On the validation, stability and control of certain biological systems

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Abstract

This thesis is concerned with the long-term behavior of certain mathematical models describing predator-prey interactions, virus propagation *in vivo* and integrated pest management strategies. Of interest are the stability and impulsive controllability of such models, since the corresponding mathematical findings are then easily interpretable in terms of biological concepts with major relevance such as disease endemicity, species extinction or permanence and pest eradication.

Threshold conditions for the global stability of the equilibria are obtained by means of Lyapunov's direct method combined with LaSalle invariance principle. These results, stated in terms of a biologically significant key parameter called the basic reproduction number, are then reconfirmed by using monotonicity methods. The models of concern are formulated in a general way, no specialization being made, for instance, on the incidence rate of the infection and on the removal rate of the virus (for the virus model) or on the functional response of the predator (for the predator-prey model). This makes the findings are applicable to a large class of real-life interactions.

Also, threshold conditions with immediate biological significance which guarantee the global success of integrated pest management strategies are derived using Floquet theory. The corresponding impulsive controllability results are then obtained by using comparison arguments. Also, a bifurcation analysis is performed via an operator theoretic approach and some situations leading to a chaotic behavior of the solutions are investigated by means of numerical simulations.

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Introduction

Despite of an active searching for general patterns and a relentless effort towards the understanding of underlying biological processes, we are still far from a thorough interpretation of certain biological phenomena, the length of the delay between contamination with HIV and the onset of AIDS being just an example which comes to mind. Consequently, mathematical models can often serve as helpful research tools for biologists, since various conflicting suppositions about the nature of the biological interactions of concern can be made precise in mathematical terms and then the predictions gained through the use of these models can be tested against real data. If proven consistent, a mathematical model can then be used for interpolating the available data and drawing conclusions about situations not previously tested, saving difficult experimentation and painful trial-and-error work in the process. Even the simple process of constructing a sound mathematical model, not necessarily very accurate, can be useful, since it forces the searching of a logical framework for the phenomena to be described and requires the identification of their main features together with precise descriptions in mathematical terms.

Mathematical biology is consequently an ever-expanding subject, which deals, for instance, with the use of mathematical models in virus dynamics, biofluid mechanics, pattern formation, angiogenesis, to name just a few applications. So broad a subject, then, cannot have its boundaries clearly delimited and its core area well defined. After all, not even its name would be universally agreed upon, as it sometimes happen with interdisciplinary sciences. Biologists, for instance, may prefer to name the subject "mathematical biology", while mathematicians may understandably favor a more self-serving term like "biomathematics". Obviously, the perception of the subject for both parties, as well as for the other parties involved (epidemiologists, geneticists, bioinformaticians and so on) will also be different. One thing is clear, though: no matter what area of mathematical biology is concerned and no matter which are the mathematical tools of choice, the only relevant research results are those which bear clear biological relevance.

The viewpoint of using predominantly analytic methods in order to reliably predict biological outcomes for given models will be embraced throughout this thesis. In this regard, only deterministic models involving the use of ordinary and impulsive differential equations will be employed and questions about validation, stability and control strategies will be answered, although the importance of statistical methods is also recognized.

This thesis is divided into three chapters, each corresponding to a major biological issue to be discussed. Chapter 1 is concerned with predator-prey interactions characterized by features such as stage structure, impulsive controls, delay caused by maturation time and also with coupled interactions in the form of a tritrophic food chain. In this regard, Section 1.1 is devoted to introducing, discussing and exemplifying the basic concepts of predator-prey interactions, such as the intrinsic growth rate of the prey and the functional and numerical response of the predator. Section 1.2 treats the global dynamics of a predator-prey model with stage structure for the predator in which the mature predator is characterized by a prey-dependent functional response in an abstract form. The global stability of the positive steady state is first obtained by using a suitable Lyapunov functional and LaSalle's invariance principle, under a persistence condition for prey and a condition upon the numerical response of the mature predator when the prey population is at the carrying capacity of the environment. This condition strikingly resembles the endemicity condition used in Section 2.2. The results are then reconfirmed by using a very different approach, that is, the theory of competitive systems. The existence of orbitally stable periodic solutions is also discussed along with the stability of the prey-only equilibrium and the biological significance of the results is motivated. This section is based on results obtained in Georgescu and Hsieh [28] and Georgescu and Morosanu [30].

Section 1.3 is concerned with another extension of the classical Lotka-Volterra model of predation, this time an impulsively perturbed tritrophic food chain system being investigated. Nonlinear general smooth functions are used to model the functional response of the intermediate consumer and of the top predator and a general prey-dependent model is consequently obtained. It is seen that the local stability of the intermediate consumer-free periodic solution is assured, provided that a certain condition on the productivity of the intermediate consumer is satisfied. This condition is then seen to be threshold-like, since it is observed that if the reverse of the productivity condition is satisfied, then the resource and intermediate consumer-free periodic solution is globally asymptotically stable.

A sufficient condition for the global stability of the intermediate consumer-free periodic solution, corresponding to the ultimate success of the pest management strategy which motivates the model, is established by means of a comparison argument and of integral estimations. It is also observed that, theoretically speaking, the control strategy can be always made to succeed by means of using highly effective pesticides or voracious top predators and by means of releasing top predators either frequently enough or in a sufficiently large amount. Any of these features alone can ensure the global success of the control strategy, although in concrete situations these requirements may or may not be biologically feasible or may require a large amount of resources. Finally, it is observed that since the impulsive perturbations induce commensurate oscillations as they act with the same period, the system displays an oscillatory behavior, tending to an impulsively perturbed periodic solution for a large portion of the parameter space. A numerical analysis of some situations leading to a chaotic behavior of the system is also provided. This section is based on the results obtained in Georgescu and Moroşanu [29].

In Section 1.4, an impulsively perturbed predator-prey model with delay, stage structure and Beddington-DeAngelis functional response for the mature predator is analyzed. The delay parameter is introduced as a constant maturation time, the novelty of the model consisting in the incorporation of the periodic human exploiting behavior due to seasonal hunting and harvesting. It is shown that if few mature predators introduced in a mature predator-free environment with prey at carrying capacity cannot reproduce fast enough, compensating through-stage mortality, as described by a certain "degree of stage structure" incorporating the delay term, then the predator-free periodic solution is globally asymptotically stable. It is also seen that systems with low resources are more likely to be stabilized to the predator-free periodic solution, while increasing the carrying capacity of the environment may destabilize an otherwise stable predator-free periodic solution. Also, it is observed that when the prey has a large intrinsic growth rate, the proportional reduction of the pest population caused by the use of the impulsive control is small and the predators can breed quickly, then the coexistence of the prey and predator populations is assured. This section is based on the results obtained in Zhang, Georgescu and Chen [138].

Chapter 2 is dedicated to analyzing the dynamics of a viral disease. To this purpose, several basic concepts of mathematical epidemiology, such as the incidence rate and the force of infection, the rationale behind using compartmental models and the basic reproduction number as a threshold parameter are presented in Section 2.1. In Section 2.2, the global dynamics of a compartmental model which describes the propagation of a virus in vivo is analyzed using an argument based on the construction of several Lyapunov

functionals and the use of LaSalle invariance principle. The main feature of this model is that the functional coefficients involved in its formulation are given in an abstract form, no specialization being made, for instance, regarding the particular form of the incidence rate of the infection and of the removal rate of the virus. In certain concrete situations, these functional coefficients are far from being well-known and an abstract functional form should consequently be employed, fact which makes our approach worth of consideration. In spite of this abstraction, results regarding the global stability of both the disease-free and the endemic equilibrium are still obtained under certain conditions, the most important of which being the monotonicity of the functional quotient between the nonlinear force of infection and the removal rate of the virus. The existence of a threshold parameter, the so-called basic reproduction number, which controls the stability of both the disease-free and the endemic equilibrium, not to mention the very existence of the latter, is consequently established. Moreover, in the absence of the above-mentioned monotonicity property, local stability results are established and estimations for the sizes of the domains of attraction are given. The biological significance of the results and a possible extension of the model are also discussed. The results in this section are based on Georgescu and Hsieh [27].

Chapter 3 is devoted to discussing a pest removal strategy. First, in Section 3.1, an overview of the basic goals and methods of integrated pest management strategies is given. The purpose of Section 3.2 is to construct a mathematical model describing a pest management strategy relying on the impulsive use of a biological and a chemical control, which are supposed to act in a periodic fashion, with the same period but not simultaneously. It is seen that if a certain inequality involving the total action of the nonlinear force of infection in a period is satisfied, then the susceptible pest-eradication solution is globally asymptotically stable, while if the opposite of this inequality is satisfied then the susceptible pest-eradication solution loses its stability and the system under consideration becomes uniformly persistent. Although the proof of the global stability result is rather computationally intensive, an immediate justification for the use of the stability condition is given through a Floquet analysis of the linearized system. It is also found out that the above persistence and stability conditions have immediate biological interpretations as balance conditions for the total loss of susceptibles in a period due to their movement to the infective class and to their removal due to pesticide spraying, on the one side, and the gain of newborn susceptibles in the same amount of time, on the other side. It is also observed that in a particular case the above results establish the existence of a certain threshold parameter for the stability of the system. In addition, is observed that, from a theoretical viewpoint, the control strategy is successful if enough resources are invested. The results in this section are based on Georgescu and Moroşanu [31].

In Section 3.3, the limiting case which separates the situations considered above is treated from a bifurcation theory viewpoint. The problem of finding nontrivial periodic solutions is reduced to a fixed point problem, which is in turn treated using the methods of bifurcation theory. It is shown that once the limiting condition is reached, then the trivial periodic solution loses its stability and a nontrivial periodic solution appears via a supercritical bifurcation. In concrete terms, a nontrivial periodic solution corresponds to the apparition of a persistent susceptible pest population, while a nontrivial periodic solution with small amplitude, below the economic injury level, indicates that the pest management strategy is still successful, although the pest population is not completely eradicated. The results in this section are based on Georgescu, Zhang and Chen [32].

Chapter 1

Predator-prey interactions: enlarging Lotka-Volterra model

1.1 Basic concepts of predator-prey interactions

The Lotka-Volterra model

The Lotka-Volterra model, proposed independently by the American ecologist Alfred J. Lotka in 1925 as a description of a predator-prey system consisting of a plant population and of a herbivorous animal which relies on this plant as its only food source and by the Italian mathematician Vito Volterra in 1926 as a model to describe the interaction between sharks and fishes in the Adriatic sea, is the simplest model of predator-prey interaction. It shall consequently be used as a vehicle to introduce a number of theoretical concepts.

Denoting by P = P(t) the density of the predator population and by N = N(t) the density of the prey population, the model can be described by the following differential system

(LV)
$$\begin{cases} N'(t) = rN(t) - aN(t)P(t), \\ P'(t) = caN(t)P(t) - dP(t), \end{cases}$$

where r, a, c, d > 0. The significance of the parameters used in the Lotka-Volterra model is as follows: r is the growth rate of the prey in the absence of the predation, d is the mortality rate of the predator, a is the search efficiency (attack rate) of the predator and c is the efficiency of the predator at converting prey into predator offsprings.

The simplicity of Lotka-Volterra model relies on certain assumptions. First, it is supposed that the prey population has unlimited food supply and will grow exponentially in the absence of the predator, as seen from the limit case equation N'(t) = rN(t), with solution $N(t) = N_0 e^{rt}$. It is also supposed that the predator species feeds on prey only and on nothing else, and will starve and become extinct in the absence of prey, rather than switch to a different type of food, as seen from the limit case equation P'(t) =-dP, with solution $P = P_0 e^{-dt}$. Other simplifying assumptions are also made upon prey searching, prey consumption and environmental complexity. That is, it is assumed that both species move randomly in a homogeneous environment, which reflects into a number of predator-prey encounters directly proportional to the product NP of prey and predator populations, respectively, among of which a fixed proportion aNP are successful. Note that the fact that the number of predator-prey encounters is directly proportional to the product NP embeds the very simple fact that there is zero interaction between these species if one of them is extinct. Finally, it is assumed that the intake of prey is transformed into predator offsprings at a fixed rate, this assumption being responsible for the term caNP in the second equation.

These simplifications lead to a number of limitations of the Lotka-Volterra model. First of all, the per-capita predator consumption rate is aN, while the per-capita predator birth rate is caN, that is, they are both unbounded when the size of the prey population grows large, which is unrealistic, as predators need time to hunt and digest prey and also manifest satiation. Also, the mathematical model is in no circumstance structurally stable and exhibits periodic oscillations during which the sizes of the predator and prey populations become much smaller than 1 and easily recover afterwards, which is obviously unacceptable. It then appears that the Lotka-Volterra model alone is not enough to describe many predator-prey systems and system-specific information should be added.

A general predator-prey model

After Lotka-Volterra model has been introduced, various studies tried to refine it in many ways and to address some of the shortcomings mentioned above. A very general model has been proposed by Yodzis in [135], in the following form

(Y)
$$\begin{cases} N'(t) = f(N(t)) - P(t)F(N(t), P(t)), \\ P'(t) = P(t)G(N(t), P(t)). \end{cases}$$

That is, in order to characterize such a model, three functions have to be given, namely: f(N), the intrinsic growth rate of the prey population, that is, the growth rate of the prey population in the absence of the predation, F(N, P), the predator's functional (behavioral) response, which represents the number of prey individuals consumed per unit area and unit time per single predator, that is, the dependence of the rate of consumption upon the density of the prey, and G(N, P), the predator's numerical response, which represents the per capita growth rate of the predator population, that is, the dependence of the represents the per capita growth rate of the prey.

Of course, in order to bear significance, a model should not only be complex enough to describe the underlying biological interactions, but should also be mathematically tractable. In this regard, a few particular forms of the functions mentioned above have been proved fit to describe certain concrete biological systems, the general form mentioned above being obviously too vague. Note also that a particular form of the model proposed by Yodzis is the following Rosenzweig-MacArthur model

(RMA)
$$\begin{cases} N'(t) = f_1(N(t)) - N(t)P(t)F_1(N(t)) \\ P'(t) = P(t) (cN(t)F_1(N(t)) - e). \end{cases}$$

The intrinsic growth rate of the prey population

The British political economist Thomas Malthus is generally credited with the idea that the populations grow exponentially over time. This type of population growth has been conjectured to occur since it has been supposed that the growth rate of the population is directly proportional to the population size.

The resources which support the prey population, however, are largely fixed and cannot grow ad infinitum. As the habitat becomes crowded, diseases act as a limiting factor in real populations and so does also intraspecific competition. Generally, it has been observed that the growth rate of the prey population declines at higher prey densities, and there is an upper limit K of the population density the population can support, called the carrying capacity.

The logistic model has been introduced by the Belgian mathematician Pierre Verhulst in 1838 in [127]. In this model the growth rate of the prey population, called hereinafter the logistic growth rate, is given by

$$f_L(N) = rN\left(1 - \frac{N}{K}\right),$$

where r can be interpreted as the intrinsic population growth rate in the absence of the intraspecific competition. Actually, the logistic model combines three ecological processes: reproduction, death and competition.

To this day, the logistic growth rate is perhaps the most used to model population growth. One of its shortcomings, however, is as follows. First, r is primarily seen, as mentioned above, a parameter which controls the population growth; there are slowly reproducing population (with low r) and rapidly reproducing populations (with high r). However, r controls not only the population growth but also the population decline (when N > K), and populations with a slow (high) reproductive rate may not have the same type of mortality rate. That is, the logistic growth model may not be appropriate for populations with different types of reproduction and mortality rates.

Another growth rate with somewhat similar properties which is especially in use in fishery industry is the one introduced by the Austrian biologist Ludwig von Bertalanffy, in which

$$f_{vB}(N) = r(K - N)$$

called the von Bertalanffy growth rate.

A growth rate which provides a good fit for situations in which growth is slower when N is close either to 0 or to the carrying capacity K is the Gompertz growth rate, introduced by the Jewish mathematician Benjamin Gompertz in 1825, for which

$$f_G(N) = fN\ln\frac{K}{N}.$$

A very general population growth model has been introduced by the British botanist Francis J. Richards in 1959, encompassing the logistic, von Bertalanffy and Gompertz growth rate. In Richards model, the growth rate has the form, called hereinafter the Richards growth rate,

$$f_R(N) = \frac{r_R}{1-\delta} N\left(\left(\frac{N}{K}\right)^{\delta-1} - 1\right), \quad \delta \neq 1.$$

That is, the growth of the prey population N is proportional to its size multiplied by a saturating function. The constant K is related to the intrinsic population growth rate, as seen from the fact that the initial growth rate is $\frac{r_R}{\delta-1}$, while δ determines the shape of the curve.

For $\delta = 2$, $f_R(N)$ reduces to

$$f_2(N) = r_R N\left(1 - \frac{N}{K}\right),$$

that is, N enjoys in this case a logistic growth rate. For $\delta = \frac{2}{3}$, one obtains

$$f_{\frac{2}{3}}(N) = 3r_R N\left(\left(\frac{N}{K}\right)^{-\frac{1}{3}} - 1\right),$$

and consequently $N^{\frac{1}{3}}$ verifies

$$\frac{d(N^{\frac{1}{3}})}{dt} = r_R K^{\frac{1}{3}} - r_R N^{\frac{1}{3}},$$

that is, a von Bertalanffy growth. Finally, for $\delta \to 1$ one obtains

$$f_{\lim_{\delta \to 1}}(N) = r_R N \ln \frac{K}{N},$$

that is, a Gompertz growth rate. A growth rate of a somewhat different nature, defined as

$$f_{NG}(N) = N\left(rN^{1-\frac{x}{K}} - d\right),$$

has also been proposed by Nisbet and Gurney in [104].

The functional response of the predator

To elaborate upon the functional and numerical response of the predator, it is important to characterize the way in which the predators interact with one another. While in some situations, especially at low predator densities, it can safely be considered that predators do not interact with one another, individual predators may interfere with each other's feeding and hunting activities, therefore negatively affecting population growth or, although less likely, may achieve a certain form of cooperation, facilitating one another's feeding activities. As mentioned by Yodzis in [135], especially for social animals such as marine mammals, this form of interaction cannot be ruled out.

Holling has developed in [51] and [52] a detailed analysis of the components of the functional response, assuming that predators do not interfere with each other. His subsequent assumptions were that the total time allotted to feeding is divided between searching for prey and handling prey and that the handling time is the same for all prey consumed.

Let us also denote by a the attack rate, that is, the amount of prey consumed per unit time, by T_S the time spent searching for prey and by T_h the time spent handling prey. Then the total amount of prey consumed is aT_S and since the functional response represents the total amount of prey consumed per unit time, one has

$$F(N,P) = \frac{aT_S}{T_S + aT_S t_h}$$

and consequently

$$F(N,P) = \frac{a}{1+at_h}$$

If no interference between predators is assumed, then the attack rate is proportional to the existing prey density, that is a = bN, b > 0. One then has

$$F_C(N,P) = \frac{bN}{1+bt_hN},$$

that is, a functional response of type II (cyrtoid) in Holling's classification from [51]. If the predators are more efficient at higher prey densities and less efficient at lower prey densities, a search rate of type $a = bN^2$ may be considered, in which case

$$F_S(N,P) = \frac{bN^2}{1+bt_hN^2},$$

that is, a functional response of type III (sigmoid) in Holling's classification. These differences in the efficiency of searching may be due to prey refuges or to the fact that the predators may detect and respond to chemicals emitted by prey by increasing their predation activity (especially when prey are insects), while some predators may switch to the most abundant prey.

