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Evaluation of continuous host-parasitoid models

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In this paper the performance of continuous host-parasitoid models were investigated. The parameter values for several well-known models: Lotka-volterra, Holling Tanner Type 2, Holling Tanner Type 3, Leslie, Bazykin, Beddington-DeAngelis, Yodzis and Rosenzwing-Macarthur models were estimated. The models were tested on 40 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 loss functions between the theoretical and experimental time series datasets following the Nelder-Mead multidimensional method. Initial values of population size and parameters were randomly chosen. Durbin-Watson statistic was applied for comparison of model outputs and experimental population trajectories. Among the eight different host-parasitoid models, Holling Tanner model Type 3 presented relatively better approximations compared to the other models.

Key words: Diamondback moth, population dynamics, model parameters estimation, biological control, parasitoid impact.

INTRODUCTION

Model utilities in ecology

Mathematical models play a central role in elucidating host-parasitoid system interactions. They help to shed some light on mechanisms that underlie these interactions, which may not be directly observable in the field (Gertsev and Gertseva, 2004). In theoretical ecology, models are used for several purposes. Models help in exploring possibilities by enabling biologists to become fully aware of potential relations between natural phenomena during variables and parameters tracking exercises (Cooper, 1990). They also offer scientists the means through which they can investigate complex systems. Models provide researchers with conceptual framework, which help ecologists carrying out experimental investigations and pose questions which can lead to the construction of concepts corresponding to various natural properties that were not striking.

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

(i) Strategic models,
(ii) Tactical models.

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

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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).

Host-parasitoid systems

Host-parasitoid system is an ecological interaction between victim (host) and exploiter (parasitoid) where the second species consume biomass from the first species (McCallum, 2000). Adult female parasitoids forage actively for hosts and oviposit in or near host individuals. After hatching, the larvae begin feeding on host tissues and complete their development either within or on host. Parasitoids are abundant in almost all terrestrial ecosystems and have been identified as one of the main causes of mortality of their hosts (Godfray, 1994).

A number of mathematical model equations will be evaluated in a view of describing the population dynamics of Diamondback Moth (DBM) and its parasitoid. The main focus of population dynamics studies has traditionally been on local stability analysis, searching studies for 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; Hassell et al., 1976; May et al., 1981; Meng et al., 2007). In this paper, it is intended to evaluate a good number of host-parasitoid models by comparing their predictive parameters with empirical time series datasets collected from the field. Eight well-known continuous mathematical models of predator-prey or host-parasitoid will be considered. These include:

(i) Lotka-Volterra (1926), (ii) Holling Tanner Type 2 and Type 3 (1959), (iii) Leslie (1945), (iv) Rosenzweig-MacArthur (1963), (v) Yodzis (1989), (vi) DeAngelis (1975), and (vii) Bazykin (1985).

DATA DESCRIPTION AND DATA COLLECTION

The data used 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. This region was selected because of its isolated location. Werugha is located on an island mountain, Taita hills, rising from an area of about 700 m elevation to 2200 m. The height of the mountain is about 10 km ×25 km high and stretches roughly in a north/south direction. Crucifer production is concentrated between 1600 m to 1800 m elevations. Additional irrigation during the dry seasons is common using bucket to draw water from shallow wells. Much of the land is terraced and crucifer production moves up on the terraces during the rainy seasons down to the valley bottom in dry seasons, ensuring year - round production. The major staple crop is maize and several species of crucifers are grown with head cabbage (*Brassica oleracea var. capitata*) as the main cash crop. Soils are mostly degraded, low in organic matter and sandy (Momanyi et al., 2006).

Data were collected by the International Centre of Insect Physiology and Ecology (ICIPE) (DBM) biological control team in Kenya. Fifteen farmer- managed cabbage farms were sampled at two-week intervals starting from two weeks after transplanting until harvest. When one field is harvested, a recently transplanted field in the immediate vicinity was chosen as its replacement. In each field, 10 plants were selected at random and a population census for larvae (1st, 2nd, 3rd, and 4th instars), pupae and adults were collected. Third and 4th instars larvae and pupae were transferred to the laboratory and observed for adult moth and parasitoid emergence. The percentage parasitism was estimated for collection and then multiplied by the total DBM population from by number of each field. This was divided by sampled plants to estimate the number of parasitoid per plant. The total number of DBM adults was also divided by number of plants to establish its population density per plant. Likewise, the total number of DBM was divided by number of plants to establish its population density per plant.

MODELS EVALUATED

Table 1 summarizes the models that were evaluated. Each model under consideration 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.

A recent publication of Deng (2008) has shown that most discrete equations used to model population dynamics in ecology are inherently pathological. For this reason, their predictions cannot be independently verified by experiments because they violet a fundamental principal of physics, which stipulates that a physical law should be the same anywhere and any time in the universe. Biological process is seen as time-invariant, which conform and allow time-independent observations that can be verified at any given state. Thus, a law must take the same mathematical form derivable from experiments carried out at independently chosen times and spaces. As a result, any mathematical formulation of a law must be endowed with such time-invariant characteristic. Accordingly, Deng suggested that continuous dynamical systems must be modelled by differential equations. In that regard, our study is in support of such an approach to make ecological modelling.

Eight well-known continuous mathematical models of predator-prey or host-parasitoid will be considered. In each case, appropriate statistical analysis is employed for the purpose of assessing model's efficiency. The models which are considered are summarised in Table 1.

Assumptions

The following assumptions were made:

(a) The two species have overlapping generations, which normally allows the use of continuous rather than discrete time differential equations.
(b) The prey or host grows unboundedly in a Malthusian way in the absence of predation and self-regulation.
(c) The effect of the predation is to reduce the prey's per capita growth rate by the term proportional to the prey and predator populations.
(d) In the absence of any prey for sustenance, the predator's death rate results in exponential asymptotical decay.
(d) The prey's contribution to predator growth rate is proportional to the prey population.

Table 1. Mathematical expressions of different models under consideration.

Author	Model	Notations and parameters
		$N(t)$ is the diamondback moth (DBM) population size at time t
		$P(t)$ is the parasitoid population size at time t
Lotka-Volterra (1926)	$$\frac{dN}{dt} = \alpha_1 N - \beta_1 N^2 - \gamma_1 NP$$ $$\frac{dP}{dt} = -\alpha_2 P - \beta_2 P^2 + \gamma_2 NP$$	α_1 is the growth rate or Malthusian parameter for the DBM populations
		α_2 is the intensity of natural death of individuals in the parasitoid populations
		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 populations
Holling Tanner Type 2 (1959)	$$\frac{dN}{dt} = \alpha_1 N - \beta_1 N^2 - \frac{\gamma_2 NP}{1 + \delta N}$$ $$\frac{dP}{dt} = \alpha_2 P - \beta_2 P^2 + \frac{\gamma_2 NP}{1 + \delta N}$$	δ is constant representing the sigmoidality of the function
Holling Tanner Type 3 (1959)	$$\frac{dN}{dt} = \alpha_1 N - \beta_1 N^2 - \frac{\gamma_1 N^2 P}{1 + \delta N^2}$$ $$\frac{dP}{dt} = \alpha_2 P - \beta_2 P^2 + \frac{\gamma_2 N^2 P}{1 + \delta N^2}$$	
Leslie (1945)	$$\frac{dN}{dt} = \alpha_1 N - \beta_1 N^2 - \gamma_1 NP$$ $$\frac{dP}{dt} = P\left(k - \frac{\gamma_1 P}{N} \right)$$	
Rosenzweig-MacArthur (1963)	$$\frac{dN}{dt} = rN\left(1 - \frac{N}{k}\right) - \frac{cNP}{d + N}$$ $$\frac{dP}{dt} = \mu \frac{cNP}{d + N} - \delta_0 P$$	r is the per capital growth rate of DBM, c is the maximum killing rate, d is the half-saturation constant (prey density at which the killing rate is half of the maximum), μ is the conversion rate of consumed prey, δ_0 is the per capital rate of consumption
Yodzis (1989)	$$\frac{dN}{dt} = rN(1 - \frac{N}{k}) - \frac{cN^2}{h^2 + N^2} P$$ $$\frac{dP}{dt} = \mu \frac{cN^2 P}{d^2 + N^2} - \delta_0 P$$	h is the handling time

Table 1. Contd.

