The Influence of Invasion Timing on Invasion Success as Predicted by an ODE Model of Competing Species in the Presence of Infectious Disease

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Honors Research Project

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ABSTRACT

We combine two standard mathematical biology models (SIR and Competing Species) to analyze the dynamics of two species who compete over resources and fight/spread disease. There is an invading species who is suddenly introduced to a native species at differing points in the native species' natural disease cycle. We simulate the natural disease progression for the native species and determine how the timing of the invading species impacts whether the invasive species can succeed in invasion (not die out). We explore cases when the invaders can and cannot get the disease with varying initial carrying capacities and initial disease prevalence.

Introduction

The model we study in this paper combines both the SIR model and the competing species model from classical biology. We first need to introduce background material on these two models.

SIR Models

One branch of models which pertain to diseases being spread between subpopulations are called the susceptible-infectious models (SI models) [2, 3]. The simplest model would have one subpopulation susceptible (not immune) to a disease and another subpopulation who has the disease and is spreading it. Those spreading the disease stay infected throughout their life and remain in contact with the susceptible subpopulation. For example, this model matches the behavior of a disease like herpes.

From this base model, we can add the possibility that an infected individual recovers from a disease. One standard version of these SIR models assumes lifetime immunity to those infected who recover, adding a third subpopulation to the model, the recovered individuals [2]. This adds a recovery subpopulation for individuals who recover from the disease and are thus immune from getting the disease again. One standard form of the model which does not take into account birth and death rates looks like

$$\frac{dS}{dt} = -\frac{\beta SI}{N}, \tag{1.1}$$

$$\frac{dI}{dt} = \frac{\beta SI}{N} - \gamma I, \tag{1.2}$$

$$\frac{dR}{dt} = \gamma I. \tag{1.3}$$

Here the dependent variables are the number of susceptible individuals (S), the number of infected individuals (I), and the number of recovered individuals (R). The parameters represent the following: the rate controlling how often a susceptible-infected contact results in a new infection (β) and the rate an infected recovers and moves into the resistant phase (γ). The parameter N represents the total population and equals S + I + R as these are the three subpopulations that all people in the population fall into. From the equations we see that $\frac{d}{dt}$N = ((S + I +R) = 0) and therefore N stays constant. Equation (1.1) states that the number of susceptible individuals decreases as susceptible individuals come into contact with the infected individuals and become infected. Equation (1.2) states that the number of infected individuals increases as susceptible individuals come into contact with infected individuals. However, the number of infected individuals decreases as infected individuals recover and become resistant to the disease. Equation (1.3) states that the recovered population increases as infected individuals become resistant to the disease. Since we do not account for births and deaths, the model typically starts with a large susceptible subpopulation, a small infected subpopulation, and no recovered subpopulation. However, as time progresses, eventually all of the susceptible subpopulation has been infected and then recovers, leaving only a recovered, immune subpopulation left (since in this model you cannot be reinfected).

If we modify equations (1.1)-(1.3) to include a birth rate ($\boldsymbol{\mu}$) and a death rate ($\boldsymbol{\nu}$) into the model and let $\boldsymbol{\mu} = \boldsymbol{\nu}$ to keep the total population constant [2], we get the model

$$\frac{dS}{dt} = \boldsymbol{\mu}\mathrm{N} - \frac{\beta SI}{N} - \boldsymbol{\nu}\mathrm{S}, \tag{1.4}$$

$$\frac{dI}{dt} = \frac{\beta SI}{N} - \gamma I - \boldsymbol{\nu} I, \tag{1.5}$$

$$\frac{dR}{dt} = \gamma I - \boldsymbol{\nu} R. \tag{1.6}$$

Here new births provide more susceptible individuals to the population, sustaining an epidemic or allowing new individuals to get and spread the disease throughout the population. For example, this is the case when diseases are endemic to a region.

Another standard recovery model is the SIRS model. In this model we assume that an individual's immunity may wane over time. This allows recovered individuals to return to a susceptible state. This is the case with a disease like influenza where getting one year's strand might protect you for that season, however, next season it provides no benefit. One standard form of the SIRS model is

$$\frac{dS}{dt} = \frac{\beta SI}{N} + \zeta R , \tag{1.7}$$

$$\frac{dI}{dt} = \frac{\beta SI}{N} - \gamma I, \tag{1.8}$$

$$\frac{dR}{dt} = \gamma I - \zeta R. \tag{1.9}$$

Here the only new parameter is the loss of immunity rate (ζ). This model predicts oscillating subpopulations of infected and susceptible individuals as individuals go from being infected, to having temporary immunity, to being susceptible again. Note that because there is no permanent resistance built up over time, individuals can be reinfected over and over again.

In any of the versions of the model just described, disease dynamics will reach a steady state or period where S, I, and R are not changing as time increases. This steady state solution can be found when $\frac{dS}{dt} = 0$, $\frac{dI}{dt} = 0$, and $\frac{dR}{dt} = 0$.

Competing Species Model

Another class of classical models in mathematical biology describes when two or more species compete over common resources. In some versions of these models, competition has two forms: interspecies and intra-species interactions, i.e., between individuals in different species and between individuals in the same species. In the absence of the other species, each species grows according to a logistic equation [4]. In logistic growth, a species grows until it hits the carrying capacity, or the maximum number of individuals that the environment can carry. Logistic growth can be modeled as

$$\frac{dN}{dt} = rN\left[1 - \frac{N}{K}\right], \tag{1.10}$$

where N(t) is the size of the population at time t, r is the intrinsic growth rate (the difference between the birth and death rates), and K is the carrying capacity. However, the presence of one species lowers the per capita growth rate of the other species since they compete for resources. Now if we extend this logistic growth model to include two species with competition effects, we get the following system

$$\frac{dN_1}{dt} = r_1 N_1\left[1 - \frac{N_1}{K_1} - \frac{N_2 c_{12}}{K_1}\right], \tag{1.11}$$

$$\frac{dN_2}{dt} = r_2 N_2 \left[1 - \frac{N_2}{K_2} - \frac{N_1 c_{21}}{K_2} \right]. \tag{1.12}$$

Here the parameters and variables are the following: N_i is the size of the population of species i at time t, r_i is the intrinsic growth rate of species i, K_i is the carrying capacity of species i, and c_{ij} is the competition coefficient which describes the effect on species i of competition with species j. Intra-specific competition, or the damage done by species i on itself, is described by $1/K_i$. Not only does the species affect its own kind, but the other species competes so that the growth of species i is hindered by species j, as seen in the third terms in both equations. As we can see, if for equation (1.11) $N_2 = 0$ (this means that the population of species 2 is 0 and has no effect on the population of N_1 with regards to our competition effects), we get the logistic equation

$$\frac{dN_1}{dt} = r_1 N_1 \left[1 - \frac{N_1}{K_1} \right],$$

which is the same as (1.10).

The Invadability Model

There is a growing body of research which combines both the competing species model and the SIR models [1, 5, 6, 7]. The model we consider comes from Turner and Bowers [1]. The Turner and Bowers model has the form

$$\frac{dH_1}{dt} = r_1 H_1(1 - c_{11}H_1 - c_{12}H_2) - \alpha_1 Y_1, \tag{2.1}$$

$$\frac{dY_1}{dt} = \beta_{11}(H_1 - Y_1)Y_1 + \beta_{12}(H_1 - Y_1)Y_2 - \Gamma_1 Y_1, \tag{2.2}$$

$$\frac{dH_2}{dt} = r_2 H_2(1 - c_{21}H_1 - c_{22}H_2) - \alpha_2 Y_2, \tag{2.3}$$

$$\frac{dY_2}{dt} = \beta_{21}(H_2 - Y_2)Y_1 + \beta_{22}(H_2 - Y_2)Y_2 - \Gamma_2 Y_2. \tag{2.4}$$

The variable H_i represents the total population of species i (either species 1 or species 2). The variable Y_i represents the total infected population of species i (either species 1 or species 2). The difference between H_i and Y_i is the total healthy population of species i. The parameters are positive constants and represent the following: r_i is the intrinsic per capita rates of population growth, c_{ij} is the competition coefficients, α_i is the per capita rates of pathogen-induced mortality, β_{ij} is the disease-transmission coefficients, Γ_i is the per capita net rates of loss of infected individuals, which includes the effects of natural mortality, pathogen-induced mortality, and recovery. In (2.1)-(2.4), all variables have been rescaled and hence all variables and parameters are dimensionless.

An important thing to notice with the disease component of the model is that the disease can be transmitted within a species or between species. The disease-transmission coefficients (β_{ij}) dictate how easily the infection can spread in either scenario. Depending on how these parameters change, either species could be more or less susceptible to getting or spreading the disease both amongst themselves or to the other species. This is important as Turner and Bowers use the model to explore invadability with the presence of disease. Invadability simply means how the introduction of another species changes both the original species population and the "invading" (the newly introduced species') population. The basic question is whether the introduction of the new species allows both species to coexist or whether one species dies out and the other survives.

