Diffusion Induced Chaos in an Insect Population

by

Dongwoook Kim

(Under the direction of Andrew Sornborger)

Abstract

A variety of ecological models exhibit chaotic dynamics because of nonlinearities in population growth and interactions. Here, we will study the LPA model (beetle *Tribolium*). The LPA model is known to exhibit chaos. In this project, we investigate two things which are the effect of noise constant and the effect of diffusion combined with the LPA model. The effect of noise is to blur the bifurcation diagram. Numerical simulations of the model have shown that diffusion can drive the total population of insects into complex patterns of variability in time. We will compare these simulations with simulations without diffusion. And we conclude that the diffusion coefficient is a bifurcation parameter and that there exist parameter regions with chaotic behavior and periodic solutions.

Index words: Theses (academic)

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B.A., Chung Ang University, 2003

A Thesis Submitted to the Graduate Faculty
of The University of Georgia in Partial Fulfillment
of the
Requirements for the Degree

Master of Science

Athens, Georgia

2006

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August 2006

Acknowledgments

I would like to thank Professor Andrew Sornborger for helping direct and proofread my thesis.

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Chapter 1

Introduction

Chaos is one aspect of the larger subject known as dynamics. This is a subject that deals with change, i.e. with systems that evolve in time. To determine whether the system in question settles down to equilibrium, keeps repeating in cycles, or does something more complicated, we analyze the dynamics to understand the behavior. There are two main types of dynamical systems; differential equations and difference equations. Differential equations describe the evolution of systems in continuous time, whereas difference equations arise in problems where time is discrete. Difference equations are very useful, both for providing simple examples of chaos, and also as tools for analyzing periodic or chaotic solutions of differential equations.

Population growth is an example of a dynamical system. In this case, we analyze the population fluctuations. Population fluctuations depend on the stability of fixed points; stable points are where every trajectory goes to a fixed point, stable periodic trajectories occur when population numbers oscillate among a finite number of values and there is a limit cycle around the fixed point, aperiodic cycles occur when populations oscillate but the characteristics of the oscillation can change, and chaos which provides an unusual, apparently random, and intuitively unexpected prediction of population behavior.

A variety of ecological models exhibit chaotic dynamics because of nonlinearities in population growth and interactions. Here, we will study a system which is difference equation, say the LPA model (beetle *Tribolium*). The LPA model is known to exhibit chaos. It has been argued that it is the only uncontroversial confirmation of chaos in a biological population [9]. In this project, we investigate the effect of diffusion combined with the LPA model. Numerical simulations of the model have shown that diffusion can drive the total population of insects into complex patterns of variability in time. We will compare these simulations with simulations without diffusion. And we conclude that the diffusion coefficient is a bifurcation parameter and that there exist parameter regions with chaotic behavior and periodic solutions.

Chapter 2

Background

2.1 Possible Dynamics in Mathematical Biology Systems

The following discussion is based on Britton's book [6].

2.1.1 First-Order Equations

We shall consider the first-order difference equation.

$$N_{t+1} = f(N_t) \tag{2.1}$$

also called a recurrence equation or map, to be solved with the initial condition N_0 given. This defines a sequence N_0, N_1, N_2 ... , called a solution of the equation with the initial condition. It is stable if another solution $N_0^{'}, N_1^{'}, N_2^{'}$,... remains close to the first solution whenever it starts close, that is $|N_t - N_t^{'}|$ is small for all t whenever $|N_t - N_t^{'}|$ is small, and asymptotically stable if also $|N_t - N_t^{'}| \to 0$ as $t \to \infty$. It is neutrally stable if it is stable but not asymptotically stable. It is a **steady state (or fixed point or equilibrium)** solution if $N_t = N^*$ for all t; it is clear from Equation (1) that the condition for N^* to be a steady state is that $N^* = f(N^*)$. It is **periodic** of period p if $N_{t+p} = N_t$ for all t, but $N_{t+q} \neq N_t$ for all t and any $q < p$, and **aperiodic** if it is not periodic.

Linearization of the system

Let N^* be a fixed point, and let $n = N - N^*$ be a small perturbation away from N^*. To see whether the perturbation grows or decays, plug the perturbation into Equation (1) and subtract $N^* = f(N^*)$ then Equation (1) gives

$$n_{t+1} = f(N^* + n_t) - f(N^*) = f'(N^*)n_t + h.o.t \tag{2.2}$$

where h.o.t. stands for higher order terms.

Let us assume that for n_t sufficiently small the higher order terms are negligible. Then we may infer that the solution of Equation (1) behaves similarly to that of the approximating equation

$$n_{t+1} = f'(N^*)n_t \tag{2.3}$$

This is known as the linearized equation. The solution is $n_t = n_0 f'(N^*)^t$. Letting $\lambda = f'(N^*)$, the steady state is oscillatorily unstable, oscillatorily asymptotically stable, monotonically asymptotically stable or monotonically unstable according to whether $\lambda < -1, -1 < \lambda < 0, 0 < \lambda < 1$ or $1 < \lambda$ respectively. The condition for asymptotic stability is

$$|\lambda| = |f'(N^*)| < 1$$

and if $|\lambda| = 1$ the steady state is stable but not asymptotically stable. The use of the notation λ reflects the fact that the place of $f'(N^*)$ will be taken by the eigenvalues of a matrix for systems of equations and we shall often refer to $f'(N^*)$ itself as an eigenvalue.

2.1.2 Systems of Nonlinear Difference Equations

We shall consider second-order systems of the form

$$N_{t+1} = f(N_t, P_t), \;\; P_{t+1} = g(N_t, P_t) \tag{2.4}$$

although the results may be extended to systems of higher dimension. Some new kinds of behavior occur here, and we need some definitions. An invariant curve is a curve Γ in (N, P)-space such that if $(N_0, P_0) \in \Gamma$, then $(N_t, P_t) \in \Gamma$ for all $t > 0$. Such a curve is stable if a solution remains close to it whenever it starts close to it, and asymptotically stable if the distance between such a solution and the curve tends to zero as $t \to \infty$. A solution N_t which starts and therefore remains on a closed invariant curve Γ may either return to its starting point after a finite number of steps, or not. We say it has a rational or irrational rotation number, respectively.

Linearization of systems

Let us assume that there exists a steady state (N^*, P^*) of this system; it satisfies Equation (2). Perturbations from this steady state may be defined by $(n, p) = (N, P) - (N^*, P^*)$. Linearizing about the steady state, in the same way as was done for the first-order equation, we obtain the approximate equations

$$n_{t+1} = \frac{\partial f}{\partial N}(N^*, P^*)n_t + \frac{\partial f}{\partial P}(N^*, P^*)p_t \tag{2.5}$$

$$n_{t+1} = \frac{\partial g}{\partial N}(N^*, P^*)n_t + \frac{\partial g}{\partial P}(N^*, P^*)p_t \tag{2.6}$$

or

$$n_{t+1} = J^* n_t \tag{2.7}$$

where n is the column vector $(n, p)^T$, J is the Jacobian of the transformation and $J^* = J(N^*, P^*)$

$J(N, P) = \begin{pmatrix} f_N(N, P) & f_P(N, P) \\ g_N(N, P) & g_P(N, P) \end{pmatrix}$ and a star denotes evaluation at the steady state.

(1) if trace$(J^*) < 0$ and determinant$(J^*) > 0$ then, the steady state is stable

(2) if trace$(J^*) > 0$ and determinant$(J^*) > 0$ then, the steady state is unstable

2.2 Bifurcation and Chaos

The following discussion is based on Strogatz's book [5]

2.2.1 Definition of Bifurcation and Chaos

Bifurcation

The qualitative structure of the solution can change as parameters are varied. In particular, fixed points can be created or destroyed, or their stability can change. These qualitative changes in the dynamics are called **bifurcations**, and the parameter values at which they occur are called **bifurcation points**.