Holling also considered a type I (linear) functional response, for which $F_L(N, P) = bN$. This functional response has been shown to model the behavior of passive predators such as spiders. An interesting conclusion can be drawn by looking at the associated mortality rates caused by predation, that is,

$$M_L(N, P) = b, \quad M_C(N, P) = \frac{b}{1 + bt_h N}, \quad M_S(N, P) = \frac{bN}{1 + bt_h N^2}.$$

Since M_S is the only mortality rate which is actually increasing on a certain subinterval (specifically, on $[0, \frac{1}{\sqrt{bt_h}}]$), a predator with a functional response of type III is the only one able to regulate a prey outbreak, but its regulatory effect is limited to prey populations with densities less than $\frac{1}{\sqrt{bt_h}}$, since for higher densities the mortality rate starts to decrease. Another functional response has been proposed by Ivlev in [59], for which

$$F(N,P) = k \left(1 - e^{-cN}\right).$$

Following the classification given in Arditi and Ginzburg [6] or in Huisman and DeBoer [55], the functional responses above may be termed as being prey-dependent, since they depend only on prey density N and not on predator density P. In this regard, an attack rate a which depends upon both N and P gives rise to a so-called predator-dependent functional response (to underline the dependence upon the predator density P, since F is assumed to depend upon N anyway), or, in the particular case in which a depends upon the prey-to-predator ratio $\frac{N}{P}$, to a ratio-dependent functional response.

Hassell and Varley used in [43] an attack rate of type $a = \frac{cN^n}{P^m}$, n, m > 0, for which

$$F(N,P) = \frac{cN^n}{P^m + cN^n t_h}$$

A problem which is common to such type of attack rates is that as $P \to 0$ one has $a \to \infty$, that is, such predators become unreasonably efficient at small densities. A different attack rate, addressing the issue mentioned above, that is, the boundedness of the attack rate when there are few predators, has been proposed by DeAngelis et al in [21] and by Beddington in [11], actually for different reasons. In this setting, $a = \frac{cN}{P_0+P}$; as $P \to 0$, one has that $a \to \frac{cN}{P_0}$. One then has

$$F(N,P) = \frac{\frac{1}{t_h}N}{N + \frac{1}{ct_h}P + \frac{1}{ct_h}P_0}.$$

It is then seen that this functional response has some qualitative features of the ratiodependent functional responses but keeps away from the "low densities problem" mentioned above. Regarding the general suitability of prey-dependent and ratio-dependent functional responses, it is believed that prey-dependent functional responses are more appropriate for situations in which predation involves random or no search process, while ratio-dependent functional responses are more appropriate for situations in which predation involves a thorough search process. See, for instance, Kuang and Beretta [72]. Other types of functional responses which account for interference between predators have also been proposed. See, for instance, Crowley and Martin [19]. See also the comprehensive paper of Skalski and Gilliam [121] for a comparison of the accuracy provided by these alternative functional responses based on statistical data for a wide range of predator-prey interactions.

The numerical response of the predator

Naturally, the reproductive rate of the predator is proportional to their predation rate, as increased food intake means more energy available for reproduction. The simplest form of a numerical response is

$$G(N, P) = -d + cF(N, P),$$

appropriate when F is a prey-dependent functional response (F = F(N)), or at least the only effect of predator interference is on each predator's rate of consumption. Here, d is the death rate of the predator, while c is a conversion coefficient. Another different form of the numerical response is Leslie's numerical response (see Leslie [78]), in the form

$$G(N,P) = r\left(1 - \frac{P}{hN}\right),$$

where r and h are positive constants. Here, it is assumed that the "carrying capacity" hN depends directly upon the available prey density N. See also Yodzis [135].

1.2 Global dynamics of a predator-prey model with stage structure for predator

1.2.1 A survey on stage-structured models

In classical models of Lotka-Volterra type it is assumed that all individuals of a single species have largely similar capabilities to hunt or reproduce. However, the life cycle of most, if not all, animals and insects consists of at least two stages, immature and mature, and the individuals in the first stage often can neither hunt nor reproduce, being raised by their mature parents. Further immediately recognizable morphological and behavioral differences may exist between these stages and other adaptive stages, such as dormancy stages, may exist for immediate survival purposes.

To study this situation theoretically, stage-structured models have been attracted much attention in the recent decades. Fundamental work towards a systematic approach to stage-structured model formulation has been made by Gurney et al. [37], Nisbet and Gurney [105], Nisbet et al. [106]. Further progress has been made by Aiello and Freedman who proposed and studied in their often quoted work [3] a single species model with stage structure and discrete delay, predicting the global attractivity of the positive steady state and thereby suggesting that the stage structure does not generate sustained oscillations, at least for a single species model. General consistency criteria to be satisfied by models which describe stage-structured ecological interactions have been laid out in Kuang [68] or Arditi and Michalski [7]. See also Liu, Chen and Agarwal [87] for a recent survey on the dynamics of stage-structured population models with an emphasis on modeling issues.

Predator-prey models with stage structure for predator have received considerable attention in recent years. Magnusson studied in [103] the destabilizing effect of cannibalism in a predator-prey system in which mature predators prey upon both immature predators and prey individuals. Wang [130] and Xiao and Chen [134] studied the global stability and persistence of a stage-structured predator-prey model by means of the theory of competitive systems. See also Wang and Chen [131], Wang et al. [132], and Gourley and Kuang [36] for stability analyses of staged predator-prey models with time delays due to the gestation of the predator and the crowding of the prey. The existence of positive periodic solutions for a delayed non-autonomous ratio-dependent predator-prey system with stage structure for predator has been established by Chen in [17] with the help of coincidence degree theory.

Apart from analyzing the stability of their delay model, Gourley and Kuang [36] also discussed its oscillatory dynamics for a linear functional response of the mature predator and observe that sustained oscillations take place only for a limited interval of maturation delays. This happens since, for small delays, their models inherits the properties of the nondelayed (of Lotka-Volterra type) system. However, if the maturation delay is too long, then the highest possible recruitment rate to adulthood drops below the adult death rate and the predator population dies out.

As far as the asymptotic behavior of predator-prey systems is concerned, it is known from Poincare-Bendixson theory that two dimensional continuous time models can approach either an equilibrium state or a limit cycle with any type of chaotic behavior being excluded, while three and higher dimensional models can exhibit more complex behavior. In this regard, staged models may provide in some situations a richer dynamics which leads to a better understanding of the interactions within the biological system under consideration. Such models may also incorporate parameters, such as different death rates for mature and immature predators and various delay effects, which are biologically more meaningful.

In [131], [130], [134] the following predator-prey model with stage structure for predator has been considered

(1.2.1)
$$\begin{cases} x'(t) = x(t) \left(r - ax(t)\right) - \frac{bx(t)}{1 + mx(t)} y_2(t), \\ y'_1(t) = k \frac{bx(t)}{1 + mx(t)} y_2(t) - (D + d_1) y_1(t), \\ y'_2(t) = Dy_1(t) - d_2 y_2(t). \end{cases}$$

Here, x(t), $y_1(t)$, $y_2(t)$ are the densities of prey, respectively of immature and mature predators at time t. It is assumed that in the absence of the predators the prey grows according to a logistic law with intrinsic growth rate r and carrying capacity r/a, while predators feed on prey only and do not contribute to the growth of the population towards the carrying capacity. It is also assumed that the immature predators are either raised by their parents or consume a resource which is available in abundance and for which they do not have to compete. As a consequence, neither crowding nor intraspecies competition terms are added into the equation which models the growth of the immature predator class. As seen in Section 1.1, the function $x \mapsto bx/(1 + mx)$ represents the Holling type 2 functional (behavioral) response of the mature predator, while the function $x \mapsto kbx/(1+mx)$ is the associated numerical (reproductive) response of the mature predator, with k representing the conversion coefficient under the assumption that the reproduction rate of the mature predators is directly proportional to the amount of prey consumed. The constants d_1 and d_2 represent the death rates of immature and mature predators. Also, it is assumed that the predators become mature after a fixed age. In this respect, D denotes the rate at which immature predators become mature predators, that is, 1/Drepresents the total time spent by a predator in its immature stage.

It was proved in Wang [130] that if the condition

$$(1.2.2) d_2(D+d_1) < \frac{kbrD}{a+mr}$$

holds, then the system (1.2.1) is uniformly persistent and a unique positive steady state $E^* = (x^*, y_1^*, y_2^*)$ exists. Moreover, it is shown that, if in addition to (1.2.2), the following conditions are also satisfied:

(1.2.3)
$$x^{*}(D+d_{1}+d_{2})(a+2max^{*}-mr)\left(D+d_{1}+d_{2}+\frac{x^{*}(a+2max^{*}-mr)}{1+mx^{*}}\right)$$
$$> \frac{by_{2}^{*}d_{2}(D+d_{1})}{1+mx^{*}}$$
$$(1.2.4) \qquad a > b + \frac{bmy_{2}^{*}}{1+mx^{*}}, \quad D+d_{1} > \frac{kbr}{a+mr} + \frac{kby_{2}^{*}}{1+mx^{*}}, \quad d_{2} > D,$$

then the positive steady state $E^* = (x^*, y_1^*, y_2^*)$ is globally asymptotically stable, where (1.2.3) alone accounts for the local stability of E^* . The proof uses the theory of competitive systems as developed in Smith [122], with condition (1.2.3) being used to establish the local stability of E^* .

More recently, Xiao and Chen [134] noted that condition (1.2.4) contradicts condition (1.2.2). Incidentally, let us note here that the same applies to relations (2.2) and (4.1) in Wang and Chen [131], albeit in a slightly different form. They also showed that the positive steady state E^* is globally asymptotically stable if (1.2.2) and (1.2.3) hold, in addition to one of the following two conditions:

(H1)
$$D + d_1 > r$$
 and $\underline{x} > \frac{r}{2a}$; (H2) $D + d_1 < r$ and $\underline{x} > \frac{r + D + d_1}{2a}$.

Here, $\underline{x} > 0$ is the persistency constant for x, which satisfies $\underline{x} \leq \liminf_{t \to \infty} x(t)$. The proof is again based on the theory of competitive systems and uses a result given by Li

and Muldowney in [81], which amounts to the fact that for competitive and permanent systems which are defined on convex and bounded sets and have the property of stability of periodic orbits, the local asymptotic stability of a unique positive steady state implies its global asymptotic stability. Essentially, the proof in [134] amounts to showing that the system (1.2.1) has the property of the stability of periodic orbits under either (H1) or (H2), a fact which is established using a criterion of Muldowney [103] and the theory of additive compound matrices.

Consider the conditions (1.2.3), (H1), and (H2). It is clear that if the inequality $\underline{x} > (r + D + d_1)/(2a)$, which is required in (H2), can be weakened to $\underline{x} > r/(2a)$ and either (H1) or (H2) can be modified to cover the case $D + d_1 = r$, then (H1) and (H2) can be combined into a single condition $\underline{x} > r/(2a)$. Moreover, condition (1.2.3), which a priori insures the local stability of the positive steady state, was motivated by specifics of the method used for the proof, which roughly inputs local asymptotic stability and outputs global asymptotic stability under certain assumptions.

However, it is clear that once the global asymptotic stability of the positive steady state is proved then its local asymptotic stability is superseded anyway. Moreover, we shall indicate that in fact (1.2.3) is satisfied if $x^* > r/(2a)$ (and consequently if $\underline{x} > r/(2a)$) in Xiao and Chen's setting, so there is no need to assume (1.2.3) separately.

In the remaining part of this section, we shall take a dual view upon studying the global dynamics of a generalized form of (1.2.1). That is, we shall first study its global dynamics by constructing a suitable Lyapunov function and using LaSalle's invariance principle in Subsection 1.1.3 and then by using the theory of competitive systems in Subsection 1.1.4, the latter method being also employed in Wang [130] and Xiao and Chen [134]. This will enable us to obtain the global asymptotic stability of the positive steady state under weaker hypotheses than those used in [134] and for a system which is slightly more general than the one studied in [130] and [134]. In our setting, the persistence condition $\underline{x} > r/(2a)$ used in [134] will appear in a natural way as a monotonicity condition in both the Lyapunov and monotonicity approaches. We shall also provide a dual view upon the persistency argument in Subsections 1.1.3 and 1.1.4. The first argument is based on the study of the flow near the boundary, while the second one relies on the use of Lyapunov-like functionals.

We shall also establish in Subsection 1.1.4 the existence of periodic solutions, together with their stability. Finally, we shall discuss the biological significance of our results and indicate possible extensions of our results to the study of more comprehensive models in Subsection 1.1.5. The results in this section are based on Georgescu and Hsieh [27] and Georgescu and Moroşanu [30].

1.2.2 A predator-prey model with stage structure for predator

In the following, we consider the following stage-structured predator-prey system

(PP)
$$\begin{cases} x'(t) = x(t)r(x(t)) - x(t)\phi(x(t))y_2(t), \\ y'_1(t) = kx(t)\phi(x(t))y_2(t) - (D+d_1)y_1(t), \\ y'_2(t) = Dy_1(t) - d_2y_2(t), \end{cases}$$

under the following hypotheses

- (H1) (a) $x \mapsto x\phi(x) \in C^1([0,\infty), [0,\infty)).$
 - (b) $x \mapsto x\phi(x)$ is strictly increasing and bounded on $[0, \infty)$.
 - (c) ϕ is strictly positive and decreasing on $(0, \infty)$.
- (H2) (a) $x \mapsto xr(x) \in C^1([0,\infty), \mathbb{R}).$
 - (b) r(0) > 0, r strictly decreasing on $[0, \infty)$, $r(x_0) = 0$ for some $x_0 > 0$.
 - (c) $x \mapsto xr(x)$ is strictly decreasing on $[x_P, \infty), 0 < x_P < x_0.$

The significance of the functions x, y_1, y_2 and of the parameters k, D, d_1, d_2 is the same as in (1.2.1). Note that (H1) is satisfied for some usual examples of predator functional response, namely for $x\phi(x) = bx^p/(1 + mx^p)$, 0 , that is, the generalized type II $Holling functional response (Holling, [51]) and <math>x\phi(x) = k(1-e^{-cx})$ (Ivlev, [59]). Also, (H2) is satisfied for some commonly used examples of growth functions, namely for xr(x) = x(1 - (x/K)), that is, the classical logistic growth, for $xr(x) = x(1 - (x/K)^{\theta})$, $\theta \in (0, 1]$, that is, the generalized logistic growth (Richards [117]) and for $xr(x) = x(re^{1-(x/K)} - d)$ (Nisbet and Gurney, [104]). As in Aiello and Freedman [3], it is assumed that the immature predators are either raised by their mature parents or grow on an abundant nutrient for which they do not have to compete with adults and consequently neither crowding terms nor intra-species competition terms are added for predators. In the following, we shall denote $x \mapsto x\phi(x)$ by f and $x \mapsto xr(x)$ by n.

First, it is easy to see that if x(0), $y_1(0)$, $y_2(0) \ge 0$, then x(t), $y_1(t)$, $y_2(t) \ge 0$ on their respective intervals of existence. To this purpose, we observe that the vector (R_1, R_2, R_3)

points inside the closed set $Q_1 = [0, \infty)^3$ at all points of ∂Q_1 , where R_1 , R_2 , R_3 are the right-hand sides appearing in (1.2.1), so Nagumo's tangency conditions are satisfied and Q_1 is a positively invariant set for (PP). See Pavel [109] for further reference on flow invariance problems for ODEs and abstract ODEs.

To prove that $Q_2 = (0, \infty)^3$ is also a positively invariant set for (1.2.1), suppose that $x(0), y_1(0), y_2(0) > 0$ and note first that $\frac{d}{dt}(y_2e^{d_2t}) = Dy_1e^{d_2t} \ge 0$, so $t \mapsto y_2(t)e^{d_2t}$ is increasing. It follows that $y_2(t) \ge y_2(0)e^{-d_2t}$ for all t for which $y_2(t)$ is well-defined, so y_2 remains strictly positive. Also, $\frac{d}{dt}(y_1e^{(D+d_1)t}) \ge 0$, so $y_1(t) \ge y_1(0)e^{-(D+d_1)t}$ and y_1 remains strictly positive. To prove that x also remains strictly positive, suppose that $x(t_0) = 0$ for some $t_0 > 0$. Then one may find $\tilde{y}_1(0)$ and $\tilde{y}_2(0) > 0$ such that the solution which starts at t = 0 from $(0, \tilde{y}_1(0), \tilde{y}_2(0))$ also reaches $(0, y_1(t_0), y_2(t_0))$ at $t = t_0$. By the uniqueness property of (PP), this solution should coincide with the solution which starts at t = 0 from $(x(0), y_1(0), y_2(0))$, which is an obvious contradiction.

We shall now show that x, y_1, y_2 are bounded on their intervals of existence, which in turn will imply by a standard continuability argument that they are defined on $[0, \infty)$. Since $x' \leq n(x)$, it follows that $x(t) \leq \max(x(0), x_0)$ for all t, which insures the boundedness of x. Let us also define $F(x, y_1, y_2) = x + (1/k)y_1 + (1/k)y_2$. Computing the derivative of F along the solutions of (PP), we obtain that

$$F + dF \le n(x) + dx,$$

where $d = \min(d_1, d_2)$, and so

$$F(x(t), y_1(t), y_2(t)) \leq F(x(0), y_1(0), y_2(0))e^{-dt} + (n_M + d\max(x(0), x_0))\frac{1 - e^{-dt}}{d},$$

for all t, where n_M is a boundedness constant for n on $[0, \max(x(0), x_0)]$, that is, on the boundedness interval for x. It follows that x, y_1, y_2 are bounded and consequently, from basic ODE theory, they are defined on all $[0, \infty)$. This means that the system (PP) is well-defined in a biological (and mathematical) sense. This implies that y_1, y_2 are also bounded and consequently defined on $[0, \infty)$.

Finally, we analyze the behavior of solutions which start with initial data (x_i, y_{1i}, y_{2i}) on the boundary of $(0, \infty)^3$. If $x_i = 0$, then $(x(t), y_1(t), y_2(t)) \rightarrow (0, 0, 0)$ irrespective of the initial values $y_{1i}, y_{2i} \ge 0$. If $x_i > 0$, then $(x(t), y_1(t), y_2(t)) \rightarrow (x_0, 0, 0)$ for $y_{1i} = y_{2i} = 0$, while $(x(t), y_1(t), y_2(t))$ enters $(0, \infty)^3$ (and stays there) otherwise.

1.2.3 The Lyapunov approach: the global stability of the predator-free equilibrium, the uniform persistence of the system and the global stability of the positive steady state

In this section, we perform a global stability analysis for the system (PP) regarding both the stability of the boundary equilibrium $(x_0, 0, 0)$ (i.e., the case in which the predator classes tend to extinction) and of the positive steady state (x^*, y_1^*, y_2^*) (i.e., the case in which the coexistence of both species is assured for all future time at stabilizing positive levels). As a result, we find sufficient conditions for the stability of the equilibria and establish the existence of a threshold parameters. The uniform persistence of the system (i.e., the case in which both species coexist, although at possibly fluctuating levels) is also discussed

Let us denote $T = d_2(D + d_1)/D$. First, we give a condition for the extinction of the predators.