Turner and Bowers have found theoretical results to see when these species coexist or whether one species dies out and the other survives. We present these results to have a theoretical understanding of the impact of invadability. Firstly, consider the case where there is no disease in the model and only competition occurs. Since we do not consider disease, the model simplifies to a competing species model, however, the results are presented in the context of invadabilty. We utilize equations 2.1 and 2.3 and set $Y_i = 0$ since the Y_i variables describe disease in the model. Consider the case when species 2 is invading species 1 at equilibrium (K_1). The average lifetime of an individual in species 2 is $1/b_2$ where b_2 is the per capita death rate of species 2. Species 2 invading species 1 can be derived from equation 2.3: ignoring the H_2 term (since it describes species 2 encountering species 2) and noticing that H_1 is the population of species 1 (which is at equilibrium K_1), we get the average increase in population for species 2 when invading species 1 at equilibrium is average lifetime multiplied by the growth rate or

$$\frac{r_2(1 - c_{21}K_1)}{b_2}. \tag{2.5}$$

An invasion of species 1 requires the population growth rate to be greater than the death rate for species 2 ($r_2 > b_2$) since if the death rate is greater than the growth rate, the species will die out. So, species 2 can invade if and only if $(1 - c_{21}K_1) > 0$. If instead of invading species 1 (with density K_1) the individual encounters its own species (with density K_2), the average increase in population is

$$\frac{r_2(1 - c_{22}K_2)}{b_2}, \tag{2.6}$$

from similar construction as (2.5). At equilibrium this must equal zero (this is the definition of equilibrium) and we obtain the provision $c_{22}K_2 = 1$. We can write the inequality

$c_{21}K_1 < c_{22}K_2$ since $c_{22}K_2 = 1 > c_{21}K_1$ and now we yield invadability results: Species 1 is invadable by species 2 when the interspecific force of competition for the invader ($c_{21}K_1$) is less than the interspecific force ($c_{22}K_2$) for the species invaded. This applies the other way when species 2 is invadable by species 1 ($c_{12}K_2 < c_{11}K_1$).

We now consider all of the possible combinations of invadability and their required invadability forces (the c_{ij}), and create a table to compare when species 1 is invadable by species 2 and vice versa. As we can see, there are four possible outcomes in our model depending on each species' invadable and not invadable forces (these are the c_{ij}). Three of those outcomes involve one species surviving and the other species being eliminated. However, if both species have weak invadability forces they can coexist.

Table 1.1: Cases for Invadability in Purely Competitive Interactions [1]

Case	Species 1	Species 2	Outcome
1	Not invadable $force_{21} > force_{22}$	Invadable $force_{12} < force_{11}$	Species 1 survives and species 2 is eliminated.
2	Invadable $force_{21} < force_{22}$	Not invadable $force_{12} > force_{11}$	Species 1 is eliminated and species 2 survives.
3	Not invadable $force_{21} > force_{22}$	Not invadable $force_{12} > force_{11}$	Species 1 survives and species 2 is eliminated. **OR** Species 1 is eliminated and species 2 survives. (Outcome Depends on Initial Densities.)
4	Invadable $force_{21} < force_{22}$	Invadable $force_{12} < force_{11}$	Species 1 and species 2 coexist.

Employing similar techniques as the purely competitive case above, we can look at purely infective interaction by letting the competition coefficients $c_{ij} = 0$. If we follow the same analysis as above we would yield a similar conclusion in regards to invadability as in the only

competitive case. The difference in the outcome simply changes from “species i survives and species j is eliminated” to “species i survives and supports the pathogen and species j is eliminated.” Of course, for case 4 this changes to “species 1 and 2 coexist and support the pathogen.”

Simulations

Using the Turner and Bowers model, we run simulations to see how invadability changes depending on what point the native species is at in their natural disease cycle. We consider two cases: One where the invaders can get the disease and another case where the invaders cannot get the disease. We first get initial condition values from the natural disease cycle to utilize for the two cases of invasion. We run these simulations in MATLAB and include a coding section for the natural disease cycle simulations, the case when the invader cannot get the disease, and the case when the invader can get the disease. We determine the influence of invasion time for each case and come up with final remarks.

The paper “Effects Of Invasion Timing In A One-Dimensional Model Of Competing Species With An Infectious Disease” [8] is closely related to this paper. In [8] the author considers a more complex case of simulating natural disease progression where spatial dimension (where species 1 and 2 are located) matters. This leads to a model that has the form of a system of coupled partial differential equations. This paper utilizes a less complex ODE model, eliminating spatial dependencies. However, both [8] and this paper have the same theme of attempting to answer the importance of disease timing in invadability.

Natural Disease Cycle Simulations

Our goal is to see how invadability changes depending on the time the invasion occurs. Firstly, we consider the case where only the native species is alive and no invasion takes place at all. We can calculate the total population and infected population of varying times throughout the natural disease cycle for the native species. Later, we use these results to simulate how the introduction of another species during these different periods in the cycle will affect whether either species will die out or if they will coexist.

Since no invasion is taking place, we will only have terms relating to the native species. From our Turner and Bowers model (2.1)-(2.4), letting H_2 and Y_2 equal 0 (since we are only interested in the natural disease cycle of the native species) yields

$$\frac{dH_1}{dt} = r_1 H_1(1 - c_{11}H_1) - \alpha_1 Y_1, \tag{3.1}$$

$$\frac{dY_1}{dt} = \beta_{11}(H_1 - Y_1)Y_1 - \Gamma_1 Y_1. \tag{3.2}$$

Recall that H_1 represents the total population of species 1 and Y_1 represents the total infected population of species 1. The difference between H_1 and Y_1 is the total healthy population of species 1. In order to simulate the natural disease cycle for the native species as well the invasions by the invading species, we obtain parameter values from Turner and Bowers [1] and utilize these values unless otherwise stated. These parameter values are given in table 2.1. Recall that (2.1)-(2.4) are rescaled so that all the parameters whose values are given in table 2.1 are dimensionless.

Table 2.1: Parameter Values

Parameter	Definition	Value
r_1	The population growth rate (native)	1
c_{11}	Competitive effect of natives on natives	0.142857
c_{12}	Competitive effect of natives on invaders	0.083333
α_1	Pathogen-induced mortality rate (native)	2
β_{11}	Disease-transmission of natives on natives	0.75
β_{12}	Disease-transmission of natives on invaders	0.4
Γ_1	Loss of infected individuals rate (native)	2
r_2	The population growth rate (invader)	0.2
c_{21}	Competitive effect of invaders on natives	0.125
c_{22}	Competitive effect of invaders on invaders	0.090909
α_2	Pathogen-induced mortality rate (invader)	4
β_{21}	Disease-transmission of invaders on natives	0.3
β_{22}	Disease-transmission of invaders on invaders	0.5
Γ_2	Loss of infected individuals rate (invader)	1

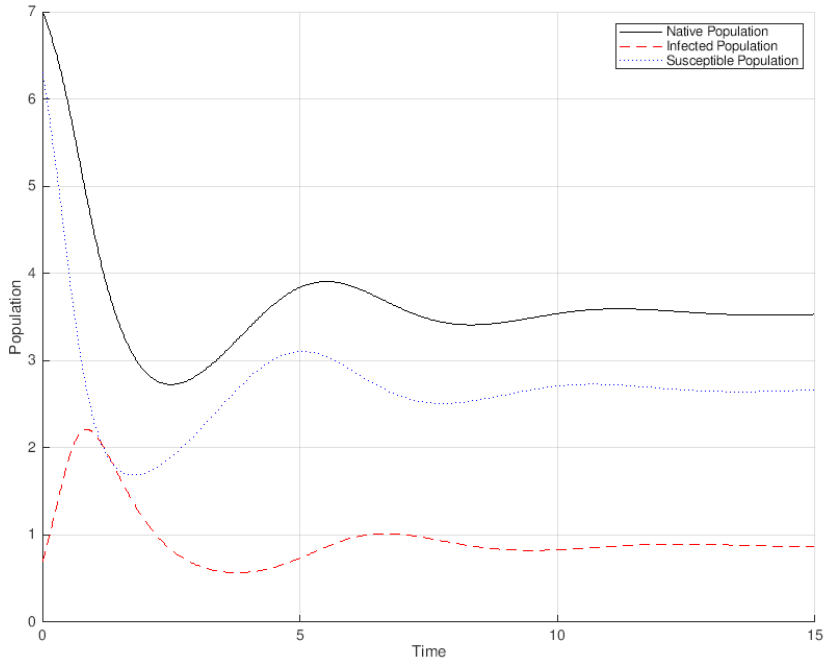


Figure 2.1: Disease Cycle

The results from a simulation with initial conditions $H_1(0) = 7$ and $Y_1(0) = .7$ are shown in figure 2.1. For times 1 through 8 we notice interesting changes in the population. The native population starts at the initial starting population of 7 (our $H_1(0) = 7$ initial condition) and decreases to a population of slightly below 3 by time 3. The native species' population then oscillates between values of 3-4 and levels off as time increases. The susceptible population follows a similar trend. However, it starts at a slightly lower initial population and has a lower minimum population value that occurs slightly earlier than the healthy population. Finally, the infected population increases for the first two units of time. However, it decreases and has decaying oscillations. This is due to the susceptible population being quickly infected. However, the infected population increases and with fewer susceptible individuals, the infected population

dies off and gives a recovery period for the susceptible population. After approximately time 8 the population has small oscillations but remains roughly at the carrying capacity. These minor oscillations occur as time increases forever and so, since there is little change beyond time 8, we will simply consider the population sizes at times 1, 2, 3,…, 8 for the initial conditions in our invasion simulations.

We consider a total of 9 cases for our initial conditions. We consider 3 initial starting populations for the native species and 3 initial infected rates. For the initial starting populations we consider 3.5, 7, and 14 since these correspond to K/2, K, and 2K where K is the carrying capacity ($K = 1/c_{11}$ or $K = 7$ for this set of parameters). We also consider an initial disease prevalence of 5%, 10%, and 20%. For figure 2.1, we utilized values $H_1(0) = 7$ and $Y_1(0) = .7$ to show that only values 1 through 8 have changes that deviate far from the carrying capacity, however, any combination would suffice to display this feature. We display the results of these natural disease cycle simulations, which are the population sizes at times 1 through 8, for these 9 initial conditions in tables 2.2-2.4. The top number represents the total population at that time and the bottom number represents the infected population at that time.

