



CHAOTIC DYNAMICS IN A POPULATION OF *TRIBOLIUM CASTANEUM*

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ABSTRACT

A nonlinear demographic model which has been used to predict the population dynamics of the flour beetle (*Tribolium castaneum*) was simulated. A set of different equations (the LPA model) which describe the nonlinear life-stage interactions, predominantly cannibalism was used. Manipulating the adult mortality rate, the changes in the dynamics from stable fixed points to periodic cycles and from periodic oscillations to chaos were observed. Phase-space graphs of the data provided evidence of chaotic behaviour. In order to take into consideration the natural fluctuations, some noise of various intensities was introduced into the system. Results show an elongation of the chaotic region and an increase in Lyapunov exponent due to the introduction of noise.

Keywords: Population dynamics, chaos, difference equation, noise.

INTRODUCTION

Complex dynamics, capable of exhibiting chaos, in biological phenomena such as neuronal behaviour, ecological systems, the rhythms of heartbeats, walking strides, and animal populations have been described and predicted by mathematical models. Mathematical models do suggest that aperiodic oscillations are ubiquitous in time and space, and play an important as well as constructive role in stabilization, self-organization, control and understanding physical systems (Pool, 1989; Fuwape, 1995; Constantino *et al.*, 1995; Constantino *et al.*, 1997; Sarbadhikari and Chakrabarty, 2001 and Fuwape *et al.*, 2007).

Tribolium castaneum (Herbst) (Coleoptera: Tenebrionidae) attack stored grain products such as flour, cereals, meal, crackers, beans, spices, pasta, cake mix, dried pet food, dried flowers, chocolate, nuts, seeds, and even dried museum specimens (Toews *et al.*, 2006). *Tribolium* has been studied and discovered to have an high reproductive rates, short life-cycle, ease of culture, and accurate censuring of all life stages, all of which make this specie easy to manipulate in the laboratory setting (Brian *et al.*, 1995). These characteristics make it a

suitable candidate for laboratory experiments in population studies.

A study of the population dynamics of *Tribolium* was carried out by Constantino *et al* (1995) and a discrete map with three variables was used to model the population dynamics of the Larva, Pupae and Adult (LPA) life stages of the flour beetle (Dennis *et al.*, 1994). The authors used a model represented by a system of three nonlinear difference equations.

$$\begin{aligned} L_{t+1} &= b A_t \\ P_{t+1} &= L_t (1 - \mu_l) \\ A_{t+1} &= P_t (1 - \mu_p) + A_t (1 - \mu_a) \end{aligned} \quad (1)$$

where b is the birth rate of the species (the number of new larvae per adult each time unit) and μ_l , μ_p , and μ_a are the death rates of the larva, pupa, and adult respectively. However, because *Tribolium* exhibit cannibalism under overpopulation stress, the standard model had to be modified to account for this trait. Under the conditions of overcrowding, adults will eat the pupae and unhatched eggs (future larvae), while larvae will also eat the eggs. Therefore, there is need for a new model that will address the cannibalistic trait. Hence, the deterministic LPA model:

$$\begin{aligned} L_{t+1} &= b A_t \exp(-C_{ea} A_t - C_{el} L_t) \\ P_{t+1} &= L_t (1 - \mu_l) \end{aligned} \quad (2)$$

$$A_{t+1} = P_t \exp(-C_{pa} A_t) + A_t (1 - \mu_a)$$

The fraction $\exp(-C_{ea}A_t)$ and $\exp(-C_{el}L_t)$ are the probabilities that an egg is not eaten in the presence of A_t adults and L_t larvae respectively. The fraction $\exp(-C_{pa}A_t)$ is the survival probability of a pupa in the presence of A_t adults. The quantity $b>0$ is the number of larva recruits per adult per unit of time in the absence of cannibalism. The values $C_{el} = 0.04$, $C_{ea} = 0.011$, $b = 7.88$, $\mu_l = 0.161$, $C_{pa} = 0.004$, $\mu_p = 0$ as proposed by McClure (2010) were used throughout this work.

