Application of differential equation models to the population dynamics of diamondback moth and its parasitoid, *Diadegma semiclausum*

*Henri E. Z. Tonnang*¹, *Lev V. Nedorezov*¹, *Horace Ochanda*², *John Owino*² and *Bernhard Lihua*³

¹ International Centre of Insect Physiology and Ecology, P. O. Box 30772, 00100 Nairobi, Kenya
² University of Nairobi Dept. of Zoology / Dept. of Mathematics, P. O. Box 30197, 00100 Nairobi, Kenya.
Corresponding author: htonnang@icipe.org

**ABSTRACT**

*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 work was to study host-parasitoid interactions using existing mathematical 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 datasets 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 curve 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.

**INTRODUCTION**

Diamondback moth (DBM), *Plutella xylostella* (L.) is the major pest of crucifer crops worldwide. Synthetic pesticides are the major control method for DBM, and pesticides cost alone has been estimated at US$1 billion annually worldwide (Talekar and Shelton 1993). In consequence, DBM has developed resistance against all major groups of pesticides, including *Bacillus thuringiensis*-based biopesticides (Tahashnik *et al.* 1990). Development and implementation of biological control as a component of Integrated Pest Management (IPM) is now considered to be the most sustainable approach to combat this
highly resistant insect pest.

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 semicalusum* (Hellen) from Taiwan province in China 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 mathematical 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 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. We tested the applicability of differential equation (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.

Sequentially, we tested 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.

**MATERIALS AND METHODS**

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. This area is situated on an island mountain, Taita Hills, rising from an area of about 700 m elevation to 2 200 m. Cabbage and kale farms are concentrated between 1 600-1 800 m elevation and are mainly rain fed; however complementary irrigation from shallow wells is commonly practiced during dry season (Momanyi
et al. 2006).

Fifteen farmer-managed farms were selected at random for collection of samples. Sampling was carried out at two week intervals starting from two weeks after transplanting until harvest. When a field had been harvested, a recently transplanted field in the immediate vicinity was chosen as replacement. In each field, ten plants were selected at random and a population census for larvae (1\textsuperscript{st}, 2\textsuperscript{nd}, 3\textsuperscript{rd} and 4\textsuperscript{th} instars), pupae and adults was undertaken. Big larvae and pupae were transported to the laboratory and were observed for adult moth and parasitoid emergence. The percentage of parasitism was estimated for each collection. The percentage of parasitism obtained was then multiplied by the total number of DBM population counted in 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.

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.

\textit{Lotka-Volterra model}

Within the framework of the Lotka-Volterra model with self-regulation (Lotka 1920, 1925, Volterra 1931), interactions between populations are described by the following differential equations “law of interacting biomass” as in molecular kinetics:

\begin{equation}
\frac{dx}{dt} = \alpha_1 x - \beta_1 x^2 - \gamma_1 xy, \quad \frac{dy}{dt} = \alpha_2 y - \beta_2 y^2 + \gamma_2 xy,
\end{equation}

\[x(0) = x_0 \geq 0, \quad y(0) = y_0 \geq 0 \text{ (Cauchy problem)} \]

[For correct presentation of the Cauchy problem we have to use non-negative initial values. However in biological situations such a problem would not occur, as initial population sizes would always be zero or positive.]

where,

\(x(t)\) is the DBM population size at time,

\(y(t)\) is the parasitoid population size at the same time,

\(\alpha_1\) is the growth rate or Malthusian parameter for DBM population,

\(\alpha_2\) is the intensity of natural death of individuals in the parasitoid population,

\(\beta_1\) and \(\beta_2\) are the coefficients of self-regulation in the respective populations,

\(\gamma_1\) and \(\gamma_2\) are the coefficients of interaction between two populations.

Note that the relation \(\alpha_2/\beta_1\) is the carrying capacity for DBM.

Theoretical studies of model (1) (Wangersky 1978) have shown that it has two dynamic regimes: elimination of the prey for all possible initial values of population sizes or stabilisation 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).

