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PII: S0022-5193(10)00109-8
DOI: doi:10.1016/j.jtbi.2010.02.034
Reference: YJTBI5887



www.elsevier.com/locate/jtbi

To appear in: *Journal of Theoretical Biology*

Received date: 23 October 2009
Revised date: 20 February 2010
Accepted date: 22 February 2010

Cite this article as: Sanyi Tang, Guangyao Tang and Robert A. Cheke, Optimum timing for integrated pest management: Modelling rates of pesticide application and natural enemy releases, *Journal of Theoretical Biology*, doi:[10.1016/j.jtbi.2010.02.034](https://doi.org/10.1016/j.jtbi.2010.02.034)

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Optimum timing for integrated pest management: modelling rates of pesticide application and natural enemy releases

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Abstract Many factors including pest natural enemy ratios, starting densities, timings of natural enemy releases, dosages and timings of insecticide applications and instantaneous killing rates of pesticides on both pests and natural enemies can affect the success of IPM control programmes. To address how such factors influence successful pest control, hybrid impulsive pest-natural enemy models with different frequencies of pesticide sprays and natural enemy releases were proposed and analyzed. With releasing both more or less frequent than the sprays, a stability threshold condition for a pest eradication periodic solution is provided. Moreover, the effects of times of spraying pesticides (or releasing natural enemies) and control tactics on the threshold condition were investigated with regard to the extent of depression or resurgence resulting from pulses of pesticide applications. Multiple attractors from which the pest population oscillates with different amplitudes can coexist for a wide range of parameters and the switch-like transitions among these attractors showed that varying dosages and frequencies of insecticide applications and the numbers of natural enemies released are crucial. To see how the pesticide applications could be reduced, we developed a model involving periodic releases of natural enemies with chemical control applied only when the densities of the pest reached the given Economic Threshold. The results indicate that the pest outbreak period or frequency largely depends on the initial densities and the control tactics.

Key-words. Optimum timing; pest control; IPM; Economic threshold; Augmentation; Predator-prey model

1 Introduction

Integrated pest management (IPM) involves choosing appropriate tactics from a range of pest control techniques including biological, cultural and chemical methods to suit individual cropping systems, pest complexes and local environments (Flint, 1987; van Lenteren, 1995, 2000; van Lenteren and Woets, 1988). Biological control is often a component of an IPM strategy (Greathead, 1992; Parker, 1971). It is defined as the reduction of pest populations by natural enemies and typically involves an active human role, such as augmentation which involves the supplemental release of natural enemies. Relatively few natural enemies may be released at a critical time of the season (inoculative release) or millions may be released (inundative release) when insufficient reproduction of released natural enemies is likely to occur and pest control will be achieved exclusively by the released individuals themselves (Hoffmann and Frodsham, 1993; Neuenschwander and Herren, 1988).

Another important method for pest control is chemical control. In most cropping systems, insecticides are still the principal means of controlling pests once the economic threshold (ET) has been reached. They can be relatively cheap and are easy to apply, fast-acting, and in most instances can be relied on to control the pests (Hoffmann and Frodsham, 1993). An ET is usually defined as the number of insect pests in the field when control actions must be taken to prevent the economic injury level from being reached and exceeded (Pedigo and Higley, 1992; van Lenteren, 1995), as shown in Fig.1. However, only if all other IPM tactics including biological and cultural control are unable to keep an insect pest population below an ET, then use of an insecticide to control the pest and prevent economic loss is justified. Even where pesticides are included as a last resort as

part of an IPM strategy, the emphasis is on rational use involving suitable active ingredient selection and careful timing of application with regard to pest population levels.

Most importantly, chemical and biological methods have often proven antagonistic pesticides limit populations of natural enemies in crops and reduce their impact on pest populations. In extreme cases of such antagonism, often called resurgence, pest populations may be increased by the application of insecticides which kill both the pest and their natural enemies (Barclay, 1982; Debach, 1974; Ruberson, 1998). So it is important to know how such antagonistic pesticides affect the outcomes of pest control measures.

One approach to understanding the range of possible ecological interactions between pest, natural enemy and pesticides is to construct and explore population models. Barclay (1982), Barlow et al. (1996) and Barclay and van den Driessche (1977) have developed continuous ODE models, with coupled predator and pest populations, both of which are affected by insecticides. Carpenter (1981) has developed a similar model for the interaction between pests, pathogens and insecticides. Recently, continuous or discrete predator-prey models concerning IPM strategies have been developed and investigated (Tang and Chen, 2004; Tang and Cheke, 2005; Tang et al., 2005; Tang and Cheke, 2008; Tang et al., 2008). However, one of the major assumptions in those publications was that all control tactics are implemented at the same time, which means that the application of pesticides can kill the released natural enemies instantly. There are three possible methods implemented in practice to avoid such antagonism when biological and chemical controls are combined: (i) spraying pesticides more frequently than releasing natural enemies; (ii) spraying pesticides less frequently than releasing

natural enemies; and (iii) releasing natural enemies frequently and spraying pesticides only when pest densities reach the ET.

Based on the above practical control methods, we first propose impulsive pest-natural enemy models with different frequencies of spraying pesticides and releasing natural enemies. The threshold conditions which guarantee that the pest dies out are derived, and several governing factors including application timing and control tactics are investigated with regard to the extent of depression or resurgence resulting from pulses of pesticide applications. Experimental observations have shown that the initial densities of pest and natural enemy populations can affect classical biological control (Burnett, 1960; Foster and Kelly, 1978; Jones, 1999). The numerical results obtained in the present paper also indicate that the simplest pest-natural enemy models with impulsive control tactics can lead to the coexistence of pests and natural enemies for a wide range of parameters, but with quite different pest amplitudes. These results indicate that the final stable states of pest-natural enemy populations depend on their initial densities as well as on their ratios, and the results are confirmed by basins of attraction of initial densities. Furthermore, the effects of random perturbations of the instant killing rates of pesticides on pests and on natural enemies, release rates and a release constant on the switch-like transitions among those attractors confirm that varying dosages and frequencies of insecticide applications and the numbers of natural enemies released are crucial.

One of the most important questions in IPM is how many natural enemies should be released and what fraction of the pest population should be killed to avoid economic damage and reduce the pesticide applications when the pest population reaches or exceeds the ET level. In many cases, the most effective

release rate or spraying rate has not been identified as it will vary depending on crop type and target host density. To avoid antagonism and reduce the pesticide applications, the pesticide is sprayed only when it is necessary, i.e. when the pest population density reaches the ET. With this in mind we developed a new hybrid impulsive dynamical model to involve a periodic releasing of natural enemies, while chemical control is applied only when the densities of the pest population reach the given ET. The results indicate that the pest outbreak period or frequency largely depends on the initial densities and the control tactics. The results also show that the selection of ET, selection of the pesticide and selection of the releasing methods (inundative or inoculation release) may be crucial in prolonging the pest outbreak period.

2 The model with periodic integrated pest control strategies

In order to address the effects of integrated control tactics on the pest-natural enemy dynamic model, we will extend the classical Lotka-Volterra model (Lotka, 1920; Volterra, 1931) by introducing an IPM strategy such as releasing of natural enemies (Parker, 1971) or spraying pesticide at a critical time and examine the consequences of population densities changing very rapidly. For instance, impulsive reduction of the pest population is possible by trapping the pests and/or by poisoning them with chemicals. An impulsive increase of the natural enemy density can be achieved by laboratory-based breeding followed by releases into the field (Tang and Chen, 2004; Tang and Cheke, 2005; Tang et al., 2005; Tang and Cheke, 2008).

The simplest case is to assume that at every period T a perturbation which incorporates a proportional (denoted by p_1) decrease of the insect pest and proportional (denoted by p_3) increase of the natural enemies and an introduction constant σ for the natural enemies which does not depend on its population sizes are considered. That is, we have the following impulsive differential equation with a fixed moment

$$\left. \begin{array}{l} \left. \begin{array}{l} \frac{dx(t)}{dt} = rx(t) [1 - \delta x(t)] - bx(t)y(t), \\ \frac{dy(t)}{dt} = y(t)(cx(t) - a), \end{array} \right\} t \neq nT, \\ \left. \begin{array}{l} x(nT^+) = (1 - p_1)x(nT), \\ y(nT^+) = (1 + p_3)y(nT) + \sigma, \end{array} \right\} t = nT, \end{array} \right\} \quad (2.1)$$

where r, δ, b, c and a are positive constants, T is the period of the impulsive effect, $q_1 \triangleq 1 - p_1$ and $q_3 \triangleq 1 + p_3$ with $0 < q_1 \leq 1, q_3 \geq 1$. The assumptions in the model (2.1) without control strategies are: (i) The prey grows in a logistic way in the absence of any predation. (ii) The effect of the predation is to reduce the prey's per capita growth rate by a term proportional to the prey and predator populations. (iii) In the absence of any prey for sustenance the predator's death rate results in exponential decay. (iv) The prey's contribution to the predator's growth rate is cxy ; that is, it is proportional to the available prey as well as to the size of the predator population.

The dynamical behavior and biological implications of the model (2.1) were extensively studied, and if $q_3 \exp(-aT) < 1$, then the complete expression of the 'pest-eradication' periodic solution of system (2.1) over the n -th time interval $t_0 = nT < t \leq (n + 1)T$ can be described as follows

$$(0, y^*(t)) = \left(0, \frac{\sigma \exp(-a(t - nT))}{1 - q_3 \exp(-aT)} \right), \quad (2.2)$$

which is globally asymptotically stable provided that the following threshold

condition

$$r < \frac{1}{T} \ln \left(\frac{1}{q_1} \right) + \frac{b\sigma}{Ta} \frac{1 - \exp(-aT)}{1 - q_3 \exp(-aT)} \quad (2.3)$$

holds true. Equivalently, we can define the threshold condition

$$R_0 = q_1 \exp \left[rT + \frac{b\sigma}{a} \frac{\exp(-aT) - 1}{1 - q_3 \exp(-aT)} \right] \quad (2.4)$$

and if $R_0 < 1$ then the pest eradication periodic solution is globally asymptotically stable.

In particular, let $q_3 = 1$ and $\sigma = 0$ (chemical control only), and the pest-eradication periodic solution (2.2) is globally stable $((0, 0)$ in this case) if the intrinsic growth rate of the pest population satisfies

$$r < \frac{1}{T} \ln \left(\frac{1}{q_1} \right)$$

which means that if the intrinsic growth rate is less than the mean pest-killing rate due to an insecticide application over period T , then the pest population eventually goes to extinction.

Similarly, let $q_1 = 1$ (biological control only), then the condition which guarantees the global stability of the pest-eradication periodic solution becomes:

$$r < \frac{b\sigma}{Ta} \frac{1 - \exp(-aT)}{1 - q_3 \exp(-aT)}$$

which means that if the intrinsic growth rate is less than the mean predation rate over period T , then the pest population will become extinct eventually.

However, for an IPM strategy ($q_1 > 0, q_3 \geq 0$ and $\sigma > 0$ here) inequality (2.3) indicates that if the intrinsic growth rate of the pest population is less than the summation of the mean killing rate and the mean predation rate over period T , then the pest population will tend to zero. Theoretically, this confirms that an IPM strategy is more effective than any single control strategy. The complex

dynamical behavior of model (2.1) has also been addressed by using numerical investigations (Tang and Cheke, 2005; Tang et al., 2005).

3 Optimum timing and rates of pesticide application and release of natural enemies

To take full advantage of existing biological control agents, it is important to understand the impact of insecticides on valuable natural enemy species. In general, pesticides tend to be harmful to most natural enemies (Ruberson, 1998), which may be associated with acute toxicity. Understanding the acute toxicity of insecticides to natural enemies is important and relevant to IPM. In fact, natural enemies must search for their prey, they are generally very mobile and spend a considerable time moving across plant tissue. This increases the likelihood that they will contact the insecticide and indicates that natural enemies are generally more adversely affected by chemical insecticides than the target pest, and even worse pest populations may be induced by the application of insecticides which kill both the pest and their natural enemies (Debach, 1974).

Undoubtedly, mathematical modelling is one of the key tools for understanding the interactions among pest, natural enemies and pesticides (Barclay, 1982; Barlow et al., 1996). Recently, continuous and discrete predator-prey models concerning IPM strategies have been developed and investigated (Barclay, 1982; Barclay and van den Driessche, 1977; Carpenter, 1981; Hassell, 1984; May, 1978; Tang and Chen, 2004; Tang and Cheke, 2005, 2008). When insecticide timing also leads to the death of parasitoids, discrete host-parasitoid models have been proposed and four different cases have been investigated according to the timing of application

(Beddington et al., 1978; Hassell, 1984; Hassell and May, 1973; May and Hassell, 1988; Waage and Hassell, 1982; Waage et al., 1985).

As noted in the introduction, all models (such as model (2.1)) developed before assumed that all control tactics are applied simultaneously. In the present work, let us take the simplest case where in each impulsive point τ_n there is an insecticide application that kills a constant fraction (denoted by p_1) of the pests and which, in addition, can kill a proportion (denoted by p_2) of natural enemies, and in each impulsive point λ_m we release a proportional amount of the natural enemies (denoted by p_3) and there is an introduction constant σ for the natural enemies which does not depend on the sizes of the populations. These modifications result in the following model

$$\left\{ \begin{array}{l} \frac{dx(t)}{dt} = rx(t) [1 - \delta x(t)] - bx(t)y(t), \\ \frac{dy(t)}{dt} = y(t)(cx(t) - a), \end{array} \right\} \quad t \neq \tau_n, t \neq \lambda_m, \quad (3.1)$$

$$\left\{ \begin{array}{l} x(\tau_n^+) = (1 - p_1)x(\tau_n), \\ y(\tau_n^+) = (1 - p_2)y(\tau_n), \end{array} \right\} \quad t = \tau_n,$$

$$y(\lambda_m^+) = (1 + p_3)y(\lambda_m) + \sigma, \quad t = \lambda_m$$

where $\tau_n (n = 1, 2, \dots)$ and $\lambda_m (m = 1, 2, \dots)$ are impulsive point series at which the chemical (or cultural) control tactics and biological control strategies are applied, respectively. Denote $q_1 = 1 - p_1$, $q_2 = 1 - p_2$ and $q_3 = 1 + p_3$ throughout the paper with $0 < q_1, q_2 \leq 1$, $q_3 \geq 1$ and $\sigma \geq 0$. It is thus possible to rank the different patterns of insecticide application in terms of their dynamic effects in relation to the timing of natural enemy releases. From a practical point of view, we consider several different cases as follows in terms of the timing of IPM applications.

Case 1 Pesticide applications more frequent than releases of natural enemies.

