MODELLING HOST- PARASITOID SYSTEM DYNAMICS APPLICABLE TO DIAMONDBACK MOTH FLUCTUATIONS

By

Henri Edouard Zefack Tonnang
M.Sc. (Physics, University of Dschang, Cameroon)
&
M.Sc. (Microprocessors and Control Engineering, University of Ibadan, Nigeria)

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DECLARATION

I, Henri Edouard Zefack Tonnang do hereby declare that this PhD thesis is my original work and it has not been presented for the award of a degree in any other university.

Signature.......................................Date........10/09/2008..................

Henri Edouard Zefack Tonnang

This thesis has been submitted with our approval as his supervisors.

Signature.......................................Date..11th September, 2008...

Prof. Horace Ochanda

Signature.......................................Date...11th -September-2008.............

Prof. John Okoth Owino

DEDICATION

To Him be all the glory

This work is dedicated to the Almighty God

And

To the advancement of sciences

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ABSTRACT

Integrated pest management (IPM) systems utilising the use/release of the parasitoid *Diadegma semiclausum* have been developed to replace the pesticides only approach to diamondback moth (DBM) *Plutella xylostella* (L.), worldwide the worst insect pest of cabbage family. The successful introduction of the DBM natural enemy in Kenya as a biological control agent under the IPM system is a good achievement towards a solution to excessive insecticides use. Data collections were done for 15 months before the release and 36 months after release of the parasitoid in two areas; in Werugha, Coast Province of Kenya and Tharuni, Central Province of Kenya, respectively. To expand the available IPM tools for better management of the pest, there is need for a model. Such a tool will help in monitoring and forecasting (early warning) of potential outbreaks, which will facilitate formulation of policies and future control strategies

The search and development of parasitoid-host models system dynamics applicable to diamondback moth (DBM) and its exotic parasitoid *Diadegma semiclausum* was done. This study is similar to predator-prey systems, in which the first species (parasitoid or predator) is dependent on the second species (host or prey) for subsistence. The first phase focused on the mechanistic modelling technique. Collected datasets were used to test most of well-known models (Lotka-Voltera model, Leslie model, Nicholson-Bailey, Hassel & Varley, Beddington, Free & Lawton, May, Holling type 2, 3 and Getz & Mills functional responses, etc...) to find the most suitable model for the dynamism and interactions between DBM and its natural enemy *D. semiclausum*. Models with continuous equations were solved via a computer program written in C/C++ using the Runge-Kutta 4^{th} algorithm with 0.01 step size. A loss function was developed, made of the square difference between the theoretical and empirical values of datasets. This routine was combined as unique function and embedded in a Nelder-Mead algorithm or Pawell,s multidimensional method and minimized with randomly chosen initial values of parameters. An attempt to evaluate the biological control impact using Lotka-Volterra model was made. Knowledge based adaptive models using artificial intelligence technique (neural networks) was applied for the prediction of DBM and *D. semiclausum* population density. The Knowledge based method showed good predictions capabilities than mechanistic models. Lack of abiotic factors for model parameters restoration may be the reasons of poor prediction for mechanistic models. More realistic procedure for model parameters restoration (Knowledge-based fitting), which can account for all factors was developed. Statistical analysis and comparison between the different developed models was performed. The Lokta-Volterra model has measured the parasitoids impact on the DBM biological control through a quantitative estimate of the effectiveness of the newly introduced species *D. semiclausum*. These equations may therefore be used as tool for decision making in the implementation for such pests management system strategy. An artificial neural network was identified as the best tool for DBM and *D.semiclausum* population density prediction.

NOTATIONS AND ABBREVIATIONS

Special notation s for specific chapters can be found in those chapters

Notations and abbreviation generally used are given below:

n: number of units in the sample size.

$n_{x:}$ number of units containing x individuals.

DBM: diamondback moth.

R: multiple correlation coefficient.

R^2: coefficient of multiple determination

D. semiclausum: diadegma semiclausum.

IMP: integrated pest management.

ANN: artificial neural network

FL: fuzzy logic

MLP: multilayer perceptron

icipe: International centre of Insect Physiology and Ecology

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Chapter 1

Introduction

1.1 Models utilities in ecology

In theoretical ecology, models are used for several purposes. Models help explore possibilities (Cooper, 1990) by enabling biologists to become fully aware of potential relations between natural phenomena during variables and parameters tracking exercises. They also offer scientists means through which they can investigate complex systems. In this case, models are used as baseline for identifying and recognizing the important ways in which more complex phenomena deviate from simple representations (Odenbaugh, 2005). Models provide researchers with conceptual framework, which help ecologists carrying out experimental investigations and pose questions that can lead to the construction of concepts corresponding to various natural properties that were not striking. Models also aid attempts to predict future changes and can be invaluable for management purposes. Finally, from models, explanations can be generated offering better understanding of the inner wor king of a system, which can lead us to making more effective decisions (Johnson and Omland, 2004).

From system management aspect, there are two groups of models, namely:

(i) Strategic Models

(ii) Tactical Models

Strategic models are designed to explore the ramifications of general questions in ecology. For example, we may want to know if an interaction between species prey-predator with discrete generations and random search by predator give rise to persistent population cycles or not?

Tactical models are specifically made for particular system and designed for forecasting reasons. This second group of models is intensively applied in integrated pest management programs to predict the likelihood success of its implementation, the number and appropriate time for parasitoid release (Godfray and Rees, 2002).

1.2 Host-parasitoid system: Diamondback moth-*Diadegma semiclausum*

Host-parasitoid system is an ecological interaction between victim (host) and exploiter (parasitoid) where the second species consume biomass from the first species (Hamish, 2000). Parasitoid is a term generally used to describe insects that develop as larva on the tissue of other arthropods (usually an insect), which they eventually kill (Hassell and Waage, 1984). Adult female parasitoids forage actively for host and deposit their eggs, on or near host individuals. After hatching, the larvae begin feeding on host tissues and complete their development either within or on the host. Godfray (1994) mentioned that parasitoids are abundant in almost all terrestrial ecosystems and they are one of the main sources of mortality for their hosts.

Diamondback moth (DBM), *plutella xylostella L.* is the major pest of Brassica crops worldwide, with the ability to develop resistance to all pesticides based against them (Talekar and Shelton, 1993). For this reason, development and implementation of Integrated Pest Management (IPM) based on biological control is now considered to be the best solution to combat this highly resistant insect pest. In the past years, development and implementation of biological control-based IPM has made remarkable achievement in the management of DBM in many parts of the world such as Southeast Asia and United States of America (Telekar and Shelton, 1993). IPM has been based on the introduction and augmentation of insect parasitoids or natural enemies in various farms where crucifer vegetables are cultivated

Figure 1.1 Diamondback moth adults

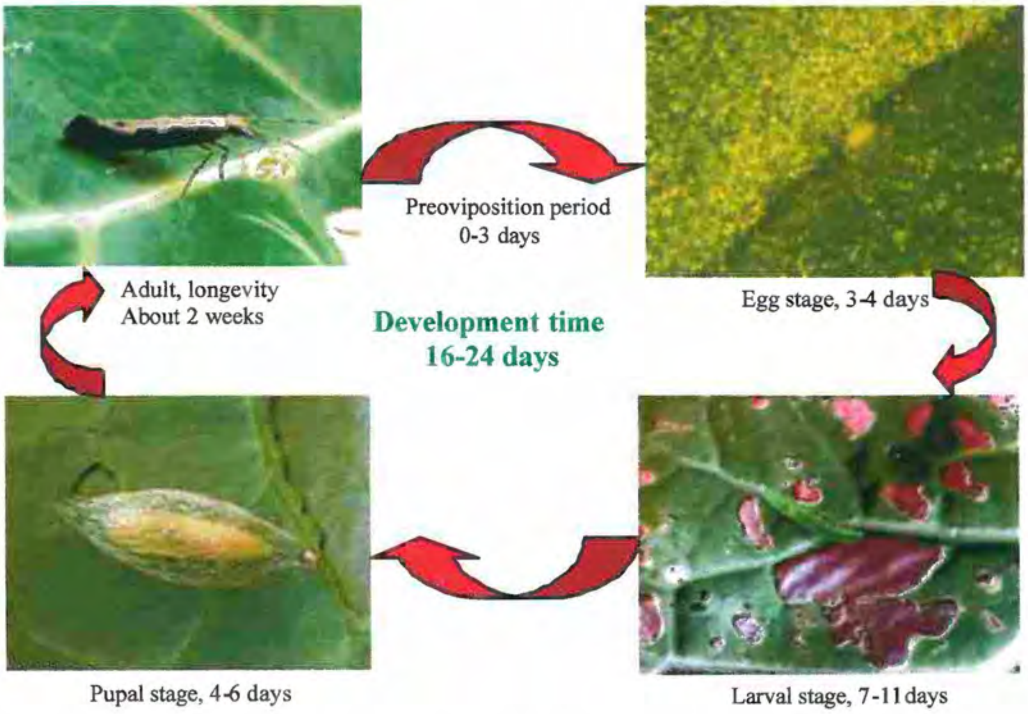

Figure 1.2 Life cycle of Diamondback moth (at ~ 25°C)

Figure 1.3 Diamondback moth damage on cabbage plant

Figure 1.4 Diamondback moth larvae damaging the cabbage leave

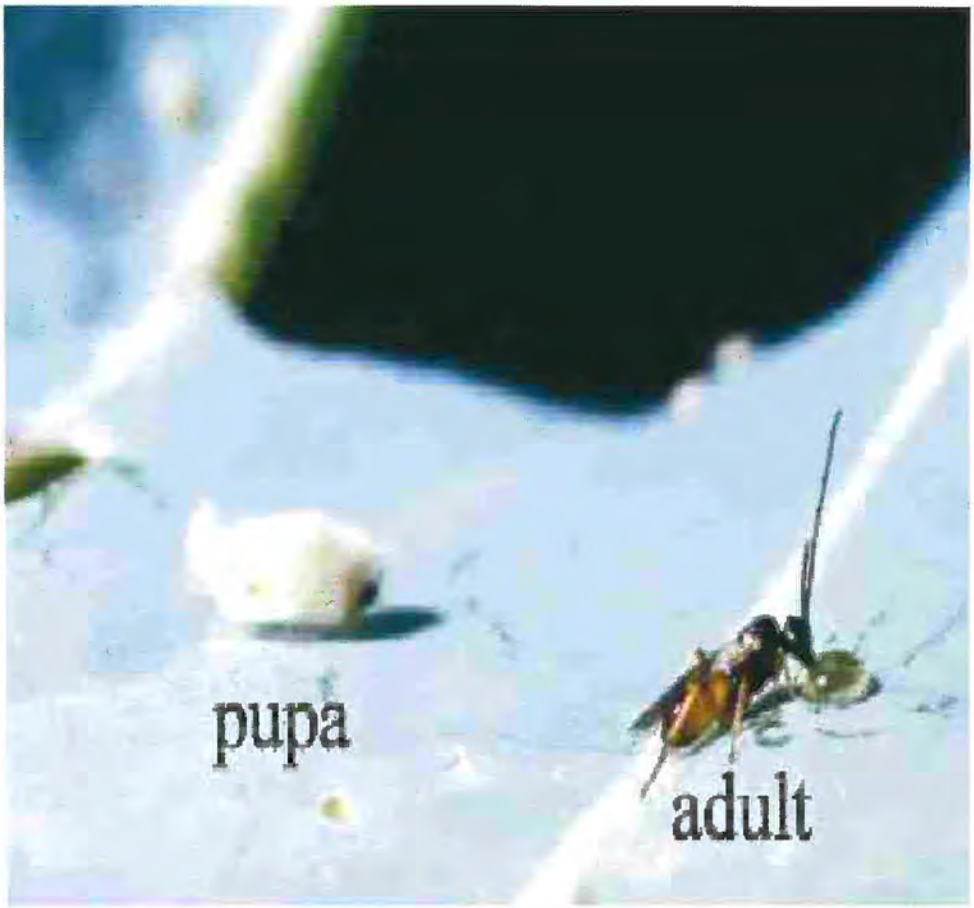

Figure1.5 *Diadegma semiclausum* pupa and adult

Diadegma semiclausum, (Hellen) is an exotic parasitoid was released in Kenya for biological control of the diamondback moth (DBM), *Plutella xylostella L.* the worst pest of crucifers in East Africa. Population dynamics of the pest and its parasitoids were studied one year before and three years after the release of the parasitoid.

1.3 Biology and ecology of the diamondback moth and the *Diadegma semiclausum*

Diamondback moth adults are slender, small, 1/3 inch (8.33mm) long, greyish-brown moths with folded wings flaring outwards and upwards at their posterior ends (Figure 1.1). They are distinguished by "having" three pale, triangular markings along the inner margin of the wings (Figure 1.1). Moth activity is greatest at dusk and dawn. They hover around plants searching for a mate or a place to deposit eggs. Male moths are attracted to the pheromones produced by females. During the day, moths can be flushed out and easily noticed by walking down between the crop rows. (Harcourt, 1957; Telekar and Shelton, 1993). Diamondback moths lay their eggs singly or in groups of two or three on the underside of lower leaves near the leaf veins or on the lower stalks. Egg hatch in 5 to 10 days depending on the prevailing temperatures (~ $25^{O}C$) (Figure 1.2). Diamondback larvae pass through four instars (growth stages). Upon hatching, they begin mining within the leaf tissue, whereas later instars feed on the leaves of young plants and/or the underside of the leaf surfaces of more mature plants (Figures 1.3-1.4). The diamondback moth larva can damage cruciferous plants by feeding and mining the leaves (Figure 1.4) (Velasco, 1982; Talekar and Yang, 1991; Konig *et al.*, 1993; Telekar and Shelton, 1993).

Diadegma -semiclausum (Figure1.5) is a solitary koinobiont endoparasitoid of DBM, black in colour and 5-7 mm long. Females live up to 37 days when fed on 10% sugar solution and 73 days when fed on dilute honey and can lay eggs 28 days after emergence. Males can survive for a period of 40 days when fed on either sugar solution or dilute honey (Ooi, 1992). The four larval stages of DBM are attacked by *Diadegma semiclausum* with preference to the second and third larval instars. Temperature in the range 15°C-25°C results in the sex ratio of about 1:1 and 25°C is considered as the optimum temperature for parasitoid development. After pupation of the host larva, the parasitoid larva completes eating up the host and thereafter forms its own cocoon. An adult parasitoid emerges in about five days after cocoon formation (at 25°C). The adult parasitoid feeds on flower nectar, mates and starts laying eggs after emergence (Fitton and Walker, 1992). Parasitism rates of this parasitoid are host-density-dependent and super parasitism is known to result in production of more female than male progeny (Koning *et al*, 1993). When the parasitoid is allowed to choose between parasitized and unparasitized DBM larvae, it is able to distinguish between parasitized and unparasitized host larvae, showing preference for the unparasitized larvae.

1.4 Brief history of modelling methods for host-parasitoid system

Until now, host-parasitoid dynamics have been modelled in two ways. The first approach uses computer simulation where virtual reality of agricultural pests with the explicit aim of improving pest management rather than understanding the underlying biology (Gutierrez and Baumgartner, 1984). The second way is based on pure mathematical differential equation with the assumption that birth and death are continuous processes as developed by (Lotka , 1925; Volterra, 1931; Turchin, 2003) or discrete processes initiated by Nicholson and Bailey (1935) and terminated by Hassel (2000).

Nicholson model was developed under the assumption that parasitoidS randomly search for the host. The phase analysis of the model shows divergent oscillation and extinction of one or both insects, what prompted the first and experimental studies on host-parasitoid. Discrepancies between model prediction and experimental results led to the development of more realistic models. In 1987, Murdoch *et al.* developed a host-parasitoid model made of considerable biological details such as age-structured and spatial processes. Spatial models are becoming fore in host-parasitoid models, Hassel *et al.* (1991) studied the behaviour of two-dimensional array of host-parasitoid populations. There show that interesting patterns emerged in particular spiral structure where waves of host are chased through time by waves of parasitoid and in other cases; a pattern that appear to be chaotic. There has been some speculation that metapopulation models may be appropriate for host-parasitoid dynamics, a case of "blinking light" metapopulation in which the whole population is susceptible to extinction, and core-satellite met populations in which one core or more "mainland" populations send out the colonist to more evanescent "island" populations (Godfray and Shimada, 1999)

Generally, these models offered tangible results, proving how host and their parasitoids show population cycles with a period approximately equal to one host generation. These cycles can be explained by temporary synchronization of the host age structure by rare events such as droughts or hurricane. With deep biological knowledge, cycles can also be explained by the fact that majority of parasitoid eggs are laid at the peak of the host generation cycle giving rise to a burst of parasitoids when host densities are at a trough in density, reinforcing the cycle (Godfray and Rees, 2002).

1.5 Problem statement

Previous studies on host-parasitoid models are limited on qualitative analysis and comparison of theoretical results with experimental time series data. The present study aims at linking equations that explain host-parasitoid dynamics and interactions to field time series data and in developing knowledge based model using artificial neural network for host-parasitoid population density.

1.6 Objectives

1.6.1 General Objective

Modelling the population dynamics and interaction between the diamondback moth and its natural enemies, *Diadegma semiclausum*

1.6.2 Specific objectives

(i) Link existing predator-prey models with collected Diamondback moth and *Diadegma semiclausum* datasets

(ii) Develop knowledge based adaptive models using ANN

(iii) Comparative studies between different models and selection of the best model for the description of DBM fluctuations

(iv) Propose a procedure for models fitting

1.7 Justification of the study

Cabbages and kale are one of the bases of smallholder vegetable farming in Kenya. They are a major vegetable consumed by a large number of the population. DBM has been for many decades; their major pest and usually farmers spend a lot of money on the purchase of insecticides to fight against this pest. We all know the negative impact of insecticide to the environment and its bad effects on human health. The successful introduction of the DBM natural enemy in Kenya as biological control agent under the IPM system is a good achievement towards solving the problem of excessive insecticide use. To expand the available IPM tools for better management of the pest, there is need for a model capable of explaining the dynamism and interactions between these two organisms: the DBM and its natural enemy. Such a tool will help in monitoring and forecasting (early warning) of potential outbreaks, which will facilitate formulation of policies and future control strategies in Kenya and other parts of the world where the pest is important.

Chapter 2

General Materials and methods

The first section of this chapter deals with material used and the second covers the methods employed in this study

2.1 Materials

In this section the site description and the crops growing are described

2.1.1 Site description

Experimental results were obtained from the pilot release areas in Werugha Location (03° 26' 16'' S; 38° 20' 24'' E) of Wundanyi Division in Taita Taveta District, Coast Province of Kenya and Tharuni Location (01° 08' 12'' S; 036° 37' 51'' E) Limuru Division, Kiambu District, Central Province (Figure 2.1). These regions were selected because of their isolated location. In case of any harmful effect of the newly introduced species in the environment, an alleviate control measures could be undertaken. The two sites are about 500 km apart and are renowned for vegetable production all year round. They are main suppliers of cabbage and kale to Kenya's biggest cities; Nairobi and Mombassa respectively.

Werugha is located on an island mountain, Taita Hills, rising from an area of about 700m elevation to 2,200m. The peak of the mountain measures about 10x25km and stretches roughly in a south/north direction. Crucifer production is concentrated between 1,600-1,800 m elevation and mainly rain fed. Additional irrigation during the dry seasons is common using buckets to draw water from shallow wells. Much of the land is terraced and crucifer production moves up on the terraces during the rainy seasons and down to the valley bottom in dry seasons, this ensures year-round production. The major staple crop is maize and several species of crucifers are grown

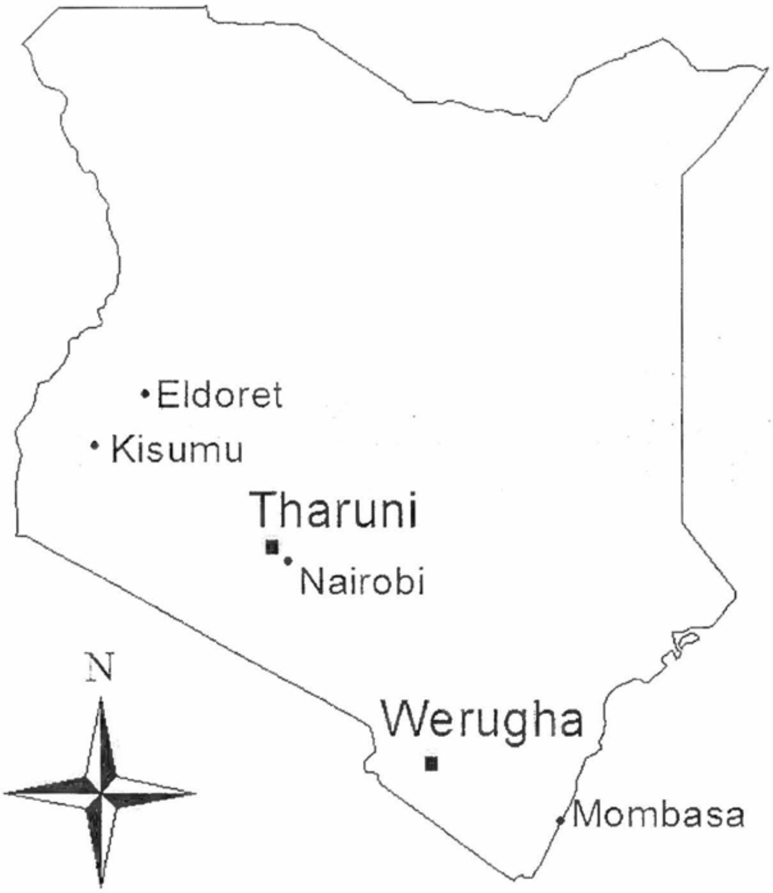

Figure 2.1 Kenya map showing the time series data sources

with head cabbage (*Brassica oleracea* var. *capitata*) as the main cash crop. Soils are mostly degraded, low in organic matter and sandy.

Tharuni is located below the ridge along the inner slope of the eastern escarpment of the Rift Valley at an altitude of approx. 2000m. Located on the leeward side, the area receives 450-700mm of rainfall per annum. The soils are sandy loam soils of low to medium fertility with a generally dusty and dry environment. Agricultural production is characterized by mixed cropping with maize and beans as the major staple crops and cabbage as the main cash crop grown mainly during the short and long rain (October to December and March to June, respectively). Kale (*Brassica oleracea acephala* L.) is grown throughout the year by all home steadand provides a refuge for both diamondback moth and natural enemies during the dry seasons.

2.2 Methods

Due to the complexity, dynamism and interaction within species in a giving ecosystem, our modelling approach was based on several modelling techniques. Firstly, searched for suitable mathematical modelling with the help of ordinary differential equations in continuous and discrete forms. Secondly, focus was made on a knowledge based adaptive modelling tool. In each part, proper statistical analysis was made to measure the models' efficiency.

In mathematical modelling technique, concentration was made on the testing well-known continuous models of prey-predator (Lotka-Voleterra, Holling-Tanner type 2 and type 3 and Leslie) and also some discrete time host-parasitoid systems such as Nicholson & Bailey and Hassel models. Continuous models equations were solved via a computer program written in C/C++ using the Runge-Kutta 4th algorithm with a

0.01 step size. A loss function was developed, made of the square difference between the theoretical and empirical values of datasets. This routine was combined as unique function and embedded in a Nelder-Mead algorithm or Pawell's multidimensional method and minimized with randomly chosen initial values of parameters.

2.2.1 Data collection

The aim was to evaluate fifteen farmer-managed farms in both areas at each sampling date. This was possible without problems in Werugha, where farmers used bucket irrigation and moved production from the terraces into valley bottoms in the dry season. In Tharuni, a place without access to irrigation water, the number of cabbage fields declined so much during the height of the long dry season, that in some occasions only six fields could be sampled. Sampling started in April 2001 in Werugha and until July 2003, fortnightly samplings were conducted which were changed to once every four weeks from August 2003 until the end of observations in July 2005. In Tharuni, fortnightly sampling was conducted from July 2001 – September 2003 followed by once every four weeks until September 2005. On July 26th, 2002, 25 pairs of *D. semiclausum* were released in five fields in Werugha and the same number was released on September 20th, 2002 in Tharuni.

Fields were selected at random with the help of the local extension officer in each area. A field was eligible for sampling from two weeks after transplanting onwards and the same field was visited until it was harvested. When a field had been harvested, a recently transplanted field in the immediate vicinity was chosen as replacement. Crop type and age, field management, pesticide applications and general conditions of the field were recorded. Ten plants were selected at random in each field and thoroughly checked, starting from the outer leaves towards the centre. The number of small larvae, big larvae, pupae and DBM adults was counted and recorded separately. Other pests found on individual plants were also recorded. The damage caused by diamondback moth was estimated using damage score of 0-5 (see Momanyi *et al.* 2006). Up to a maximum of five DBM larvae (3rd instar or older) or pupae were collected from each plant and put in individual vials for further investigations in the laboratory. Larvae were retained singly on a fresh cabbage leaf in labeled 30ml plastic vials at ambient temperatures of 21±2°C and checked daily until emergence of adult moths or parasitoids. Emerged parasitoids were identified, sexed and counted. Parasitism was calculated as the number of parasitized larvae/pupae divided by the total number collected. The percentage of parasitism was estimated for each collection. This was then multiplied by the total number of DBM population counted on the field and divided by 150 to estimate the number of parasitoids per plant. At the same time, the total number of DBM was divided by 150 to evaluate its population density per plant (Momanyi *et al.*, 2006).

A data logger (Hobo Pro Series, Onset Computer Corp. Pocasset, MA, USA) was used to record temperatures and relative humidity (hourly records), while rainfall records were obtained from the Kenya Meteorological Services.

2.2.2 Statistical criteria for parameter estimation

Parameter determination is a crucial phase in the analysis of empirical datasets. Several methods can be used for the estimation of model parameters; such as laboratory experiments to determine parameters like fecundity and survival. In this case, model parameters have concrete numerical values. An alternative for model parameter estimation is minimization of the value of the following function that uses empirical and theoretical dataset:

$$Q(\bar{\alpha},\bar{I})=\sum_{j=1}^{N}[x_j^{*}-G^{(j-1)}(\alpha_{dbm},x_0)]^2+\sum_{j=1}^{N}[y_j^{*}-G'^{(j-1)}(\alpha_{ds},y_0)]^2\rightarrow\min_{\bar{\alpha},\bar{I}} \qquad (2.1)$$

where,

x_j^{*} is the empirical value of DBM population density at time j,

y_j^{*} is the empirical value of parasitoid population density at time j,

G is the solution of the Cauchy problem for the respective system of differential equations, which describes the DBM dynamics in time,

$G^{(j)}$ are the values of function G calculated at times j,

G' is the solution of the Cauchy problem for the respective system of differential equations, which describes the dynamics of parasitoids,

$G'^{(j)}$ are the values of function G' calculated at time j,

$\bar{\alpha}=(\alpha_{dbm},\alpha_{ds})$, α_{dbm} is the set of parameters for function G,

and α_{ds} is the set of parameters for the function G'

$\bar{I}=(x_0,y_0)$ is the initial vector of population size.

Considering the fact that the initial values of population size x_0 and y_0 are also used as a parameter in (2.1), the space dimensions of the confidence domains become larger than those of the model parameters. In this case, the space of model parameters presents its own structure that is specified by bifurcation surfaces, which when transited, lead to quality changes of the dynamical regime of population fluctuations.

2.2.3 Nelder-Mead multidimensional algorithm

This method belongs to a class of nonlinear optimization techniques known as simplex searches. It uses a non-degenerate simplex as its design for function sampling. A non-degenerate simplex is a set of $n+1$ vertices in R^n that has the property that the set of simplex edges are adjacent to any given vertex spans R^n. A simplex is a line in R^1, a triangle in R^2, a tetrahedron in R^3, and so on (Gurson, 1999; Press *et al.* 1992).

The Nelder-Mead search algorithm has four steps: reflection, expansion, contraction, and shrink. These four steps are labeled respectively by the coefficients: ρ (reflection), χ (expansion) γ (contraction) and σ (shrink), governed by the rules:

$$\rho>0,\ \chi>1,\ \chi>\rho,\ 0<\gamma<1, \text{ and } 0<\sigma<1. \qquad (2.2)$$

While these are general rules, they are always seen by the convention yielding the following value: $\rho=1,\ \chi=2,\ \gamma=\frac{1}{2},\ \sigma=\frac{1}{2}.$ (2.3)

0. **Initially**. Start with a no degenerate simplex for $\Re^n$ and calculate the function values at all the vertices. Then at each iteration k, $k\geq 0$.

1. **Order**. Order the vertices $x_0^k, x_1^k, \ldots\ldots, x_{n-1}^k, x_n^k$ such that

$$f(x_0^k)\leq f(x_1^k)\leq \ldots\leq f(x_{n-1}^k)\leq f(x_n^k). \qquad (2.4)$$

2. **Reflect.** After computing the centroid $\bar{x}^k=\frac{1}{n}\sum_{i=0}^{n-1}x_i^k$, compute the reflection point x_r^k from $x_r^k=\bar{x}^k+\rho(\bar{x}^k-x_n^k)$. (2.5)

If $f(x_0^k)\leq f(x_r^k)<f(x_{n-1}^k)$, replace x_n^k with x_r^k and go to step 6.

a) Reflection Step.

b) Expansion Step

c) Inside Contraction

d) Outside Contraction.

Figure 2.2 Nelder-Mead algorithm geometrical Steps for a triangle

3. **Expand**. If $f(x_r^k) < f(x_0^k)$, calculate the expansion point x_e^k from

$$x_e^k = \bar{x}^k + \chi(x_r^k - \bar{x}^k). \tag{2.6}$$

If $f(x_e^k) < f(x_r^k)$ replace x_n^k with x_e^k and go to Step 6, otherwise $(f(x_e^k) \geq f(x_r^k))$,

Replace x_n^k with x_r^k and go to Step 6.

4. **Contract.** If $f(x_r^k) \geq f(x_{n-1}^k$ perform a contraction between $\bar{x}^k$ and whichever of x_r^k and x_n^k has the lower function value.

a. **Outside.** If $f(x_{n-1}^k) \leq f(x_r^k) < f(x_n^k)$, perform an outside contraction:

Calculate $$x_{oc}^k = \bar{x}^k + \gamma(x_r^k - \bar{x}^k) \tag{2.7}$$

If $f(x_{0c}^k) \leq f(x_r^k)$, replace x_n^k with x_{oc}^k and go to Step 6; otherwise perform a shrink (Step 5).

b. **Inside.** If $f(x_r^k) \geq f(x_n^k)$ perform an inside contraction: calculate

$$x_{ic}^k = \bar{x}^k + \gamma(x_n^k - \bar{x}^k). \tag{2.8}$$

If $f(x_{ic}^k) < f(x_n^k)$, replace x_n^k with x_{ic}^k and go to Step 6; otherwise perform a shrink (Step5).

5. **Shrink.** Shrink the simplex around x_o^k by replacing x_i^k with

$$\hat{x}_i^k = x_i^k + \frac{1}{2}(x_o^k - x_i^k),\ i = 1,\ldots,n \tag{2.9}$$

where $\hat{x}_i^k$ is the calculated shrink value

6. **Check Termination.** Termination if any of the possible stopping criteria in force are satisfied. Otherwise, set $k = k + 1$ and return to Step 1 (Gurson, 1999).

2.2.4 Powell's multidimensional algorithm

Good numbers of methods have been developed for minimizing a mono-dimensional cost function without applying derivatives, such as the dichotomy algorithm, the Fibonnacci's method or the golden section method (Press *et al.*, 1992).

In general, to minimize a multidimensional function, it is possible to repeat mono-dimensional minimization successively in the direction of each parameter axis. If the cost function contains a valley that is not oriented along a parameter axis, this requires a lot of small displacements. The Powell's method rather minimizes the cost function by changing search direction to valley direction, thereby speeding up the optimization process. In another words, the Powell's algorithm is simply based on conjugacy relations such as, for a given cost function the iterations are repeated until a point sufficiently close to a minimum has been reached (Powell, 1964; Press *et al.*, 1992).