Bifurcations are important scientifically – they provide models of transitions and instabilities as some control parameter is varied. For example, consider the buckling of a beam. If a small weight is placed on top of the beam, the beam can support the load and remain vertical. But if the load is too heavy, the vertical position becomes unstable, and the beam may buckle. Here the weight plays the role of the control parameter, and the deflection of the beam from vertical plays the role of the dynamical variable.

Chaos

No definition of the term chaos is universally accepted yet, but almost everyone would agree on the three ingredients used in the following working definition:

Chaos is aperiodic long-term behavior in a deterministic system that exhibits sensitive dependence on initial conditions.

1. "Aperiodic long-term behavior" means that there are trajectories which do not settle down to fixed points, periodic orbits, or quasiperiodic orbits as $t \to \infty$. For practical reasons, we should require that such trajectories are not too rare. For instance, we could insist that there be an open set of initial conditions leading to aperiodic trajectories, or perhaps that such trajectories should occur with nonzero probability, given a random initial condition.

2. "Deterministic" means that the system has no random or noisy inputs or parameters. The irregular behavior arises from the system's ***nonlinearity***, rather than from noisy driving forces.

3. "Sensitive dependence on initial conditions" means that nearby trajectories separate exponentially fast, i.e., the system has a positive Liapunov exponent (which I'll explain later)

2.2.2 Bifurcation Parameter

In this section, we will discuss bifurcation and chaos with an example of the logistic-like equation [8].

$$N_{t+1} = cN_t^2(1 - N_t) \tag{2.8}$$

Here $N_t \geq 0$ is a dimensionless measure of the population in the t-th generation and $c \geq 0$ is the intrinsic growth rate. We restrict the control parameter c to the range $5 \leq c \leq 6.6$ to see well-behaved solutions. For many values of c, the sequence $\{N_t\}$ never settles down to a fixed point or a periodic orbit. This is a discrete time version of chaos.

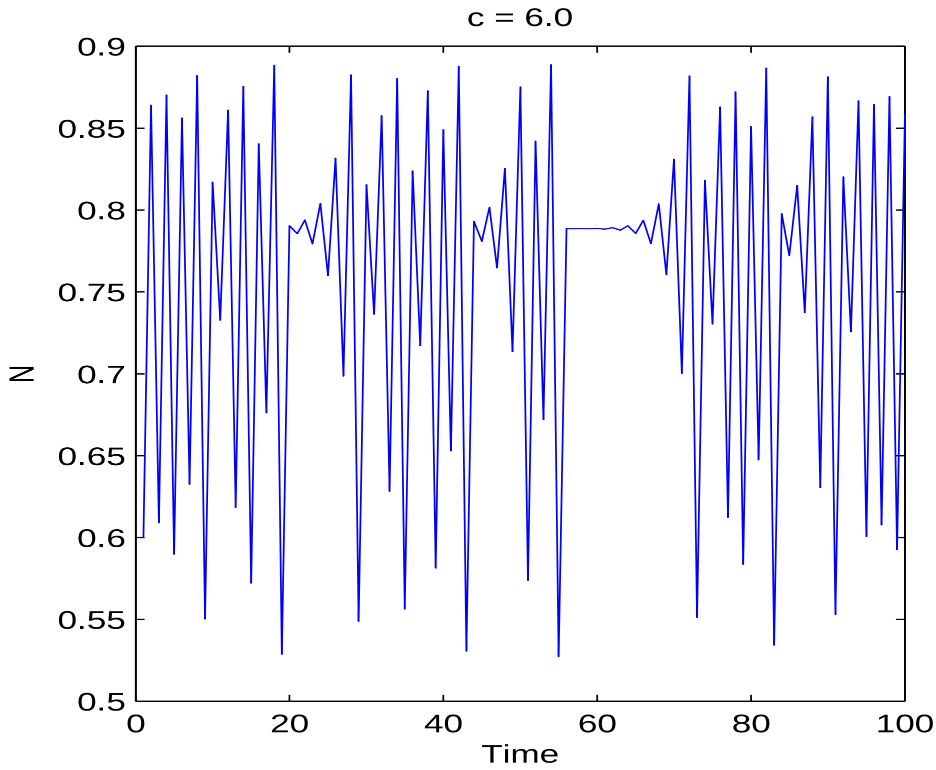


FIGURE 1: TIME-SERIES OF LOGISTIC EQUATION SOLUTION FOR C = 6.0

One might guess the system would become more and more chaotic as c changes, but in fact the dynamics are more subtle than that. To see the long-term behavior for all values of c at once, we plot the bifurcation diagram[1] (Figure 2).

Smoothly distributed parts in Figure 2 are evidence of chaos, and the lines represent periodic cycles. For $C \in [5, 5.8]$, it shows periodic behavior and for $C \in [5.9, 6.2]$, it shows chaotic behavior. For C=5.4, the bifurcation occurs from 1 to 2 periodic cycles. From the bifurcation diagram, we can see the long-term behavior as the control parameter, C, changes.

[1]The bifurcation diagram shows the possible long-term values a variable of a system can obtain as a function of a parameter of the system.

Liapunov Exponent

We have seen that the logistic map can exhibit aperiodic orbits for certain parameter values, but how do we know that this is really chaos? Here is the intuition. Given some initial condition x_0, consider a nearby point $x_0 + \delta_0$, where the initial separation δ_0 is extremely small. Let δ_n be the separation after n iterates. If $|\delta_n| \approx |\delta_0| e^{n\lambda}$, then λ is called the **Liapunov Exponent** (λ is defined to be the long-term exponential rate of divergence between two trajectories with an infinitesimally small difference in their initial conditions). A positive Liapunov exponent is a signature of a chaotic system, while a negative or zero Liapunov exponent represents a non-chaotic system. Figure 3 is a plot of the Liapunov exponent in the logistic equation as a function of C. We can compare it with Figure 2. For $C \in [5, 5.8]$, λ (Liapunov exponent) is negative which means it shows periodic behavior. In Figure 3, for that interval ([5,5.8]), it shows lines (periodic solutions). And for $C \in [5.9, 6.2]$, λ is positive which means it shows chaotic behavior, as you see in Figure 2.