Assume $\lambda_{m+1} - \lambda_m \equiv T_N$ for all $m (m \in \mathcal{N})$, where T_N is the period of releasing

natural enemies. For this case the model (3.1) is said to be a T_N periodic system if there exists a positive integer k_P such that

$$\tau_{n+k_P} = \tau_n + T_N.$$

This implies that in each period T_N , k_P pesticide applications are used.

Case 2 Natural enemy releases more frequent than pesticide applications.

Assume $\tau_{n+1} - \tau_n \equiv T_P$ for all $n(n \in \mathcal{N})$, where T_P is the period of pesticide applications. For this case the model (3.1) is said to be a T_P periodic system if there exists a positive integer k_N such that

$$\lambda_{m+k_N} = \lambda_m + T_P.$$

This implies that in each period T_P , k_N natural enemy releases are applied.

Case 3 Chemical and biological control tactics applied with different periods.

Assume $\lambda_{m+1} - \lambda_m \equiv T_N$ for all m , and $\tau_{n+1} - \tau_n \equiv T_P$ for all n . In this case, T_P is the period of pesticide applications, T_N is the period of natural enemy releases, $m, n \in \mathcal{N}$. Denote $\rho = T_P/T_N$, then ρ either is rational (i.e. T_P and T_N are rational dependent) or is irrational (i.e. T_P and T_N are rational independent). If ρ is rational, then $\rho = p/q$, $p, q \in \mathcal{N}$ and p, q are relatively prime. Let $T_0 = pT_N (= qT_P)$, then the model (3.1) is T_0 periodic system. This means that if ρ is rational, the model (3.1) can be investigated by using similar methods as Cases 1 and 2; If ρ is irrational, then the dynamical behavior of model (3.1) becomes more complex. For this special case, it is quite difficult to investigate the dynamical behavior theoretically, please see more details from the reference (Liu and Chen , 2004).

The main purposes of the following are to focus on Cases 1 and 2, and investigate the effects of timing of application of IPM tactics and rates of spraying

or releasing on the pest management. We also study the effects of initial densities of pest and natural enemies on the pest control and dynamical complexities.

4 Dynamical analysis of Case 1 and its biological implications

For Case 1, there are k_P pesticide applications during period T_N . Denote

$\Delta_i = \tau_{i+1} - \tau_i, i = 0, 1, 2, \dots, k_P$, where $\Delta_0 = \tau_1, \Delta_{k_P} = T_N - \tau_{k_P}$. Firstly, the basic properties of the following subsystem

$$\begin{cases} \frac{dy(t)}{dt} = -ay(t), t \neq \lambda_m \\ y(\tau_n^+) = q_2 y(\tau_n), t = \tau_n, \\ y(\lambda_m^+) = q_3 y(\lambda_m) + \sigma, t = \lambda_m \end{cases} \quad (4.1)$$

play a key role in analyzing the pest control.

It is shown in Appendix A, that there exists a globally stable periodic solution $y^{T_N}(t)$ for the subsystem (4.1) if the inequality

$$q_3 q_2^{k_P} \exp(-aT_N) < 1 \quad (4.2)$$

holds true. Therefore, the complete expression for the 'pest-eradication' periodic solution of system (3.1) over the h -th time interval $hT_N < t \leq (h+1)T_N$ is given by $(0, y^{T_N}(t))$. Furthermore, if the following threshold condition

$$R_0^N \triangleq q_1^{k_P} \exp \left[rT_N + \frac{b}{a} Y^* \sum_{j=0}^{k_P} q_2^j \left(e^{-a(\sum_{i=0}^j \Delta_i)} - e^{-a(\sum_{i=0}^{j-1} \Delta_i)} \right) \right] < 1 \quad (4.3)$$

is satisfied, then the pest-eradication periodic solution $(0, y^{T_N}(t))$ is globally attractive, where $Y^* = \sigma / [1 - q_3 q_2^{k_P} \exp(-aT_N)]$.

In particular, if $\Delta_i \equiv \Delta$ for all $i = 0, 1, 2, \dots, k_P$, then the above condition becomes as follows:

$$R_0^N = q_1^{k_P} \exp \left[rT_N + \frac{b}{a} Y^* (e^{-a\Delta} - 1) \frac{1 - q_2^{k_P+1} e^{-(k_P+1)a\Delta}}{1 - q_2 e^{-a\Delta}} \right] < 1$$

i.e.

$$R_0^N = q_1^{k_P} \exp \left[rT_N + \frac{b}{a} Y^* (e^{-a\Delta} - 1) \frac{1 - q_2^{k_P+1} e^{-aT_N}}{1 - q_2 e^{-a\Delta}} \right] < 1. \quad (4.4)$$

Equivalently, the above inequality can become as follows

$$r < \frac{1}{T_N} \ln \left(\frac{1}{q_1^{k_P}} \right) + \frac{b}{aT_N} Y^* (1 - e^{-a\Delta}) \frac{1 - q_2^{k_P+1} e^{-aT_N}}{1 - q_2 e^{-a\Delta}}$$

which can be explained as for those examples shown in the section 2.

What we want to address in the following is how control tactics including killing rates p_1 and p_2 , release rate p_3 and release constant σ , timing of pesticide application τ_i (or k_P) and timing of release period T_N affect the threshold condition R_0^N .

In Fig.2(A-C), we fixed the release period T_N and let the killing rate p_2 vary. The simulation results indicate that if the pesticide kills the natural enemies with a relatively higher killing rate p_2 (for example $p_2 = 0.07$), the threshold value R_0^N is a monotonically increasing function with respect to the number of pesticide applications k_P (Fig.2(A)). This shows that if the pesticide has a strong effect on the natural enemies, repeated use of the same pesticides can result in target pest resurgence. If the killing rate p_2 on the natural enemies is slightly reduced from 0.07 to 0.05, Fig.2(B) shows that the threshold value R_0^N is not monotonic with respect to the number of pesticide applications k_P . So in this case we must carefully select the number of pesticide applications (two or three events in this case). If the pesticides do not kill the natural enemies so much, Fig.2(C) clarifies that the threshold value R_0^N is a monotonically decreasing function with respect to

the number of pesticide applications k_P . All these simulations show that for a given releasing period, the number of application pesticide within this period and the killing rate of this pesticide on natural enemies are crucial.

Biological controls can be supported by augmentation of natural predators (and / or parasites or parasitoids), which includes the introduction of naturally occurring predators at either an inundative or inoculative level (Parker, 1971; Udayagiri et al., 2000). Fig.3 provides the details on how different release (augmentation) rates p_3 affect the threshold value R_0^N . For the given killing rates p_1 and p_2 , release period T_N , and if the number of pesticide applications is relatively small, Fig.3 shows that slightly increasing the release rate p_3 can dramatically reduce the quantity of threshold parameter R_0^N . However, for a relatively larger number of pesticide applications, different killing rates p_1 and p_2 , a different release period T_N may result in target pest resurgence, as shown in Figs.3 and 4.

Fig.4 shows the effects of different parameter sets on the quantity of the threshold condition R_0^N . All simulation results shown in Fig.4 indicate that the R_0^N appear to be quite sensitive to small changes in killing rates p_1 and p_2 , release constant σ and releasing period T_N . All these results clarify that the effect of pesticide timing, effectiveness of natural enemies and pesticide selectivity are crucial to pest depression and resurgence. This information may also help the field operator to decide on the optimum timing for spray applications and optimum rate for release.

Experimental observations have confirmed that the initial densities of pest and natural enemy populations can affect the outcome of classical biological control (Foster and Kelly, 1978; Jones, 1999). The results obtained for Case 1 indicate

that the simplest Lotka-Volterra model with integrated control tactics has various coexistence possibilities with a wide range of parameters, including several interior attractors where the pest and natural enemy populations coexist, as shown in Fig.5. The final stable states of pest and natural enemy populations depend on their initial densities as well as on their ratios, and those results are confirmed by basins of attraction of initial densities (Fig.6).

To avoid insecticide resistance, resistance strategies most often involve either mixing and applying pesticides together or alternating the use of available pesticides. But can such variations in doses and types of insecticides used and the numbers of natural enemies introduced affect the dynamics? Different numbers of natural enemies released and various dosages of pesticide applications or different pesticide applications can be mathematically expressed in terms of four parameters, q_1 , q_2 , q_3 and σ in model (3.1). That is, random perturbations due to variations in the dosages applied or releases (migration) of natural enemies can be taken into account with these four additional parameters, i.e.

$q_{1\eta} = q_1 + \eta_1 u$, $q_{2\eta} = q_2 + \eta_2 u$, $q_{3\eta} = q_3 + \eta_3 u$, $\sigma_\eta = \sigma + \eta_4 u$ and u is a random variable uniformly distributed on $[-1, 1]$ and $\eta_i > 0$ for $i = 1, 2, 3, 4$ to represent the intensity of noise. One view of this noise is that it represents small random events of spraying, augmentation, immigration and mortality.

In order to understand how these small random perturbations affect the final state of the pest population, we numerically studied system (3.1) with respect to the switch-like transitions among the attractors shown in Fig.5. That is, we asked do these stable attractors switch from one attractor to another once small random perturbations have been introduced? As an example, with all other parameter values fixed as in Fig.5, it has been shown that there are three stable attractors

which can coexist. If we choose the initial condition $(x_0, y_0) = (0.6, 1.5)$ (or $(2.6, 1)$), the stable attractor without random perturbation is an attractor at which the pest population oscillates with a larger amplitude (see Fig.5). When small random perturbations are introduced in one of the parameters q_1, q_2, q_3, σ , numerical simulations imply that this solution can switch to another attractor with smaller amplitude at a random time (Figs.7 and 8). However, extensive numerical simulations indicate that the attractors with a smaller amplitude are robust and are not affected by these types of small random perturbations. These numerical results confirm that different doses of pesticide application and natural enemy releases can influence the dynamics of the classical pest-natural enemy system, and small random perturbations on parameters q_1, q_2, q_3, σ may play key roles in insect pest control.

5 Dynamical analysis of Case 2 and its biological implications

For Case 2 there are k_N natural enemy releases during period T_P . Denote $\Delta_i = \lambda_{i+1} - \lambda_i, i = 0, 1, 2, \dots, k_N$, where $\Delta_0 = \lambda_1, \Delta_{k_N} = T_P - \lambda_{k_P}$.

It is shown in Appendix B, that there exists a globally stable periodic solution $y^{T_P}(t)$ for the subsystem (4.1) if the inequality

$$q_2 q_3^{k_N} \exp(-aT_P) < 1 \quad (5.1)$$

holds true. Therefore, the complete expression for the 'pest-eradication' periodic solution of system (3.1) over the h -th time interval $hT_P < t \leq (h+1)T_P$ is given

by $(0, y^{TP}(t))$. Furthermore, if the following threshold condition

$$\begin{aligned}
 R_0^P \triangleq & q_1 \exp[rT_P + \frac{b}{a}Y^*(\exp(-a\Delta_0) - 1) \\
 & + \frac{b}{a}[q_3Y^*\exp(-a\Delta_0) + \sigma](\exp(-a\Delta_1) - 1) + \dots + \\
 & \frac{b}{a}\left[q_3^{k_N}Y^*\exp\left(-a\sum_{i=0}^{k_N-1}\Delta_i\right) + \sigma\sum_{i=0}^{k_N-1}q_3^i\exp\left(-a\sum_{j=k_N-i}^{k_N-1}\Delta_j\right)\right] \cdot \\
 & (\exp(-a\Delta_{k_N}) - 1) < 1
 \end{aligned} \tag{5.2}$$

is satisfied, then the pest-eradication periodic solution $(0, y^{TP}(t))$ is globally attractive, where Y^* is given in Appendix B. In particular, if $\Delta_i \equiv \Delta$ for all $i = 0, 1, 2, \dots, k_P$, then the above condition becomes as follows

$$R_0^P = q_1 e^{\left[rT_P + \frac{b}{a}(e^{-a\Delta} - 1) \left(\frac{Y^* \left(\frac{1 - q_3^{k_N+1} e^{-aT_P}}{1 - q_3 e^{-a\Delta}} \right) + \sigma \sum_{i=1}^{k_N} (k_N + 1 - i) q_3^{i-1} e^{-a(i-1)\Delta}} \right) \right]} < 1. \tag{5.3}$$

Since the release of natural enemies in this case is more frequent than spraying pesticides, the side-effects of pesticides on the natural enemy population are largely reduced. Moreover, the threshold condition R_0^P can be significantly affected by the supplemental release of natural enemies. For example, if we fixed all parameters as those in Fig.9 and chose different releasing constant σ and different k_N , the simulation results indicate that slight increases of the release constant σ can significantly reduce the threshold value R_0^P (Fig.9), while increasing the number of natural enemy releases as well. This clarifies that repeated releases of a small number of natural enemies at a critical time of the season can successfully suppress the pest population. In practice, an example of inoculative release occurs in greenhouse production of several crops. Periodic releases of the parasitoid *Encarsia formosa* are used to control greenhouse whitefly *Trialeurodes vaporariorum*, and the predaceous mite, *Phytoseiulus persimilis*, is used for control of the two-spotted spider mite *Tetranychus urticae* (Parker, 1971).

We can also employ the methods provided in Case 1 to investigate the effects of all other parameters on the threshold value R_0^P . Furthermore, bifurcation analyses also indicate that multiple attractors can coexist for a wide range of parameters for this case. For example, the two attractors with quite different pest amplitudes that can coexist (see Fig.10), and the switch-like transitions between the two attractors shown in Fig.11. This further indicates that different dosages of pesticide applied and numbers of natural enemies released are crucial for controlling pests.

6 Hybrid impulsive model with Economic

Threshold

As mentioned before, pesticides may kill or harm natural enemies following exposure by contact, ingestion or, less commonly, by respiration. They may also affect natural enemies indirectly by killing or contaminating their hosts or prey. An understanding of the effectiveness of natural enemies is essential to avoid applying pesticides when biological control is adequate, as shown in Cases 1 and 2. Probably the best method for reducing the overall negative impact of chemicals on natural enemies is to apply pesticides only when necessary. In practice, the pesticides can only be applied when the density of the pest population reaches the Economic Threshold (ET), and model (3.1) becomes

$$\left\{ \begin{array}{l} \frac{dx(t)}{dt} = rx(t) [1 - \delta x(t)] - bx(t)y(t), \quad x(t) < ET, \\ \frac{dy(t)}{dt} = y(t)(cx(t) - a), \quad t \neq \lambda_m, \\ \left. \begin{array}{l} x(t^+) = (1 - p_1)x(t), \\ y(t^+) = (1 - p_2)y(t), \end{array} \right\} \quad x(t) = ET, \\ y(\lambda_m^+) = (1 + p_3)y(\lambda_m) + \sigma, \quad t = \lambda_m, \end{array} \right. \quad (6.1)$$

where $\lambda_m (m = 1, 2, \dots)$ is an impulsive point series at which the natural enemies are released. For simplification, we assume $\lambda_{m+1} - \lambda_m = T$ for all m , i.e. the periodic releasing of natural enemies is applied.