Theorem 1.2.1. Suppose that $T \ge kf(x_0)$. Then $(x_0, 0, 0)$ is globally asymptotically stable on $(0, \infty)^3$.

Proof. Let us consider the Lyapunov function

$$U_1(x, y_1, y_2) = \int_{x_0}^x \frac{f(\tau) - f(x_0)}{f(\tau)} d\tau + \frac{1}{k} y_1 + \frac{1}{k} \frac{D + d_1}{D} y_2$$

We now compute the derivative of U_1 along the solutions of (PP). One then has

$$\dot{U}_{1} = \frac{f(x) - f(x_{0})}{f(x)} (n(x) - f(x)y_{2}) + \frac{1}{k} (kf(x)y_{2} - (D + d_{1})y_{1}) + \frac{1}{k} \frac{D + d_{1}}{D} (Dy_{1} - d_{2}y_{2}) = \frac{f(x) - f(x_{0})}{f(x)} n(x) + \frac{1}{k} \left(kf(x_{0}) - \frac{(D + d_{1})d_{2}}{D} \right) y_{2}.$$

Since f is strictly increasing on $[0, \infty)$ and $\operatorname{sgn} n(x) = \operatorname{sgn}(x_0 - x)$ for $x \in (0, \infty)$, it is seen that $U_1 \leq 0$, with equality if and only if $x = x_0$ and either $y_2 = 0$ or $T = kf(x_0)$. In both cases, the only invariant subset \tilde{M} within the set $M = \{(x, y_1, y_2); x = x_0\}$ is $\tilde{M} = \{(x_0, 0, 0)\}.$

Since $U_1 \leq 0$ on $(0, \infty)^3$ and the only possible ω -limit sets of $(x(t), y_1(t), y_2(t))$ on the boundary of $(0, \infty)^3$ are $\{(x_0, 0, 0)\}$ and $\{(0, 0, 0)\}$, our conclusion follows from LaSalle's invariance principle (see Appendix A or LaSalle [77]).

We now attempt to analyze the existence of the positive steady state E^* and the persistence of the system (PP).

Definition 1.2.1. The system (PP) is said to be uniformly persistent (or permanent) if there is $\varepsilon_0 > 0$ such that any solution of (PP) which starts with $x(0), y_1(0), y_2(0) > 0$ satisfies

 $\liminf_{t \to \infty} x(t) \ge \varepsilon_0, \quad \liminf_{t \to \infty} y_1(t) \ge \varepsilon_0, \quad \liminf_{t \to \infty} y_2(t) \ge \varepsilon_0.$

Uniform persistence (permanence) is an important property of systems arising in ecology, epidemics, population dynamics and not only. It is actually a concept which is important and meaningful in itself, addressing the long-term survival of some or all components of a system. For other (weaker) types of persistence and criteria to establish the persistence of a given system, see Butler, Freedman and Waltman [14], Freedman, Ruan and Tang [25], Hofbauer and So [49].

Theorem 1.2.2. Suppose that $T < kf(x_0)$. Then the positive steady state E^* exists, is unique and the system (PP) is uniformly persistent.

Proof. Let us consider the Lyapunov function

$$U_2(x, y_1, y_2) = \frac{1}{k}y_1 + \frac{1}{k}\frac{D+d_1}{D}y_2.$$

We now compute the derivative of U_2 along the solutions of (PP). One then has

$$\dot{U}_2 = \frac{1}{k} (kf(x)y_2 - (D+d_1)y_1) + \frac{1}{k} \frac{D+d_1}{D} (Dy_1 - d_2y_2)$$
$$= \left(f(x) - \frac{(D+d_1)d_2}{kD} \right) y_2.$$

If $T < kf(x_0)$, then U_2 is positive in all strictly positive points of a vicinity of $(x_0, 0, 0)$ and so $(x_0, 0, 0)$ is unstable. Since the only invariant subsets on the boundary of $(0, \infty)^3$ are $\{(x_0, 0, 0)\}$ and $\{(0, 0, 0)\}$ and their stable manifolds are also contained in the boundary of $(0, \infty)^3$, it follows from a result of Hofbauer and So [49] that the system (PP) is uniformly persistent.

To show the existence of E^* , we need to find positive solutions for the system

(1.2.5)
$$\begin{cases} n(x^*) = f(x^*)y_2^*, \\ kf(x^*)y_2^* = (D+d_1)y_1^*, \\ Dy_1^* = d_2y_2^*. \end{cases}$$

After some algebraic manipulations, one obtains that x^* is the positive root of $kf(x^*) = T$, which is unique and belongs to $(0, x_0)$, as kf is strictly increasing and continuous, kf(0) < T and $kf(x_0) > T$. Moreover, it is seen that y_1^* and y_2^* are given by

$$y_1^* = \frac{d_2}{D} \frac{n(x^*)}{f(x^*)}, \quad y_2^* = \frac{n(x^*)}{f(x^*)}$$

and are positive, as x^* belongs to $(0, x_0)$, where *n* is positive. Consequently x^* , y_1^* , y_2^* are all unique and positive. We also remark that since the system (PP) is uniformly persistent, it follows that there is an $\underline{x} > 0$ such that $\liminf_{x \to 0} x(t) \ge \underline{x}$.

From Theorems 1.2.1 and 1.2.2, combined with the remark about the behavior of the solutions starting on the boundary of $[0, \infty)^3$ which was made at the end of Subsection 1.1.2, it also follows that (0, 0, 0) is an unstable equilibrium and its stable manifold consists of the positive quadrant $\{(0, y_{1i}, y_{2i}); y_{1i}, y_{2i} \ge 0\}$. That is, our model predicts that the predator and the prey cannot simultaneously face extinction, with the sole exception of the case in which the size of the initial prey populations equals zero, justified by the fact that the predators feed on prey only and do not consume other resource, so in the absence of prey they are condemned to extinction.

Having established the existence and uniqueness of the positive steady state E^* , we now turn our attention to its stability. For this purpose, we employ a condition on the persistence constant \underline{x} , which ensures that the prey population remains ultimately higher than a certain value.

Theorem 1.2.3. Suppose that $T < kf(x_0)$ and $\underline{x} > x_P$. Then the positive steady state E^* is globally asymptotically stable on $(0, \infty)^3$.

Proof. Since $\underline{x} > x_P$, it is seen that there is $t_0 \ge 0$ such that $x(t) > x_P$ for all $t \ge t_0$ and also that $x^* > x_P$. Let us consider the Lyapunov function

$$U_3(x, y_1, y_2) = \int_{x^*}^x \frac{f(\tau) - f(x^*)}{f(\tau)} d\tau + \frac{1}{k} \int_{y_1^*}^{y_1} \frac{\tau - y_1^*}{\tau} d\tau + \frac{1}{k} \frac{D + d_1}{D} \int_{y_2^*}^{y_2} \frac{\tau - y_2^*}{\tau} d\tau.$$

It is easily seen that $U_3(x, y_1, y_2) \ge 0$ and $U_3(x, y_1, y_2) = 0$ if and only if $x = x^*$, $y_1 = y_1^*$, $y_2 = y_2^*$. We now compute the derivative of U_3 along the solutions of (PP). One obtains

that

$$\begin{split} \dot{U}_3 &= \frac{f(x) - f(x^*)}{f(x)} \left(n(x) - f(x)y_2 \right) + \frac{1}{k} \frac{y_1 - y_1^*}{y_1} \left(kf(x)y_2 - (D+d_1)y_1 \right) \\ &+ \frac{1}{k} \frac{D+d_1}{D} \frac{y_2 - y_2^*}{y_2} \left(Dy_1 - d_2y_2 \right) \\ &= n(x) \frac{f(x) - f(x^*)}{f(x)} + f(x^*)y_2 - \frac{D+d_1}{k} y_1^* \left(\frac{f(x)}{f(x^*)} \frac{y_2}{y_2^*} \frac{y_1^*}{y_1} + \frac{y_2^*}{y_2} \frac{y_1}{y_1^*} + \frac{f(x^*)}{f(x)} - 3 \right) \\ &+ \frac{D+d_1}{k} y_1^* \frac{f(x^*)}{f(x)} - \frac{D+d_1}{k} y_1^* - \frac{D+d_1}{kD} d_2y_2. \end{split}$$

Since $f(x^*) = (D + d_1)d_2/(kD)$, this yields

$$\dot{U}_{3} = n(x)\frac{f(x) - f(x^{*})}{f(x)} - \frac{D + d_{1}}{k}y_{1}^{*}\left(\frac{f(x)}{f(x^{*})}\frac{y_{2}}{y_{2}^{*}}\frac{y_{1}^{*}}{y_{1}} + \frac{y_{2}^{*}}{y_{2}}\frac{y_{1}}{y_{1}^{*}} + \frac{f(x^{*})}{f(x)} - 3\right)$$

$$+ \frac{D + d_{1}}{k}y_{1}^{*}\left(\frac{f(x^{*})}{f(x)} - 1\right)$$

$$= \frac{1}{f(x)}(n(x) - n(x^{*}))(f(x) - f(x^{*}))$$

$$- \frac{D + d_{1}}{k}y_{1}^{*}\left(\frac{f(x)}{f(x^{*})}\frac{y_{2}}{y_{2}^{*}}\frac{y_{1}^{*}}{y_{1}} + \frac{y_{2}^{*}}{y_{2}}\frac{y_{1}}{y_{1}^{*}} + \frac{f(x^{*})}{f(x)} - 3\right).$$

From AM-GM inequality, it is clear that

$$\frac{f(x)}{f(x^*)}\frac{y_2}{y_2^*}\frac{y_1^*}{y_1} + \frac{y_2^*}{y_2}\frac{y_1}{y_1^*} + \frac{f(x^*)}{f(x)} \ge 3,$$

with equality if and only if

$$\frac{f(x)}{f(x^*)}\frac{y_2}{y_2^*}\frac{y_1^*}{y_1} = \frac{y_2^*}{y_2}\frac{y_1}{y_1^*} = \frac{f(x^*)}{f(x)} = 1,$$

that is, $x = x^*$ and $y_1/y_1^* = y_2/y_2^*$.

If $x(t) > x_P$ for $t \ge t_0$, then since n is strictly decreasing on $[x_P, \infty)$ and f is strictly increasing on $[0, \infty)$, it follows that

$$\frac{1}{f(x)}(n(x) - n(x^*))(f(x) - f(x^*)) \le 0$$

with equality if and only if $x = x^*$. This implies that $U_3 \leq 0$, with equality if and only if $x = x^*$ and $y_1/y_1^* = y_2/y_2^*$. We now find the invariant subsets \tilde{M} within the set

$$M = \left\{ (x, y_1, y_2); x = x^*, \frac{y_1}{y_1^*} = \frac{y_2}{y_2^*} \right\}$$

Since $x = x^*$ on \tilde{M} and consequently $x' = n(x^*) - f(x^*)y_2$, it follows that $x' = f(x^*)(y_2 - y_2^*)$ and so $y_2 = y_2^*$. This implies $y_1 = y_1^*$ and consequently the only invariant set in M is $\tilde{M} = \{(x, y_1^*, y_2^*)\}$. From LaSalle's invariance principle one then obtains the desired conclusion.

1.2.4 Monotonicity methods: global stability results and the existence of periodic solutions

In the following, we shall also introduce a different method of proving the uniform persistence of our model and showing the global stability of its positive steady state, based on the use of monotonicity methods. The existence of periodic solutions shall also be considered.

Let us denote

$$h = \frac{n}{f} = \frac{r}{\phi}.$$

It is easy to see that h(0) > 0, $h(x_0) = 0$ and h is strictly decreasing on $[x_P, +\infty)$. We start by proving a quantitative property of the solutions of (PP).

Lemma 1.2.1. For all $\rho > 0$ small enough, if

$$\limsup_{t \to \infty} y_2(t) \le \rho$$

then

$$\liminf_{t \to \infty} x(t) \ge h^{-1}(\rho).$$

Proof. In these circumstances, it is seen that

$$x'(t) = f(x(t)) \left[\frac{n(x(t))}{f(x(t))} - y_2 \right]$$

$$\geq f(x(t)) \left[h(x(t)) - (\rho + \varepsilon) \right]$$

for t large enough and $\varepsilon > 0$ arbitrary. The conclusion follows easily, if ρ is chosen small enough, so that $0 < \rho < h(0)$ and consequently $h^{-1}(\rho)$ is well-defined.

We now introduce a few notions regarding the persistence of a semidynamical system. Let π_1 be a semidynamical system defined on a closed subset F of a locally compact metric space (X, d).

Definition 1.2.2. It is said that a subset S of F is a uniform repeller if there is $\eta > 0$ such that for each $x \in F \setminus S$, $\liminf_{t\to\infty} d(\pi_1(x,t),S) > \eta$.

Of course, the semidynamical system is then uniformly persistent if the boundary of F is a uniform repeller. We now state an elegant result of Fonda ([24, Corollary 1]) about uniform repellers for semidynamical systems on abstract metric spaces.

Theorem 1.2.4. Let π be a semidynamical system defined on a locally compact metric space X and let S be a compact subset of X such that $X \setminus S$ is positively invariant. A necessary and sufficient condition for S to be a uniform repeller is that there exists a neighborhood U of S and a continuous function $P: X \to \mathbb{R}^+_0$ satisfying

- 1. P(x) = 0 if and only if $x \in S$.
- 2. For all $x \in U \setminus S$ there is a $T_x > 0$ such that $P(\pi(x, T_x)) > P(x)$.

Using the above result, it is possible to prove that the set $B = \{(x, y_1, y_2) \in [0, M]^3; y_2 = 0\}$ is a uniform repeller, where M is a suitable boundedness constant.

Theorem 1.2.5. Suppose that $T < kf(x_0)$ is satisfied. Then B is a uniform repeller.

Proof. It is seen that *B* is compact and that $[0, M]^3 \setminus B$ is positively invariant. Let $P : [0, M]^3 \to [0, \infty)$ defined by $P(x, y_1, y_2) = y_2$. Define also

$$U = \left\{ (x, y_1, y_2) \in [0, M]^3, P(x, y_1, y_2) < \rho \right\}$$

where ρ is small enough, so that $kf(h^{-1}(\rho))D/(D+d_1) > d_2$ and $h^{-1}(\rho)$ is well defined.

Suppose by contradiction that there is $z \in U$ such that for all t > 0 one has

$$P(\pi(z,t)) \le P(z) < \rho,$$

where $z = (x^z, y_1^z, y_2^z)$ and $\pi(z, \cdot)$ is the solution of (PP) with initial data $x(0) = x^z$, $y_1(0) = y_1^z, y_2(0) = y_2^z$.

Let us consider

$$\xi(t) = y_2(t) + \frac{D}{D+d_1}(1-\rho^*)y_1(t)$$

with ρ^* small enough, so that

$$\frac{D}{D+d_1}(1-\rho^*)kf(h^{-1}(\rho)) - d_2 > 0$$

One then has

$$\begin{aligned} \xi'(t) &= (Dy_1(t) - d_2y_2(t)) + \frac{D}{D+d_1}(1-\rho^*) \left[kf(x)y_2 - (D+d_1)y_1\right] \\ &= Dy_1 - d_2y_2 - D(1-\rho^*)y_1 + \frac{D}{D+d_1}(1-\rho^*)kf(x)y_2 \\ &= \rho^*y_1 + \left[\frac{D}{D+d_1}(1-\rho^*)kf(x) - d_2\right]y_2 \\ &\geq \rho^*y_1 + \left[\frac{D}{D+d_1}(1-\rho^*)kf(h^{-1}(\rho)) - d_2\right]y_2. \end{aligned}$$

As a result, $\xi'(t) \ge C\xi(t)$ for some sufficiently small C and consequently $\xi(t) \to \infty$ as $t \to \infty$, which contradicts the boundedness of x, y_1, y_2 . It then follows by Theorem 1.2.4 that B is an uniform repeller, which finishes the proof.

It is then easy to see that under the hypotheses of Theorem 1.2.5, the system (PP) is uniformly persistent provided that condition $\underline{x} > x_P$ holds. Consequently, we obtain the following result.

Theorem 1.2.6. If $T < kf(x_0)$ and $\underline{x} > x_P$ holds, then (PP) is uniformly persistent.

Proof. By Theorem 1.2.5, the boundedness of x, y_1, y_2 and inequality $\underline{x} > x_P$, there are m, M > 0 such that

(1.2.6)
$$m \le \liminf_{t \to \infty} \varphi(t) \le \limsup_{t \to \infty} \varphi(t) \le M$$

for $\varphi \in \{x, y_2\}$. From the second equation in (PP) one infers that

$$y_1(t_2) = e^{-(D+d_1)(t_2-t_1)}y_1(t_1) + \int_{t_1}^{t_2} kf(x(s))y_2(s)e^{-(D+d_1)(t_2-s)}ds,$$

 \mathbf{SO}

$$y_1(t_2) \ge e^{-(D+d_1)(t_2-t_1)}y_1(t_1) + kf(m)\rho \frac{1 - e^{-(D+d_1)(t_2-t_1)}}{D+d_1}$$

for $t_2 \ge t_1 \ge t^*$, t^* great enough, which implies that

$$\liminf_{t \to \infty} y_1(t) \ge \frac{kf(m)\rho}{D+d_1}$$

Since y_1 is bounded, it follows that (1.2.6) holds for $\varphi = y_1$ as well, with suitable m, M and consequently (PP) is persistent and in the long term both the predator and prey populations reach at least a certain level not depending on the initial population sizes. \Box

The biological interpretation of the above result is very simple. Once few mature predators introduced in a prey-only equilibrium can reproduce fast enough $(kf(x_0) > d_2(D + d_1)/D)$ and there is an abundance of prey on the long term $(\underline{x} > x_P)$, then the survival of all populations is assured for all future time. For other related arguments pertaining to the persistence of certain epidemiologic systems, see Margheri and Rebelo [96].

To prove again the global stability of the positive endemic equilibrium E^* by an alternate method, which will also yield the stability of the periodic solutions as a byproduct, we need now introduce a few notions and results about competitive systems and the orbital stability of their periodic orbits. See Smith [123] for a comprehensive treatment of asymptotic behavior of finite and infinite dimensional competitive systems.

Definition 1.2.3. The autonomous differential system

(1.2.7)
$$x' = f(x), \quad f : \mathcal{D} \subset \mathbb{R}^n \to \mathbb{R}^n,$$

is said to be competitive in \mathcal{D} if there is a diagonal matrix $H = \text{diag}(\varepsilon_1, \varepsilon_2, \dots, \varepsilon_n)$, $\varepsilon_i \in \{-1, 1\}, i = 1, \dots, n$ such that $HJ_{(1,2,7)}H$ has nonpositive off-diagonal elements for all $x \in \mathcal{D}$.

It is known (see, for instance, Smith [122, Theorem 4.1]) that three-dimensional competitive systems defined on convex sets have the Poincare-Bendixson property, in the sense that any nonempty compact *w*-limit set of (1.2.7) which contains no equilibria is a closed orbit of (1.2.7).

Definition 1.2.4. An orbit \mathcal{O} of (1.2.7) is called orbitally stable if and only if for all $\varepsilon > 0$ there is $\delta > 0$ with the property that any solution x(t) starting in an initial data x(0) with the property that the distance from x(0) to \mathcal{O} is less than δ remains at distance less than ε from \mathcal{O} for any $t \ge 0$. The orbit \mathcal{O} is then called orbitally asymptotically stable if it is orbitally stable and the distance from x(t) to \mathcal{O} tends to 0 as $t \to \infty$.