The main characteristics of the algorithm are the following: Initialize the set of directions u_i to the basis vectors, $u_i = e_i, i = 1,...,n$ and then repeat the following sequence of steps until the function stops decreasing: (Powell, 1964; Press *et al.*, 1992).

- Save the starting position as p_0.
- For $i = 1,....,n-1$, move $p_{i=1}$ to the minimum along direction u_i and call this point p_i.

- For $i = 1,\dots,n-1$, set $u_i \leftarrow u_{i+1}$.
- Set $u_n \leftarrow p_n - p_0$
- Move p_n to the minimum along direction u_n and call this point p_0.

This algorithm is simply based on conjugacy relations and for a given function f the iterations are repeated until a point sufficiently close to a minimum has been reached.

2.2.5 Artificial Neural Networks

This technique belongs to a group of methods called artificial intelligence. Artificial Neural Networks (ANNs) are inspired by the neural network structure of the brain, and consist of interconnected processing units (artificial neuron) that use a mathematical or computational model for information processing, based on a connectionist approach to computation. The application of ANN for modelling necessitates three stages namely, the training, the validation and performance testing stage.

2.3 Analysis of residuals

The Durbin Watson test which is used for analysis of serial correlation was applied on the discrepancy between theoretical (obtained from the model) and experimental trajectories (from field datasets). Before its application, the residuals were subjected to the Shapiro-Wilk W test and Kolmogorov-Smirnov test for conformation to a normal distribution (Shapiro *et al.*, 1968). The Durbin Watson criterion (d) usually ranges in value from 0 to 4. A value near 2 indicates no-autocorrelation whereby a value toward 0 indicates positive autocorrelation and toward 4 indicates negative autocorrelation between residuals. The existence of positive or negative correlations of residuals indicates dependence between empirical and model trajectories, which lead to the rejection of the null hypothesis and the model validity. The case of no-autocorrelation indicates independence among residuals, assertion could then be made that model and data are in concern. The Durbin-Watson criterion (d) is calculated using the following expression:

$$d = \frac{\sum_{i=2}^{n} (e_i - e_{i=1})^2}{\sum_{i=1}^{n} e_i^{\ 2}} \tag{2.10}$$

where n is the sample size and e_i the residual value at point i.

Chapter 3

Fitting continuous host-parasitoid models with field time series data

Summary

Diadegma semiclausum, an exotic parasitoid, was released in Kenya for biological control of the diamondback moth (DBM), the worst pest of crucifers in East Africa. Population dynamics of the pest and its parasitoids were studied for three years after the release of the parasitoid. The objective of the present chapter was to study host-parasitoid interactions using existing continuous equations models (Lotka-Volterra, Holling-Tanner type 2, Holling Tanner type 3 and Leslie model) and search for mathematical tools that can be used to predict, on the basis of the available data, the likelihood of success of the biological control agent in the entire East African region. For each model, we estimated model parameters from the minimization of the loss function between the theoretical and experimental time series data following the Nelder-Mead multidimensional method. Initial values of population size and parameters were randomly chosen. Isaev's classification of insect outbreak types was applied to describe the periods of DBM and parasitoid population dynamics. The DBM trajectory presented periods of cyclical eruptive, pulse eruptive and stability zones whereby the parasitoid was mainly characterized by sustainable line behaviour. For all sets of parameters, boundaries of confidence domains were determined. Carrying capacity and the coefficient of fecundity for both species were calculated. Levels of population stability were also determined and for almost every model, the population stabilized at values of 1.01 DBM per plant and approximately 0.05 parasitoids per plant. Tests on residuals showed that they were normally distributed.

Application of the Durbin-Watson criteria for comparison of model outputs and experimental population trajectories produced a positive correlation with all selected models. Consequently, it was concluded that none of the chosen models is appropriate to explain the population dynamics of either species.

3.1 Introduction

The International Centre of Insect Physiology and Ecology (ICIPE), Nairobi, Kenya, embarked on a project to reduce reliance on pesticides for DBM control and introduced a well-known exotic parasitoid, *Diadegma semiclausum* (Hellen) from Taiwan in October 2001. The first release was made in July 2002 at Werugha in Taita Taveta District (Momanyi *et al.* 2006). Diamondback moth and parasitoid population dynamics were studied for one year before and three years after the release Macharia *et al.* (2005) conducted an extensive *ex ante* impact assessment and estimated the effect of parasitoid introduction on pesticide use and reduction of crop damage. They found that investment in the DBM biological control programme was beneficial for Kenya and for the funding agency with a benefit cost ratio of 24:1. The results obtained encouraged the extension of the project to neighbouring countries in the region to make optimal use of the research investment and create economies of scale. In this case, a mathematical model predicting the influence of different ecological parameters would greatly help in the prediction of the likelihood of success of similar parasitoid introductions in other areas where the pest is of importance.

In ecological modelling, numerous continuous equation models have been developed to describe population and ecosystem dynamics (Silvert, 1993; Wilder *et al.*, 1994; Hsu and Huang, 1995). However, very few of these models were tested against concrete experimental datasets on a quantitative level. Generally, researchers limit their studies to qualitative comparison of theoretical results to experimental data, which does not allow conclusions to be drawn on the adequacy of the models to describe observed population dynamics. On the other hand, choosing a mathematical model to describe a biological process is difficult as there are no standard criteria for the selection of a mathematical model to describe a particular population dynamics (Isaev *et al.* 1984; 2001). Often there are only two choices: proceed on a sequential check of the existing models starting from the simplest one (Lyapunov and Bagrinovskaya, 1975) or create a new model to describe the population dynamics of the species in question.

In this study, the first approach was chosen. The applicability of differential equations (prey-predator or host-parasitoid) models for the description of DBM interactions with the parasitoid based on a time series dataset collected during the three-year post-release period was tested.

Sequentially, tests were done on the simplest, the Lotka-Volterra model (Lotka, 1920; 1925; Volterra, 1931) followed by the Holling models with functional response type 2 (Isaev *et al.*, 1984; 2001) and type 3 (Poletaev, 1966; 1973; 1975) and finally, the Leslie model of prey-predator systems (Leslie, 1948). These models were selected because they were constructed based on the assumptions of continuous birth and death processes and that the generations of the interacting populations overlap completely. Also important was that, in practice, successful parasitoid development always kills the host, which is similar to the well-known prey-predator system.

3.2 Materials and Methods

3.2.1 Site description and data collection

Experimental results were obtained from the pilot release area in Werugha Location (03° 26' 16'' S; 38° 20' 24'' E) of Wundanyi Division in Taita Taveta District, Coast Province of Kenya as described in section 2.1.1.

3.2.2 Models used to fit the dataset

A great number of mathematical models are devoted to the description of prey-predator or host-parasitoid system dynamics (Gilpin, 1974; Hassell, 1978; Hadeler and Gerstmann, 1990). Every model has its own set of dynamic regimes for population fluctuations, with a specific set of parameters, and also specific functions that describe the processes of self-regulation and interactions between populations. The models used are listed below and for easy reference; the main characteristics of each of the models are briefly explained.

i) Lotka-Volterra model

The Lotka-Volterra model is one of many differential mathematical models devoted to the description of prey-predator or host-parasitoid system dynamics. The following assumptions were made during their elaboration (Lotka, 1920; 1925; Volterra, 1931; Pielou, 1977; Murray, 2001; Turchin, 2003)

(i) The prey or host grows unboundedly in a Malthusian way in the absence of predation and self-regulation;

(ii) The effect of the predation is to reduce the prey's per capita growth rate by the term proportional to prey and predator populations: Volterra's principle of "pair interaction" (Volterra, 1931);

(iii) In the absence of any prey for sustenance, the predator's death rate results in exponential asymptotical decay;

(iv) The prey's contribution to predator growth rate is proportional to the prey population.

Within this framework interactions between populations are described by the law of interacting biomass as in molecular kinetics by:

$$\frac{dx}{dt} = \alpha_1 x - \beta_1 x^2 - \gamma_1 xy, \frac{dy}{dt} = -\alpha_2 y - \beta_2 y^2 + \gamma_2 xy, \qquad (3.1)$$

$x(0) = x_0 \geq 0$, $y(0) = y_0 \geq 0$ (Cauchy problem)

where,

$x(t)$ is the DBM population size at moment t,

$y(t)$ is the parasitoid population size at the same moment,

α_1 is the growth rate or Malthusian parameter for the DBM population,

α_2 is the intensity of natural death of individuals in the parasitoid population,

β_1 and β_2 are the coefficients of self-regulation in the respective populations,

γ_1 and γ_2 are the coefficients of interaction between the two populations,

α_1 / β_1 is the equilibrium number for DBM at the absence of parasitoid,

x_0 is the initial value of DBM population density, and

y_0 is the initia l value of the parasitoid population density.

For correct presentation of the Cauchy problem, non-negative initial values have to be used. However, in biological situations such a problem does not occur as initial population sizes would always be positive.

ii) Holling Tanner Models type 2 and type 3

Holling (1959) modified model (3.1) taking into account the existence of the effect of saturation (using a 'Monod' type of function) in interaction within populations and obtained the following system of differential equations:

$$\frac{dx}{dt}=\alpha_1 x-\beta_1 x^2-\frac{\gamma_1 xy}{1+\delta x},\frac{dy}{dt}=-\alpha_2\ y-\beta_2 y^2+\frac{\gamma_2\ xy}{1+\delta x} \tag{3.2}$$

where, δ is constant representing the sigmoidality of the function,

γ_1/δ characterizes the maximum intensity of DBM population,

γ_2/δ is the maximum intensity of parasitoid population increase.

This function is generally called the Holling's type 2 functional response and its characteristics is as follows: at low prey densities, the predation rate per capita increases approximately linearly with prey density and at high prey densities, the predation rate levels off (Holling, 1959; Alexeev, 1976; Bazykin, 1985; Isaev *et al.* 1984; 2001; Turchin, 2003).

Another model (Type 3 in Holling's classification), with a different type of population interaction was also investigated. In the Holling's type 3 functional response, the predation rate initially increases faster than linearly, before levelling off in a manner like that of a type 2 functional response.

$$\frac{dx}{dt}=\alpha_1 x-\beta_1 x^2-\frac{\gamma_1 x^2 y}{1+\delta x^2},\frac{dy}{dt}=-\alpha_2 y-\beta_2 y^2+\frac{\gamma_2 x^2 y}{1+\delta x^2}, \tag{3.3}$$

where, all parameters are the same as in (3.2).

iii) Leslie model

Leslie (1945) assumed that the dynamics of a parasitoid depends on the relation between sizes of both populations. He introduced a parameter K as maximum intensity of parasitoid population growth, which is realized when the host population is large enough for maximum parasitism and obtained the following equations (Leslie, 1945; 1948).

$$\frac{dx}{dt} = \alpha_1 x - \beta_1 x^2 - \gamma_1 xy, \frac{dy}{dt} = y\left(K - \frac{\gamma_1 y}{x}\right) \qquad (3.4)$$

3.2.3 Statistical criteria and residuals analysis for parameters estimation

This section was carried out using the methodology described in sections 2.2.2, 2.2.3 and 2.3. More emphasis was given to the determination of the parameters borders of confidence domains. These borders (Ω_i) were determined by finding the intersections of minimized function of equation 2.1 with the plane Q = constant, which can be expressed as follows:

$$Q(\vec{\alpha}) = Q(\vec{\alpha}_{\min})[1 + \frac{m}{n-m} * F(m, n-m, \beta)] \qquad (3.5)$$

where F is the quantile function, which depends on sample size (n) and the number of parameters (m) for minimization at a chosen level of significance (β). For calculation, the two nearest values of the calculated model parameter are selected as starting points. Small increments and decrements are made from their original value, and the Q-function is recalculated for each value. This process is followed until the boundaries of the confidence domains are determined. The results were obtained from a computer program written in C. In this program, model equations were solved in a routine using the Runge-Kutta 4th algorithm with 0.01 step size (Press *et al.,* 1992).

3.3 Results

DBM and parasitoid population fluctuations with time are displayed in Figure 3.1. Examination of these trajectories under the assumption that DBM and parasitoid population dynamics can be explained based on Isaev's classification of insect outbreaks (Isaev *et al.*, 1980; 1984; 2001; Berryman, 1992; Berryman and Munster-Swendsen; 1994) leads to the following conclusions. Points 1-5 on the DBM line correspond to a high cyclical eruption, points 16-18 and points 37-39 both correspond to a pulse eruption; points 9-14 and 20-24 are low cyclical eruptions. Points 6-8 represent the decline phase boundaries of high cyclical eruption and low cyclical eruption. The parasitoid line presents a low sustained trajectory at point 1-14 and a sustained eruption trajectory at points 16-19, 24-27 and 36-39. Points 31-36 and 41-49 in the DBM and parasitoid lines respectively correspond to sustained population fluctuations towards stabilization. Other parts of the DBM line and parasitoid line such as points 27-30 on DBM and parasitoid lines cannot be explained under the hypothesis that the population dynamics correspond to the regime of a proper outbreak.

Evaluation of the quotients Skewness/Standard Error and Kurtosis/Standard Error gave values < 3. In addition, the results of the Shapiro-Wilcoxon and Kolmogorov-Smirnov tests showed that the residuals for all models were normally distributed; this demonstrates the validity of application of Durbin Watson criteria for analysis of the sequence of deviations. The results obtained from the minimization of function (5) and from statistical analysis are presented in Table 3.1. Following are the analysis and interpretation of these results for each model.

Table 3.1. Estimates of model parameters and values of statistical criteria for four differential population models fitted to an empirical times series of the diamondback moth and its parasitoid, *Diadegma semiclausum*, Werugha, Wundanyi Division, Taita Taveta District of Kenya (calculated with the help of formula (2.1).

Models	**DBM growth rate** (α_1)	**Natural death rate** (α_2) **(parasitoid)**	**DBM self-regulation coefficient** (β_1)	**Self-regulation coefficient** (β_2) **(parasitoid)**	**Interaction coefficient** (γ_1) **(DBM/ parasitoid)**	**Interaction coefficient** (γ_2) **(parasitoid/ DBM**	**Carrying capacity** (α_1 / β_1) **DBM**	**Sigmoidality constant** (δ)	**Maximum population growth (parasitoid)** (K)	**Initial population size** (x_0) **(DBM)**	**Initial population size** (y_0) **(parasitoid)**	**Loss-function*** (Q_{min})	**Durbin-Watson criterion** (*d*) **DBM**	**Durbin-Watson criterion** (*d*) **parasitoid**
Lokta-Volterra	1.45	2.49	42.19	9.07	0.03	120.58	0.03	-	-	9.36	0.03	80.5	1.20	0.56
Holling Type 2	0.40	2.47	3.77	0.59	2.23	0.30	0.11	0.001	-	12.36	0.09	96.9	1.05	0.60
Holling Type 3	1.72	2.00	3.51	0.41	1.75	0.75	0.49	0.022	-	12.40	0.24	95.6	1.11	0.49
Leslie	0.55	-	0.21	-	36.91	-	2.57	-	0.08	10.72	0.29	88.0	1.13	0.65

* - squared deviations between empirical and theoretical time series

3.3.1 Lotka-Volterra model

We obtained a value of 1.45 for the growth rate of DBM and 42.19 for the self-regulation coefficient. Figure 3.2 represents the DBM population variation with time. The model predicted a monotonously decreasing line starting at 9.36 as initial DBM population size, which stabilized at a value of 0.80 DBM/plant. The carrying capacity according to the model was 0.03 DBM/plant (Table 3.1).

The model estimated a self-regulation coefficient of 9.07 for the parasitoid and 2.49 as its death rate. Parasitoid population grew from 0.05/plant following an increasing function for a period of 12 weeks and reached its peak at 0.41, after which the population decreased and stabilized at an approximate value of 0.06 (Figure 3.3).

Analysis of the deviations between model and experimental values produced d = 1.20 and d = 0.56 for the Durbin-Watson criteria of DBM and parasitoid, respectively. The critical values are d_L= 1.32 for 1% and d_L= 1.50 for 5%. In both cases d $<d_L$. Consequently, there is a positive correlation between residuals and we have to reject the hypothesis that this model is suitable for describing the population dynamics of either species.

The behaviour of function Q on the plane (α_1, α_2) and the boundaries of confidence domains Ω_k, $k = 1,2,3$ for 1, 5 and 10% confidence levels are illustrated in Figure 3.4. These trajectories are within the plane surface with the following coordinates α_1= 5.90 and α_2=22.50.

3.3.2 Holing-Tanner type 2 model

This model generated a DBM growth rate of 0.40 and a self-regulation coefficient of 3.77 for DBM (Table 3.1). Figure 3.2 depicts the variation in DBM population density with time. The model predicted a line with a starting population of

12.36 DBM/plant declining monotonously at a decreasing rate and stabilizing to a value of 0.88. The calculated carrying capacity was 0.11 DBM/plant.

Model predictions for parasitoid numbers began with a very small monotonous increase in population size starting with 0.09. This initial value increased to a maximum of 0.10 where the trajectory started declining at an increasing rate before stabilizing at 0.05/plant (Figure 3.3). Self-regulation for the parasitoid was estimated at 0.59 and the death rate value was 2.47.

Values of the Durbin-Watson criteria were determined as d = 1.05 and d = 0.60 (DBM and parasitoid, respectively). As in the Lotka-Volterra model, d $< d_L$, consequently there is a dependence between residuals and the model cannot be accepted as suitable for the description of the population dynamics of either species.

Function Q on the plane (α_2, γ_1) and the boundaries of confidence domain Ω_k, $k = 1,2,3$ for 1, 5 and 10% confidence levels are presented in Figure 3.5 This Figure shows concentric surfaces with an approximate centre at coordinate point 2.80, 2.60).

3.3.3 Holling-Tanner type 3 model

The growth rate for DBM was calculated at 1.72 and the self-regulation coefficient was estimated at 3.51 (Table 3.1). The model predicted a monotonous decline at decreasing rate starting at 12.40 as initial DBM population per plant and stabilizing at 1.02 (Figure 3.2).

The self-regulation coefficient for the parasitoid was 0.41 and the death rate 2.00. Parasitoid population density was calculated to follow a monotonously increasing function from 0.24 which reached its peak at 0.43 and began to decline at increasing rate to stabilize at 0.26/plant (Figure 3.3)

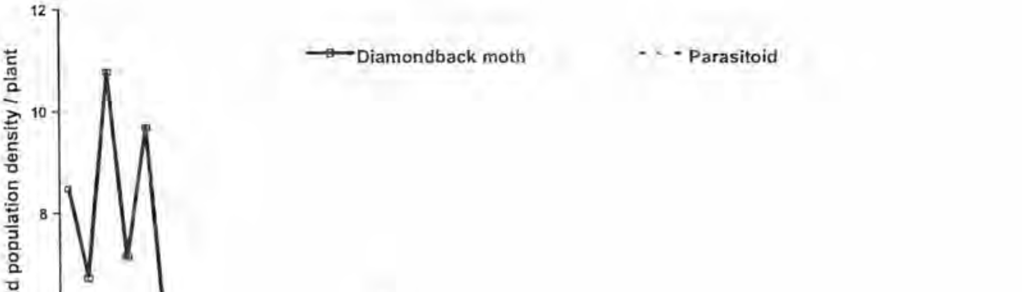

Figure 3.1 Changes in the population dynamics of diamondback moth (*Plutella xylostella*) and its parasitoid, *Diadegma semiclausum* after introduction and release of the parasitoid. Werugha, Wundanyi Division, Taita Taveta District of Kenya.

Deviations between model and experimental values resulted in d = 1.11 and d = 0.49 for the Durbin-Watson criteria (DBM and parasitoid, respectively). As in the previous cases, d < d_L, indicating a positive correlation between residuals.

Figure 3.6 depicts the function Q on the plane $(\alpha_1, \gamma_1)$and the boundaries of confidence domain Ω_k, $k = 1,2,3$ for 1, 5 and 10% confidence levels, respectively. These boundaries of confidence domains are annular trajectories with a common centre at coordinates (2.50, 2.50) and $r_1 = 2.00$, $r_2 = 2.40$ and $r_3 = 3.80$ as approximated radius values for 1, 5 and 10% confidence levels, respectively.

3.3.4 Leslie model

The Leslie model produced a growth rate of 0.55 for DBM and a very small self-regulation coefficient (0.21), the carrying capacity was 2.57 (Table 1). The model predicted a monotonously decreasing population line starting at 10.72, which stabilizedat a value of 0.60 DBM/plant (Figure 3.2).

The prediction for the parasitoid population was a line declining at an increasing rate which stabilized at a value of 0.05/plant (Figure 33). This model predicted 0.08 as intensity of parasitoid population growth.

Durbin-Watson values for the deviations between model and experimental values were 1.13 and 0.65 for DBM and parasitoid, respectively. Again, there was a positive correlation between residuals and we have to reject the hypothesis that the Leslie model is appropriate for the fitting of DBM-parasitoid population fluctuations.

Figure 3.7 shows the loss function Q on the plane $(\alpha_1, \gamma_1)$and the boundaries of confidence domain Ω_k, $k = 1,2,3$ for 1, 5 and 10% confidence levels respectively, which are concentric circles.

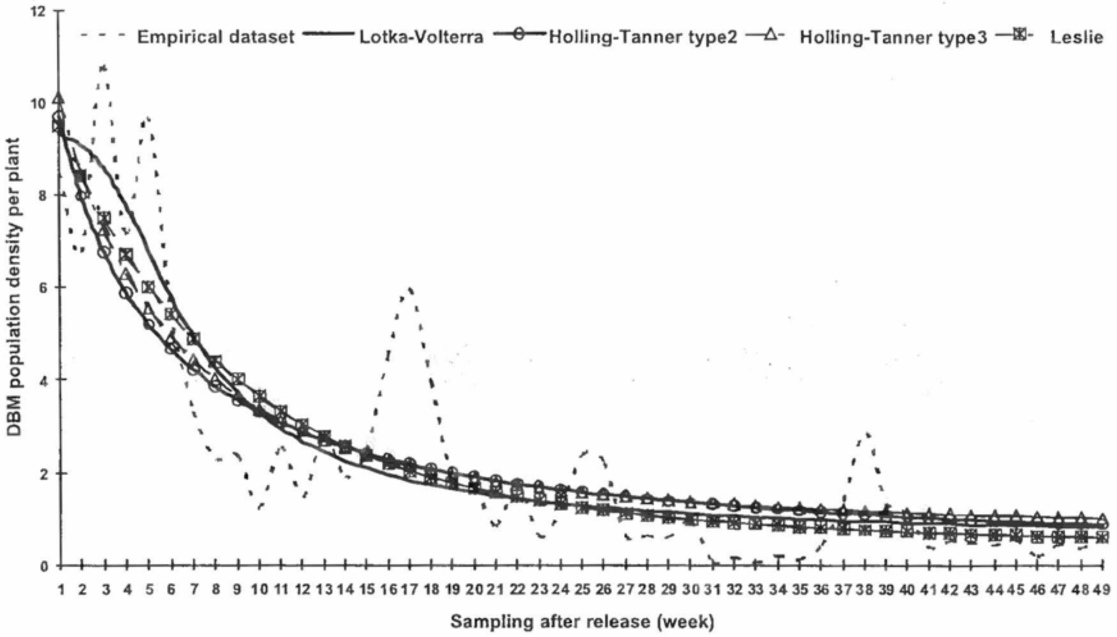

Figure 3.2 Trajectories of the diamondback moth populations predicted by various predator-prey models. Predictions are based on an empirical dataset collected after the initial release of an exotic parasitoid, *Diadegma semiclausum* Werugha, Wundanyi Division, Taita

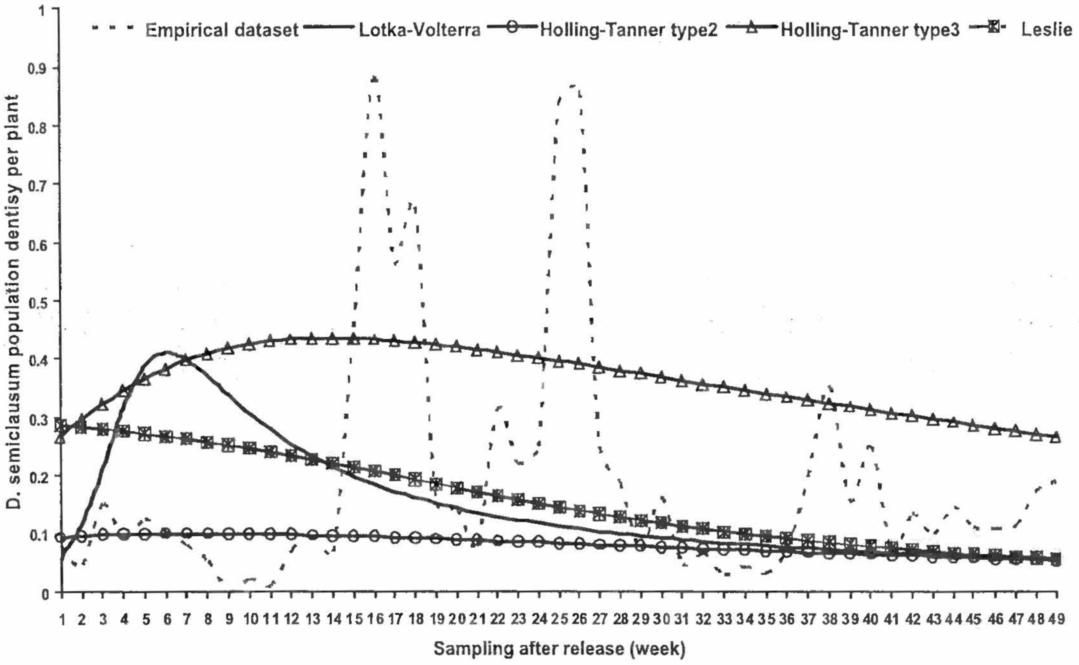

Figure 3.3 Population trajectories of the diamondback moth parasitoid, *Diadegma semiclausum* predicted by various predator-prey models after an initial introduction and release. Predictions are based on an empirical dataset collected after initial release of the parasitoid, Werugha, Wundanyi Division, Taita Taveta District of Kenya.

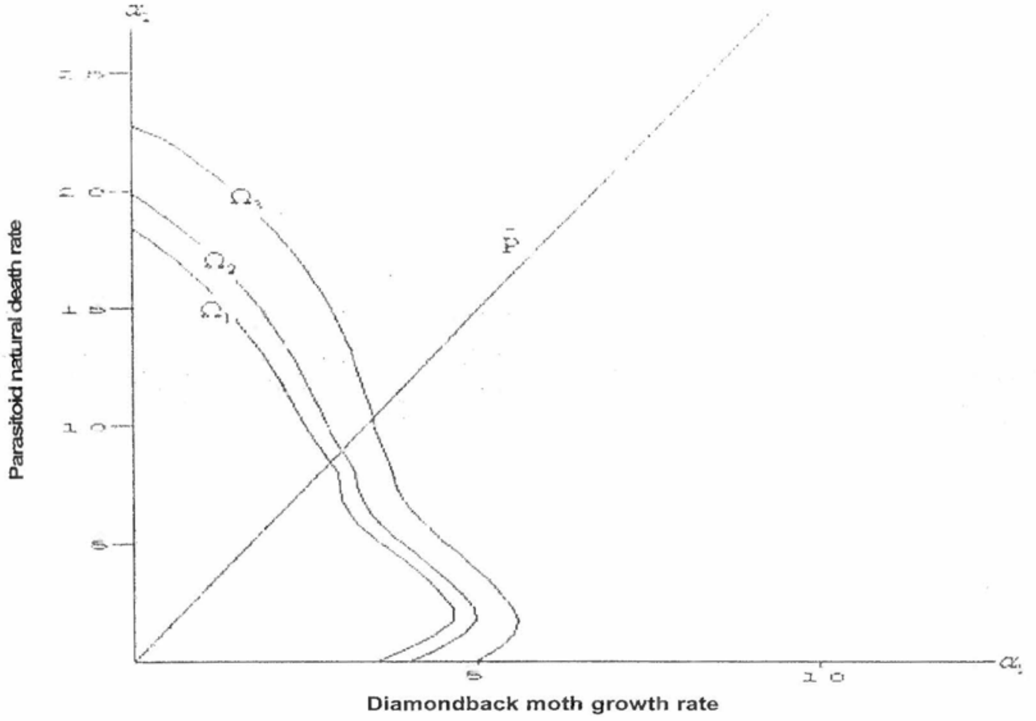

Figure 3.4 Boundaries of confidence domains for estimated parameters of Lotka-Volterra model at fixed initial values of diamondback moth (x_0) and parasitoid, *Diadegma semiclausum* (y_0) population / plant. Ω_1 is the boundary for 10% confidence level, Ω_2 - for 5% confidence level and Ω_3 - for 1% respectively. $\bar{P}: \alpha_2 = 2.86\alpha_1$ is the bifurcation line.

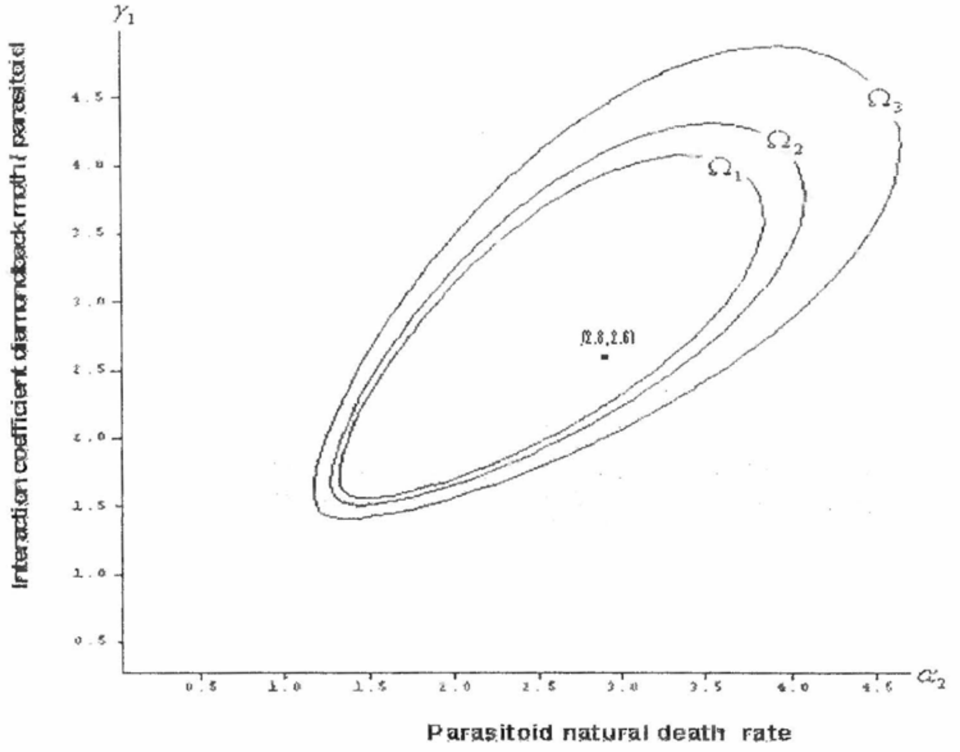

Figure 3.5 Boundaries of confidence domains for estimated parameters of Holling-Tanner type 2 model at fixed initial values of diamondback moth (x_0) and parasitoid, *Diadegma semiclausum* (y_0) population / plant. Ω_1 is the boundary for 10% confidence level, Ω_2 - for 5% confidence level and Ω_3 - for 1% respectively.