From the biological point of view, the effective testing of natural enemy release strategies and timing of insecticide applications require the use of replicated treatments in independent greenhouses (Hoddle et al., 1997a,b) and the use of experimental controls either in cages or separate greenhouses (Hoddle et al., 1997a,b). Thus, experimental methods in combination with the model approaches presented in this paper are the most cost effective method. However, the intrinsic growth rate of pests, r , predator searching efficiency, b , instant killing rates q_1 and q_2 , releasing rate q_3 and constant σ , and other factors (such as ET) can vary amongst pest and natural enemy species. How do these factors affect the control strategies? In particular, what we want to know is how do the ET and various pest-natural enemy ratios affect the control strategies.

For a given ET, we suggest that successful control strategies largely depend on the initial density and pest-natural enemy ratios. To show this, we fix all parameter values as those in Fig.12. The results shown in Fig.12 provide some examples of different possible cases. In Fig.12(A) the initial densities of pest-natural enemy populations are (1.8,1.7) and the simulation result indicates that the density of the pest population never reaches the given ET, which shows that the solution initiating from (1.8,1.7) is free from pesticide applications. If we set the initial densities as (0.6,1), Fig.12(B) indicates that the system is free from chemical control after one pesticide application. If we set the initial densities as (1.2, 0.8) or (2.1,0.5) or (2.7, 0.4), Fig.12(C-E) indicates that the system is free from chemical control after two, four or five pesticide applications. If we further

increase the pest-natural enemy ratio and set the initial densities as (1.8, 0.2), the pest outbreak frequency is significantly increased, as shown in Fig.12(F).

We have conducted many other numerical simulations (not shown here) on model (6.1) with different initial densities and different pest-natural enemy ratios, and found that there are only three possible control cases that model (6.1) has: (a) infinite repeats of chemical control tactics such as in periodic control strategies; (b) finite numbers of chemical control tactics; (c) no chemical control required. These results clarify that the models proposed here can help us to understand pest-natural enemy interactions, help us to design appropriate control strategies and to make management decisions in insect pest control.

Consequently, we denote the time points at which the solution reaches ET as $t_n (n = 1, 2, \dots)$. If $\text{mod}(t_n, T) \equiv 0$, a chemical control is applied at t_n and after that a biological control is also applied at the same time. If $\text{mod}(t_n, T) \neq 0$, only a chemical control programme is applied. Further, denote

$$T_n = t_n - t_{n-1} \quad (6.2)$$

with $t_0 = 0$ as pest-outbreak duration (or period), where n may be finite or infinite which depends on the solutions of the models.

The effect of control tactics (here parameters T, ET, q_1, q_2, q_3 and σ) on pest mean outbreak period (or outbreak frequency) can be calculated from the model (6.1) and formula (6.2) numerically (Fig.13). Mean pest outbreak period is an average over several pest outbreaks (here outbreaks indicate that the densities of the pest reach the given ET) or pest cycle periods. Model (6.1) predicts that the densities of the pest do not reach the ET if the natural enemies are released frequently enough (here smaller T , Fig.13(A)), and the mean outbreak period is decreasing as the release period T or survival rate of the pest on pesticide

application q_1 increases (Fig.13(A) and (C)). Conversely, model (6.1) predicts that the larger ET, or survival rate (here q_2) of the natural enemy on the pesticide application, or releasing rate (here q_3) and or release constant (here σ) is, the longer is the mean outbreak period (Fig.13(B), (D), (E) and (F)). Note that the mean outbreak period can suddenly jump from a small value to a larger value at some critical points of ET, q_3 and σ , which indicates that the selection of ET and releasing methods (inundative or inoculation release) may be crucial in prolonging the pest outbreak period. Moreover, the different ET, or different values of the release rate q_3 and or different values of the release constant σ may have the same mean outbreak period (Fig.13(B), (E) and (F)). Finally, we emphasize here that the effects of the other parameters r, b, c, d on the mean outbreak period can be investigated similarly.

7 Discussion

Natural enemies are usually more susceptible to the effects of pesticides than plant-feeding hosts or prey owing to their searching habits, usually less-developed enzyme-based detoxification systems and preening behavior. Usually, target pest resurgence can occur when natural enemies are destroyed. Thus, when using integrated pest management as an approach to control insect pests one must be committed to a long term strategy. If it is decided that spraying must occur, it is best to make sure that it is carried out at a time of the day or even season when there is the lowest chance of adversely affecting natural enemies. Apart from selecting pesticides that are likely to be less harmful to natural enemies and other non-target organisms such as pollinators, further selectivity can be gained by

judicious pesticide application involving minimization of the pesticide concentration and appropriate timing of pesticide applications.

Due to the antagonism between chemical and biological methods, understanding the range of possible ecological interactions among pest, natural enemy and pesticides is quite important for successful pest control. Here we have extended the classical continuous pest-natural enemy models to include an IPM control strategy in order to (a) understand why different release methods result in different pest control outcomes; (b) to estimate and predict the timing of a pesticide application and the instantaneous killing rates of insecticide applications on pest and natural enemy, and (c) to investigate the effects of initial densities of pest-natural enemy populations on insect pest control.

Two possible cases are investigated firstly according to the relations between spraying frequency of pesticides and release frequency of natural enemies. Whatever releases taken place more or less frequently than the sprays, the threshold conditions which guarantee the existence and stability of the pest eradication periodic solution are provided. Moreover, the effects of times of spraying pesticides (or releasing natural enemies) and control tactics on the threshold condition were carefully investigated. In particular, the effects of the releasing rate and releasing constant, instantaneous killing rates of pesticides for pest and natural enemy populations, releasing and spraying period on the stability of the pest-eradication periodic solution were discussed with regard to the extent of depression or resurgence resulting from pulse pesticide applications. The results imply that the modelling methods described can help in the design of appropriate control strategies and assist management decision-making.

If the integrated control methods can not completely eradicate the pest

population, i.e. the threshold condition does not hold true any more, the pest population can have outbreaks at different scales. By extensive numerical bifurcation investigations, we found that when choosing different parameter spaces, multiple attractors from which the pest population oscillates with different amplitudes can coexist for a wide range of parameters. The results indicate that the dynamic behavior of a population may be affected dramatically by small changes in the values of initial densities of the pest and natural enemy populations, and the switch-like transitions among these attractors showing that varying dosages and frequencies of insecticide applications and the numbers of natural enemies released are crucial for pest control. Meanwhile, the stable pest outbreak solutions with large amplitudes can switch to the stable pest outbreak solution with relatively small amplitude at a random time while the stable pest outbreak solutions with a smaller amplitude are robust to random perturbation. These results confirm that varying dosages of pesticide applications and numbers of natural enemies released are important for pest control and pesticide resistance.

In practice, a good pest control programme should reduce pest populations to levels acceptable (here ET level) to the public rather than eradication. Our second type of model is proposed based on this ideal. To reduce the pesticide application and avoid the antagonism, we assumed that the pesticides are released only when the densities of the pest population reach the ET and periodic repeated releases of natural enemies are applied. The factors which affect the pest outbreak frequency and mean outbreak period are discussed. The simulation results indicate that the pest outbreak period or frequency largely depends on the initial densities, control tactics and given ET.

We must emphasize here that proper identification of insect pests, natural

enemies and a basic knowledge of economic thresholds are essential for an IPM programme to be successful, which can help us to determine parameters p_1, p_2, p_3 and ET. Therefore, in order to keep track of both pest and natural enemy populations, regular field monitoring are necessary, and these data are quite important for making management decisions. However, regular field monitoring needs lots of manpower and time, and consequently increases the costs. Further, the ET is dynamic and depends on many factors, see more details on how to determine the ET from the literature (Tang and Cheke, 2005).

The majority of this work is based on deterministic models of the pest-natural enemy interaction with pulse perturbations and ET. This raises the interesting question of how robust the models are to various forms of environmental and demographic stochasticity, as it is well known that stochasticity can significantly affect the persistence and dynamics of populations (Bonsall and Hastings, 2004; Tang and Heron, 2008). The switch-like behavior in response to small random perturbations confirms that environmental stochasticity has little effect on the coexistence of attractors. However, demographic noise may affect the population dynamics more broadly, and is most influential in small populations. Stochastic fluctuations at small population sizes tend to be amplified by the dynamics to cause massive population variability, i.e. demographic stochasticity has a destabilizing effect. How do environmental and demographic stochasticity affect the rich dynamic behaviors described in this paper and influence the IPM strategy, including coexistence and the structure of the basin attractors? The introduction of stochasticity also allows us to investigate the interesting question of whether stochasticity is beneficial to IPM strategies or not, a question for future research directions.

This work focused entirely on the simplest pest-natural enemy model with impulsive effects and the temporal interactions of an insect pest and its natural enemy. A number of stabilizing factors such as spatial heterogeneity, density dependent growth of the pest and functional responses of the predator will be considered in future and will be reported elsewhere.

Acknowledgements

We would like to thank the referees for their careful reading of the original manuscript and many valuable comments and suggestions that greatly improved the presentation of this paper. The first author is supported by the National Natural Science Foundation of China NSFC 10871122(S.Y. Tang).

Appendix A

In any given time interval $(hT_N, (h+1)T_N]$, where h is a positive integer, we investigate the dynamical behavior of model (4.1). In fact, integrating the first equation of model (4.1) from hT_N to $\tau_1 + hT_N$ yields

$$y(t) = y(hT_N^+) \exp[-a(t - hT_N)], \quad t \in (hT_N, \tau_1 + hT_N].$$

At time $\tau_1 + hT_N$, one pesticide application occurs and

$$y((\tau_1 + hT_N)^+) = q_2 y(hT_N^+) \exp[-a\tau_1] = q_2 y(hT_N^+) \exp[-a\Delta_0].$$

Again, integrating the first equation of model (4.1) from $\tau_1 + hT_N$ to $\tau_2 + hT_N$ yields

$$y(t) = y((\tau_1 + hT_N)^+) \exp[-a(t - \tau_1 - hT_N)], \quad t \in (\tau_1 + hT_N, \tau_2 + hT_N].$$

At time $\tau_2 + hT_N$, one time pesticide application occurs and

$$y((\tau_2 + hT_N)^+) = q_2 y((\tau_1 + hT_N)^+) \exp[-a\Delta_1] = q_2^2 y(hT_N^+) \exp[-a(\Delta_0 + \Delta_1)].$$

By induction, we can see that

$$y(t) = q_2^{k_P} y(hT_N^+) \exp[-a(\Delta_0 + \Delta_1 + \dots + \Delta_{k_P-1})] \exp[-a(t - \tau_{k_P} - hT_N)], \quad (\text{A.1})$$

for all $t \in (\tau_{k_P} + hT_N, (h+1)T_N]$. At time $(h+1)T_N$, release of natural enemies occurs once and

$$y((h+1)T_N^+) = q_3 q_2^{k_P} y(hT_N^+) \exp[-aT_N] + \sigma. \quad (\text{A.2})$$

Denote $Y_h = y(hT_N^+)$, then we have the following difference equation

$$Y_{h+1} = q_3 q_2^{k_P} \exp[-aT_N] Y_h + \sigma,$$

which has a unique steady state

$$Y^* = \frac{\sigma}{1 - q_3 q_2^{k_P} \exp[-aT_N]}. \quad (\text{A.3})$$

Therefore if $q_3 q_2^{k_P} \exp[-aT_N] < 1$, then the model (4.1) has a globally stable T_N periodic solution (denoted by $y^{T_N}(t)$), which can be calculated as follows

$$y^{T_N}(t) = \begin{cases} Y^* \exp[-a(t - hT_N)], & t \in (hT_N, \tau_1 + hT_N], \\ q_2 Y^* \exp[-a\Delta_0] \exp[-a(t - \tau_1 - hT_N)], & t \in (\tau_1 + hT_N, \tau_2 + hT_N], \\ \vdots \\ q_2^{k_P} Y^* \exp\left[-a \sum_{i=0}^{k_P-1} \Delta_i\right] e^{[-a(t - \tau_{k_P} - hT_N)]}, & t \in (\tau_{k_P} + hT_N, (h+1)T_N]. \end{cases} \quad (\text{A.4})$$

Furthermore, we obtain the complete expression for the 'pest-eradication' periodic solution, $(0, y^{T_N}(t))$, of system (3.1) over the h -th time interval $hT_N < t \leq (h+1)T_N$.