Definition 1.2.5. The system (1.2.7) is then said to have the property of stability of periodic orbits if all its periodic orbits are orbitally asymptotically stable in the sense mentioned above.

We now show that our system (PP) is competitive and that, under certain conditions, has the property of stability of periodic orbits.

Theorem 1.2.7. The system (PP) is competitive. If $kf(x_0) > T$ is satisfied and $\underline{x} > x_P$ holds, then (PP) also has the property of stability of periodic orbits.

Proof. Consider

$$\mathcal{D} = [0,\infty]^3, \quad H = \left(egin{array}{ccc} 1 & 0 & 0 \\ 0 & -1 & 0 \\ 0 & 0 & 1 \end{array}
ight).$$

It is seen that

(1.2.8)
$$J_{(PP)}(x, y_1, y_2) = \begin{pmatrix} n'(x) - f'(x)y_2 & 0 & -f(x) \\ kf'(x)y_2 & -(D+d_1) & kf(x) \\ 0 & D & -d_2 \end{pmatrix},$$

and consequently

$$HJ_{(\text{PP})}H = \begin{pmatrix} n'(x) - f'(x)y_2 & 0 & -f(x) \\ -kf'(x)y_2 & -(D+d_1) & -kf(x) \\ 0 & -D & -d_2 \end{pmatrix},$$

and so $HJ_{(PP)}H$ has nonpositive off-diagonal entries on \mathcal{D} , that is, it is competitive on \mathcal{D} .

We attempt to show that the system (PP) has the property of stability of periodic orbits by applying Theorem B.2.1, provided that $kf(x_0) > T$ is satisfied and $\underline{x} > x_P$ holds. Let $p = (x(t), y_1(t), y_2(t))$ be a positive periodic orbit of (PP).

Let us consider the system

(1.2.9)
$$Z'(t) = J^{[2]}_{(\text{PP})}(p(t))Z(t), \quad Z = (z_1, z_2, z_3)^T$$

and prove that this system is asymptotically stable. Let us define

$$V(z_1(t), z_2(t), z_3(t)) = \left\| \left(z_1(t), \frac{y_1(t)}{y_2(t)} z_2(t), \frac{y_1(t)}{ky_2(t)} z_3(t) \right) \right\|,$$

where $\|\cdot\|$ is a norm on \mathbb{R}^3 , defined by

$$||(z_1, z_2, z_3)|| = \max(|z_1|, |z_2| + |z_3|).$$

Note that V is well defined, since (PP) is persistent under the given hypotheses. Then system (1.2.9) can be expanded as

(1.2.10)
$$\begin{cases} z_1' = -(-n'(x) + f'(x)y_2 + (D+d_1))z_1 + kf(x)z_2 + f(x)z_3, \\ z_2' = Dz_1 + (n'(x) - f'(x)y_2 - d_2)z_2, \\ z_3' = kf'(x)y_2z_2 - (D+d_1+d_2)z_3. \end{cases}$$

By using (1.2.10), it is possible to derive the estimations

(1.2.11)
$$\begin{cases} D_{+} |z_{1}| \leq -(-n'(x) + f'(x)y_{2} + (D + d_{1})) |z_{1}| + kf(x) |z_{2}| + f'(x) |z_{3}|, \\ D_{+} |z_{2}| \leq D |z_{1}| - (-n'(x) + f'(x)y_{2} + d_{2}) |z_{2}|, \\ D_{+} |z_{3}| \leq kf'(x)y_{2} |z_{2}| - (D + d_{1} + d_{2}) |z_{3}|. \end{cases}$$

Then

$$(1.2.12) \quad D_+|z_1| \le -(-n'(x) + f'(x)y_2 + (D+d_1))|z_1| + \frac{kf(x)y_2}{y_1}\left(\frac{y_1}{y_2}\left(|z_2| + \frac{|z_3|}{k}\right)\right)$$
and

and

(1.2.13)
$$D_+\left(|z_2| + \frac{|z_3|}{k}\right) \le D|z_1| - (d_2 + \min(-n'(x), D + d_1))\left(|z_2| + \frac{|z_3|}{k}\right).$$

From the above, we may infer that

$$D_{+}\left(\frac{y_{1}}{y_{2}}\left(|z_{2}|+\frac{|z_{3}|}{k}\right)\right) = \frac{\dot{y_{1}}y_{2}-y_{1}\dot{y_{2}}}{y_{2}^{2}}\left(|z_{2}|+\frac{|z_{3}|}{k}\right) + \frac{y_{1}}{y_{2}}\left(D_{+}\left(|z_{2}|+\frac{|z_{3}|}{k}\right)\right)$$
$$\leq \left(\frac{\dot{y_{1}}}{y_{1}}-\frac{\dot{y_{2}}}{y_{2}}\right)\frac{y_{1}}{y_{2}}\left(|z_{2}|+\frac{|z_{3}|}{k}\right)\frac{y_{1}}{y_{2}}D|z_{1}|-k\frac{y_{1}}{y_{2}}\left(|z_{2}|+\frac{|z_{3}|}{k}\right)$$

and therefore

$$D_{+}\left(\frac{y_{1}}{y_{2}}\left(|z_{2}|+\frac{|z_{3}|}{k}\right)\right)$$

$$\leq \frac{y_{1}}{y_{2}}D|z_{1}|+\left(\frac{y_{1}}{y_{1}}-D\frac{y_{1}}{y_{2}}-\min\left(-n'(x),D+d_{1}\right)\right)\frac{y_{1}}{y_{2}}\left(|z_{2}|+\frac{|z_{3}|}{k}\right)$$

It is now possible to evaluate the time derivative of V. Let $t_0 > 0$. If $V(t) = |z_1(t)|$ in a vicinity of t_0 , then

$$D_{+}V(t_{0}) \leq -(-n'(x) + f'(x)y_{2} + (D + d_{1}))|z_{1}| + \frac{kf(x)y_{2}}{y_{1}} \left(\frac{y_{1}}{y_{2}} \left(|z_{2}| + \frac{|z_{3}|}{k}\right)\right)$$
$$\leq \left[\frac{kf(x)y_{2}}{y_{1}} + n'(x) - f'(x)y_{2} - (D + d_{1})\right]|z_{1}|$$
$$\leq \left[\frac{\dot{y}_{1}}{y_{1}} + n'(x) - f'(x)y_{2}\right]V(t_{0}).$$

If $V(t) = \frac{y_1(t)}{y_2(t)} \left[|z_2(t)| + \frac{z_3(t)}{k} \right]$ in a vicinity of t_0 , then

$$D_{+}V(t_{0}) \leq \frac{y_{1}}{y_{2}}D|z_{1}| + \left(\frac{\dot{y_{1}}}{y_{1}} - D\frac{y_{1}}{y_{2}} - \min\left(-n'(x), D + d_{1}\right)\right)\frac{y_{1}}{y_{2}}\left(|z_{2}| + \frac{|z_{3}|}{k}\right)$$
$$\leq \left[\frac{\dot{y_{1}}}{y_{1}} - \min\left(-n'(x), D + d_{1}\right)\right]V(t_{0}).$$

If neither of these situations happens, then

$$|z_1(t_0)| = \frac{y_1(t_0)}{y_2(t_0)} \left[|z_2(t_0)| + \frac{|z_3(t_0)|}{k} \right]$$
$$D_+ |z_1(t)| \Big|_{t=t_0} = D_+ \left[\frac{y_1(t)}{y_2(t)} \left(|z_2(t)| + \frac{|z_3(t)|}{k} \right) \right] \Big|_{t=t_0}$$

and consequently, by the same argument,

$$D_{+}V(t_{0}) \leq \min\left(\left[\frac{\dot{y}_{1}}{y_{1}} + n'(x) - f'(x)y_{2}\right], \left[\frac{\dot{y}_{1}}{y_{1}} - \min\left(-n'(x), D + d_{1}\right)\right]\right)V(t_{0})$$

Then, for all t > 0, one has

$$D_{+}V(t) \leq \max\left(\left[\frac{\dot{y_{1}}}{y_{1}} + n'(x) - f'(x)y_{2}\right], \left[\frac{\dot{y_{1}}}{y_{1}} - \min\left(-n'(x), D + d_{1}\right)\right]\right)V(t)$$

$$\leq \max\left(\left[\frac{\dot{y_{1}}}{y_{1}} + n'(x) - f'(x)y_{2}\right], \left[\frac{\dot{y_{1}}}{y_{1}} + \max\left(n'(x), -(D + d_{1})\right)\right]\right)V(t)$$

$$\leq \frac{\dot{y_{1}}}{y_{1}} + \max\left(n'(x), -(D + d_{1})\right)V(t).$$

Note that if $\underline{x} > x_P$, then n'(x(t)) is strictly negative on some $[t_*, \infty)$. It follows that

$$V(t) \le V(t^*) \frac{y_1(t)}{y_1(t^*)} e^{-\delta(t-t^*)}$$

so $\lim_{t\to\infty} V(t) = 0$. It then follows from the persistence of (PP) that

$$\lim_{t \to \infty} z_1(t) = \lim_{t \to \infty} z_2(t) = \lim_{t \to \infty} z_3(t) = 0.$$

so the null solution of (1.2.9) is asymptotically stable. By Theorem B.2.1, the system (PP) has the property of stability of periodic solutions.

It is then possible to prove that for three-dimensional competitive systems which are uniformly persistent, the local asymptotic stability of a unique positive equilibrium and the property of stability of periodic orbits insure that the endemic equilibrium is actually globally asymptotically stable. More precisely, the following result ([134, Theorem 2.2]) holds.

Proposition 1.2.1. Assume that n = 3 and that D is convex and bounded. If the system (1.2.7) is competitive and uniformly persistent in D, it has a unique equilibrium in D and it also has the property of stability of periodic orbits, then the interior equilibrium is globally asymptotically stable in Int D.

By Theorem 1.2.7 and Proposition 1.2.1, it then follows that the positive equilibrium is globally asymptotically stable in $(0, \infty)^3$ since condition $\underline{x} > x_P$ implies that $x^* > x_P$ and consequently, as previously noted, the positive equilibrium is locally asymptotically stable. From all our previous considerations, it is then possible to conclude with the following global stability result, which characterizes the global asymptotic stability of the positive equilibrium. **Theorem 1.2.8.** Suppose that $kf(x_0) > T$ and $\underline{x} > x_P$ holds. Then (PP) is uniformly persistent and there is a unique positive equilibrium $E^* = (x^*, y_1^*, y_2^*)$, which is globally asymptotically stable on $(0, \infty)^3$.

For f(x) = bx/(1 + mx) and n(x) = x(r - ax), our Theorem 1.2.8 improves [134, Theorem 2.1], since (H1) and (H2) in [134] are unified in a single weaker assumption, while being observed that there is no need to assume *a priori* the local asymptotic stability of the positive endemic equilibrium.

Suppose now that $T < kf(x_0)$. Consequently, from Theorem 1.2.8, it follows that the system (PP) is persistent and the positive steady state E^* exists and is unique. As seen in Xiao and Chen [134], it is possible to study the local stability of the positive steady state and the existence of the periodic solutions together with their orbital stability by using a result on the behavior of three-dimensional competitive systems established by Zhu and Smith in [147].

It has been seen that the Jacobian $J_{(PP)}(x, y_1, y_2)$ of the system (PP) at (x, y_1, y_2) is given by (1.2.8). Moreover, the coordinates x^* , y_1^* , y_2^* of the equilibrium point E^* verify the equilibrium relations (1.2.5). From the equilibrium relations (1.2.5), it follows that the characteristic equation at (x^*, y_1^*, y_2^*) is given by

(1.2.14)
$$\lambda^{3} + \left[(D + d_{1} + d_{2}) + f'(x^{*})y_{2}^{*} - n'(x^{*}) \right] \lambda^{2} + \lambda \left[(D + d_{1} + d_{2})(f'(x^{*})y_{2}^{*} - n'(x^{*})) \right] + (D + d_{1})d_{2}f'(x^{*})y_{2}^{*} = 0.$$

By the Routh-Hurwitz theorem, all roots of (1.2.14) have negative real parts if

(1.2.15)
$$[(D+d_1+d_2)+f'(x^*)y_2^*-n'(x^*)][(D+d_1+d_2)(f'(x^*)y_2^*-n'(x^*))]$$

> $(D+d_1)d_2f'(x^*)y_2^*,$

while if the reverse of (1.2.15) is satisfied, then two characteristic roots have positive real parts. Note that since $(D + d_1)d_2f'(x^*)y_2^* > 0$, there is always a negative real root of (1.2.14). Note also that if $x^* > x_P$, then $n'(x^*) < 0$ and consequently

$$\begin{split} & [(D+d_1+d_2)+f'(x^*)y_2^*-n'(x^*)]\left[(D+d_1+d_2)(f'(x^*)y_2^*-n'(x^*))\right] \\ & > (D+d_1+d_2)^2 f'(x^*)y_2^* \\ & \ge 4(D+d_1)d_2f'(x^*)y_2^*, \end{split}$$

so (1.2.15) is satisfied if the inequality $x^* > x_P$ holds and consequently any positive equilibrium $E^* = (x^*, y_1^*, y_2^*)$ for which $x^* > x_P$ is locally asymptotically stable.
In the particular case treated in Georgescu and Hsieh [27], in which

(1.2.16)
$$xr(x) = x(r-ax), \quad x\varphi(x) = bx/(1+mx),$$

a quick inspection of our argument shows that E^* is also stable for some $x^* < r/(2a)$ (corresponding to $x^* < x_P$, since in this case $x_P = r/(2a)$), provided that $x^* > r/(2a) - \tilde{c}/(2m)$, where

(1.2.17)
$$\tilde{c} = \left(1 + \frac{a}{mr} - \sqrt{1 - \left(1 - \frac{a}{mr}\right)^2 + 4\frac{a}{mr}\frac{d_2\left(D + d_1\right)}{\left(D + d_1 + d_2\right)^2}}\right)\frac{mr}{2a}$$

In particular, this shows that the inequality of type (1.2.15), which has been a priori assumed in Xiao and Chen [134] (stated under the equivalent form (1.2.3)), does actually follow if either (H1) or (H2) are assumed, since $\underline{x} > r/(2a)$ implies $x^* > r/(2a)$, so there is no need to assume this inequality separately. Also, it is perhaps interesting to remark that while the inequality $\underline{x} > x_P$ insures the global stability of E^* , a somewhat similar but weaker estimate $x^* > x_P$ insures its local stability. We do not know, however, whether the inequality $\underline{x} > x_P$ (or $\underline{x} > r/(2a)$ in our particular case) is sharp or not, that is, if x_P is the smallest constant C with the property that $\underline{x} > C$ (or $\underline{x} > r/(2a)$ insures the converge of the respective solution of (1.2.1) to E^* , under the condition $kf(x_0) > T$ (or kf(r/a) > T).

By the previously established competitiveness, persistence and boundedness results, it follows that (PP) is point dissipative. It is also easy to see that (PP) is irreducible in $[0, \infty) \times (-\infty, 0] \times [0, \infty)$.

Since (PP) has an unique equilibrium point $E^* = (x^*, y_1^*, y_2^*)$ and

$$\det J_{(\text{PP})}(x^*, y_1^*, y_2^*) = -(D+d_1)d_2f'(x^*)y_2^* < 0,$$

it follows from Theorem 1.2 in Zhu and Smith [147] that either E^* is stable, or, if it is unstable, there is at least one but no more than finitely many periodic orbits and at least one of these is orbitally asymptotically stable. Also, if E^* is stable but not globally stable, then since (PP) is a three-dimensional competitive system, it follows from Theorem 4.1 in Smith [123, Chapter 3] that (PP) has a periodic orbit which is necessarily orbitally unstable. Moreover, if E^* is hyperbolic and unstable with a 2-dimensional unstable manifold, it follows from Theorem 4.2 in Smith [123, Chapter 3] that the ω -limit of any orbit of (PP) which does not start on the stable manifold of E^* is a nontrivial periodic orbit. Summarizing the above discussion, one obtains the following result. **Theorem 1.2.9.** Suppose that $T < kf(x_0)$ and that E^* is not globally asymptotically stable.

- 1. If either (1.2.15) or its reverse is satisfied, then E^* is hyperbolic and there is at least a nontrivial periodic orbit. The ω -limit of any orbit with positive initial data is either E^* or a nontrivial periodic orbit.
- 2. If (1.2.15) is satisfied (which happens in particular when $x^* > x_P$), then the positive equilibrium E^* is locally asymptotically stable and there is at least a periodic orbit which is necessarily orbitally unstable.
- 3. If the reverse of (1.2.15) is satisfied, then the positive equilibrium E* is unstable with a 2-dimensional unstable manifold and there is at least one but no more than finitely many periodic orbits and at least one of these is orbitally asymptotically stable. Any solution which does not start on the one-dimensional stable manifold of E* converges to a nontrivial periodic orbit.

Unfortunately, we are not able to study analytically whether the periodic solutions mentioned in parts (2) and (3) above are unique or not.

1.2.5 Numerical simulations and the biological interpretations of the stability results

First, we discuss the biological significance of our results. From the above results, we know that $T = d_2(D+d_1)/D$ is a threshold parameter for the stability of the system and that the numerical response of the mature predator plays a major role in the long-term behavior of the stage-structured predator-prey system (PP). More precisely, Theorem 1.2.1 indicates that if the numerical response of the mature predator for the prey at carrying capacity is lower than the threshold value T, i.e., if few mature predators introduced in a predator-free ambient with prey at carrying capacity cannot reproduce fast enough, the predator classes tend to extinction. This bears a striking resemblance to the nonendemicity conditions used in mathematical epidemiology. Moreover, we can define the basic reproduction number of the system by $R_0 = kf(x_0)\frac{D}{D+d_1}\frac{1}{d_2}$ and then the condition $T \ge kf(x_0)$ is equivalent to $R_0 \le 1$. This basic reproduction number has a clear biological interpretation: the first term in R_0 , $kf(x_0)$, gives the mean number of newborn predators per mature predator; the second term, $\frac{D}{D+d_1}$, gives the probability that an immature predator will survive to adulthood and the third term, $\frac{1}{d_2}$, is simply the average lifespan of a mature predator. Subsequently, the product of these three terms yields the mean number of offspring by every predator, which is precisely the biological meaning of a basic reproduction number. Similar threshold condition for coexistence of predator-prey system had previously been formulated and explained by Pielou [110], among others, but had not been termed as "basic reproduction number" to our best knowledge.

Furthermore, if the numerical response of the mature predator for the prey at carrying capacity is higher than the threshold value T and the size of the prey population ultimately remains higher than another value $\underline{x} > x_P$, that is, if the prey is always abundant enough, it is seen from Theorem 1.2.3 that the system tends to a positive steady state. We also note that if the death rate d_1 of the immature predator is negligible compared to the rate D at which the immature predators become mature predators, then the inequality $T < kf(x_0)$ becomes a very simple comparison between the death rate of the mature predators and their rate of reproduction. Moreover, the stage structure affects the capability of the predator species to survive and become uniformly persistent, since it is now $(D + d_1)/D$ times easier for the predator species to become extinct, as can be seen from Theorem 1.2.1. This means that if it takes too much for the immature predators to mature, or the through-stage death rate of the immature predator is high (that is, D is small compared to d_1 , then the total number of offsprings produced during the adult stage will not be enough to compensate the total loss of immature predators and the predator classes will tend to extinction.