However, due to inherent biological complexity and variation we cannot expect the model to always yield results that fits experimental data perfectly. This is because the LPA model does not take into account all biological factors related to the beetle. Processes such as birth rates and death rates may vary across a population and fluctuate with time, and so we will not be able to find a set of parameter values under which the model exactly matches the data. The best we can hope for are parameter values which give us model predictions closest to the observed data.

We incorporated “noise,” into our model in order to account for the fluctuations factors. The two main types of noise are environmental and demographic in nature. The main source of demographic noise is variation in model parameters, such as birth and death rates within a population. Environmental stochasticity reflects disturbances affecting the entire population, such as fluctuations in weather. Demographic noise typically predominates at low population levels, while environmental noise is often the main source of variation at high population levels (Robertson, 2009).

We introduce noise on the logarithmic scale to equation (2), as follows:

$$\begin{aligned} L_{t+1} &= b A_t \exp(-C_{ea} A_t - C_{el} L_t + E_{1t}) \\ P_{t+1} &= L_t (1 - \mu_l) \exp(E_{2t}) \end{aligned} \quad (3)$$

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

Here E_{1t} , E_{2t} , E_{3t} are random noise variables assumed to have a joint multivariate normal distribution with means of zero. The noise variables represent the unpredictable departures of the observations from the deterministic model due to environmental and other factors.

MATERIALS AND METHODS

The model was solved by stepping forward in time x_{n+1} from a known time x_n using a time step Δt over a time span, N . From a mathematical point of view, a small other than a large value of Δt will yield results of higher accuracy. Therefore, we employed a time step $\Delta t = 0.001$ over a time span $N = 100000$.

The easiest way to observe changes in a chaotic system is by varying a parameter in the system with time (a **time series**). The axis that normally represents time can also be used for some other variable. In other words, the new graph involves more than one variable (besides time). In more formal terms, phase space or state space is an abstract mathematical space in which **coordinates** represent the variables needed to specify the phase (or state) of a dynamical system.

Numerous algorithms and techniques have been developed to detect chaos in both discrete and continuous systems. One of the most commonly used methods is by evaluating the Lyapunov Exponent given by (4).

$$\lambda = \lim_{n \rightarrow \infty} \frac{1}{n} \sum_{t=0}^{n-1} \ln |f'(x)| \quad (4)$$

where λ is the Lyapunov exponent and $f'(x)$ is a function of the original time series and n is the length of the time series under consideration. The case of $\lambda > 0$ is of particular interest. A dynamical system with positive Lyapunov exponent is said to be chaotic. The path of such a system is extremely sensitive to change in the initial conditions (Wolf *et al.*, 1985).

A uniformly distributed noise (f) is used to simulate environmental and other factors. This is given by

$$f(x, \mu, \sigma) = \frac{1}{\sigma \sqrt{2\pi}} e^{-\frac{(x-\mu)^2}{2\sigma^2}}$$

where μ is the mean of the data set and σ is the standard deviation. The noise is created to have a mean value of zero and standard deviation of 1. The software Lyapunov Exponents Toolbox (LET) using an algorithm proposed by Wolt *et al.* (1985) was used in this work to evaluate the Lyapunov Exponent. Initial conditions of $[L,P,A]=[1, 3, 5]$ is used throughout this research. Bifurcation diagrams are qualitative changes in the dynamics of a system as a parameter is varied (Strogatz, 1994).

RESULTS

The LPA model was solved numerically as described in the above section. Noise strengths are in the range [0 1], therefore, sample noise values 0.2, 0.5 and 0.9 were chosen to represent low, average and high noise levels. The population of larva after a time (t) without noise introduced into the system is shown in figure 1a while the same system with noise of strength $d = 0.2, 0.5$ and 0.9 are shown in figures 1b, c and d respectively. The total population of beetles (pupa + larvae + adult) is plotted against mortality rate for the case of noiseless system (figure 2a) and noise strength of 0.2 and 0.9 (figures 2b and 2c respectively). In comparison with figure 1a, a shrink in the chaotic region is seen in figures (3b – 3c) coupled with an elongation of stable region in the range 0.75 – 0.95 for the system with noise strength $d = 0.2$ and $d = 0.5$ respectively. To compare the effect of noise on the nonlinearity in the LPA model, a plot of Lyapunov exponent was made for the different noise levels and compared with the noiseless system. The results are presented in figures 6a and 6b. A system with at least one positive Lyapunov exponent is regarded as chaotic (Strogatz, 1994).