It follows from system (3.1) that we have $y(t) > y^{T_N}(t) - \epsilon$ for t large enough and ϵ small enough. For simplification we may assume $y(t) > y^{T_N}(t) - \epsilon$ holds for all $t \geq 0$. Thus we have

$$\begin{cases} \frac{dx(t)}{dt} \leq rx(t) - bx(t)[y^{T_N}(t) - \epsilon], & t \neq \tau_n, \\ x(\tau_n^+) = q_1 x(\tau_n), & t = \tau_n. \end{cases} \quad (\text{A.5})$$

Again from the comparison theorem on impulsive differential equations we get

$$\begin{aligned} x(\tau_1 + hT_N) &\leq x(hT_N) \exp\left[\int_{hT_N}^{\tau_1 + hT_N} (r - b(y^{T_N}(t) - \epsilon)) dt\right], \\ x(\tau_2 + hT_N) &\leq x((\tau_1 + hT_N)^+) \exp\left[\int_{\tau_1 + hT_N}^{\tau_2 + hT_N} (r - b(y^{T_N}(t) - \epsilon)) dt\right] \\ &= q_1 x(\tau_1 + hT_N) \exp\left[\int_{\tau_1 + hT_N}^{\tau_2 + hT_N} (r - b(y^{T_N}(t) - \epsilon)) dt\right], \\ &\vdots \\ x((h+1)T_N) &\leq x((\tau_{k_P} + hT_N)^+) \exp\left[\int_{\tau_{k_P} + hT_N}^{(h+1)T_N} (r - b(y^{T_N}(t) - \epsilon)) dt\right] \\ &= q_1 x(\tau_{k_P} + hT_N) \exp\left[\int_{\tau_{k_P} + hT_N}^{(h+1)T_N} (r - b(y^{T_N}(t) - \epsilon)) dt\right], \end{aligned} \quad (\text{A.6})$$

which indicates that

$$\begin{aligned}
x((h+1)T_N) &\leq q_1^{k_P} x(hT_N) \exp \left[\int_{hT_N}^{\tau_1+hT_N} (r - b(y^{T_N}(t) - \epsilon)) dt \right. \\
&\quad + \sum_{j=1}^{k_P-1} \int_{\tau_j+hT_N}^{\tau_{j+1}+hT_N} (r - b(y^{T_N}(t) - \epsilon)) dt \\
&\quad \left. + \int_{\tau_{k_P}+hT_N}^{(h+1)T_N} (r - b(y^{T_N}(t) - \epsilon)) dt \right] \\
&= q_1^{k_P} x(hT_N) \exp \left[(r + b\epsilon)T_N + \frac{b}{a} Y^* \left(e^{-a\Delta_0} - 1 + q_2 \left(e^{-a \sum_{i=0}^1 \Delta_i} - e^{-a\Delta_0} \right) \right. \right. \\
&\quad + q_2^2 \left(e^{-a \sum_{i=0}^2 \Delta_i} - e^{-a \sum_{i=0}^1 \Delta_i} \right) + q_2^3 \left(e^{-a \sum_{i=0}^3 \Delta_i} - e^{-a \sum_{i=0}^2 \Delta_i} \right) \\
&\quad \left. \left. + \dots + q_2^{k_P} \left(e^{-a \left(\sum_{i=0}^{k_P} \Delta_i \right)} - e^{-a \left(\sum_{i=0}^{k_P-1} \Delta_i \right)} \right) \right) \right] \\
&= q_1^{k_P} x(hT_N) e^{\left[(r+b\epsilon)T_N + \frac{b}{a} Y^* \sum_{j=0}^{k_P} q_2^j \left(e^{-a \left(\sum_{i=0}^j \Delta_i \right)} - e^{-a \left(\sum_{i=0}^{j-1} \Delta_i \right)} \right) \right]} \\
&\triangleq x(hT_N) R_\epsilon^N
\end{aligned} \tag{A.7}$$

where $\sum_{i=0}^{-1} \Delta_i = 0$ and

$$R_\epsilon^N = q_1^{k_P} \exp \left[(r + b\epsilon)T_N + \frac{b}{a} Y^* \sum_{j=0}^{k_P} q_2^j \left(e^{-a(\sum_{i=0}^j \Delta_i)} - e^{-a(\sum_{i=0}^{j-1} \Delta_i)} \right) \right].$$

Therefore, if $R_0^N < 1$ then $x(hT) \leq x(0^+)(R_0^N)^h$ and $x(hT) \rightarrow 0$ as $h \rightarrow \infty$.

Consequently, $x(t) \rightarrow 0$ as $t \rightarrow \infty$. Similarly, we can prove $y(t) \rightarrow y^{T_N}(t)$ as

$t \rightarrow \infty$. This indicates that if $R_0^N < 1$ then the pest eradication periodic solution

$(0, y^{T_N}(t))$ is globally attractive.

Appendix B

In any given time interval $(hT_P, (h+1)T_P]$, where h is a positive integer, we

investigate the dynamical behavior of model (4.1). Integrating the first equation of

model (4.1) from hT_P to $\lambda_1 + hT_P$ yields

$$y(t) = y(hT_P^+) \exp[-a(t - hT_P)], \quad t \in (hT_P, \lambda_1 + hT_P].$$

At time $\lambda_1 + hT_P$, one release of natural enemies occurs and

$$y((\lambda_1 + hT_P)^+) = q_3 y(hT_P^+) \exp[-a\lambda_1] + \sigma = q_3 y(hT_P^+) \exp[-a\Delta_0] + \sigma.$$

Again, integrating the first equation of model (4.1) from $\lambda_1 + hT_P$ to $\lambda_2 + hT_P$ yields

$$y(t) = y((\lambda_1 + hT_P)^+) \exp[-a(t - \lambda_1 - hT_P)], \quad t \in (\lambda_1 + hT_P, \lambda_2 + hT_P].$$

At time $\lambda_2 + hT_P$, one release of natural enemies occurs and

$$\begin{aligned} y((\lambda_2 + hT_P)^+) &= q_3 y((\lambda_1 + hT_P)^+) \exp[-a\Delta_1] + \sigma \\ &= q_3^2 y(hT_P^+) \exp[-a(\Delta_0 + \Delta_1)] + q_3 \sigma \exp[-a\Delta_1] + \sigma. \end{aligned}$$

Similarly, we have

$$\begin{aligned} y((\lambda_3 + hT_P)^+) &= q_3 y((\lambda_2 + hT_P)^+) \exp[-a\Delta_2] + \sigma \\ &= q_3^3 y(hT_P^+) \exp[-a(\Delta_0 + \Delta_1 + \Delta_2)] \\ &\quad + q_3^2 \sigma \exp[-a(\Delta_1 + \Delta_2)] + q_3 \sigma \exp[-a\Delta_2] + \sigma \\ &= q_3^3 y(hT_P^+) \exp[-a(\Delta_0 + \Delta_1 + \Delta_2)] + \sigma \sum_{i=0}^2 q_3^i \exp\left[-a \sum_{j=3-i}^2 \Delta_j\right]. \end{aligned}$$

By induction, we can see that

$$y((\lambda_{k_N} + hT_P)^+) = q_3^{k_N} y(hT_P^+) \exp\left[-a \sum_{i=0}^{k_N-1} \Delta_i\right] + \sigma \sum_{i=0}^{k_N-1} q_3^i \exp\left[-a \sum_{j=k_N-i}^{k_N-1} \Delta_j\right]$$

and

$$y(t) = y((\lambda_{k_N} + hT_P)^+) \exp[-a(t - \lambda_{k_N} - hT_P)], \quad t \in (\lambda_{k_N} + hT_P, (h+1)T_P], \quad (\text{B.1})$$

At time $(h+1)T_P$, one pesticide application occurs and

$$\begin{aligned} y((h+1)T_P^+) &= q_2 y((\lambda_{k_N} + hT_P)^+) \exp[-a(T_P - \lambda_{k_N})] \\ &= q_2 q_3^{k_N} y(hT_P^+) \exp\left[-a \sum_{i=0}^{k_N} \Delta_i\right] + q_2 \sigma \sum_{i=0}^{k_N-1} q_3^i \exp\left[-a \sum_{j=k_N-i}^{k_N} \Delta_j\right]. \end{aligned} \quad (\text{B.2})$$

Denote $Y_h = y(hT_P^+)$, then we have the following difference equation

$$\begin{aligned} Y_{h+1} &= q_2 q_3^{k_N} \exp \left[-a \sum_{i=0}^{k_N} \Delta_i \right] Y_h + q_2 \sigma \sum_{i=0}^{k_N-1} q_3^i \exp \left[-a \sum_{j=k_N-i}^{k_N} \Delta_j \right] \\ &= q_2 q_3^{k_N} \exp [-aT_P] Y_h + q_2 \sigma \sum_{i=0}^{k_N-1} q_3^i \exp \left[-a \sum_{j=k_N-i}^{k_N} \Delta_j \right] \\ &\triangleq \phi Y_h + \psi \end{aligned}$$

which has a unique steady state

$$Y^* = \frac{\psi}{1 - \phi}. \quad (\text{B.3})$$

Therefore if $q_2 q_3^{k_N} \exp [-aT_P] < 1$, then model (4.1) has a globally stable T_P periodic solution (denoted by $y^{T_P}(t)$), which can be calculated as follows

$$y^{T_P}(t) = \begin{cases} Y^* \exp[-a(t - hT_P)], & t \in (hT_P, \lambda_1 + hT_P], \\ [q_3 Y^* \exp(-a\Delta_0) + \sigma] \exp[-a(t - \lambda_1 - hT_P)], & t \in (\lambda_1 + hT_P, \lambda_2 + hT_P], \\ \vdots \\ \left\{ q_3^{k_N} Y^* \exp \left[-a \sum_{i=0}^{k_N-1} \Delta_i \right] + \sigma \sum_{i=0}^{k_N-1} q_3^i \exp \left[-a \sum_{j=k_N-i}^{k_N} \Delta_j \right] \right\} e^{[-a(t - \lambda_{k_N} - hT_P)]}, & t \in (\lambda_{k_N} + hT_P, (h+1)T_P]. \end{cases} \quad (\text{B.4})$$

Once again for Case 2, we obtain the complete expression for the 'pest-eradication' periodic solution, $(0, y^{T_P}(t))$, of system (3.1) over the h -th time interval $hT_P < t \leq (h+1)T_P$.

It follows from system (3.1) that we have $y(t) > y^{T_P}(t) - \epsilon$ for t large enough and ϵ small enough. For simplification we may assume $y(t) > y^{T_P}(t) - \epsilon$ holds for all $t \geq 0$. Thus we have

$$\begin{cases} \frac{dx(t)}{dt} \leq rx(t) - bx(t)[y^{T_P}(t) - \epsilon], & t \neq \tau_n, \\ x(\tau_n^+) = q_1 x(\tau_n), & t = \tau_n. \end{cases} \quad (\text{B.5})$$

Again from the comparison theorem on impulsive differential equations we get

$$\begin{aligned}
x((h+1)T_P) &\leq x(hT_P^+) \exp \left[\int_{hT_P^+}^{(h+1)T_P} (r - b(y^{T_P}(t) - \epsilon)) dt \right] \\
&= x(hT_P^+) \exp \left[\int_{hT_P^+}^{\lambda_1+hT_P} (r - b(y^{T_P}(t) - \epsilon)) dt \right. \\
&\quad + \sum_{j=1}^{k_N-1} \int_{\lambda_j+hT_P}^{\lambda_{j+1}+hT_P} (r - b(y^{T_P}(t) - \epsilon)) dt \\
&\quad \left. + \int_{\lambda_{k_N}+hT_P}^{(h+1)T_P} (r - b(y^{T_P}(t) - \epsilon)) dt \right] \\
&= x(hT_P^+) \exp \left[(r + b\epsilon)T_P + \frac{b}{a} Y^* (\exp(-a\Delta_0) - 1) \right. \\
&\quad + \frac{b}{a} [q_3 Y^* \exp(-a\Delta_0) + \sigma] (\exp(-a\Delta_1) - 1) + \dots + \\
&\quad \left. \frac{b}{a} \left[q_3^{k_N} Y^* \exp \left(-a \sum_{i=0}^{k_N-1} \Delta_i \right) + \sigma \sum_{i=0}^{k_N-1} q_3^i \exp \left(-a \sum_{j=k_N-i}^{k_N-1} \Delta_j \right) \right] \right. \\
&\quad \left. (\exp(-a\Delta_{k_N}) - 1) \right] \\
&\triangleq x(hT_P^+) \Theta_\epsilon^P,
\end{aligned} \tag{B.6}$$

which indicates that

$$x((h+1)T_P^+) \leq q_1 x(hT_P^+) \Theta_\epsilon^P \triangleq x(hT_P^+) R_\epsilon^P \tag{B.7}$$

where $\sum_{i=0}^{k_N-1} \Delta_i = 0$.

Therefore, if $R_0^P < 1$ then $x(hT_P^+) \leq x(0^+) (R_0^P)^h$ and $x(hT_P^+) \rightarrow 0$ as $h \rightarrow \infty$.

Consequently, $x(t) \rightarrow 0$ as $t \rightarrow \infty$. Similarly, we can prove $y(t) \rightarrow y^{T_P}(t)$ as $t \rightarrow \infty$. This indicates that if $R_0^P < 1$ then the pest eradication periodic solution $(0, y^{T_P}(t))$ is globally attractive.

In particular, if $\Delta_i \equiv \Delta$ for all $i = 0, 1, 2, \dots, k_N$, then the condition $R_0^P < 1$ becomes as follows:

$$\begin{aligned}
R_0^P &= q_1 \exp \left[rT_P + \frac{b}{a} (e^{(-a\Delta)} - 1) \left[Y^* + q_3 Y^* e^{(-a\Delta)} + \dots + q_3^{k_N} Y^* e^{(-ak_N\Delta)} \right. \right. \\
&\quad \left. \left. + \sigma + \dots + \sigma \sum_{i=0}^{k_N-1} q_3^i \exp \left(-a \sum_{j=k_N-i}^{k_N-1} \Delta_j \right) \right] \right] \\
&= q_1 e \left[rT_P + \frac{b}{a} (e^{-a\Delta} - 1) \left(\frac{Y^* (1 - q_3^{k_N+1} e^{-aT_P})}{1 - q_3 e^{-a\Delta}} + \sigma \sum_{i=1}^{k_N} (k_N+1-i) q_3^{i-1} e^{-a(i-1)\Delta} \right) \right]
\end{aligned} \tag{B.8}$$

and

$$Y^* = \frac{\psi}{1 - \phi} \quad (\text{B.9})$$

with $\phi = q_2 q_3^{k_N} \exp[-aT_P]$ and

$$\begin{aligned} \psi &= q_2 \sigma \sum_{i=0}^{k_N-1} q_3^i \exp \left[-a \sum_{j=k_N-i}^{k_N} \Delta \right] = q_2 \sigma \sum_{i=0}^{k_N-1} q_3^i \exp[-a(i+1)\Delta] \\ &= q_2 \sigma \frac{(\exp(-a\Delta) - q_3^{k_N} \exp(-aT_P))}{1 - q_3 \exp(-a\Delta)}. \end{aligned}$$

References

- Barclay, H.J., 1982. Models for pest control using predator release, habitat management and pesticide release in combination. *J. Appl. Ecol.* 19,337-348.
- Barclay, H.J., van den Driessche, P. 1977. Predator-prey models with added mortality. *Can. Entomol.* 109,763-768.
- Barlow, N.D., Moller, H., Beggs, J.R., 1996. A model for the effect of *Sphecophaga vesparum* as a biological control agent of the common wasp in New Zealand. *J. Appl. Ecol.* 33,31-34.
- Beddington, J.R., Free, C.A., Lawton, J.H., 1978. Characteristics of successful natural enemies in models of biological control of insect pests. *Nature* 273,513-519.
- Bonsall, M.B., Hastings, A., 2004. Demographic and environmental stochasticity in predator-prey metapopulation dynamics. *J. Anim. Ecol.* 73,1043-1055.
- Burnett, T., 1960. Effects of initial densities and periods of infestation on the growth forms of a host and parasite population. *Can. J. Zool.* 38,1063-1077.
- Carpenter, S.R., 1981. Effect of control measures on pest populations subject to regulation by parasites and pathogens. *J. Theor. Biol.* 92,181-184.
- Debach, P., 1974. *Biological control by natural enemies*. Cambridge University Press, London.
- Flint, M.L., 1987. *Integrated Pest Management for Walnuts*, University of California Statewide Integrated Pest Management Project, Division of Agriculture and Natural Resources, Second Edition, University of California, Oakland, CA, publication 3270, pp 3641.