\textit{Holling tanner models type 2 and type 3}

Holling (1959) modified model (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:
\[
\frac{dx}{dt} = \alpha_1 x - \beta_1 x^2 - \frac{\gamma_1 \beta y}{1 + \delta x^2} \quad \frac{dy}{dt} = -\alpha_2 y - \beta_2 y^2 + \frac{\gamma_2 \beta y}{1 + \delta x^2},
\]
(2)

where, \( \delta \) is constant representing the sigmoidality of the function,
\( \gamma_1/\delta \) characterizes the maximum intensity of DBM population,
\( \gamma_2/\delta \) is the maximum intensity of parasitoid population increase.

This function is generally called the Holling’s type 2 functional response and its characteristics are 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, Bazyn 1985, Isaev et al. 1984, 2001).

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.

\[
\frac{dx}{dt} = \alpha_1 x - \beta_1 x^2 - \frac{\gamma_1 x^2 y}{1 + \delta x^2} \quad \frac{dy}{dt} = -\alpha_3 y - \beta_3 y^2 + \frac{\gamma_3 x^2 y}{1 + \delta x^2},
\]
(3)

where, all parameters are the same as in (2).

**Leslie model**

Leslie 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).

\[
\frac{dx}{dt} = \alpha_1 x - \beta_1 x^2 - \gamma_1 xy \quad \frac{dy}{dt} = y \left( K - \frac{\gamma_1 y}{x} \right)
\]
(4)

**Statistical Criteria for Parameter Estimation**

Parameter determination is a crucial phase of 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, survival etc. In this case, model parameters have specific numerical values. An alternative method of parameter estimation is minimization of the value of the following function using the empirical dataset:

\[
Q(\vec{\alpha}, \vec{y}) = \sum_{i=1}^{N} \left( x_i - G^{(K-1)}(\alpha_{\text{data}}, x_0) \right)^2 + \sum_{i=1}^{N} \left( y_i - G^{(K-1)}(\alpha_{\text{data}}, y_0) \right)^2 \rightarrow \min \frac{\partial Q}{\partial \vec{x}}
\]
(5)

where,
\( x_i \) is the empirical value of DBM population density at time \( j \),
\( y_i \) 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,
\( G' \) is the value of function calculated at time \( j \),
\( G' \) is the solution of Cauchy problem for the respective system of differential equations, which describes the dynamics of parasitoids,
\( G'' \) is the value of function \( G' \) calculated at time \( j \),
\( \vec{\alpha} = (\alpha_{\text{data}}, \alpha_{\text{data}}) \), \( \alpha_{\text{data}} \) is the set of parameters for function \( G \),
and \( \alpha_{\text{data}} \) is the set of parameters for function \( G' \),
\( \vec{y} = (x_0, y_0) \) is the initial vector of population size.
\( x_0 \) is the initial value of DBM population density.

\( y_0 \) is the initial value of the parasitoid population density.

Searching for model parameters is vital because it helps in characterizing the population. However, during this exercise it has to be remembered that our estimated parameters are stochastic variables. For this reason, the confidence domains in which these parameters can be found with their corresponding level of significance should be indicated (Draper and Smith 1981).

The borders of confidence domains are determined by finding the intersections of minimized function (5) with the plane \( Q = \text{constant} \), where the value of the constant depends on sample size and the number of parameters for minimization at a chosen level of significance. 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.

Considering the fact that the initial values of population size \( x_0 \) and \( y_0 \) are also used as parameters in (5), the space dimensions of the confidence domains become larger than those of the model parameters. In this case, the space of model parameters present is its own structure that is specified by bifurcation surfaces, which when transited, lead to quality changes of the dynamical regime of population fluctuations.

**Minimization Method: the 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, each labeled by the coefficients: \( \rho \) (reflection), \( \chi \) (expansion) \( \gamma \) (contraction) and \( \sigma \) (shrink), and is governed by the rules:

\[
\rho > 0, \chi > 1, \gamma > \rho, 0 < \gamma < 1, \text{ and } 0 < \sigma < 1. \tag{6}
\]

While these are general rules, they are always seen by the convention yielding the values \( \rho = 1, \chi = 2, \gamma = \frac{1}{2} \) and \( \sigma = \frac{1}{2} \) (Gurson 1999).

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 4\(^{\text{th}}\) algorithm with 0.01 step size (Press et al. 1992). A loss function was developed, made of the squared difference between the theoretical and empirical values of datasets. This routine was combined as a unique function and embedded in a Nelder-Mead algorithm for minimization with randomly chosen initial values of parameters.