DISCUSSION

One of the evidence of chaos is the period doubling window in bifurcation diagrams. From the results obtained with the noiseless system, period doubling windows were observed. Also periodic oscillations could be seen showing a period doubling route to chaos. However, with noise introduced into the system, it is observed that windows are found in the chaotic state with some periodic oscillations. Compared with the noiseless system, the windows in the noisy system are seen to be elongated. The Lyapunov exponent of the population of larvae and adult are shown in figures 6a and b respectively. The Lyapunov exponents are seen to increase with increasing noise level in both cases.

It can be deduced from the analysis that fluctuations of experimental flour beetle populations are explained largely by known nonlinear forces involving cannibalistic-stage interactions. The population fluctuations are a blend of deterministic forces and stochastic events. Using standard mathematical techniques to analyse the model, changes in adult mortality rate produces substantial shifts in population dynamic behaviour. Manipulating the adult mortality rate, it can be

concluded that there is a change in the dynamics from stable fixed points to periodic cycles to periodic oscillations.

Furthermore, from the graph of Lyapunov Exponent (figure 6), it can be inferred that the flour beetle system is deterministic in nature as its chaotic nature is independent of environmental factor (noise). Noise in the system, however, increases the Lyapunov exponent in both the Larva and Pupa population while its effect in the Adult population is reduced as time evolves.

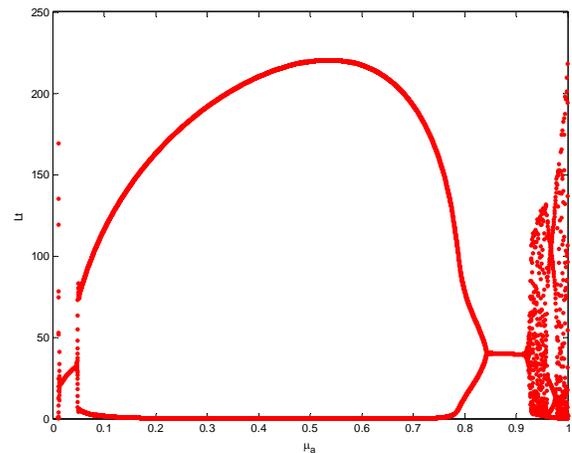


Figure 1(a): Bifurcation diagram showing the population of Larva (L_t) as the adult mortality rate (μ_a) is varied without noise.

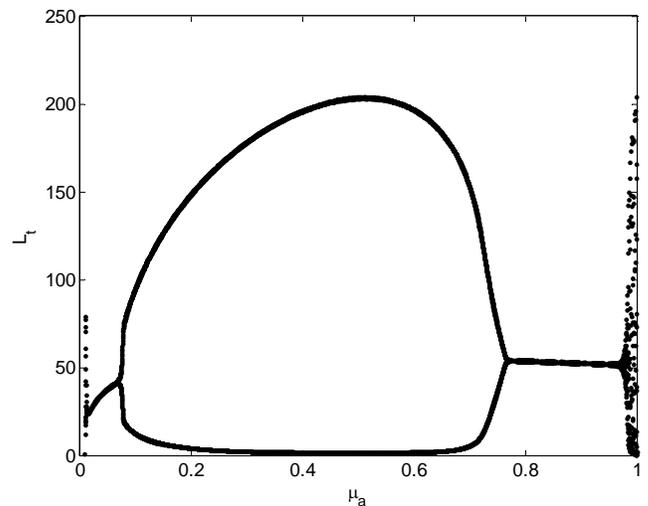


Figure 1(b) A graph of number of larva (L_t) against adult mortality rate (μ_a) (Between 0.01 and 1.0) with noise added to the system. Noise strength 0.2.