Table 2.2: Disease Cycle Simulations for 5% Initial Disease Prevalence (total population above diseased population)

Time	1	2	3	4	5	6	7	8
K = 3.5	4.6416 0.4285	4.6254 1.1550	3.6619 1.3069	3.1610 0.9403	3.2517 0.7419	3.5418 0.7424	3.7028 0.8509	3.6488 0.9334
K = 7	5.1449 2.0824	3.1144 1.3815	2.7839 0.7425	3.2243 0.5805	3.7417 0.6842	3.8775 0.9132	3.6548 1.0095	3.4482 0.9318
K = 14	4.1111 3.1741	2.1798 0.9235	2.4796 0.4241	3.4092 0.3869	4.1589 0.6429	4.1097 1.0674	3.5815 1.1097	3.3087 0.9091

Table 2.3: Disease Cycle Simulations for 10% Initial Disease Prevalence (total population above diseased population)

Time	1	2	3	4	5	6	7	8
K = 3.5	4.2789 0.6435	4.1520 1.1167	3.5477 1.1267	3.2746 0.8970	3.3692 0.7780	3.5650 0.7935	3.6507 0.8705	3.6009 0.9161
K = 7	4.4755 2.1656	2.8682 1.1545	2.8289 0.6549	3.3702 0.5741	3.8384 0.7340	3.8553 0.9643	3.5883 1.0056	3.4198 0.9062
K = 14	3.6608 2.8673	2.0917 0.8161	2.5128 0.3876	3.4951 0.3774	4.2262 0.6649	4.1029 1.1019	3.5442 1.1077	3.2918 0.8951

Table 2.4: Disease Cycle Simulations for 20% Initial Disease Prevalence (total population above diseased population)

Time	1	2	3	4	5	6	7	8
K = 3.5	3.7360 0.8244	3.6960 0.9422	3.5410 0.9420	3.4651 0.8827	3.4925 0.8470	3.5488 0.8522	3.5718 0.8743	3.5575 0.8863
K = 7	3.7864 2.0325	2.6620 0.9372	2.9005 0.5707	3.5374 0.5707	3.9360 0.7946	3.8200 1.0157	3.5177 0.9955	3.3946 0.8787
K = 14	3.2680 2.5645	2.0159 0.7209	2.5468 0.3539	3.5791 0.3672	4.2922 0.6857	4.0969 1.1349	3.5094 1.1057	3.2758 0.8820

The data in tables 2.2 to 2.4 display several noteworthy trends. Firstly, we can see that the time with the lowest total population differs slightly depending on the carrying capacity. Time 4 has the lowest total population for K = 3.5, time 2 for K = 14, and times 2 and 3 for K = 7. Thus a lower carrying capacity allows the total population to reach its lowest value at a later time than a greater carrying capacity can. We can see initial disease prevalence plays a role in total population rate with those having higher initial disease prevalence having lower total populations at both the beginning and ending times but having greater total populations during the middle of the disease cycle.

Now that we have our native species' disease cycle for varying initial conditions, we can see how timing affects invadabilty. We consider two different cases. Firstly, we consider the case when only the native species can get the disease. We then consider the case when both the native species and the invaders can get the disease. We compare how these two cases differ and offer remarks in both scenarios.

Case when Invaders cannot get the Disease

In the case when the invaders cannot get the disease we set $Y_2 = 0$ in 2.4 since this is the size of the subpopulation of the diseased invaders. Thus we are left with the model

$$\frac{dH_1}{dt} = r_1 H_1(1 - c_{11}H_1 - c_{12}H_2) - \alpha_1 Y_1, \tag{3.3}$$

$$\frac{dY_1}{dt} = \beta_{11}(H_1 - Y_1)Y_1 - \Gamma_1 Y_1, \tag{3.4}$$

$$\frac{dH_2}{dt} = r_2H_2(1 - c_{21}H_1 - c_{22}H_2). \quad (3.5)$$

To run our simulations we do the following: Firstly, we plug in our disease cycle values from tables 2.2-2.4 for our initial conditions for the native species to simulate that they are getting invaded by the invading species at the corresponding times in the disease cycle. For our third initial condition (since we have a system of 3 ordinary differential equations), we utilize whatever the original initial population size was for the native species. Thus we assume the invaders total population size is equivalent to the original population size of the native species' (either k = 3.5, 7, or 14).

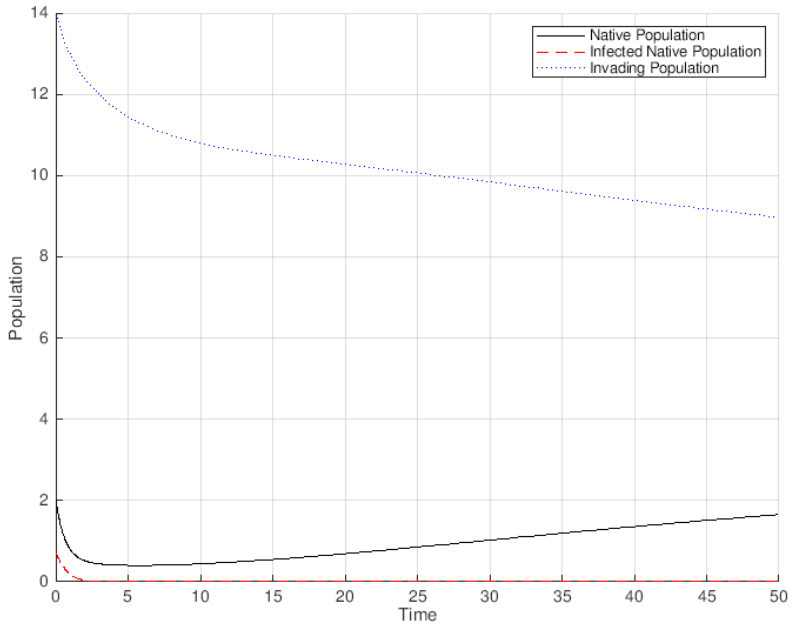


Figure 2.2: Simulation when Invaders are Immune

If we run every simulation from tables 2.2-2.4 we notice that for all but three cases, both species survive (neither species dies out) and are able to coexist. Figure 2.2 displays an example when both species survive using the values carrying capacity 14, disease prevalence = 20%, and the invasion occuring at time = 2 in the natural disease cycle. We can see that the invading

population decreases to its steady solution while the native species is able to recover and increase to its steady solution. The disease dies out quickly (by time = 3), as indicated by the dashed curve in the lower left corner of figure 2.2.

To analyze the effect of invasion timing we utilize the following approach: We consider times 1, 4, and 8 from tables 2.2-2.4 for each carrying capacity and display the simulations to see how they differ. We choose these three times since these approximately correspond to the beginning, middle, and end of the possible "interesting" invasion times. The different carrying capacities will yield significant changes to the population dynamics. However, our results indicate that the initial disease prevalence does not make significant changes to the population dynamics. So, we will not discuss these changes until mentioning how carrying capacity changes the results of the invasions. Thus we will display a total of nine graphs consisting of the carrying capacities 3.5, 7, and 14 with each carrying capacity at times 1, 4, and 8. Then we compare how initial disease prevalence affects results. A 5% initial disease prevalence will be assumed for all simulations but the final initial disease prevalence case. There we compare the 5% initial disease prevalence to 20% initial disease prevalence to compare how they differ.