**Analysis of Residuals**

The Durbin Watson test was applied on the discrepancy between theoretical (obtained from the model) and experimental trajectories (from field datasets), before its application residuals were subjected to Shapiro-Wilcoxon (Shapiro and Luppov 1983) test and Kolmogorov-Smirnov test for confirmation of their random distribution.

**RESULTS**

DBM and parasitoid population fluctuations with time are displayed in Figure 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 curve 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 curve presents a low sustained trajectory at points 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 curves, respectively, correspond to sustained population fluctuations towards stabilization. Other parts of the DBM curve and parasitoid curve, such as points 27-30 on DBM and parasitoid curves, cannot be explained under the hypothesis that the population dynamics correspond to the regime of a proper outbreak.

![Graph](image)

**Figure 1** Changes in the population dynamics of diamondback moth (*Plutella xylostella*) and its parasitoid, *Diadegma semiclausum*, after introduction and release of the parasitoid.

WeruAM, Wundanyi Division, Taita Taveta District of Kenya

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 1. Following are the analysis and interpretation of these results for each model.

**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 2 represents the DBM population variation with time. The model predicted a monotonously decreasing curve 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 1).
Table 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* (calculated with the help of formula 5). Werauga, Wundanyi Division, Taita Taveta District of Kenya

<table>
<thead>
<tr>
<th>Models</th>
<th>DBM growth rate ($\alpha_1$)</th>
<th>Natural death rate ($\alpha_2$)</th>
<th>DBM self-regulation coefficient ($\beta_1$)</th>
<th>Interaction coefficient ($\gamma_1$) (DBM/parasitoid)</th>
<th>Interaction coefficient ($\gamma_2$) (parasitoid/DBM)</th>
<th>Carrying capacity ($\alpha_1/\beta_1$) (DBM)</th>
<th>Sigmoidality constant ($\delta$)</th>
<th>Maximum population size ($x_0$) (DBM)</th>
<th>Initial population size ($y_0$) (parasitoid)</th>
<th>Loss-function* (Qmin)</th>
<th>Durbin-Watson criterion (d)</th>
<th>Durbin-Watson criterion (d)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lokta-Voltera</td>
<td>1.45</td>
<td>2.49</td>
<td>42.19</td>
<td>9.07</td>
<td>0.03</td>
<td>120.58</td>
<td>—</td>
<td>9.36</td>
<td>0.03</td>
<td>80.5</td>
<td>1.20</td>
<td>0.56</td>
</tr>
<tr>
<td>Holling Type 2</td>
<td>0.40</td>
<td>2.47</td>
<td>3.77</td>
<td>0.59</td>
<td>2.23</td>
<td>0.30</td>
<td>0.11</td>
<td>0.001</td>
<td>12.36</td>
<td>0.09</td>
<td>96.9</td>
<td>1.05</td>
</tr>
<tr>
<td>Holling Type 3</td>
<td>1.72</td>
<td>2.00</td>
<td>3.51</td>
<td>0.41</td>
<td>1.75</td>
<td>0.75</td>
<td>0.49</td>
<td>0.022</td>
<td>12.40</td>
<td>0.24</td>
<td>95.6</td>
<td>1.11</td>
</tr>
<tr>
<td>Leslie</td>
<td>0.55</td>
<td>—</td>
<td>0.21</td>
<td>—</td>
<td>36.91</td>
<td>—</td>
<td>2.57</td>
<td>—</td>
<td>10.72</td>
<td>0.29</td>
<td>88.0</td>
<td>1.13</td>
</tr>
</tbody>
</table>

* squared deviations between empirical and theoretical time series.
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).

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 $(\alpha_1, \alpha_3)$ and the boundaries of confidence domains $\Omega_k$, $k = 1, 2, 3$, for 1, 5 and 10% confidence levels are illustrated in Figure 4. These trajectories are within the plane surface with the following coordinates $\alpha_1 = 5.90$ and $\alpha_3 = 22.50$.

**Holling-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 1). Figure 2 depicts the variation in DBM population density with time. The model predicted a curve 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). 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,
Figure 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.

Wenugha, Wundanyi Division, Taita Taveta District of Kenya.