Beddington-DeAngelis (1975)	$$\frac{dN}{dt} = rN\left(1 - \frac{N}{k}\right) - \frac{cNP}{d + bP + N}$$ $$\frac{dP}{dt} = \mu\frac{cNP}{d + bP + N} - \delta_0 P$$	b is the parasitoid or predator searching rate
Bazykin (1985)	$$\frac{dN}{dt} = rN\left(1 - \frac{N}{k}\right) - \frac{cNP}{d + N}$$ $$\frac{dP}{dt} = \mu\frac{cNP}{d + N} - \delta_0 P - \delta_1 P^2$$	δ_1 is the self-limitation

(e) Other potential sources of mortality like fungi which could have made some contribution to host population trajectory were not included.

Statistical criteria for parameters estimation

Model-based parameters can be derived either on the basis of laboratory data on fecundity, survivorship, etc., in which case the parameters have concrete numerical values, or by numerical calculation through minimization of the following Loss functions made of the squared difference between the theoretical and empirical values of dataset:

Loss function 1:

$$F = \sum_{i=1}^{n}\left[\left(H_{\exp i} - H_{theoi}\right)^2 + \sum_{i=1}^{n}\left(P_{\exp i} - P_{theoi}\right)^2\right]$$

Loss function 2:

$$F = \sum_{i=1}^{n}\left[\frac{\left(H_{\exp i} - H_{theoi}\right)^2}{H_{\exp i}} + \frac{\left(P_{\exp i} - P_{theoi}\right)^2}{P_{\exp i}}\right]$$

Loss function 3:

$$F = \sum_{i=1}^{n}\left[w_h\left(H_{\exp i} - H_{theoi}\right)\right]^2 + \left[w_p\left(P_{\exp i} - P_{theoi}\right)\right]^2$$

where,

$n =$ the sample size,

$H_{\exp i} =$ the experimental density of host,

$H_{theoi} =$ the theoretical density of host,

$P_{\exp i} =$ the experimental density of parasitoid,

$P_{theoi} =$ the theoretical density of parasitoid,

$W_p =$ the ratios of standard deviations of parasitoid,

$W_h =$ the ratios of standard deviations of host group.

The calculations are carried out with a computer program written in C/C++ programming language. In this program, model equations were solved in a routine using the Runge-Kutta 4th order algorithm with step size of 0.01. This routine was combined as a unique function and embedded in a Nelder-Mead algorithm for minimization with randomly chosen initial values of parameters (Press, 1992; Gurson, 1999).

Durbin-Watson statistic

The Durbin-Watson statistic is given by

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

Where

$n =$ the sample size and

$e_i =$ the residual value at point i.

The Durbin-Watson statistic, which is used as sensitivity analysis of the serial correlation, was applied on the discrepancy between theoretical data and experimental data. The Durbin -Watson statistics d usually range from 0 to 4. A value near 2 indicates no-autocorrelation whereby a value toward 0 indicates positive autocorrelation, and that towards 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's validity. The case of

Table 2. Estimate of model parameters by Nelder-Mead method with Loss function 1.

Parameter	Lotka	HollTy2	HollTy3	Leslie	Rose	Yodzis	DeA	Bazykin
N	2.71	7.090	2.973	3.479	10.119	2.028	8.271	7.248
P	0.0	0.023	0.145	0.021	1.386	3.657	1.133	0.163
α_1	0.036	0.006	0.476	0.020	-	-	-	-
α_2	0.028	0.555	0.061	-	-	-	-	-
β_1	0.08	0.066	0.029	0.013	-	-	-	-
β_2	0.04	0.076	0.042	-	-	-	-	-
γ_1	0.320	0.005	0.032	0.009	-	-	-	-
γ_2	0.014	0.016	0.013	-	-	-	-	-
κ	-	-	-	0.310	0.408	0.503	0.333	0.592
r	-	-	-	-	0.057	0.161	0.047	0.237
μ	-	-	-	-	0.016	0.224	0.013	0.054
c	-	-	-	-	0.008	0.371	0.007	0.029
d	-	-	-	-	0.024	0.037	0.020	0.067
δ_0	-	-	-	-	0.008	0.037	0.007	-
δ_1	-	-	-	-	-	-	-	0.039
b	-	-	-	-	-	-	0.013	-
h	-	-	-	-	-	0.017	-	-
δ	-	0.066	0.055	-	-	-	-	-
FLI	155.598	167.090	146.234	450.596	2485.346	1173.989	4543.766	632.195
dD	0.292	0.256	0.463	0.354	0.293	0.185	0.255	0.235
dP	0.515	0.115	0.457	0.545	0.021	0.001	0.009	0.041

Where: HollTy2 = The Holling Tanner Model Type 2, HollTy3 = the Holling Tanner Model Type 3, Rose = the Rosenzweig Mac-Arthur Model, DeA = the DeAngelis Model, dD = DBM Durbin-Watson criterion value, dP = Parasitoid Durbin-Watson criterion value, FL1 = loss function one values, FL2 = Loss function two values, FL3 = Loss function three values.

no-autocorrelation indicates independence among residuals, and assertion can then be made that a close fit between a model output and empirical data exists. The computed d statistic is then compared to a critical value from the Durbin-Watson significance table (Savin and White, 1978). The Durbin -Watson d is conducted at 5% level of significance.

RESULTS

The results obtained using Durbin-Watson statistics are as summarized in Tables 2 to 4 depending on the model.

Model population size predictions at different initial DBM population sizes

The model functional responses in Tables 1 to 4 were used to develop graphs which allow predictions of future DBM population sizes as a function of a constant number of parasitoids. The DBM data in Tables 1 to 4 were plotted on the plane at fixed values of parasitoid/plant.

DISCUSSION

Among the eight different host-parasitoid models, Holling Tanner model Type 3 presented relatively better approximations compared to other models. The model with Holling Tanner model Type 3 functional responses is used to develop a graph that allows predictions of future DBM population size as a function of 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. The trajectories show that the DBM population size at 2weeks intervals

Table 3. Estimate of model parameters by Nelder-Mead method with loss function 2.

Parameter	Lotka	HollTy2	HollTy3	Leslie	Rose	Yodzis	DeA	Bazykin
N	1.81	7.215	3.552	4.367	10.255	2.094	8.162	3.210
P	0.07	0.024	0.174	0.081	1.405	3.777	1.119	0.072
α_1	0.023	0.006	0.569	0.694	-	-	-	-
α_2	0.648	0.565	0.073	-	-	-	-	-
β_1	0.08	0.067	0.035	0.043	-	-	-	-
β_2	0.034	0.078	0.049	-	-	-	-	-
γ_1	1.40	0.005	0.038	0.047	-	-	-	-
γ_2	0.015	0.057	0.016	-	-	-	-	
k	-	-	-	0.019	0.413	0.520	0.328	0.262
r	-	-	-	-	0.058	0.166	0.046	0.105
μ	-	-	-	-	0.017	0.231	0.013	0.024
c	-	-	-	-	0.008	0.383	0.007	0.013
d	-	-	-	-	0.025	0.033	0.020	0029
δ_0	-	-	-	-	0.008	0.038	0.007	0.029
δ_1	-	-	-	-	-	-	-	0.017
b	-	-	-	-	-	-	0.013	-
h	-	-	-	-	-	0.018	-	-
δ		0.024	0.066		-	-	-	-
FL2	78.41	53.108	1199.578	18581.787	35168.520	13676.174	61342.60	4888.981
dD	0.521	0.263	0.417	0.064	0.297	0.174	0.253	0.199
dP	0.469	0.386	0.631	0.736	0.020	0.019	0.009	0.045

kept increasing, but the rate of increase declined with an increase in parasitoid number. This demonstrates the efficiency of parasitoid in reducing the DBM population size. The models which were considered could not all offer perfect prediction for the trajectories of the collected data. This just demonstrates the reality that exists in choosing a mathematical model to describe a particular population dynamics. 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-up of the existing models starting from the simplest or create a new model to describe the population.