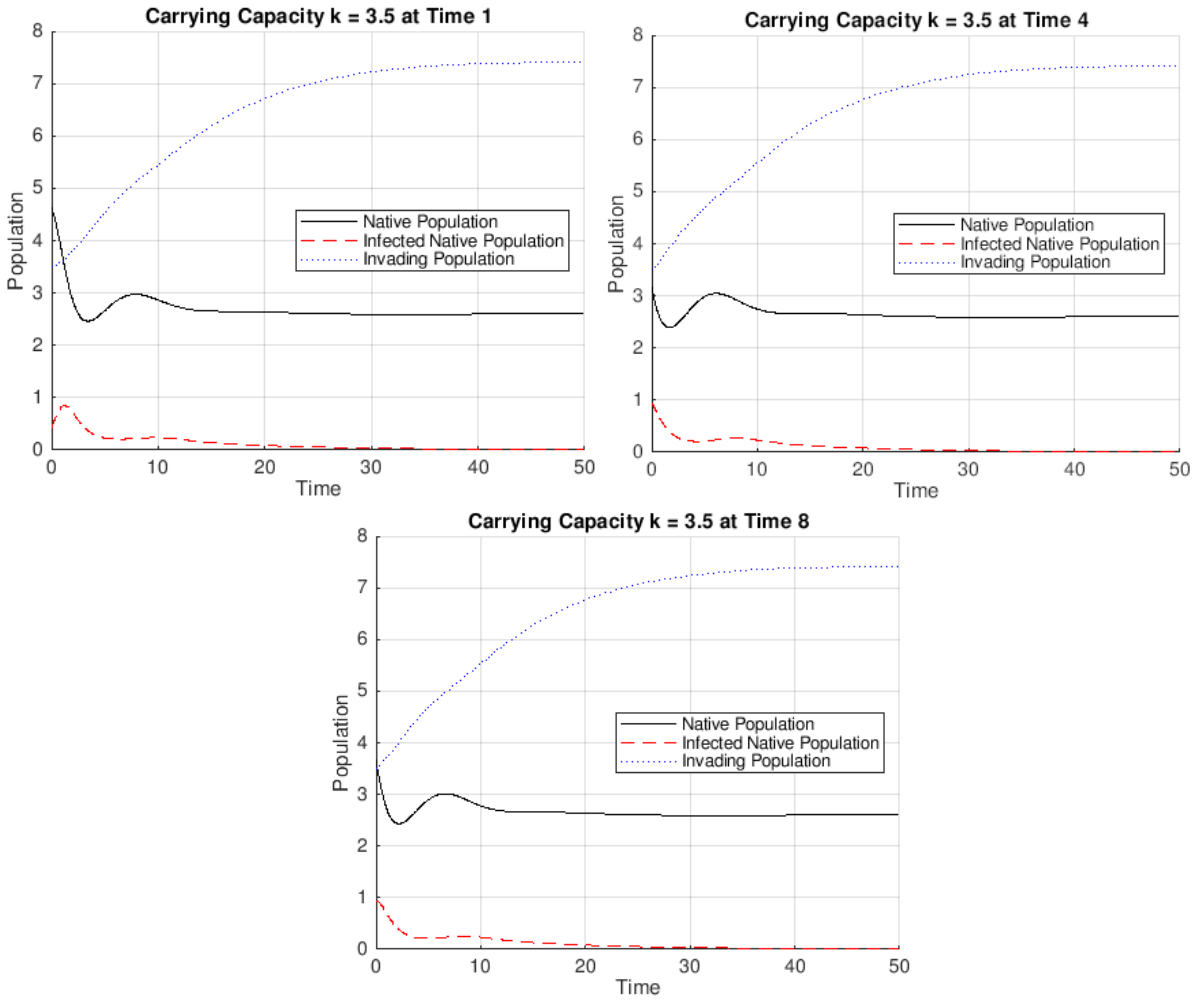
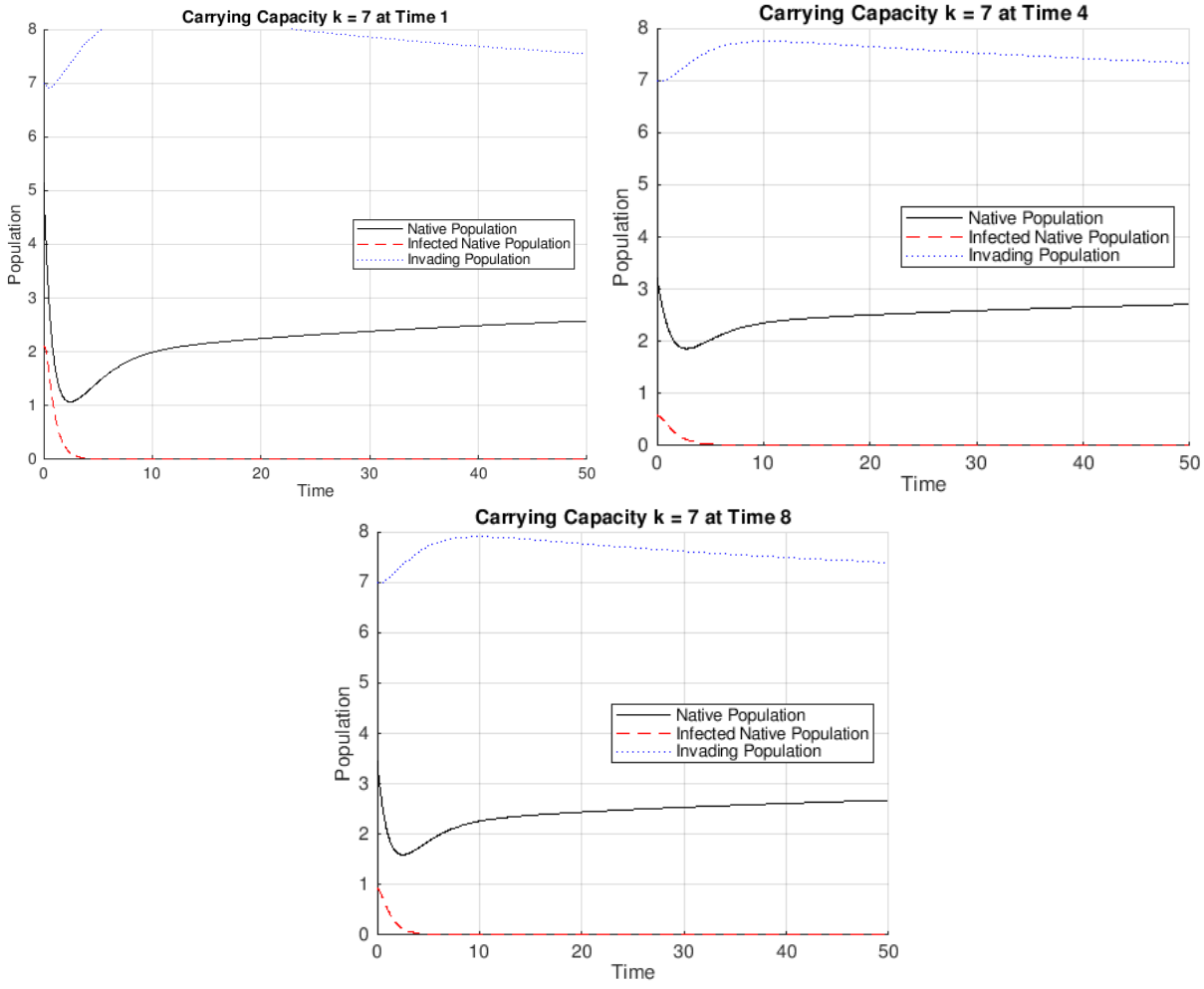


Figure 2.3-2.5 (Clockwise): Simulations for K = 3.5 at Times 1, 4, and 8

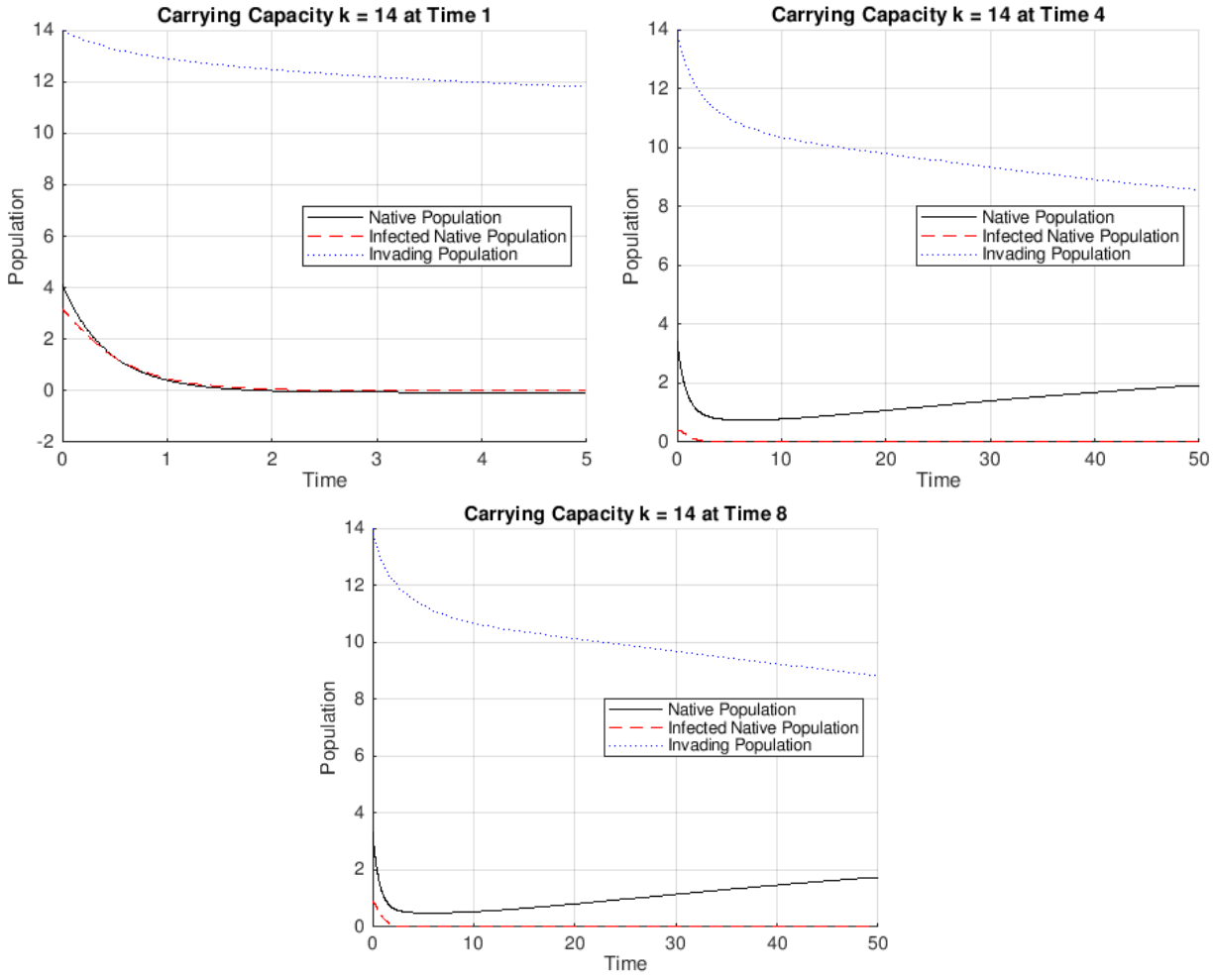
In figures 2.3-2.5 we display simulations for times 1, 4, and 8 with a carrying capacity of 3.5 and initial disease prevalence of 5% (table 2.2). The first and most noticeable difference between these simulations at different times is the starting population for the native population. At time 1 the native population starts in between 4 and 5, at time 4 it starts slightly greater than 3, and at time 8 it starts between 3 and 4. All three simulations have a dip in native population at slightly different times depending on the timing of the invasion. However, all simulations then

follow a similar increase and decrease in native population until the native population stables off with significantly smaller oscillations. The invading population increases similarly in all 3 simulations, appropraching some steady state. Finally, the infected native population follows similarly to the native population where the initial populations are different. However, at some slightly different time they have similar decreasing and then increasing oscillations and continue oscillating downwards to a smaller population until they reach a population of 0.