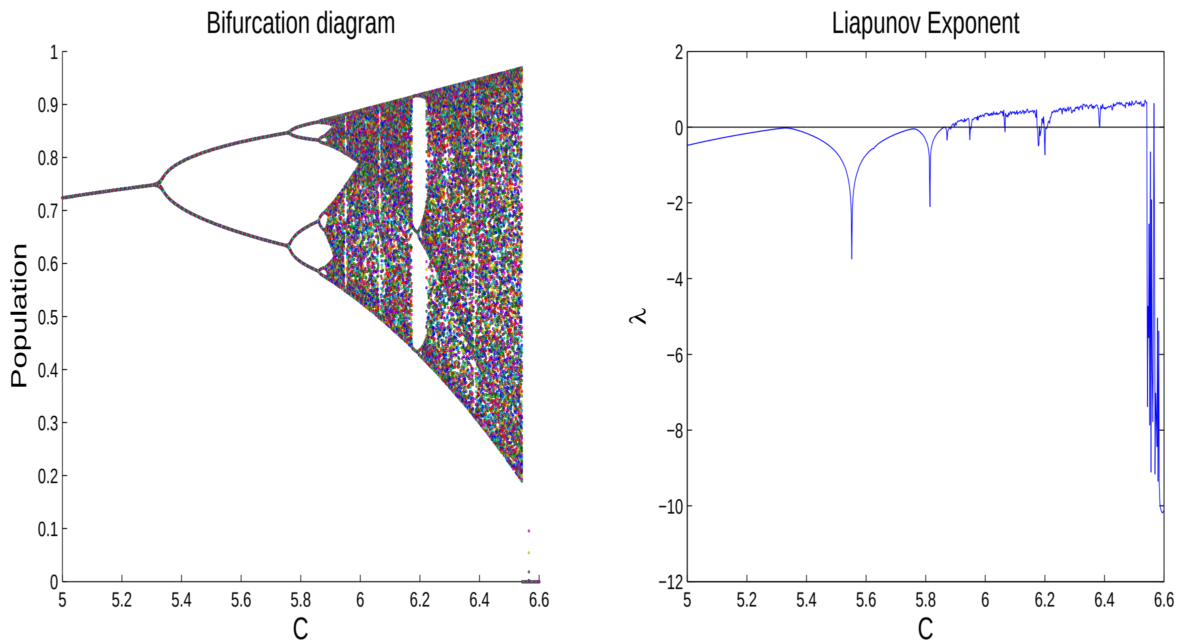


Figure 2 : Bifurcation diagram, Figure 3: Liapunov Exponent

2.3 Diffusion

The following discussion is based on Brown's book [10]. and Murray's book [11]

Transport is one of the fundamental processes of biology. Animals move from regions of high to low density because of shortage of resources, or in a trial-and-error search for better conditions. They also need to search for food and for a mate. Plant seeds disperse to avoid competing with the parent plant. On a smaller scale, materials need to be transported from the site of synthesis within the organism to the utilization site, for metabolism or growth or some other need.

Diffusion is a form of transport due to the continual random motion of particles. This ranges from the Brownian motion of very small particles (named after the biologist R. Brown who first wrote about the random walks of invertebrates and small animals, such as those of the larvae of *Trichostrongylus retortaeformis*). In these cases, the random motion usually results in a rate of spread from one region to another which is proportional to the concentration difference between the two regions.

2.3.1 Diffusion Model

Suppose a particle moves randomly backward and forward along a line in fixed steps Δx that are taken in a fixed time Δt. If the motion is unbiased then it is equally probable that the particle takes a step to the right or left. After time $N\Delta t$ the particle can be anywhere from -$N\Delta x$ to $N\Delta x$ if we take the starting point of the particles as the origin. The spatial distribution is clearly not going to be uniform if we release a group of particles about $x = 0$ since the probability of a particle reaching $x = N\Delta x$ after N step is very small compared with that for x nearer $x = 0$.

2.3.2 Example of Diffusion

One of the classic examples of diffusion as applied to animal dispersal is that of the muskrat which spread across entire countries within a decade or two. The spread was so fast because the new center of population acted as breeding colonies in their own right, and this very much accelerated the spread. If the population locally is reproducing at a rate, ρ, and the density is denoted by N, then the growth rate for unaided diffusion is incremented by ρN, and so we obtain the equation

$$\frac{\partial N}{\partial t} = D\frac{\partial^2 N}{\partial^2 x} + \rho N \tag{2.9}$$

where, D is diffusion coefficient. The first term is diffusion term and the second term is growth term.

2.3.3 Rule for Interaction between Spatial Points

When we consider the diffusion equation in a discrete context on a line, there must be a rule for movement between spatial points (bins). Suppose we have 10 different bins (groups), a fraction of the population can move to an adjacent bin (each bin has 2 adjacent bins which are its left and right bins except for the initial and final bins which are the 1st and 10th bins.) at each time step. And let's assume that the rate of diffusion, called d, is the same in both directions.

From the 2nd bin to 9th bin, the diffusion process (see Figure 4) is the same. But the 1st bin and 10th bin will have different diffusion processes. Eq (2.10) is the diffusion equation for the 2nd to 9th bin. In this process, adults in the jth bin move at rate d to the $(j-1)$st and $(j+1)$st bins and adults in the $(j-1)$st and $(j+1)$st bins move at rate d to the jth bin

$$N_{t+1}^{j} = N_t^j + d(N_t^{j+1} - 2N_t^j + N_t^{j-1}) \tag{2.10}$$

where $2 \leq j \leq 9$, t = time, and j = space. Note that second term of the right hand side equation is a finite difference version of the diffusion term above.

Eq (2.11) is the diffusion equation for the 1st bin. Here, the adults in the 1st bin move at rate d to the 2nd bin and the adults in the 2nd bin move at rate d to the 1st bin.

$$N_{t+1}^{j} = N_t^j + d(N_t^{j+1} - N_t^j) \tag{2.11}$$

where j=1.

Eq (2.12) is the diffusion equation for the 10th bin. Here, the adults in the 9th bin move at rate d to the 10th bin and the adults in the 10th bin move at rate d to the 9th bin.

$$N_{t+1}^{j} = N_t^j + d(N_t^{j-1} - N_t^j) \tag{2.12}$$

where j=10.

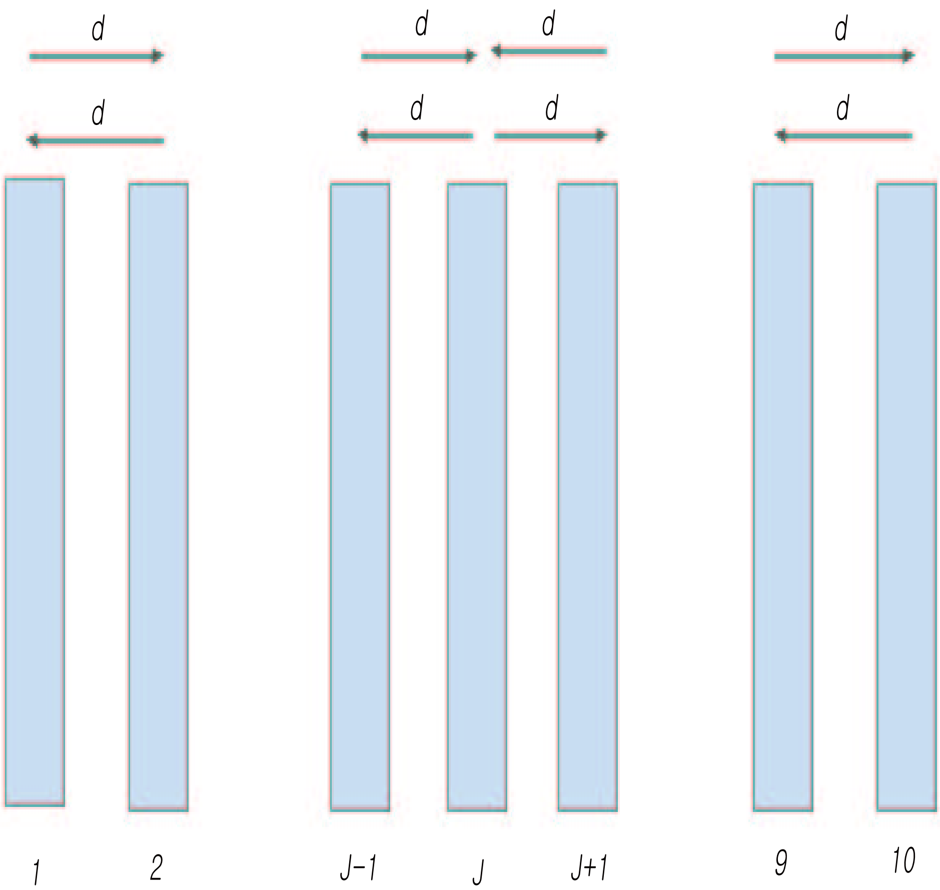


FIGURE 4 : THE RULE FOR DIFFUSION PROCESS; J INDICATES J-TH BIN.