The Durbin-Watson criteria applied to the deviation between theoretical and empirical data yielded results for each model as shown in Tables 2 to 4 in both models. The gap between the calculated Durbin-Watson value (dD) and (dP) (Tables 2 to 4) shows that there is an existence of positive or negative correlations of residuals between empirical and theoretical datasets. Several reasons may account for the existence of positive or negative correlations (inadequacy) of the models. For example, the fitting procedure typically tries to maximize fits at a very short or very long time scales.

However, intermediate scales that may better reflect parameter predictions are not selected during the process. Also, the algorithm for the set of parameters that fit the model well may introduce some noise to the model time series.

Moreover, these models were evaluated with time series obtained from highly unstable situation after the introduction of parasitoid. In such a condition, the introduced species may have not begun to play a major role on the pest population regulations. In this perspective more complex models, which will take into account time lag reaction of DBM intra self-regulation disease, should be investigated as they may offer better results.

Table 4. Estimate of model parameters by Nelder-Mead method with Loss function 3.

Parameter	Lotka	HollTy2	HollTy3	Leslie	Rose	Yodzis	DeA	Bazykin
N	3.813	3.176	2.184	1.914	10.504	2.532	0.829	5.034
P	1.754	0.011	0.107	0.012	1.439	1.165	0.381	0.113
α_1	0.023	0.003	0.349	0.011	-	-	-	-
α_2	0.648	0.249	0.045	-	-	-	-	-
β_1	0.034	0.030	0.021	0.008	-	-	-	-
β_2	0.023	0.034	0.031	-	-	-	-	-
γ_1	0.015	0.002	0.023	0.005	-	-	-	-
γ_2	0.010	0.025	0.009	-	-	-	-	-
K	-	-		0.017	0.423	0.010	0.003	0.411
r	-	-	-	-	0.059	0.015	0.005	0.164
μ	-	-	-	-	0.017	0.039	0.013	0.038
c	-	-	-	-	0.008	0.007	0.002	0.021
d	-	-	-	-	0.025	0.023	0.141	0.046
δ_0	-	-	-	-	0.008	0.015	0.005	0.046
δ_1	-	-	-	-	-	-	-	0.027
b	-	-	-	-	-	-	0.007	-
h	-	-	-	-	-	0.430	-	-
δ	-	0.066	0.040	-	-	-	-	-
FL3	1.813	4.699	4.662	8.265	2116.489	733.866	88.055	268.632
dD	0.443	0.288	0.415	0.315	0.305	0.189	0.221	0.205
dP	0.369	0.869	0.285	0.500	0.021	0.017	0.002	0.057

Fitting the host parasitoid models with the field data

The data in Tables 1 to 5 were used to draw the graphs as shown in Figures 1 to 16 for the purpose of showing the relationship between the experimental and theoretical.

Conclusions

In this study eight continuous mathematical models were considered for the evaluation of the population dynamics of diamondback moth (DBM) and its parasitoid. The models considered were those authored by; Lotka-Volterra, Holling Tanner Type 2, Holling Tanner Type 3, Leslie, Bazykin, DeAngelis, Yodzis and Rosenzweig-Macarthur models. The results were obtained from a computer program written in C/C++ programming language using the Runge-Kutta 4th algorithm with 0.01 step size. A Loss function was developed, made of the squared difference between the theoretical and empirical values of dataset. This routine was combined as a unique function and embedded in a Nelder-Mead algorithm for minimization with randomly chosen initial values of parameters. The Durbin-Watson statistics was used to determine the correlation between the theoretical and experimental data.

Applying the Durbin-Watson statistics, it was found that, among the eight models, Holling Tanner Type 3 functional response presented better approximations compared to the others.

All in all it would be unrealistic to expect any model to perfectly fit census field data because of the irregularities in nature, since parameter values are expected to vary. It is also generally accepted that field collected time series data are never 100% accurate and may show a deviation of up to 20.
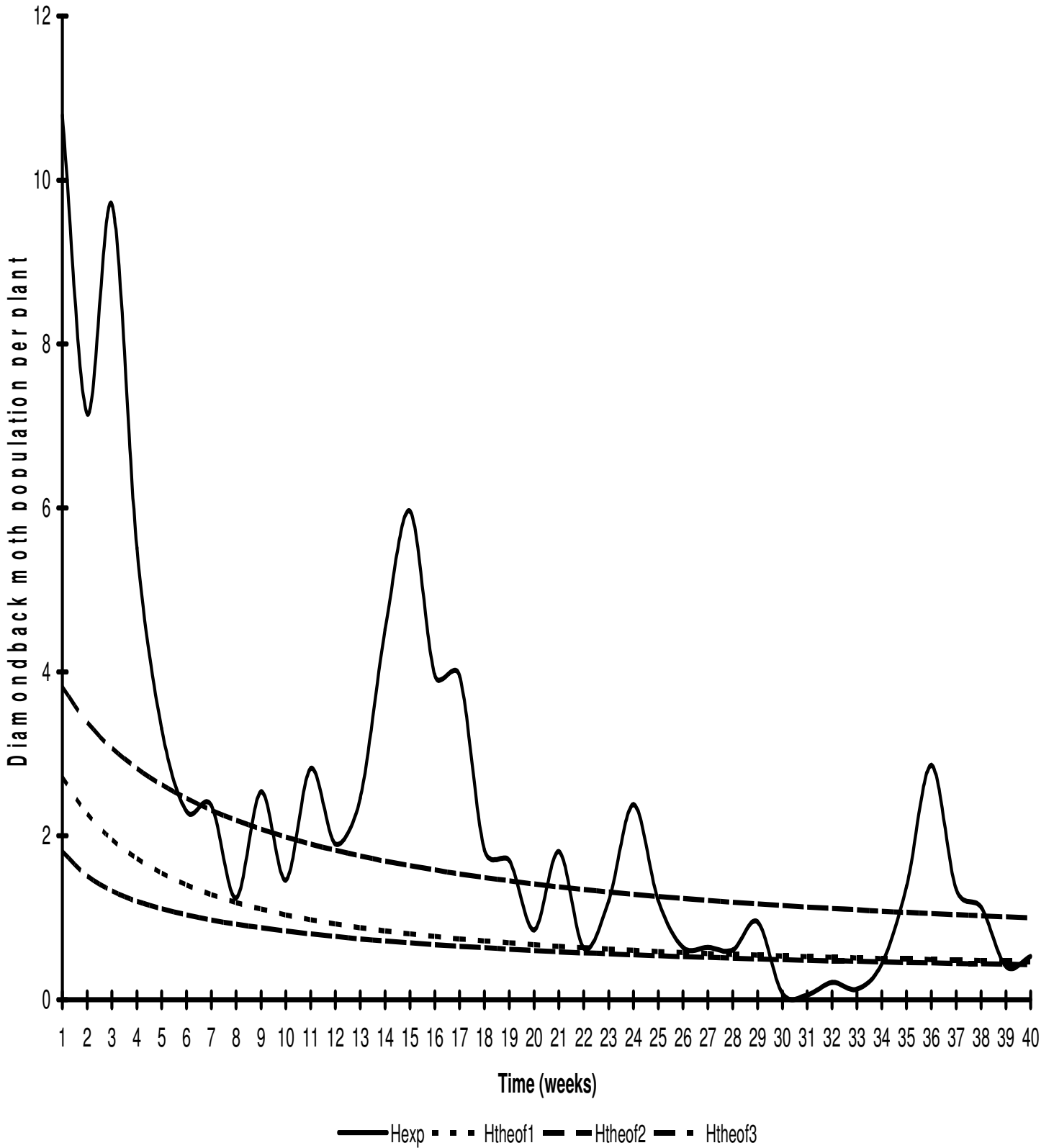
Figure 1. Trajectories of the diamondback moth population for empirical datasets and those predicted by Lotka -Volterra Model using Loss functions 1, 2 and 3.where, Hexp is the Diamondback moth empirical datasets, Htheof1 is the diamondback moth theoretical datasets from models for Loss function 1, Htheof 2 is the Diamondba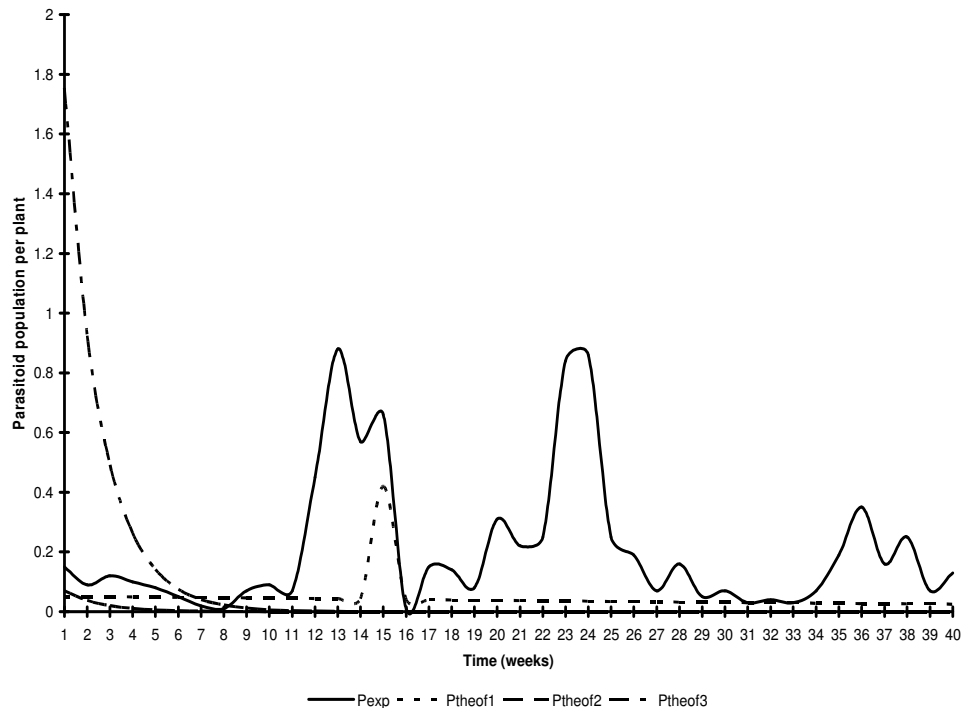ck moth theoretical datasets from models for Loss function 2, Htheof 3 is the Diamondback moth theoretical datasets from models for Loss function 3.