However, the situation where $R_0 > 1$ (or $T < kf(x_0)$) but $\underline{x} \leq x_P$ is more complicated. When $x^* > x_P$, we know that E^* is locally asymptotically stable, but we do not know of its global properties. The same happens for the case $x^* \leq x_P$ and (1.2.15) holds (see Theorem 1.2.9). Moreover, the precise conditions for existence and uniqueness of periodic orbits, namely when E^* is not globally stable, are unknown under (ii) of Theorem 1.2.9. Therefore, we proceed to investigate further by using numerical simulations.

In the following, we shall use the particular forms of xr(x) and $x\phi(x)$ from Georgescu and Hsieh [27] which were given in (1.2.16), that is, xr(x) = x(r - ax), $x\phi(x) = bx/(1 + mx)$. For case 1 (see Fig. 1.2.1) we let r = 1 and a = 2. Subsequently, $x_0 = \frac{r}{a} = 0.5$, $R_0 = \frac{kbx_0}{1+mx_0} \frac{D}{d_2(D+d_1)} = 1.515 > 1$, $x_P = \frac{r}{2a} = 0.25$ and $x^* > \frac{r}{2a}$. Since $x^* > \frac{r}{2a}$, the positive steady state E^* is locally asymptotically stable. Numerical simulations of trajectories starting at various initial populations seem to indicate that the stability is also global for the parameter values we used. For case 2 (see Fig. 1.2.2), we let r = 1 and a = 1 so

Figure 1.2.1: Simulation for case 1 with $R_0 = 1.515 > 1$ and $x^* > \frac{r}{2a}$. All trajectories approach E^* .



that $x_0 = \frac{r}{a} = 1$, $R_0 = 2.273 > 1$, $x_P = \frac{r}{2a} = 0.5$, $x^* < \frac{r}{2a}$ and (1.2.15) holds. Since (1.2.15) holds, we know that the positive equilibrium E^* is locally asymptotically stable. Numerical simulations seem also to indicate that the stability is global. It is interesting to note that we are unable to find parameter values under which E^* satisfies (1.2.15) and hence it is locally asymptotically stable, but not globally stable.

We also consider case 3 (see Fig. 1.2.3), where r = 3 and a = 2 and subsequently $x_0 = \frac{r}{a} = 1.5$, $x_P = \frac{r}{2a} = 0.75$, $R_0 = 2.727 > 1$, $x^* < \frac{r}{2a}$ but (1.2.15) doesn't hold. From part (iii) of Theorem 1.2.9, we know that the positive equilibrium E^* is unstable and there exists an orbitally asymptotically stable periodic orbit. Our simulation shows that this orbitally stable periodic orbit is unique and its orbital stability appears to be global. We summarize our stability results in Table 1.2.5. The three cases described by last three rows of the table are illustrated with Figs. 1.2.1-1.2.3, respectively. We note that, biologically, when (1.2.15) fails to hold and E^* becomes unstable, the coexistence of the prey and predator populations is still ensured for initial populations not on the 1-dimensional stable region of E^* , albeit with fluctuating population sizes.

We now continue with few comments regarding the *a priori* estimate $\underline{x} > r/(2a)$, which was used to establish the global asymptotic stability of the positive steady state in

Figure 1.2.2: Simulation for case 2 with $R_0 = 2.273 > 1$, $x^* < \frac{r}{2a}$ and (1.2.15) holds. All trajectories approach E^* .



R_0	E_0	x^*	\underline{x}	(4.2)	E^*	$(x, y_1, y_2) \rightarrow$
≤ 1	GAS	NE	NI	NA	NE	E_0
		$> \frac{r}{2a}$	$> \frac{r}{2a}$	YES	GAS	E^*
> 1	unstable	$> \frac{\overline{r}}{2a}$	$\leq \frac{\overline{r}}{2a}$	YES	LAS	$E^{*(1)}$
× -		$\leq \frac{r}{2a}$	$\leq \frac{r}{2a}$	YES	LAS	$E^{*(1)}$
		$\leq \frac{\overline{r}}{2a}$	$\leq \frac{\overline{r}}{2a}$	NO	unstable	$OASLC^{(1)}$

Table 1.2.1: Asymptotic states of the system. "NE" denotes does not exist, "NA" denotes not applicable, , "NI" denotes no influence, "OASLC" denotes orbitally asymptotically stable limit cycle, "GAS" and "LAS" denote globally and locally asymptotically stable, respectively, and "⁽¹⁾" denotes conclusion based on simulation results.

our particular case described in (1.2.16).

Let 0 < l < r/a. It is seen that

$$x^* > l \Leftrightarrow bkDl < (1+ml)(D+d_1)d_2,$$

from which it is easy to infer that

$$x^* > l \Leftrightarrow kf(l) < T.$$

Since $\underline{x} > l$ necessarily implies that $x^* > l$ (though this condition is only necessary and is not sufficient), it is seen that in order to have the inequality $\underline{x} > l$ satisfied, it is necessary

Figure 1.2.3: Simulation for case 3 with $R_0 = 2.727 > 1$, $x^* < \frac{r}{2a}$ but (1.2.15) doesn't hold. E^* is unstable and all trajectories approach an orbitally stable periodic orbit.



that kf(l) < T. Note that this inequality alone does not suffice to establish that $\underline{x} > l$. Again, this inequality has a certain biological interpretation. In order to have the prey population ultimately staying above a certain level l, one needs as a pre-requirement that the numerical response of the predator for prey at density l be lesser than the threshold value T. Particularizing l = r/(2a), it is seen that in order to obtain that $\underline{x} > r/(2a)$, one needs the inequality kf(r/(2a)) < T satisfied.

Also, it is perhaps fitting to give sufficient conditions here which insure the validity of our boundedness estimate $\underline{x} > r/(2a)$. From the first equation in (PP) adapted to our particular case, one obtains that

$$(1+mx)x'(t) = x(t)\left[(r-ax(t))(1+mx(t)) - by_2(t)\right]$$

which implies

$$(1+mx)x' \ge x\left[(r-b(\bar{M}+\varepsilon)) + x(rm-a) - amx^2\right]$$

for t large enough, where \overline{M} is a ultimate upper bound for y_2 and $\varepsilon > 0$ is an arbitrary constant. If $r - b(\overline{M} + \varepsilon) > 0$, it follows that $\liminf_{t \to \infty} x_t(t) \ge x_2$, where x_2 is the positive root of

$$(r - b(\bar{M} + \varepsilon)) + x(rm - a) - amx^2 = 0.$$

From the above relations, one may deduce that $\underline{x} > r/(2a)$ whenever the following conditions are satisfied

$$r - b(\bar{M} + \varepsilon) > 0$$
, $a + \sqrt{(a - rm)^2 + 4(r - b(\bar{M} + \varepsilon))am} > 2mr$.

Since $\varepsilon > 0$ was arbitrary, a set of conditions which ensures that $\underline{x} > r/(2a)$ is therefore

(1.2.18)
$$r > b\bar{M}, \quad a + \sqrt{(a - rm)^2 + 4(r - b\bar{M})am} > 2mr.$$

However, it is difficult to give a clear biological interpretation of the inequalities in (1.2.18) and we would like to point out that our *a priori* estimate $\underline{x} > r/(2a)$ (or, in the general case, $x > x_P$) is easier to interpret and represents a theoretical device readily adaptable for the study of other systems of a certain structure, in connection with monotonicity properties. For explicit estimations of type (1.2.18), this sort of adjustment may not be transparent. Note that, from the discussions in Subsection 1.1.2 on the boundedness of the solutions of system (PP), an ultimate upper bound for y_2 is $\overline{M} = k \max(r/a, x(0))(r+d)/d$, where $d = \min(d_1, d_2)$. See also Xiao and Chen [134] for a numerical example regarding the feasibility of the condition $\underline{x} > r/(2a)$.

Since the mature predator functional response f depends only on the size of the prey population x, our model (PP) together with its particular form (1.2.1) may be called, following the terminology given in Section 1.1, prey-dependent. It is also easy to see that the model (PP) can be thought as a stage-structured version of the classical predator-prey model with Holling type II functional response given below:

(H)
$$\begin{cases} x' = rx(1 - \frac{x}{K}) - \frac{bx}{1 + mx}y, \\ y' = k\frac{bx}{1 + mx}y - dy \end{cases}$$

It is therefore not surprising that, as it is easily seen from (1.2.5), our model inherits the structure which generates the so-called paradox of enrichment, formulated by Hairston et al. [39] and by Rosenzweig [119], which states that increasing the carrying capacity of the environment will cause an increase in the sizes of the predator classes at equilibrium, but not in that of prey. Also, since the left-hand side of (1.2.15) is a decreasing function of the carrying capacity r/a while the right-hand side of (1.2.15) is an increasing function of the same variable, it is seen that an increase in the carrying capacity may destabilize an otherwise stable positive equilibrium.

It has already been noted that all prey equilibria x^* for which $x^* > r/(2a)$ are locally asymptotically stable, that is, high prey equilibrium densities are stable. Moreover, it can also be observed that low prey equilibrium densities are unstable, since the limit of lefthand side of (1.2.15) as x^* tends to 0 is also 0, while the same limit of the right-hand of side (1.2.15) is positive. Consequently, the model (PP) is also affected by the so-called paradox of biological control (Luck [94]), which states that the low prey equilibrium densities of a Lotka-Volterra model are inherently unstable

Note that, by Rosenzweig-MacArthur graphical stability criterion, any equilibrium of (H) with $x^* > r/(2a) - 1/(2m)$ is stable, while any equilibrium of (H) with $x^* < r/(2a) - 1/(2m)$ is unstable. Furthermore, by Theorem 3.2 in Kuang [70], one may prove that if $\underline{x} > r/(2a)$ then (x^*, y^*) is globally asymptotically stable. One may then expect a stability threshold for (1.2.1) which is sharper than r/(2a). Unfortunately, this result does not carry out nicely for our system (PP) in its particular form (1.2.1) (see (1.2.17)). Note also that the equilibria of (1.2.1) with x^* close to r/(2a) - 1/(2m) are unstable, as the left-hand side of (1.2.15) becomes arbitrarily small, while the right-hand side remains above a strictly positive lower bound.

This model, or similar ones accounting for the effects of further biological interactions, may be used to provide details about the survival of endangered mammal and reptilian species. See Zhang, Chen and Neumann [145], where the problem of optimal harvesting is also addressed, for a somewhat more complicated model, but under the assumption that all the functions which are used to model the biological interactions are linear, except for the logistic term. In [145], the case of the Chinese Alligator is considered, as a stage-structured species preying on aquatic animals, and some recommendations for the species preservation are provided. Similarly, the conclusion which arises from our Theorem 1.2.8 is very simple: to guarantee the survival of the endangered predators at a stable and sure level, its reproduction rate should be improved, so that $R_0 > 1$ (perhaps by artificial insemination) and the prey should be kept numerically above a certain level, so that $\underline{x} > x_P$ (perhaps by raising prey offsprings in dedicated facilities and subsequently releasing them into the natural habitat). Both measures are necessary and an improvement in a single area would not suffice.

It has also been observed in this study that, for the most part of the parameter space, the dynamical outcome does not depend on the initial population sizes and the prey and predator species cannot face extinction simultaneously. These are hallmarks of preydependent models, as opposed to ratio-dependent models. As seen, for instance, in Jost et al. [61] or in Beretta and Kuang [12], mutual extinction may occur for ratio-dependent models, together with other rich dynamics, and the behavior of the system may depend on the initial population sizes (see also Kuang [71]).

The population ecology models involving ordinary differential equations are often not as descriptive or as realistic as those using delay differential equations. In this regard, it has been observed by Harrison in [41] by validating a variety of predator-prey models against a known data set regarding the interaction between *Paramecium aurelia* and its predator *Didinium nasutum* presented by Luckinbill in [95] that the best numerical fit has been given by a delayed numerical response of the predator coupled with a sigmoid functional response. However, the stability analysis for the nondelayed model is much easier to be carried out, as time delays generally have a destabilizing effect and may introduce bifurcations and other rich dynamics under certain conditions. This simplification has been done for our model, where the delaying effect of the gestation period for predators is not taken under consideration. Also, the logistic part of the equation which models the growth of the prey class may need to contain a delay term, for similar reasons. We plan to address these issue in a subsequent work.

Our considerations may be easily extended to systems of the form

(1.2.19)
$$\begin{cases} x' = n(x) - f(x)g(y_2), \\ y'_1 = kf(x)g(y_2) - c_1h(y_1) \\ y'_2 = c_2h(y_1) - c_3r(y_2), \end{cases}$$

to encompass different types of functional responses from the mature predator and possible nonlinearity in the behavior of species, including nonlinearity in the predation process, under appropriate monotonicity assumptions on the functions f, g, h, r. Some examples of f and n which fit into our framework are $f(x) = mx^c$, $0 < c \leq 1$, $f(x) = m(1 - e^{-cx})$, m, c > 0, $f(x) = bx^p/(1 + mx^p)$, $0 and <math>n(x) = x(r - ax)/(1 + \varepsilon x)$, $\varepsilon > 0$, $n(x) = rx(1 - (x/(r/a))^c)$, $0 < c \leq 1$, provided that the threshold value T and the minimal value r/(2a) for \underline{x} are modified accordingly. Another simple extension is to a model in which predators pass through p > 2 life stages, as long as the consumption of prey occurs only in the last stage. Note that the last form of n(x) given above is the Richards growth rate, often used to model growth of biological populations [117] or severity of disease outbreak [53].

The function n need not be monotone on its whole domain, but only on $[\underline{\tilde{x}}, +\infty), \underline{\tilde{x}}$ being the persistency constant of the prey for the system under consideration. In this situation, condition $\liminf_{t\to\infty} x(t) \geq \underline{\tilde{x}}$ is used to restrict n to its monotonicity domain. See Section 2.2 or Georgescu and Hsieh [28] for a related argument concerning the global stability of the endemic equilibrium for the propagation of a virus *in vivo*, with the remark that in this situation there is no need to impose any *a priori* lower bound condition since the function which corresponds to n is monotone on the whole feasibility domain. Finally, regarding our construction of a Lyapunov function, we mention that functions of type $V(x_1, x_2, x_3, x_4) = \sum_{i=1}^4 a_i(x_i - x_i^* \ln x_i)$, to which our function U_3 relates, have also been found useful for the study of SEIR epidemiological models. See Korobeinikov [64], Korobeinkov and Maini [66] for details. In this regard, global stability results for models which incorporate nonlinear incidence rates of a very general form have recently been obtained by Korobeinikov and Maini in [67].

1.3 Impulsive perturbations of a three-trophic prey-dependent food chain system

1.3.1 An introduction to food chains

Classical two species continuous time models have constituted for a long time the main tool used to investigate the interactions between ecological populations (see, for instance, Volterra [128], Leslie-Gower [79], May [97]). However, as seen from Poincaré's theorem, such models have only two behavior patterns, that is, they approach either a limit cycle or an equilibrium point and consequently fail to capture the complex behavior of some natural ecosystems. Further, other shortcomings of certain two-species models have also been pointed out. These are the paradox of enrichment and the paradox of biological control, mentioned in the previous section. To eliminate these shortcomings, ratio-dependent type models have been introduced as a replacement of Lotka-Volterra models, but these models have also attracted criticism (see Abrams [1], Deng et al [22]).

Consequently, another paradigm started to prevail, that is, the idea that the behavior of a complex system can be understood only when mutual interactions between a larger number of species are considered in a single model (Rosenzweig [119]). As a result, complex behavior, in the form of stable equilibria, limit cycles, multiple attractors and chaos, has been observed in three or more species models (Gilpin [33]) and it has also been noted that the dynamical outcome may depend on the initial population sizes, which is more in line with the results of field experiments and observations.

To understand the dynamical behavior of ecological communities, one should start by tracing their food webs and quantifying the strength of the respective interspecies interactions. It has been observed by Hastings and Powell in [44] and by Klebanoff and Hastings in [63] that since food webs often describe a net of nonlinear predator-prey interactions, there is a natural tendency of food webs to oscillate and chaos may ultimately arise when two or more predator-prey subsystems oscillate with incommensurate frequencies. Mc-Cann and Yodzis [100] mention that the parameter values chosen by Hastings and Powell in [44] may be biologically unfeasible, but the conclusions obtained in [44] are valid, and indicate biologically reasonable sets of parameter values which also produce chaos. They also provide comments about which biological conditions (metabolic types) favor the apparition of chaos. Six natural types of food web configurations are studied in McCann et al. [98] and it is also found that the dominance of strong consumer-resource interactions may generate cyclic dynamics when the frequencies of oscillation are commensurate, respectively chaotic dynamics when the frequencies of oscillation are incommensurate, while the dominance of weak coupling between interactions may dampen the total oscillation of the system, together with other biological factors, such as omnivory and food-chainpredation mechanisms. See also Bascompte et al. [10].

The so-called simple food chain, which is studied in this section, is a tritrophic food chain which appears when a top predator P feeds on an intermediate consumer C, which in turn feeds on a resource R. In this model, neither the intermediate consumer nor the top predator feed on other resources and nutrient recycling is not accounted for. The qualitative behavior of the simple food chain model with Holling type II functional responses for both the top predator and the intermediate consumer, that is, for $g_i(x) = \frac{a_i x}{1+b_i x}$, $i \in \{1, 2\}$, has been studied in detail by Hastings and Powell in [44] and by Klebanoff and Hastings in [63]. See also McCann and Yodzis [99], Kuznetsov and Rinaldi [73]. In these papers, it has been found that the model may exhibit chaotic behaviour in the neighborhood of the intermediate consumer-free equilibrium and it has also been observed that the clearance rate b_1 of the intermediate consumer is a key parameter for the stability of the model. A thorough analysis of the simple food chain model with ratio-dependent functional response for both the top predator and the intermediate consumer has been performed in Hsu et al [54]. Particularly, a tristability situation has been observed, in which different solutions tend to the origin, intermediate consumer-free equilibrium and positive equilibrium, respectively, for the same set of parameters and a discussion of the feasibility of the biological control has also been provided. Chaotic-looking solutions have also been found to exist for certain parameter values.

Simple food chain models may naturally appear as a result of the combined use of different methods which are specifically suited to the target pest and minimize the harmful effects on the environment or on non-target organisms. An approach to biological control is augmentation, relying on supplementing or manipulating the existing natural enemies of the pest in order to enhance their effectiveness. A way to achieve augmentation is to breed natural predators of the pest in laboratories and to release them periodically in the ecosystem. Consequently, in our food chain model R is the resource to be protected, C is the pest which should be regulated and P is a natural predator of the pest which is augmented by means of periodic and impulsive release of laboratory-bred individuals. Also, R, C and P are regulated by means of responsible use of chemical controls (pesticide spraying) and the use of mechanical accessories, such as pest barriers and pest traps. See Section 3.1 for general details upon biological controls and pest management strategies.