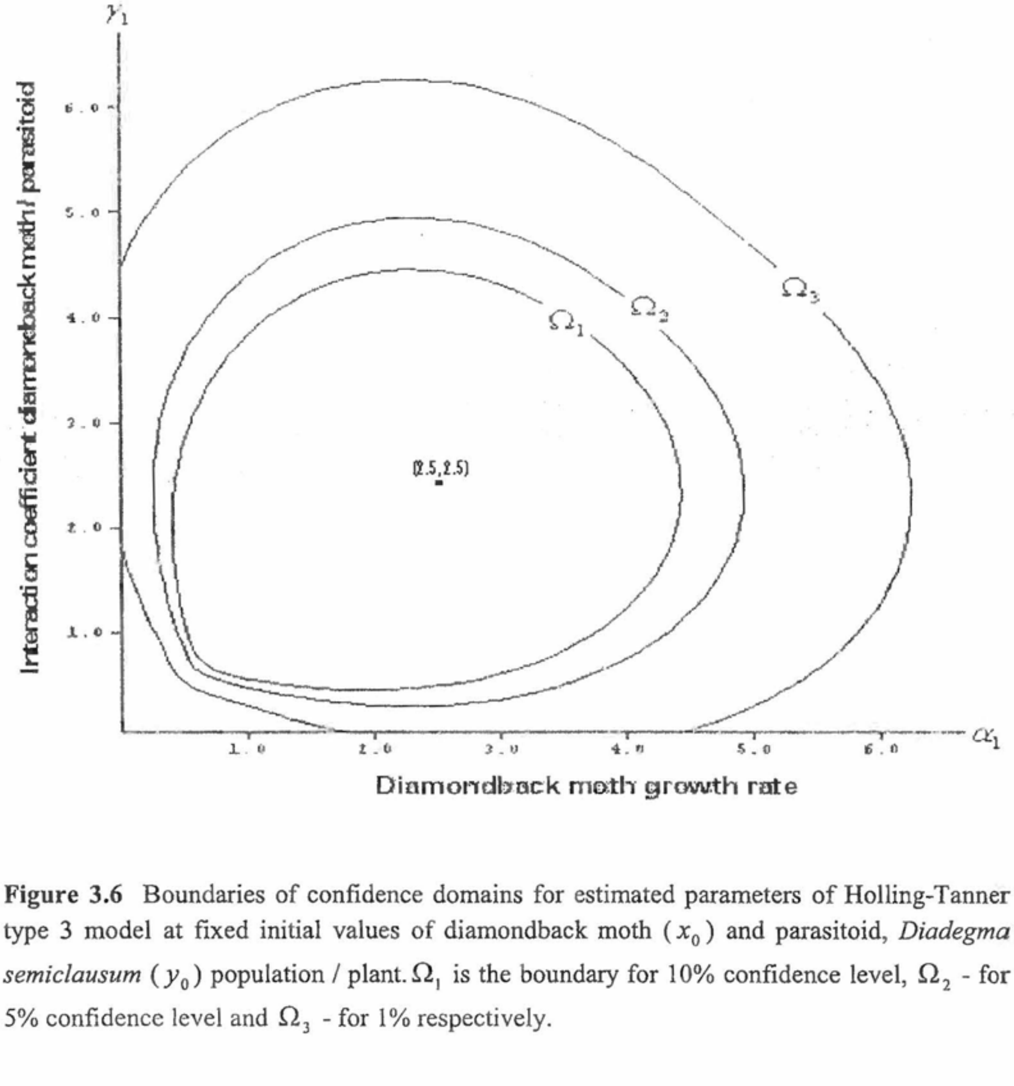

Figure 3.6 Boundaries of confidence domains for estimated parameters of Holling-Tanner type 3 model at fixed initial values of diamondback moth (x_0) and parasitoid, *Diadegma semiclausum* (y_0) population / plant. Ω_1 is the boundary for 10% confidence level, Ω_2 - for 5% confidence level and Ω_3 - for 1% respectively.

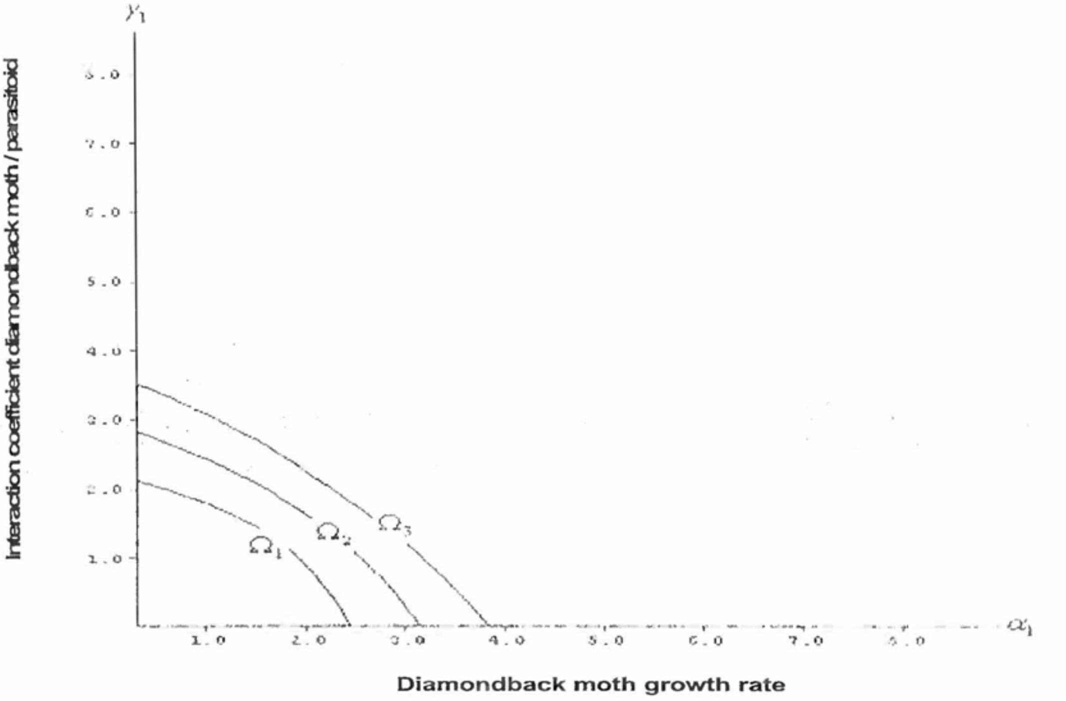

Figure 3.7 Boundaries of confidence domains for estimated parameters of Leslie model at fixed initial values of diamondback moth (x_0) and *Diadegma semiclausum* (y_0) population / plant. Ω_1 is the boundary for 10% confidence level, Ω_2 - for 5% confidence level and Ω_3 - for 1% respectively.

3.4 Discussion

The unstable cyclic eruptive pulses of the DBM population cannot be explained from the analysis carried out in this study, but their appearance may be due to favourable environmental conditions and abundance in food that trigger an outbreak which immediately collapses due to parasitism and others factors such as rainfall, which have been reported as major factors of DBM population regulation (Gunn, 1917; Wakisaka *et al.*, 1991). In addition, good explanation of population dynamics is obtained when time lag reaction of DBM intra self-regulation and effects of parasitoid on DBM population size are both taken into consideration. Low parasitoid population density at the beginning of the collection after release in Figure 1 shows the period of adaptation of this insect to its new environment. An increase in DBM population leads to more hosts that can be parasitized and therefore causes an increase on the parasitoid population. Sustained population fluctuations are zones of stabilization where the parasitoid successfully regulates the DBM. Points on the trajectory that could not be explained using Isaev's classification of insect outbreaks can be considered as stochastic near stable (or unstable) level.

This work explores a standard methodology for model parameter restoration. The analyzed models are all autonomous mathematical equations, i.e. without the variable time on the right hand site of their respective functions. Absence of this variable leads to the assumption that the time interval between measurements is equal to 1. In other words, real values for model parameters cannot be estimated; nevertheless, identified parameters are proportional to real values with an unknown coefficient of proportionality. From the four different host-parasitoid models, best estimated sets of parameters for each model derived from the minimization of the loss function all correspond to a regime of population stabilization at non zero level for both insects.

The Lotka-Volterra model demonstrated a very strong self-regulative mechanism for the DBM and lesser for its parasitoid. In contrast, Holling-Tanner type 2 and type 3 showed a weak self-regulation phenomenon especially for the parasitoid. This may be explained considering the fact that self-regulative intra-population mechanisms are strongest at big population size and their influence is negligible at small population size. DBM population was large enough before the release of *D. semiclausum*, which increased in size after a brief adaptation period.

The DBM growth rate coefficient was highest for Holling-Tanner type 3 and Lowest for Holling-Tanner type 2 models. The discrepancy observed among models may be due to the ability for each model in fitting empirical data, or the difference in mathematical expression of model equations. Syed and Abro (2003) estimated an intrinsic rate of increase of 0.23 when DBM fed on *Brassica oleracea capitata* under laboratory conditions. Considering that the intrinsic rate of increase is equivalent to the growth and is defined as the difference between the birth rate and death rate, it can be assume that the estimated intrinsic rate value obtained by Syed and Abro (2003) was uniform everywhere. With these considerations the Holling's type 2 model estimated DBM growth rate is the closest value to the experimental result. However, the comparison of the intrinsic rate of increase reported by Syed and Abro (2003) with our estimates would not be realistic since the intrinsic rate of increase is highly dependant on environmental condition, especially temperature. Syed and Abro (2003) did not state the temperature conditions under which their experiments were conducted. Despite the variance on the predicted DBM growth rate from model to model, its evaluation indicates that it still lies within acceptable range with non-negative value indicating that the DBM birth rate is higher than the death rate.

The natural death rate of the parasitoid for all models was estimated between 2 to 2.5, which is higher than the natural death rate obtained for DBM. Hence the parasitoid has to be considered an endangered insect, which is justified by its total dependence on DBM for multiplication and perpetuation. In the absence of DBM, parasitoid populations may rapidly decrease until extinction. However detailed evaluation of the ability of this parasitoid to thrive on its alternate hosts should be carried out to evaluate its potential to survive in the system without DBM.

Another puzzling result of this study was the big divergence between predicted self-regulation and interaction coefficients of DBM and the parasitoid. Biologically, the high value of self-regulation produced by the Lotka-Volterra model does not make much sense because the empirical population never reached the numbers where high intra-specific competition could be expected. However, the same model also produced a very high self-regulation coefficient for the parasitoid. This indicates strong competition for host larvae. Momanyi *et al.* (2006) showed that one year after release, competition between parasitoids was so strong that even first instar larvae that were still mining were parasitized. In contrast, all models produced a high positive interaction coefficient between DBM and the parasitoid. Considerable variation existed for DBM and parasitoid initial population sizes predicted by the different models. These variations could be explained by the power for each model in fitting empirical time series.

The maximum calculated value of carrying capacity from these models was about 3 DBM/plant, which is an unrealistic result if compared to empirical datasets where in outbreak situations and without effective parasitism, especially in maturing crops, the actual numbers recorded can surpass 10 DBM/plant (Karimzadeh *et al.* 2004). However, with total effectiveness of the parasitoid in controlling the DBM, and during period of stabilization for both populations, with less food availability and unfavourable climatic conditions for DBM, this value of carrying capacity could be realistic. In the same line the estimated set of parameters depends on the time step between measurements. Knowing that the carrying capacity is obtained from relation between two values of estimated parameters, its value may not always be the same as soon as change occurs in time step value. From this perspective, it will be very difficult to discuss the relation between absolute value of carrying capacity to observed value in the field, at the same time.

All the disparities pointed out above confirm the existence of a sizeable gap between a mathematical approach and its application in ecological and biological systems. Mathematicians and ecologists use different symbols, terms and definitions that are sometimes very explanatory and meaningful in mathematics and meaningless in biology. The models investigated in this study were pioneer work in mathematical biology, and generally, they do not include biological constraints, which could enable them map biological processes more precisely. An example would be that none of the models analysed considers possibilities such as nature of parasitoid (solitary or gregarious), inter and intra-specific competitions, impact of alternate hosts, physiological reactions of organism in the population, etc. The algorithm for parameter estimation applied then searches for the minimum of the loss function and generates values that result in better convergence of the equations. What may have also contributed to this outcome is that we applied the models in a highly unstable situation after the introduction of an exotic parasitoid. Such an introduction purposefully intends to move the system equilibrium to a different level and therefore, creates instability that must have affected the outcome of the calculations.

The boundaries of the confidence domains of all models described circular trajectories. These surfaces are areas where all possible combinations of model parameters can be found with a minimum value of the loss function Q. For the Lotka-Volterra model, this domain was divided in to two areas by a bifurcation line $\bar{P}$ determined by the equation $\alpha_2 = 2.85\alpha_1$. The surface below the bifurcation line $\bar{P}$ corresponds to the regime of elimination of the parasitoid and the surface above this line is the area of stabilization of both populations.

Generally the existence of positive or negative correlations of residuals between empirical and model trajectories indicates dependence. The application of the Durbin-Watson criteria, which is a powerful tool for testing the dependence between residuals, showed a positive correlation for all tested models. This leads to the conclusion that none of the studied models can be applied to describe the dynamics of the DBM/parasitoid system. More complex models, which will take into account time lag reaction of DBM intra self-regulation and effects of parasitoid on changes in DBM population size and others factors such as temperature, rainfall and diseases, should be investigated, as they may offer better results. In this perspective we have to reject our original intention for using these models for the prediction of likelihood success of the biological control agent in the entire East Africa region.

Chapter 4

Fitting discrete host-parasitoid models with field time series data

Summary

The applicability of discrete mathematical models for the description of the population dynamics of diamondback moth (DBM) (*Plutella xylostella* L.) and its parasitoid *D. semiclausum* was investigated. The parameter values for several well-known models (Nicholson-Bailey (1935), Hassel & Varley (9176), Beddington, Free & Lawton (1976), May (1978), Holling type 2, 3 (1959) and Getz & Mills (1997) functional responses) were estimated The models were tested on 20 consecutive sets of time series data collected at 14 days interval for pest and parasitoid population obtained from a highland cabbage growing area in eastern Kenya. Model parameters were estimated from the minimization of the squared difference between the numerical solution of the model and the empirical data using Powell's method, as well as determination of boundaries of their confidence domains. Maximum calculated DBM growth rates varied between 0.02 and 0.07. The carrying capacity determined at 16.5 DBM/plant by the Beddington *et al* (1975). model was within the range of field data. All the estimated parameter values related to the parasitoid including the instantaneous searching rate (0.07 to 0.28), per capita searching efficiency (0.20 to 0.27), search time (5.20 to 5.33), handling time (0.77 to 0.90), and parasitism aggregation index (0.33) were well outside the range encountered empirically. Independence between residuals of the theoretical and experimental population trajectories for DBM under Durbin-Watson criteria for all tested models, except the May (1978) model, proved their adequacy. In contrast, the criteria applied to the

parasitoid residuals showed a strong correlation. Consequently, all models failed in estimating parasitoid dynamics. We concluded that the population dynamics of DBM and its parasitoid and their interactions could not be mutually explained by any of the models tested. Two reasons were pointed out: the parasitoid, in this integrated biological control system perhaps has not played the major role on pest population regulation; or the models used could not encompass all factors affecting population behaviour within this era where human activities and climate change have seriously affected most ecos ystems.

4.1 Introduction

Mathematical models play a central role in the study of host-parasitoid system interactions. With the help of models, we may comprehend some mechanisms of their interaction, and which phenomena may not be directly observed in the field (Gertsev and Gertseva, 2004). Difference equations are widely used for the study of dynamics between insect populations in temperate regions because of the discrete nature of their generations (Royama, 1971; Hassel and May, 1974; Hassel *et al.*, 1976; May *et al.*, 1981). These models are less suitable for tropical insects where continuous generations and life cycles of host and parasitoid of different length are to be expected. However, Royama (1971) suggested that discrete models could be applied to populations with overlapping generations provided age structure and the period of observation is shorter than a generation.

We used, difference equation models to the study of population dynamics of the Diamondback moth, *Plutella xylostella* (Lep.: Plutellidae) and its parasitoid *Diadegma semiclausum* (Hellen) (Hym.: Icheumonidae). The main focus of population dynamic studies has traditionally been on local stability analysis, searching the equilibrium points, determining the nature of their stability and spatial synchrony in which model parameters are obtained through trial and error (Hassel and May, 1974; Hassel *et al.*, 1976; May *et al.*, 1981; Nguyen *et al.*, 2006; Meng *et al.*, 2007). In that regard, a good number of models have been developed, and this gives us a possibility to compare some of the well-known host-parasitoid models with time series datasets collected from the field. Each mathematical model used here possesses a rich set of dynamical regimes. If we fail to find a model which offers good approximation for empirical time series, the base for the following assertions could be made: 1) Parasitoids in an integrated biological control system may not play the major role on pest population regulation. In that case, recommendation of more complicated mathematical models, which include some additional density-dependent or density-independent factors, should be used to fit such field data. 2) The applied models, originally designed to answer qualitative questions about population dynamics may not be capable to encompass all factors affecting population behaviour within this era where human activities and changes on climate have seriously affected most ecosystems. Therefore, new host-parasitoid models which incorporate these aspects may be thought of.

4.2 Materials and Methods

4.2.1 Site description and Data collection

The data were obtained from pilot release areas in Werugha as previously described in section 2.1.1 and the collection was done as summarised in section 2.2.1

4.2.2 Models used to fit the datasets

The data were mainly used with mathematical models that studied the interaction between insects and their natural enemies. We concentrated, in particular, on models of insect parasitoids and their insect hosts. This is because much of the theoretical work by entomologists has centred on host-parasitoid interactions. With some caution, however, host parasitoid models can be extended to include interactions with other kinds of natural enemies. Successive tests of difference equations models were conducted based on the empirical time series dataset collected during three-year post-release period.

Conforming to the discrete seasonality of most arthropods, the models are phrased finite recursive equations of the basic form:

$$N_{t+1} = \lambda N_t f(N_{t,} P_t)\ P_{t+1} = cN_t[1 - f(N_t, P_t)] \qquad (4.1)$$

where, N_t , N_{t+1} , P_t , P_{t+1} give the host and the parasitoid population densities in successive generations respectively, λ is the geometric growth factor for the host ($\lambda = e^r$ where r is the intrinsic rate of increase), and c is the number of parasitoid produced for each host individual attacked. The function f , gives host survival with respect to parasitoid and host densities and can be varied to reflect various parasitoid foraging behaviours (May *et al.*, 1981). Two major features of the parasitoid life cycle well lend themselves to this model structure. First, it is the adult female parasitoid that searches for hosts and second, parasitoids normally oviposit in or on or near hosts making reproduction closely dependent on the number of host parasitized. Table 4.1 summarise the models used.

Table 4.1 Mathematical expression of different models used from publications.

Comments	Model equations	Authors
Growth factor (λ) Parasitoid per capita searching efficiency (a) Number parasitoid produced each host attacked(c)	$N_{t+1} = \lambda N_t \exp(-aP_t)$ $P_{t+1} = cN_t[1-\exp(-aP_t)]$ (4.2)	Nicholson Bailey (1935)
Parasitoid constant searching efficiency (q) Slope parasitoid searching efficiency (m)	$N_{t+1} = \lambda N_t \exp(-qP_t^{1-m})$ $P_{t+1} = cN_t[1-\exp(-qP_t^{1-m})]$ (4.3)	Hassell and Varley (1976)
Carrying capacity for host in the absence of the parasitoid (K)	$N_{t+1} = N_t \exp(r[1-\frac{N_t}{K}]-aP_t)$ $P_{t+1} = cN_t[1-\exp(-aP_t)]$ (4.4)	Beddington *et al.* (1975)
Index parasitism aggregation (k)	$N_{t+1} = \lambda N_t (1+\frac{aP_t}{k})^{-k}$ $P_{t+1} = cN_t[1-(1+\frac{aP_t}{k})^{-k}]$ (4.5)	May (1978)
Parasitoid instantaneous search rate (a') Parasitoid search time (T) Parasitoid handling time (T_h)	$N_{t+1} = \lambda N_t \exp(\frac{-a'TP_t}{1+a'T_hN_t})$ $P_{t+1} = cN_t[1-\exp(\frac{-a'TP_t}{1+a'T_hN_t})]$ (4.6)	Holling type 2 (1959)
Parasitoid constant for search rate (b)	$N_{t+1} = \lambda N_t \exp(\frac{-bTN_tP_t}{1+cN_t+bT_hN_t^2})$ $P_{t+1} = cN_t[1-\exp(\frac{-bTN_tP_t}{1+cN_t+bT_hN_t^2})]$ (4.7)	Holling type 3 (1959)
Upper bound encounter rate (β)	$N_{t+1} = \lambda N_t (1+\frac{a\beta P_t}{k(\beta+aN_t)})^{-k}$ $P_{t+1} = cN_t[1-(1+\frac{a\beta P_t}{k(\beta+aN_t)})^{-k}]$ (4.8)	Getz and Mills (1997)

4.2.3 Assumptions

The following assumptions were made:

a) In some part of Kenya, there are two seasons with favourable and unfavourable weather conditions each year associated with bimodal rainfall distributions (Sutherst *et al.*, 1999). This leads to the seasonality of some species such as DBM which become rare in the field during the rainy season.

b) The two species (DBM and *D. semiclausum*) have overlapping generations which normally allows the use of continuous rather than discrete time and differential equations. Previous experience with such models showed that they could not predict values within the conventional biological confidence level range (5%) (Tonnang *et al.*, 2006). Therefore, we chose the period of observation shorter than the generation of insects (Royama, 1971). As DBM probably has a generation time of about 3 weeks in coastal Kenya, the time series represents intrageneration as well as intergenerational dynamics. c) Insect species have an age structure (Royama, 1971), therefore sometimes both were not abundant enough to be measured by integer numbers thus real numbers were used; consequently a model that can be applied to cases with just a few individuals was chosen.

d) In reality, three years data collection was made after the release of the *D. semiclausum* (Lohr *et al.,* 2007). Only 20 datasets of consecutive collection, corresponding to period of maximum parasitism were used.

e) Other sources of mortality which could have been responsible for the host population trajectory were neglected.

e) Lohr *et al.* (2007) indicates 3 other parasitoids that attack DBM in the region before release of *D. semiclausum*. However, after release their parasitism rate became extremely low hence their effect was neglected.

f) Models were selected within the constraint imposed by the simplicity which eases the analysis and the ability for parameters to fulfil basic biological meaning.

4.2.4 Statistical criteria for parameter estimation Analysis of residuals

Parameter determination was carried out using the methodology already described on the second chapter sections 2.2.2 and 2.2.3. Minimization of the loss function equation 2.1 was done by Powell's multidimensional algorithm (see section 2.2.4). Analysis of residuals was done with Durbin Watson Criteria shown in section 2.3

4.2.5 Model population size predictions at different DBM initial population size

The model with Holling type 3 functional responses was used to develop a graph that allows predictions of future DBM population size as a function of a constant number of parasitoids. The choice for this model was made because it has shown better approximation of the empirical data for DBM and parasitoid than others. For a random selection of DBM initial population size between 0 to 30 DBM/plant, the model was used to estimate the values of DBM at given time interval of 2n weeks (where $n \in N$ ensemble of integers) for a fixed number of parasitoids. The above DBM data was plotted on the plane at fixed value of parasitoid/plant. A projection for any given DBM population from the abscissa to the parasitoid population line will give an estimation of the DBM population size at the next time interval.

4.3 Results

Evaluation of the quotients Skewness/Standard Error and Kurtosis/Standard Error gave values < 3. In addition, the results of the Shapiro-Wilcoxon and Kolmogorov-Smirnov tests showed that the residuals for all models were normally distributed. This demonstrates the validity of application of Durbin Watson criteria for analysis of the sequence of deviations. The results obtained from the minimization of function (9) and from statistical analysis are presented in Table 4.2.

Nicholson-Bailey model predicted an oscillating trajectory composed of a monotonously increasing function starting with 7.5 (initial DBM population size) and reached the first peak between 6 to 8 weeks. After this point, the line began to decline at decreasing rate until the 18th week of collection, then recommenced increasing (Figure 4.1a). The parasitoid population density for the model followed an increasing function starting from 0.02, reaching its peak at 1.69 and then declining until 0.001parasitoid/plant (Figure 4.1b).

The Hassel & Varley (1976) model predicted a DBM and parasitiod clines with similar trajectory behaviour as in Nicholson Bailey model (Figures 4.1).

The carrying capacity, according to Beddington et al.(1975) model was 16.50 DBM/plant. The model DBM populations line started at 8.72 DBM per plant, reached 8.80 DBM per plant, then began decreasing up to 2.64 then gained low increment. The parasitoid population density fluctuation also displays an oscillating trajectory but with small amplitude compared to the DBM line (Figures 4.2).

The May (1978) model generated a line with a starting population of 9.97 DBM/plant declining at a decreasing rate until 4.34 (Figure 4.2a). The model predictions for parasitoid numbers began with 1.12 parasitoid per plant then decreased to around 0.01 parasitoid / plant (Figure 4.2b).

Table 4.2 Estimates of model parameters and values of statistical criteria for seven recurrent models fitted to an empirical times series of the diamondback moth and its parasitoid, *Diadegma semiclausum*, after release in Werugha, Wundanyi Division, Taita Taveta District, Coast Province of Kenya.

	Nicholson-Bailey	Hassel & Varley	Biddington et al.	May	Holling type 2	Holling type3	Getz and Mills
DBM growth rate (r)	0.06	0.07	0.05	0.02	-	-	-
DBM carrying capacity (K)	-	-	16.50	-	-	-	-
Parasitoid per capita searching efficiency (a)	0.27	-	0.24	0.20	-	-	-
Parasitoid constant searching efficiency (q)	-	0.28	-	-	-	-	-
Parasitoid instantaneous search rate (a')	-	-	-	-	0.07	-	0.28
Parasitoid constant for search rate (b)	-	-	-	-	-	0.14	-
Parasitoid search time (T)	-	-	-	-	5.33	5.20	-
Parasitoid handling time (T_h)	-	-	-	-	0.77	0.90	-
Upper bound encounter rate (β)	-	-	-	-	-	-	19.29
Slope parasitoid searching efficiency (m)	-	0.02	-	-	-	-	-
Index parasitism aggregation (k)	-	-	-	0.33	-	-	0.90
Initial DBM population size (N_0)	7.58	7.45	8.72	9.97	6.21	4.53	7.61
Initial parasitoid population size (P_0)	0.02	0.02	0.05	1.12	0.04	0.02	0.05
Loss-function* (Q_{min})	45.31	44.51	47.84	104.18	52.17	61.73	51.85
DBM Durbin-Watson criterion value (dd)	2.03	2.07	1.86	0.95	1.93	1.96	1.85
Parasitoid Durbin-Watson criterion (dp)	0.24	0.23	0.20	0.15	0.20	0.46	0.18

* - squared deviations between empirical and theoretical time series.

- For each model, the number of parasitoid produced per host individual attacked is equal to 1 (c = 1) because *Diadegma semiclausum* is a solitary parasitoid

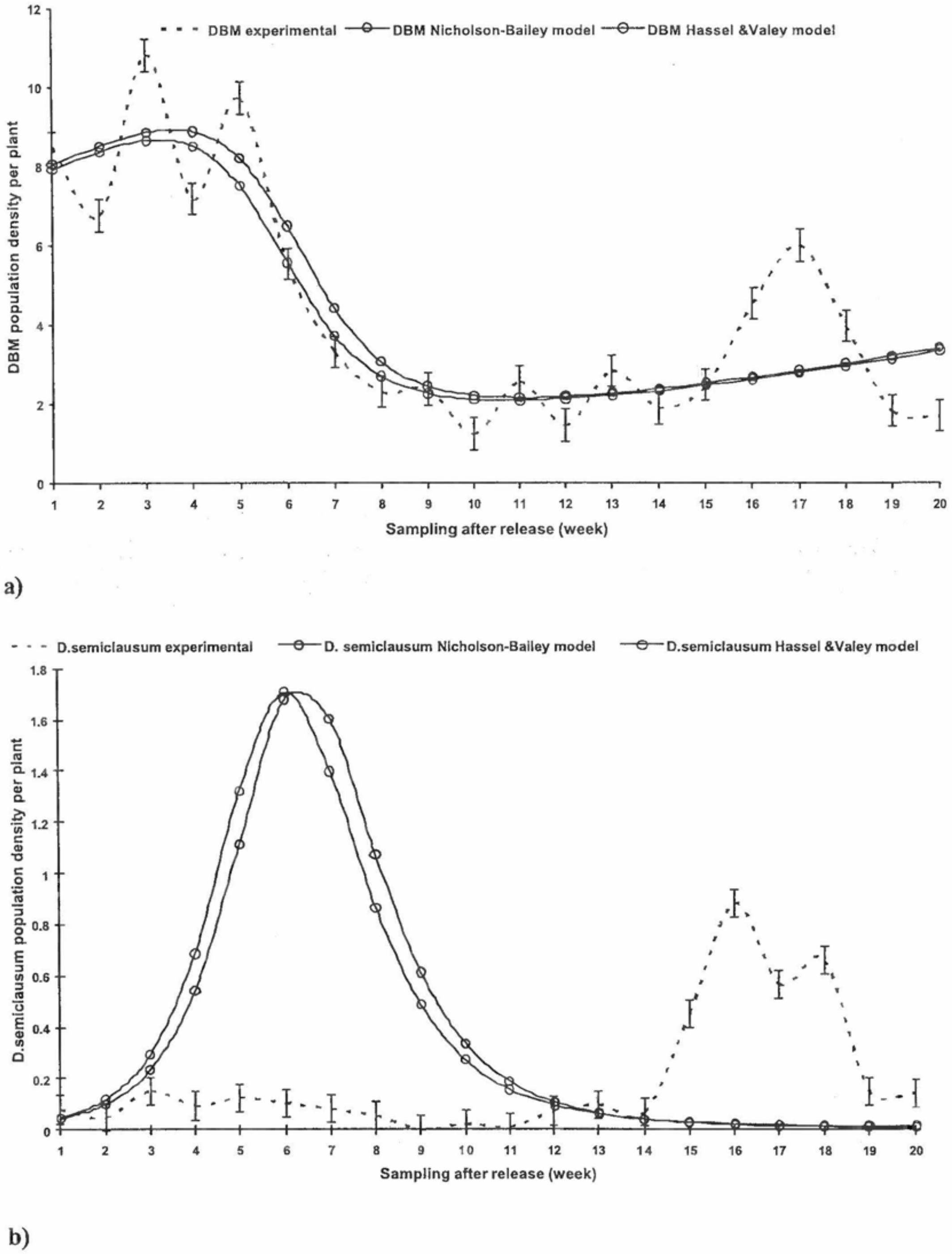

Figure 4.1 Trajectories of the diamondback moth (a) and *Diadegma semiclausum* (b) population for empirical datasets and predicted by Nicholson-Bailey and Hassel & Valey models. Predictions are based on an empirical dataset collected after the initial release of an exotic parasitoid, *Diadegma semiclausum,* Werugha, Wundanyi Division, Taita Taveta District, Coast Province of Kenya.