- Foster, G.N., Kelly, A., 1978. Initial density of glasshouse whitefly (*Trialeurodes vaporariorum* (Westwood), Hemiptera) in relation to the success of suppression by *Encarsia formosa* Gahan (Hymenoptera) on glasshouse tomatoes. *Hortic Res* 18,55-62.
- Greathead, D.J., 1992. Natural enemies of tropical locusts and grasshoppers: their impact and potential as biological control agents. In: Lomer, C. J.; Prior, C., eds. *Biological control of locusts and grasshoppers*. Wallingford, UK: C.A.B. International: 105-121.
- Hassell, M.P., 1984. Insecticides in host-parasitoid interactions. *Theor. Popul. Biol.* 26, 378-386.
- Hassell, M.P., May, R.M., 1973. Stability in insect host-parasite models. *J. Anim. Ecol.* 42,693-726.
- Hoddle, M.S., van Driesche, R.G., Sanderson, J.P., 1997. Biological control of *Bemisia argentifolii* (Homoptera: Aleyrodidae) on poinsettia with inundative releases of *Encarsia formosa* "Beltsville Strain" (Hymenoptera: Aphelinidae): Can parasitoid reproduction augment inundative releases? *J. Econ. Entomol.* 90,910-924.
- Hoddle, M.S., van Driesche, R.G., Sanderson, J.P., 1997. Biology and use of the whitefly parasitoid *Encarsia formosa*. *Annu. Rev. Entomol.* 43,645-669.
- Hoffmann, M.P., Frodsham, A.C., 1993. *Natural enemies of vegetable insect pests*. Cooperative Extension, Cornell University, Ithaca, NY, pp. 63.
- Jones, W.A., Greenberg, S.M., Legaspi, J.R., 1999. The effect of varying *Bemisia argentifolii* and *Eretmocerus mundus* ratios on parasitism. *BioControl* 44,13-28.
- Liu, X.N., Chen, L.S. 2004. Global dynamics of the periodic logistic system with periodic impulsive perturbations. *J. Math. Anal. Appl.* 289, 279-291.
- Lotka, A.J., 1920. Undamped oscillations derived from the law of mass action. *J. Amer. Chem. Soc.* 42, 1595-1599.
- May, R.M., 1978. Host-parasitoid systems in patchy environments: a phenomenological model. *J. Anim. Ecol.* 47,833-843.
- May, R.M., Hassell, M.P., 1988. Population dynamics and biological control. *Phil. Trans. R. Soc. Lond. B* 318,129-169.

- Neuenschwander, P., Herren, H.R., 1988. Biological Control of the Cassava Mealybug, *Phenacoccus manihoti*, by the Exotic Parasitoid *Epidinocarsis lopezi* in Africa. *Phil. Trans. R. Soc. Lond. B* 318,319-333.
- Parker, F.D., 1971. Management of pest populations by manipulating densities of both host and parasites through periodic releases, In: Huffaker, C. B., ed. *Biological control*. New York: Plenum Press.
- Pedigo, L.P., Higley, L.G., 1992. A new perspective of the economic injury level concept and environmental quality. *Amer. Entomol.* 38,12-20.
- Ruberson, J.R., Nemoto, H., Hirose, Y., 1998. Pesticides and conservation of natural enemies in pest management. In: P. Barbosa (ed.), *Conservation Biological Control*, pp. 207-220. Academic Press, New York.
- Tang, S.Y., Chen, L.S., 2004. Modelling and analysis of integrated pest management strategy. *Dis. Cont. Dyna. Sys. B* 4,759-768.
- Tang, S.Y., Cheke, R.A., 2005. State-dependent impulsive models of integrated pest management (IPM) strategies and their dynamic consequences. *J. Math. Biol.* 50,257-292.
- Tang, S.Y., Xiao, Y.N., Chen, L.S., Cheke, R.A., 2005. Integrated pest management models and their dynamical behavior. *Bull. Math. Biol.* 67,115-135.
- Tang, S.Y., Heron, E.A., 2008. Bayesian inference for a stochastic logistic model with switching points. *Ecol. Mod.* 215,153-169.
- Tang, S.Y., Cheke, R.A., 2008. Models for integrated pest control and their biological implications. *Math. Biosci.* 215,115-125.
- Tang S.Y., Xiao Y.N., Cheke, R.A., 2008. Multiple attractors of host-parasitoid models with integrated pest management strategies: Eradication, persistence and outbreak. *Theor. Popul. Biol.* 73,181-197.
- Udayagiri, S., Norton, A.P., Welter, S.C., 2000. Integrating pesticide effects with inundative biological control: interpretation of pesticide toxicity curves for *Anaphes iole* in strawberries. *Entomologia Experimentalis et Applicata* 95,87-95.
- Van Lenteren, J.C., 1995. Integrated pest management in protected crops, in: D.Dent (Ed.), *Integrated pest management*, Chapman & Hall, London 311-320.

- van Lenteren, J.C., 2000. Measures of success in biological control of arthropods by augmentation of natural enemies, in: S.Wratten, G.Gurr(Eds.), Measures of Success in Biological Control, Kluwer Academic Publishers, Dordrecht, 77-89.
- Van Lenteren, J.C., Woets, J., 1988. Biological and integrated pest control in greenhouses, *Ann. Rev. Ent.* 33,239-250.
- Volterra, V., 1931. Variations and fluctuations of a number of individuals in animal species living together. Translation In: R.N. Chapman: *Animal Ecology*, New York: McGraw Hill, 409-448.
- Waage, J.K., Hassell, M.P., 1982. Parasitoids as biological control agents-a fundamental approach. *Parasitology* 84,241-268.
- Waage, J.K., Hassell, M.P., Godfray, H.C.J., 1985. The dynamics of pest-parasitoid-insecticide interactions. *J. Appl. Ecol.* 22,825-838.

Figure Legends

Figure 1: Economic Injury Level (EIL) = lowest population density that will cause economic damage. Economic Threshold (ET) = population density at which control measures should be introduced to prevent an increasing pest population from reaching the economic injury level. The arrows indicate points when pest levels exceed the economic threshold and an IPM strategy would be applied.

Figure 2: The effects of number of pesticide applications and release period T_N on the threshold level R_0^N . The parameter values are as follows: $r = 1.1755, b = 1, a = 0.307, q_1 = 0.85, q_3 = 1.0, \sigma = 5.1$, and $k_p = 1, 2, 3, \dots, 12$ with $\Delta_i \equiv \Delta$.

Figure 3: The effects of the number of pesticide applications and release rate q_3 on the threshold level R_0^N . The parameter values are as follows: $r = 1.3, b = 1, a = 0.42, \sigma = 0.5$, and $k_p = 1, 2, 3, \dots, 12$ with $\Delta_i \equiv \Delta$. (A) $q_1 = 0.45, q_2 = 0.94, T_N = 4.2$; (B) $q_1 = 0.65, q_2 = 0.94, T_N = 4.2$; (C) $q_1 = 0.45, q_2 = 0.94, T_N = 4$; (D) $q_1 = 0.65, q_2 = 0.98, T_N = 4.2$.

Figure 4: The effects of times of spraying pesticides and parameter sets on the threshold level R_0^N . The parameter values are as follows: $r = 1.2, b = 1, a = 0.307, q_3 = 1.0$, and $k_p = 1, 2, 3, \dots, 12$ with $\Delta_i \equiv \Delta$. (A) $q_2 = 0.95, \sigma = 5, T_N = 14$; (B) $q_1 = 0.65, \sigma = 5, T_N = 14$; (C) $q_1 = 0.75, q_2 = 0.95, T_N = 14$; (D) $q_1 = 0.75, q_2 = 0.95, \sigma = 5$.

Figure 5: Three coexisting attractors of system (3.1) with parameters as follows: $r = 1.5, b = 1, a = 0.6, q_1 = 0.85, q_2 = 0.95, q_3 = 4.12, \sigma = 0.5, \delta = 0, c = 0.3, k_N = 2, T_N = 4$. The initial conditions are: (A-B) (2.6, 2); (C-D) (2.6, 1); (E-F) (0.6, 1.5).

Figure 6: Basins of attraction of the three attractors shown in Fig.5 with the parameters identical to those in Figure 5. The white, green and red points are attracted to the attractors shown in Fig.5 from top to bottom, respectively.

Figure 7: Attractors' switch-like behavior of system (3.1) with small random perturbation on parameters q_2 and σ , i.e. $\eta_2 = 0.05, \eta_4 = 0.05$ and $\eta_1 = \eta_3 = 0$. The other parameters are identical to those in Fig.5.

Figure 8: Attractors' switch-like behavior of system (3.1) with small random perturbation on parameters q_1 and q_3 , i.e. $\eta_3 = 0.1, \eta_1 = 0.05$ and $\eta_2 = \eta_4 = 0$. The other parameters are identical to those in Fig.5.

Figure 9: The effects of times of releasing natural enemies and releasing constant σ on the threshold level R_0^N . The parameter values are as follows: $r = 0.8, b = 1, a = 0.2, T_P = 5, q_1 = 0.75, q_2 = 0.9, q_3 = 1.1$ with $\Delta_i \equiv \Delta$.

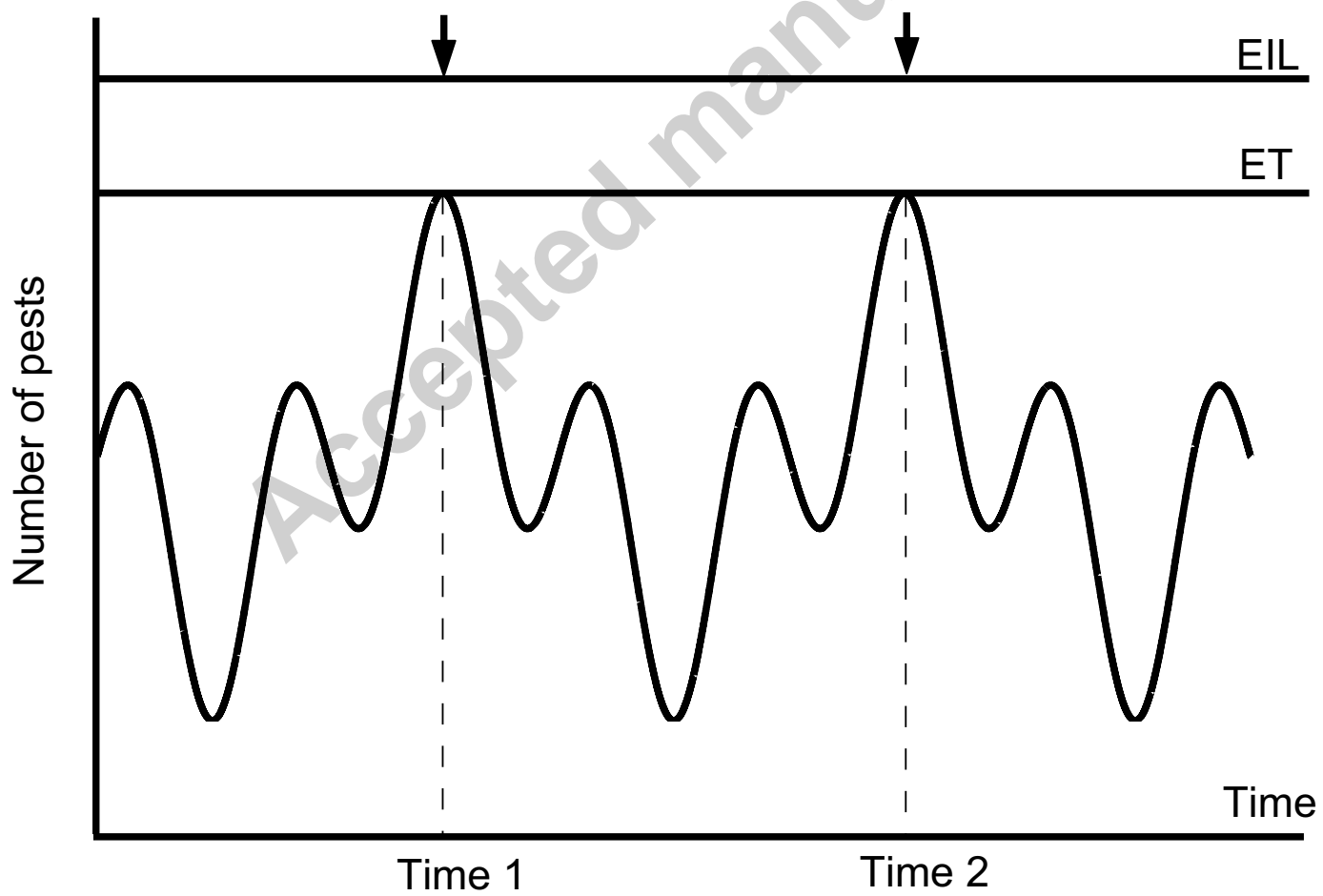
Figure 10: Two coexisting attractors of system (3.1) with parameters as follows: $r = 3, b = 1, a = 0.2, q_1 = 0.65, q_2 = 0.98, q_3 = 1.2, \sigma = 0.5, \delta = 0, c = 0.3, T_P = 8.22, k_N = 2$. The initial conditions are: (A-B) (0.6, 1); (C-D) (0.6, 0.7).

Figure 11: Attractors' switch-like behavior of system (3.1) with small random perturbation on parameters q_1 and q_3 , i.e. $\eta_3 = 0.1, \eta_1 = 0.05$ and $\eta_2 = \eta_4 = 0$. The other parameters are identical to those in Fig.10.