Due to the inherent discontinuity of human activities (that is, pesticides cannot be sprayed all year round but only during certain periods of the year), a natural choice is to use discrete impulsive controls rather than continuous controls for our pest management strategy. In this regard, the effect of impulsive perturbations on the simple food chain model has been studied by Zhang and Chen [141] assuming linear responses for the top predator and the intermediate consumer, by Zhang and Chen in [139] assuming Holling type II functional responses, by Zhang et al in [144] assuming Holling type IV (or simplified Monod-Haldane) functional responses and by Zhang et al in [143] and Zhang and Chen in [140] assuming Beddington-DeAngelis functional responses. In all these papers, only the case of a constant impulsive perturbation has been considered. See also Zhang et al [142], Zhang et al [146], Liu et al [84] for related results regarding the impulsive control of predator-prey systems and Georgescu and Moroşanu [31] for the discussion of an integrated pest management strategy involving biological and chemical impulsive controls. State-dependent impulsive control strategies are investigated in Meng et al [101] and Jiao et al [60], while a different approach to the control of a model related to ours, based on the use of Pontryagin's principle, is employed in Apreutesei [5].

In the following, it is seen by means of the Floquet theory of impulsively perturbed systems of ordinary differential equations that the local stability of the intermediate consumer-free periodic solution is governed by a threshold-like inequality, provided that a certain condition on the productivity of the resource is satisfied. If the reverse of the productivity condition is satisfied, then the resource and intermediate consumer-free periodic solution is globally asymptotically stable.

A sufficient condition for the global stability of the intermediate consumer-free periodic solution, corresponding to the ultimate success of our pest management strategy, is established, while it is observed that, biologically speaking, the integrated pest management strategy can be considered successful when the intermediate consumer population stabilizes under a certain economic injury level, not necessarily when it is completely eradicated. Formally, both the local and global stability condition display a significant dependence on the functional response of the top predator. Note that, due to the impulsive top predator release of constant strength, our controlled system does not exhibit the domino effect, characteristic to the unperturbed food chain system, that is, if one species dies out then all the species at higher trophic levels die out as well (although the extinction of the resource will attract the extinction of the intermediate consumer, of course). Due to the proportional impulsive perturbations at t = (n+l-1)T, $n \in \mathbb{N}^*$, the resource and intermediate consumer-free periodic solution is no longer unstable for any values the parameters involved, as it is the case when only constant impulsive perturbations of the top predator are employed, and the existence of a threshold parameter which controls its stability is also established. It is observed that, theoretically speaking, the control strategy can be always made to succeed by the use of proper pesticides, while as far as the biological control is concerned, its global effectiveness can also be reached provided that the top predator is voracious enough, or the amount μ of top predator released each time is large enough or the period T is small enough. Any of these features alone can ensure the global success of our control strategy, although in concrete situations these may or may not be biologically feasible or may require a large amount of resources. Also, our food chain system may be interpreted as the nonlinear coupling of two predator-prey subsystems (intermediate consumer-resource and top predator-intermediate consumer) through the mediation of the intermediate consumer, while the impulsive perturbations induce commensurate oscillations, as they act with the same period T. It is therefore expected that the system will display an oscillatory behavior, tending to a (impulsively perturbed)

limit cycle of period T for an important portion of the parameter space, corresponding to impulsive and periodic perturbations with significant strength. Finally, a numerical analysis of some situations leading to a chaotic behavior of the system is also provided. This section is based on the results obtained in Georgescu and Moroşanu [29].

1.3.2 The impulsively perturbed food chain system

The abundance and interaction of resource, intermediate consumer and top predator populations may be expressed in terms of their biomass per spatial unit. In this regard, let x(t), y(t), z(t) be the biomass per spatial unit of the resource, intermediate consumer and top predator, respectively. As previously mentioned, we assume that the top predator feeds on the intermediate consumer only and in turn the intermediate consumer feeds on the resource only, while the nutrient recycling is not accounted for.

The functional responses of the intermediate consumer and of the top predator are denoted by the nonlinear smooth functions g_1 , g_2 , depending only on the resource biomass density and on the intermediate consumer biomass density, respectively, and satisfying a few assumptions which will be outlined below. Due to the assumption above, our model is a prey dependent one. It is also supposed that in the absence of predation from the intermediate consumer, the resource grows according to a logistic growth with intrinsic growth rate r and carrying capacity r/a.

The processes of resource conversion into intermediate consumer biomass and of intermediate consumer into top predator biomass, respectively, are characterized by constant conversion rates k_1 and k_2 . The death rates d_1 and d_2 of the intermediate consumer and of the top predator, respectively, are also assumed to be constant

It is assumed that top predators are bred in laboratories and subsequently released in an impulsive and periodic fashion of period T, in a fixed amount μ each time. It is also assumed that pesticides are sprayed in an impulsive and periodic fashion, with the same period as the action of releasing top predators, but at different moments. As a result of pesticide spraying, fixed proportions δ_1 , δ_2 , δ_3 of the resource, intermediate consumer and top predator biomass are degraded each time.

On the basis of the above assumptions, we may formulate the following impulsively

perturbed model

$$\{ \begin{aligned} x'(t) &= x(t)[r - ax(t)] - g_1(x(t))y(t), & t \neq (n+l-1)T, \ t \neq nT; \\ y'(t) &= k_1g_1(x(t))y(t) - g_2(y(t))z(t) - d_1y(t), & t \neq (n+l-1)T, \ t \neq nT; \\ z'(t) &= k_2g_2(y(t))z(t) - d_2z(t), & t \neq (n+l-1)T, \ t \neq nT; \\ \Delta x(t) &= -\delta_1 x(t), & t = (n+l-1)T; \\ \Delta y(t) &= -\delta_2 y(t), & t = (n+l-1)T; \\ \Delta z(t) &= -\delta_3 x(t), & t = (n+l-1)T; \\ \Delta x(t) &= 0, & t = nT; \\ \Delta y(t) &= 0, & t = nT; \\ \Delta z(t) &= \mu, & t = nT. \end{aligned}$$

Here, $T > 0, 0 < l < 1, \Delta \varphi(t) = \varphi(t+) - \varphi(t)$ for $\varphi \in \{x, y, z\}$ and $t > 0, 0 \le \delta_1, \delta_2, \delta_3 < 1$, $n \in \mathbb{N}^*$. The functions g_1, g_2 are assumed to satisfy the following assumptions.

(G) g_i is of class C^1 on \mathbb{R}_+ , $g_i(0) = 0$, increasing and such that $x \mapsto g_i(x)/x$ is decreasing on \mathbb{R}_+ , $|g'_i(x)| \leq L_i$ for $x \in \mathbb{R}_+$, $i \in \{1, 2\}$, where $L_1, L_2 \geq 0$.

Note that hypothesis (G) is satisfied if functions g_1, g_2 represent Holling type II functional responses, that is, $g_i(x) = \frac{a_i x}{1+b_i x}$, $i \in \{1, 2\}$, in which $a_i, i \in \{1, 2\}$ are the search rates of the resource and of the intermediate consumer, respectively, and $b_i, i \in \{1, 2\}$, represent the corresponding clearance rates, that is, search rates multiplied by the (supposedly constant) handling time. Also, the above-mentioned constants L_1 and L_2 can be taken as globally Lipschitz constants for g_1, g_2 , respectively.

Impulsive perturbations of our three trophic food chain model have also been considered by Zhang and Chen in [139], in the form of the periodic constant impulsive perturbations of the top predator only (that is, no second group of conditions in (FC)), with particular Holling type II functional responses for the intermediate consumer and for the top predator. In [139], the local asymptotic stability of the intermediate consumerextinction periodic solution is established, provided that the impulsive period T is small enough, and it is also shown that the resource and intermediate consumer-free periodic solution is unstable.

We shall now establish the biological well-posedness of the Cauchy problem associated to our system (FC) for strictly positive initial data. First, using Lemma C.1.2, it is possible to prove that the Cauchy problem with strictly positive initial data is well-posed for our system (FC), that is, solutions (x, y, z) starting with strictly positive initial data remain strictly positive and bounded on their whole domains.

Lemma 1.3.1. The positive orthant $(\mathbb{R}^*_+)^3$ is an invariant region for the system (FC).

Proof. Let us consider $(x, y, z) : [0, T_0) \to \mathbb{R}^3$ a saturated solution for (FC) which starts with strictly positive x(0), y(0), z(0). Under our assumptions (G), it is easy to see that

$$\begin{cases} x'(t) \ge x(t) \left[r - ax(t) - g_1'(0)y(t) \right], & 0 \le t < T_0, \ t \ne (n+l-1)T, nT; \\ y'(t) \ge y(t) \left[k_1 g_1(x(t)) - g_2'(0)z(t) - d_1 \right], \\ z'(t) = z(t) \left[k_2 g_2(y(t)) - d_2 \right]. \end{cases}$$

as long as the solution remains positive. It then follows from Lemma C.1.2 that

$$\begin{cases} x(t) \ge x(0) \left(1 - \delta_1\right)^{\left[\frac{t + (1 - l)T}{T}\right]} e^{\int_0^t p_1(s)ds}, & 0 \le t < T_0; \\ y(t) \ge y(0) \left(1 - \delta_2\right)^{\left[\frac{t + (1 - l)T}{T}\right]} e^{\int_0^t p_2(s)ds}, \\ z(t) \ge z(0) \left(1 - \delta_3\right)^{\left[\frac{t + (1 - l)T}{T}\right]} e^{\int_0^t p_3(s)ds}, \end{cases}$$

where

$$\begin{cases} p_1(t) = r - ax(t) - g'_1(0)y(t); \\ p_2(t) = k_1g(x(t)) - g'_2(0)z(t) - d_1; \\ p_3(t) = k_2g_2(y(t)) - d_2, \end{cases}$$

that is, x, y, z remain strictly positive on $[0, T_0)$.

Also, using Lemma C.1.2, it is possible to show that all solutions of (FC) starting in $(\mathbb{R}^*_+)^3$ remain bounded and are actually defined on the whole \mathbb{R}_+ .

Lemma 1.3.2. All solutions $(x(\cdot), y(\cdot), z(\cdot))$ of (FC) with initial data $(x(\cdot), y(\cdot), z(\cdot)) \in (\mathbb{R}^*_+)^3$ are bounded and defined on \mathbb{R}_+ .

Proof. Let us consider a solution $(x(\cdot), y(\cdot), z(\cdot))$ of (FC) starting with strictly positive x(0), y(0), z(0) and define $u_1 : \mathbb{R}_+ \to \mathbb{R}_+$ by

$$u_1(t) = x(t) + \frac{1}{k_1}y(t) + \frac{1}{k_1k_2}z(t), \quad t \ge 0.$$

One then has

(1.3.1)
$$\frac{du_1}{dt} = x(t)[r - ax(t)] - \frac{d_1}{k_1}y(t) - \frac{d_2}{k_1k_2}z(t), \quad t > 0, \ t \neq (n+l-1)T, \ t \neq nT.$$

Let us denote $D = \min(d_1, d_2)$. It follows that

(1.3.2)
$$\frac{du_1}{dt} + Du_1 \le x(t) \left[r + D - ax(t) \right], \quad t > 0, \ t \ne (n+l-1)T, \ t \ne nT.$$

As the right-hand side of (1.3.2) is bounded from above by $C = (r + D)^2/(4a)$, it follows that

$$\frac{du_1}{dt}(t) + Du_1(t) \le C, \quad t > 0, \ t \ne (n+l-1)T, \ t \ne nT,$$

together with

$$u_1((n+l-1)T+) \le (1-\delta)u_1((n+l-1)T)$$

and

$$u_1(nT+) = u_1(nT) + \frac{\mu}{k_1k_2},$$

where $\delta = \min(\delta_1, \delta_2, \delta_3)$. By Lemma C.1.2, it follows that

$$(1.3.3) \quad u_1(t) \le u_1(0+) \left[\prod_{0 < (n+l-1)T < t} (1-\delta) \right] e^{-Dt} + C \int_0^t \left[\prod_{s \le (n+l-1)T < t} (1-\delta) \right] e^{-D(t-s)} ds + \sum_{0 < nT < t} \frac{\mu}{k_1 k_2} e^{-D(t-nT)}, \quad t > 0,$$

which yields

(1.3.4)
$$u_1(t) \le u_1(0+)e^{-Dt} + \frac{C(1-e^{-Dt})}{D} + \frac{\mu}{k_1k_2}\frac{e^{DT}}{e^{DT}-1}, \quad t > 0.$$

and since the limit of the right-hand side of (1.3.4) for $t \to \infty$ is

$$L = \frac{C}{D} + \frac{\mu}{k_1 k_2} \frac{e^{DT}}{e^{DT} - 1} < \infty,$$

it easily follows that u is bounded on its domain. Consequently, x, y, z are bounded and it follows by an easy continuability argument that they are defined on the whole \mathbb{R}_+ . \Box

It is also important to note that by a very similar procedure one may obtain that

$$u_2(t) \le u_2(0+)e^{-d_1t} + \frac{C_1}{d_1} \left(1 - e^{-d_1t}\right),$$

where $u_2(t) = x(t) + (1/k_1)y(t)$ and $C_1 = (r + d_1)^2/(4a)$. Consequently,

$$x(t) + \frac{1}{k_1}y(t) \le \left[x(0+) + \frac{1}{k_1}y(0+)\right] + \frac{(r+d_1)^2}{4ad_1} \quad \text{for } t > 0$$

At this point, it is useful to note that from the above it may be seen that y is bounded, with boundedness constant

(1.3.5)
$$B = k_1 \left[x(0+) + \frac{1}{k_1} y(0+) + \frac{(r+d_1)^2}{4ad_1} \right]$$

Of course, this boundedness constant is not necessarily optimal, but it is important to note that it is T and μ -independent. In the following, we shall also be interested in finding an ultimate boundedness constant for y, that is, a boundedness constant for y after the transient effects of the initial data are eliminated, rather than a boundedness constant; the former can be much smaller.

Also, certain results pertaining to the Floquet theory of impulsive ordinary differential equations which are mentioned in Appendix C are of interest to our discussion. Note that we shall be able to use Lemma C.2.1 in our settings even though we also employ the constant impulse $\Delta z = \mu$ apparently not covered by our Lemma C.2.1. This happens since we shall actually study the stability of certain periodic discontinuous solutions by means of the small amplitude perturbations method and the above-mentioned jump condition disappears after we reduce our problem to the stability of the null solution for certain systems, using the proper change of variables which involves discontinuous functions.

1.3.3 Periodically forced subsystems

When the intermediate consumer y is eradicated, it is easy to see that the equations in (FC) decouple and we are led to consider the properties of the subsystems

(RS;x)
$$\begin{cases} x'(t) = x(t)[r - ax(t)], & t \neq nT, (n+l-1)T; \\ \Delta x(t) = -\delta_1 x(t), & t = (n+l-1)T; \\ \Delta x(t) = 0, & t = nT; \\ x(0+) = x_0, \end{cases}$$

and

(RS;z)
$$\begin{cases} z'(t) = -d_2 z(t), & t \neq nT, \ (n+l-1)T; \\ \Delta z(t) = -\delta_3 z(t), & t = (n+l-1)T; \\ \Delta z(t) = \mu, & t = nT; \\ z(0+) = z_0, \end{cases}$$

which describe the dynamics of the resource and of the top predator, respectively, in the absence of the intermediate consumer. First, it is seen that if a certain inequality which characterizes resource productivity is satisfied, then the system formed with the first three equations in (RS;x) has a periodic solution, to which all solutions of (RS;x) starting with strictly positive x_0 tend as $t \to \infty$, while if the opposite inequality is satisfied, then all solutions of (RS;x) tend to 0 as $t \to \infty$. The above-mentioned periodic solution will be labeled as x_r^* rather than, for instance, x_{r,a,δ_1}^* , as systems of type (RS;x) will always occur with the same a and δ_1 , but sometimes with different r's, so there is no danger of confusion.

Lemma 1.3.3. The following statements hold.

1. Suppose that $\ln(1 - \delta_1) + rT > 0$. Then the system formed with the first three equations in (RS;x) has a periodic solution x_r^* . With this notation, the following properties are satisfied.

(a)
$$\int_0^T x_r^*(t) dt = (1/a) \left[\ln(1 - \delta_1) + rT \right].$$

(b) $\lim_{t\to\infty} |x(t) - x_r^*(t)| = 0$ for all solutions x(t) of (RS;x) starting with strictly positive x_0 .

(c)
$$\sup_{t\geq 0} |x_{r_1}^*(t) - x_{r_2}^*(t)| \le f_1(r_1, r_2; T, a, \delta_1), \text{ with } \lim_{r_1 \to r_2} f_1(r_1, r_2; T, a, \delta_1) = 0.$$

2. Suppose that $\ln(1-\delta_1) + rT \leq 0$. Then $\lim_{t\to\infty} x(t) = 0$ for all solutions of (RS;x).

Proof. First, it is easy to see that

(1.3.6)
$$u(t) = \frac{(r/a)u(t_0)e^{r(t-t_0)}}{(r/a) + u(t_0)(e^{r(t-t_0)} - 1)}, \quad (n+l-1)T \le t_0 < t \le (n+l)T$$

for any solution u of the first equation in (RS;x), and so

$$u((n+l)T) = \frac{(r/a)u((n+l-1)T+)e^{rT}}{r/a + u((n+l-1)T+)(e^{rT}-1)}$$

Then

(1.3.7)
$$u((n+l)T+) = (1-\delta_1)\frac{(r/a)u((n+l-1)T+)e^{rT}}{(r/a)+u((n+l-1)T+)(e^{rT}-1)}$$

for any solution u of the first equation in (RS;x). Suppose now that $\ln(1 - \delta_1) + rT > 0$. By the periodicity requirement, it follows that

$$x_r^*((n+l-1)T+) = \frac{(r/a)\left[(1-\delta_1)e^{rT}-1\right]}{e^{rT}-1}$$

and so

$$x_r^*(lT+) = \frac{(r/a)\left[(1-\delta_1)e^{rT}-1\right]}{e^{rT}-1}.$$

Obviously, as $\ln(1 - \delta_1) + rT > 0$, the periodic solution x_r^* does indeed exist, is unique and strictly positive. Actually, it may be seen that

(1.3.8)
$$x_r^*(t) = \frac{(r/a)Ae^{r(t-(n+l-1)T)}}{1+A\left(e^{r(t-(n+l-1)T)}-1\right)}, \quad (n+l-1)T < t \le (n+l)T,$$

where

(1.3.9)
$$A = \frac{(1-\delta_1)e^{rT}-1}{e^{rT}-1}$$

Also, since

$$\frac{x_r^{*\prime}(t)}{x_r^{*}(t)} = r - ax_r^{*}(t), \quad t \in ((n+l-1)T, (n+l)T],$$

it follows that

$$\ln\left(x_r^*(t_2)\right) - \ln\left(x_r^*(t_1)\right) = \int_{t_1}^{t_2} \left[r - ax_r^*(s)\right] ds, \quad (n+l-1)T < t_1 \le t_2 \le (n+l)T$$

and so

$$\ln\left(x_r^*((n+l)T)\right) - \ln\left(x_r^*((n+l-1)T+)\right) = \int_{(n+l-1)T}^{(n+l)T} \left[r - ax_r^*(s)\right] ds.$$

By the periodicity of x_r^* , it follows that

$$-\ln(1-\delta_1) = \int_0^T [r - ax_r^*(s)] \, ds,$$

from which the first assertion follows. Note also that

$$\ln(1 - \delta_1) + \int_0^T \left[r - ax_r^*(s)\right] ds = 0.$$

Let now x(t) be a solution of (RS;x) starting with strictly positive initial data. We shall prove that $\lim_{t\to\infty} |x(t) - x_r^*(t)| = 0.$

If $x(lT+) = x_r^*(lT+)$, then obviously $x \equiv x_r^*$. Suppose now that $x(lT+) > x_r^*(lT+)$; if the reverse inequality is satisfied one can devise a similar argument to obtain the conclusion mentioned above.