Figures 2.6-2.8 (Clockwise): Simulations for K = 7 at Times 1, 4, and 8

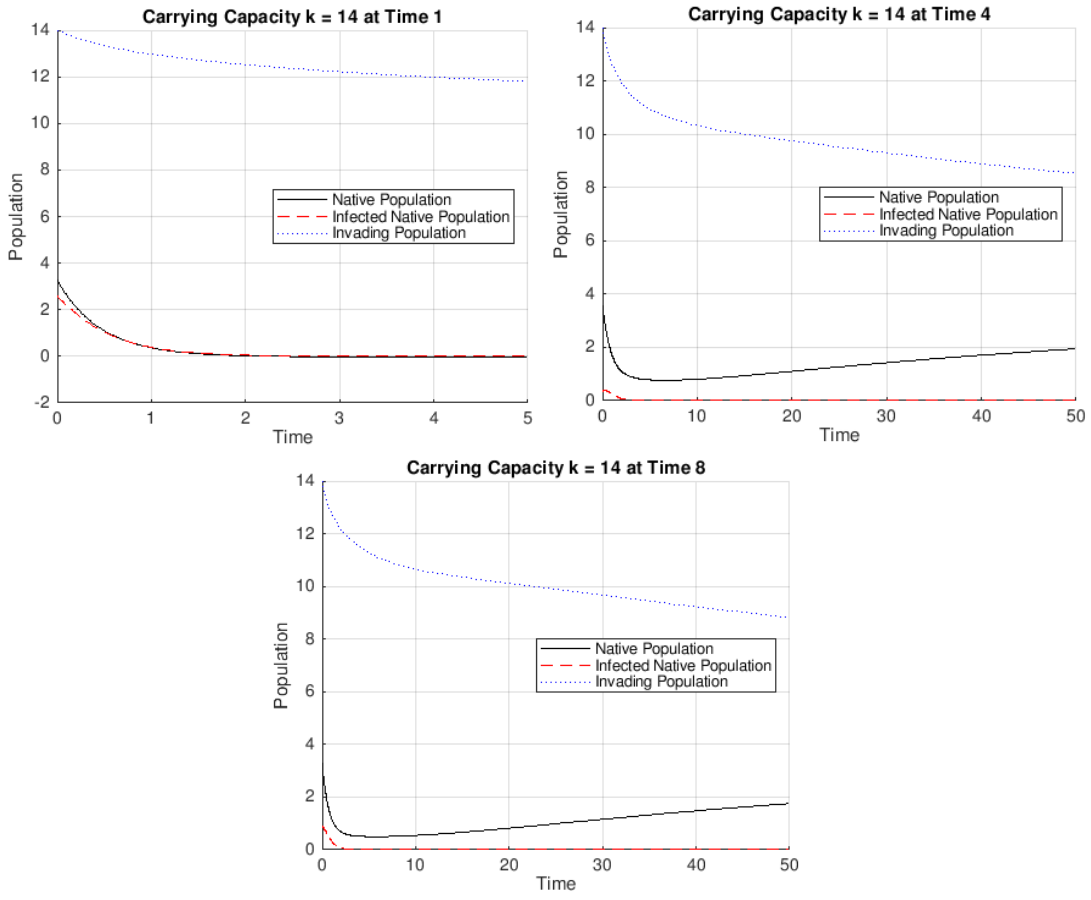
In figures 2.6-2.8 we display simulations for times 1, 4, and 8 with a carrying capacity of 7 and initial disease prevalence of 5% (table 2.2). A similar pattern exists here as with the case where the carrying capacity was 3.5. The invading population approaches a steady state in a similar manner in all three simulations. The main difference between the native populations in these three simulations is the starting population and its drop to the population value between 1 and 2 (and how much it differs). The general shape of the curve is similar as is the value it appears to approach, however, the initial population determines how much the native population will drop to (a larger initial native population means a lower minimum population as the first drop). Finally, the infected native population starts at different populations between the simulations. However, they all drop to 0 quickly and have similarly shaped curves (a larger initial native infected population will make the time when they reach a population of 0 happen sooner).



Figures 2.9-2.11 (Clockwise): Simulations for k = 14 at Times 1, 4, and 8

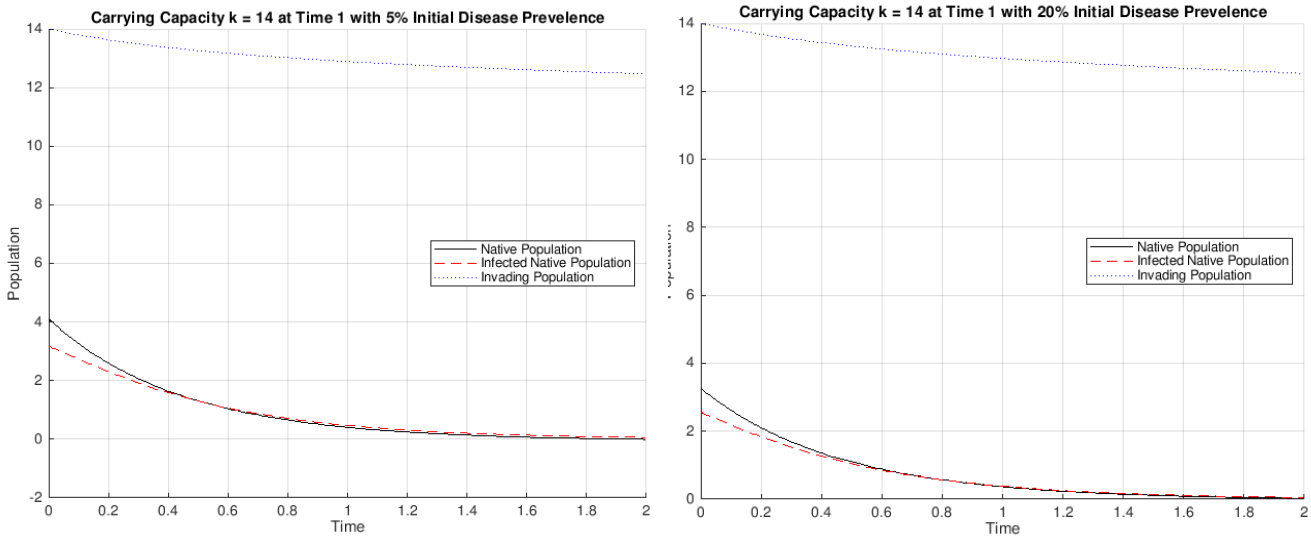
In figures 2.9-2.11 we display simulations for times 1, 4, and 8 with a carrying capacity of 14 and initial disease prevalence of 5% (table 2.2). Here we notice a very interesting result. For the simulation at time 1, the native population dies out, however, for the time 4 and time 8 simulations, the native species survives and they have similar curves as in the previous cases with carrying capacity 3.5 and 7. The infected native population dies out quickly in all three simulations. Finally, the invading population is approaching similar values in the time 4 and time

8 simulations. However, due to the lack of a competing species after it dies out, the time 1 simulations invading population will approach a greater value than in the other two cases.



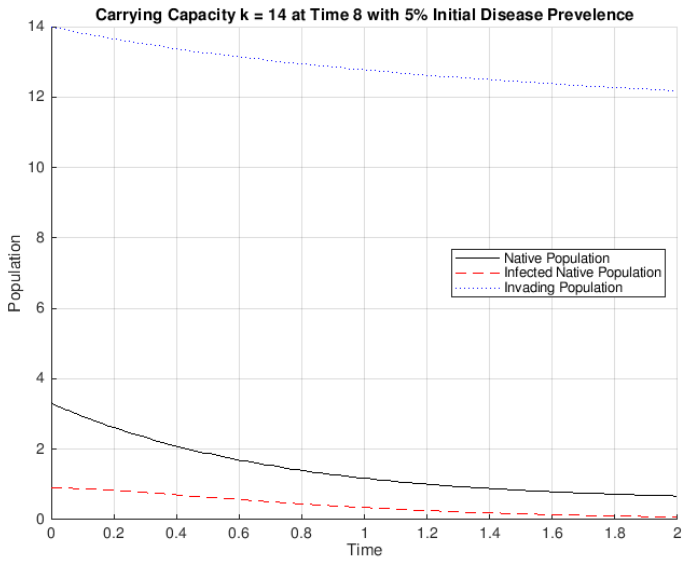
Figures 2.12-2.14 (Clockwise): Simulations for k = 14 at Times 1, 4, and 8 with initial disease prevalence of 20%

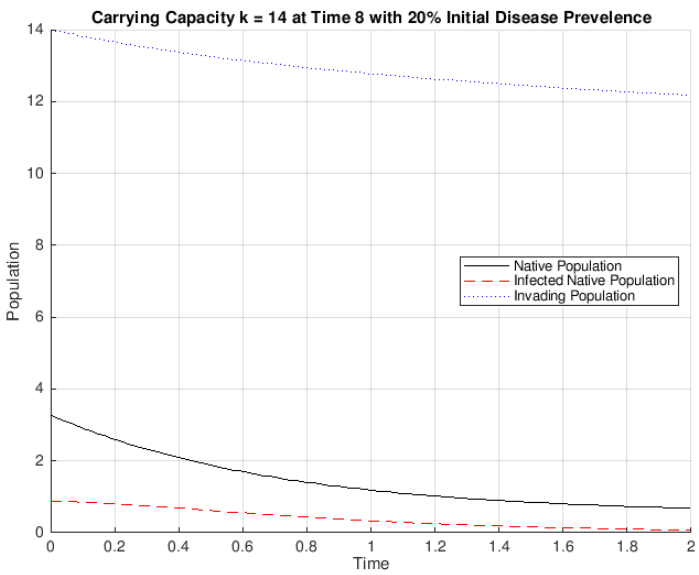
We can see no noticable effects of the initial disease prevalence comparing the 20% initial disease prevalence at carrying capacity 14 (Figures 2.12-2.14) with the initial disease prevalence of 5% with carrying capacity 14 (Figures 2.9-2.11) with this window range. To better compare the changes, we look at times 1 and 8 at a smaller time interval (time = 0-2).