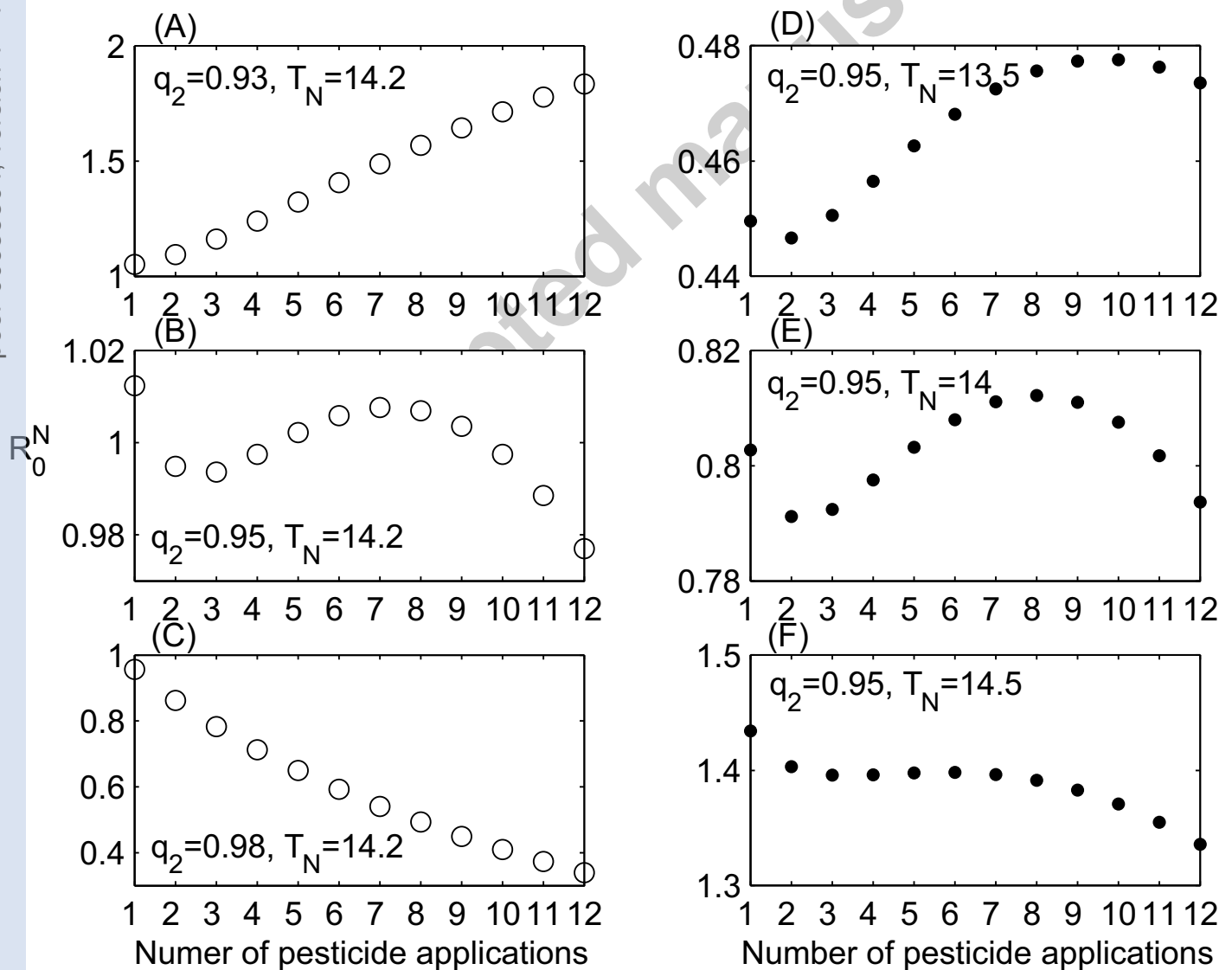
Figure 12: Illustrating the effects of ET and initial densities of pest and natural enemy populations of model (6.1) on the control strategies. The parameters are fixed as follows: $r = 3, b = 1, a = 0.3, q_1 = 0.65, q_2 = 0.95, q_3 = 1.2, \sigma = 1, \delta = 0, c = 0.3, T = 4$. Initial densities in (A) is (1.8, 1.7), in (B) is (0.6,1), in (C) is (1.2, 0.8), in (D) is (2.1,0.5), in (E) is (2.7, 0.4), and in (F) is (1.8, 0.2).

Figure 13: The mean outbreak period of model (6.1), as a function of T in (A), as a function of ET in (B), as a function of q_1 in (C), as a function of q_2 in (D), as a function of q_3 in (E), and as a function of σ in (F). The basic parameter set is fixed as follows: $r = 2, b = 1, a = 0.6, q_1 = 0.65, q_2 = 0.95, q_3 = 1.2, \sigma = 1, \delta = 0, c = 0.1, T = 4, ET = 5$. Initial densities are $(H_0, P_0) = (1, 1)$. Simulations were run for $100 \times T$ to rule out transients, and then run for $50 \times T$ to get T_n which allows us determine the average outbreak period.