Chapter 3

Methods and Data

3.1 LPA Model with Stochastic Terms

Many species of Tribolium (flour beetle) are cannibalistic, including the species Tribolium castaneum that we analyze in this thesis. The following model, which is called the LPA model, describes the dynamics of larval, pupal, and adult Tribolium populations at time $t+1$ as a function of the populations at time t by means of a system of three difference equations

$$L_{t+1} = bA_t \exp(-C_{el}L_t - C_{ea}A_t + E_{1t}) \tag{3.1}$$

$$P_{t+1} = L_t(1 - \mu_l) \exp(E_{2t}) \tag{3.2}$$

$$A_{t+1} = [P_t \exp(-C_{pa}A_t) + A_t(1 - \mu_a)] \exp(E_{3t}) \tag{3.3}$$

In this model [1], L_t is the number of feeding larvae (referred to as the L-stage) at time t, P_t is the number of large larvae, non-feeding larvae, pupae, and callow adults (collectively the P-stage) and A_t is the number of sexually mature adults (A-stage animals). The unit of time is taken to be the feeding larval maturation interval so that after one unit of time a larva either dies or survives and pupates. The unit of time is 2 weeks and is, approximately, the average amount of time spent in the feeding larval stage under standard experimental conditions described in the reference [1]. The unit of time is also approximately the average duration of the P-stage. The quantity b is the number of larval recruits per adult per unit time in the absence of cannibalism. The fractions μ_l and μ_a are the larval and adult rates of mortality, respectively, in one time unit.

The exponential nonlinearities account for the cannibalism of eggs by both larvae and adults and the cannibalism of pupae by adults. The fractions $\exp(-C_{el}L_t)$ and $\exp(-C_{ea}A_t)$ are the probabilities that an egg is not eaten in the presence of L_t larvae and A_t adults, respectively, in one time unit [1]. The fraction $\exp(C_{pa}A_t)$ is the survival probability of a pupa in the presence of A_t adults in one time unit. The terms E_{1t}, E_{2t} and E_{3t} are random noise variables assumed to have a joint multivariate normal distribution with a mean vector of zeros and a variance-covariance matrix denoted by Σ (The variance-covariance matrix is estimated from experimental data in [1]. The maximum likelihood estimates in the variance-covariance matrices are $\sigma_{11} = 0.3412, \sigma_{22} = 0.2488, \sigma_{33} = 1.627 \times 10^{-4}, \sigma_{12} = 7.312 \times 10^{-2}, \sigma_{13} = -1.719 \times 10^{-3}$, and $\sigma_{23} = 3.374 \times 10^{-4}$). The deterministic skeleton of the model is identified by setting $\sum = 0$, or equivalently, by letting E_{1t}, E_{2t} and E_{3t} equal to zero in Eqs. 1–3.

The noise variables represent unpredictable departures of the observations from the deterministic behavior (resulting from environmental and other causes) and are assumed to be correlated with each other within a time unit but uncorrelated on longer time scales. These assumptions were found acceptable for many previous data sets by standard diagnostic analysis of time-series residuals. The adult mortality rate, μ_a, may be experimentally set to 0.96 by removing or adding adults at time of census. In Costantino *et al.* 1997 [1], recruitment into the adult stage was manipulated by removing or adding young adults at the time of census to make the number of new adult recruits consistent with the treatment value of C_{pa}..

3.2 Various Dynamics with LPA Model

In this section, we will discuss population evolution solutions for the LPA model. By using numerical iteration (with MATLAB), we will describe the dynamics of the total population (larvae+pupae+adults) versus time for each fixed parameter, C_{pa}. In this description, we will see when we change C_{pa}, the evolution of the total population will be changed from steady state (equilibrium) to periodic cycles or periodic cycles to chaos. The results will be the same with the bifurcation diagram of the total population which we will discuss in next section.

3.2.1 Numerical Method

Here, we assume that E_{1t}, E_{2t} and E_{3t} in Eqs. 1–3 are zero. By changing the parameter, C_{pa}, the population dynamics changes giving rise to bifurcations in dynamics. In the case where $\Sigma = 0$, for each C_{pa}, the dynamics of the adult population shows a stable equilibrium, periodic cycles or chaos. For the deterministic skeleton, we iterated the LPA model for 10000 steps to see the long term behavior of the total population. Fixing C_{pa}, we calculate the total population for each time point. And then we graphed the total population as a function of time. These graphs give us a good visualization of the dynamics of the total population. By changing C_{pa}, we can conclude that the dynamics of the total population has different asymptotic behaviors (stable equilibrium, periodic cycles and chaos). In the next section, we will graph some solutions (3 different cases; stable equilibrium, periodic cycles and chaos).

3.2.2 Dynamics of the Total Population

Here, we plot three different total population dynamics; steady state, periodic and chaotic behavior (see Figure 5).

For $C_{pa} = 0.0$, there is a horizontal straight line; we call it a stable equilibrium or steady state. That means the population of adults does not change after some time (or long time). In this case, the dynamics is very simple. It's easy to predict long term behavior of the total population since the population dynamics does not change.

For $C_{pa} = 0.55$ and 0.9, these graphs show periodic cycles. As you see in the two graphs, the total population is oscillating periodically. For $C_{pa} = 0.55$, there are 8 periodic cycles. And for $C_{pa} = 0.9$, there are 3 periodic cycles.

For $C_{pa} = 0.1$, 0.3 and 0.45, the graphs show aperiodic cycles or chaos. These solutions are oscillating. However there is no fixed period for oscillations.

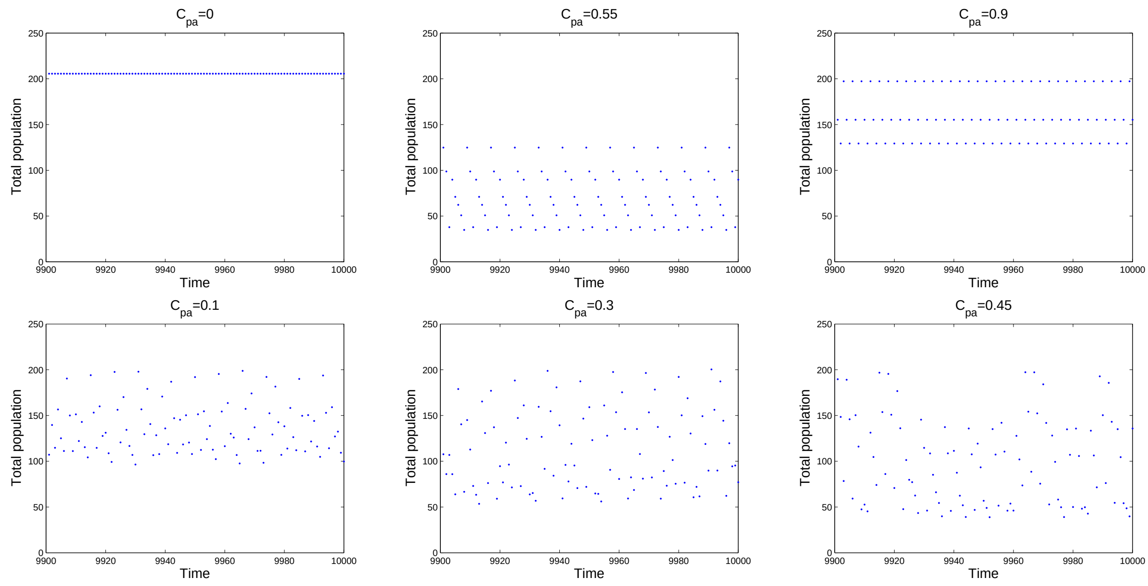


Figure 5: Dynamics of the LPA model for different values of C_{pa}

Now, from the above graphs, we know that the parameter, C_{pa}, determines the nature of bifurcations.