Figure 4  Boundaries of confidence domains for estimated parameters of Lotka-Volterra model at fixed initial values of diamondback moth (*x*<sub>n</sub>) and parasitoid, *Diadegma semiclausum* (*y*<sub>n</sub>) population / plant

Ω<sub>1</sub> is the boundary for 10% confidence level, Ω<sub>2</sub> for 5% confidence level and Ω<sub>3</sub> for 1% respectively.

P: \( \alpha_1 = 2.86 \alpha_c \) is the bifurcation line.

respectively). As in the Lotka-Volterra model, \( d < d_c \), 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*<sub>1</sub>, *γ*<sub>1</sub>) and the boundaries of confidence domain \( \Omega_k \), \( k = 1, 2, 3 \), for 1, 5 and
10% confidence levels are presented in Figure 5. The Figure shows concentric surfaces with an approximate centre at coordinate point (2.80, 2.60).

![Diagram showing boundaries of confidence domains](image)

**Figure 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

$\Omega_1$ is the boundary for 10% confidence level, $\Omega_2$ for 5% confidence level and $\Omega_3$ for 1% respectively.

**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 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 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).

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, $d < 2$, indicating a positive correlation between residuals.

Figure 6 depicts the function $Q$ on the plane $(\alpha, \gamma)$ and the boundaries of confidence domain $\Omega_k$, $k = 1, 2, 3$, 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.

**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 curve starting at 10.72, which stabilized at a value of 0.60 DBM/plant (Figure 2).

The prediction for the parasitoid population was a curve declining at an increasing rate which stabilized at a value of 0.05/plant (Figure 3). 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...
Figure 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

$\Omega_1$ is the boundary for 10% confidence level, $\Omega_2$ for 5% confidence level and $\Omega_3$ for 1% respectively.

Figure 7 shows the loss function $Q$ on the plane ($\alpha_1, \gamma_1$) and the boundaries of confidence domain $\Omega_k$, $k = 1, 2, 3$, for 1%, 5% and 10% confidence levels respectively, which are concentric circles.

Figure 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

$\Omega_1$ is the boundary for 10% confidence level, $\Omega_2$ for 5% confidence level and $\Omega_3$ for 1% respectively.

**DISCUSSION**

The unstable cyclic eruptive pulses of the DBM population (Figure 1) 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 other factors such as rainfall, which have been reported as major factors of DBM population regulation (Gunn 1917, Wakisaka et al. 1991). In addition, a 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 Isaac’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 side 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 large population sizes and their influence is negligible at small population sizes. DBM population was large enough before the release of Diadegma 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 assumed 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 dataset.

The maximum calculated value of the 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 the relation between two values of estimated parameters, its value may not always be the same as soon as change occurs in the time step value. From this perspective, it will be very difficult to discuss the relation between the 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 sometimes are 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 to map biological processes more precisely. An example would be that none of the models analysed considers possibilities such as the 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 two areas by a bifurcation line $\bar{P}$ determined by the equation $\alpha_2 = 2.85\alpha_1$ (Figure 4). 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 models tested. 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 other 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 of success of the biological control agent in the entire East Africa region.

Acknowledgements

The data used in the work presented here were collected by the DBM Biocontrol Team of ICIPE, in particular Ruth Gathu and Gatama Gichini, with support of Paul Onano and Shadrack Juma of the local extension office. We also acknowledge M. Knapp and S. Subramanian for valuable suggestions on the manuscript. The DBM Biocontrol Project is financed by the German Federal Ministry of Economic Cooperation and Development (BMZ) through the German Agency of Technical Cooperation (GTZ). The senior author is a student under ICIPE’s African Regional Postgraduate Programme in Insect Science (ARPPIS) and funded by the German Academic Exchange Service. All are gratefully acknowledged.

REFERENCES


Isaev, AS, Nedorezov, LV and Khlebopros, RG. (1980) Qualitative analysis of the phenomenological model of the forest insect number dynamics. Pest and Pathogen Control, IASA, Austria 9: 1-44.

Dynamics of Forest Insects. (In Russian) Nauka, Novosibirsk.


Lotka, Al. (1925) Elements of Physical Biology. Williams and Wilkins, Baltimore, MD.


No. 92-368.