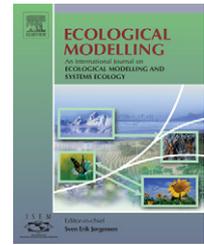


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Assessing the impact of biological control of *Plutella xylostella* through the application of Lotka–Volterra model

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ABSTRACT

The Lotka–Volterra model was applied to the population densities of diamondback moth (DBM), *Plutella xylostella* (L.) and its exotic larval parasitoid *Diadegma semiclausum* (Hellen) data that was collected earlier by icipe's DBM biological control team. The 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. 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 in Werugha and from 6.11 to 3.76 and 3.45 (with and without exclusion of the time before *D. semiclausum* recovery) in Tharuni when transiting from the pre- and post-release periods, respectively. This change was a consequence of the newly introduced parasitoid, in the areas. The study presented a successful and detailed technique for non-linear model parameters restoration which was demonstrated by the correct mimicking of empirical datasets from the classical biological control with *D. semiclausum*, in different areas of Kenya. The applied 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.

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1. Introduction

The diamondback moth (DBM), *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), adults are slender, very small, 1/3 in.

(8 mm) long, greyish-brown with folded wings flaring outward and upward at their posterior ends. They fly around plants searching for a mate or a place to deposit eggs. Male DBM are attracted to the pheromone produced by females. The DBM lay

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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 occurs in 5–10 days depending on the prevailing temperatures. The DBM larvae pass through four instars (growth stages). 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. The DBM are the dangerous pests of all cultivated crucifers with a worldwide distribution. For many years, synthetic pesticides have been the major control method for DBM. Cost of pesticides alone used for the control of DBM has been estimated at US \$1 billion annually worldwide (Talekar and Shelton, 1993) and the pest has developed resistance against all major groups of pesticides, including *Bacillus thuringiensis* (Berliner) based biopesticides (Tabashnik et al., 1990). The situation is similar in Kenya, where cabbage and kale are among the main vegetables and are consumed on a daily basis by large proportion of the population: pesticide resistance has developed to most commercially available products and farmers have resorted to pesticide cocktails (Kibata, 1996).

Hymenopteran parasitoids of the genera *Diadegma* (Hymenoptera: Ichneumonidae) and *Cotesia* (Hymenoptera: Braconidae) are among the most effective natural enemies of DBM. *Diadegma semiclausum* is a solitary koinobiont endoparasitoid of DBM, black in colour and 5–7 mm long. The four larval stages of DBM are attacked by *D. 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 5 days after cocoon formation.

In October 2001, the International Centre of Insect Physiology and Ecology (*icipe*) in Nairobi, Kenya, imported *D. semiclausum* from the Asian Vegetable Research and Development Center (AVRDC) in Taiwan. Two pilot releases were made: 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 3 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 famous Lotka–Volterra equations play a fundamental role in the mathematical modelling of various ecological and chemical systems. This model has been widely applied in several areas of ecological modelling. On finding the optimal between two species harvesting policy, Mesterton-Gibbons (1996) utilized the Lotka–Volterra model. Piana et al. (2006) fitted the Lotka–Volterra predation model and its modifications to a time-series datasets for fish assemblage collected from an isolated lagoon of the upper Parana River floodplain. In the application of biological control, analysis of cassava pest in Africa was conducted with the help of mathematical model (Gutierrez et al., 1988). Buffoni and Gilioli (2003) developed a lumped parameter model for acarine predator–prey population interactions. A dynamics component modelling for integrated pest management with chemicals in atmospheric surface layers was presented in Bisignanesi and Borgas (2007). Using simple models for host–parasitoid interactions, May and Hassel (1988) presented a basic framework for examining the

outcome of releasing natural enemies against a target pest population in classical biological control programme.