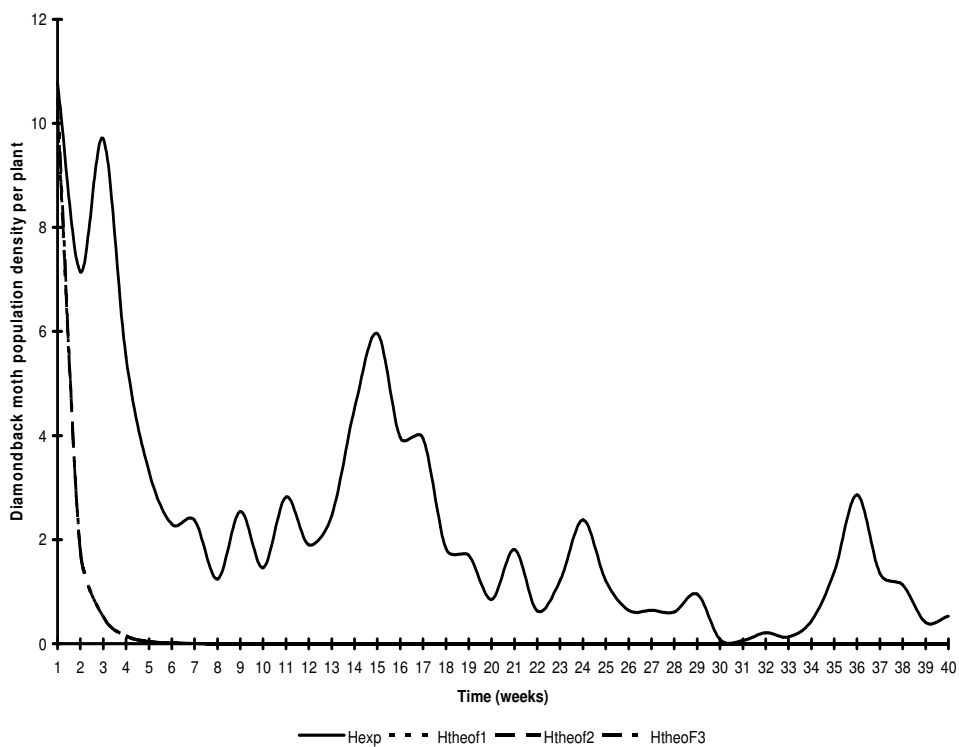**Figure 2.** Trajectories of the parasitoid population for empirical datasets and those predicted by Lotka-Volterra Model using Loss functions 1, 2 and 3. where, Pexp is the Parasitoid empirical datasets,Ptheof1 is the Parasitoid theoretical datasets from models for Loss function 1, Ptheof2 is the Parasitoid theoretical datasets from models for Loss function 2, Ptheof3 is the Parasitoid theoretical datasets from models for Loss function 3.
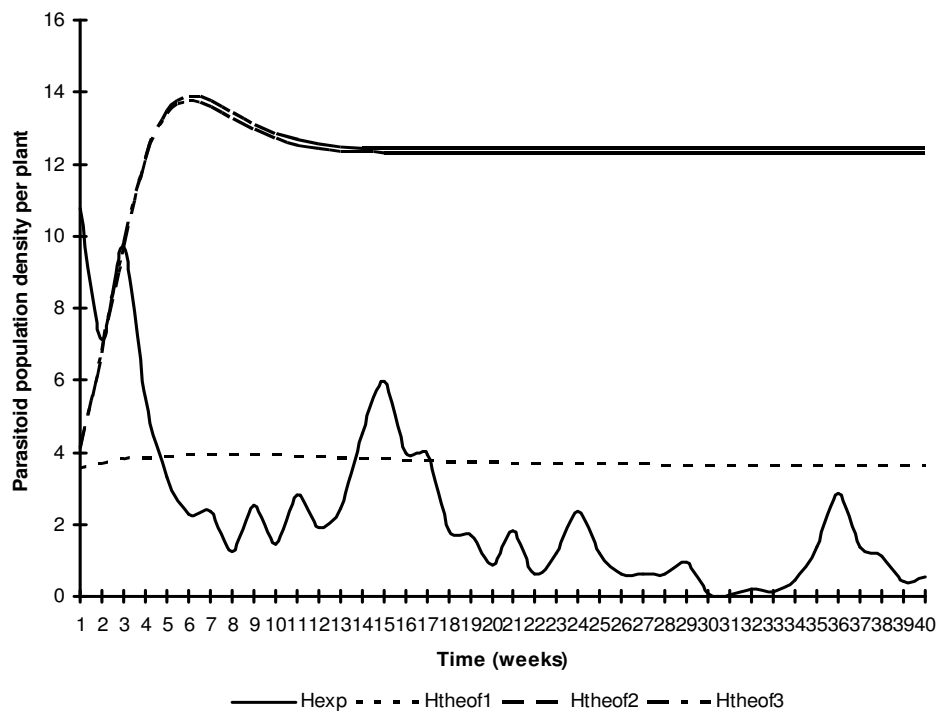
Figure 3. Trajectories of the Diamondback moth population for empirical datasets and those predicted by Holling Tanner Model Type 2 using Loss functions 1, 2 and 3.