3.2.3 Histogram

In this section, we will see the density of the total population for the values of C_{pa} in the previous Figure. In the above, we showed the dynamics of the LPA model for different values of C_{pa}.

Figure 6 is the histogram of the dynamics of the total population for each C_{pa}. This Figure shows how many times the solution has a value within a given population bin for various values of the C_{pa}. As you see in Figure 6, for $C_{pa} = 0$, the histogram shows 1 vertical line since there is an equilibrium in Figure 5.

For $C_{pa} = 0.55$, the histogram shows 8 vertical lines since it takes on 8 different values in one cycle and for $C_{pa} = 0.9$, the histogram shows 3 vertical lines since it takes on 3 different values in one cycle in Figure 5.

For $C_{pa} = 0.1$, 0.3 and 0.45, chaotic solutions, the solution gives a distribution of values.

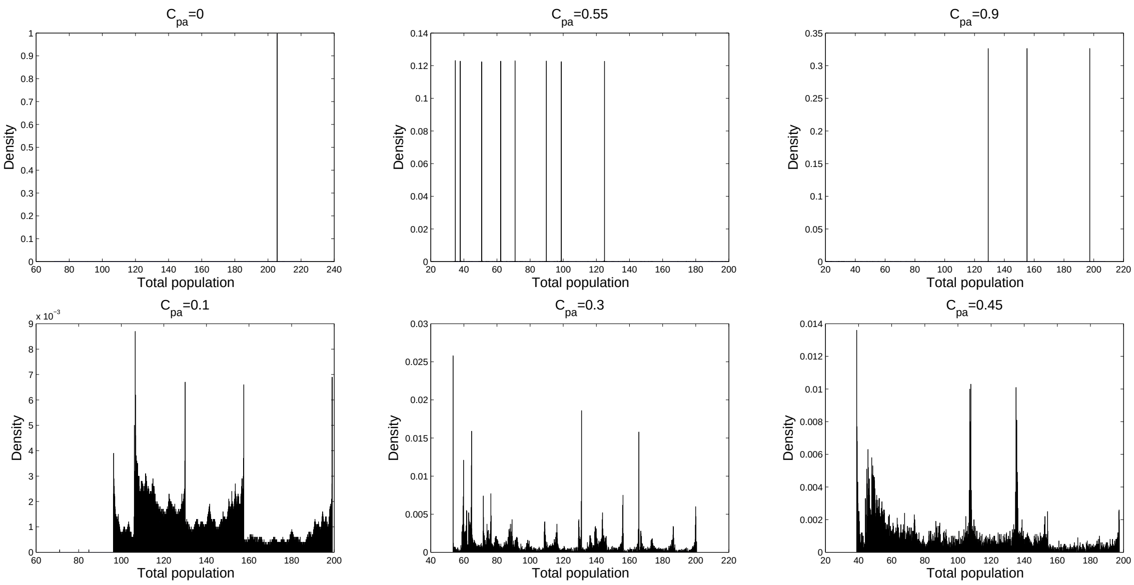


Figure 6: The histogram of the Dynamics of the LPA model for different values of C_{pa}

3.3 Bifurcation Diagram without Random Noise

Above, we showed when the parameter C_{pa} is changed, the dynamics of adult population also changes. In this section, we investigate the dynamics of total insect-population by changing C_{pa} via the bifurcation diagram.

3.3.1 Numerical Method

For the case $\Sigma = 0$ and $b = 6.598$, $C_{el} = 1.209 \times 10^{-2}$, $C_{ea} = 1.155 \times 10^{-2}$, $\mu_l = 0.2055$, and $\mu_a = 7.629 \times 10^{-3}$ [1], we plot the bifurcation diagram. In this thesis, the initial values are from [1] which are 250 larvae, 50 pupae and 100 adults. The number of time steps is 6400 steps. The last 200 time points are assumed to represent the asymptotic behavior of the solutions and are used to calculate the density bifurcation diagram (see below).

3.3.2 Density Bifurcation Diagram

The bifurcation diagram conveys information about how the dynamics of the total population changes as a function of the parameter, C_{pa}. In this plot, we plot the population density (i.e. histogram) as a function of C_{pa}. Figure 7 is the density bifurcation diagram of the total population for the LPA model. In Figure 7, black means zero population and white indicates high populations with gray scales in between.

Smoothly distributed regions are evidence of quasiperiodicity or chaos, and the sharp lines represent periodic cycles. For $C_{pa} = 0.0$, the population dynamics shows a stable equilibrium (not shown in Figure 5). For $C_{pa} \in [\ 0.1,\ 0.3\ ]$, chaotic behavior occurs. Again, for $C_{pa} \in [\ 0.1,\ 0.2\ ]$, and 0.45, it shows chaos. For $C_{pa} = 0.75$ and 0.9, there are 8 lines and 3 lines, respectively. Those lines mean that the dynamics of population has 8 periodic cycles or 3 periodic cycles. In this region of parameter space, if we change the initial values, the solution may change and the trajectory may enter a different periodic attractor.

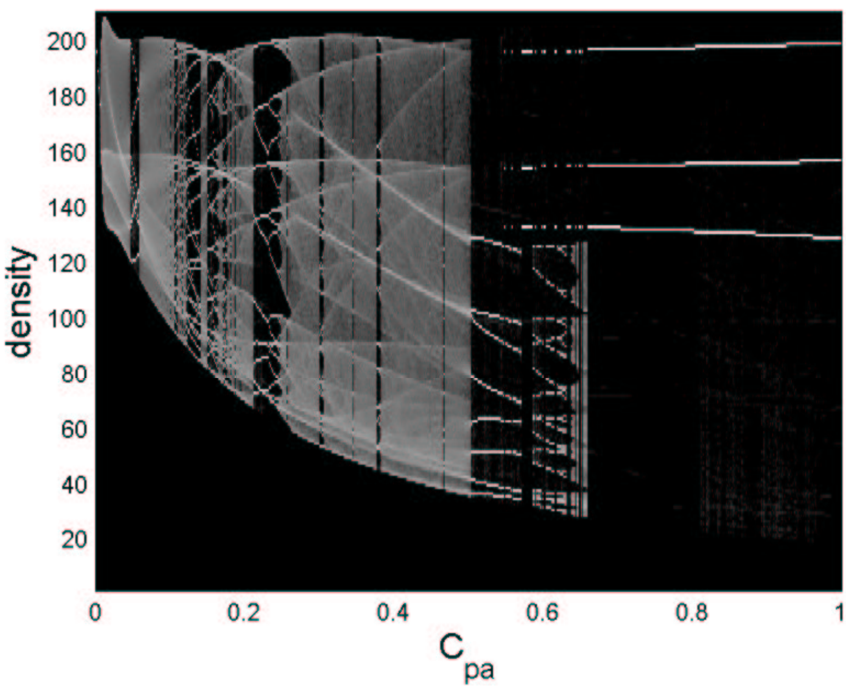
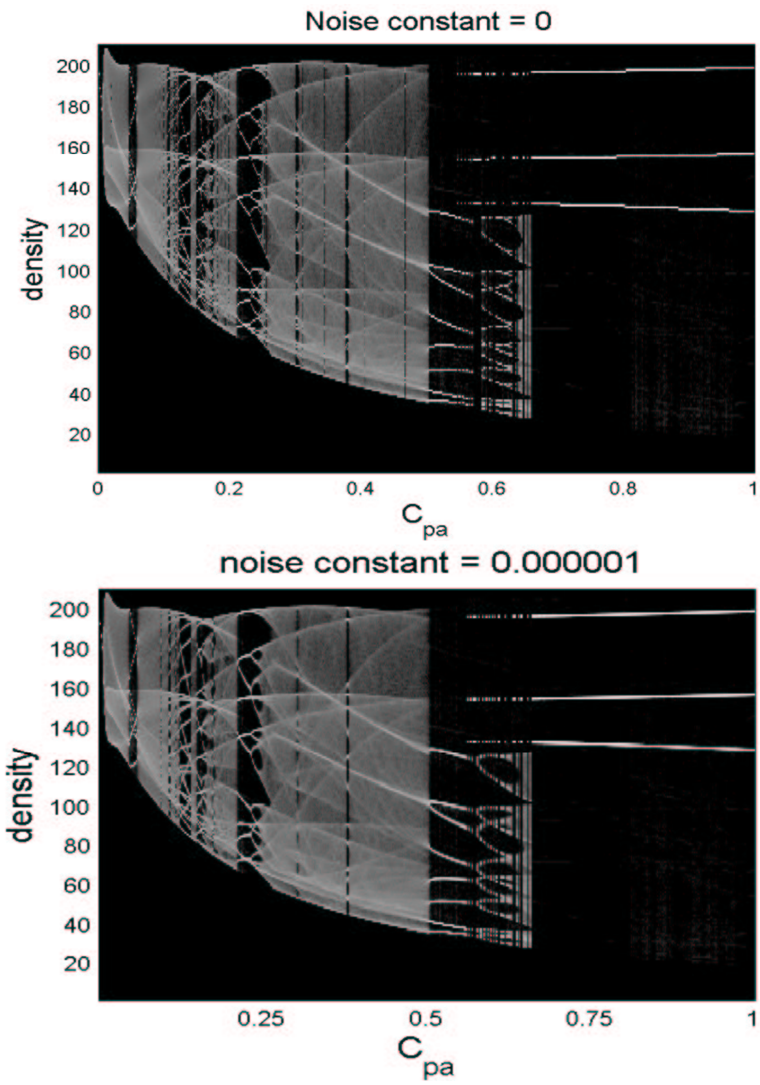