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; May and Hassel, 1988; Wilder et al., 1994; Hsu and Huang, 1995; Mesterton-Gibbons, 1996; Legaspi et al., 1996; Nguyen-Huu et al., 2006; Meng et al., 2007) 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. A general sensitivity analysis and stability patterns of two-species pest model using artificial neural networks was conducted by Park et al. (2007). This study provides an idea of the response of the model dynamics to a variation in the values of some parameters without involving the state where a regulator has been introduced to control the pest. The objective of the present work was measuring the parasitoids impact on the DBM biological control through a quantitative estimate of the effectiveness of the newly introduced species *D. semiclausum*. The process of quantification commenced by fitting the Lotka–Volterra equations with the DBM and *D. semiclausum* population density field datasets, and to make use of the estimated parameter values to evaluate the system's steady state before and after the release of the exotic parasitoid and comparison. In case the results confirm the positive impact in reducing pest (DBM) population density as shown by the empirical datasets, the utilized model could therefore be used as tool for decision making in the implementation for strategies in pest management systems in the region.

2. Materials and methods

2.1. Data source and collection method

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. A detailed description of the pilot release areas was provided in (Momanyi et al., 2006). Cabbage and kale were the main rain fed vegetable crops in both regions, with complementary irrigation during the dry season from shallow wells using buckets (Momanyi et al., 2006).

The model was applied to DBM and *D. semiclausum* population densities data collected earlier by *icipe*'s DBM biological control team. Data collection was described in detail in (Löhr et al., 2007). The total number of all parasitoids collected before release was lumped together as "indigenous parasitoids". After release, consideration was only given to *D. semiclausum*, as the parasitism by the indigenous parasitoids became insignificant, less than 5% (Löhr et al., 2007). Whereas in Werugha, the exotic parasitoid was recovered immediately after release, in Tharuni area, the first recovery was made after 4 months, corresponding to eight samplings. This gap lead to the consideration of two cases: Tharuni after release¹ where the complete time series made up of 52 collections for after

release period was used; and Tharuni after release² where the first eight collections without *D. semiclausum* recovery were excluded from the analysis.

2.2. Lotka–Volterra model

The Lotka–Volterra model is one of many continuous (Gertsev and Gertseva, 2004) 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; Filho et al., 2005).

Within this framework interactions between populations are described by the following equations:

$$\begin{aligned} \frac{dx}{dt} &= \alpha_1 x - \beta_1 x^2 - \gamma_1 xy, & \frac{dy}{dt} &= -\alpha_2 y - \beta_2 y^2 + \gamma_2 xy, \\ x(0) = x_0 \geq 0, & y(0) = y_0 \geq 0. & & \text{(Cauchy problem)} \end{aligned} \quad (1)$$

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.

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.

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. The steady state or non-trivial equilibrium of the system is given by:

$$\bar{x} = \frac{\alpha_1\beta_2 + \alpha_2\gamma_1}{\gamma_1\gamma_2 + \beta_1\beta_2}, \quad \bar{y} = \frac{\alpha_1 - \beta_1\bar{x}}{\gamma_1} \quad (2)$$

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

2.3. Other considerations

The following considerations were made:

- The total number of all parasitoids collected before release was lumped together and called “indigenous parasitoid”. The assumption was made just to have a bigger number for parasitoids before release as their individual figure were very small.
- The two species (DBM and *D. semiclausum*) have overlapping generations which normally allows the use of continuous rather than discrete time differential equa-

tions except other assumptions are made (Royama, 1971).

- 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.

2.4. Statistical criteria for parameters estimation

The model parameters estimation was done through minimization of the value of the following function that uses empirical and theoretical dataset:

$$\begin{aligned} Q(\bar{\alpha}, \bar{I}) &= \sum_{k=1}^N [x_k^* - G^{(K-1)}(\alpha_{dbm}, x_0)]^2 + \sum_{k=1}^N [y_k^* - G'^{(K-1)}(\alpha_{ds}, y_0)]^2 \\ &\rightarrow \min_{\bar{\alpha}, \bar{I}} \end{aligned} \quad (3)$$

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.

The borders of confidence domains (Ω_I) are determined by finding the intersections of minimized Eq. (4) with the plane $Q = \text{constant}$, which can be expressed as follows:

$$Q(\bar{\alpha}) = Q(\bar{\alpha}_{\min}) \left[1 + \frac{m}{n-m} * F(m, n-m, \beta) \right] \quad (4)$$

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.