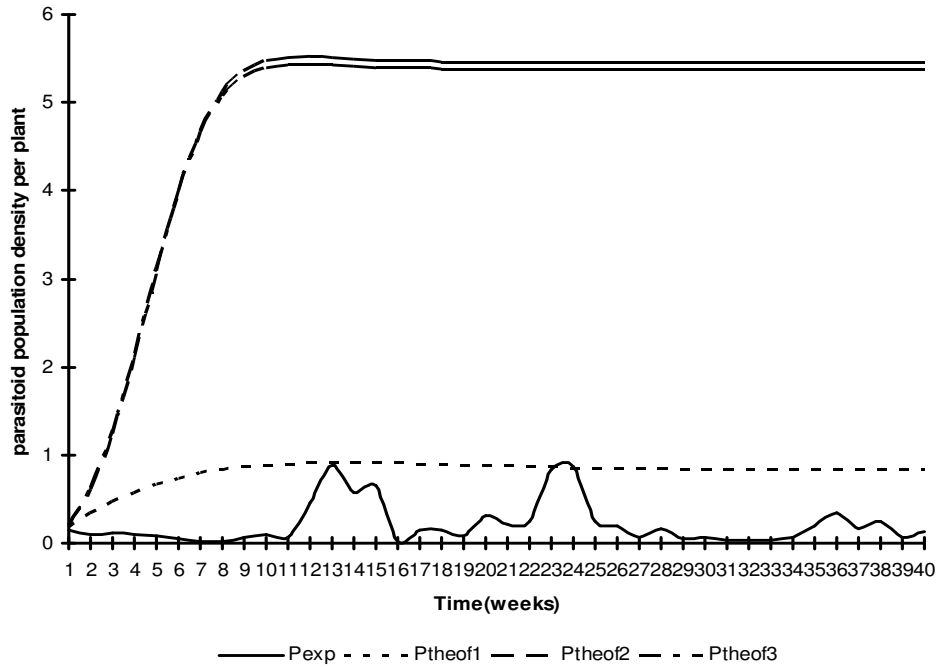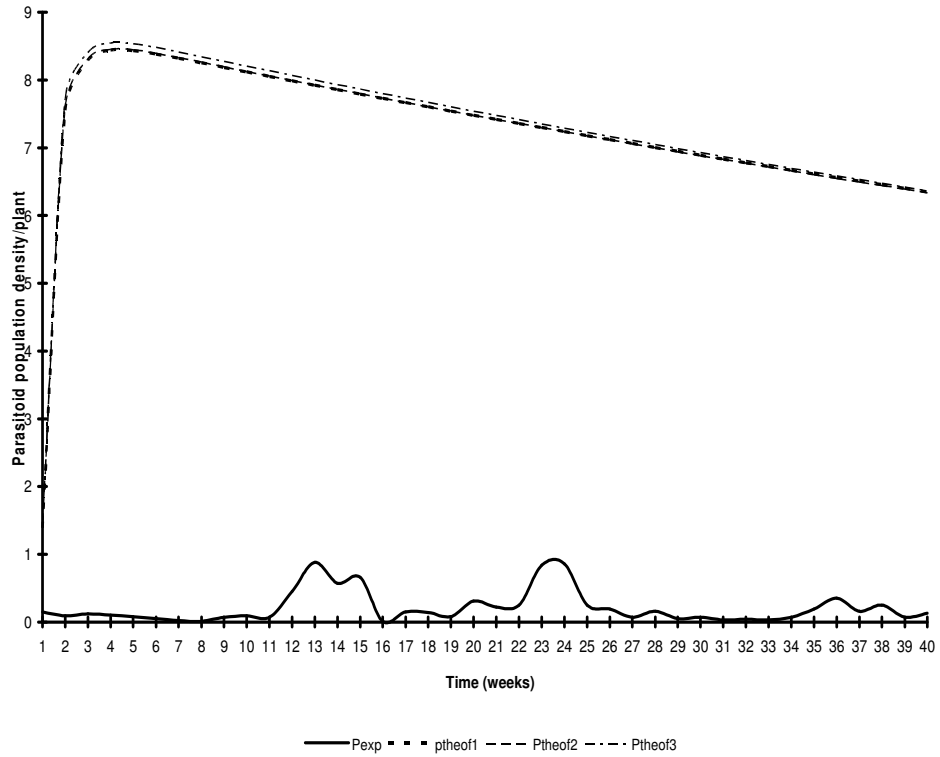
Figure 4. Trajectories of the parasitoid population for empirical datasets and those predicted by Holling Tanner Model Type 2 using Loss functions 1, 2 and 3.
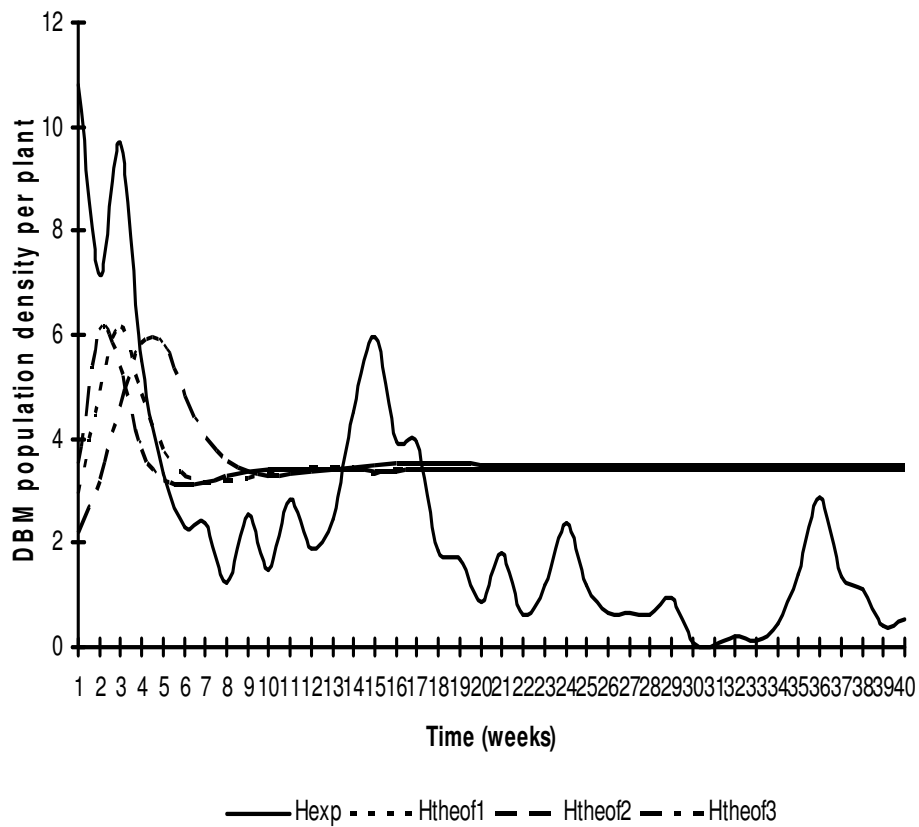
Figure 5. Trajectories of the Diamondback moth population for empirical datasets and those predicted by Holling Tanner Model Type 3 using loss functions 1, 2 and 3.
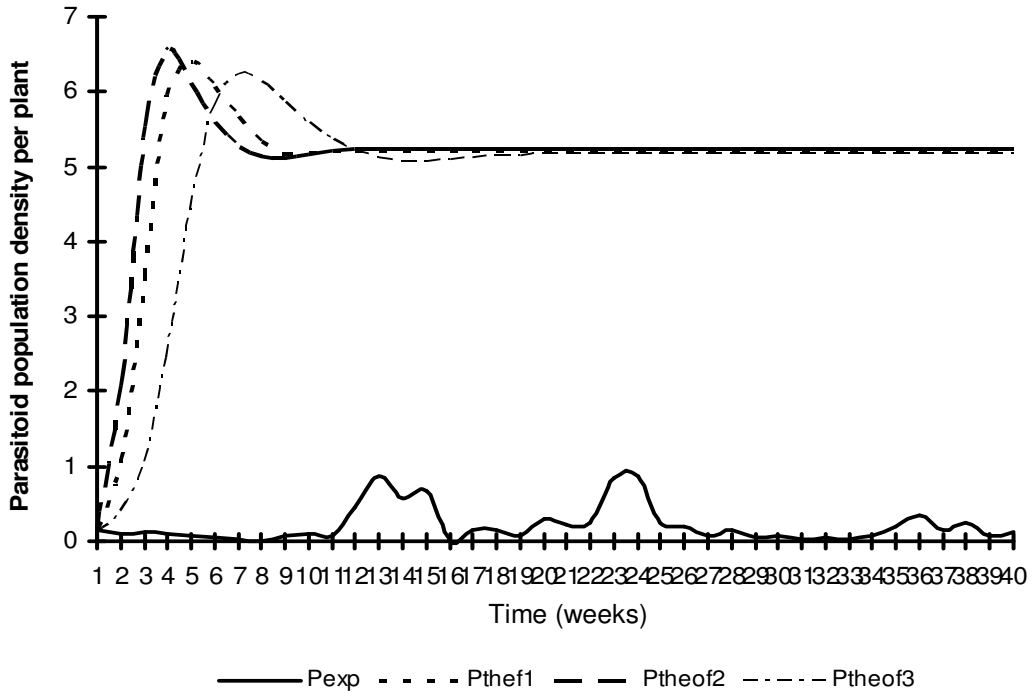
Figure 6. Trajectories of the Parasitoid population for empirical datasets and those predicted by Holling Tanner Model Type 3 using Loss functions 1, 2 and 3.
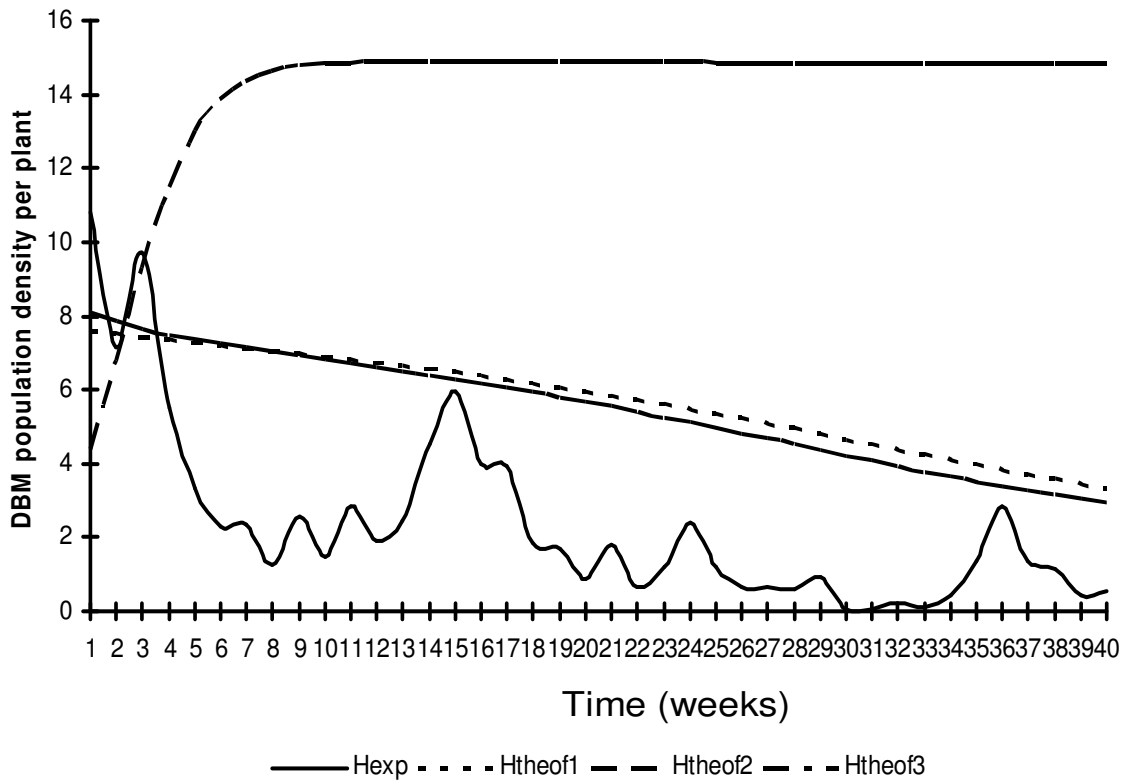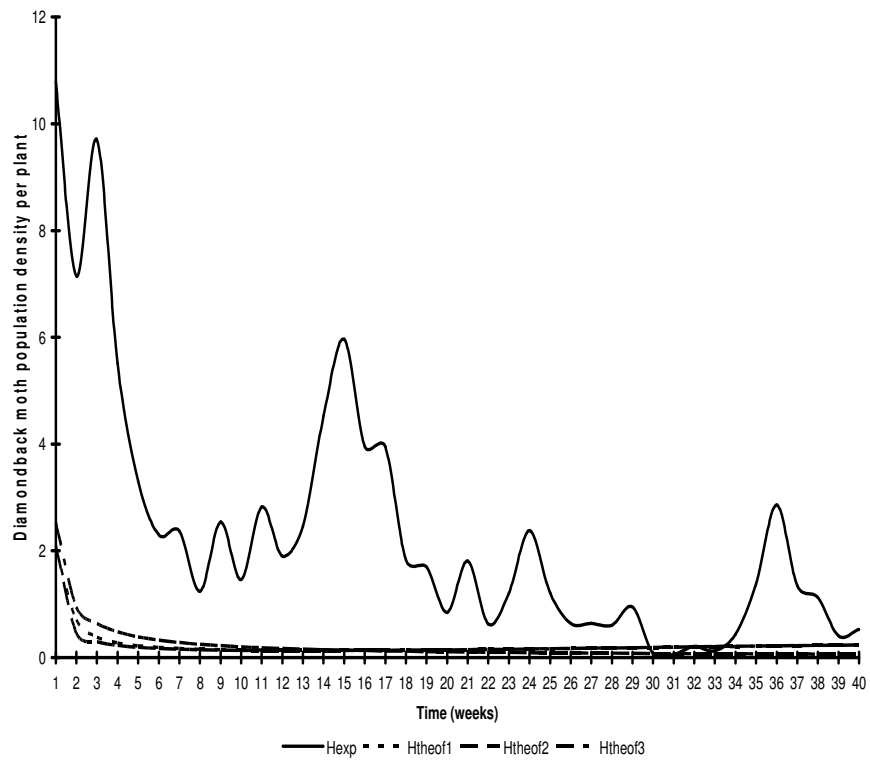