4. Figure 1

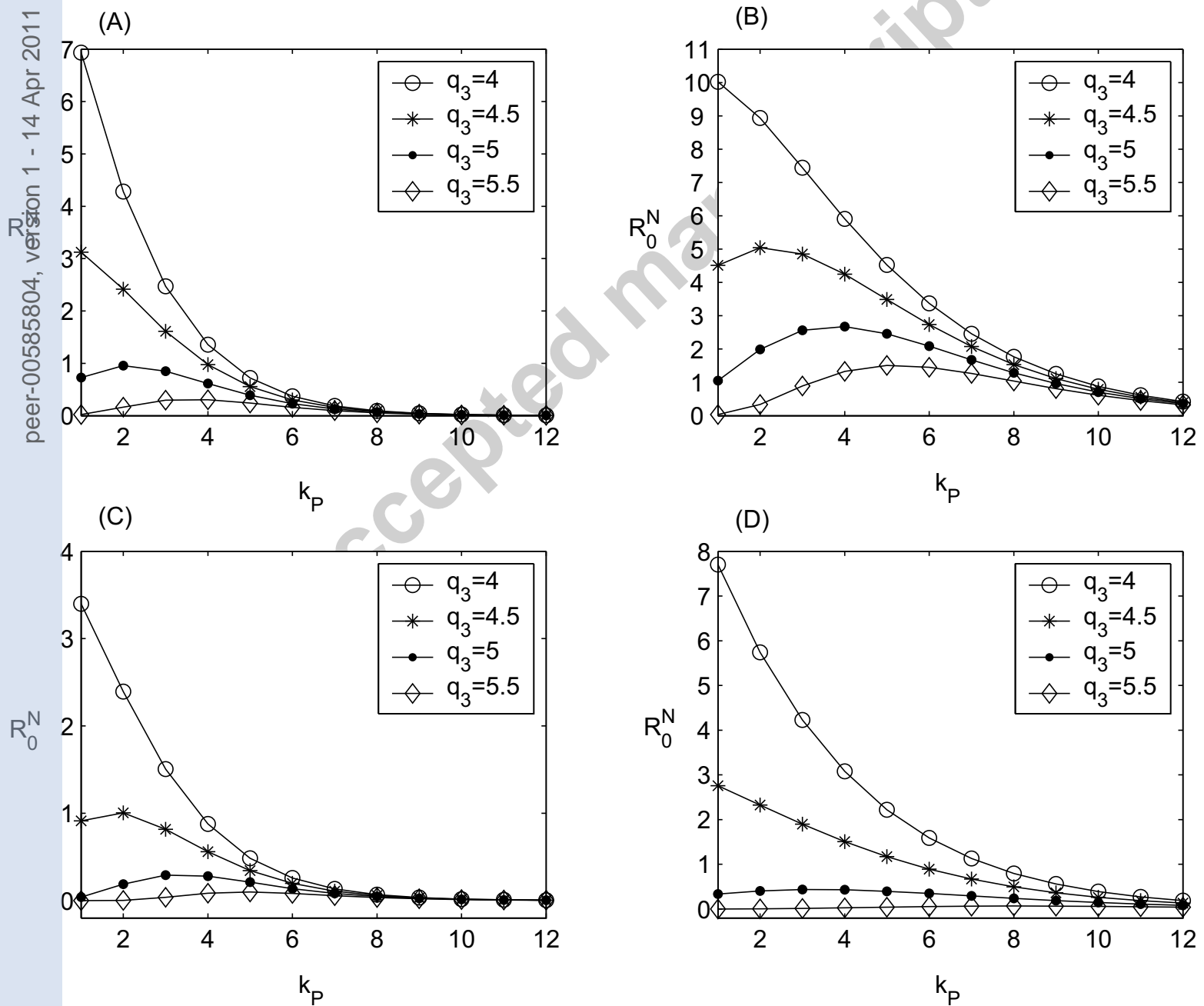


4. Figure 2

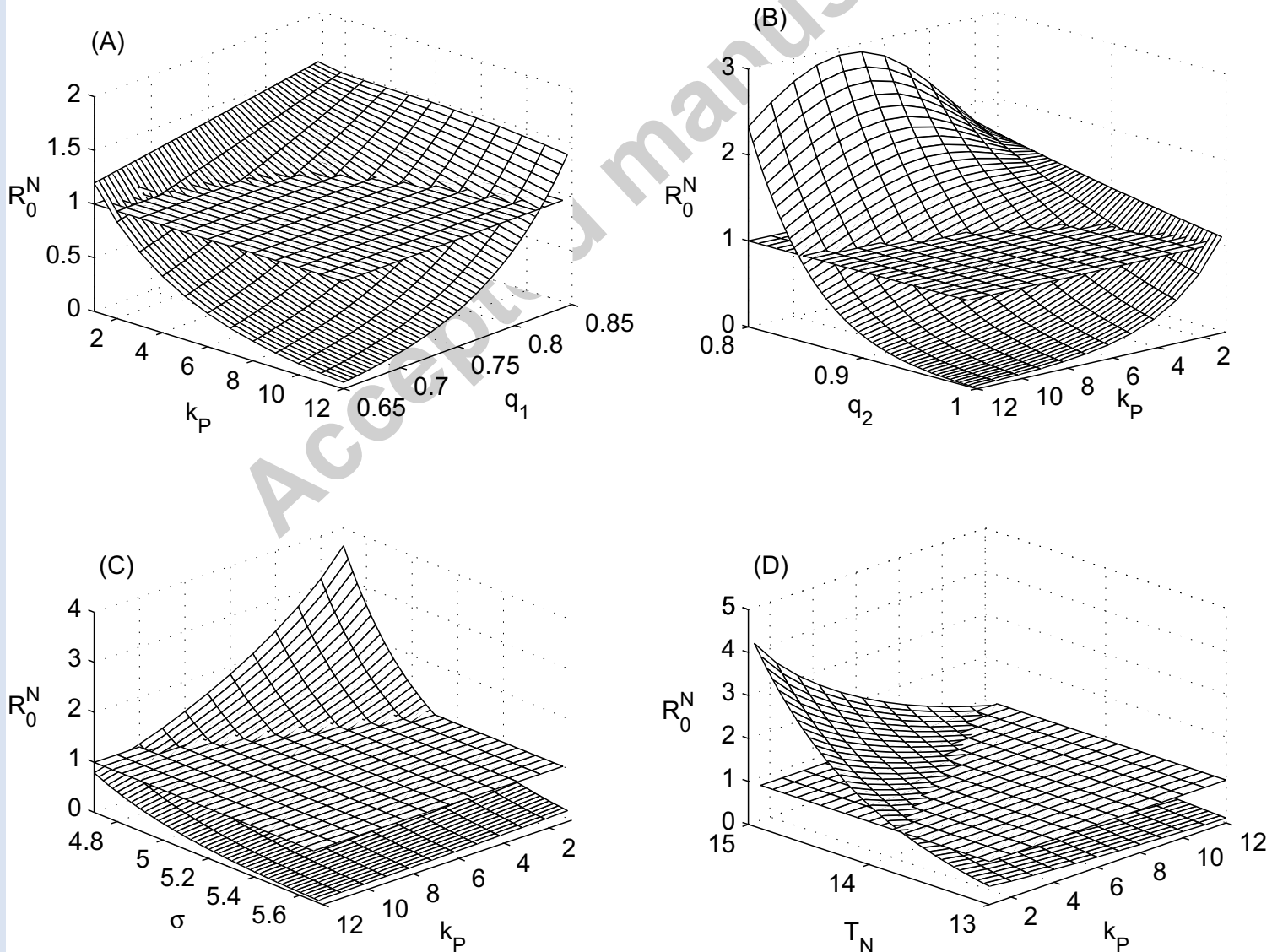


4. Figure 3

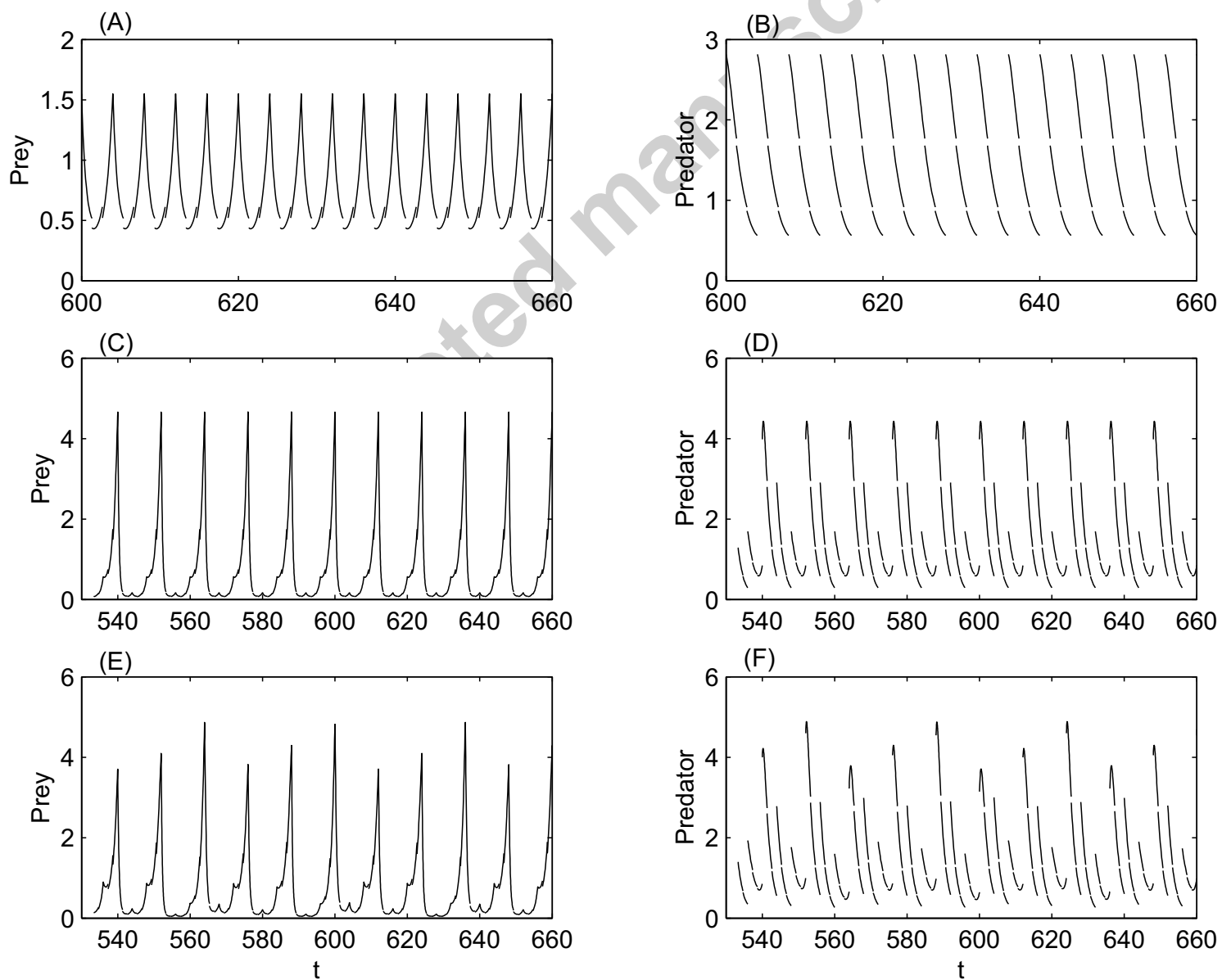
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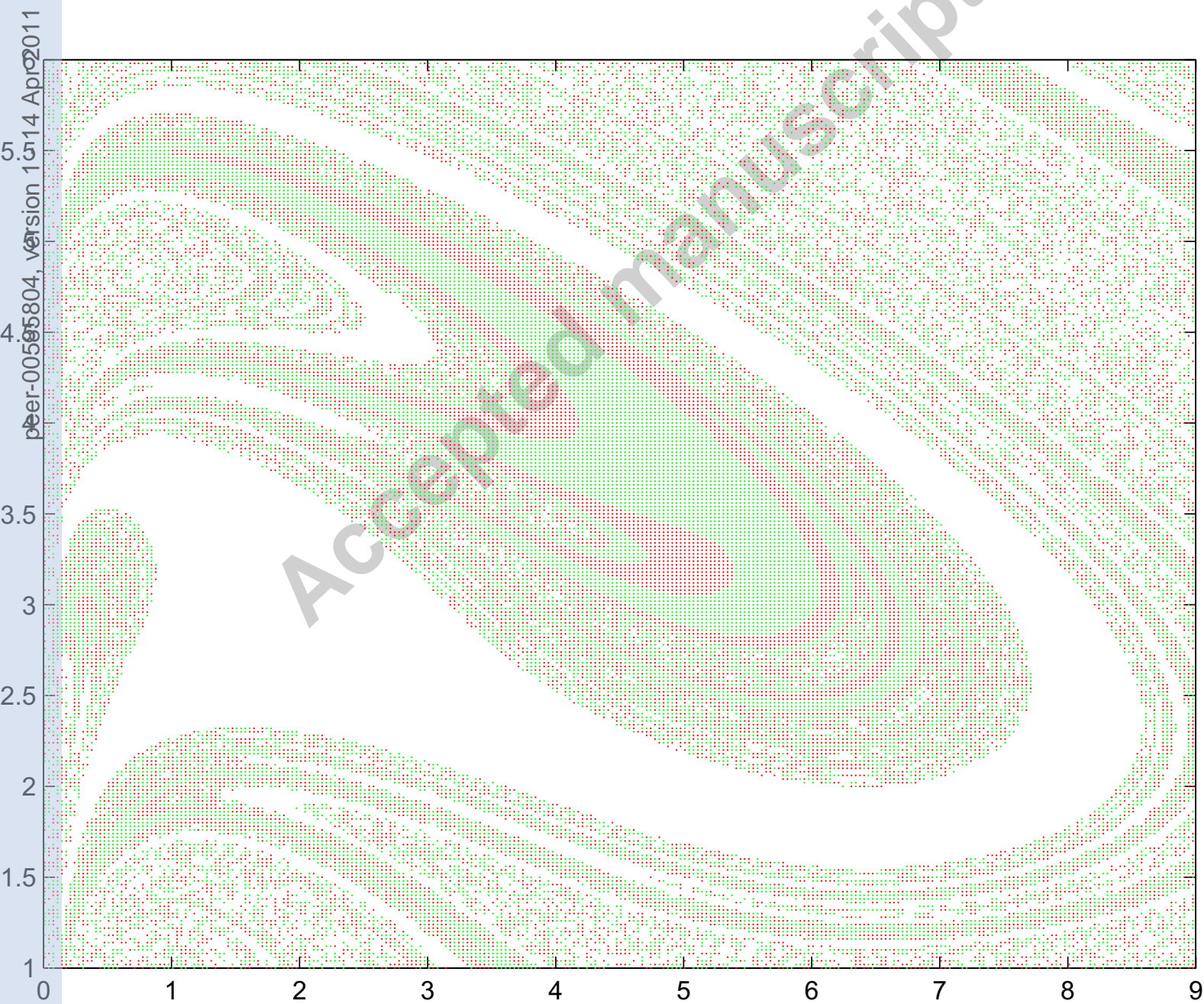
4. Figure 4