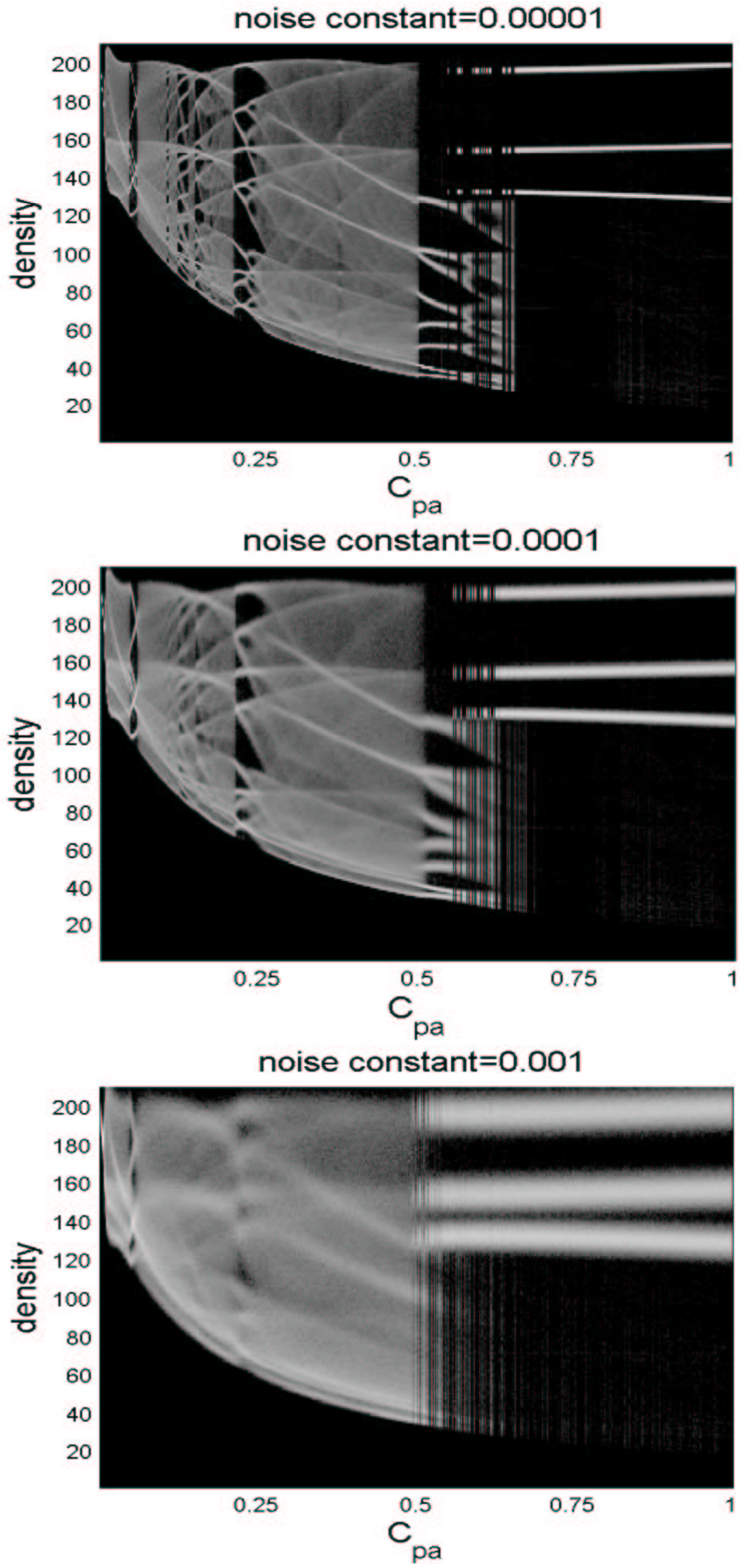
Figure 7: Density Bifurcation diagram for total population numbers (L-stage+P-stage+A-stage) using deterministic skeleton ($\sum = 0$)

3.4 Bifurcation Diagram with Noise

Let us look at the LPA Model (Eq 1-3) again. In the above section, we ignored the noise terms which are E_{1t}, E_{2t} and E_{3t}. The reason is that if we ignore the noise terms in the LPA model, then we can see the dynamics of population easily for each species. This means that we can predict the behavior of the population exactly for some parameters.

Now, if there are noise terms, what happens in the LPA model? In this section, we will discuss the effect of stochastic terms in the LPA model. And we will show when we change the noise constant, called ϵ (which is a constant multiplying Σ), what occurs in the bifurcation diagram. We will show the bifurcation diagram as a function of the amplitude of the noise.