Considering the fact that the initial values of population size x_0 and y_0 are also used as a parameter in (3), 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.

2.5. Minimization method: the Nelder-Mead multidimensional algorithm

The Nelder-Mead search algorithm was used for parameter estimation (Press et al., 1992; Gurson, 1999; Small and Wang, 2003).

The calculations were carried out with 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). 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 for minimization with randomly chosen initial values of parameters.

2.6. 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 and 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 curve 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.

3. Results

3.1. Werugha before release

The values of the estimated model parameters are shown in Table 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 curve began to decline at decreasing rate until 2.3 before increased again (Fig. 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 (Fig. 1).

Fig. 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.

3.2. Werugha after release

The model predicted a monotonously decreasing curve starting at 8.48 as initial DBM population size, with stabilization starting at 0.74 DBM/plant (Fig. 3). The *D. semiclausum* population shows a slowly oscillating curve from 0.15 increases to 0.23 and declines 0.17/plant (Fig. 3).

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

Table 1 – Estimates of Lotka–Volterra model parameters and values of statistical criteria for Lotka–Volterra 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.

Estimated parameters	Werugha		Tharuni		
	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 ^b	5.25	11.58 ^b	9.70 ^b
Initial population size (y_0) (parasitoid)	0.05	0.15	1.58	0.05	0.04
Loss-function ^a (Q_{min})	101.61	92.87	143.31	242.49	110.36

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

^a Squared deviations between empirical and theoretical time series.

^b DBM population size at release.

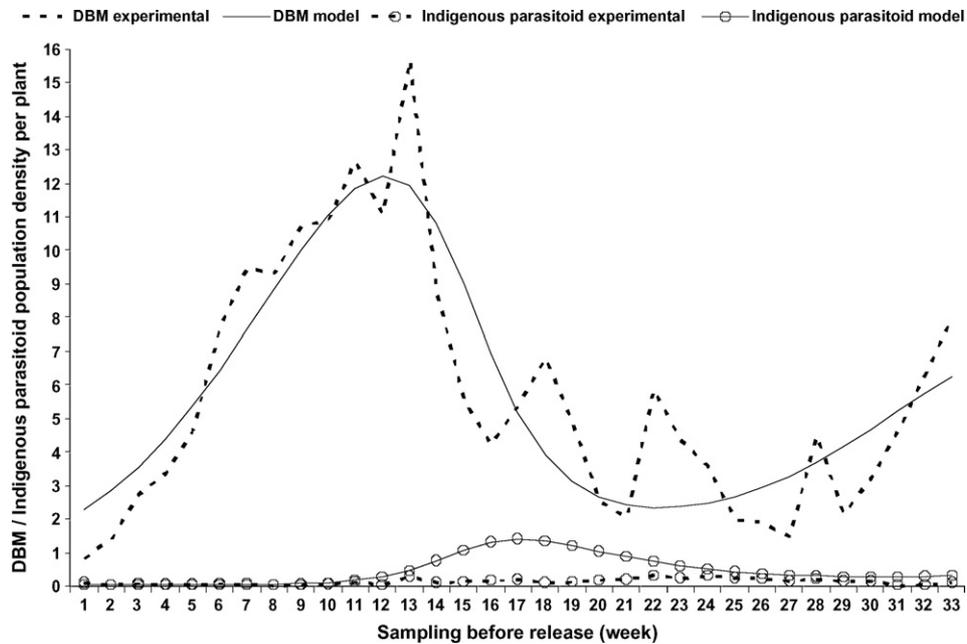


Fig. 1 – Empirical population trajectories of diamondback moth and its indigenous parasitoids and predictions of the Lotka–Volterra model. Predictions are based on data collected before the first release of the exotic parasitoid. Werugha, Wundanyi Division, Taita Taveta District, Coast Province of Kenya.

and reached the second minimum of 4.0 DBM/plant where the curve recommenced increasing (Fig. 4). The indigenous parasitoids population density fluctuation also displayed an oscillating trajectory but with small amplitude compared to the DBM curve. The curve began with 1.58 indigenous parasitoids/plant declined at a decreasing rate until 0.15 where the growth commences at decreasing rate. The curve reaches the peak at 1.03 indigenous parasitoids/plant then declined again (Figs. 4 and 5).