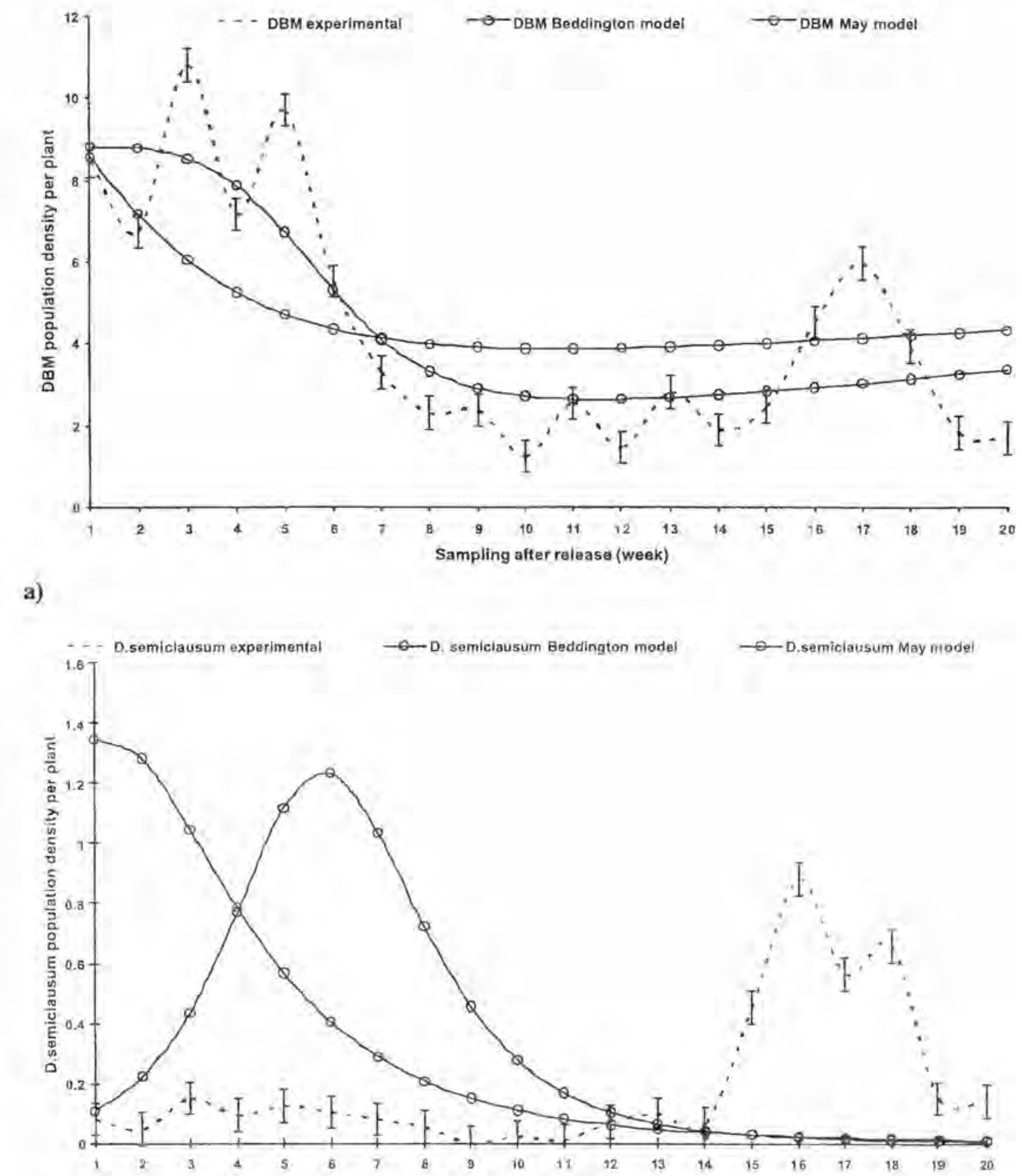

Figure 4.2 Trajectories of the diamondback moth (a) and *Diadegma semiclausum* (b) diamondback moth population for empirical datasets and predicted by Biddington *et al.* and May models. Predictions are based on an empirical dataset collected after the initial release of an exotic parasitoid, *Diadegma semiclausum*, Werugha, Wundanyi Division, Taita Taveta District, Coast Province of Kenya.

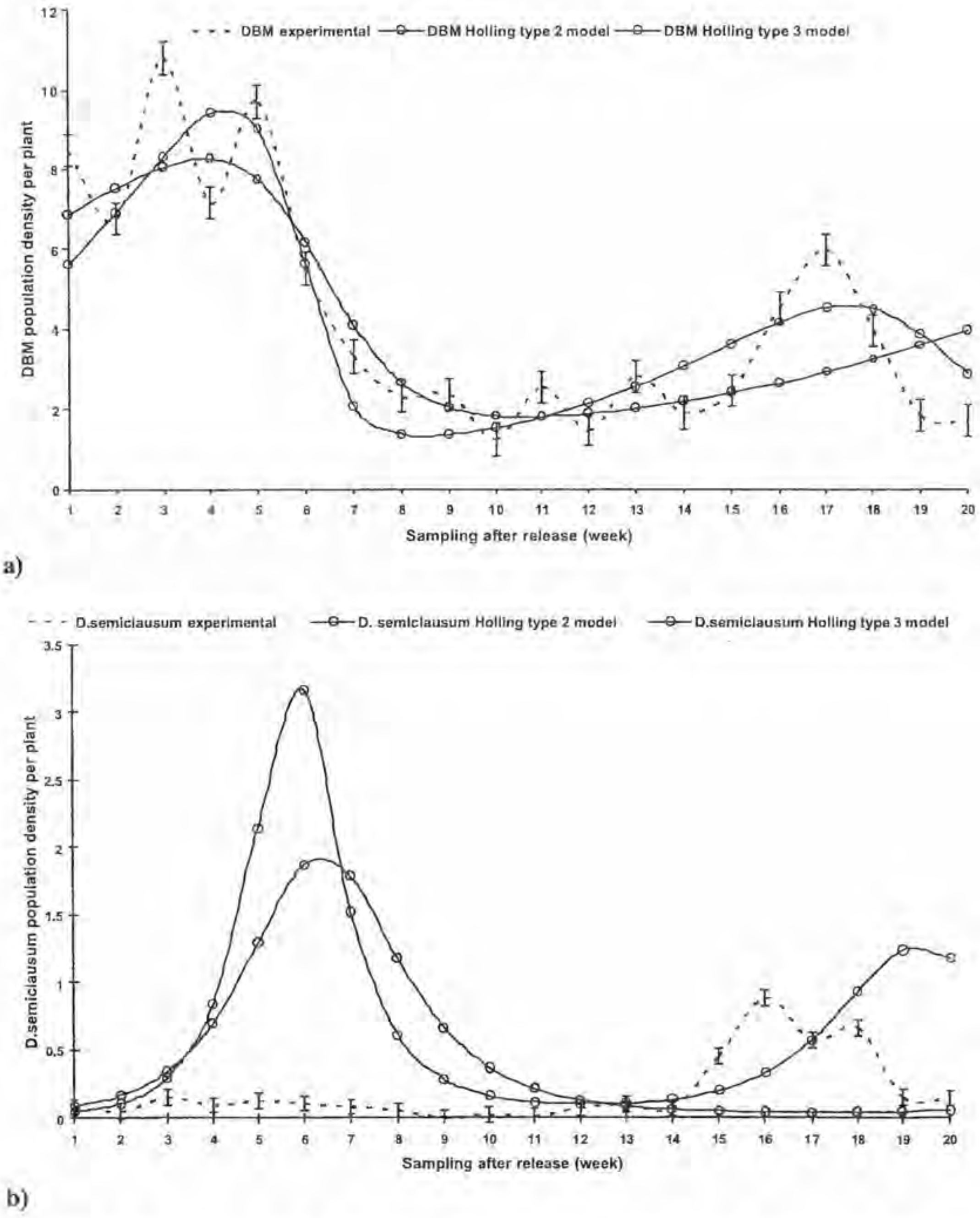

Figure 4.3 Trajectories of the diamondback moth (a) and *Diadegma semiclausum* (b) diamondback moth population for empirical datasets and predicted by Holling type 2 and type 3 functional response models. Predictions are based on an empirical dataset collected after the initial release of an exotic parasitoid, *Diadegma semiclausum*, Werugha, Wundanyi Division, Taita Taveta District, Coast Province of Kenya.

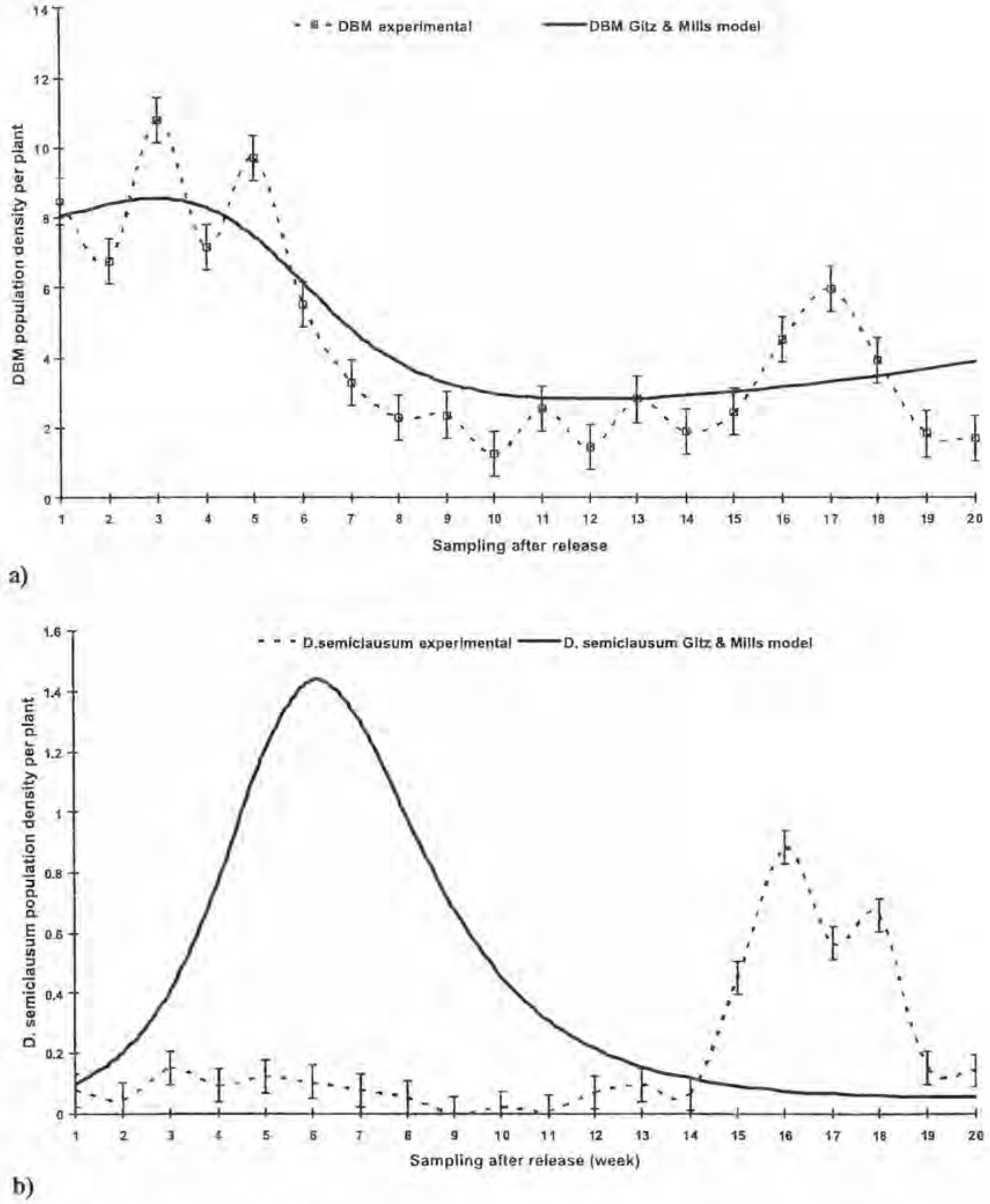

Figure 4.4 Trajectories of the diamondback moth (a) and *Diadegma semiclausum* (b) diamondback moth population for empirical datasets and predicted by Getz and Mills functional responses model. Predictions are based on an empirical dataset collected after the initial release of an exotic parasitoid, *Diadegma semiclausum*, Werugha, Wundanyi Division, Taita Taveta District, Coast Province of Kenya.

DBM and parasitiod population density predicted by model with Holling type 2 functional responses are shown in Figures 4.3. The trajectories behaviour is similar to Nicholson-Bailey model.

Among the applied models, Holling type 3 functional responses presented better line predictions compared to others models. In mapping empirical datasets the model formed an oscillating trajectory starting with 4.53 (initial DBM population size) increase up to 9.40 DBM/plant where the line began to decline until 1.35 then recommenced increasing until 4.53 and decreased again (Figure 4.3a). The parasitoid population density followed an increasing function starting from 0.02, reaching its first peak at 3.16 and then declining until 0.01parasitoid/plant and increased again (Figure 4.3b).

Model with Getz and Mills functional responses population line started at 7.61, reached 8.55 DBM / plant, and then began decreasing to 2.81 where it regained low increment.

The Durbin-Watson criteria applied to the deviations between model and experimental values produced results for each model as shown in Table 4.1 The boundaries of critical values are d_L= 1.20 and $d_u = 1.41$ at 5% level of significance. The Calculated DBM (*dd*) value for all models except for May (1978) model were outside the critical bounds interval and near to 2, meaning that there was no dependence between residuals. In other words, we failed to reject the hypothesis of no negative correlation and no positive correlation for DBM. For the parasitoid, and for all models, the Durbin-Watson value *d* was less than the lower bound of critical value ($dp < d_L$), proving a positive correlation between residuals for the insect.

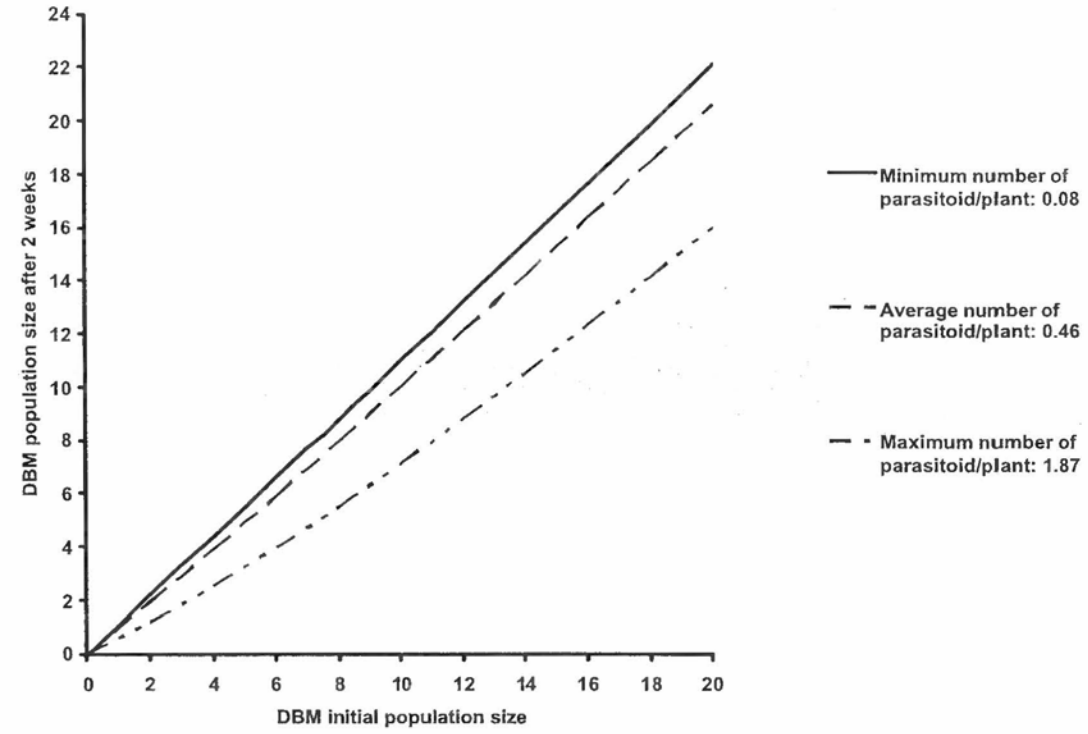

Figure 4.5 Model with Holling type 2 functional response predictions for changes in diamondback moth population size at fixed initial values of parasitoids population, Werugha, Wundanyi Division, Taita Taveta District, Coast Province of Kenya

4.3.1 Outcome of model population size predictions at different DBM initial population

Figure 4.5 is an example which illustrates the model with Holling type 3 functional response predictions for changes in diamondback moth population size at fixed initial values of parasitoids population (0.08, 0.46 and 1.87) respectively. The lines show that the DBM population size at 2 weeks interval kept increasing with an increase in DBM initial population size, but the rate of increase reduced with an increase in parasitoid number. This demonstrates the efficiency of parasitoid in reducing the DBM population size. The graph is a direct biological application of the model and its estimated parameters. If the time interval between collections was identical to the duration of the insect generation time, this can lead to the estimation of the respective insect population size after chosen generations and the obtained results can be compared to what is given from life table analysis.

4.4 Discussion

The unstable cyclic eruptive pulses of the empirical DBM population cannot be clearly explained from the analysis carried out in this chapter. However, their appearance may be due to favourable environmental conditions and abundance in food that trigger an outbreak which immediately collapses due to parasitism and others factors such as rainfall, which have been reported as major factors of DBM population dynamics (Wakisaka *et al.,* 1991). In addition, good explanation of population dynamics is obtained when time lag reaction of DBM intra self-regulation and effects of parasitoid on DBM population size are both taken into consideration. Low parasitoid population density at the beginning of the collection after release may reflect the period of adaptation of this insect to its new environment. An increase in

DBM population leads to more hosts that can be parasitized and therefore causes an increase on the parasitoid population. Sustained population fluctuations are zones of stabilization where the parasitoid successfully regulates the DBM. Points on the trajectory that could not be explained using Isaev's classification of insect outbreaks can be considered as stochastic near stable (or unstable) level.

The DBM growth rate in our models is what is usually called in biology the intrinsic rate of increase. Models with Holling type 3 functional responses produced the highest value for this coefficient whereas the May (1978) model estimated the lowest. The discrepancy observed among models may be due to the ability for each model in fitting empirical data, or the difference in mathematical expression of model equations. Sarnthoy *et al.* (1989) showed that intrinsic rate of increase for DBM is higher at higher temperature. With a mean temperature of 17.6 °C they obtained a DBM intrinsic rate of increase of 0.11 and at 29 °C this parameter value became 0.23. Assuming that the DBM intrinsic rate of increase was uniform everywhere where the same climatic conditions are applied, model with Holling's type 2 functional responses should have offered the best estimation. However, the comparison of the intrinsic rate of increase reported by Sarnthoy *et al.* (1989) with our estimates would not be realistic since this parameter is highly dependant on environmental conditions, especially temperature. The annual average temperature was 16.7 at the study site, a different value from what was considered by the mentioned authors in their experiment close to 17.6.

Among the studied models, only one (Beddington, Free and Lawton) model estimated the value of DBM carrying capacity. The calculated carrying capacity is realistic because several experiments have shown that more than 20 DBM per plant is a good measure of the steady-state density for a cabbage plant to sustainable support diamondback moth species (Wang and Keller, 2003; Karimzadeh *et al.*, 2004).

Early host-parasitoid models only described the outcome of parasitoid searching behaviour in terms of constants (Thompson, 1924; Nicholson, 1933). As studies have increased in the area and more data on the population dynamics has been accumulated; it offers better understanding of the system and new factors that could influence the levels of parasitism per capita efficiency of parasitoid abundance has been suggested. This leads to the proliferation of models with functional responses that differentiate host-parasitoid for predator-prey systems. The majority of these host-parasitoid models incorporate parameters such as search time and handling time (Hassel *et al.,* 1976, Getz and Mills, 1997). Unfortunately, none of the authors properly explained the dimension in which these model parameters are measured. In their laboratory study, Wang and Keller (2002) evaluated the oviposition time for *D. semiclausum* between 3 to 5 seconds and total handling including the time spent waiting for a host of 973 s. They also enumerated ways (wriggling and dropping off leaf, underside feeding) by which DBM larvae can avoid parasitoids. If we assume the second or minute as the time unit in this study for all models, our obtained predictions for these parameters will still be very small compared to experimental results obtained by the above authors. Lack of consideration of the host defensive behaviour in the models could be responsible for the discrepancy between our obtained results and experimentation.

A good number of authors have observed active aggregation in parasitoid and some have stipulated that aggregation response of parasitoids is an important factor that contributes to host regulation (Hassell and May, 1974; Waage, 1983; Smith and Maelzer, 1986; Murdoch *et al.,* 1987; Sheehan, and Shelton, 1989). The May model predicted 0.33 as the index parasitism aggregation for *D. semiclausum*. Experimental work revealed that the *D. semiclausum* parasitism index falls in between 0.6 and 0.9. The same study also demonstrated that high degree of aggregation seems to generate density-dependant parasitism by *D. semiclausum*(Wang and Keller, 2003). In almost every case, our estimated models parameters related to the parasitoid failed to approximate existing experimental results. In general, the existence of positive or negative correlations of residuals between empirical and model trajectories indicates dependence. The application of the Durbin-Watson criteria, which is a tool for testing the dependence between residuals, showed a total independence (no positive and no negative correlation) of residuals for the DBM with all models except May model. In the contrary, a strong residual correlation was demonstrated by the same criteria for the parasitoid. At this stage it is clear that none of the studied models was capable of mutually capturing the dynamics and interactions between DBM and its natural enemies. Several reasons may be responsible for the inadequacy of the models. The fitting procedure which typically try to maximize fit at either very short or very long time scales whereas as the main measuring features for these parameters are for the intermediate scale which may not have been selected during the fitting. Again, the fitting algorithm in searching for the set of parameters that fit the model well, may introduce some noise to the model time series. Lack of sufficient biological constraints and environmental factors in the models can lead to poor predictions. Legaspi *et al.* (1996) largely discuss the possible importance of temperature and other diurnal events on functional response for simulation models applied to biological control. What may have also contributed to this outcome is that we applied the models in a highly unstable situation after the introduction of an exotic parasitoid. In such condition, the introduced species may have not played the major role on pest population regulation. In that case, a recommendation for mathematical models, which include some additional density-dependent or density-independent factors, should be used to fit the field data. It might again be possible that, the applied models which, originally were designed to answer qualitative questions about population dynamics could not encompass this human activity coupled with actual climate change effects. Therefore, new host-parasitoid models which incorporate these aspects may be thought of. Process-based models built using the results of laboratory and/or field experimentation which will explicitly account for all important system interactions are proposed. However, because of the complexity of the ecosystems, it is unlikely ever to be possible to include all appropriate variables and interactions in a model. Also, the more parameters a model has, the less are its chances in providing good fit to independent data. Only by combining a wide range of consensus methodologies well built and fitted models are likely to emerge. From other angles, more effort should be given in fitting procedure too. It can be improved by developing a likelihood function that incorporates the best information on the structure of the measurement and dynamic noise.

Chapter 5

Assessing the impact of biological control of *Plutella xylostella* through the application of Lotka-Volterra model

Summary

Population dynamics of diamondback moth (DBM), *Plutella xylostella* (L.) and its larval exotic parasitoid *Diadegma semiclausum* (Hellen) were studied for 15 months before the release of parasitoid and 36 months after release in two areas at Werugha, Coast Province of Kenya and Tharuni, Central Province of Kenya, respectively. One hundred and twenty five (125) pairs (males and female s) of *D. semiclausum* were released once at each location. For the pre-release period, the individual counts of all parasitoid species was summed up as "indigenous parasitoids" whereas for the post-release period, only the *D. semiclausum* population density was accounted for; as the parasitism rate by indigenous parasitoids was extremely low. For each area in pre and post release periods, we estimated Lotka-Volterra model parameters from the minimization of the loss function between the theoretical and experimental time series datasets following the Nelder-Mead multidimensional method. The model estimated a reduction in the value of the steady state of DBM population from 4.86 to 2.17 at Werugha and from 6.11 to 3.76 and 3.45 (with and without exclusion of the time before *D. semiclausum* recovery) at Tharuni when transiting from the pre-release and post-release periods, respectively. This change is a consequence of the newly introduced parasitoid, in the areas. The study presents a detailed technique for model parameters restoration and proved that the classical

biological control effort with *D. semiclausum,* in different areas of Kenya has had a positive impact in reducing pest (DBM) population density.

5.1 Introduction

The Diamondback moth (DBM), *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), adults are slender, very small, 1/3 inch (8mm) long, greyish-brown with folded wings flaring outward and upward at their posterior ends. They lay their eggs singly or in groups of two or three on the underside of lower leaves near the leaf veins or on the lower stalks. Upon hatching, they begin mining within the leaf tissue, whereas later instars feed on heart leaves of young plants and/or the underside of the leaf surfaces of more mature plants.

Hymenopteran parasitoids of the genera *Diadegma* (Hymenoptera: Ichneumonidae) are among the most effective natural enemies of DBM. The four larval stages of DBM are attacked by *Diadegma semiclausum* with preference to the second and third larval instars. After pupation of the host larva, the parasitoid larva completes eating up the host and thereafter forms its own cocoon. An adult parasitoid emerges in about five days after cocoon formation. Parasitism rates of this parasitoid are host-density-dependent and super parasitism is known to result in to production of more female than male progeny (Konig *et al.*, 1993). When the parasitoid is allowed to choose between parasitized and unparasitised DBM larvae, it is well able to distinguish between parasitized and unparasitised host larvae, showing preference for the unparasitised larvae (Konig *et al.*, 1993).

Diadegma semiclausum (Hellen) and *Diadromus collaris* (Gravenhorst) (Hymenoptera: Ichneumonidae) were introduced into New Zealand from England (Hardy, 1938; Thomas and Ferguson, 1989) as biological control agents against

DBM. For the same purpose, in 1950 *D. semiclausum* was taken to Indonesia (Sastrosiswojo and Sastrodihardjo, 1986). Talekar *et al.* (1990) and Talekar (1992) reported that the introduction of *D. semiclausum* caused more than 70% parasitism in highland areas of Taiwan, providing substantial savings in DBM control. In several highland regions of Asia, biological control of DBM through introduction of *D. semiclausum* has been a success (Biever, 1997; Poelking, 1992). With cabbage growing in Kenya also predominantly concentrated in the cool highlands, the importation and release of *D. semiclausum* in the country was expected to produce similar results as in the highlands of tropical Asia.

In October 2001, two pilot releases areas were created in Kenya: the first release at Werugha in Taita Hills on July 2002 and the second release at Tharuni in Central Highlands of Kenya in September of the same year (Momanyi *et al.*, 2006). DBM and parasitoid population dynamics were studied for 15 months before and three years after the release in each pilot site in order to measure the effect of the releases on DBM population and cabbage damage as well as the effect on indigenous natural enemies (Löhr *et al.*, 2007). The objective of the present work was to study the biological control impact of the exotic parasitoid *D. semiclausum* in Kenya, using the Lotka-Volterra prey-predator model with self-regulation mechanism. This impact study was done through estimation of the model steady state values before and after the release of the exotic parasitoid and compares

5.2 Materials and Methods

5.2.1 Site description and Data collection

Experimental results were obtained from pilot release areas in Werugha, Wundanyi Division in Taita Taveta District, Coast Province of Kenya and Tharuni

Limuru Division, Kiambu District, Central Province. A detailed description of the pilot release areas was provided in section 2.1.1. It was mention that cabbage and kale are the main rain fed vegetable crops in both regions, with complementary irrigation during the dry season from shallow wells using buckets. The model was applied as explained earlier, (see sections 2.2.1, 2.2.2 and2.2.3). These paragraphs also provide detailed explanations for DBM and *D. semiclausum* population density collection.

5.2.2 Lotka-Volerra model

Detailed description of the The Lotka-Volterra was made in section 3.3.2. The models equations are expressed as follows:

$$\frac{dx}{dt} = \alpha_1 x - \beta_1 x^2 - \gamma_1 xy, \frac{dy}{dt} = -\alpha_2 y - \beta_2 y^2 + \gamma_2 xy, \tag{3.1}$$

$x(0) = x_0 \geq 0$, $y(0) = y_0 \geq 0$ (Cauchy problem)

Where,

$x(t)$ is the DBM population size at moment t,

$y(t)$ is the parasitoid population size at the same moment,

α_1 is the growth rate or Malthusian parameter for the DBM population,

α_2 is the intensity of natural death of individuals in the parasitoid population,

β_1 and β_2 are the coefficients of self-regulation in the respective populations,

γ_1 and γ_2 are the coefficients of interaction between the two populations,

α_1 / β_1 is the equilibrium number for DBM at the absence of parasitoid,

x_0 is the initial value of DBM population density, and

y_0 is the initial value of the parasitoid population density.

Theoretical studies of model (1) by Wangersky (1978) have shown that it has two dynamic regimes: elimination of the predators for all possible initial values of population sizes if $\alpha_1\gamma_2 > \alpha_2\beta_1$ or stabilization of both populations at a unique, non-zero, stable level (under the additional assumption that the Malthusian parameter $\alpha_1 > 0$. If $\alpha_1 < 0$, both populations fade asymptotically for all non-negative initial values). The steady state or non-trivial equilibrium of the system is given by:

$$\bar{x} = \frac{\alpha_1\beta_2 + \alpha_2\gamma_1}{\gamma_1\gamma_2 + \beta_1\beta_2}, \quad \bar{y} = \frac{\alpha_1 - \beta_1\bar{x}}{\gamma_1}. \qquad (5.1)$$

The model was applied before the release with the interacting system DBM/ indigenous parasitoids and with only DBM/*D. semiclausum* interacting system after release.

5.2.3 Other considerations

The following considerations were made:

a) The total number of all parasitoids collected before release was lumped together and called “indigenous parasitoid”. The assumption was made to have a bigger number for parasitoids before release as their individual figure were very small.

b) The two species (DBM and *D. semiclausum*) have overlapping generations which normally allows the use of continuous rather than discrete time differential equations except other assumptions are made (Royama, 1971).

c) Insect were not abundant enough to be measured by integer numbers therefore real numbers were used; consequently a model that can be apply to cases with just a few individuals was chosen.

d) Choosing a model with time-delay should have been an ideal choice, but as our goal was to evaluate the steady state point, must of such model in the literature are either not stable or their steady state is difficult to evaluate (Royama, 1971).

e) Other sources of mortality which could have also been responsible for the host population trajectory were neglected.

f) Godfray and Rees (2002) mentioned three main reasons that justified the importance of a population growth rate parameter in the study of population biology. First, the population growth rate is central to population projection. Secondly, it is often the most natural response variable for the statistical analysis of the factors influencing a species population dynamics and, finally, this parameter intimately links population dynamics and evolutionary biology. Lotka-Volterra model predicts the growth rate of the insect pest (DBM) and offers straight forward means of calculating the steady state of population which is the leading parameter in achieving the study goal.

5.2.4 Statistical criteria and residuals analysis for parameter estimation

The statistical criteria and residual analysis for estimated parameters was carried out as explained in section 3.2.3.

5.2.5 Model population size predictions

The model was used to develop a graph that allows predictions of future DBM population size at fixed initial number of parasitoids. For a random selection of DBM initial population size between 0 to 30 DBM/plant, the model was used to estimate the values of DBM at given time interval of 2n weeks (where $n \in N$ ensemble of integers) at fixed number of parasitoids. The above DBM data was plotted on the plane at fixed value of parasitoid/plant. A projection for any given DBM population from the abscissa to the parasitoid population line will give an estimation of the DBM population size at the next time interval. The same procedure could be performed with a chosen initial parasitoid population at fixed value of DBM/plant, leading to the parasitoid population prediction at given time intervals.

5.3 Results

5.3.1 Werugha before release

The values of the estimated model parameters are shown in Table 5.1. The model predicted an oscillating trajectory composed of a monotonously increasing function starting with 1.91 (initial DBM population size) and reached the first peak at 12.22 DBM/plant where the line began to decline at decreasing rate until 2.3 before increased again (Figure 5.1). The indigenous parasitoids population followed a monotonously slow increasing function starting from 0.05, reaching its peak at 1.41 and then declined to 0.3/plant (Figure 5.1).

Figure 5.2 depicts the function Q on the plane (α_1, β_1) and the boundaries of the confidence domain Ω_k, $k = 1,2,3$ for 1, 5 and 10% confidence levels, respectively. The boundaries of the confidence domains were hyperbolic trajectories. The trace $\bar{P}$ with equation $\beta_1 = 0.21\alpha_1$ is the bifurcation line.