noise constant=0.00001
density
200
180
160
140
120
100
80
60
40
20
0.25
0.5
0.75
1
C_{pa}
noise constant=0.0001
density
200
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80
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40
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C_{pa}
noise constant=0.001
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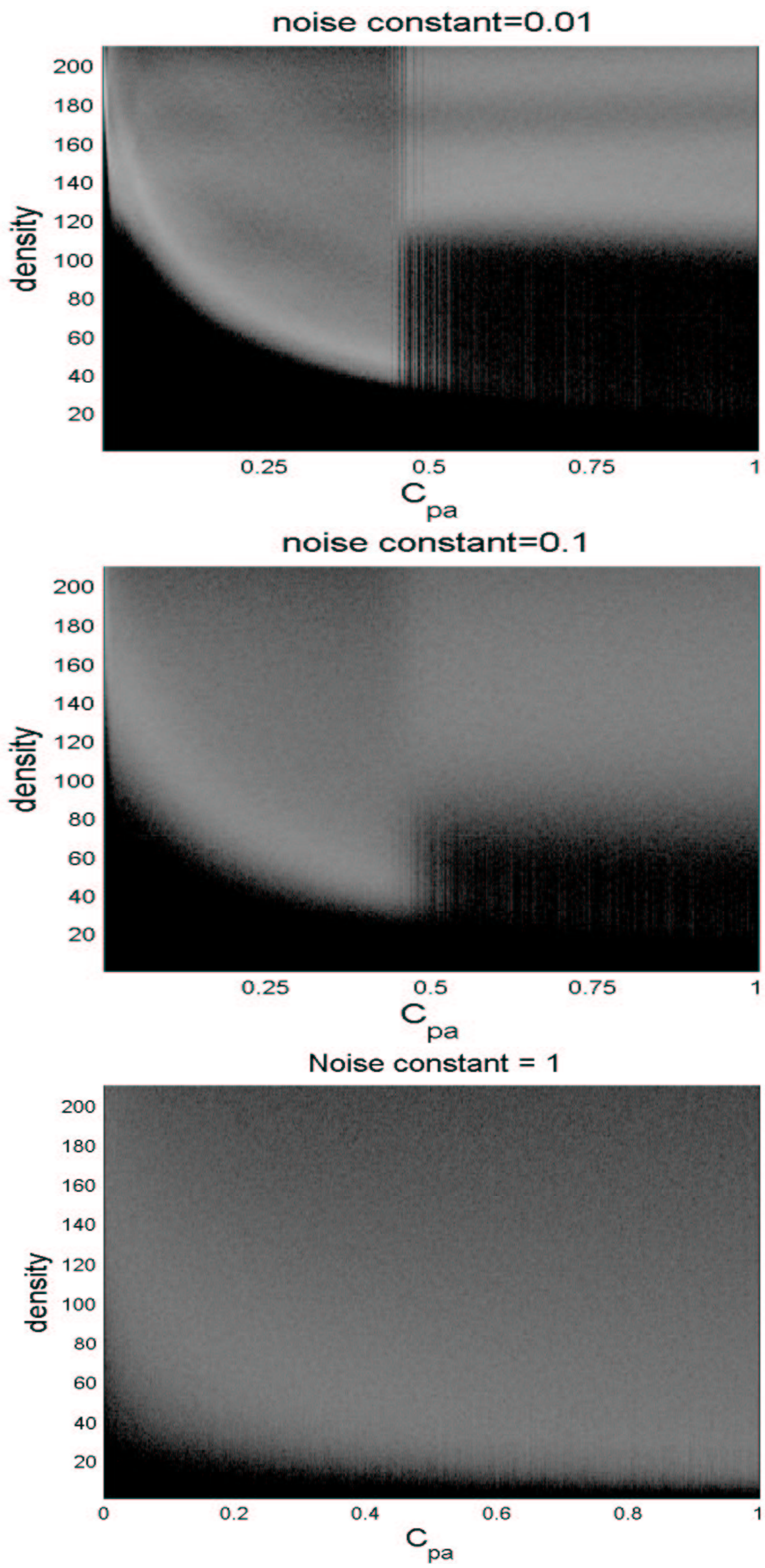

Figure 8: Density bifurcation diagram for various noise constant.

For very small amplitude noise, the form of the graph looks similar to the bifurcation diagram without noise terms. However, we can no longer predict where we can be sure of periodicity. For $\epsilon = 0.001$, there is a 3-periodic cycle around $C_{pa} = 0.9$. If we choose the noise constant small enough, then the bifurcation diagram will approach the old bifurcation diagram. The effect of noise is to blur the bifurcation diagram. Structure is still apparent even for $\epsilon = 0.1$. But, as the noise constant increases, more and more structure is destroyed.

Chapter 4

Diffusion

The few ecological studies of chaos in spatial systems consider models in discrete time and space [3] or in discrete time and continuous space [4]. In all these models, the diffusive dispersal of organisms drives the biological system (prey-predator or host-parasitoid system) into chaotic dynamics. The results of discrete models cannot be applied directly to nonlinear interactions and dispersal in continuous time and space. It is well known that discrete models exhibit chaos more readily than their continuous counterparts. For example, chaotic dynamics is possible for discrete time models of even a single species, but require at least three variables in continuous time. In this section, we will investigate the behavior of the insect population with diffusion.

Simulations of the model have shown that diffusion can drive adults into complex patterns of variability in time. The main point of my thesis is to determine whether these patterns are chaotic. We will demonstrate that there is diffusion–induced chaos and diffusion–induced periodicity in the LPA model with diffusion.

4.0.1 The Model

To pose the problem in its simplest form, we will assume that we are investigating the deterministic skeleton and $\Sigma = 0$. We will also assume that only adults move to other insect niches and no unpredictable external factors are acting. We set the rate of diffusion, d, to be the same for all niches.

With these assumptions, we can generalize the LPA model to include the effects of diffusion. Consider a single dimension along which adults diffuse at the same constant rate d.

Larvae and pupae do not move. Thus, there is no diffusion term in the populations of larvae and pupae .

$$L^j_{t+1} = bA^j_t \exp(-C_{el}L^j_t - C_{ea}A^j_t); \tag{4.1}$$

$$P^j_{t+1} = L^j_t(1-\mu_l); \tag{4.2}$$

where j is jth bin and t is the time

Now, consider the dynamics of the adult population. We will assume that adults can diffuse between bins. The equations in this case become

$$A^j_{t+1} = P^j_t \exp(-C_{pa}A^j_t) + A^j_t(1-\mu_a) + d(A^{j+1}_t - 2A^j_t + A^{j-1}_t) \tag{4.3}$$

$$A^j_{t+1} = P^j_t \exp(-C_{pa}A^j_t) + A^j_t(1-\mu_a) + d(A^{j-1}_t - A^j_t) \tag{4.4}$$

$$A^j_{t+1} = P^j_t \exp(-C_{pa}A^j_t) + A^j_t(1-\mu_a) + d(A^{j+1}_t - A^j_t) \tag{4.5}$$

where d is a diffusion coefficient.

Eq (4.3) is the case for interior bins, Eq (4.4) is the case for the right boundary, and Eq (4.5) is the case for the left boundary.

Numerical Method

For the case $\Sigma = 0$ and the parameter which we indicated in section 3.4.1, we plot the density bifurcation diagram for the LPA model with diffusion. The time iteration is 64000 steps. We consider 10 bins. When we change the diffusion coefficient, we will see the dynamics change.

We will show results from two cases; $C_{pa} = 0.55$ (periodic when $d = 0$) and $C_{pa} = 0.3$ (chaotic when $d = 0$).

Density Bifurcation Diagram

Figure 9 is the diffusion density bifurcation diagram for $C_{pa} = 0.55$. For various values of the diffusion coefficient, the total population density changes. The first figure of Figure 9 has a range of diffusion coefficient from 0.001 to 0.02 and below two graphs are for $d = 0.001$

to 0.0015 and for d = 0.017 to 0.02. For d = 0.001 to 0.005, it seems that there are only periodic cycles. However, between periodic cycles, some chaotic behavior occurs. For $d \in$ [0.005 0.0173], chaotic behavior occurs. In that region, periodic cycles do not appear. Look at the right figure of Figure 9. This figure is focused on the range of d from 0.0170 to 0.02. As you see it, the bifurcation occurs at $d = 0.0177$ from chaotic to periodic cycles and again for d = 0.0183, the periodic cycles change to chaotic behavior. For this parameter ($C_{pa} = 0.55$), we conclude that changing the diffusion coefficient can induce either chaos or periodic dynamics.