The behaviour of function Q on the plane (α_1, β_1) and the boundaries of confidence domains $\Omega_k, k = 1, 2, 3$ for 1, 5 and 10% confidence levels are illustrated in Fig. 6. \bar{P} is the bifurcation line determined by: $\beta_1 = 0.16\alpha_1$.

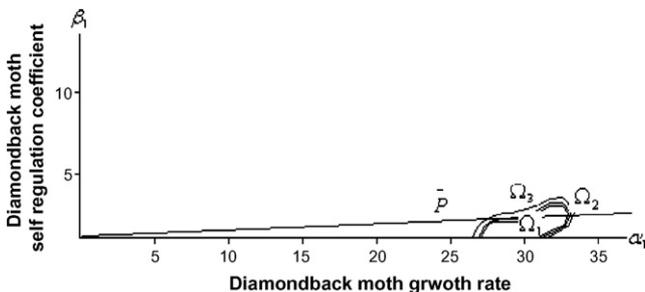


Fig. 2 – Boundaries of confidence domains for estimated parameters of the Lotka–Volterra model at fixed initial population values of the diamondback moth (x_0) and its indigenous parasitoids (y_0). Werugha, Wundanyi Division, Taita Taveta District, Coast Province of Kenya. Ω_1 is the boundary for 10% 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.

3.4. Tharuni after release¹

The predicted population curve 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 (Fig. 6). Model predictions for *D. semiclausum* 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 (Fig. 6).

3.5. Tharuni after release²

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 (Fig. 7). For *D. semiclausum* numbers the Lotka–Volterra model predictions is an oscillation with low amplitudes (Fig. 7).

3.6. Comparison between Tharuni after release¹ and Tharuni after release²

Table 1 shows that the Tharuni after release¹ data set yielded in most cases higher model parameter values than Tharuni after release². In addition, the value of the loss function (Q_{min}) for Tharuni after release¹ was substantially bigger than the value obtained from Tharuni before release and after release². 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