Table 5.1 Estimates of Lotka-Volterra model parameters and values of statistical criteria for Lotka-Voltera fitted to an empirical times series of the diamondback moth and its parasitoid, *Diadegma semiclausum*, before and after release in Werugha, Wundanyi Division, Taita Taveta District, Coast Province of Kenya and Tharuni, Limuru Division, Kiambu District, Central Province of Kenya.

	Werugha		Tharuni		
Estimated parameters	Before release (66 weeks)	After release (98 weeks)	Before release (66 weeks)	After release[1] (104 weeks)	After release[2] (88 weeks)
DBM growth rate (α_1)	27.76	27.76	27.63	27.63	27.63
Natural death rate (α_2) (parasitoid)	33.28	1.80	58.6	74.18	58.67
DBM self-regulation coefficient (β_1)	1.40	1.40	0.98	0.98	0.98
Self-regulation coefficient (β_2) (parasitoid)	2.04	0.43	1.10	375.25	26.77
Interaction coefficient (γ_1) (DBM/parasitoid)	35.14	145.19	40.69	242.98	72.27
Interaction coefficient (γ_2) (parasitoid/DBM)	7.07	0.95	9.68	29.51	19.56
Steady state population (DBM) ($\bar{x}$)	4.86	2.17	6.11	3.76	3.45
Steady state population (parasitoid) ($\bar{y}$)	0.60	0.17	0.53	0.1	0.33
Initial population size (x_0) (DBM)	1.91	8.48**	5.25	11.58**	9.70**
Initial population size (y_0) (parasitoid)	0.05	0.15	1.58	0.05	0.04
Loss-function* (Q_{min})	101.61	92.87	143.31	242.49	110.36

* - Squared deviations between empirical and theoretical time series

** - DBM population size at release

Tharuni after release[1]: Time series datasets made of 52 data were considered, these data correspond to all the post-releasing collections where the number of *D. semiclausum* is zero in the first 8 collections.

Tharuni after release[2]: Time series datasets made of 44 data were considered, these data correspond to 44 collections, excluding the 8 collections where no *D. semiclausum* was found on the field

5.3.2 Werugha after release

The model predicted a monotonously decreasing line starting at 8.48 as initial DBM population size, with stabilization starting at 0.74 DBM/plant (Figure 5.3). The *D. semiclausum* population shows a slowly oscillating line from 0.15 increases to 0.23 and declines 0.17 /plant (Figure 5.3).

5.3.3 Tharuni before release

The model predicted an oscillating trajectory starting at 5.3 as initial DBM population size, which reached its first minimum at approximately 2.7 DBM/plant; then began increasing up 10.0 where started to decline again at increasing rate and reached the second minimum of 4.0 DBM/plant where the line recommenced increasing (Figure 5.4). The indigenous parasitoids population density fluctuation also displayed an oscillating trajectory but with small amplitude compared to the DBM line. The line began with 1.58 indigenous parasitoids/plant declined at a decreasing rate until 0.15 where the growth commences at decreasing rate. The line reaches the peak at 1.03 indigenous parasitoids/plant then declined again (Figure 5.4).

The behaviour of function Q on the plane (α_1, β_1) and the boundaries of confidence domains Ω_k, $k = 1,2,3$ for 1, 5 and 10% confidence levels are illustrated in Figure 5.6. $\bar{P}$ is the bifurcation line determined by: $\beta_1 = 0.16\alpha_1$.

5.3.4 Tharuni after release[1]

The predicted population line started with 11.58 DBM/plant and declined monotonously at a decreasing rate until 2.93 and then commenced increasing to later stabilize towards a value of 3.76 (Figure 5.6). Model predictions for *D. semiclausum*

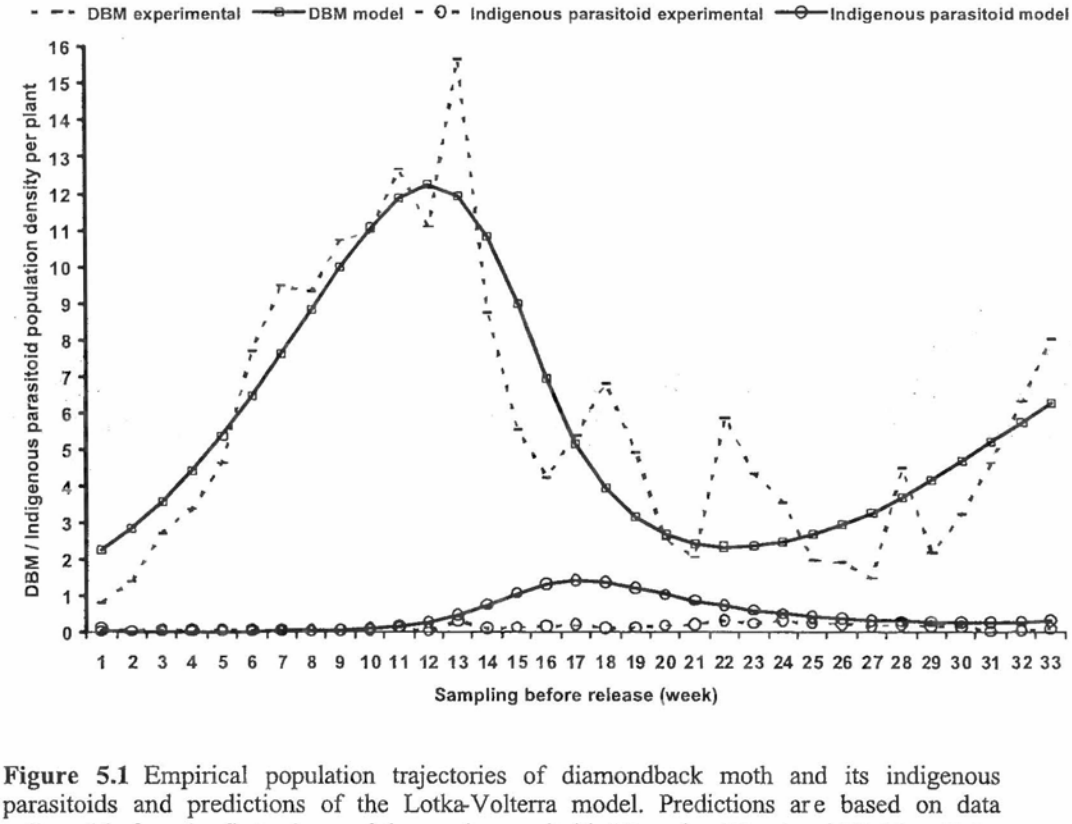

Figure 5.1 Empirical population trajectories of diamondback moth and its indigenous parasitoids and predictions of the Lotka-Volterra model. Predictions are based on data collected before the first release of the exotic parasitoid. Werugha, Wundanyi Division, Taita Taveta District, Coast Province of Kenya.

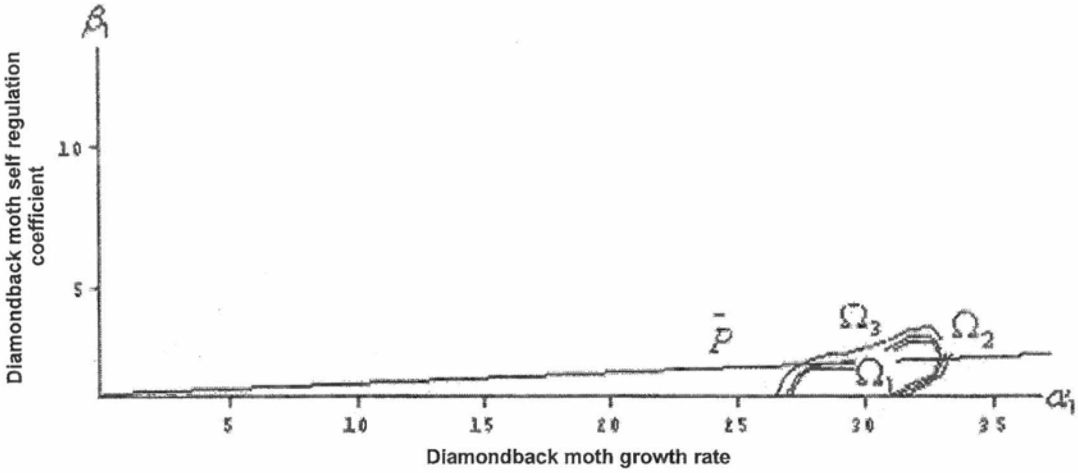

Figure 5.2 Boundaries of confidence domains for estimated parameters of the Lotka-Volterra model at fixed initial population values of the diamondback moth (x_0) and its indigenous parasitoids (y_0). Werugha, Wundanyi Division, Taita Taveta District , Coast Province of Kenya.

Ω_1 is the boundary for 10% confidence level, Ω_2 for 5% confidence level and Ω_3 - for 1%, respectively. $\bar{P}$: $\beta_1 = 0.21\alpha_1$ is the bifurcation line.

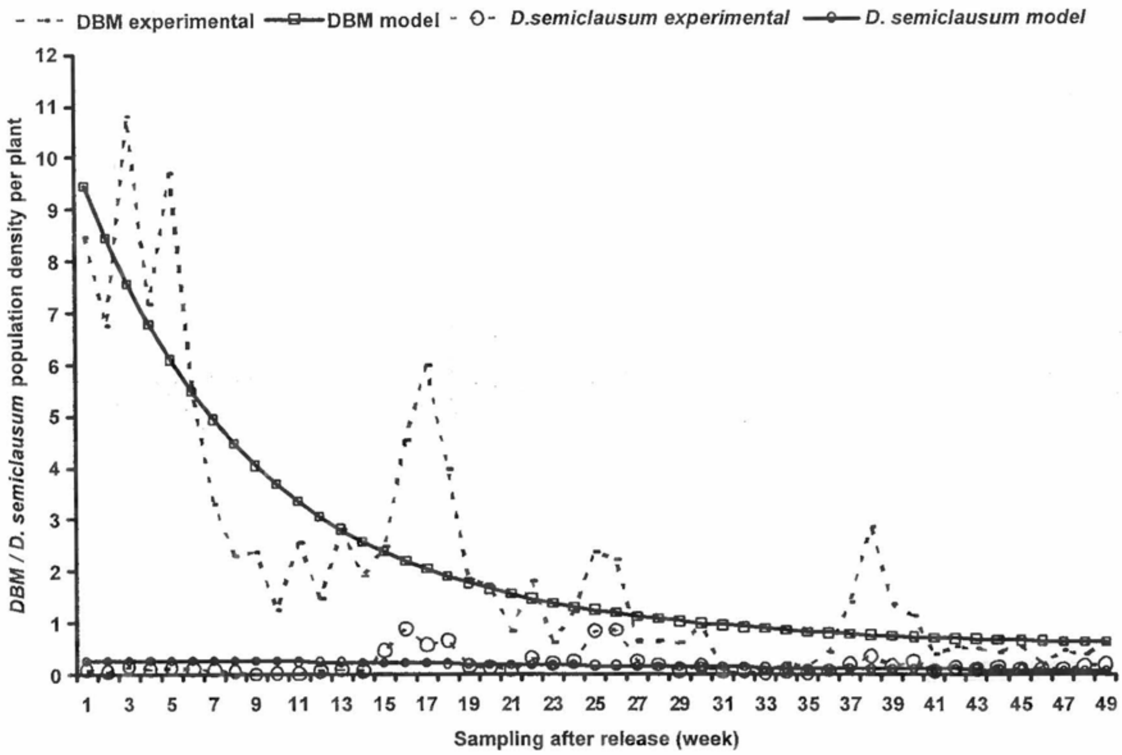

Figure 5.3 Empirical population trajectories of the diamondback moth and its exotic parasitoid, *Diadegma semiclausum,* and predictions of the Lotka-Volterra model. Predictions are based on data collected after the first release of the exotic parasitoid. Werugha, Wundanyi Division, Taita Taveta District, Coast Province of Kenya.

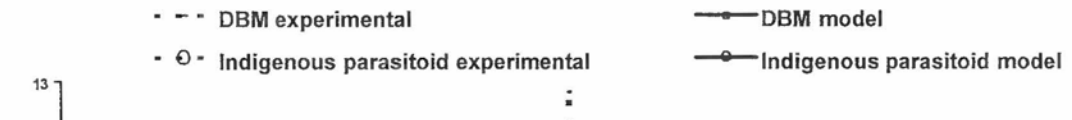

Figure 5.4 Empirical population trajectories of diamondback moth and indigenous parasitoids and predictions of the Lotka-Volterra model. Predictions are based on data collected before the first release of the exotic parasitoid. Tharuni, Limuru Division, Kaimbu District, Central Provinceof Kenya

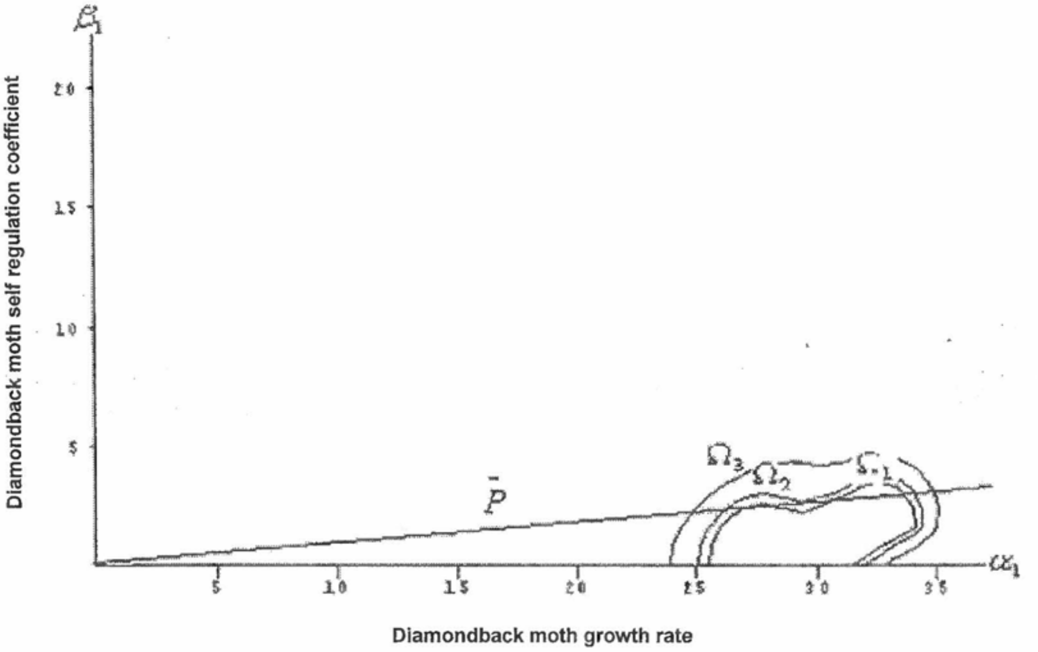

Figure 5.5 Boundaries of confidence domains for estimated parameters of the Lotka-Volterra model at fixed initial values of diamondback moth (x_0) and indigenous parasitoid (y_0) population. Tharuni, Limuru Division, Kiambu District, Central Province of Kenya.

Ω_1 is the boundary for 10% confidence level, Ω_2 for 5% confidence level and Ω_3 - for 1%, respectively. $\bar{P}$: $\beta_1 = 0.21\alpha_1$ is the bifurcation line.

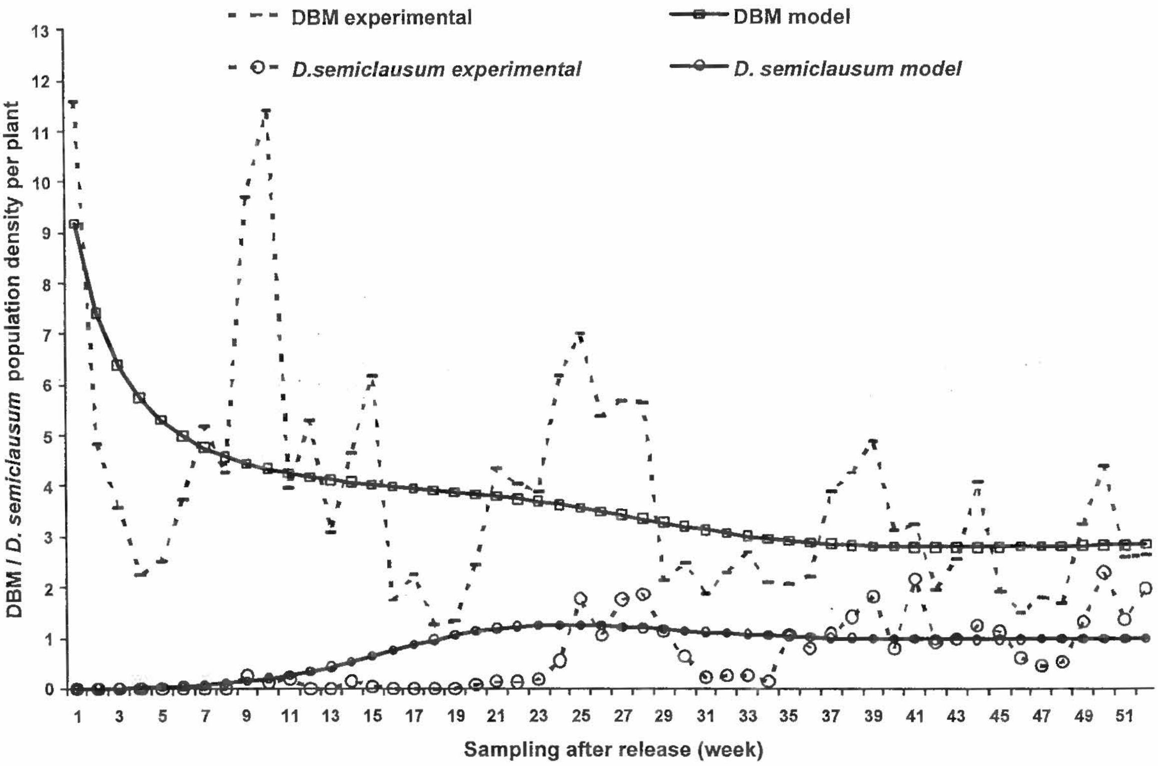

Figure 5.6 Empirical population trajectories of the diamondback moth and its exotic parasitoid, *Diadegma semiclausum,* and predictions of the Lotka-Volterra model. Predictions are based on data collected after the first release of the exotic parasitoid without exclusion of the initial period where no *Diadegma semiclausum* were recovered. Tharuni, Limuru Division, Kaimbu District, Central Provinceof Kenya.

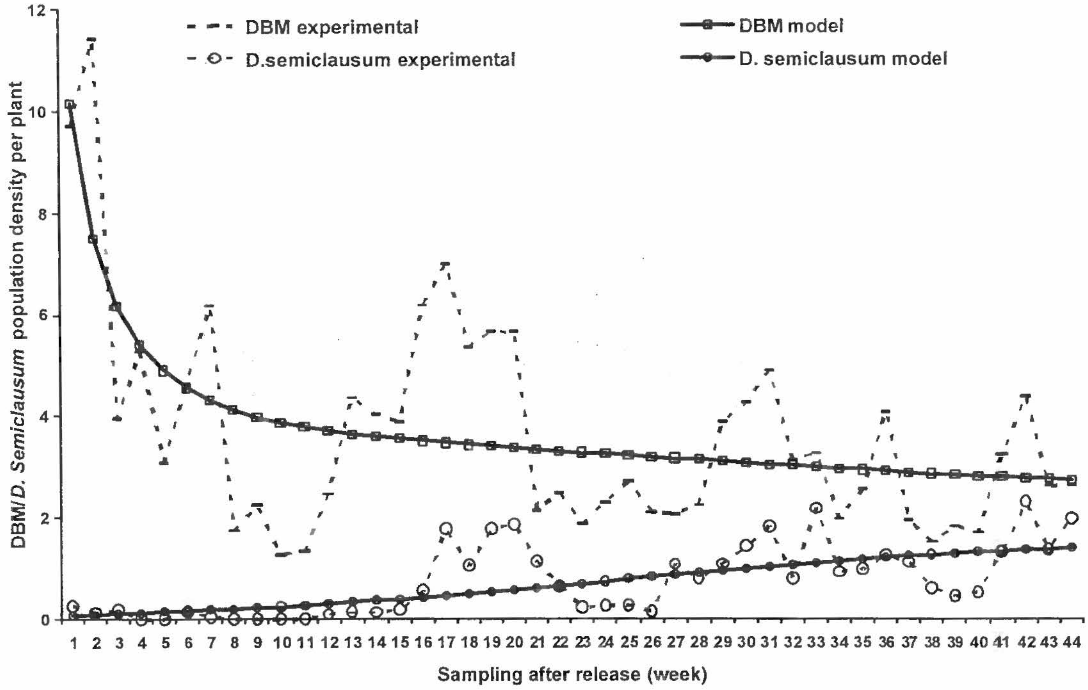

Figure 5.7 Empirical population trajectories of the diamondback moth and its exotic parasitoid, *Diadegma semiclausum,* and predictions of the Lotka-Volterra model. Predictions are based on data collected after the first release of the exotic parasitoid excluding the initial period where no *Diadegma semiclausum* were recovered. Tharuni, Limuru Division, Kiambu District, Central Province of Kenya.

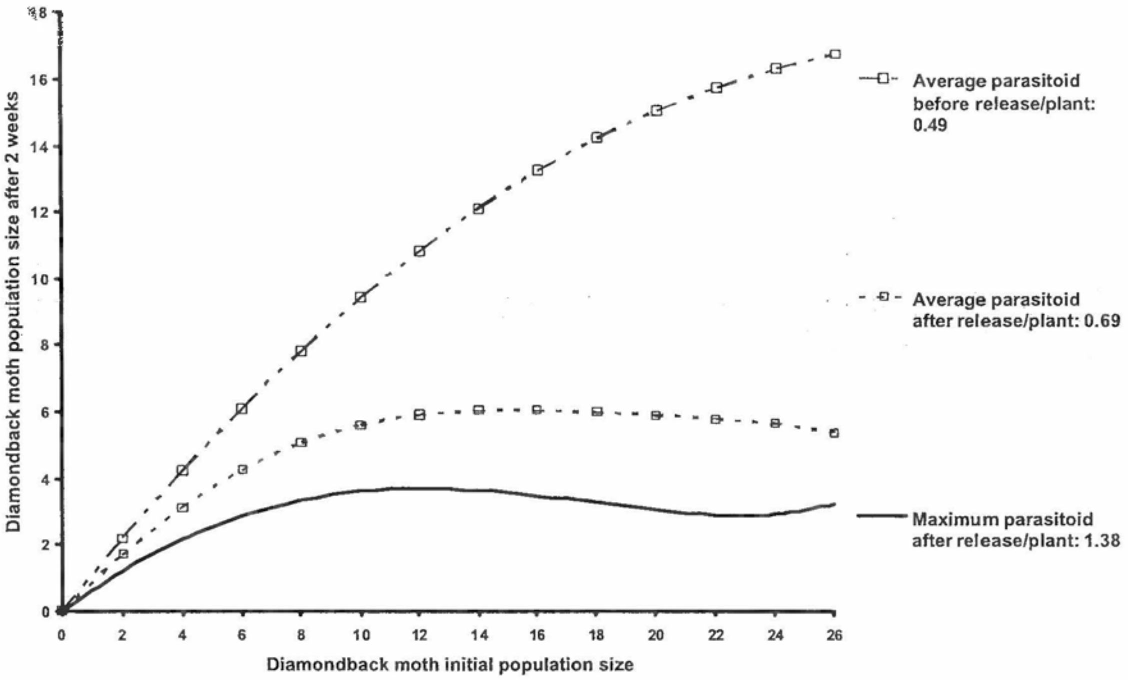

Figure 5.8 Model predictions for changes in diamondback moth population size at fixed initial values of parasitoids population, Tharuni, Limuru Division, Kiambu District, Central Province of Kenya.

numbers began with a very small monotonous increase in population size starting at 0.05. This initial value increased to 0.31 then decreased at around 0.98 *D. semiclausum* / plant (Figure 5.6).

5.3.5 Tharuni after release[2]

The model prediction for the population development was an initial population size of 9.7 DBM/plant followed by steeply decreasing values for the first five samplings. Thereafter population size began oscillating with continuous peak reduction (Figure 5.7). For *D. semiclausum* numbers the Lotka-Volterra model predictions is an oscillation with low amplitudes (Figure 5.7).

5.3.6 Comparison between Tharuni after release[1] and Tharuni after release[2]

Table 5.1 shows that the Tharuni after release[1] data set yielded in most cases higher model parameter values than Tharuni after release[2]. In addition, the value of the loss function ($Q_{\min}$) for Tharuni after release[1] was substantially bigger than the value obtained from Tharuni before release and after release[2]. We compare the loss function of different datasets from the logic that before release, DBM was abundant in the field than after release. In contrary, parasitoids became abundant after release. Our loss function been made of the square difference between the number of these two insects and the theoretical results, expectation was to obtain lower value of $Q_{\min}$ after the release. As intension was to measure the impact of *D. semiclausum*, in the following discussion while mentioning the post-release period in Tharuni, reference should be given to Tharuni after release[2]

5.3.7 Outcome of model population size predictions

Figure 5.8 is an example that illustrates the model predictions for changes in diamondback moth population size at fixed initial values of the parasitoid population (0.49, 0.69 and 1.38) respectively in Tharuni. With an average parasitoid before release of 0.49/plant, the DBM population size at 2 weeks interval keeps on increasing with an increase in DBM initial population size. This demonstrates the inefficiency of the indigenous parasitoids. After release, with an average population size of 0.69 *D. semiclausum*/plant, the population size of DBM after 2 weeks increase with an increase in DBM initial population size until 12 DBM/plant where the line slowly reduced when approaching 28 DBM/plant. Considering the maximum number of *D. semiclausum*/plant equal to 1.38, similar line behaviour was obtained as for the previous with reduction rate on the DBM population size after 2 weeks and an earlier decrease, which started increase near 28 DBM/plant. Figure 5.8 is a direct biological application of the model and its estimated parameters, if the time interval between collection was identical to the duration of the insects generations time, this can lead to the estimation of the respective insects population size after chosen generations and the obtained results can be compared to what is given from life table analysis.

5.4 Discussion

In spite of the great number of mathematical models used to explain the dynamics and interactions between host and parasitoid, (Lotka, 1920; 1925; Volterra, 1931; Hsu and Huang, 1995) and the numerous reports of success of *D. semiclausum* in controlling DBM in various part of the world (Talekar *et al*, 1990, Biever, 1997; Poelking, 1992), no attempt has been made to assess and predict the impact of this parasitoid using pure mathematical models.

Standard methodology for model parameter restoration was applied. The model used is made of autonomous mathematical equations, i.e. without the variable time on the right hand side of their respective functions. Absence of this variable leads to the assumption that the time interval between measurements is unity. In other words, real values for model parameters cannot be estimated; nevertheless, identified parameters are proportional to real values with an unknown coefficient of proportionality. Best estimated sets of parameters for the model in both studied sites before and after the release of the exotic parasitoid *D. semiclausum* correspond to a regime of population stabilization at non zero level for both insects.

Normally, in the field of insect population, a deterministic description of phenomena is quite difficult, an empirical equations can only be casually adopted (Royama, 1971). The choice of these equations was hard to rationalise as there exists other forms of equations which could fit the same observed data. Obtaining good fit does not necessary imply that the chosen equations could clearly explain the type of interaction between the insects and well predict their population density. Consequently, we limited the scope on model parameters, estimation, casual comparison with empirical results and evaluation of the system steady states.

The growth rate in our model equations is what is called in pure biological sense the "intrinsic rate of natural increase". This rate is dependant upon the genetics of the population and the physical quality of the environment such as temperature (Wangersky, 1978). Sarnthoy *et al.* (1989) estimated 0.11 and 0.25 at mean temperatures of 17.6 ^{0}C and 28.9 ^{0}C respectively for the Thailand DBM strain. In both pilot areas, temperature fluctuated between 13. ^{0}C to 35 ^{0}C, the model predicted growth rate is very high compared to these values and the value obtained at Werugha differs from what was obtained at Tharuni. The discrepancy could be explained by the climatic differences in particular higher temperature and lower rainfall at Tharuni (Löhr *et al*, 2007). Momanyi *et al.* (2006) also point out that these factors were responsible for the delay in the establishment of the newly introduce parasitoid at Tharuni.

Honestly, comparison of different results requires identical time and space scale between the studies. Unfortunately, attempts to predict species density are usually hampered by mismatches between the spatial and temporal scales at which we make measurements and the scale at which ecological phenomena influence patterns of species life requirements. Each author define its own time and space scale what make results comparison inadequate. Lack of information on natural history of the insects severely limits the ability to confidently offer accurate population density prediction. Which ability is further complicated by often non-linear response of species to habitat and vice versa. Sometimes, the size and ecological context of habitat patches influence the demography of the insects.

The model predicted higher value of self regulation coefficient for DBM in Werugha than Tharuni, this is explained by the favourable environmental conditions for proper DBM development in the first area rather than the latter. In other part, low rainfall in Tharuni has lead to dusty conditions and deficit in evapotranspiration which resulted to discontinuity of cabbage (DBM host plant) production in the area. The model produced a high value for parasitoid self-regulation. We know from data presented by Momanyi *et al.* (2006) that one year after release in Werugha, competition between parasitoids was so strong that even first instar larvae that were still mining were parasitized So the high self-regulation parameter may truly reflect strong competition for host larvae. This becomes much clearer if we calculate a parasitoid/host ratio from our dataset: while the average value before release was 0.02

for Werugha before release, this increase to 0.06, 0.26, and 0.30 for the 1st, 2nd and 3rd year after release, respectively. Corresponding values for Tharuni were much higher (0.03 before, 0.06, 0.28 and 0.47 for the three years after release).

Based on the self-regulation mechanism for insect population (Nicholson, 1958), the following analysis may possibly be made as tentative explanation for the DBM and *D. semiclausum* population fluctuation. The continued existence of DBM is necessarily limited to areas where all it requires for living is supplied in quantity and quality. Inside these areas the DBM population tends to increase progressively, but this increase automatically face some limiting factors such as climatic variations. This is the most likely explanation for the DBM population fluctuations before release in Werugha and Tharuni. After the release of *D. semiclausum,* especially in Werugha where the establishment of the parasitoid was very fast, the newly introduced species reduced the DBM population to such scarcity that it started to experience difficulty in finding enough hosts to parasitize and its population also declined. This phenomenon progressively tends to reduce the peak of DBM population density and increase the *D. semiclausum* population density, which both later began to stabilize.

Wangersky (1978) defined the interaction coefficient host/parasitoid (γ_1) as a constant of proportionality, linking the parasitoid-inflicted mortality to the numbers of host and parasitoid. The same author defined the interaction coefficient parasitoid/host (γ_2) as a relation between the increase in parasitoid population density to the number of hosts and parasitoids. In both studied areas, the values of these coefficients changed after the release demonstrating different interactions between DBM and *D. semiclausum* than DBM and indigenous parasitoid. This is justified by the *D. semiclausum* superior host searching capability and better association with cabbage host plants, at least as far as its congeneric indigenous species is concerned (Rossbach *et al.,* 2005).

Wallner (1987) stated that natural multi-species assemblages of plants, animals and insects may possess several steady states or non trivial equilibrium points. The change in the steady state can be caused by a sudden shift in population number as a consequence of a newly introduced species or changes in environmental conditions or food availability. In both studied sites we found reduction of the steady state of DBM population after the release of *D. semiclausum,* other factors (food availability, environmental conditions etc.) remaining unchanged. Such an introduction moves the system non-trivial equilibrium point to a different level by decreasing the DBM population density and increasing the parasitoid population density with both populations later may converge and stabilize.