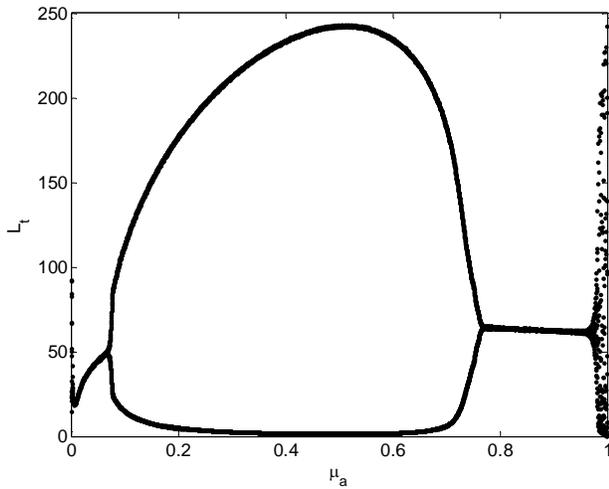


Figure 1(c) A graph of number of larva (L_t) against adult mortality rate (μ_a) (Between 0.01 and 1.0) with noise added to the system. Noise strength 0.5

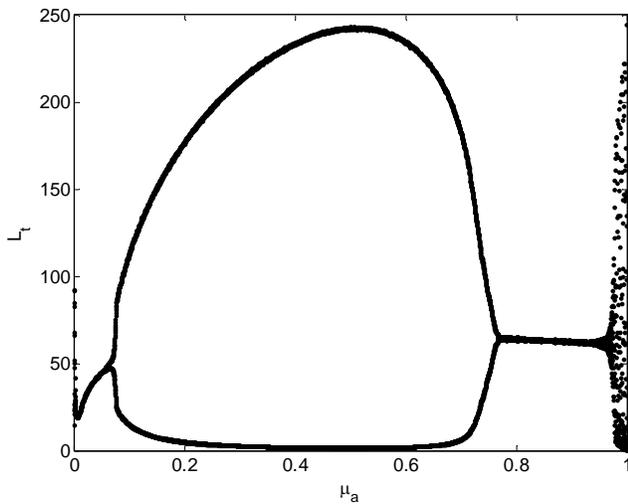


Figure 1(d) A graph of number of larva (L_t) against adult mortality rate (μ_a) (Between 0.01 and 1.0) with noise added to the system. Noise strength 0.9

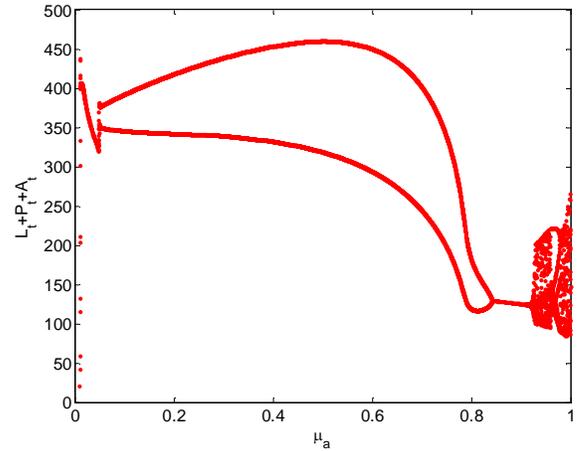


Figure 2a: Total population of flour beetle under investigation with varying adult mortality ratio while external noise is removed.

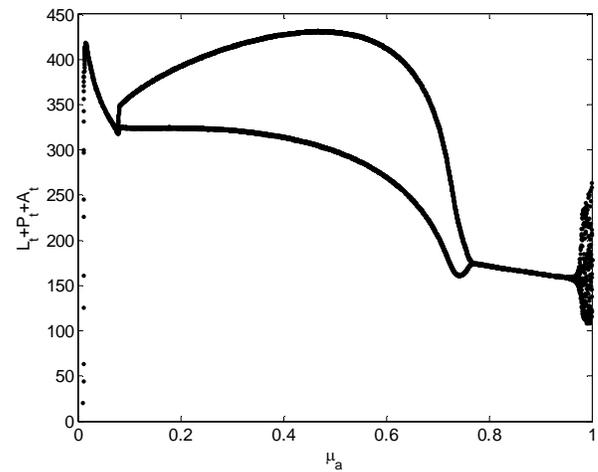


Figure 2b: Total population of flour beetle under investigation with varying adult mortality ratio while external noise is introduced. Noise strength is 0.2.