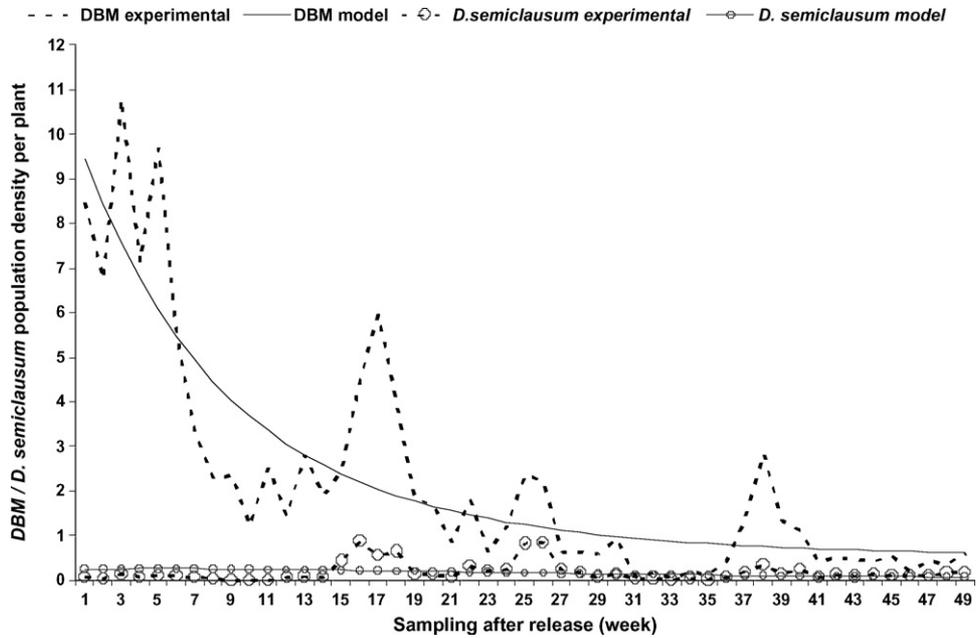


Fig. 3 – Empirical population trajectories of the diamondback moth and its exotic parasitoid, *Diadegma semiclausum*, and predictions of the Lotka–Volterra model. Predictions are based on data collected after the first release of the exotic parasitoid. Werugha, Wundanyi Division, Taita Taveta District, Coast Province of Kenya.

release. Our loss function been made of the square difference between the number of these two insects and the theoretical results, we expect to obtain lower value of Q_{min} after the release. As we intend to measure the impact of *D. semiclausum*, in the following discussion while mentioning the post-release period in Tharuni, we basically refer to Tharuni after release²

3.7. Outcome of model population size predictions

Fig. 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

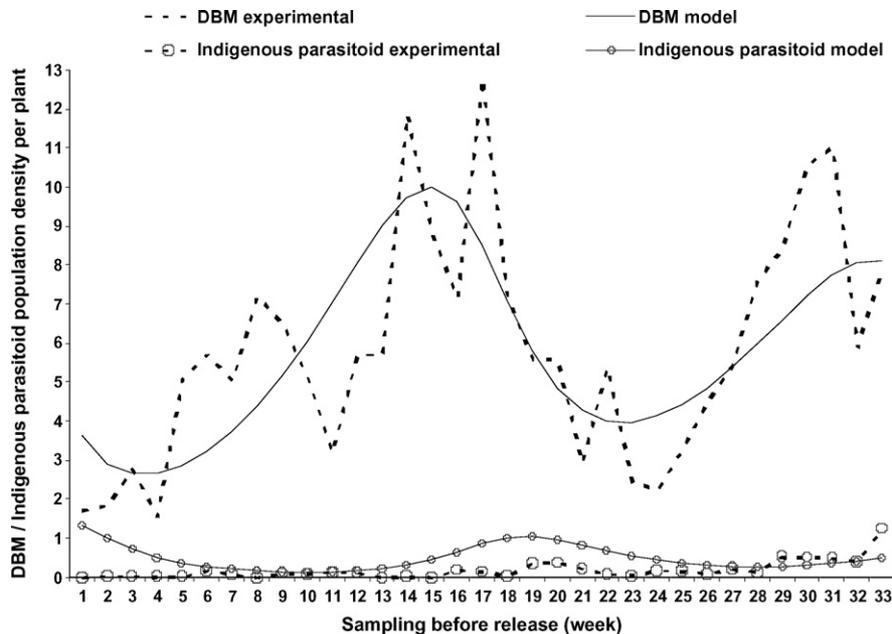


Fig. 4 – Empirical population trajectories of diamondback moth and indigenous parasitoids and predictions of the Lotka–Volterra model. Predictions are based on data collected before the first release of the exotic parasitoid. Tharuni, Limuru Division, Kaimbu District, Central Province of Kenya.

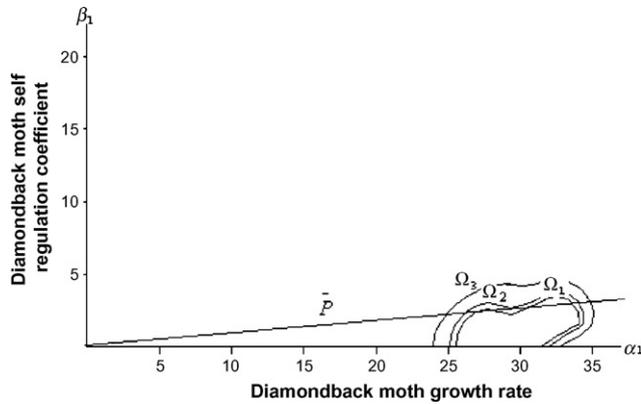


Fig. 5 – Boundaries of confidence domains for estimated parameters of the Lotka–Volterra model at fixed initial values of diamondback moth (x_0) and indigenous parasitoid (y_0) population. Tharuni, Limuru Division, Kiambu District, Central Province of Kenya. Ω_1 is the boundary for 10% confidence level, Ω_2 for 5% confidence level and Ω_3 – for 1%, respectively. \bar{P} : $\beta_1 = 0.21\alpha_1$ is the bifurcation line.