Figures 2.15-2.16 (Left then Right): Simulations for k = 14 at Time 1 with initial disease prevalence of 5% and 20%

With this smaller time interval in figures 2.15-2.16 we can see the change that occurs. With the 5% initial disease prevalence the native starting population is larger than the 20% native population, as is the infected native population. However the underlying curve does not seem to change as in both cases both the native and infected native population drop to a population of 0 quickly.





Figures 2.17-2.18 (Left then Right): Simulations for k = 14 at Time 8 with initial disease prevalence of 5% and 20%

In figures 2.17-2.18 the differences are hardly noticeable. The native populations differ by less than .2 at all times on this interval. The populations follow similar trends for both initial disease prevalences. Therefore, for cases where the initial total population and diseased population for the native populations disease cycle are similar, the differences between initial disease prevalence is minimal. However, there are more profound changes for native population disease cycles which have a greater difference in their values.

Case when Invaders can get the Disease

In the case when the invaders are immune, we use the entire Turner and Bowers model (2.1)-(2.4). We use the same initial conditions as in the previous subsection, when the invaders cannot get the disease, except we add an initial diseased population rate for the invading species (since now there are 4 ordinary differential equations and we need a 4th initial condition). We use the same initial disease population rate as the original native species' initial disease population rate (5%, 10%, and 20%). This is similar to how we utilized whatever the original initial population size was for the native species for the previous case when the invaders cannot get the disease.

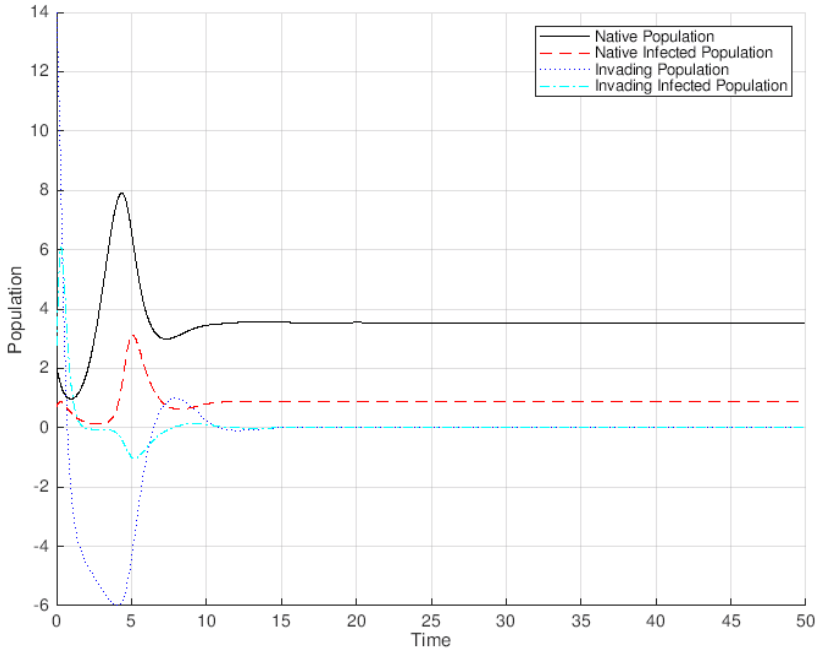
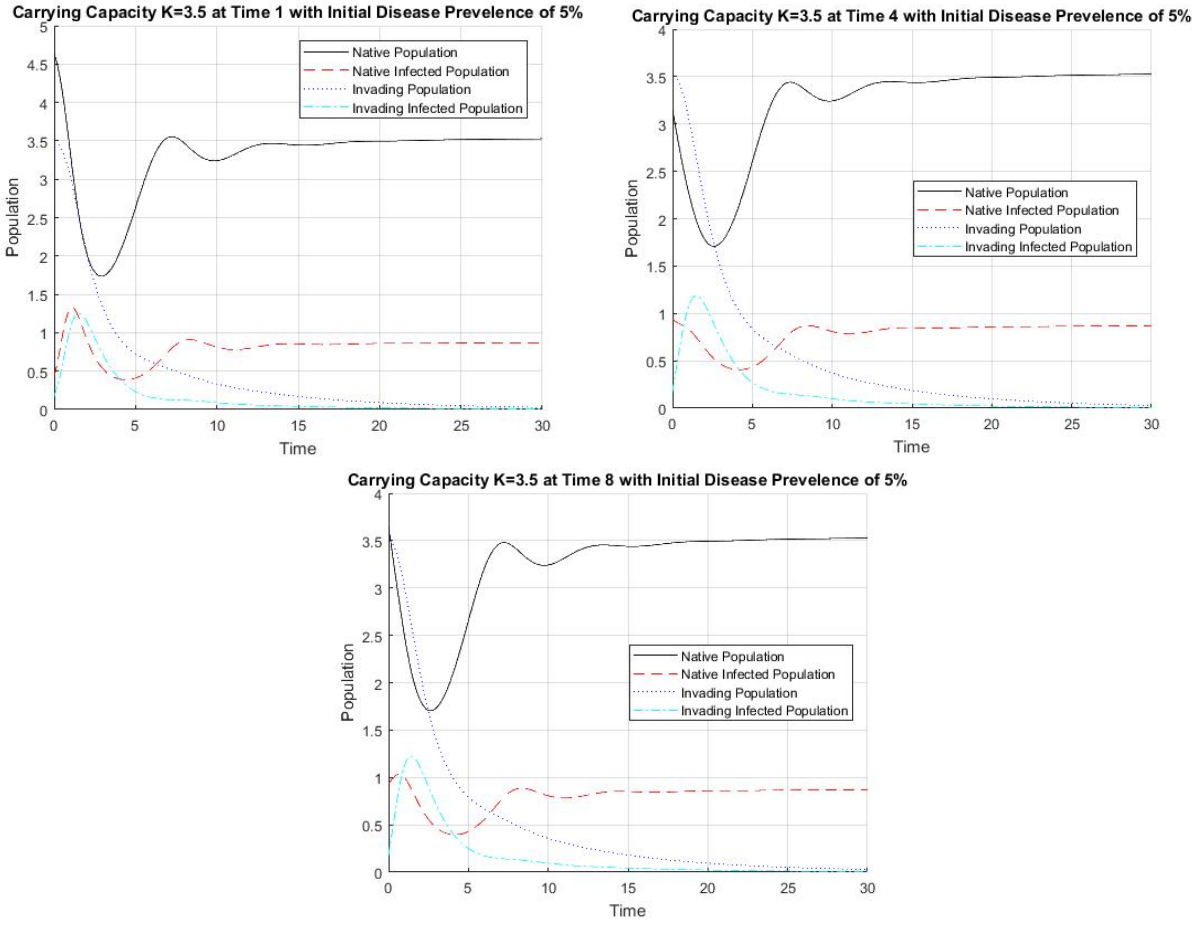


Figure 2.19: Simulation when Invaders can get Disease

Figure 2.19 displays an example when the native species is at its lowest total initial population (Carrying Capacity = 14, Disease Prevalence = 20%, time = 2). We can see that the invading population decreases significantly within several units of time while the native species

recovers from the low initial population. Obviously populations cannot be negative and we ignore the invading population after it reaches a total population of 0 (it cannot recover from a population of 0). However, the model still relies on these below 0 values and thus, they are still important. However, we decided to change a parameter value to avoid getting negative populations. For the remainder of this paper we let $\alpha_2 = 1$. This will give us positive population values for all our considered cases.