Figure 7. Trajectories of the Diamondback moth population for empirical datasets and those predicted by Leslie Model using Loss functions 1, 2 and 3.
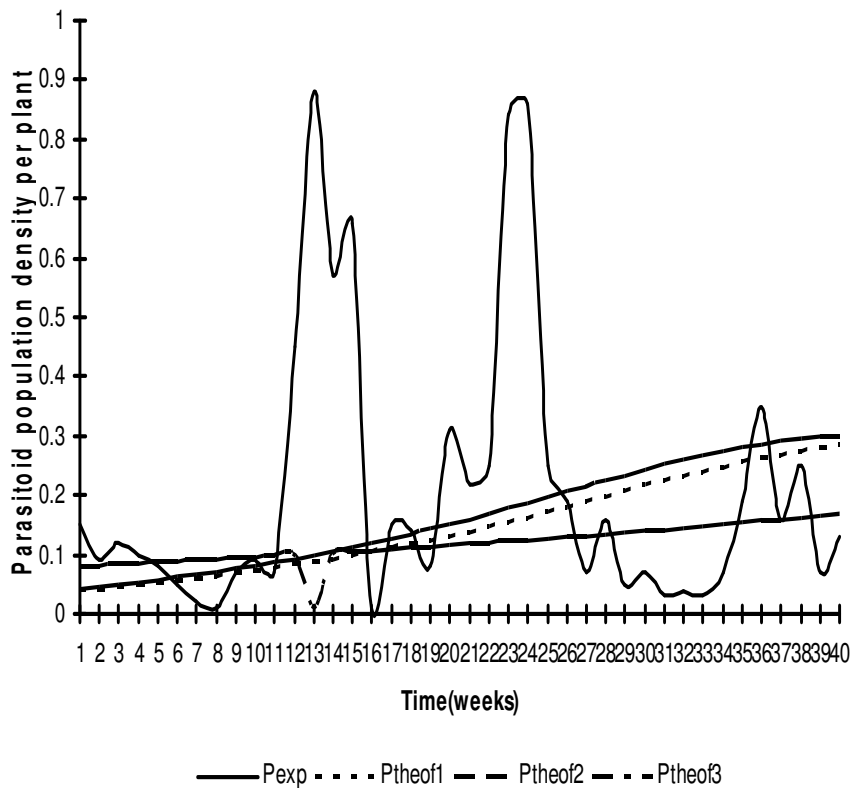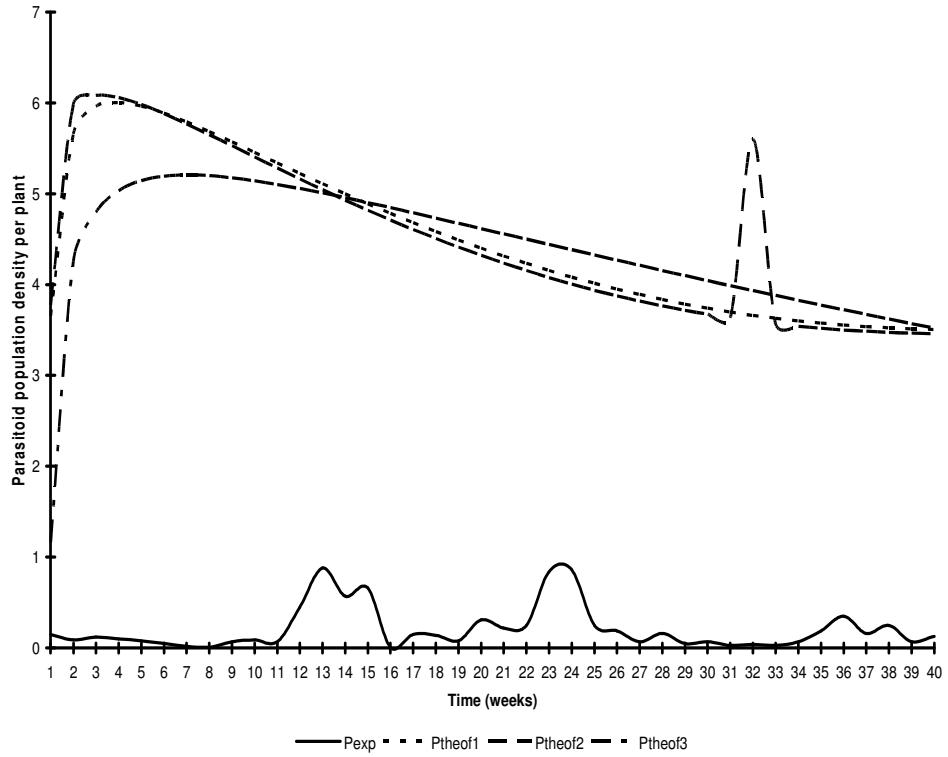
Figure 8. Trajectories of the Parasitoid population for empirical datasets and those predicted by Leslie Model using Loss functions 1, 2 and 3.