The boundaries of the confidence domains for the model in most cases described hyperbolic trajectories in form of annular surfaces. These surfaces are areas where all possible combinations of model parameters can be found with a minimum value of the loss function Q. These domains were divided in two areas by a bifurcation line $\bar{P}$. The surface below the bifurcation line $\bar{P}$ corresponds to stable coexistence of DBM and "indigenous parasitoids" before release, DBM and *D. semiclausum* after the release respectively. The surface above the line corresponds to elimination of the parasitoids. In the model, the DBM never go to extinction.

From the graphs, it is clear that the model after the release could not properly capture the subtleties of ecological reality as before release. This could be due to the shifting of the system non trivial equilibrium. This was demonstrated by the gap obtained between the steady state of DBM population ($\bar{x}$) before and after release.

The estimated values at the same area in different periods, post and pre-release presented large reduction proving the impact of the newly released exotic parasitoid in the two areas. From this result, conclusion could be made that the biological control based on the introduction and release of *D. semiclausum,* in two different sides *at* the Central and Coast Provinces of Kenya has had a positive impact in suppressing pest (DBM) population density. The results obtained could encourage the expansion of the project to neighbouring countries with similar natural conditions in the entire East Africa region to help the farmer in controlling DBM and consequently minimize the unnecessary use of insecticides.

Chapter 6

Host-parasitoid population density prediction using artificial neural networks

Summary

Integrated pest management (IPM) systems utilizing the use/release of the parasitoid *D. semiclausum* have been developed to replace the pesticides only approach to diamondback moth (DBM) *Plutella xylostella* (L.), worldwide the worst insect pest of cabbage family. Artificial Neural Networks (ANNs) methodology was applied to generate predictions for the population density of diamondback moth (DBM) *Plutella xylostella* (L.) and its larval parasitoid *Diadegma semiclausum* (Hellén). Two data sets, each from a different release area in the Kenya highlands, and both collected during a three year period after release of the parasitoid, were used in the study. Two ANN models were developed using 48 data points (Werugha) and 51 data points (Tharuni). The datasets were divided as follows: 30 were used for the training stage, 8 for cross-validation and 10 for testing at the first pilot site. At the latter pilot site, 30 were used for the training stage, 10 for cross-validation and 11 for testing.

The results of developed ANNs models gave satisfactory results over the whole range of the dependent variable values for DBM and *D. semiclausum* ($r^2 = 0.81$ and $r^2 = 0.99$), and ($r^2 = 0.90$ and $r^2 = 0.99$) at Werugha and Tharuni respectively. The ANNs provided a powerful tool for host-parasitoid system modelling with few assumptions on the data and allowed for highly accurate predictions. The successful introduction of the DBM natural enemy in Kenya as biological control agent under the IPM system is a good achievement towards solution on excessive insecticides use.

To expand the available IPM tools for better management of the pest, there is a need for a model. Such a tool will help in monitoring.

6.1 Introduction

The importance of studies of host-parasitoid systems cannot be overemphasized, especially at this period marked by the development of integrated pest management (IPM) systems with emphasis on the use/release of parasitoids. Such studies date back to Lotka (1925) and Volterra (1931) where the main goal of studying host-parasitoid systems was to understand which biological factors are capable of generating cycle dynamics. Unfortunately such mechanistic approach had limited accuracy especially in predicting population density.

Artificial Neural Networks (ANNs) models are highly flexible function approximators, which have shown their utility in a broad range of ecological, environmental and engineering modelling applications (Levine et al., 1996; Tonnang, 2004; Deng, 2007). The rapid emergence of ANNs applications in many fields can be attributed to their advantages over standard statistical approaches. Their flexibility provides a powerful tool for forecasting and prediction, however, the large number of parameters that must be selected only serves to complicate the design process (Maier and Dandy, 2000). In most practical circumstances, the design of ANNs is heavily based on heuristic trial and error processes with only broad rules of thumb for guidance.

Many authors have used ANNs technique in ecological and environmental modelling. For example, Levine et al. (1996) classified soil structure from soil sample data with the help of ANNs, Zhang and Stanley (1997) adopted neural networks for water demand forecasting. Moreau et al. (1999) embedded neural networks in Lotka-

Volterra predator prey model. Dreyfus-Leon et al. (2006) used ANNs to model the performance and information exchange between fishes. There are a range of papers that illustrate phytoplankton occurrence and succession (Recknagel et al., 1997) and their production using ANNs (Scardi, 1996, 2001; Scardi and Hardi, 1999). However, while ANNs have been employed by several researchers in ecological modelling, no attempts have been made on host-parasitoid population density prediction using this technique.

The DBM been a major pest of cruciferous crops worldwide, has increasingly developed resistance to all major classes of insecticides (Talekar and Shelton, 1993). Iga (1985) revealed, based on the study of DBM population dynamics using life table analysis, that natural enemies played an important role in regulating its population. Harcout (1963) and Sivapragasam *et al.* (1988) focused on the effect of rainfall on DBM. Wakisaka *et al.* (1991) made use of life table analysis and simulated rainfall to evaluate the effect of precipitation on loss of DBM eggs from the surface of plant leaves. Kobori and Amano (2003) later studied the effect of rainfall on a population of DBM under artificial conditions. They tried to determine the detailed effect of rainfall on DBM population on cabbage such as the quantity, duration and drop size of precipitation which can lead to the washing off of DBM eggs laid on cabbage leaf surface.

Integrated pest management systems with emphasis on the use/release of parasitoids have been developed to replace the pesticides only approach to DBM control. When researchers found that local natural enemies did not provide adequate control of DBM in East Africa, a classical biological control programme was initiated by the International Centre of Insect Physiology and Ecology (*icipe*) in Kenya and neighbouring countries. Subsequently, *D. semiclausum* was imported into Kenya in

2000 and released in April 2001 (Löhr *et al.,* 2007). The population dynamics of DBM and its parasitoids was studied for one year before and three years after release in order to assess impact of the introduction. The present chapter was therefore geared to developing ANNs models that would allow for more general predictions of DBM and parasitoid populations, based on the data collected in two different pilot areas in Kenya. It was thought that ANNs based models, adequately trained with several parameters that affect the population density of these insects could be a better approach with more precise predictions than differential and discrete equation models. We further conducted some sensitivity analyses to measure the effect on rainfall on DBM population density.

6.2 Materials and Methods

6.2.1 Sites and observed data

Experimental results were obtained from the pilot release areas in Werugha and in Tharuni. A detailed description of pilot release areas has been described elsewhere (see section 2.1.1).

In Werugha the collected dataset contained 48 points and in Tharuni 51 points. These datasets were subdivided in three groups for (training, cross-validation and testing) in the both regions as (30, 8 and 10) and (30, 10 and 11) respectively.

A data logger (Hobo Pro Series, Onset Computer Corp. Pocasset, MA, USA) was used to record temperatures and relative humidity (hourly records), while rainfall records were obtained from the Kenya Meteorological Services.

6.2.2 Development of the models

The development of an artificial neural network model involves several phases namely designing, topology, data normalization, training, cross-validation and testing.

i) Design phase

This phase includes; selection of neural paradigm, types of processing elements (PEs) or "artificial neurons", number of layers, the connectivity of the layers, the transfer function, the learning algorithm, momentum factor and learning coefficient.

ii) Transfer function

Schalkoff (1996) reported that ANNs PE has many inputs that are multiplied by a weight and then summed. A non-linear function called transfer function is applied to calculate each output of the PE. A commonly used transfer function is the sigmoid function, which was also used in this study:

$$f(x) = \frac{1}{1+e^{-x}} \tag{6.1}$$

iii) Topology

A typical back propagation neural network consists of three or more layers namely; input, hidden and output layers. Each layer is made of a number of PEs, whereby each PE is connected to every PE in the preceding layer by a simple weighted link (Wong and Henderson, 1997). The first step to form the network topology is to select the number of PEs in each layer. This number in the input layer depends on the data points of the input data. Five PEs (rainfall, relative humidity, temperature, DBM and *Diadegma semiclausum* population density at time (t-1)) were considered as inputs for the developed models. The number of PEs in the hidden layers was determined through trial and error. When the networks did not converge, more PEs were added to the hidden layers. At Werugha and Tharuni, the ANN models developed have two hidden layers of 10 PEs and 12 PEs respectively (Figure 6.1 (a,b)). The number of PEs in the output layer depends on the number of patterns to be recognized. Two PEs were considered in this study, representing DBM and *D. semiclausum* population density at time (t) respectively.

iv) Data normalization

In theory, the input-output data can have a very large domain of variation, so if the domain of variation of the input-output data is large, then the ANNs tends to be less stable. Therefore, this difficulty must be eliminated before the ANN enters its learning phase. This was done by pre-processing or scaling the input-output data in order to have small variation of the range of input-output data. This means that instead of using the input-output variables in term of their usual physical units, they were represented in dimensionless forms with values ranging from 0 to 1. To obtain the dimensionless input-output data, the following formula was used (Erahaghi *et al.*, 1993):

$$O_{new} = \frac{Oold - O\min}{O\max - O\min} \tag{6.2}$$

where, O_{new}, O_{old}, O_{max} and O_{min} are the newly obtained values of a parameter, the old value of a parameter, the maximum value and minimum value among a choose set of parameters respectively.

v) Training phase

Training is the stage where the ANN learns the recognition task by adjusting the weights in the links between PEs created by processing representative examples (input and output pairs). This was done by finding of a set of suitable weights that minimizes the error between the predicted and the actual output. The values of these weights were first set randomly. During the training, the network error was computed using a back-propagation training algorithm following the procedure below.

1) Maximum PE error was defined, 2) The weights in all the network links were randomized, 3) Sets of training patterns were selected (a pattern includes input and output pairs), 4) Outputs at the output layer were evaluated by propagating the input from the input layer to the output layer in a feed- forward manner, 5) Error at the output layer was calculated, 6) If the sum -square error between this output and desired output was acceptable, the calculation was stopped, 7) If step (6) was not satisfied, a minimization of the errors was effected by adjusting the weights between the PEs in the following manner: i) Output PEs and their weights were adjusted, ii) Propagated backward to the layer adjacent to the output layer by calculating errors and adjusting weights, iii) the backwards calculations were continued until all errors were calculated and weights were adjusted (Tonnang, 2004; Deng, 2007).

vi) Cross-validation and testing phases

The cross-validation phase was divided in two steps: 1) The ANN was subjected to data points not seen during the training phase, and the output was predicted. 2) The ANNs was subjected to intermediate data points seen during the training phase to ensure that oscillation (over fitting) did not occur (Deng, 2007). Testing the ANN performance on new data sets was important to ensure generalization, which was defined as the ability of the ANNs to recognize patterns for which its networks were not specifically trained (Schalkoff, 1996).

vii) Models implementation

A computer program writing in object oriented C^{++} programming language as described by Jeoy (1997) was used in this research to implement the developed ANN models in both pilot sites.

6.2.3 Analysis of residuals

The Durbin Watson test was applied on the discrepancy between theoretical (obtained from the model) and experimental (from field datasets) trajectories as described in section 2.3.

6.2.4 Rainfall analyses

To study the effect of rainfall on the DBM population density, a common approach was used. It consisted to perturb (increase or decrease) rainfall value and recording the response of the built model, whilst holding all other parameters constant at their most likely point estimates.

6.3 Results

The trial and error procedure to get the desired topology of the ANN models begins by varying the rate of learning from 0.01 - 0.1 at step 0.01 and the number of hidden layers from 4 - 12, (4,4), (5,5), (6,6), (7,7), (8,8), (9,9), (10,10) to (12,12). Several topologies were examined and the best result of the training phase was obtained with (0.15) learning rate and (10, 10) hidden layers and (0.2) learning rate and (12, 12) hidden layer at Werugha (Figure 6.1 (a)) and Tharuni (Figure 6.1 (b)) respectively.

The predicted population densities of DBM and its parasitoid in two areas of Kenya resulting from the ANNs developed are presented in Figures 6.2-6.6. The determination coefficient between experimental and ANN model prediction testified the predictive power of the models. Figures 6.2-6.3 show that ANNs gave satisfactory results over the whole range of the dependent variable values for DBM ($r^2 = 0.81$) and *D. semiclausum* ($r^2 = 0.998$) at Werugha. In Tharuni, similar results with very high R^2- values; 0.90 and 0.99 was obtained for DBM and *D. semiclausum* respectively (Figures 6.4-6.5). The points on these figures are well aligned on the diagonal of the perfect-fit line. There are more discard values for the DBM compare to *D. semiclausum* but the highest are better predicted.

Evaluation of the quotients skewedness/standard error and kurtosis/standard error for residuals gave values < 3. In addition, the results of the Shapiro-Wilk and Kolmogorov-Smirnov tests showed that the residuals for the models in both pilot sites were normally distributed. This demonstrates the validity of the application of the Durbin Watson criteria for analysis of the sequence of deviations. Successively, 2.27 and 1.79 was obtained for Durbin Watson (*d*) value for DBM and *D. semiclausum* in Werugha and 2.20, 1.99 in Tharuni. These values being closer to 2 demonstrate complete independence of residuals and confirm the validity of the developed models. Figure 6.6 displays the contribution of rainfall on the DBM population density. The figure shows that DBM population keeps on increasing at very low rainfall value and drastically drop when the rainfall value become more important. Although there appeared to be a general trend toward increasing rainfall rate with decrease in DBM population density, the DBM population reached a point where, increasing rainfall did not have any effect.

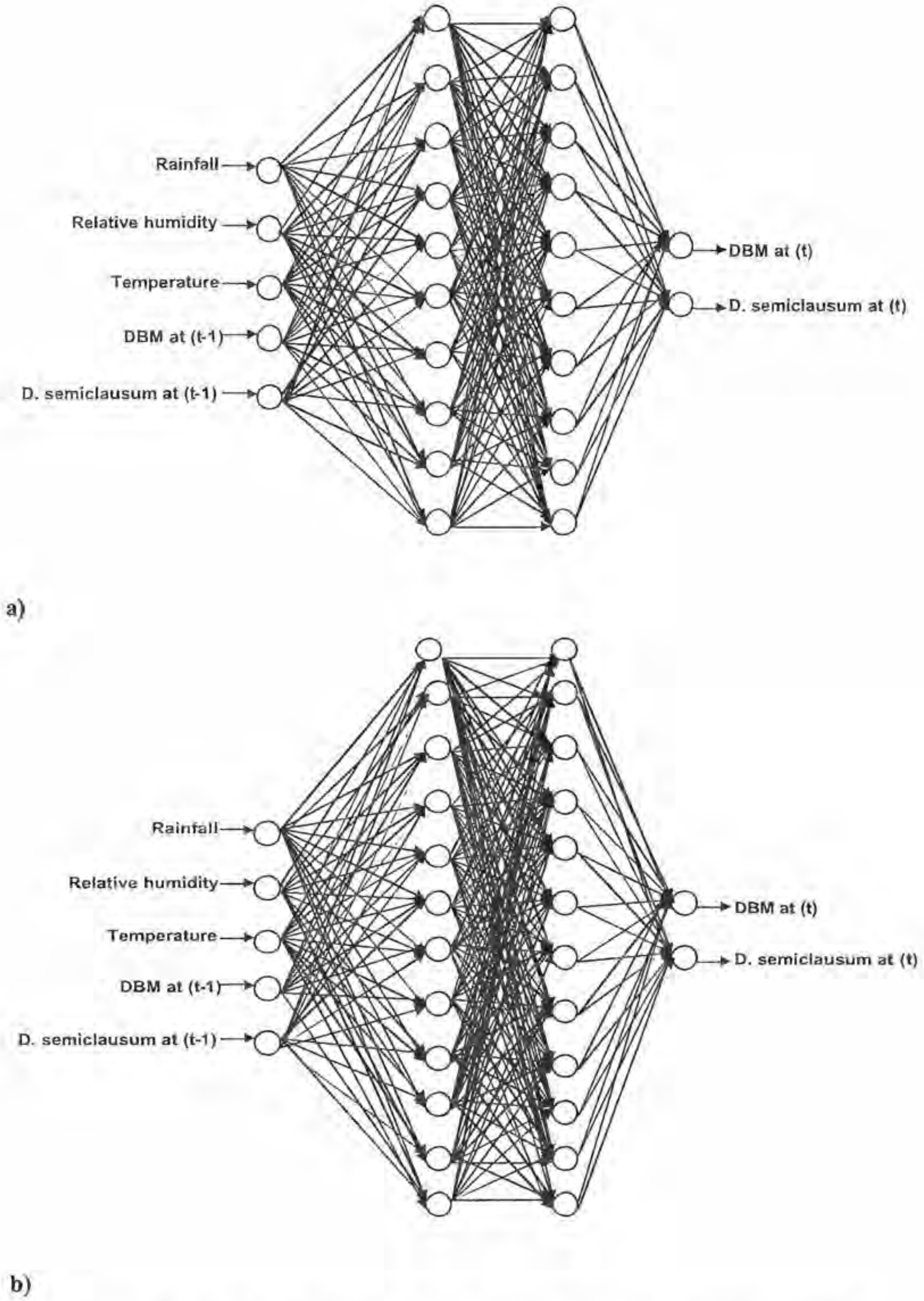

Figure 6.1 Developed ANNs model for the diamondback moth and its parasitoid *D. semiclausum* in Werugha (a), Wundanyi Division, Taita Taveta District, Coast Province of Kenya and in Tharuni (b), Limuru Division, Kiambu District, Central Province of Kenya

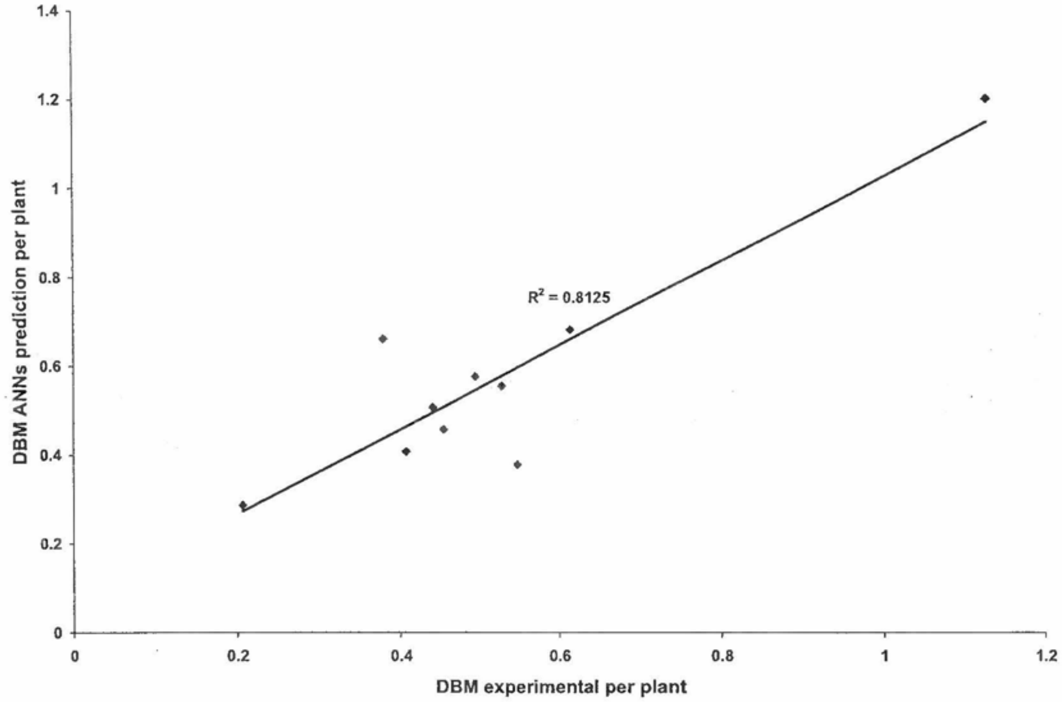

Figure 6.2 Relationship between experimental and ANNs model prediction for diamondback moth in Werugha, Wundanyi Division, Taita Taveta District, Coast Province of Kenya.

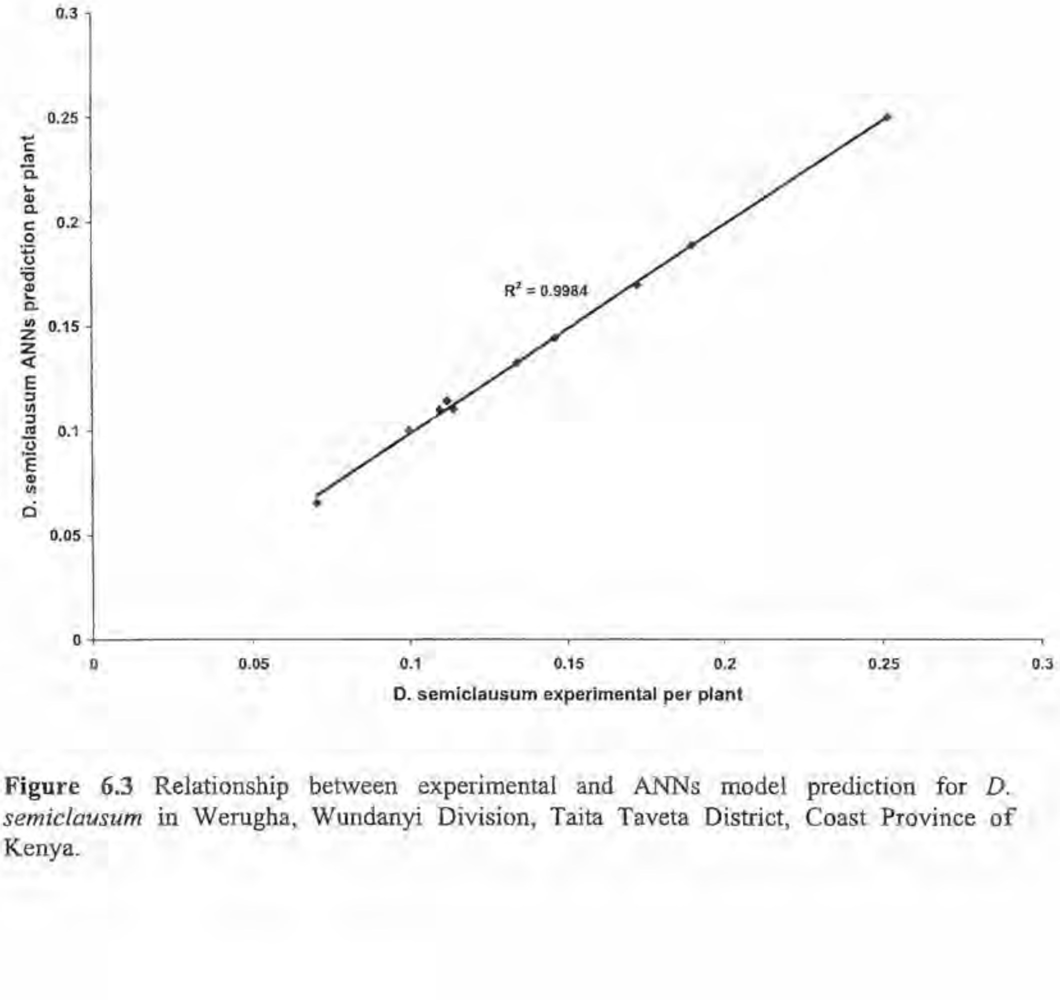

Figure 6.3 Relationship between experimental and ANNs model prediction for *D. semiclausum* in Werugha, Wundanyi Division, Taita Taveta District, Coast Province of Kenya.

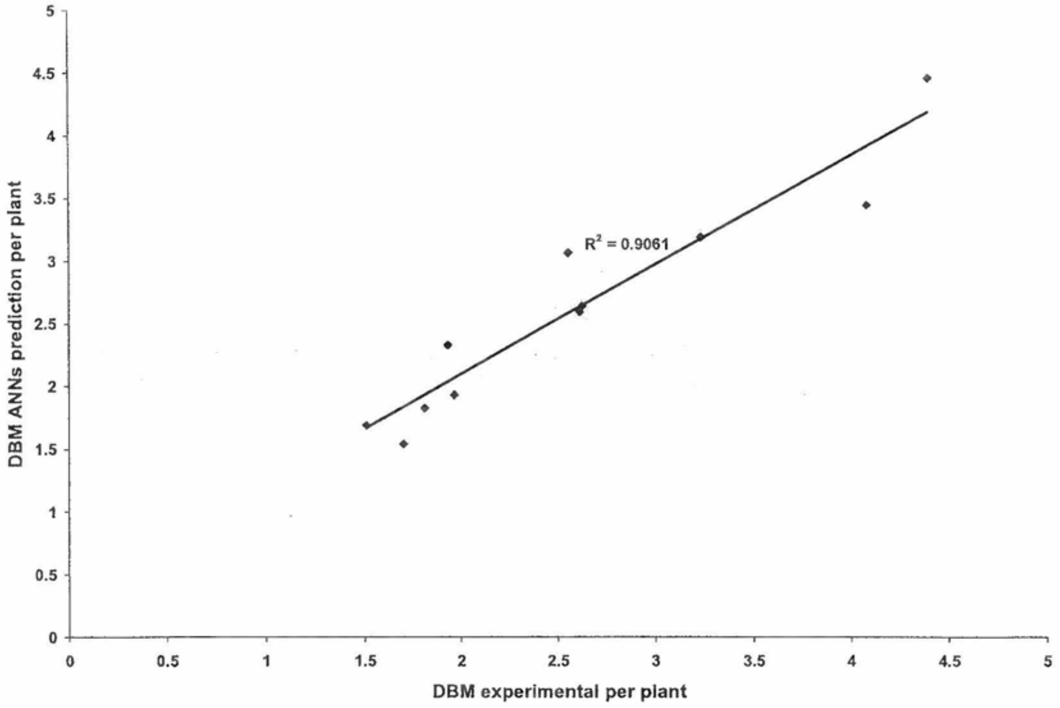

Figure 6.4 Relationship between experimental and ANNs model prediction for diamondback moth in Tharuni, Limuru Division, Kiambu District, Central Province of Kenya.

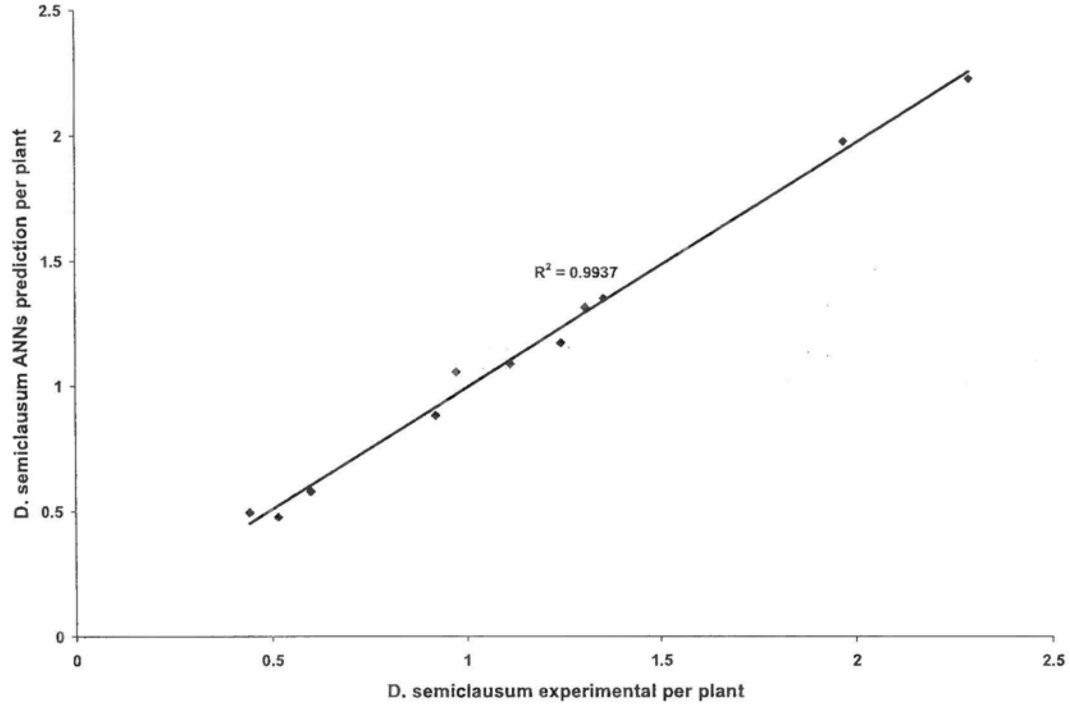

Figure 6.5 Relationship between experimental and ANNs model prediction for *D. semiclausum* in Tharuni, Limuru Division, Kiambu District, Central Province of Kenya.

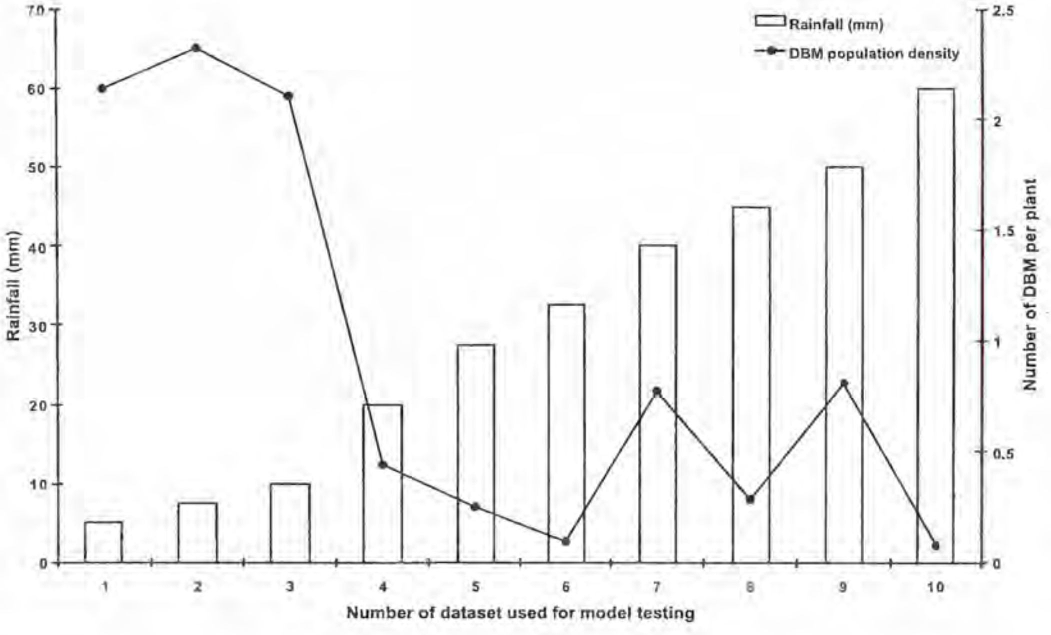

Figure 6.6 Effect of rainfall on DBM population density at Werugha, Wundanyi Division, Taita Taveta District, Coast Province of Kenya.

6.4 Discussions

Host-parasitoid systems, such as DBM-*D. semiclausum*, are distinctly non-linear, dynamic and complex. Powerful mathematical and computational techniques are usually required to elucidate and predict their behaviours. These tools generally include ordinary and recurrent differential equations, which lead to the construction of mechanistic models. The approach, which dates back to Lotka (1925) and Volterra (1931) is typically focused to understand the causes of generic phenomenon. These models are explicitly constructed following biological principles and contain the major mechanisms or processes that are believed to generate the dynamic behaviour. After the construction, the mechanistic models are parameterized. Major bottlenecks arise during the fitting of the models to real experimental data. On the one hand, no explicit method with satisfactory accuracy of fitting has been developed. On the other hand, choosing a mathematical model to describe a biological process is difficult because of the non-existence of standard criteria for selection of a mathematical model describing a particular population dynamics (Isaev *et al.* 1984; 2001).

