(t))J_{(r1)}$$

$$J_{r3} = (1 - d(t))J_{(r2)}$$

$$J_{nr1} = \ell(1 - r_g(t))G_{nr3,nr} + (1 - \alpha)\ell(1 - r_g(t))G_{r3,nr} + (1 - \beta)(1 - r_g(t))bG_{nr3,r}$$

$$J_{nr2} = (1 - d(t))J_{(nr1)}$$

$$J_{nr3} = (1 - d(t))J_{(nr2)}$$

$$W_{r1} = (1 - d(t))J_{r3}$$

$$W_{r2} = (1 - q(t))W_{r1}$$

$$W_{r3} = (1 - q(t))W_{r2}$$

$$W_{nr1} = (1 - d(t))J_{nr3}$$

$$W_{nr2} = (1 - q(t))W_{nr1}$$

$$W_{nr3} = (1 - q(t))W_{nr2}$$

$$\begin{aligned} B_r &= (1 - q(t))W_{r3} + (1 - r_l)L_{r3,r} + (1 - r_l)L_{r3,nr} - c(A_r, A)p_r(t)B_r \\ &\quad - c(A_{nr}, A)p_r(t)B_r - r_{br}(t)B_r + B_r \end{aligned}$$

$$\begin{aligned} B_{nr} &= (1 - q(t))W_{nr3} + (1 - r_l)L_{nr3,r} + (1 - r_l)L_{nr3,nr} - c(A_r, A)p_{nr}(t)B_{nr} \\ &\quad - c(A_{nr}, A)p_{nr}(t)B_{nr} - r_{bnr}(t)B_{nr} + B_{nr} \end{aligned}$$

$$G_{r1,r} = c(A_r, A)p_r(t)B_r$$

$$G_{r2,r} = (1 - r_g(t))G_{r1,r}$$

$$G_{r3,r} = (1 - r_g(t))G_{r2,r}$$

$$G_{r1,nr} = c(A_{nr}, A)p_r(t)B_r$$

$$G_{r2,nr} = (1 - r_g(t))G_{r1,nr}$$

$$G_{r3,nr} = (1 - r_g(t))G_{r2,nr}$$

$$G_r = G_{r,r1} + G_{r2,r} + G_{r3,r} + G_{r1,nr} + G_{r2,nr} + G_{r3,nr}$$

$$G_{nr1,r} = c(A_r, A)p_{nr}(t)B_{nr}$$

$$G_{nr2,r} = (1 - r_g(t))G_{nr1,r}$$

$$G_{nr3,r} = (1 - r_g(t))G_{nr2,r}$$

$$G_{nr1,nr} = c(A_{nr}, A)p_{nr}(t)B_{nr}$$

$$G_{nr2,nr} = (1 - r_g(t))G_{nr1,nr}$$

$$G_{nr3,nr} = (1 - r_g(t))G_{nr2,nr}$$

$$G_{nr} = G_{nr1,nr} + G_{nr2,nr} + G_{nr3,nr} + G_{nr1,r} + G_{nr2,r} + G_{nr3,r}$$

$$L_{r1,r} = (1 - r_l(t))G_{r3,r}$$

$$L_{r2,r} = (1 - r_l)L_{r1,r}$$

$$L_{r3,r} = (1 - r_l)L_{r2,r}$$

$$L_{r1,nr} = (1 - r_g(t))G_{r3,nr}$$

$$L_{r2,nr} = (1 - r_l)L_{r1,nr}$$

$$L_{r3,nr} = (1 - r_l)L_{r2,nr}$$

$$L_r = L_{r1,r} + L_{r2,r} + L_{r3,r} + L_{r1,nr} + L_{r2,nr} + L_{r3,nr}$$

$$L_{nr1,r} = (1 - r_g(t))G_{nr3,r}$$

$$L_{nr2,r} = (1 - r_l)L_{nr1,r}$$

$$L_{nr3,r} = (1 - r_l)L_{nr2,r}$$

$$L_{nr1,nr} = (1 - r_g(t))G_{nr3,nr}$$

$$L_{nr2,nr} = (1 - r_l)L_{nr1,nr}$$

$$L_{nr3,nr} = (1 - r_l)L_{nr2,nr}$$

$$L_{nr} = L_{nr1,nr} + L_{nr2,nr} + L_{nr3,nr} + L_{nr1,r} + L_{nr2,r} + L_{nr3,r}$$

$$A_r = B_r + G_r + L_r$$

$$A_{nr} = B_{nr} + G_{nr} + L_{nr}$$

$$A = A_r + A_{nr}$$

Chapter 5

Conclusions and Future Work

Our simulations or experiments of the normalized basic phenotype and age class model suggest the possibility of a fixed point, where $\underline{P} \neq \underline{0}$. Since we used the normalized basic model in our simulations showing coexistence we would like to know whether we can prove the existence and stability of a fixed point in $\bar{\Phi}$, from Equation 2.5. However linearizing this map is overly complicated; the partial derivatives of the Jacobian, $J_{\underline{P}}(J_r, J_{nr}, A_r, A_{nr})$, prove too difficult to produce by hand. Because of this, in the future we would like to use outward interval arithmetic and computational topology over the domain to prove the existence of a fixed point by verifying the hypothesis of Brouwer Fixed Point Theorem.

Theorem 1. *Brouwer Fixed Point Theorem* Let $\Delta \subset R^n$. If $\Theta : \Delta \rightarrow \Delta$ is continuous and $\Delta \approx D^n$, then there exists a fixed point.

By finding a fixed point in our normalized basic model, this biologically means that the white-footed mouse population will limit and remain at certain proportions of responsive and non-responsive phenotypes.

Another natural next step would be to look at a range of α and β values near to the values found that show coexistence. We can use computational topology to measure these two parameters in a more rigorous manner, to see if there exists a

range that produces coexistence among the two phenotypes. Also it is important to find out which α and β values make biological sense and if this is already known in the literature.

We would also like to include a density dependent death rate or carrying capacity in the extended model, to prevent population explosion. Using a carrying capacity would also be more biologically realistic since both phenotypes of mice are competing for resources, and therefore extensive population growth would increase death rate [1]. An example of a function we may use is a logistic function of the following:

$$death(\underline{P}) = \frac{1}{1 + b \cdot e^{-c\underline{P}}}$$

Here \underline{P} is the population in the extended model and a, b, c are parameters that we can alter to produce a death rate. We can see as $\underline{P} \rightarrow \infty$ then $d(\underline{P}) \rightarrow 1$, so the death rate would equal 1 or 100% of the population.

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