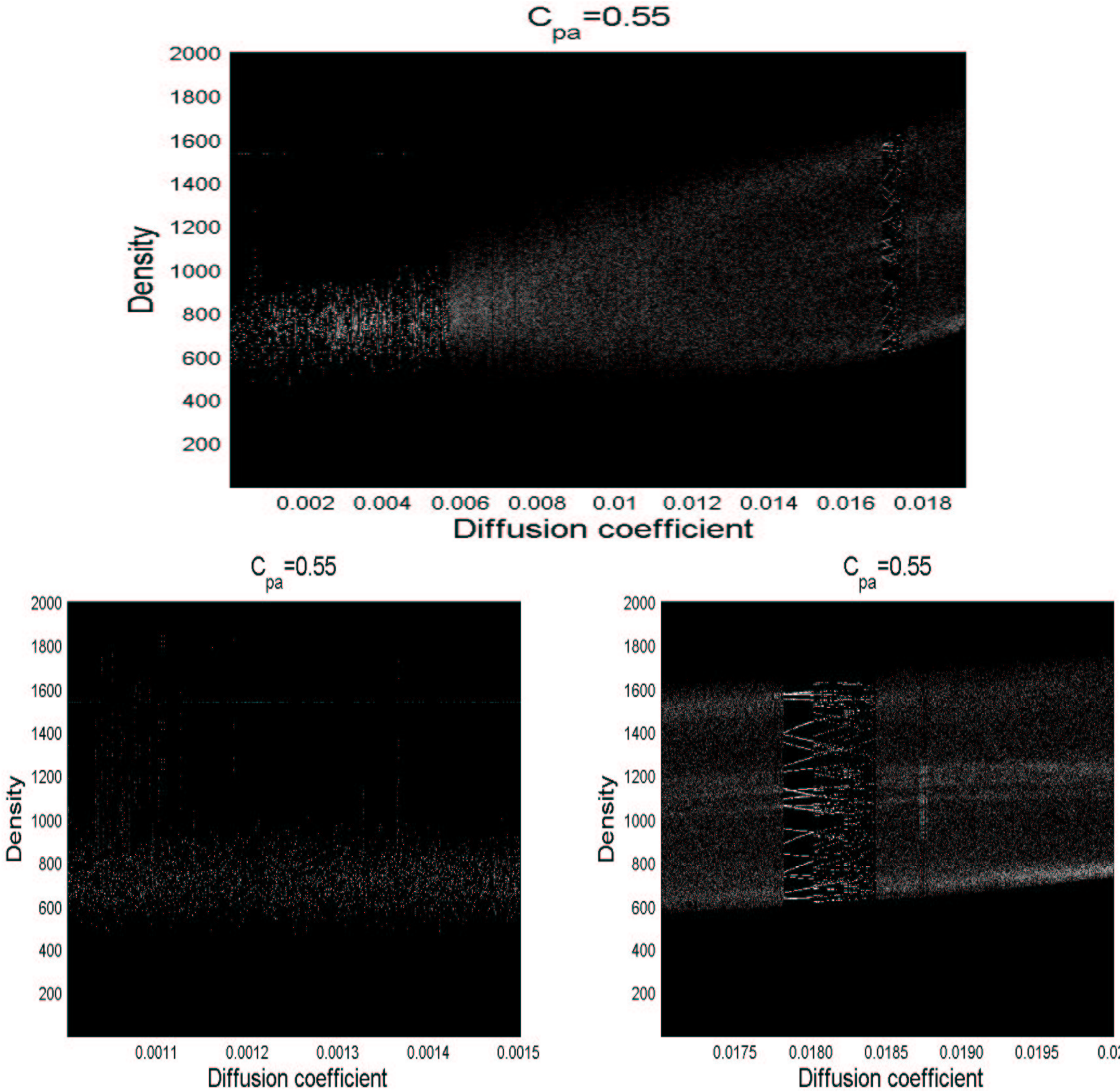

Figure 9: Diffusion Density Bifurcation diagram for total population numbers with diffusion ($C_{pa} = 0.55$) using deterministic skeleton ($\sum = 0$)

Figure 10 shows the diffusion density bifurcation diagram for $C_{pa} = 0.3$. For $d = 0$, there is chaotic behavior. For $d \neq 0$, for various values of d, there are both chaotic and periodic cycles. Almost all regions exhibit chaos, however, for $d = 0.0186$, the bifurcation occurs from chaotic to periodic cycles. In this case, the diffusion coefficient induces periodic cycles in a previously chaotic system.

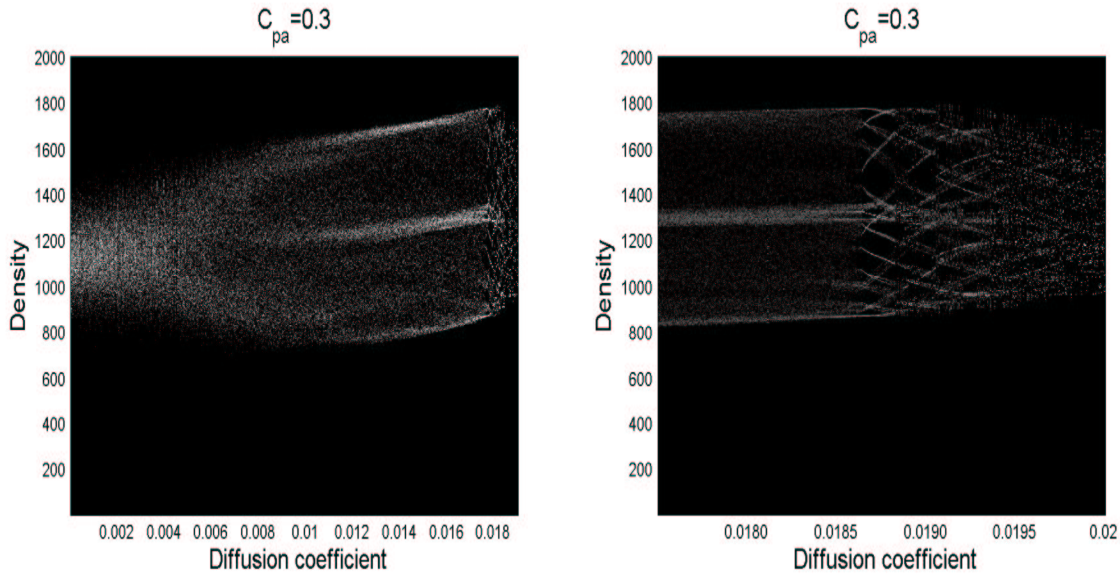

FIGURE 10: DENSITY BIFURCATION DIAGRAM FOR TOTAL POPULATION NUMBERS WITH DIFFUSION ($C_{pa} = 0.3$) USING DETERMINISTIC SKELETON ($\sum = 0$)

Chapter 5

Conclusion

We discussed the dynamics of total population with the LPA model. In this discussion, we used the density bifurcation diagram (without noise and with noise) to see the dynamics.

The effect of noise is to blur the density bifurcation diagram. Small-scale features blur most easily and large-scale features retain their characteristics longer as the amplitude of noise increases. In the experimental setting ($\epsilon = 1$), therefore, in the last panel of Figure 8, we show predicted population densities for $C_{pa} = 0$ to 1. No fine detail is visible. The only relic of the solution is the change in the lower population limit as a function of C_{pa}. Even if the noise constant is large enough, the dynamics of total population is not extinct.

In the diffusion case, we have shown that there is another parameter that may induce chaos, the diffusion coefficient, d. Conversely, we have also shown that diffusion can also induce periodicity in a previously chaotic system.

Can diffusion induced chaos be observed? In an experimental setting, if the equations for the evolution of the system are unknown, then one is at most able to determine if the dynamics is chaotic or not. However, in deliberately designed experiment, when the equations for the dynamics are known and the diffusion coefficient can be freely control, one can certainly study if diffusion induced chaos has occurred and what diffusion coefficient level can induce chaos.

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