In our previous studies Tonnang *et al.* (2006), we attempted to minimize the mean squared difference between the numerical solution of mechanistic model equations (Lotka-Volterra, Leslie, Holling type 2, 3) and the experimental data for model parameter restoration. The obtained parameters failed in all cases in offering a satisfactory prediction via the employed models.

In the present work, the power of ANNs was verified by a very high determination coefficient between DBM-*D. semiclausum* experimental values and predicted values for both developed models. The results are in agreement with the literature, in which ANN performances have repeatedly been reported in other ecological modelling studies to surpass the majority of traditional methods, especially referring to prediction (Brey *et al.*, 1996; Paruelo *et al.*, 1997, Whitehead *et al.,* 1997). This may find its explanation in the predominantly non-linear relationships and complexity that exit between the studied variables on the one hand, and the ability of ANNs to take directly into account any non-linear relationship relating the dependant variables to each independent variable of the system (Lek *et al.*, 1996). Others parameter such as food should have been taken into consideration in this study, but its non-consideration was due to the fact that both pilot sites are permanent crucifer growing areas. Food was always in abundance hence its subtraction as one of the factors influencing the DBM population density.

The application of the Durbin-Watson criteria, showed a total independence (no positive and no negative correlation) of residuals for the DBM and *D. semiclausum* in both pilot sites respectively. While residual testing is not a sufficient condition for model adequacy, it is nevertheless a necessary condition to demonstrate that the model has offered good approximation to the data generating process, particularly for ANN whose estimation procedures could be susceptible to partial convergence.

The method also presents some weaknesses. For example, no information about the underlying biological mechanisms between interacting insects is provided, while abiotic factors can be taken into consideration. The ANNs usefulness for forecasting often is limited by problems of over fitting and the lack of rigorous procedures for model identification, selection and adequacy testing.

Harcourt (1963), Sivapragasam *et al.* (1988) and Wakisaka *et al.* (1991) conducted studies on the effect of rainfall on DBM population. Their results only mention that rainfall affects the DBM population without precision on the volume and how. The present work make allusion of rainfall impact on DBM population without any emphasis on which stage the population of the insect is affected. More elaborate studies were conducted by Kobori and Amano (2003). Their work pointed that DBM eggs laid on the upper leaf surface were washed off with precipitation of 17.3 mm in 1 hour with 2.5 mm diameter drop while few eggs on the lower surface were washed off. The results illustrated that under same conditions as for the eggs, the falling rate of larvae decreased with advancing larval stadium except for the first larval stage. The rate of falling larvae increased with increasing treatment time. Kobori and Amano (2003) worked with artificial rain, whereas the present study was done under field conditions with real precipitation. Our results show that after a certain threshold (around 20 mm), the rainfall volume does not have any effect on the DBM population. Increase in rainfall volume at this level does not lead to a reduction in DBM population. This is in agreement with Kobori and Amano (2003), who pointed out that even a rainfall of one hour duration with volume greater than 30 mm does not lead to a complete removal of the larvae. Before this rainfall analysis was performed with ANN, an attempt to measure the level of dependence between this variable and DBM population density using classical method such as Pearson correlation was done. The obtained results could not clearly state the type and level of relationship that exists between these parameters. We assume it could be a non-linear dependence. However, lack of precise duration and drop size of the precipitations limited the full understanding of rainfall effects on the DBM population in field condition.

Overall ANNs can provide a powerful tool for host-parasitoid system modeling with few assumptions on the data. They will allow the user to achieve highly accurate predictions, which can greatly assist in decision making. The method also provides room for sensibility analyses, which consists of the arbitrary modification of a parameter value and recording the response of the built model, whilst holding all other parameters constant at their most likely point estimates.

Chapter 7

Knowledge-based fitting technique for ecological models

Summary

Appropriate fitting for a model can demonstrate whether it is really capable of producing observed dynamics or not. Restoration of ecological model parameters from experimental datasets has been and remains a very difficult task. An evaluation of an approach to tackle this problem was conducted. The technique began by obtaining the time series data to be fitted into a model. Chose a model with unknown parameters, studied the biotic and abiotic factors which are involved in the particular ecological phenomena and determined the range of the model parameters. Created a database for model initial values by slight changes on parameter magnitude values. For each set of parameter initial values, numerically and repeatedly solved the model equations. The results were used as inputs to an Artificial Neural Network (ANN) and their corresponding initial parameter value as outputs. The developed ANN was trained with back propagation algorithm for the networks to map and memorise the nonlinearity of the system. When the ANN model was properly set-up, field-time series datasets were then introduced to estimate the corresponding parameter values of the designated system.

Two models were chosen (Lotka-Volterra and Beddington, Free & Lawton) to fit pest and parasitoid population obtained from a highland cabbage growing area in eastern Kenya. Model parameters were firstly estimated from the minimization of the squared difference between the numerical solution of the models and the empirical data using Nelder-Mead and Powell's method. Secondly, knowledge-based technique was applied for both models. The results showed that the parameter estimates

obtained from ecological time series datasets were quite realistic and biologically acceptable. The study presents a more elaborate fitting procedure, which incorporates the best information on the structure of the measurement and dynamic noise, taking into consideration possibilities of long-term drifts in weather and environmental parameters.

7.1 Introduction

Wood (2001) stated many reasons, which could facilitate model fitting. For example, mortality rate being a very difficult factor to be directly measure in the field, and population density is easier, good fitting of the latter to model may possibly infer the former. Comparison between different mechanisms for ecological interactions can be made with the help of fed models (Carpenter *et al*, 1994). Appropriate fitting can demonstrate whether a model is really capable of producing observed dynamics or not, as well as pinpointing the features of data that are not explained by theory embodied in a badly fed model. A good model-based calibration of data enhances the predictive potential of a model. Models that fit to time series datasets can be used to predict changes in a given populations and for potential effects of management interventions (Jassby and Powell, 1990; Hilborn and Walters, 1992). They can also be used to infer possible causes of temporal variability and to test consequences of natural or deliberate perturbations (Carpenter and Kitchell, 1993).

Most dynamic ecological models are non-linear and standard methods that can guarantee the finding of the best fit to experimental datasets do not generally exist (Wood, 2001). There are a series of alternative of non-linear optimisation technique to choose from. For some models, fitting is straightforward. For others the practical difficulties have substantially undermined the usefulness of model fitting for scientific usage.

Thee main factors have been associated with difficulties in model fitting (Wood, 2001). First, the choice of measuring function, because, complex function may be difficult to minimize. Second, for well-behaved measures of model fit, numerically calculation of model solution should be carefully performed to avoid slowness and unreliable convergence. Third, it is difficult to quantify the efficiency and reliability of a method applied it fails to make good use of the structure of the model-fitting problem. Others obstacles for good models include elements that are not derived entirely from mechanistics first principles. Sometimes, some parts of the models are phenomenological characterisations of a process or a relationship. These terms introduce incidental assumptions into a model that may have nothing to do with the biological or ecological mechanisms on which the model was constructed. It is usually assumed that these incidental assumptions will have little effect on the qualitative facets of the model's dynamics, but this is not always the reality (Wood and Thomas, 1999). Further examples arise in pure estimation problems. The form of a parameter such as mortality rate is usually not known from observed population time series (Wood and Nisbet, 1991). Carpenter *et al.* (1994) pointed out that estimation of model parameters estimation is difficult because the incidental unknown relation that may exist between observation and predictor.

In view of these difficulties, a number of techniques have been explored to address efficient fitting of models. These include, modified likelihood estimators that incorporate model sensitivity to uncertain predictors (Chandler, 1972). Reilly and Patino-Leal (1981) proposed a Bayesian approach in which the incidental parameters are integrated out of the joint posterior density function. A method called direct fit whereby a relation is established between current and future values of the model state variables has also been used. Once relevant state variables are estimated, nonlinear least squares regression is applied to find the set of parameters that best fit the data (Carpenter *et al.*, 1994). The direct fitting approach usually failed with majority of nonlinear models and a nonlinear forecasting technique that can allow fitting of model process-error have been proposed To detect chaos in ecological data sets, Ellner and Turchin (1995) developed a method based on statistical theory for parameter estimation in nonlinear time-series models. Conditional least squares and maximum likelihood were described for general ecological time series models by Dennis *et al.*, (1995) and better illustration and presentation of these methods were done by Ives *et al.* (2003). Gould and Pollock (1997) have focused on maximum likelihood estimation under the robust design in lieu of least squares regression. Zeng *et al.* (1998) applied the Kalman filter and likelihood function to estimate their model parameters. Wood (2001) proposed partially specified models construction with part of the structure represented by unknown function, with other parts containing conventional model elements with only unknown parameters. Ellner *et al.* (2002) described a method of fitting population dynamics models to time series data by gradient matching. The technique involves smoothing the population time series, in order to estimate the gradient, and then fitting rate equation using penalized regression splines.

7.2 Models

Relative to temporal representation of the dynamics of the system, ecological models can be written as system of delay differential equations with a finite number of continuities and discontinuities which include ordinary and discrete time equations.

Consider x_i as the value of the *ith* state variable and x as the vector of all state variables at time *t*. Similarly $x_{t-\tau_i}$ is the value of state variable at $t-\tau_i$ then,

$$\frac{dx_i}{dt} = f_i(x\ , x_{t-\tau_1}, x_{t-\tau_2}, \ldots, t) \text{ for all } t > 0, t \neq \{T_1, T_2, \ldots\}, \qquad (7.1)$$

where $\{T_1, T_2, \ldots\}$ is the points at which the state of the system changes discontinuously (the elements of this set may be state variable dependant). Assuming that f_i does not actually depend on the system state prior to $t = 0$, so that initial state, $x_i(0)$, rather than initial histories, are required to integrate the models. In other words, f_i is subject to the restriction that its partial differential with respect to any element of $x_{t-\tau_i}$ is zero if $t < \tau_i$. The models may be supplemented by discontinuities as follows (Wood, 2001)

$$x_i(T_j^+) = d_i(x(T_j^-), j)\ , \qquad (7.2)$$

where T_j^+ is the instant after T_j and T_j^- the instant before. The particular models given above and in Examples provide illustrations from the class of models.

Majority of discrete time models and all ordinary differential equation models are special cases of this class of models. For example, by setting $f_i(.) = 0$ for all, we get the general class of models that can be written as systems of difference equations:

$$x_i(T_{j+1}) = d\,(x(T_j), T_j)\,. \qquad (7.3)$$

This class includes matrix models and discrete difference equation models. Similarly, by having no discontinuities and no lags the general model becomes a model written as a system of ordinary differential equations.

$$\frac{df_i}{dt} = f_i(x, t)\,. \qquad (7.4)$$

The class of models chosen covers a high proportion of models actually used in ecology.

7.3 Example: host-parasitoid system (diamondback moth-*Diadegma semiclausum*)

The example presented here used field data for an insect diamondback moth (DBM), *Plutella xylostella* (L.) (Lepidoptera: Plutellidae) and its exotic parasitoid *Diadegma semiclausum*. The system dynamic is the one which has been studied throughout this work. Good explanation of the system was done in the introduction. This section utilized the time series data collected after release of the parasitoid in Werugha.

7.3.1 Reasons for models selection

a) Godfray and Rees (2002) mentioned three main reasons that justified the importance of a population growth rate parameter in the study of population biology. First, the population growth rate is central to population projection. Secondly, it is often the most natural response variable for the statistical analysis of the factors influencing a species population dynamics and, finally, this parameter intimately links population dynamics and evolutionary biology. In this context, the Lotka-Volterra and Beddington et al. (1975) models both predicted the growth rate of the insect pest (DBM).

b) The two species (DBM and *D. semiclausum*) have overlapping generations in Kenya, which normally allows the use of continuous (Lotka, 1920; Volterra, 1931 model equations) rather than discrete time and differential equations except some considerations are made (Royama, 1971). Among those, are the periods of observation, which must be shorter than the generation of insects (Royama, 1971). As DBM probably has a generation time of about 3 weeks in coastal Kenya (Rossbach *et* *al.*, 2005), only 20 datasets of consecutive collection, corresponding to period of maximum parasitism and exactly 14 days interval between collections was used with Beddington *et al.*(1975) model.

c) Models were selected within the constraint imposed by the simplicity necessary to their analysis and the ability for parameters to fulfil basic biological meaning.

After models selection, the following assumptions were made: i) other sources of mortality which could have also been responsible for the host population trajectory were neglected. ii) Lohr *et al.* (2007) indicates 3 other parasitoids that attack DBM in the region before release of *D. semiclausum.* However, after release their parasitism rate became extremely low hence their effect was neglected.

7.3.2 Ordinary differential equation: Lotka-Volerra model

The Lotka-Volterra model has already been very well developed and explained in section 3.2 of chapter (see equation 3.1).

7.3.3 Discrete equation: Beddington, Free and Lawton model

Conforming to the discrete seasonality of most arthropods, their models are phrased finite recursive equations of the basic form

$$x_{t+1} = \lambda x_t f(x_t, y_t), \; y_{t+1} = c x_t [1 - f(x_t, y_t)], \qquad (7.5)$$

where, x_t, x_{t+1}, y_t, y_{t+1} give the host and the parasitoid population densities in successive generations respectively, λ is the geometric growth factor for the host ($\lambda = e^r$ where r is the intrinsic rate of increase), and c is the number of parasitoid produced for each host individual attacked. The function $f(x_t, y_t)$, gives host survival with respect to parasitoid and host densities and can be varied to reflect various parasitoid foraging behaviours (May *et al.*, 1981). The Nicholson-Bailey model, one of the pioneer models of this class, stipulates that, in the absence of parasitoids, the host population will grow geometrically, which is not realistic. Beddington *et al.* (1975) modified the Nicholson-Bailey model by introducing intraspecific competition between hosts after the reproduction phase and came out with the proposed equations:

$$x_{t+1} = x_t \exp(r[1-\frac{x_t}{K}]-ay_t)\,,\; y_{t+1} = cx_t[1-\exp(-ay_t)]\,, \tag{7.6}$$

where K is the "carrying capacity" for the host in the absence of the parasitoid and (a) the parasitoid per capita searching efficiency. This model implies that host density-dependence acts at a particular time in the life cycle in relation to the stage attacked by the parasitoids.

7.4 Multilayer Perceptron (MLP) using the Back propagation algorithm

There are different types of artificial neural networks (ANN). The most widely used ANN is known as Multilayer Perceptron (MLP) using the Back propagation algorithm. This type of ANN is excellent at prediction and classification tasks. This type of network has two modes of operation during the training or learning phase: Feed forward computation and the weights updating operation. In feed forward computation, when an input pattern is presented to the input layer, the units in the next layer use the weighted sum of inputs and the activation function to calculate their outputs. These outputs are passed forward for computation in the next layer until the output layer is reached. During the weight updating operation, an error signal, which is based on the discrepancy between the desired response and the actual output of the network, is back propagated through the network for the updating of weights. The back propagation algorithm is generally represented by:

$$w_{ij}^{k+1} = w_{ij}^{k} + \eta \delta_j I_i f'(s), \qquad (7.7)$$

where, w_{ij}^{k} stands for the weights of the connection from unit i in layer k to unit j in layer $k+1$, η is a small constant called the learning rate, δ_j^k is the signal error, I_i is input vector to the network, $f'()$ is the derivative of the network transfer function and s is the sum of all the weights.

The recursive formula (7.8) is the key to back propagation learning. It allows the error signal of a lower layer (δ_j^k) to be computed as linear combination of the error signal of upper layer (δ_j^{k+1}). In this manner, the error signals (δ_j^k) are back propagated through all the layers from the top to the down. This also implies that the influences from an upper layer to a lower layer (and vice versa) can only be affected via the error signals of the intermediate layer. The MLP received inputs and predicts outputs. The error between the desired outputs and the obtained outputs are used to validate the effectiveness of the model and fine-tune the weights to more accurately map the process dynamics.

7.5 Fitting Lotka-Volterra and Beddington *et al.* models by direct minimization

Previous chapters (3, 4) have largely shown how to fit such models by direct minimization. For each model, the technique was rigorously follows in restoring their parameters. Nelder-Mead and Powell's methods for minimization were used respectively in each model. Analysis of residual was carried out with Durbin Watson criteria.

7.6 Knowledge-based fitting technique

Ecological models are made of parameters. Fitting these models to time series involve finding values of the parameters and usually the initial values that best matched the data according to some modeller defined criterion. We implemented an iterative framework (Table 1).

7.7 Fitting Lotka-Volterra and Beddington *et al.* models by Knowledge-based technique

To demonstrate the procedure above, the fitting of Lotka-Volterra and Beddington et al. models with time series data was conducted for the diamondback moth and its parasitoid, *D. semiclausun*. The procedure began with step3 as the data was already available and the model chosen.

Table 7.1 Descriptive steps of the knowledge-based fitting technique

	Rule of procedure
Step 1	Obtain the time series data to be fitted into the model.
Step 2	Choose a model with unknown parameters.
Step 3	Study the biotic and abiotic factors which involve in the ecological phenomena, this will help figure out the boundaries of the model parameters
Step 4	Create a database of model initial values (by slight change on parameter) in respective of the biological and physical inference range obtained from step 3
Step 5	For each set of parameter initial values, numerically and repeatedly solve the model equations and saved the results $x(t)$and $y(t)$ obtained
Step 6	Build an artificial neural network model (ANN) with multilayer perceptron (MLP)
Step 7	Optimisation of the network architecture, the number of hidden layers and the number units in the hidden layers are determined and conduct an independent test on the model to verify model prediction and accuracy.
Step 8	Fed the ANN with time series data to estimate the values of parameters corresponding to your system.

Step 3. The physical and biological environments factors, which involve the diamondback moth and its parasitoid, population fluctuations, were studied. Life cycle for both insects were properly understood, this help in choosing the ranges of the model parameters. For example, the DBM growth rate was chosen to belong at [0.20, 0.34] (Shirai, 2000, Shu-Sheng *et al.*, 2002) and the Parasitoid death rate at [3.00, 6.00] (Fitton and Walker, 1992; Konig *et al.*, 1993).

Step 4. Created a data base by slightly change on parameter values in respective of the ranges obtained from step 3 for each parameter.

Step 5. With each set of parameters initial values, we numerically and repeatedly solve the model equations and saved the results $x(t)$ or x_t and $y(t)$ or y_t obtained.

Step 6. Built an artificial neural network model (ANN) with multilayer perceptron (MLP). The MLP modelling process generally proceeds as follows: we began by determine the form of the pre- and post-processing of the data $x(t)$ or x_t and $y(t)$ or y_t that will be used as inputs to ANN and their corresponding initial parameter value as outputs. These values were standardized so that they are all on the same order of magnitude. After standardization, determination of the network parameters such as learning rate and momentum was done.

Step 7. The developed MLP uses back propagation as training algorithm. The network architecture consists of three layers. The input layer was made of two neurons numerical values for $x(t)$, $y(t)$ (Lotka-Volterra model) and x_t and y_t (Beddington et al. model).

The training was done by finding a set of suitable weights that minimizes the error between the predicted and the actual output. The values of these weights were first set randomly. During the training, the network error was computed using a back-propagation training algorithm.

The cross-validation phase was divided in two steps: a) The MLP was subjected to data points not seen during the training phase, and the output was predicted. a) The MLP was subjected to intermediate data points seen during the training phase to ensure that oscillation (over fitting) did not occur. Sensitivity analyses and independent test on the MLP to verify its prediction and accuracy was conducted.

Step 8. Fed the MLP with field time series data to estimate the values of parameters corresponding to DBM-*D. semiclausum*.

7.8 Parameter estimates

The sum of squared deviation between empirical and theoretical time series with Nelder-Mead and Powell's methods and knowledge-based parameter estimates for Lotka-Volterra and Beddington *et al.* models are given in Tables 7.2 and 7.3. The models both estimated the value of DBM growth rate. This parameter is equivalent in pure biological sense to the "intrinsic rate of natural increase". This rate is dependant upon the genetics of the population and the physical quality of the environment such as temperature (Wangersky, 1978). Sarnthoy *et al.* (1989) estimated 0.11 and 0.25 at mean temperatures of 17.6 ^{0}C and 28.9 ^{0}C respectively for the Thailand DBM strain. In our pilot area, temperature fluctuated between 13. ^{0}C to 35 ^{0}C, it was found that the models predictions for this parameter were rather too high or too low when estimated by minimization of the sum of squared deviations between empirical and theoretical time series. With reference to Sarnthoy *et al.* (1989) laboratory results and some knowledge about the genetic variation of the Kenya DBM strain (Rossbach *et al.*, 2005), the proposed knowledge based fitting technique estimated a DBM growth rate of 0.30 for both models. The obtained result is quite realistic and biologically acceptable.

The natural death rate of the parasitoid was high with Nelder-Mead and very low with Powell's method. From biological point of view (Rossbach *et al.,* 2005, Momanyi *et al.,* 2006) the parasitoid is a solitary insect, which is justified by its total dependence on DBM as its host for multiplication and perpetuation. In the absence of DBM, parasitoid populations may rapidly decrease until extinction.

Biologically, a self-regulation greater than 1 does not make much sense because the empirical population never reached the numbers where high intra-specific competition could be expected. We however, expected a self-regulation coefficient close to 1 for the parasitoid, which can explain the strong competition for host larvae in the field. Momanyi *et al.* (2006) showed that one year after release, competition between parasitoids was so strong that even first instar larvae that were still mining were parasitized. Some studies conducted in the pilot site has shown that the *D. semiclausum* host searching capability is high and the insect better association with cabbage host plants, at least as far as its congeneric indigenous species is concerned (Rossbach *et al.* 2005). This justified the strong interactions between this parasitoid and its host and vice versa.

The estimated value of carrying capacity from Beddington *et al.* model (Table 7.3) was about 160, 16, and 9 DBM/plant with Nelder-Mead, Powell and Knowledge based method respectively. The problem is the estimated first two values, which are an order of magnitude higher than the value suggested from field data. Nevertheless, in outbreak situations and without effective parasitism, especially in maturing crops, the DBM numbers recorded can surpass 16 DBM/plant (Karimzadeh *et al.,* 2004).

From the studies made by Rossbach et al. (2005) and Momanyi *et al.* (2006) we deduced that the parasitoid per capita searching efficiency might be greater than the values predicted by Nelder-Mead and Powell's methods, what justify the value obtained with knowledge-based technique.

The observed time series together with the model outputs are sketches in Figures (7.1-7.4). Most of these figures presented poor fitting of the models to data, especially for parasitoid. Good fitting was observed for DBM with Beddington *et al.* model. To confirm the suitability of the models, Durbin-Watson test for autocorrelation between residuals was conducted. The Durbin-Watson criteria applied to the deviations between model and experimental values produced results for each model as shown in Tables 7.2 and 7.3. The closest these values are to 2, the greater independence exists between residuals. Knowledge based technique has shown an improvement in fitting the models. For both models, the gap between the Durbin-Watson criteria values (dd and dp) and 2 are considerably reduced. The reductions were very high with DBM than the parasitoid at the point that parameters estimates with our propose technique shown perfect fit to Beddington *et al.* model (Figure 7.3).

Table 7.2 Estimates of Lotka-Volterra model parameters fitted to an empirical times series of the diamondback moth and its parasitoid, *Diadegma semiclausum*, after release in Werugha, Wundanyi Division, Taita Taveta District, Coast Province of Kenya using sum squared deviations between empirical and theoretical time series and Knowledge-based fitting

	Sum squared deviations between empirical and theoretical time series with:		
Estimated Parameters	**Nelder-Mead method**	**Powell's method**	**Knowledge-based technique**
BM growth rate (α_1)	27.76	8.71	0.30
Natural death rate (α_2) (parasitoid)	1.80	0.08	5.25
DBM self-regulation coefficient (β_1)	1.40	0.25	0.86
Self-regulation coefficient (β_2) (parasitoid)	0.43	9.84	0.98
Interaction coefficient (γ_1) (DBM/parasitoid)	145.19	69.59	23.45
Interaction coefficient (γ_2) (parasitoid/DBM)	0.95	0.35	1.55
Initial population size (x_0) (DBM)	8.48	10.66	10.74
Initial population size (y_0) (parasitoid)	0.15	0.25	0.17
Loss-function* ($Q_{\min}$)	92.87	87.79	-
DBM Durbin-Watson criterion (dd)	1.05	1.13	1.27
Parasitoid Durbin-Watson criterion (dp)	0.79	0.73	0.84

* - Squared deviations between empirical and theoretical time series

Table 7.3 Estimates of Bedington *et al.* model parameters fitted to an empirical times series of the diamondback moth and its parasitoid, *Diadegma semiclausum*, after release in Werugha, Wundanyi Division, Taita Taveta District, Coast Province of Kenya using sum squared deviations between empirical and theoretical time series and Knowledge-based fitting.

Estimated Parameters	Sum squared deviations between empirical and theoretical time series with:		Knowledge-based technique
	Nelder-Mead method	Powell's method	
DBM growth rate (r)	0.07	0.05	0.30
DBM carrying capacity (K)	160.15	16.50	9.00
Parasitoid per capita searching efficiency (a)	0.27	0.24	0.37
Initial DBM population size (x_0)	7.60	8.72	8.48
Initial parasitoid population size (y_0)	0.02	0.05	0.004
Loss-function* ($Q_{\min}$)	45.25	47.84	-
DBM Durbin-Watson criterion (dd)	2.08	1.87	2.05
Parasitoid Durbin-Watson criterion (dp)	0.22	0.21	0.37

* - Squared deviations between empirical and theoretical time series

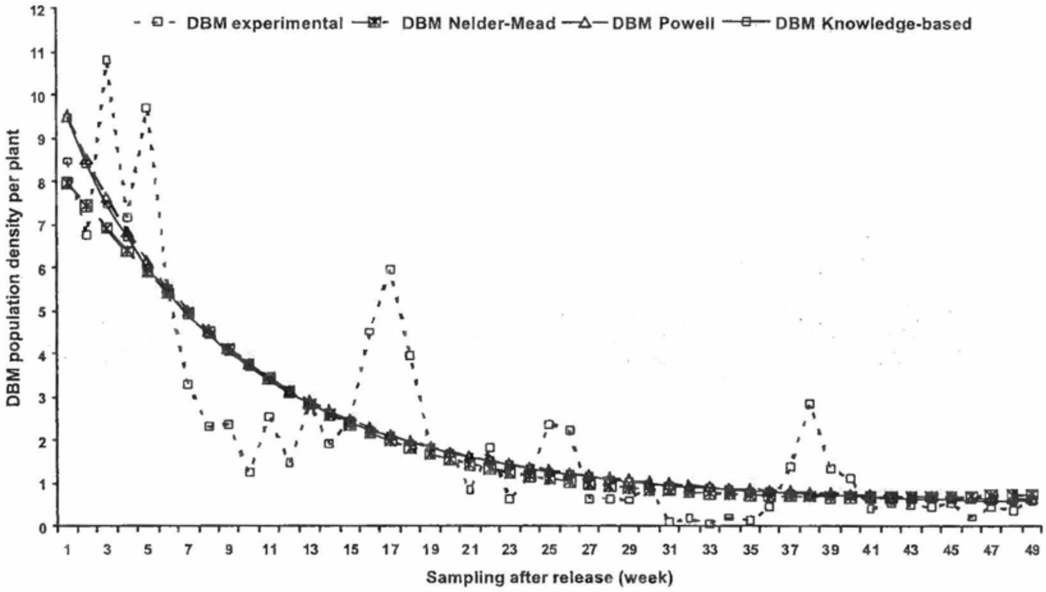

Figure 7.1 Population trajectories of diamondback moth estimates of Lotka-Volterra model parameters fitted to an times series after release of its parasitoid, *Diadegma semiclausum* in Werugha, Wundanyi Division, Taita Taveta District, Coast Province of Kenya using sum squared deviations between empirical and theoretical time series and Knowledge-based fitting.

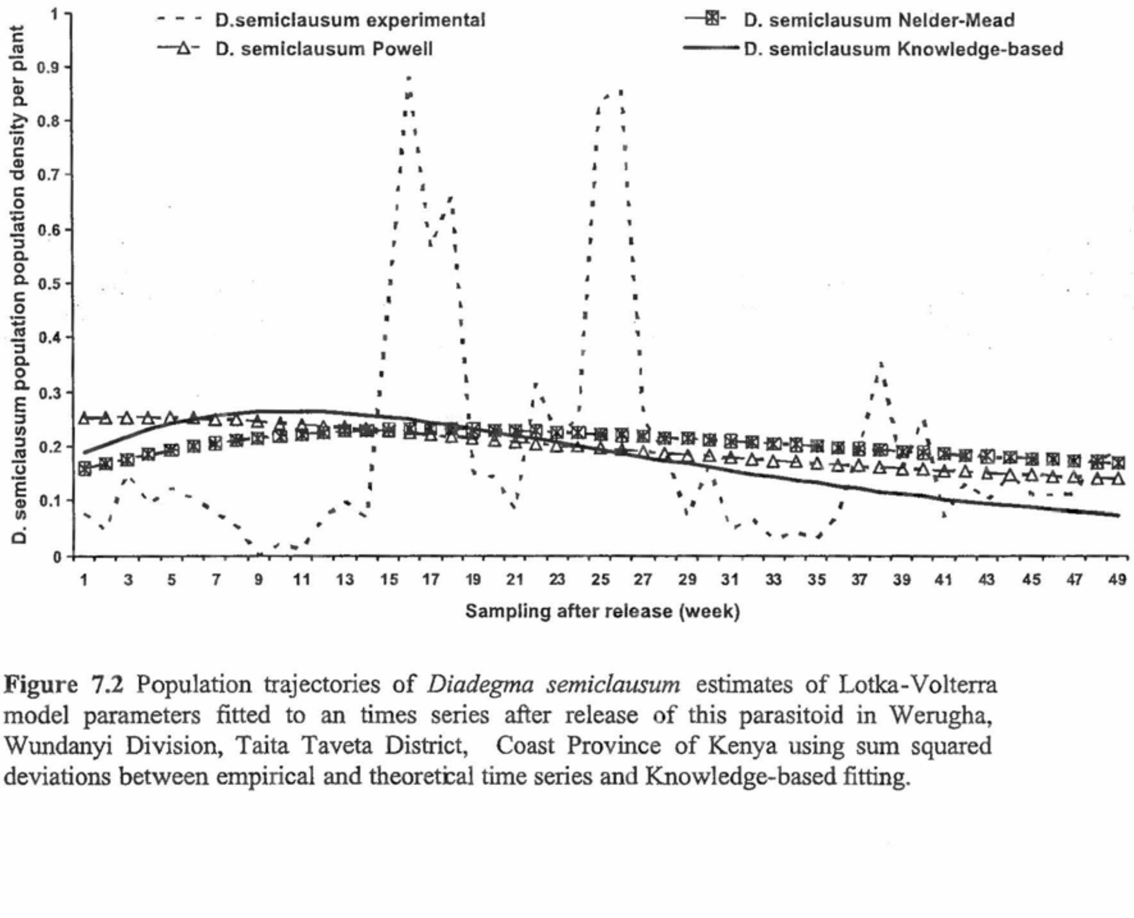

Figure 7.2 Population trajectories of *Diadegma semiclausum* estimates of Lotka-Volterra model parameters fitted to an times series after release of this parasitoid in Werugha, Wundanyi Division, Taita Taveta District, Coast Province of Kenya using sum squared deviations between empirical and theoretical time series and Knowledge-based fitting.