Figure 9. Trajectories of the Diamondback moth population for empirical datasets and those predicted by Rosenzweing Model using Loss functions 1, 2 and 3.

Figure 10. Trajectories of the parasitoid population for empirical datasets and those predicted by Rosenzweig Model using Loss functions 1, 2 and 3.

Figure 11. Trajectories of the Diamondback moth Population for empirical datasets and those predicted by Yodzis Model using Loss functions 1, 2 and 3.

Figure 12. Trajectories of the Parasitoid population for empirical datasets and those predicted by Yodzis Model using Loss functions 1,2 and 3.
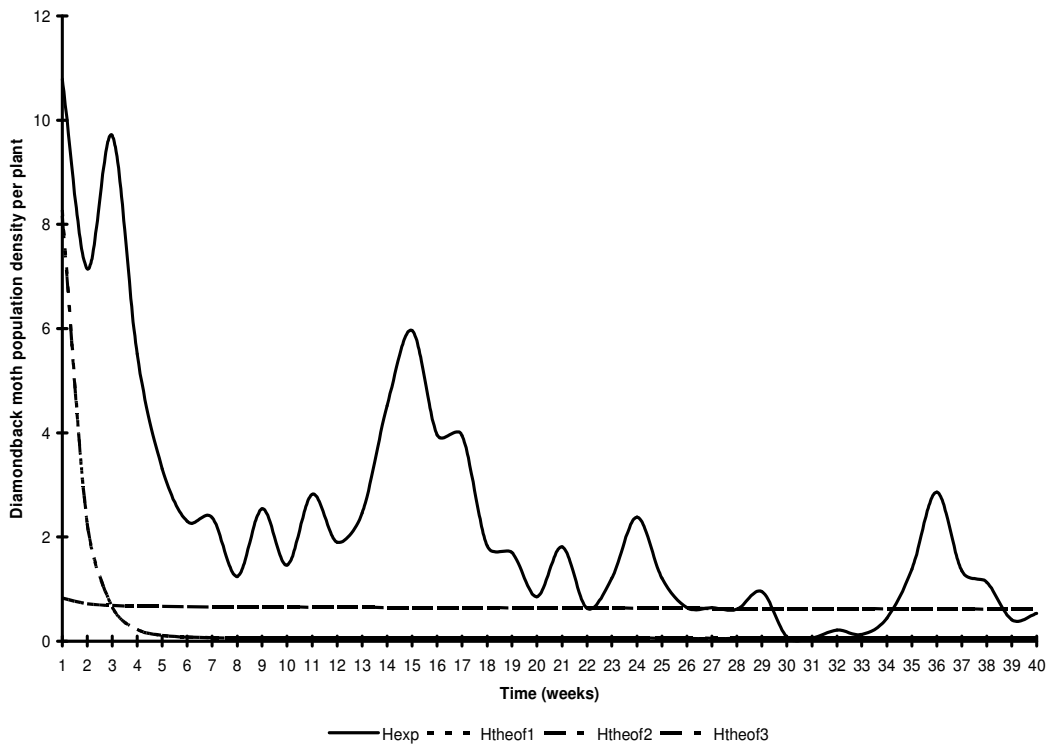