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 curve slowly reduced when approaching 28 DBM/plant. Considering the maximum number of *D. semiclausum*/plant equal to 1.38, we obtained similar curve behaviour to the previous with reduction earlier rate on the DBM population size after 2 weeks and an earlier decrease, which started increase near 28 DBM/plant. Fig. 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.

4. Discussion

We applied a standard methodology for model parameter restoration. The model used is made up 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.

The Lotka–Volterra model has played and continues to play a fundamental role in the mathematical modelling of various biological systems. On the finding of optimal two species harvesting policy, Mesterton-Gibbons (1996) applied the Lotka–Volterra model and came to the conclusion that even if two species would coexist in the absence of harvesting, one species may be driven to extinction by optimal policy if it is sufficiently more catchable than the other. Piana et al. (2006) fitted the Lotka–Volterra predation model and some of its modifications to a time-series datasets for fish assemblage collected from an isolated lagoon of the upper Parana River

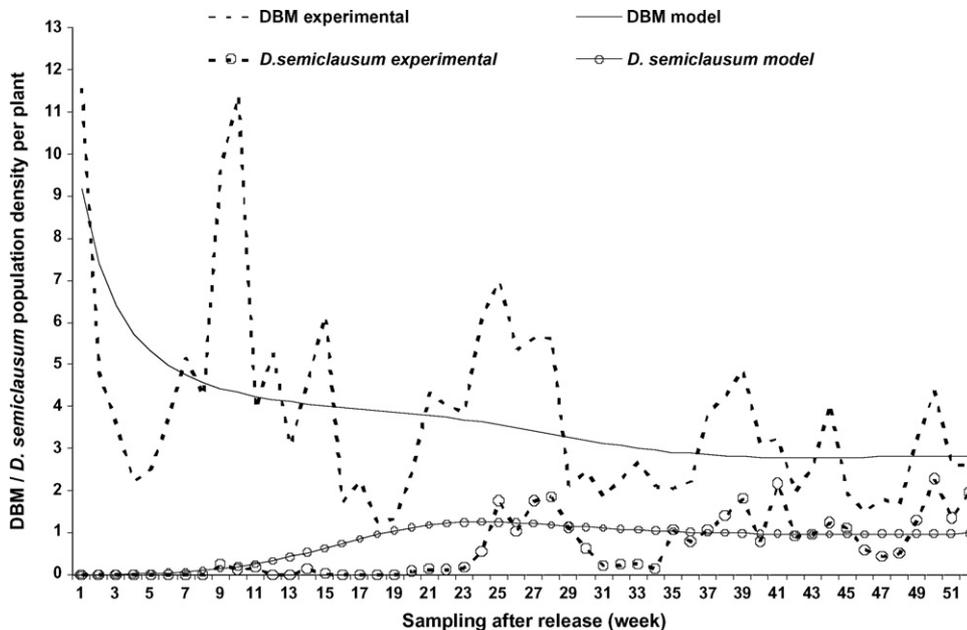


Fig. 6 – Empirical population trajectories of the diamondback moth and its exotic parasitoid, *Diadegma semiclausum*, and predictions of the Lotka–Volterra model. Predictions are based on data collected after the first release of the exotic parasitoid without exclusion of the initial period where no *Diadegma semiclausum* were recovered. Tharuni, Limuru Division, Kaimbu District, Central Province of Kenya.