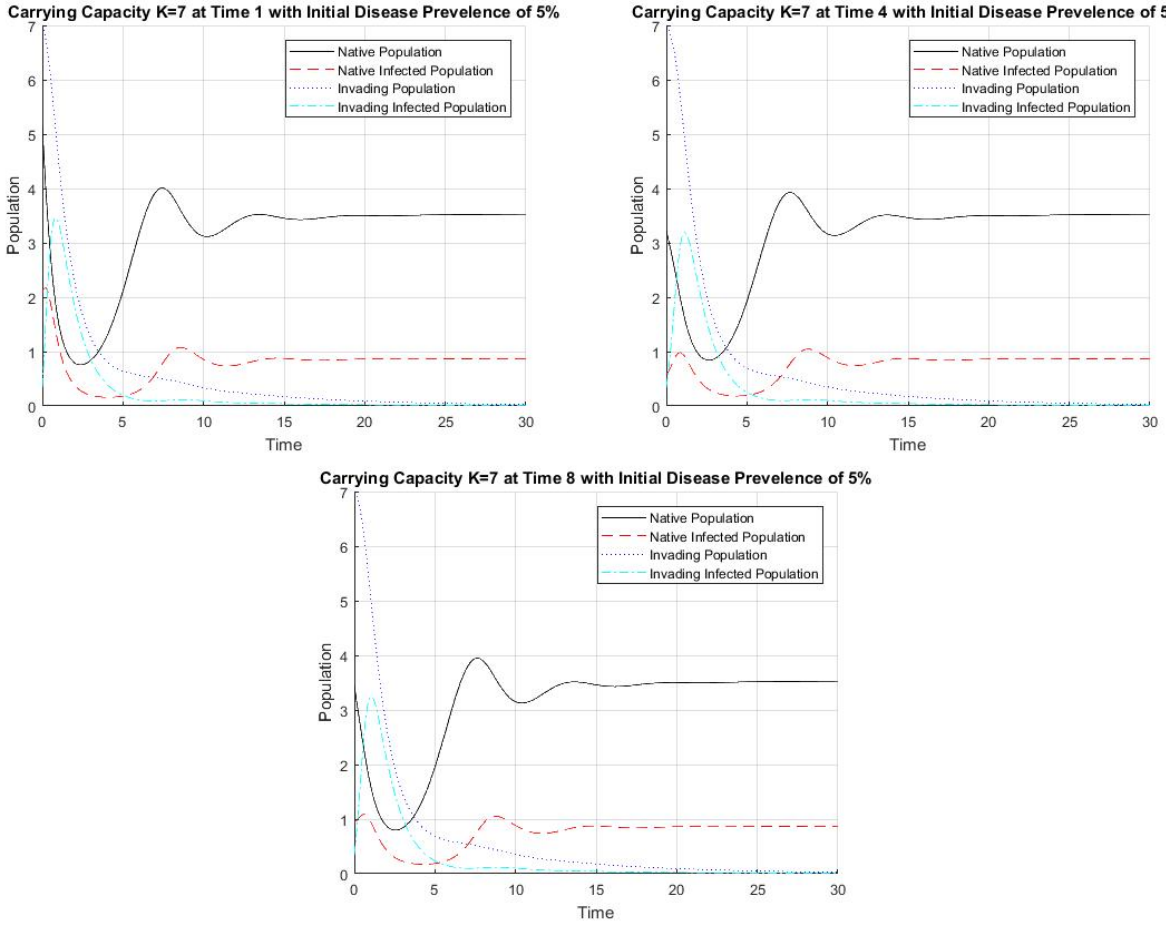
Similarly to how we analyzed the case where the invaders cannot get the disease, we consider times 1, 4, and 8 from tables 2.2-2.4 for each carrying capacity and display the simulations to see how they differ. Again, the different carrying capacities will yield significant changes to the population dynamics. However, the initial disease prevalence will not make significant changes to the population dynamics. So, we will not discuss these changes until mentioning how carrying capacity changes the results of the invasions. Thus we will display a total of nine graphs consisting of the carrying capacities 3.5, 7, and 14 with each carrying capacity at times 1, 4, and 8. Then we compare how initial disease prevalence affects results. All our simulations will be done at the initial disease prevalence of 5% except the final initial disease prevalence case to more consistently compare results.



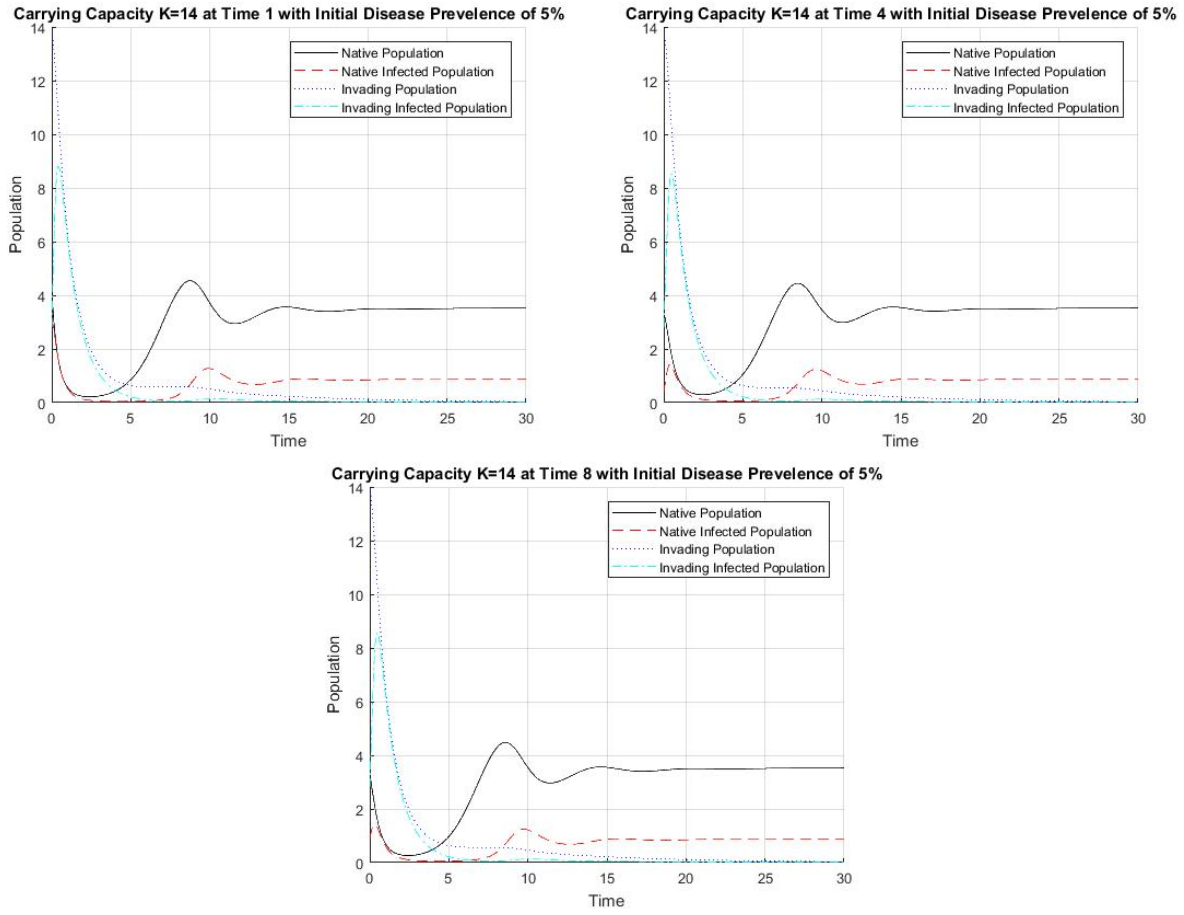
Figures 2.20-2.22 (Clockwise): Simulations for K=3.5 at Times 1, 4, and 8

There are several noteworthy observations to make about figures 2.20-2.22 . Firstly, we notice how the invading population and invading infected population have exactly the same population at time 0 for all three cases. This is logical since the initial conditions for each were the same and therefore, they all start at the same values and change as the model progresses (they are similar for all three cases for the entire time interval [0, 30]). Also, the total invading and the infected invading populations die out in all three simulations. We see similar changes to the native and native infected populations as in the case where the invaders could not get the disease. The starting population for the native population and native infected population are different and

change the initial decline in population (as well as how long it takes), however, the qualitative nature of the curves does not change. They all approach the same steady state populations in all three simulations (the natives all approach a certain value, the infected native all approach a certain value, invading and infected native populations cases are similar). These observations are consistent with the case where the invaders could not get the disease. Since the simulations where K=7 and K=14 are similar to these simulations we display both consecutively.



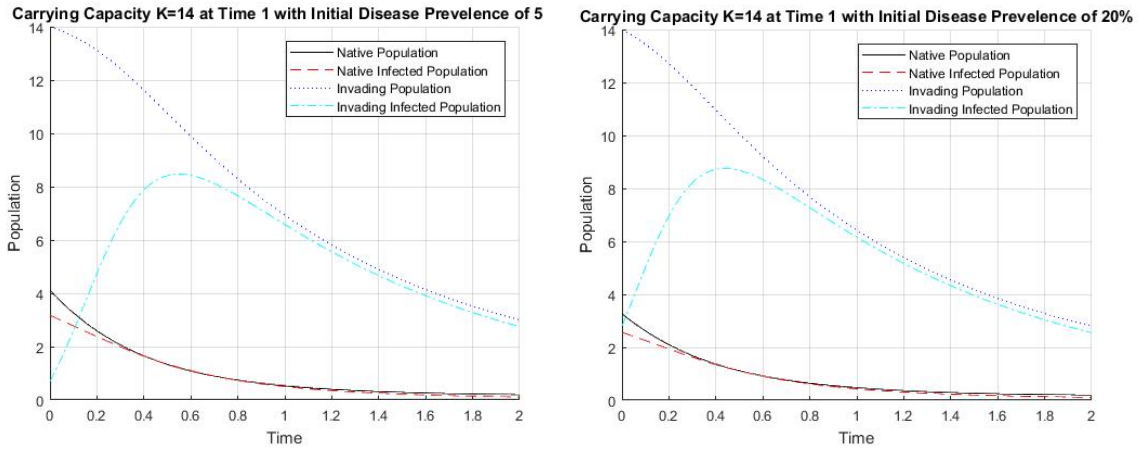
Figures 2.23-2.25 (Clockwise): Simulations for K=7 at Times 1, 4, and 8