Let us denote $f : \mathbb{R}_+ \to \mathbb{R}_+$,

$$f(x) = (1 - \delta_1) \frac{(r/a) x e^{rT}}{(r/a) + x (e^{rT} - 1)}.$$

It is then seen that $x \mapsto f(x)$ is strictly increasing on \mathbb{R}_+ , while $x \mapsto f(x)/x$ is strictly decreasing on \mathbb{R}_+ . By (1.3.6), it is also seen that

$$x_r^*((l+1)T+) = f(x_r^*(lT+)), \quad x((l+1)T+) = f(x(lT+))$$

and by the periodicity of x_r^* it is seen that $x_r^*((l+1)T+) = x_r^*(lT+)$. It follows that

$$x((l+1)T+) = f(x(lT+)) > f(x_r^*(lT+)) = x_r^*(lT+),$$

since f is strictly increasing on \mathbb{R}_+ . Also,

$$x((l+1)T+) = f(x(lT+)) = \frac{f(x(lT+))}{x(lT+)}x(lT+) < x(lT+),$$

since $x(lT+) > x_r^*(lT+)$, $f(x_r^*(lT+)) = x_r^*(lT+)$ and $x \mapsto f(x)/x$ is strictly decreasing on \mathbb{R}_+ .

Similarly, by an induction argument,

$$x((n+l+1)T+) = f(x((n+l)T+)) > f(x_r^*((n+l)T+)) = f(x_r^*(lT+))$$
$$= x_r^*(lT+)$$

and

$$\begin{aligned} x((n+l+1)T+) &= f(x((n+l)T+)) = \frac{f(x((n+l)T+))}{x((n+l)T+)} x((n+l)T+) \\ &< x((n+l)T+). \end{aligned}$$

One then obtains that $(x((n+l)T+))_{n\geq 0}$ is monotonically decreasing and bounded from below by $x_r^*(lT+)$, so it is convergent to some $w_1 > 0$. Also,

$$x((n+l+1)T+) - x((n+l)T+) = f(x((n+l)T+)) - x((n+l)T+) \to 0 \quad \text{as } n \to \infty.$$

From the above, it follows that $f(w_1) = w_1$, and so $w_1 = x_r^*(lT+)$, since the equation f(t) = t has a single strictly positive solution. It then follows that $(x((n+l)T+))_{n\geq 0} \rightarrow x_r^*(lT+)$ for $n \rightarrow \infty$. Also, by (1.3.6), one may prove that

$$|x(t) - x_r^*(t)| \le e^{rT} |x((n+l)T+) - x_r^*((n+l)T+)|, \quad \text{for } t \in ((n+l)T, (n+l+1)T],$$

from which the second assertion follows. The remaining assertion can be proved by direct computation, making use of the explicit representation formula (1.3.8) and of the T-periodicity of $x_{r_1}^*$ and $x_{r_2}^*$. In fact, one may obtain that

$$\left|x_{r_1}^*(t) - x_{r_2}^*(t)\right| \le |r_1 - r_2| \left[\frac{1}{a} + \frac{(1-A)^2}{a}\right] + \frac{A(1-A)}{a} \left|r_1 e^{r_2 T} - r_2 e^{r_1 T}\right| \quad \text{for } t \ge 0.$$

Suppose now that $\ln(1 - \delta_1) + rT \leq 0$. Again, by (1.3.7), it is seen that

$$\begin{aligned} x((n+l)T+) &= (1-\delta_1) \frac{(r/a)x((n+l-1)T+)e^{rT}}{(r/a)+x((n+l-1)T+)(e^{rT}-1)} \\ &= x((n+l-1)T+) \frac{(r/a)(1-\delta_1)e^{rT}}{(r/a)+x((n+l-1)T+)(e^{rT}-1)} \\ &\leq x((n+l-1)T+), \end{aligned}$$

as $(1-\delta_1)e^{rT} \leq 1$. It then follows that $(x((n+l-1)T+))_{n\geq 0}$ is monotonically decreasing and bounded from below by 0, so it converges to some $w_2 \geq 0$. Since x((n+l)T+) = f(x((n+l-1)T+)), it follows that $f(w_2) = w_2$. Then

$$w_2 = w_2 \frac{(r/a)(1-\delta_1)e^{rT}}{(r/a) + w_2 (e^{rT} - 1)}$$

and, since $\ln(1 - \delta_1) + rT \leq 0$, it easily follows that $w_2 = 0$. By (1.3.6), it also follows that

$$x(t) \le x((n+l-1)T+)e^{rT} \quad \text{for } t \in ((n+l-1)T, (n+l)T]$$

or $x(t) = 0.$

and so $\lim_{t\to\infty} x(t) = 0.$

We now suggest an approximate interpretation of the hypotheses in Lemma 1.3.3. Let us suppose that x approaches 0 in (RS;x). Then rT approximates the total growth (per unit biomass) of the resource biomass in a period, while $\ln(1 - \delta_1)$ is a correction term which accounts for the loss of resource biomass (per unit biomass) due to pesticide spraying. If the total growth rT does not exceed the loss $\ln(1 - \delta_1)$, there is a net loss of resource biomass when x approaches 0 and so the resource biomass x(t) tends to 0 as $t \to \infty$, while if $\ln(1 - \delta_1) + rT > 0$, there is a net gain of resource biomass when x approaches 0 which prevents the extinction of the resource x.

Secondly, it is seen that the system formed with the first three equations in (RS;z) has a periodic solution to which all solutions of (RS;z) starting with strictly positive z_0 tend as $t \to \infty$, irrespective of the sign of $\ln(1-\delta_1)+rT$. This happens since the survival of the top predator is assured by the periodic impulse μ and does not depend upon the survival or extinction of the resource, although the peristence level is, of course, indirectly affected. Again, this solution will be labeled as $z_{d_2}^*$, for reasons similar to those outlined above.

Lemma 1.3.4. The system formed with the first three equations in (RS;z) has a periodic solution $z_{d_2}^*$. With this notation, the following properties are satisfied.

1.
$$\int_0^T z_{d_2}^*(t) dt = \frac{\mu}{1 - e^{-d_2 T}(1 - \delta_3)} \left[(1 - e^{-d_2 lT}) + (1 - \delta_3)(e^{-d_2 lT} - e^{-d_2 T}) \right].$$

2. $\lim_{t \to \infty} |z(t) - z_{d_2}^*(t)| = 0 \text{ for all solutions } z(t) \text{ of } (RS;z) \text{ starting with strictly positive } z_0.$

3.
$$\sup_{t \ge 0} \left| z_{d_2}^*(t) - z_{\tilde{d}_2}^*(t) \right| \le f_2(d_2, \tilde{d}_2; T, \mu, \delta_3), \text{ with } \lim_{\tilde{d}_2 \to d_2} f_2(\tilde{d}_2, d_2; T, \mu, \delta_3) = 0.$$

Proof. First, it is easy to see that

(1.3.10)
$$u(t) = e^{-d_2(t-t_0)}u(t_0)$$
 $t, t_0 \in ((n+l-1)T, nT)$ or $(nT, (n+l+1)T)$

for any solution u of the first equation in (RS;z) and so

$$\begin{aligned} z_{d_2}^*((n+1)T+) &= z_{d_2}^*((n+1)T) + \mu \\ &= e^{-d_2(1-l)T} z_{d_2}^*((n+l)T+) + \mu \\ &= e^{-d_2(1-l)T} (1-\delta_3) e^{-d_2lT} z_{d_2}^*(nT+) + \mu \\ &= e^{-d_2T} (1-\delta_3) z_{d_2}^*(nT+) + \mu. \end{aligned}$$

By the periodicity requirement, it follows that

$$z_{d_2}^*(nT+) = e^{-d_2T}(1-\delta_3)z_{d_2}^*(nT+) + \mu$$

and so

(1.3.11)
$$z_{d_2}^*(0+) = \frac{\mu}{1 - e^{-d_2T}(1-\delta_3)}$$

Obviously, by (1.3.11), the periodic solution searched for does indeed exist, is unique and strictly positive. Actually, it may be seen that

(1.3.12)
$$z_{d_2}^*(t) = \begin{cases} \frac{\mu}{1 - e^{-d_2 T}(1 - \delta_3)} e^{-d_2(t - nT)}, & t \in (nT, (n+l)T] \\ \frac{\mu}{1 - e^{-d_2 T}(1 - \delta_3)} e^{-d_2(t - nT)}(1 - \delta_3), & t \in ((n+l)T, (n+1)T]. \end{cases}$$

The first assertion follows then by direct computation.

Let now z be a solution of (RS;z) with strictly positive initial data. We shall prove that $\lim_{t\to\infty} |z(t) - z_{d_2}^*(t)| = 0.$

It is seen that $z - z_{d_2}^*$ verifies the system

$$\begin{cases} (z - z_{d_2}^*)'(t) = -d_2(z - z_{d_2}^*)(t), & t \neq (n+l-1)T, \ t \neq nT; \\ \Delta(z - z_{d_2}^*)(t) = -\delta_3(z - z_{d_2}^*)(t), & t = (n+l-1)T; \\ \Delta(z - z_{d_2}^*)(t) = 0, & t = nT. \end{cases}$$

Consequently,

$$(1.3.13) z(t) - z_{d_2}^*(t) = \begin{cases} e^{-d_2(t - (n-1)T)} & \left(z(0+) - \frac{\mu}{1 - e^{-d_2T}(1 - \delta_3)}\right) (1 - \delta_3)^{n-1}, \\ t \in ((n-1)T, (n+l-1)T]; \\ e^{-d_2(t - (n-1)T)} & \left(z(0+) - \frac{\mu}{1 - e^{-d_2T}(1 - \delta_3)}\right) (1 - \delta_3)^n, \\ t \in ((n+l-1)T, nT]; \end{cases}$$

from which the second assertion follows. The third assertion can be proved by direct computation, as done for Lemma 1.3.3. $\hfill \Box$

1.3.4 Local stability results. A Floquet analysis

In this section we study the local stability of the resource and intermediate consumerfree periodic solution $(0, 0, z_{d_2}^*(t))$ and of the intermediate consumer-free periodic solution $(x_r^*(t), 0, z_{d_2}^*(t))$ by means of Floquet theory, supposing that the productivity condition for the resource $\ln(1 - \delta_1) + rT > 0$ is satisfied. In this sense, it will be seen that the local stability of the intermediate consumer-free periodic solution is governed by a thresholdlike condition expressed in terms of an integral involving the periodic solutions x_r^* and $z_{d_2}^*$ introduced in the previous section, while the resource and intermediate consumer-free periodic solution is always unstable.

Theorem 1.3.1. Suppose that $\ln(1 - \delta_1) + rT > 0$. The following properties hold.

- 1. The resource and intermediate consumer-free periodic solution $(0, 0, z_{d_2}^*(t))$ is unstable.
- 2. The intermediate consumer-free periodic solution $(x_r^*(t), 0, z_{d_2}^*(t))$ is locally asymptotically stable provided that

(1.3.14)
$$\ln(1-\delta_2) + \int_0^T \left[k_1 g_1(x_r^*(s)) - g_2'(0) z_{d_2}^*(s) - d_1 \right] ds < 0$$

and unstable provided that the reverse inequality holds.

Proof. To study the stability of the resource and intermediate consumer-free periodic solution $(0, 0, z_{d_2}^*(t))$, let us denote

(1.3.15)
$$x(t) = u(t), \quad y(t) = v(t), \quad z(t) = w(t) + z_{d_2}^*(t),$$

u, v and w being understood as small amplitude perturbations. Substituting (1.3.15) into the first three equations of (FC), one obtains

(1.3.16)
$$\begin{cases} u'(t) = u(t) [r - au(t)] - g_1(u(t))v(t) \\ v'(t) = k_1 g_1(u(t)) - g_2(v(t)) [w(t) + z_{d_2}^*(t)] - d_1 v(t) \\ w'(t) = k_2 g_2(v(t))) [w(t) + z_{d_2}^*(t)] - d_2 w(t) \end{cases}$$

The corresponding linearization of (1.3.16) at (0, 0, 0) is

(1.3.17)
$$\begin{cases} u'(t) = ru(t) \\ v'(t) = -\left[g'_2(0)z^*_{d_2}(t) + d_1\right]v(t) \\ w'(t) = k_2g'_2(0)z^*_{d_2}(t)v(t) - d_2w(t) \end{cases}$$

and so a fundamental matrix of (1.3.17) is

(1.3.18)
$$\Phi_L^1(t) = \begin{pmatrix} e^{rt} & 0 & 0\\ 0 & e^{-\int_0^t \left[g_2'(0)z_{d_2}^*(s) + d_1\right]ds} & 0\\ 0 & \left(\int_0^t k_2 g_2'(0)z_{d_2}^*(s)e^{-\int_0^s \left[g_2'(0)z_{d_2}^*(\tau) + d_1\right]d\tau}ds\right)e^{-d_2t} & e^{-d_2t} \end{pmatrix}.$$

The linearization of the jump conditions at (n+l-1)T reads as

(1.3.19)
$$\begin{cases} \Delta u(t) = -\delta_1 u(t), & t = (n+l-1)T; \\ \Delta v(t) = -\delta_2 v(t), \\ \Delta w(t) = -\delta_3 w(t), \end{cases}$$

while the linearization of the jump conditions at nT reads as

(1.3.20)
$$\begin{cases} \Delta u(t) = 0, \quad t = nT; \\ \Delta v(t) = 0, \\ \Delta w(t) = 0. \end{cases}$$

Consequently, the local stability of the resource and intermediate consumer-free periodic solution $(0, 0, z_{d_2}^*(t))$ can be analyzed by studying the eigenvalues of the monodromy matrix

$$M_1 = \begin{pmatrix} 1 - \delta_1 & 0 & 0 \\ 0 & 1 - \delta_2 & 0 \\ 0 & 0 & 1 - \delta_3 \end{pmatrix} \Phi_L^1(T).$$

Since the eigenvalues of M_1 are

,

$$\lambda_1 = (1 - \delta_1)e^{rT}, \quad \lambda_2 = (1 - \delta_2)e^{-\int_0^T \left[g_2'(0)z_{d_2}^*(s) + d_1\right]ds}, \quad \lambda_3 = (1 - \delta_3)e^{-d_2T}$$

and $\lambda_1 > 1$, it follows that the resource and intermediate consumer-free periodic solution $(0, 0, z_{d_2}^*(t))$ is unstable, with an one-dimensional unstable manifold.

We now study the stability of the intermediate consumer-free periodic solution $(x_r^*(t), 0, z_{d_2}^*(t))$. Let us denote

(1.3.21)
$$x(t) = u(t) + x_r^*(t), \quad y(t) = v(t), \quad z(t) = w(t) + z_{d_2}^*(t),$$

u, v, w being understood again as small amplitude perturbations. Substituting (1.3.21) into the first three equations of (FC), one obtains

(1.3.22)
$$\begin{cases} u'(t) = u(t) \left[r - a(u(t) + x_r^*(t)) \right] - g_1(u(t) + x_r^*(t))v(t) \\ v'(t) = k_1 g_1(u(t) + x_r^*(t))v(t) - g_2(v(t))(w(t) + z_{d_2}^*(t)) - d_1v(t) \\ w'(t) = k_2 g_2(v(t))(w(t) + z_{d_2}^*(t)) - d_2w(t). \end{cases}$$

The corresponding linearization of (1.3.22) at (0, 0, 0) is

(1.3.23)
$$\begin{cases} u'(t) = u(t) \left[r - a x_r^*(t) \right] - g_1(x_r^*(t)) v(t) \\ v'(t) = \left[k_1 g_1(x_r^*(t)) - g_2'(0) z_{d_2}^*(t) - d_1 \right] v(t) \\ w'(t) = k_2 g_2'(0) z_{d_2}^*(t) v(t) - d_2 w(t). \end{cases}$$

Let us define

$$\varphi : \mathbb{R}_+ \to \mathbb{R}, \quad \varphi(t) = \int_0^t \left[r - a x_r^*(s) \right] ds,$$

$$\psi : \mathbb{R}_+ \to \mathbb{R}, \quad \psi(t) = \int_0^t \left[k_1 g_1(x_r^*(s)) - g_2'(0) z_{d_2}^*(s) - d_1 \right] ds.$$

Then a fundamental matrix of (1.3.23) is

$$\Phi_L^2(t) = \begin{pmatrix} e^{\varphi(t)} & -e^{\varphi(t)} \int_0^t g_1(x_r^*(s))e^{\psi(s)-\varphi(s)}ds & 0\\ 0 & e^{\psi(t)} & 0\\ 0 & e^{-d_2t} \int_0^t k_2 g_2'(0) z_{d_2}^*(s)e^{d_2s+\psi(s)}ds & e^{-d_2t} \end{pmatrix}$$

The linearization of the jump conditions at (n + l - 1)T and nT gives again (1.3.19) and (1.3.20). Consequently, the local stability of the intermediate consumer-free periodic

solution $(x_r^*(t), 0, z_{d_2}^*(t))$ can be analyzed by studying the eigenvalues of the monodromy matrix

$$M_2 = \begin{pmatrix} 1 - \delta_1 & 0 & 0 \\ 0 & 1 - \delta_2 & 0 \\ 0 & 0 & 1 - \delta_3 \end{pmatrix} \Phi_L^2(T).$$

It is seen that the eigenvalues of M_2 are

$$\lambda_1 = (1 - \delta_1)e^{\varphi(T)}, \quad \lambda_2 = (1 - \delta_2)e^{\psi(T)}, \quad \lambda_3 = (1 - \delta_3)e^{-d_2T}$$

It is obvious that $0 < \lambda_3 < 1$. Also, $\lambda_1 = 1$, from Lemma 1.3.3. If (1.3.14) is satisfied, then $0 < \lambda_2 < 1$ and $\lambda_1 = 1$ is a simple eigenvalue, which implies that $(x_r^*(t), 0, z_{d_2}^*(t))$ is stable. If the reverse of (1.3.14) is satisfied, then $\lambda_2 > 1$ and $(x_r^*(t), 0, z_{d_2}^*(t))$ is unstable. Finally, noting that $\int_0^T g_1(x_r^*(s))e^{\psi(s)-\varphi(s)}ds > 0$, since the integrand is strictly positive, one sees that if

(1.3.24)
$$\ln(1-\delta_2) + \int_0^T \left[k_1 g_1(x_r^*(s)) - g_2'(0) z_{d_2}^*(s) - d_1\right] ds = 0.$$

then $(x_r^*(t), 0, z_{d_2}^*(t))$ is again unstable, since $\lambda = 1$ is an eigenvalue of multiplicity 2 and its elementary divisor its not simple.