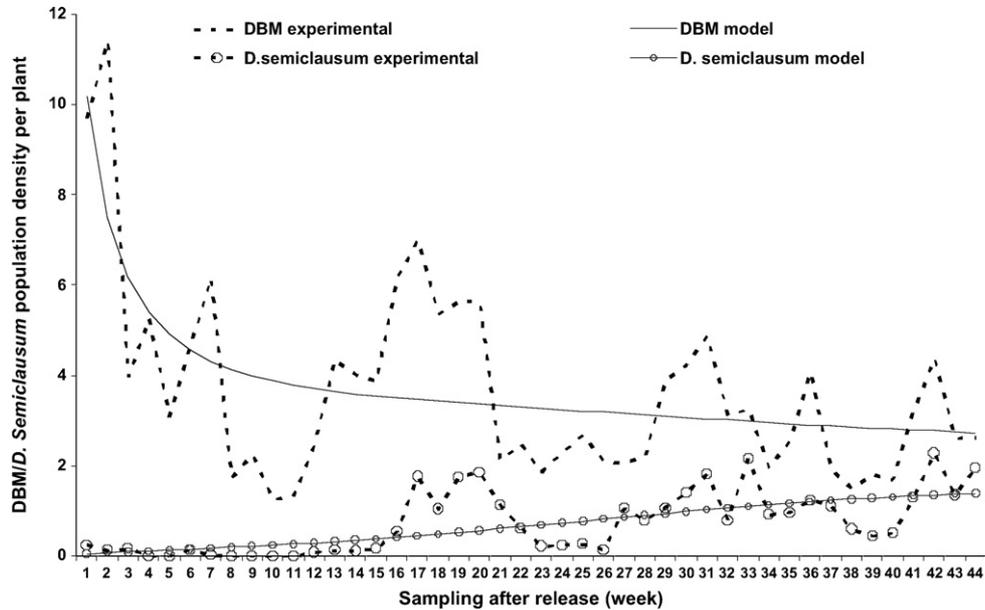


Fig. 7 – Empirical population trajectories of the diamondback moth and its exotic parasitoid, *Diadegma semiclausum*, and predictions of the Lotka–Volterra model. Predictions are based on data collected after the first release of the exotic parasitoid excluding the initial period where no *Diadegma semiclausum* were recovered. Tharuni, Limuru Division, Kiambu District, Central Province of Kenya.

floodplain. In their study, all prey species were grouped as prey and the same was done to predators. We applied a similar assumption by grouping all parasitoids found in the field before release as “indigenous parasitoid.” Results from this study allowed the authors to make some suggestions about the predator–prey relationship when applied to the environment studied such as: predators were efficient in controlling prey population and refuge did not present intense interference in the predator–prey relationship. These conclusions motivated our choice of the Lotka–Volterra model and

justify our use of model without the introduction of a refuge parameter.

The literature presented several model applications in biological control. Analysis of cassava pest biological control in Africa was done with the help of mathematical model (Gutierrez et al., 1988). The model provides a reasonable base for examining the effects of pests on plant yield and natural enemies on cassava pests. Buffoni and Gilioli (2003) developed a lumped parameter model for acarine predator–prey population interactions. In this work, the methodology was