Figures 2.26-2.28 (Clockwise): Simulations for K=14 at Times 1, 4, and 8

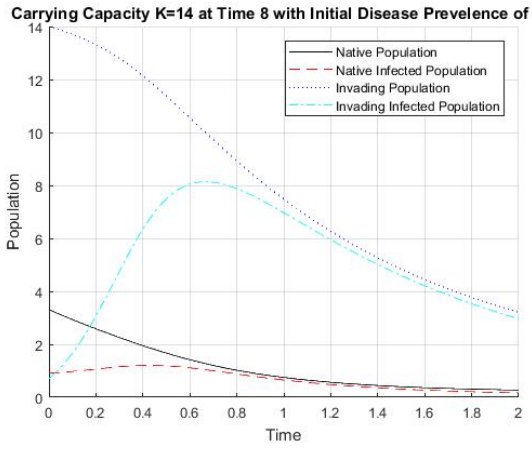
In figures 2.23-2.25 and 2.26-2.28 we display simulations which have common themes similar to those simulations which we have previously presented. The invading and infected invading population die out in all cases. However, we see a lower minimum invading population for K=14 than other carrying capacity levels. Again, the differing times change starting sizes for the native population and native infected population and change the initial decline in population (as well as how long it takes). However, the qualitative nature of the curves does not change. They all approach the same end populations in both sets of three cases (the native, infected

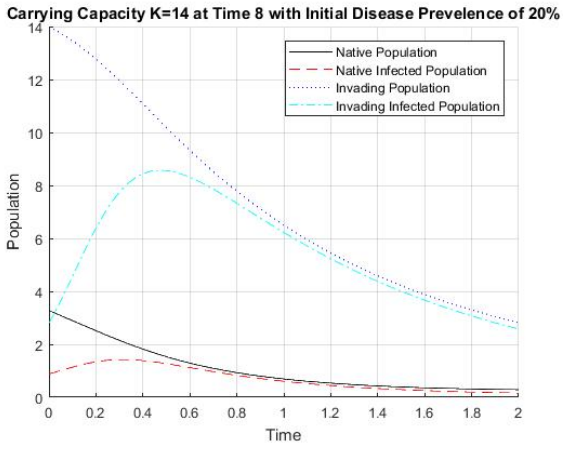
native, invading, and infected native populations all approach the same values for all three natural disease cycle times).



Figures 2.29-2.30 (Left then Right): Simulations for K=14 at Time 1 with initial disease prevalence of 5% and 20%

In figures 2.29-2.30 we look at the effect of the initial disease prevalence on these simulations. Again, with the 5% initial disease prevalence the native starting population is larger than the 20% native population, as is the infected native population. However, the underlying curve does not seem to change. The invading infected population has a noticeable shift as well but similarly, the underlying curve is the same. This occurs because of our assumption of the initial disease prevalence for the invading population. Our starting infected population is the carrying capacity times the initial disease prevalence rate (.7 and 2.8 here respectively). This is why we start at these population values when time = 0.





Figures 2.31-2.32 (Left then Right): Simulations for K=14 at Time 8 with initial disease prevalence of 5% and 20%

In figures 2.31-2.32, similar to the case where the invaders cannot get the disease, the differences are much smaller at this higher natural disease cycle time value. This is again due to the initial total population and diseased population for the native populations disease cycle being similar, so the differences between initial disease prevalence is minimal. However, there are more profound changes for the native population disease cycles which have a greater difference in their values.

Conclusion

With the simulations we have run for both cases (when invaders can/cannot get the disease) we can establish several important relationships (based on these specific parameter values). The main way the natural disease cycle plays a role in invadabilty is determining the initial starting population of the native and infected native populations and the initial drop in native and infected native populations. The general shape of the curve is similar and so is the value the populations all approach. This does not change invadability. If the shift is strong enough, however, it is possible that the invadability case changes (going from coexistence to one species dying out or vice versa). We saw this case when invaders could not get the disease, carrying capacity = 14, at time 1, for any initial disease prevalence. Finally, the role of the native populations disease cycle depends on the initial disease prevalence. Those having higher initial disease prevalence rates have a lower total population at both the beginning and ending times but during the middle of the disease cycle, have greater total populations.

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Matlab Code

Natural Disease Cycle Simulations

```
%Script File for Natural Disease Cycle Simulations
%Name of File is Interspec_Infect_and_CompFig1.m
global rone coneone conetwo alphaone betaoneone betaonetwo gammaone;
global rtwo ctwoone ctwotwo alphatwo betatwoone betatwotwo gammatwo;
rone = 1;
coneone = .142857;
conetwo = .083333;
alphaone = 2;
betaoneone = .75;
betaonetwo = .4;
gammaone = 2;
rtwo = .2;
ctwoone = .125;
ctwotwo = .090909;
alphatwo = 4;
betatwoone = .3;
betatwotwo = .5;
gammatwo = 1;
figure
hold on
init = [7 .7];  %Initial Conditions
t = [0 20];
options = odeset('RelTol',1e-8, 'AbsTol',1e-8);
[t,y] = ode45(@Interspec_Infect_and_Comp_rhs,t,init,options)
plot(t,y(:,1),'k');
plot(t,y(:,2),'--r');
plot(t,y(:,1) - y(:,2),':b')
hold off
xlabel('Time')
ylabel('Population')
legend('Native Population','Infected Population','Susceptible Population')

%Function File for Natural Disease Cycle Simulations
%Name of File is Interspec_Infect_and_Comp_rhs.m
function dy = Interspec_Infect_and_Comp_rhs(t,y)
global rone coneone conetwo alphaone betaoneone betaonetwo gammaone;
global rtwo ctwoone ctwotwo alphatwo betatwoone betatwotwo gammatwo;
dy = zeros(2,1);
dy(1) = (rone).*y(1).*(1-(coneone.*y(1))) - alphaone.*y(2);
dy(2) = (betaoneone).*(y(1) - y(2)).*y(2) - gammaone.*y(2);
% H1 = y(1)
% Y1 = y(2)
% H2 = y(3)
% Y2 = y(4)
```

When Invaders cannot get Disease Simulations

```
%Script File for When Invaders cannot get Disease
%Name of File is Times1to8.m
global rone coneone conetwo alphaone betaoneone betaonetwo gammaone;
global rtwo ctwoone ctwotwo alphatwo betatwoone betatwotwo gammatwo;
rone = 1;
coneone = .142857;
conetwo = 0.091;
alphaone = 2;
betaoneone = .75;
betaonetwo = .4;
gammaone = 2;
rtwo = .2;
ctwoone = .125;
ctwotwo = .090909;
alphatwo = 4;
betatwoone = .3;
betatwotwo = .5;
gammatwo = 1;
figure
hold on
init = [4.2789 0.6435 3.5];
t = [0 200];
options = odeset('RelTol',1e-8, 'AbsTol',1e-8);
[t,y] = ode45(@Times1to8rhs,t,init,options)
plot(t,y(:,1),'k');
plot(t,y(:,2),'--r');
plot(t,y(:,3),':b');
grid
legend('Native Population','Infected Native Population','Invading Population')
xlabel('Time')
ylabel('Population')

%Function File for When Invaders cannot get Disease
%Name of File is Times1to8rhs.m
function dy = Times1to8rhs(t,y)
global rone coneone conetwo alphaone betaoneone betaonetwo gammaone;
global rtwo ctwoone ctwotwo alphatwo betatwoone betatwotwo gammatwo;
dy = zeros(3,1);
dy(1) = (rone).*y(1).*(1-(coneone.*y(1)) - (conetwo.*y(3))) - alphaone.*y(2);
dy(2) = (betaoneone).*(y(1) - y(2)).*y(2) - gammaone.*y(2);
dy(3) = (rtwo).*y(3).*(1-(ctwoone.*y(1)) - (ctwotwo.*y(3)));
% H1 = y(1)
% Y1 = y(2)
% H2 = y(3)
% Y2 = y(4)
```

When Invaders can get Disease Simulations

```
%Script File for When Invaders can get Disease
%Name of File is f4equationmodel.m
global rone coneone conetwo alphaone betaoneone betaonetwo gammaone;
global rtwo ctwoone ctwotwo alphatwo betatwoone betatwotwo gammatwo;
rone = 1;
coneone = .142857;
conetwo = 0.083333;
alphaone = 2;
betaoneone = .75;
betaonetwo = .4;
gammaone = 2;
rtwo = .2;
ctwoone = .125;
ctwotwo = .090909;
alphatwo = 4;
betatwoone = .4;
betatwotwo = .75;
gammatwo = 1;
figure
hold on
init = [3.6488 0.9334 50 .175];
t = [0 50];
options = odeset('RelTol',1e-8, 'AbsTol',1e-8);
[t,y] = ode45(@f4equationmodelrhs,t,init,options)
plot(t,y(:,1),'k');
plot(t,y(:,2),'--r');
plot(t,y(:,3),':b');
plot(t,y(:,4),'-.c');
grid
xlabel('Time')
ylabel('Population')
legend('Native Population','Native Infected Population','Invading Population','Invading Infected Population')

%Function File for When Invaders can get Disease
%Name of File is f4equationmodelrhs
function dy = f4equationmodelrhs(t,y)
global rone coneone conetwo alphaone betaoneone betaonetwo gammaone;
global rtwo ctwoone ctwotwo alphatwo betatwoone betatwotwo gammatwo;
dy = zeros(4,1);
dy(1) = (rone).*y(1).*(1-(coneone.*y(1)) - (conetwo.*y(3))) - alphaone.*y(2);
dy(2) = (betaoneone).*(y(1) - y(2)).*y(2) + (betaonetwo).*(y(1) - y(2)).*y(4) - gammaone.*y(2);
dy(3) = (rtwo).*y(3).*(1-(ctwoone.*y(1)) - (ctwotwo.*y(3))) - alphatwo.*y(4);
dy(4) = (betatwoone).*(y(3) - y(4)).*y(2) + (betatwotwo).*(y(3) - y(4)).*y(4) - gammatwo.*y(4);
% H1 = y(1)
% Y1 = y(2)
% H2 = y(3)
% Y2 = y(4)
```