Figure 13. Trajectories of the parasitoid population for empirical datasets and those predicted by Beddington-DeAngelis Model using Loss functions 1, 2 and 3.
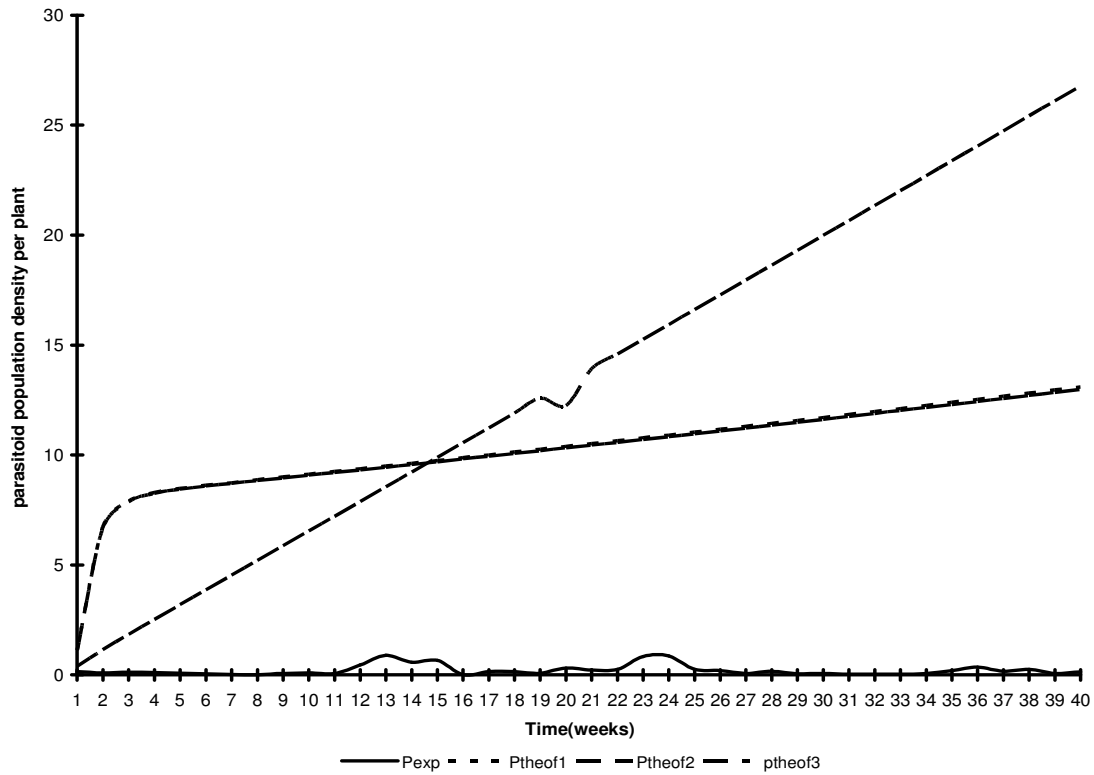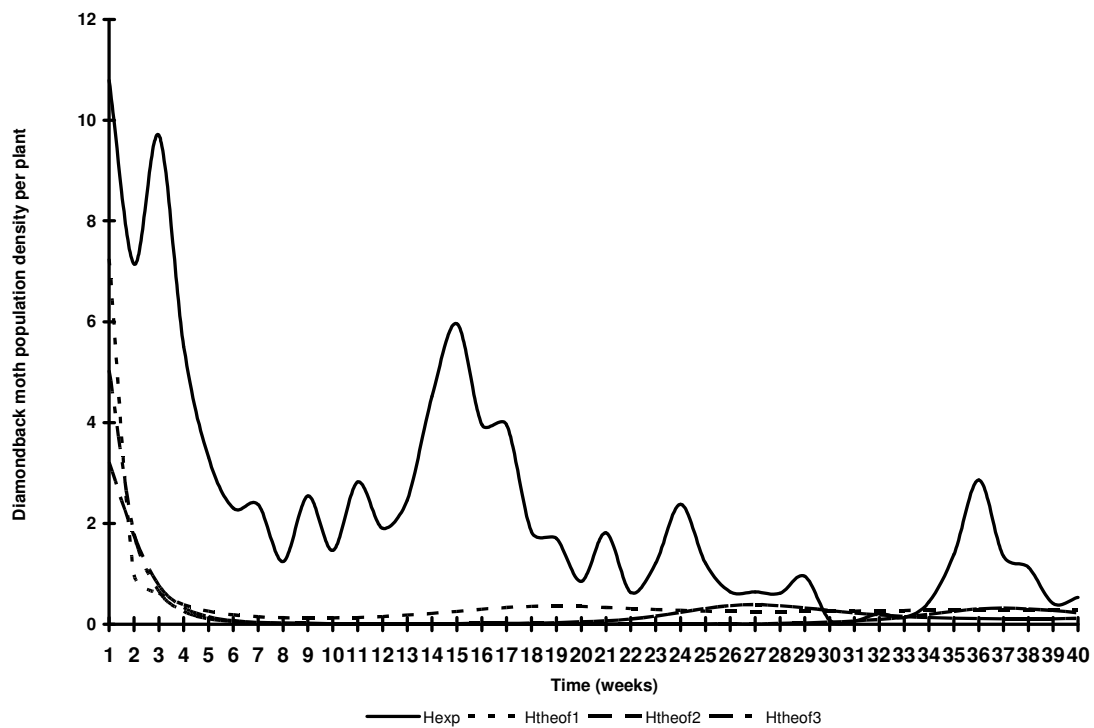
Figure 14. Trajectories of the parasitoid population for empirical datasets and those predicted by Beddington-DeAngelis Model using Loss functions 1, 2 and 3.

Figure 15. Trajectories of the Diamondback moth population for empirical datasets and those predicted by Bazykin Model using loss functions 1, 2 and 3.
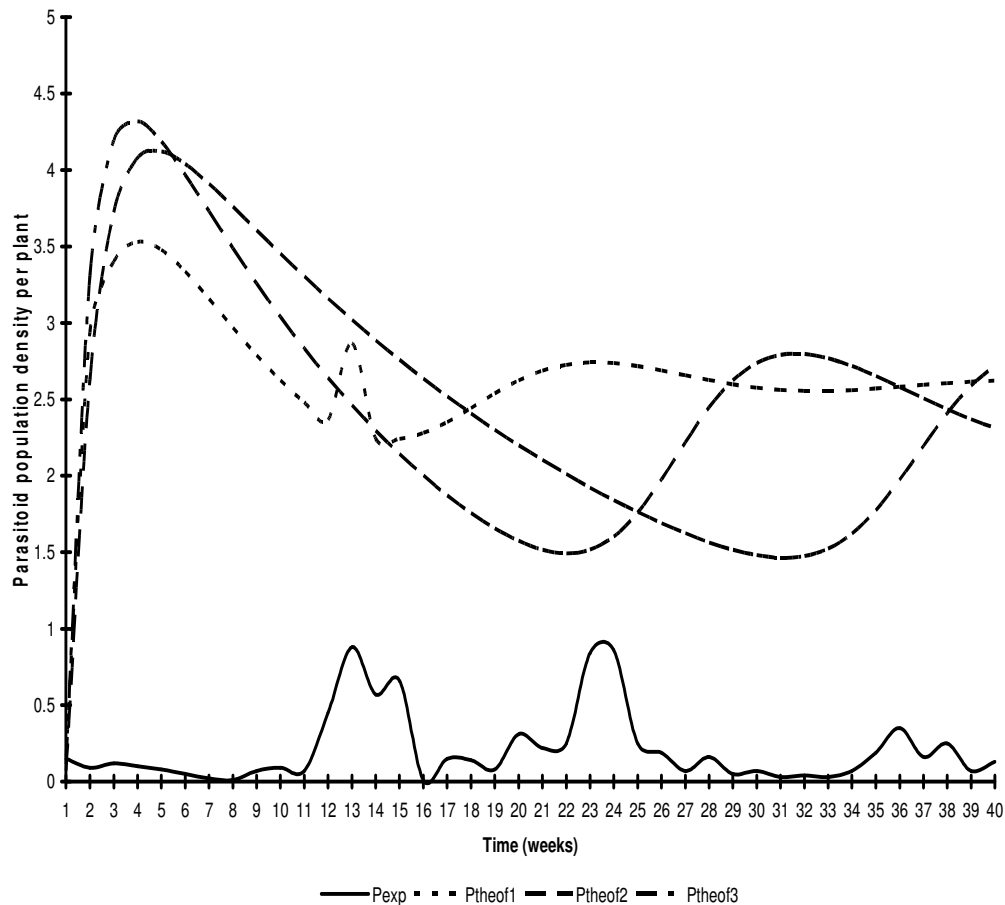
Figure 16. Trajectories of the parasitoid population for empirical datasets and those predicted by Bazykin Model using Loss functions 1, 2 and 3.

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