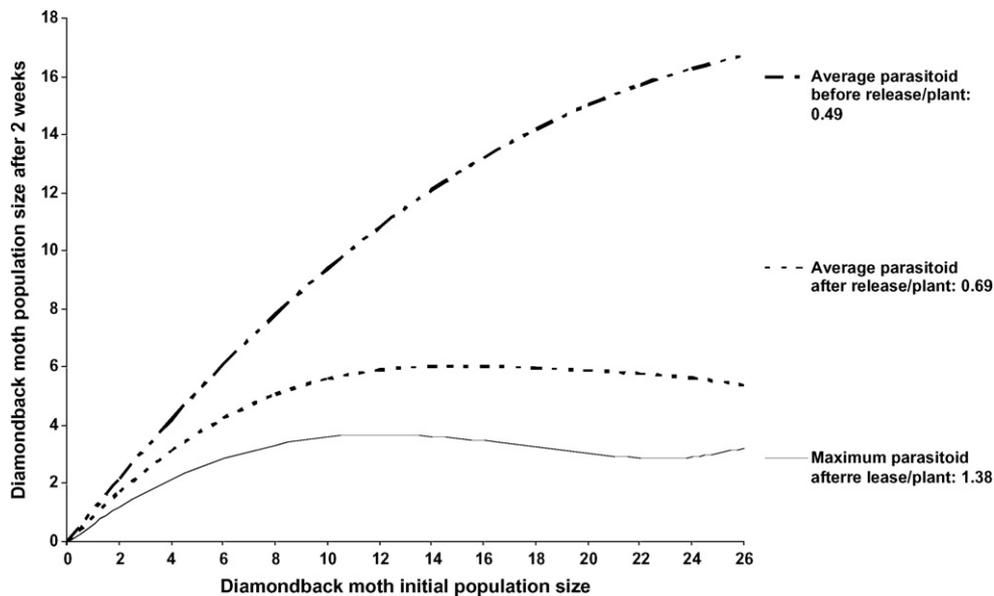


Fig. 8 – Model predictions for changes in diamondback moth population size at fixed initial values of parasitoids population, Tharuni, Limuru Division, Kiambu District, Central Province of Kenya.

numerically simulated and results were compared to a case study of the mite *Tetranychus urticae* Koch and its biological control agent, the predatory mite *Phytoseiulus persimilis* Athias Henriot. They were exploring the influence of the release strategies on the success of the biological experiment. However in the present study, we have fitted and make use of the model to confirm the already executed biological control experiment. Using simple models for host–parasitoid interactions, May and Hassel (1988) presented a basic framework for examining the outcome of releasing natural enemies against a target pest population in classical biological control programme. These authors particularly examined the conditions for the initial invasion and establishment of a natural enemy species, for maximum depression of the host population, and for the persistence of the populations in stable interaction. The main part of their discussion focused on host–parasitoid interactions with discrete, synchronized generations which correspond well for insects in temperate zone situations where seasonality often synchronizes the populations and provides a natural interval between the appearances of successive generations. Such models, however, did not seem appropriate (except special considerations were made) to the host–parasitoid interactions in our tropical climate condition, where the hosts and parasitoids life cycles may be of quite different lengths and where one would expect continuous generations with all stages present at the same time.

In insect population, a deterministic description of phenomena is often difficult that an empirical equation 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 datasets. Obtaining good fit does not necessarily imply that the chosen equations could clearly explain the type of interaction between the chosen insects and better predict their population densities. 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 depends on 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 °C and 28.9 °C, respectively for the Thailand DBM strain. In both pilot areas, temperature fluctuated between 13 °C and 35 °C, the model predicted growth rate is very high compared to these values and the value obtained at Werugha differs from what was obtained in Tharuni. The discrepancy could be explained by the climatic differences in particular higher temperature and lower rainfall in 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 introduced parasitoid in Tharuni.

The correct 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 defines their own time and space scale on what

makes 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 may influence the demography of the insects.

The model predicted higher value of self-regulation coefficient for DBM in Werugha than in Tharuni, this is explained by the favourable environmental conditions for proper DBM development in the first area rather than the latter. In order words, low rainfall in Tharuni led 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 the 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 was 0.02 for Werugha before release, this increased 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 3 years after release respectively).

Based on the mechanism of self-regulation in insect population (Nicholson, 1958), the following analysis could be made as tentative explanation of the DBM and *D. semiclausum* population fluctuations. 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 automatic increase faces 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 change in values of these coefficients after the release demonstrated a difference in interactions between DBM/indigenous parasitoid and DBM/*D. semiclausum*. 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 (Roszbach 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 the 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. From these results, we concluded that the model was properly fitted to field datasets, this was justified by the model ability in confirming the positive impact caused by the newly introduced species in reducing pest (DBM) population density as shown by the empirical datasets. The Lotka–Volterra model provided a quantitative estimate of the effectiveness of the newly introduced species and could therefore be used as a tool for decision making in the implementation for strategies in pest management system in the region.

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