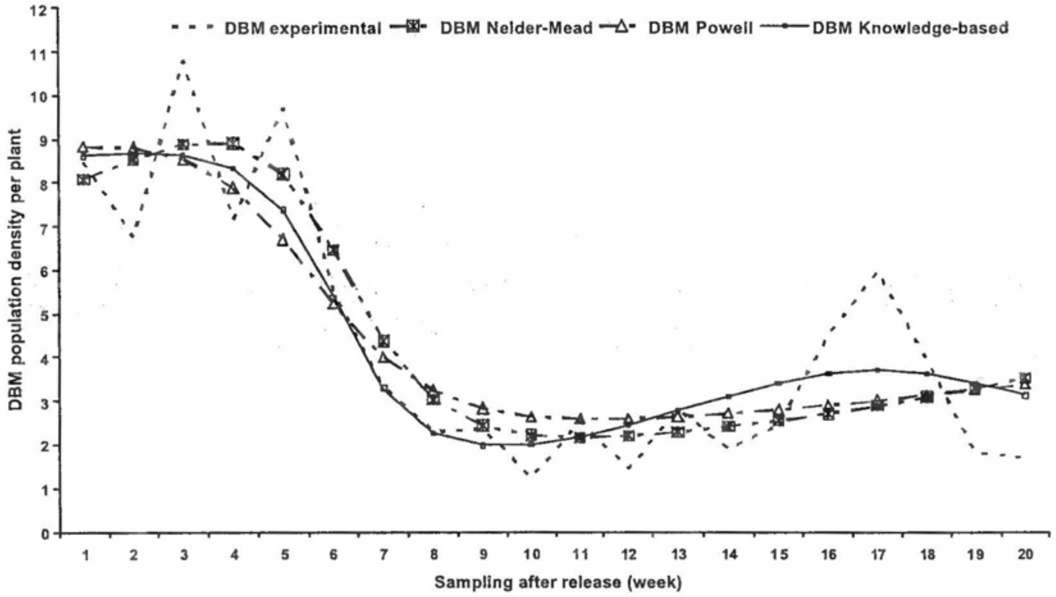

Figure 7.3 Population trajectories of diamondback moth estimates of Beddington *et al.* model parameters fitted to an times series after release of its parasitoid, *Diadegma semiclausum* in Werugha, Wundanyi Division, Taita Taveta District, Coast Province of Kenya using sum squared deviations between empirical and theoretical time series and Knowledge-based fitting

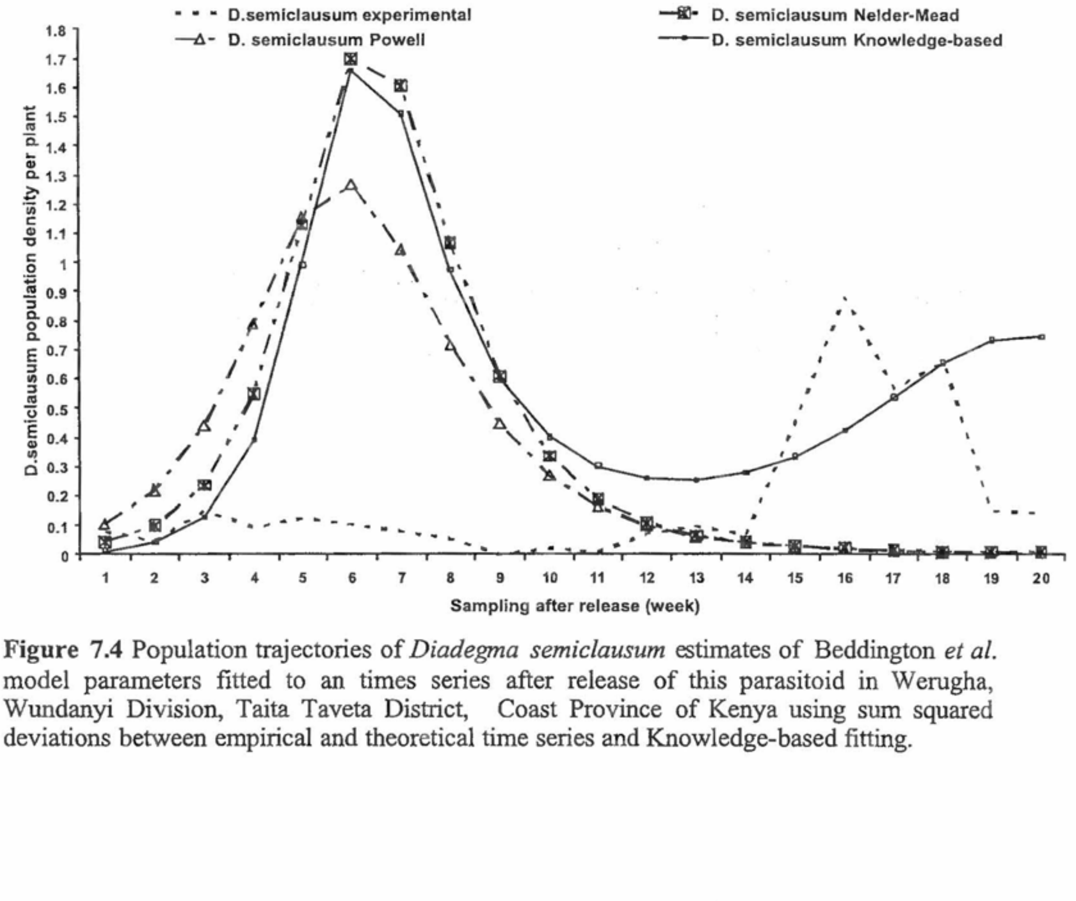

Figure 7.4 Population trajectories of *Diadegma semiclausum* estimates of Beddington *et al.* model parameters fitted to an times series after release of this parasitoid in Werugha, Wundanyi Division, Taita Taveta District, Coast Province of Kenya using sum squared deviations between empirical and theoretical time series and Knowledge-based fitting.

7.9 Discussion

The approach described in this work provides a way of fitting ecological models, which estimates parameters that precisely accounts for the physical and biological environments factor s involve in the system. More importantly, it provides a practical means of connecting models to data with inferential knowledge through proper mapping of nonlinearity and good prediction. Knowledge based technique stands on two major computing stages: 1) Numerically solve the models equations to obtain the database for initial values and corresponding model parameters, 2) Develop, train test and make use of the MPL for prediction. The first stage is obvious to majority of theoretical ecological modeller. In the contest of mapping and predicting nonlinear systems, the superiority of MLP over standard statistical methods is well known (Paruelo and Tomasel, 1997; Karul and Soyupak, 2006). MLP are highly flexible function approximators, which provide a powerful tool for forecasting and prediction.

The method described has several practical benefits in fitting ecological models. For example , missing values, uneven sampling, and unobserved state variables present no major difficulties. Generally, at the second stage of computing, when training a MLP, our goal is to find an optimal set of connection weights. But we can go one step beyond. After the trained weights are found, we can find optimal input patterns, which produced any desired output pattern by, simply imagine that the input neurons are actually a new hidden layer at the front of the MPL network. By doing this, the fitting method becomes efficient, reliable and makes it possible to have some confidence in the notion that differences in model fit reflect real differences in model performances. Rather than differences in how much help was given to the fitting routine. Going one step beyond also, provides the means, of new parameter estimates to be done in case a change in environmental factors that occur over year or generation time scale is inferred. Sometimes ecological models present chaotic behaviour with certain set of parameters. Fitting chaotic system with method such as trajectory matching is problematic, but knowledge based technique offer no nuisance features. The approach make use of data collected at any appropriate scale of the system, bypassing the assumptions and uncertainties that could have arise when parameters are imported from other systems or small-scale of field collections.

In general, puzzling results from our examples at some part of this study are the big divergence between estimated parameters from one technique to another and especially within difference minimization methods. Firstly, a query may arise to the fitting procedure, whichin this case, typically tries to maximize fit at either very short or very long time scales. The minimization may be following this direction whereas the main measuring features for the parameters are for the intermediate scale, which initially may not have been selected. Secondly, the fitting algorithm with sum of square minimization in searching for the set of parameters that fit the model well, may introduce some noise to the model time series. Thirdly, these algorithms once applied search for the minimum of the loss function and generates values that result in better convergence of the equations. Two type of minimum usually exist (local and global), the latter means the truly lowest function value has been found. But, finding global minimum in reality is a very difficult problem that is why the loss function Q has different values for the two methods. For each value of the loss function Q corresponds a set of parameters. With knowledge-based technique, the issue of global and local minimum is overcome by ANN, which powerfully optimizes the function. Fourthly, the application of the models in a highly unstable situation after the introduction of an exotic parasitoid could have also contributed to the discrepancy outcome. Because, such an introduction purposefully intends to move the system equilibrium to a different level and therefore creates instability that must have affected the outcome of the calculations. In this case appropriate methods, which can easily map nonlinearity, have to be applied.

It is unfortunate that the models selected to illustrate knowledge fitting technique could not all offered perfect prediction for the trajectories of the collected data. This just demonstrates the critical reality that exists in choosing a mathematical model to describe a particular population fluctuation. Isaev *et al.* (2001) stated clearly that there is no standard criterion for a mathematical model selection. Often, we can only proceed on a sequential check of the existing models starting from the simplest or create a new model to describe the population. We opted for the first option, because, during the process of developing a new mechanistic model for the collected time series data, we may be confronted by three issues: i) what are the state variables? ii) How are the states variables functionally interrelated? iii) What are the numerical values of model parameters? These should have brought news challenges that are not in the scope of the study.

An elaborate fitting procedure was proposed, which incorporates the best information on the structure of the measurement and dynamic noise, taking in consideration possibilities of long-term parameters drift (weather, environmental and evolutionary). Our approach demonstrated an ability to improve parameter estimates by accounting for observation errors. Nevertheless, let acknowledge the fact that, even modest errors cause substantial difficulties in model identification. Perfect manipulation and understanding of a system within an ecosystem, can substantially increases the probability of detecting the underlying model, reduces uncertainty in parameter estimates and yields models capable of predicting wider range of system or the entire ecosystem state.

The approach presented is not a panacea. Let not intend to say that any model well fitted will be good to explain an ecological or biological phenomenon. Before any fitting attempt, the model must incorporate some ecological factors, including freak catastrophic events and density dependence, which can be important in particular circumstances. Bad fit may be consequence of lack of these factors and not the fitting procedure performance. Nonetheless it is believed that part of the difficulties in ecological modelling stems from lack of explicit connection tools between models and data. Most often, theoretical models in ecology tend to emphasize on qualitative dynamics. In normal situation, the end product of such investigation should have been a broad map of the phase parameter space, which should have lead to perfect understanding of the system and offer guideline for decision-making. In this context, we think the interface between model and data presented here, will be helpful toward making new theories more accountable to experimental data.

Chapter 8

General discussion, Conclusion and Prospects

8.1 General discussion

Relatively few attempts have been made to fit predator-prey models to field time series directly. A major challenge in fitting such models is that these data usually include process error, which is random variation in the actual numbers of organism present, and observation error, which occurs because the data are estimates only from those numbers. The presented work in chapters 3, 4 and 5 is a detailed technique for restoration of parameters. A loss function, which measures the discrepancy between the models values and observed values, was defined, and a numerical process was used to select the parameters which minimize this function. Results from the fitted mechanistic models were unable to identify a suitable model that could mutually explain the dynamics of Diamondback moth and its exotic parasitoid, *Diadegma semiclausum*.

Poor fitting may be due to many reasons :

1. The population dynamics of these insects are inherently nonlinear. The rate of population change may be affected not only by the current population density but also by lagged density. Consequently specific mechanisms may involve either intrinsic or extrinsic factors. This lag structure of population may be too complex and can incorporate several delays on the population rate of increase. In such situation, direct model parameters restoration becomes extremely studious.
2. The critical issue when applying methods that estimate parameters associated with interacting populations such as Diamondback moth and *Diadegma semiclausum* at a

particular time in models is to ensure that they are the most appropriate parameters for the specific question the model is intended to address. For example, the survival rate of Diamondback moth measured in the field at a particular time for a specific period might not be a good description for the same population at different period. It would then be inappropriate to use the same measurement for all periods. This is the result from how complex the situation in nature.

3. When fitting models to our ecological data, we find ourselves in the situation where the functional form of the model is not known, and then the only task is the estimation of its parameters. From theory several alternative models were chosen, and each one was contracted with the data in order to determine which one offered the best fit. Owing to the fact that good number of models explaining dynamics between host and parasitoid has been developed, it is challenging to choose the exact one for a particular time series.

However, the fitting exercise is full of merits. The effort of fitting models is exemplified by the information that it provides about the dynamics. First, the form of the fitted model may suggest underlying mechanism, or narrow the range of possible mechanisms, so that the model is a step toward obtaining an improved model. Second, the fitted model can be used to characterize the significant features of the system dynamics. Such features of interest for population and epidemic dynamics are the overall extent of chaos versus stability, the level of predictability versus unpredictable noise in the dynamics, and how both of these varied as a function of current state of the system. Finally the fitted model can be used to evaluate a proposed mechanistic model, or compare alternative proposed models, by fitting the same model to output from the mechanistic model and comparing with the model fitted to data.

The polar alternatives of fitting simple mechanistic model, is purely descriptive statistical model, which has been the dominant approach for modelling and quantifying population fluctuations. While it is recognized that both approaches have limitations, both are widely used. Our research suggests that a combination of mechanistic and statistical population modelling, reflecting the actual state of knowledge about the system, can be useful in practice for improved forecasting and characterization of population dynamics. Moreover, the fitted model can provide information on the mechanisms driving the observed dynamics. By applying this approach it is thought that, an improvement in the model parameter estimates has been made. The remarkable achievement is that parameters ranges coincide with biological borders.

Another successful result from this study was the development and implementation of an adaptive model using artificial neural network for host-parasitoid population density prediction. It was shown that artificial neural network can provide a powerful tool for host-parasitoid system modelling with few assumptions on the data. It will allow the user to achieve highly accurate predictions, which can greatly assist in decision making. The method also provides room for sensibility analysis, which consist of the arbitrary modification of a parameter value and recording the response of the built model, whilst holding all other parameters constant at their most likely point estimates.

8.2 Conclusion

It would be unrealistic to expect any mechanistic model to perfectly fit census field data because of the irregularities in nature, since parameter values are expected to change. It is also generally accepted that field collected time series data are never

100% accurate and may show a deviation of up to 20%. Thus our estimated parameters are only well-informed guesses at best. Stanfield and Bleloch (1986) sum it up with: "We can never really validate the sort of model that we have built, we can only hope to gain confidence in it" In the present work was successful in the sense that: 1) This provides guidance on the possibilities that most actual mechanistic host-parasitoid model may not be accurate in the full prediction of DBM and *Diadegma semiclausum* population dynamics. 2) This elucidates a useful application of models for impact assessment of the effect for a newly introduce species within the region. 3) It proves and demonstrates the predictive power of artificial neural network for host-parasitoid population density. 4) The work proposes and elucidates an interface between model and data which may be helpful toward making new theories for models to become more accountable to experimental data. Our wishes is that let this practical exercise become useful to modellers, either in terms of mathematical interpretation of ecological information or stimulating innovative thinking about an old field of research.

8.3 Prospects

From this study, the following suggestions were made

8.3.1 Recommendations directed to the fitting of mechanistic models

1. Before fitting, the model parameters should be considered as variable which may depend on abiotic factors such as climate (rainfall and temperature).
2. Laboratory studies and field experiments should be conducted if possible to determine value of some parameters before the fitting exercise.

3. Direct estimation of parameters from time series for predator-prey or host-parasitoid are rarely done in practice and would be advisable for good understanding and studies of the systems.

4. Fitting models to time series has significant advantages for estimating and forecasting parameters. Data can be collected at appropriate scales for the system of interest, thus by passing the assumptions and uncertainties that arise from small-scale experiments. Parameter estimates could be improved by accounting for observation errors. However, even modest observation errors cause substantial difficulties in model identification.

8.3.2 Considerations which may help models end users in terms of management and making policies

1. The first problem is scale which could be considered general to all ecologists. When time comes to apply results from models in management and policy, the main challenge is to deal with the wide array of scales that are often incompatible with one another. Frequently, management and policy are exercises that operate at different scales of ecology. Management scales are determined by administrative boundaries, land ownership, and policy is developed at even broader scales. To think that Nature, which follows its own scaling rules, can somehow be made to fit within the arbitrary scales of management and policy is fantasy. To argue further based on the present work, organisms such as insects follow their own algorithms in responding to their respective habitat and this determines the scales at which they operate and over which variation in environmental conditions may be relevant to them.

2. It is important to be clear about the goals and objectives both within a study and, among subjects studied. A model developed for our purpose is not immediately

transferable to some other purpose, even if it is a "good" model. Investigations may be conducted for multiplicity of purposes and at a variety of levels.

3. It must be noted that the species scientists wishes to predict the dynamics, interactions and fluctuations are nature dependant entities and any conclusions or actions are bound to be accompanied by uncertainty as the nature self .

Appendix A: Runge-Kutta algorithm

The Lotka-volterra model is made up of nonlinear ordinary differential equations that cannot directly be solved. For finding approximate solutions, numerical methods are generally used. The Runge-Kutta algorithm belongs to a family of numerical methods which use several intermediate points with $\lfloor x^k, x^k + h \rfloor$ to make a better prediction of y^{k+1}.

$$y^{k+1} = y^k + \alpha_0 h f_0 + \alpha_1 h f_1 + \alpha_2 h f_2 + \ldots \tag{A.1}$$

where f_0, f_1, $f_2 \ldots$; are the intermediate points being used and h the step size.

Because of its fast convergence, the fourth order Runge-Kutta algorithm was applied in this work, its iterations are as follow:

$$f_0 = f(x^k, y^k),$$

$$f_1 = f(x^k + \frac{h}{2}, y^k + \frac{h}{2} f_0),$$

$$f_2 = f(x^k + \frac{h}{2}, y^k + \frac{h}{2} f_1),$$

$$f_3 = f(x^k + h, y^k + h f_2),$$

$$y^{k+1} = y^k + \frac{h}{6}(f_0 + 2f_1 + 2f_2 + f_3). \tag{A.2}$$

Appendix B: Sample Computer program in C/C++ programming language for Lotka-Volterra model parameter restoration with Nerlder-Mead Algorithm

```
#include <stdio.h>
#include <math.h>
#include <stdlib.h>
#include <time.h>
#include <windows.h>
#define  MP  22
#define  NP  21   //Maximum value for NDIM=20

typedef  double MAT[MP][NP];
MAT P;
double Y[MP], PT[MP];
//int   I,ITER,J,NDIM;
int   I,ITER,J,NDIM;
double FTOL;
 double Random()
{
   float x;
   /* Set evil seed (initial seed) */
   srand( (unsigned)time( NULL ) );
    x = (float) rand()/RAND_MAX;
   return x;
}

/*********** Lotka Volterra Equations *****************/
double prey(double t, double h, double p, double r, double c, double a)
{
        double result;
        result = r * h - c*h*h - a * h * p;
        return result;
}
double predator(double t, double h, double p, double m, double e, double b)
{
        double result;
        result = - m * p - e*p*p + b * p * h ;
        return result;
}
/* Utility function */
double square(double value)
{
   return value * value;
}
// user defined function to minimize .by chep
double FUNC(double *P)
{
   int i;
```

```
   double preyPopulationDensity, predatorPopulationDensity;
   double qht, qpt;
   double a,b,c,e,r,m,A,B,H,Pp,T,W1,W2,X11,X12,X21,X22,X31,X32,X41,X42;
   double n, s;
   double populationPrey[49];
   double populationPredator[49];
   double result;

double dbm[49] = {};

double NaturalEnemy[49] = {};

double q = 0.0, step = 0.01;

         r=P[1]*Random();
         c=P[2]*Random();
         a=P[3]*Random();
         m=P[4]*Random();
         e=P[5]*Random();
         b=P[6]*Random();
         H=P[7]*Random();
         Pp=P[8]*Random();
         W1 = H;
          W2 = Pp;

          A = 0;
          B = 49;
           s = 1;
   // The Runge-Kutta Method of order four for systems of differential equations
         n = (B - A) / s;
         T = A;
  for (i = 0; i < n; i++)

  {
         X11 = s * step * prey(T, W1, W2, r, c, a);
         X12 = s * step * predator(T, W1, W2, m, e, b);

         X21 = s * step * prey(T + s/2.0, W1 + X11/2.0, W2 + X12/2.0, r, c, a);
         X22 = s * step * predator(T + s/2.0, W1 + X11/ 2.0, W2 + X12/2.0, m, e, b);

         X31 = s * step * prey(T + s/2.0, W1 + X21/2.0, W2 + X22/2.0, r, c, a);
         X32 = s * step * predator(T + s/2.0, W1 + X21/2.0, W2 + X22/2.0, m, e, b);

         X41 = s * step * prey(T + s, W1 + X31, W2 + X32, r, c, a);
         X42 = s * step * predator(T + s, W1 + X31, W2 + X32, m, e, b);

         W1 = W1 + (X11 + 2.0 * X21 + 2.0 * X31 + X41) / 6.0;
         W2 = W2 + (X12 + 2.0 * X22 + 2.0 * X32 + X42) / 6.0;

                T = A + (i + 1)  * s;
```

```
                populationPrey[i] = W1;
                populationPredator[i] = W2;
        }

  qht = qpt = 0.0;

  for (i = 0; i < 49; i++)
        {
     preyPopulationDensity = populationPrey[i] - dbm[i];
     preyPopulationDensity *= preyPopulationDensity;
     qht += preyPopulationDensity;

     predatorPopulationDensity = populationPredator[i] - NaturalEnemy[i];
     predatorPopulationDensity *= predatorPopulationDensity;
     qpt += predatorPopulationDensity;
  }
       result=qht + qpt;
       printf("Q: %f\n", result);

       return result;
   }

void AMOEBA(MAT P, double *Y, int NDIM, double FTOL,int *ITER)
 {
/*---------------------------------------------------------------------
! Multidimensional minimization of the function FUNC(X) where X is
! an NDIM-dimensional vector, by the downhill simplex method of
! Nelder and Mead. Input is a matrix P whose NDIM+1 rows are NDIM-
! dimensional vectors which are the vertices of the starting simplex
! (Logical dimensions of P are P(NDIM+1,NDIM); physical dimensions
! are input as P(NP,NP)). Also input is the vector Y of length NDIM
! +1, whose components must be pre-initialized to the values of FUNC
! evaluated at the NDIM+1 vertices (rows) of P; and FTOL the fractio-
! nal convergence tolerance to be achieved in the function value. On
! output, P and Y will have been reset to NDIM+1 new points all within
! FTOL of a minimum function value, and ITER gives the number of ite-
! rations taken.
!--------------------------------------------------------------------*/
// Label: e1
const NMAX=20.00, ITMAX=50000000000.00;
//Expected maximum number of dimensions, three parameters which define
// the expansions and contractions, and maximum allowed number of
//iterations.

  double PR[MP], PRR[MP], PBAR[MP];
  double ALPHA=1.0, BETA=0.5, GAMMA=2.0;
  int I,IHI,ILO,INHI,J,MPTS;
  double RTOL,YPR,YPRR;
 MPTS=NDIM+1;
```

```
*ITER=0;
e1:ILO=1;

 if (Y[1] > Y[2])
 {
  IHI=1;
  INHI=2;
 }
 else
 {
  IHI=2;
  INHI=1;
 }
 for (I=1; I<=MPTS; I++)
 {
  if (Y[I] < Y[ILO])  ILO=I;
         if (Y[I] > Y[IHI])
         {
    INHI=IHI;
    IHI=I;
  }
  else if (Y[I] > Y[INHI])
         if (I != IHI)  INHI=I;
 }
//Compute the fractional range from highest to lowest and return if
//satisfactory.

 RTOL=2.0*fabs(Y[IHI]-Y[ILO])/(fabs(Y[IHI])+fabs(Y[ILO]));
 if (RTOL < FTOL)  return;  //normal exit
 if (*ITER == ITMAX)


 {
   printf(" Amoeba exceeding maximum iterations.\n");
   return;
 }

 *ITER= (*ITER) + 1;

 for (J=1; J<=NDIM; J++)  PBAR[J]=0.0;
 for (I=1; I<=MPTS; I++)
   if (I != IHI)
     for (J=1; J<=NDIM; J++)
       PBAR[J] += P[I][J];
 for (J=1; J<=NDIM; J++) {
   PBAR[J] /= 1.0*NDIM;
   PR[J]=(1.0+ALPHA)*PBAR[J] - ALPHA*P[IHI][J];
 }
 YPR=FUNC(PR);
 if (YPR <= Y[ILO])
```

```
 {
   for (J=1; J<=NDIM; J++)
     PRR[J]=GAMMA*PR[J] + (1.0-GAMMA)*PBAR[J];
   YPRR=FUNC(PRR);
          if (YPRR < Y[ILO])
           {
     for (J=1; J<=NDIM; J++) P[IHI][J]=PRR[J];
     Y[IHI]=YPRR;
   }
   else {
     for (J=1; J<=NDIM; J++) P[IHI][J]=PR[J];
     Y[IHI]=YPR;
           }
 }
 else if (YPR >= Y[INHI])
 {
          if (YPR < Y[IHI])
           {
     for (J=1; J<=NDIM; J++)  P[IHI][J]=PR[J];
     Y[IHI]=YPR;
    }
   for (J=1; J<=NDIM; J++)  PRR[J]=BETA*P[IHI][J] + (1.0-BETA)*PBAR[J];
   YPRR=FUNC(PRR);
           if (YPRR < Y[IHI])
           {
     for (J=1; J<=NDIM; J++)  P[IHI][J]=PRR[J];
     Y[IHI]=YPRR;
    }
   else
                       for (I=1; I<=MPTS; I++)
                       if (I != ILO)
                       {
                         for (J=1; J<=NDIM; J++)
                         {
           PR[J]=0.5*(P[I][J] + P[ILO][J]);
                   P[I][J]=PR[J];
                         }
                       Y[I]=FUNC(PR);
           }
  }
  else {
    for (J=1; J<=NDIM; J++)  P[IHI][J]=PR[J];
    Y[IHI]=YPR;
  }
  goto e1;
}
void main()
{
  NDIM=8; // 2 variables
  FTOL=1e-8;   // User given tolerance
```

```
 //define NDIM+1 initial vertices (one by row)

 P[1][1]=.07; P[1][2]=.5; P[1][3]=.01; P[1][4]=.03;
 P[1][5]=.02; P[1][6]=.01; P[1][7]=12.41; P[1][8]=1.7;

 P[2][1]=.09; P[2][2]=.17; P[2][3]=.05; P[2][4]=.29;
 P[2][5]=.02; P[2][6]=.02;P[2][7]=15.6; P[2][8]=2.9;

 P[3][1]=.32; P[3][2]=.04;  P[3][3]=.8;  P[3][4]=.073;
 P[3][5]=.09;  P[3][6]=.053; P[3][7]= 9.8; P[3][8]=0.22;

 P[4][1]=.03; P[4][2]=.02; P[4][3]= .013; P[4][4]=.85;
 P[4][5]=.045; P[4][6]=.03; P[4][7]= 5.00; P[4][8]=2.3;

 P[5][1]=1.0; P[5][2]=.052; P[5][3]=.01; P[5][4]=.029;
 P[5][5]=.01; P[5][6]=.02; P[5][7]=7.41; P[5][8]=2.9;

 P[6][1]=.72; P[6][2]=.044; P[6][3]= .048;P[6][4]=.093;
 P[6][5]=.02;P[6][6]=.083;P[6][7]=4.5;P[6][8]=0.22;

 P[7][1]=.008; P[7][2]=.083; P[7][3]= .097; P[7][4]=.703;
 P[7][5]=.071; P[7][6]=.03; P[7][7]= 8.98; P[7][8]=0.03;

 P[8][1]=.23; P[8][2]=.72; P[8][3]= .53; P[8][4]=.025;
 P[8][5]=.045;  P[8][6]=.053; P[8][7]= 2.9; P[8][8]=5.23;

 P[9][1]=.8; P[9][2]=.02; P[9][3]= .03; P[9][4]=.05;
 P[9][5]=.045; P[9][6]=.93; P[9][7]= 9.60; P[9][8]=1.9;

//Initialize Y to the values of FUNC evaluated
//at the NDIM+1 vertices (rows] of P

 for (I=1; I<=NDIM+1; I++)
 {
        for (int v=1;v<=8;v++)
        {
   //PT[1]=P[I][1]; PT[2]=P[I][2];
        PT[v]=P[I][v];
        }
  Y[I]=FUNC(PT);
 }
//for (I=1; I<=NDIM+1; I++) printf(" %14.10f\n", PT[I]);
 //call main function

 for (I=1 ; I<=NDIM+1; I++)
 {
  for (J=1; J<=NDIM; J++)  printf("  %f", P[I][J]);
  printf("\n");
 }
```

```
 AMOEBA(P,Y,NDIM,FTOL,&ITER);

 //print results
 printf("\n Number of iterations: %d\n\n", ITER);
 printf(" Best values of Parameters :\n");

 for (I=1 ; I<=NDIM+1; I++)
 {
  for (J=1; J<=NDIM; J++)  printf("  %5.4f", P[I][J]*Random());
  printf("\n");
 }

 printf("\n Best mimimum values of the Q function:\n");
 for (I=1; I<=NDIM+1; I++) printf(" %5.4f\n", Y[I]);
 printf("\n");

}
```

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ACHIEVEMENTS TO DATE (relevant publications)

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2. **Henri E. Z. Tonnang (2004).** Building an automated controller for a distillation column. In: Workshop on New methods in Process Control. Nigeria National Petroleum Corporation-Petroleum Refining Company (NNPC-PRC), PortHarcout, December, 13-18 2004.
3. **Henri E. Z. Tonnang (2006).** Modelling the population dynamics of Diamondback moth and its parasitoid-*Diadegma semiclausum with* differential equations. ARPPIS Scholars Association (ASA) Meeting Dar es Salaam November 27-29.
4. **Henri E. Z. Tonnang,** Lev V. Nedorezov, Horace Ochanda, John Owino and Bernhard Löhr **(2007).** Application of differential equation models to the population dynamics of Diamondback moth and its parasitoid - *Diadegma semiclausum* (Hellen)" 5th International workshop on "Management of Diamondback Moth and Other Crucifer Insect Pests" October 24-27, 2006, Beijing, China, pp 24.
5. **Henri E. Z. Tonnang,** Lev V. Nedorezov, Horace Ochanda, John Owino and Bernhard Löhr **(2008).** Step-by-step guideline for the development of an artificial neural network for host-parasitoid population density prediction" ICE, July,06-12, 2008, Durban, South Africa.

Thesis

1. **Henri E. Z.Tonnang (1998).** Conversion of the Aeolian Energy to Electricity. M.Sc research thesis submitted and defended at the Department of Physics, Faculty of Sciences of the University of Dschang, in partial fulfillment of the award of Master's Degree in Physics Science. ***Grade: Very Good with special congratulation from the Jury.***

2. **Henri E. Z. Tonnang (2004).** Distillation Column Control using Artificial Neural Network. M.Sc research thesis submitted and defended at the Department of Electrical and Electronics Engineering, Faculty of Technology, University of Ibadan, in partial fulfillment of the award of Master's Degree in Microprocessors and Control Engineering. ***Grade: Very Good***

3. **Henri E. Z. Tonnang (2008).** Modeling Host-Parasitoid System Dynamics and Fluctuations Applicable to Diamondback Moth. Ph.D research thesis School of Biological Sciences/School of Mathematics of the University of Nairobi, in partial fulfillment of the award of the Degree of Doctor of Philosophy.

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1. **Henri E. Z. Tonnang (2005).** Data Mining Model Controller of crude oil Fractionator based Back propagation algorithm Feed forward neural networks. In: Proceeding 6th European Advanced Equipment Control/Advanced Process Control (AEC/APC) Conference, April 6-8, Dublin, Ireland.

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1. Henri E. Z .Tonnang and Oni David **(2008).** Using Data Mining Techniques to Control Crude oil Fractionator. International Journal of Science Environmental and Enginering Technology.

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1. Henri E. Z. Tonnang, Lev V. Nedorezov, Horace Ochanda, John Owino and Bernhard Löhr. Fitting discrete host-parasitoid models with field time series data. Population Ecology (POEC-S-08-00111)

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