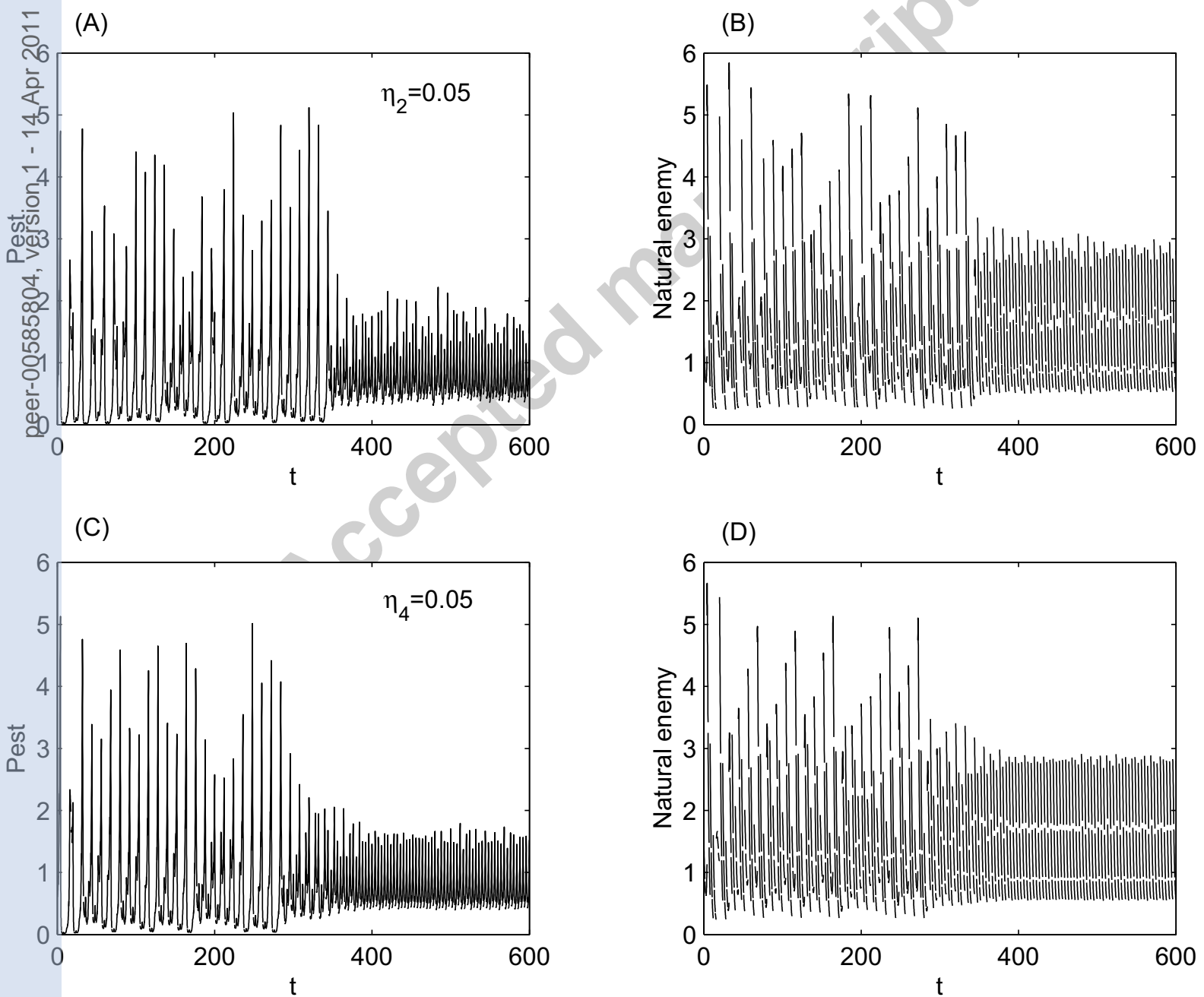
4. Figure 5



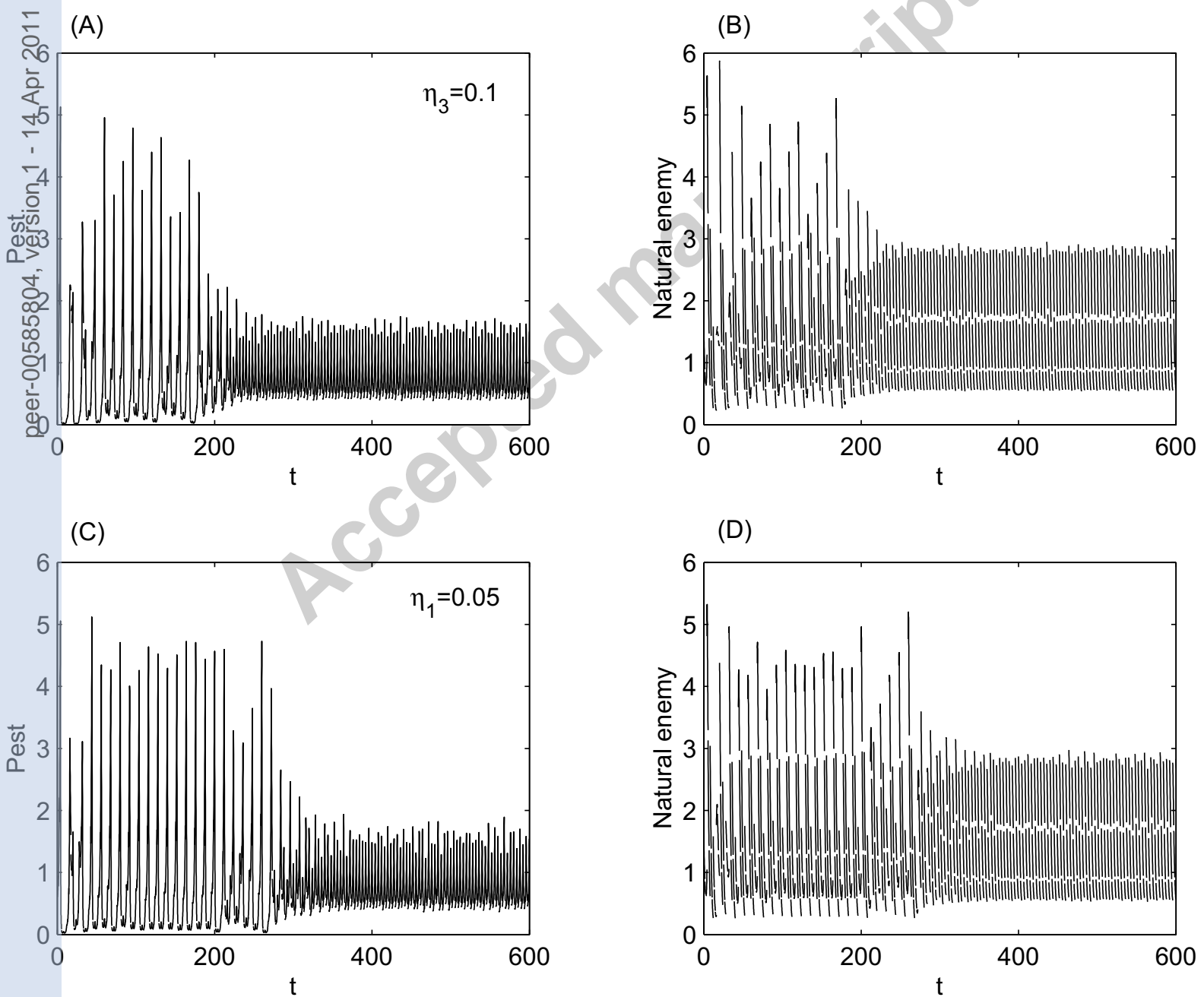
4. Figure 6



4. Figure 7

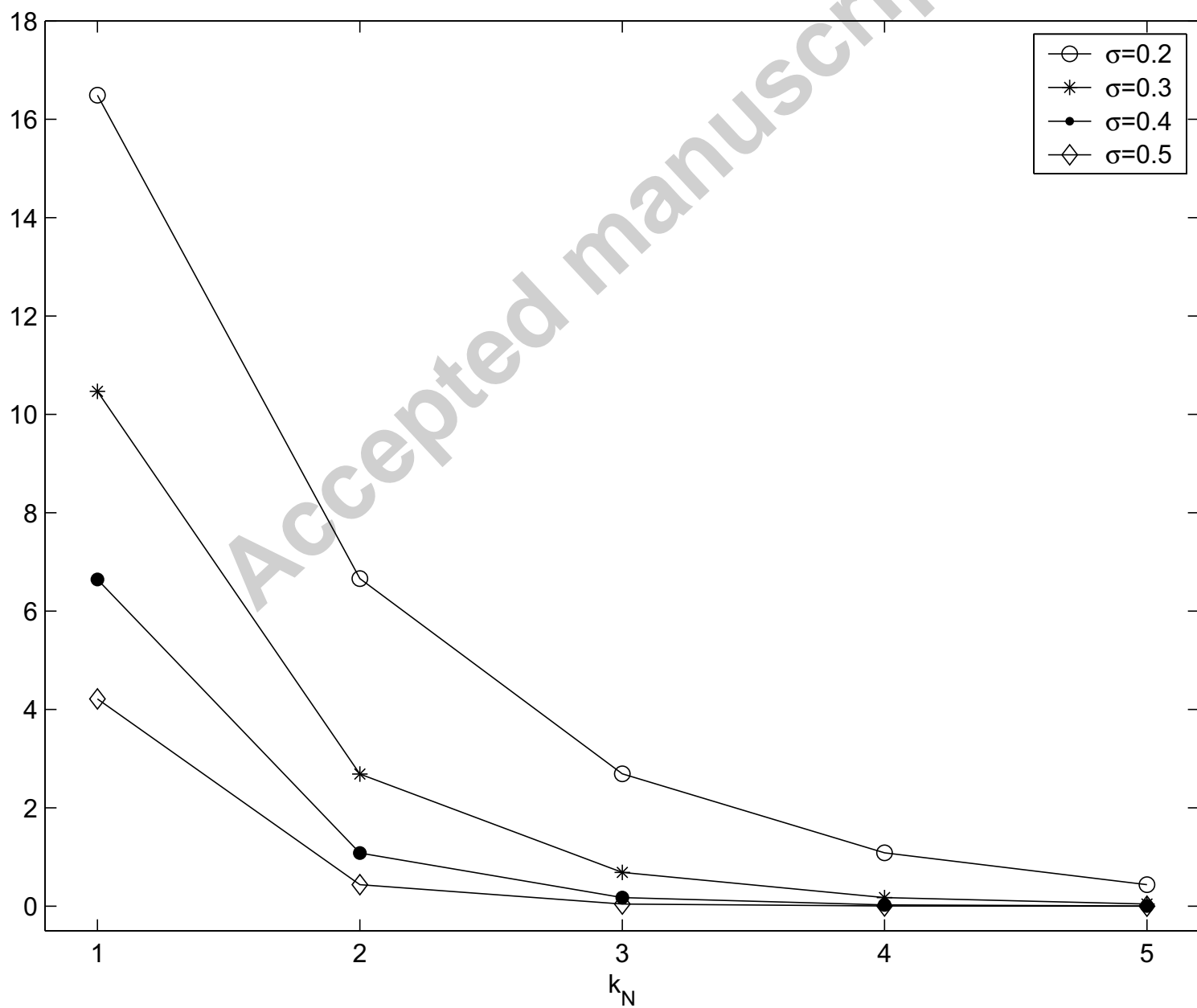


4. Figure 8



4. Figure 9

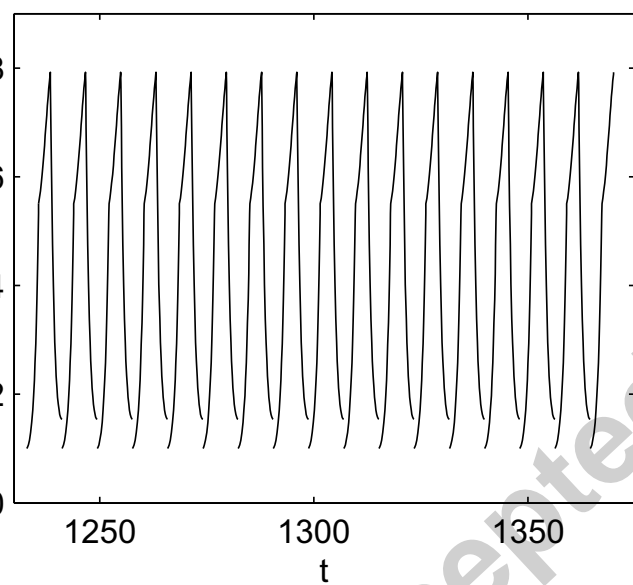
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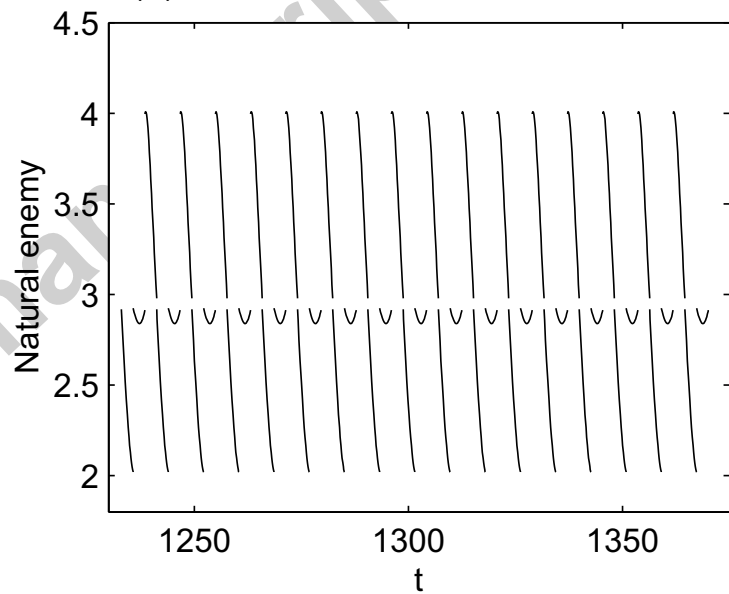
4. Figure 10

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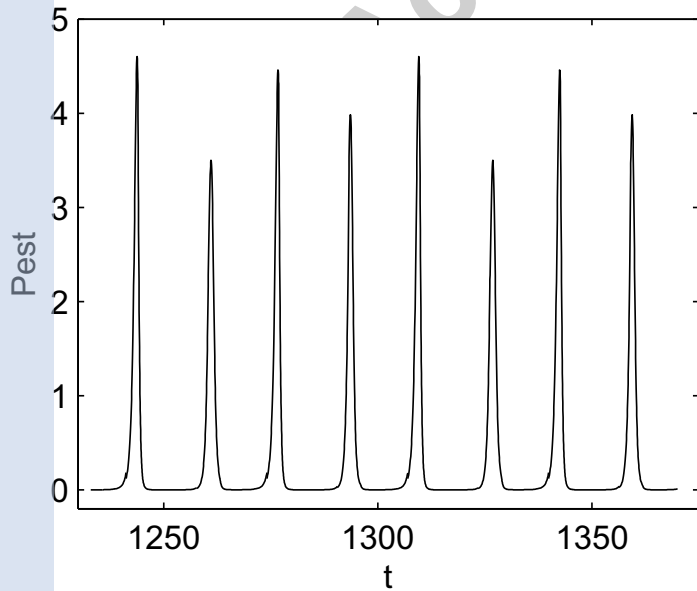
(A)



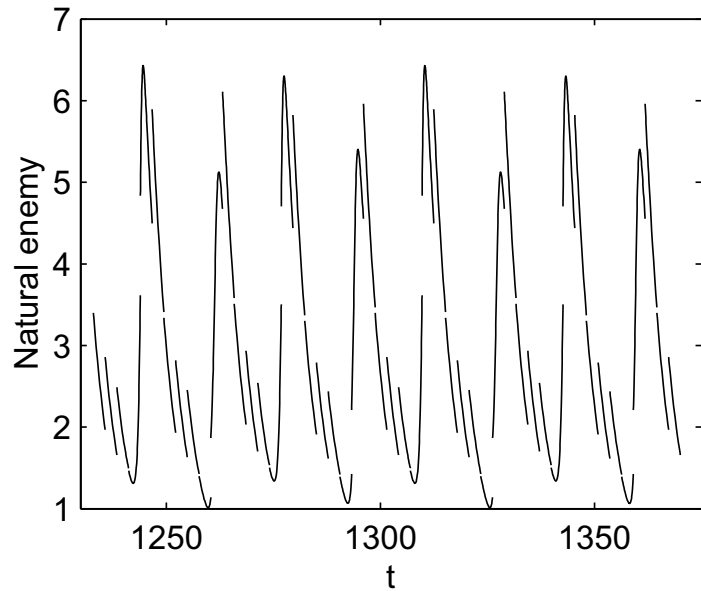
(B)



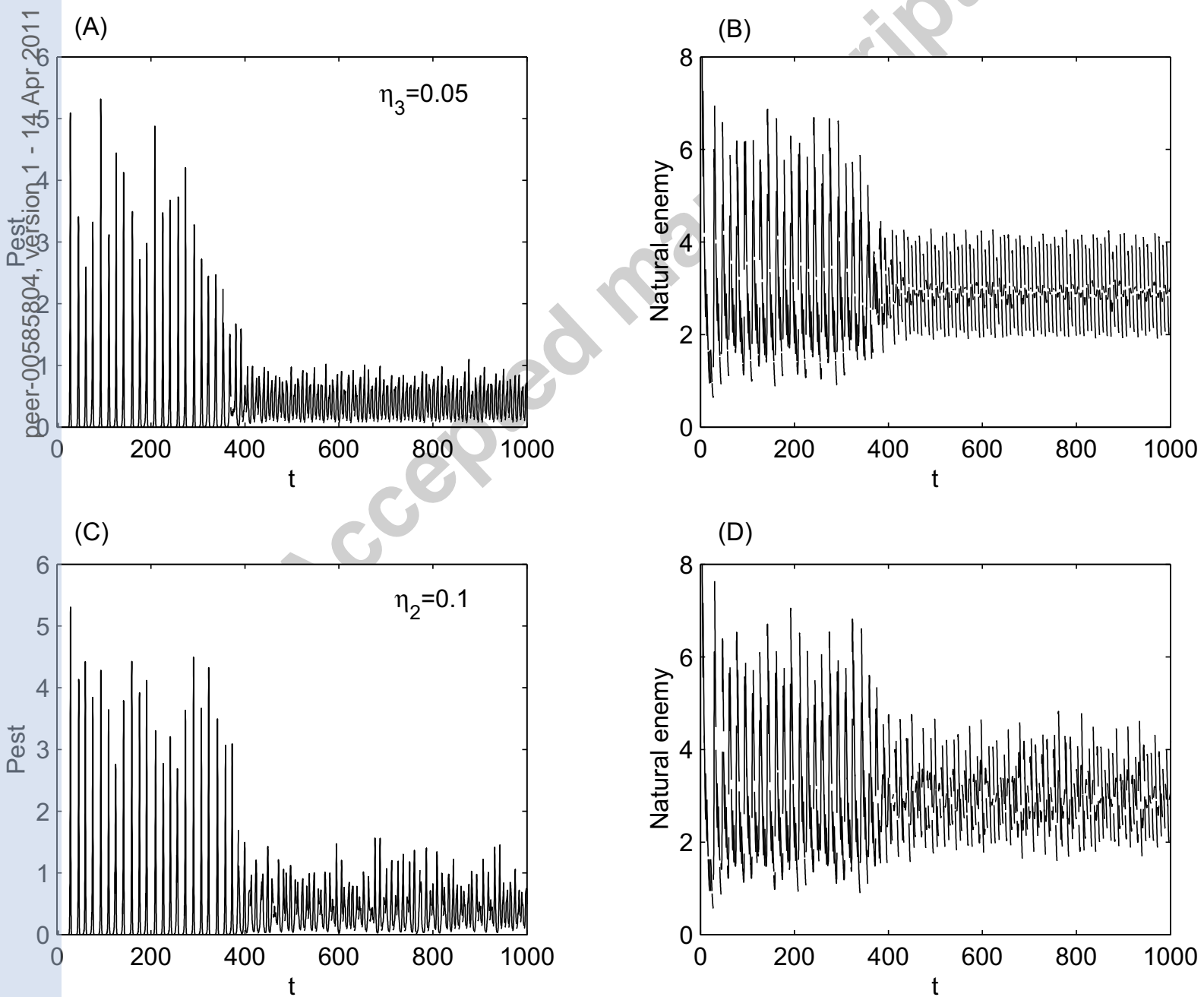
(C)



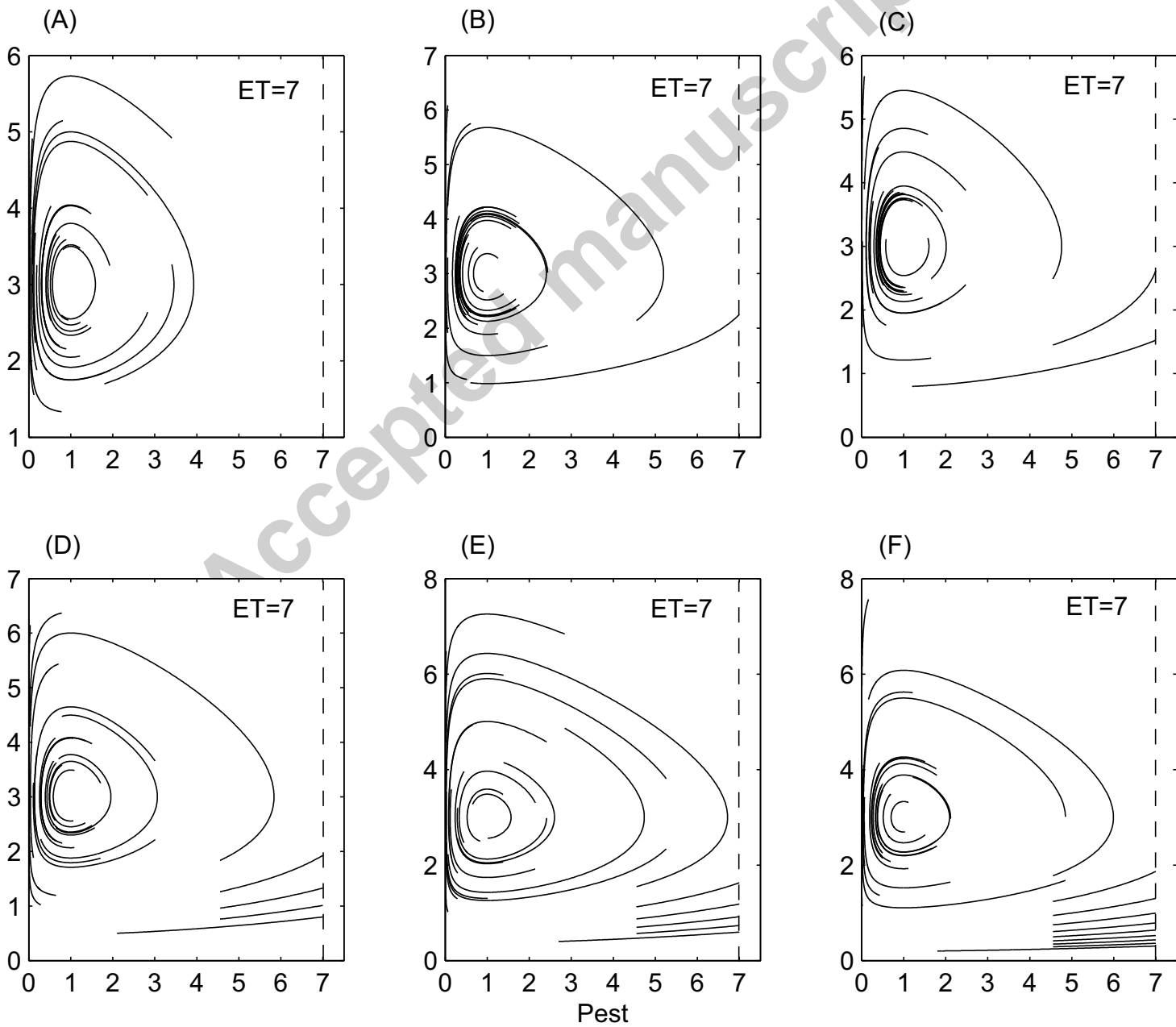
(D)



4. Figure 11



4. Figure 12



4. Figure 13