Note that the meaning of condition (1.3.14) is completely similar to that of condition $\ln(1 - \delta_1) + rT < 0$, but applied to the dynamics of y this time. Namely, suppose that y approaches 0. Then $\int_0^T [k_1g_1(x_r^*(s)) - g'_2(0)z_{d_2}^*(s) - d_1] ds$ approximates the total growth (per unit biomass) of the intermediate consumer biomass in a period (note that $\lim_{t\to 0} (g(t)/t) = g'_2(0)$), while $\ln(1 - \delta_2)$ is a correction term which accounts for the loss of intermediate consumer biomass (per unit biomass) due to pesticide spraying. If the total growth exceeds the loss $\ln(1 - \delta_2)$, then there is a net gain of consumer biomass when y approaches 0 which prevents the extinction of the intermediate consumer, while if the loss $\ln(1 - \delta_2)$ exceeds the total growth, there is a net loss of consumer biomass when y approaches 0 and so y(t) tends to 0 as $t \to \infty$. Also, condition $\ln(1 - \delta_1) + rT > 0$ ensures the instability of the resource and intermediate consumer-free periodic solution, since it prevents the extinction of the resource.

Since g_1 and g_2 are general functional responses, we have to state our stability condition (1.3.14) in terms of the periodic solutions x_r^* and $z_{d_2}^*$ rather than in a more explicit form. Actually, this form may make more sense even when the particular forms of g_1 and g_2 are known (for instance, when g_1 , g_2 are Holling type II functional responses), as the resulting explicit inequalities are rather cumbersome and their interpretations are not transparent.

1.3.5 Global stability results

In this section, we perform a global stability analysis of the resource and intermediate consumer-free periodic solution $(0, 0, z_{d_2}^*(t))$ and of the intermediate consumer-free periodic solution $(x_r^*(t), 0, z_{d_2}^*(t))$, respectively.

Theorem 1.3.2. The following statements hold.

- 1. Suppose that $\ln(1-\delta_1)+rT \leq 0$. Then the resource and intermediate consumer-free periodic solution $(0,0,z_{d_2}^*(t))$ is globally asymptotically stable.
- 2. Suppose that $\ln(1 \delta_1) + rT > 0$. Then the intermediate consumer-free periodic solution $(x_r^*(t), 0, z_{d_2}^*(t))$ is globally asymptotically stable provided that

(1.3.25)
$$\ln(1-\delta_2) + \int_0^T \left[k_1 g_1(x_r^*(s)) - c_{g_2} z_{d_2}^*(s) - d_1 \right] ds < 0,$$

where

$$c_{g_2} = \inf_{0 \le u \le M_y} g_2'(u),$$

 M_y being an ultimate boundedness constant for y.

Proof. Suppose first that $\ln(1 - \delta_1) + rT \leq 0$. Let $\varepsilon_1 > 0$ such that $k_1g_1(\varepsilon_1) < d_1$ (this is always possible since $\lim_{\varepsilon \to 0} g_1(\varepsilon) = 0$) and let also $\eta = (1 - \delta_1)e^{(k_1g_1(\varepsilon_1) - d_1)T}$. Note that $0 < \eta < 1$. It is seen that

$$x'(t) = x(t) [r - ax(t)] - g_1(x(t))y(t) \le x(t) [r - ax(t)]$$

and so, by Lemma C.1.1, $x(t) \leq \tilde{x}(t)$ for $t \geq 0$, where \tilde{x} is the solution of (RS;x) with the same initial data at 0+ as x. As any such solution \tilde{x} tends to 0 for $t \to \infty$, by Lemma 1.3.3, x tends to 0 as well and there is $T_1 > 0$ such that $x(t) \leq \varepsilon_1$ for $t \geq T_1$. For the sake of simplicity, we suppose that $x(t) \leq \varepsilon_1$ for all t > 0. One then obtains that

$$y'(t) = k_1 g_1(x(t)) y(t) - g_2(y(t)) z(t) - d_1 y(t)$$

$$\leq y(t) [k_1 g_1(\varepsilon_1) - d_1], \quad t \neq (n+l-1)T.$$

By integrating the above inequality on ((n+l-1)T, (n+l)T], one obtains

$$\ln(y((n+l)T)) - \ln(y((n+l-1)T+)) \le (k_1g_1(\varepsilon_1) - d_1)T \text{ for } n \ge 1$$

and so

$$\ln(y((n+l)T)) - \ln(y((n+l-1)T)) - \ln(1-\delta_1) \le (k_1g_1(\varepsilon_1) - d_1)T \text{ for } n \ge 1.$$

It then follows that

$$y((n+l)T) \le y((n+l-1)T)\eta$$

and consequently

$$y((n+l)T) \le y(lT)\eta^n,$$

which implies that $y((n+l)T) \to 0$ as $n \to \infty$. Also,

$$y(t) \le y((n+l-1)T+)e^{(k_1g_1(\varepsilon_1)-d_1)(t-(n+l-1)T)}, \quad t \in ((n+l-1)T, (n+l)T]$$

which implies that

$$y(t) \le y((n+l-1)T+), \quad t \in ((n+l-1)T, (n+l)T]$$

and consequently $y(t) \to 0$ as $t \to \infty$.

We finish by proving that $z(t) - z_{d_2}^*(t) \to 0$ as $t \to \infty$. To this purpose, let $0 < \varepsilon_2 < d_2/(k_2L_2)$. Since $y(t) \to 0$ as $t \to \infty$, there is some $T_2 > 0$ such that $y(t) \le \varepsilon_2$ for all $t \ge T_2$. For the sake of simplicity, we suppose that $y(t) \le \varepsilon_2$ for all t > 0.

It follows that

$$z'(t) = k_2 g_2(y(t)) z(t) - d_2 z(t)$$

$$\leq k_2 L_2 y(t) z(t) - d_2 z(t)$$

$$\leq -(d_2 - k_2 L_2 \varepsilon_2) z(t), \quad t \neq (n+l-1)T, \ t \neq nT$$

Consequently, one infers from Lemma C.1.1 that

$$\tilde{z}_1(t) \le z(t) \le \tilde{z}_2(t)$$

where \tilde{z}_1 is the solution of (RS;z) with the same initial data at 0+ as z and \tilde{z}_2 is the solution of (RS;z) with d_2 changed into $d_2 - k_2 L_2 \varepsilon_2$ and the same initial data at 0+ as z.

As these solutions become close to $z_{d_2}^*(t)$, respectively to $z_{d_2-k_2L_2\varepsilon_2}^*(t)$ as $t \to \infty$, by Lemma 1.3.4, it follows that, for t large enough,

$$z_{d_2}^*(t) - \varepsilon_2 \le z(t) \le z_{d_2 - k_2 L_2 \varepsilon_2}^*(t) + \varepsilon_2$$

and the conclusion follows from Lemma 1.3.4. The first assertion is now established.

Suppose now that $\ln(1 - \delta_1) + rT > 0$. We first show that $y(t) \to 0$ as $t \to \infty$. To this purpose, choose $\varepsilon_3 > 0$ such that

$$\ln(1-\delta_2) + \int_0^T \left[k_1 g_1(x_r^*(s) + \varepsilon_3) - c_{g_2}(z_{d_2}^*(s) - \varepsilon_3) - d_1 \right] ds < 0$$

This choice is obviously feasible, as $|g_1(x_r^*(s) + \varepsilon_3) - g_1(x_r^*(s))| \le L_1\varepsilon_3$ and (1.3.25) is satisfied. Let us also denote

$$\xi = (1 - \delta_2) e^{\int_0^T \left[k_1 g_1(x_r^*(s) + \varepsilon_3) - c_{g_2}(z_{d_2}^*(s) - \varepsilon_3) - d_1\right] ds}$$

and observe that $0 < \xi < 1$.

It is seen that

$$x'(t) = x(t) [r - ax(t)] - g_1(x(t))y(t) \le x(t) [r - ax(t)],$$

and so, by Lemma C.1.1, $x(t) \leq \tilde{x}(t)$ for $t \geq 0$, where \tilde{x} is the solution of (RS;x) with the same initial data at 0+ as x. As any such solution becomes close to $x_r^*(t)$ for $t \to \infty$, by Lemma 1.3.3, there is some $T_3 > 0$ such that $x(t) \leq x_r^*(t) + \varepsilon_3$ for $t \geq T_3$. For the sake of simplicity, we suppose that $x(t) \leq x_r^*(t) + \varepsilon_3$ for all t > 0.

Also,

$$z'(t) = k_2 g_2(y(t)) z(t) - d_2 z(t) \ge -d_2 z(t),$$

and so, by Lemma C.1.1, $z(t) \ge \tilde{z}(t)$ for $t \ge 0$, where \tilde{z} is the solution of (RS;z) with the same initial data at 0+ as z. As any such solution becomes close to $z_{d_2}^*(t)$ for $t \to \infty$, by Lemma 1.3.4, there is some $T_4 > 0$ such that $z(t) \ge z_{d_2}^*(t) - \varepsilon_3$ for $t \ge T_4$. For the sake of simplicity, we suppose that $z(t) \ge z_{d_2}^*(t) - \varepsilon_3$ for all t > 0.

Since y(t) is ultimately bounded, there is $T_5 > 0$ such that $y(t) \leq M_y$ for all $t \geq T_5$, where M_y is an ultimate boundedness constant for y. For the sake of simplicity, we suppose that $y(t) \leq M_y$ for all t > 0. Also, note that in this situation $g_2(y(t)) \geq c_{g_2}y(t)$ for $t \geq 0$. One then obtains that

$$y'(t) = k_1 g_1(x(t)) y(t) - g_2(y(t)) z(t) - d_1 y(t)$$

$$\leq y(t) \left[k_1 g_1(x_r^*(t) + \varepsilon_3) - c_{g_2}(z_{d_2}^*(t) - \varepsilon_3) - d_1 \right], \quad t \neq (n+l-1)T,$$

and it consequently follows that

$$\frac{y'(t)}{y(t)} \le k_1 g_1(x_r^*(t) + \varepsilon_3) - c_{g_2}(z_{d_2}^*(t) - \varepsilon_3) - d_1, \quad t \ne (n+l-1)T.$$

By integrating the above inequality on ((n+l-1)T, (n+l)T], one obtains

$$\ln(y((n+l)T)) - \ln(y((n+l-1)T+))$$

$$\leq \int_{(n+l-1)T}^{(n+l)T} \left[k_1 g_1(x_r^*(t) + \varepsilon_3) - c_{g_2}(z_{d_2}^*(t) - \varepsilon_3) - d_1 \right] dt$$

and so

$$\ln(y((n+l)T)) - \ln(y((n+l-1)T)) - \ln(1-\delta_2))$$

$$\leq \int_0^T \left[k_1 g_1(x_r^*(t) + \varepsilon_3) - c_{g_2}(z_{d_2}^*(t) - \varepsilon_3) - d_1 \right] dt$$

by periodicity. It then follows that

$$y((n+l)T) \le y((n+l-1)T)\xi$$

and consequently

$$y((n+l)T) \le y(lT)\xi^n,$$

which implies that $y((n+l)T) \to 0$ as $n \to \infty$. Also

$$\frac{y'(t)}{y(t)} \le k_1 g_1(x(t)) \le \tilde{k},$$

 \tilde{k} being a suitable boundedness constant, so

$$y(t) \le y((n+l-1)T+)e^{\tilde{k}(t+(n+l-1)T)}, \quad t \in ((n+l-1)T, (n+l)T]$$

which implies that

$$y(t) \le (1 - \delta_2)y((n + l - 1)T)e^{kT}, \quad t \in ((n + l - 1)T, (n + l)T],$$

and consequently $y(t) \to 0$ as $t \to \infty$. We now prove that $x(t) - x_r^*(t) \to 0$ as $t \to \infty$. To this purpose, let $0 < \varepsilon_4 \le r/L_1$. Since $y(t) \to 0$ as $t \to \infty$, there is $T_6 > 0$ such that $y(t) < \varepsilon_4$ for $t \ge T_6$. For the sake of simplicity, we suppose that $y(t) < \varepsilon_4$ for all t > 0.

It follows that

$$x'(t) = x(t) [r - ax(t)] - g_1(x(t))y(t)$$
$$= x(t) \left[r - \frac{g_1(x(t))}{x(t)}y(t) - ax(t) \right]$$
$$\ge x(t) [(r - L_1\varepsilon_4) - ax(t)]$$

for $t \neq (n+l-1)T$, $t \neq nT$. Consequently, one infers from Lemma C.1.1 that

$$\tilde{x}_1(t) \le x(t) \le \tilde{x}_2(t)$$

where \tilde{x}_2 is the solution of (RS;x) with the same initial data at 0+ as x and \tilde{x}_1 is the solution of (RS;x) with r changed into $r - L_1 \varepsilon_4$ and the same initial data at 0+ as x.

As these solutions become close to $x_r^*(t)$, respectively to $x_{r-L_1\varepsilon_4}^*(t)$ as $t \to \infty$, by Lemma 1.3.3, it follows that, for t large enough,

$$x_{r-L_1\varepsilon_4}^*(t) - \varepsilon_4 \le x(t) \le x_r^*(t) + \varepsilon_4$$

and the conclusions now follow again from Lemma 1.3.3. To prove that $z(t) - z_{d_2}^*(t) \to 0$ as $t \to \infty$, we may proceed as done for the proof of the first assertion. The second assertion is now established.

Note that condition (1.3.25) has a somewhat theoretical value and is only sufficient for the global asymptotic stability of the intermediate consumer-free periodic solution. One may not expect, though, an integral condition of type (1.3.25) to be threshold-like (to be necessary as well). This happens since (FC) has to inherit, at least partially, the chaotic behavior of the unperturbed system, which is attained for a certain window in the parameter space, as noted in Klebanoff and Hastings [63]. At this point, the availability of a good estimate of the ultimate boundedness constant for y or of c_{g_2} is crucial. In this regard, if one considers the case in which g_2 is a Holling type II functional response, $g_2(y) = (a_2y)/(1+b_2y)$, then $g'_2(y) = a_2/(1+b_2y)^2$ and then $\inf_{y\in\mathbb{R}_+} g'_2(u) = 0$. Consequently, if no good estimations for the ultimate boundedness constant are available and B is large, then the only sensible way to ensure the validity of (1.3.25) is to assume that

$$\ln(1-\delta_2) + \int_0^T \left[k_1 g_1(x_r^*(s)) - d_1\right] ds < 0,$$

but this is a rather crude estimation, which ensures the extinction of the intermediate consumer even if no top predator is present.

Note also that, at least formally, both the local stability condition (1.3.14) and the global stability condition (1.3.25) display a significant dependence on the functional response g_2 of the top predator, with a dominance on the dependence on a_2 .

1.3.6 Biological outcomes of the stability results

From Theorem 1.3.2, we note that if the pesticide is not selective enough, that is, if δ_1 is large enough to make $\ln(1 - \delta_1) + rT$ negative, or, in other words, if the pesticide has a significant negative effect on the growth of the resource biomass, then the resource and intermediate consumer-free periodic solution is globally asymptotically stable, which means that our control strategy fails. Alternatively, this means that a non-selective pesticide should not be applied very often (T should be large enough) in order to avoid resource extinction. Of course, this may have a negative impact on the overall success of the integrated pest management strategy.

From Theorem 1.3.2, it is seen that, theoretically speaking, our control strategy can be always made to succeed globally by the use of proper pesticides, provided that δ_1 is small enough, in order to have the inequality $\ln(1-\delta_1)+rT > 0$ satisfied, and δ_2 is large enough to have (1.3.25) satisfied, for any given top predator functional response g_2 . Also, it is seen that an aggressive ($g'_2(0)$ large enough) top predator may stabilize an otherwise unstable intermediate consumer-free periodic solution, at least locally (see (1.3.14)). In order to stabilize the intermediate consumer-free periodic solution globally, the top predator should be aggressive enough, even at large intermediate consumer densities, when saturation effects are supposed to appear, so that

$$\inf_{0 \le u \le M_y} g_2'(u) > \frac{\ln(1 - \delta_2) + \int_0^T \left[k_1 g_1(x_r^*(s)) - d_1\right] ds}{\int_0^T z_{d_2}^*(s) ds}.$$

If g_2 is a Holling type II functional response (see above) or a Ivlev functional response $(g_2(x) = k(1 - e^{-bx}))$, which are convex regarded as functions of x, then the above reduces to

$$g_2'(M_y) > \frac{\ln(1-\delta_2) + \int_0^T \left[k_1 g_1(x_r^*(s)) - d_1\right] ds}{\int_0^T z_{d_2}^*(s) ds}$$

Note that $\int_0^T k_1 g_1(x_r^*(s)) ds$ and $\int_0^T z_{d_2}^*(s) ds$ are g_2 -independent.

Since $\lim_{\mu\to\infty} \int_0^T z_{d_2}^*(s) ds = +\infty$, from Lemma 1.3.4, and x_r^* does not depend upon μ , it is seen from (1.3.2) that the intermediate consumer-free periodic solution can be stabilized globally by means of increasing μ alone. Note that B, the global boundedness constant for y which is indicated in (1.3.5) and which may also serve as an ultimate boundedness constant for y, is μ -independent.

Also,

$$\int_0^T k_1 g_1(x_r^*(s)) ds < k_1 L_1 \int_0^T x_r^*(s) ds = k_1 L_1(1/a) \left(\ln(1-\delta_1) + rT \right),$$

from Lemma 1.3.3, so

$$\limsup_{T\downarrow-(\ln(1-\delta_1))/r}\int_0^T k_1g_1(x_r^*(s))ds \le 0.$$

As

$$\liminf_{T \downarrow -(\ln(1-\delta_1))/r} c_{g_2} \int_0^T (z_{d_2}^*(s) + d_1) ds > 0$$

from Lemma 1.3.4 and c_{g_2} is *T*-independent, it is seen from (1.3.2) that the intermediate consumer-free periodic solution can also be globally stabilized by means of decreasing *T* alone, in such a way that $\ln(1 - \delta_1) + rT$ remains strictly positive.

However, the purpose of a pest management strategy is to drive the intermediate consumer population under the economic injury level rather to eradicate it completely, so we may considered ourselves successful even in situations in which (1.3.25) is not satisfied, provided that the intermediate consumer population stabilizes under the economic injury level.

Accepting $(1/T) \int_0^T f(t) dt$ as an averaging measure for the oscillations of a periodic and positive function f of period T (an average level of persistence, that is), it is seen from Lemma 1.3.4 that an increase in μ causes an increase in the average level of $z_{d_2}^*$, while from Lemma 1.3.3 is is seen that an increase in μ has no effect on the average level of x_r^* .

From Lemma 1.3.3, it may also be observed that an increase in the carrying capacity of the environment (a decrease of a while keeping r constant, that is) causes an increase in the average level of x_r^* , while having no effect on the average level of $z_{d_2}^*$. This is certainly conceivable, since if y tends to extinction, then the resource x and the top predator z are essentially independent, as the top predator z does not feed upon the resource x. Also, as seen from (1.3.14) and (1.3.25), an increase in the carrying capacity of the environment may not necessarily destabilize the intermediate consumer-free periodic solution $(x_r^*(t), 0, z_{d_2}^*(t))$, at least when the functional response g_1 of the intermediate consumer is a Holling type II functional, since $\int_0^T g_1(x_r^*(s))ds$ is bounded from above as a function of a, but it certainly reduces the chances of having a stable intermediate consumer-free periodic solution, since $\int_0^T g_1(x_r^*(s))ds$ is decreasing as a function of a. It is then seen that we obtain a paradox of enrichment for our food chain model, albeit in a weaker form. Also, noting that all terms in (1.3.14) are negative except for $k_1 \int_0^T g_1(x_r^*(s)) ds$, we observe that periodic solutions $(x_r^*(t), 0, z_{d_2}^*(t))$ with low x_r^* 's are inherently stable rather than unstable, so the paradox of biological control is not present in our model.

To show that our pest management strategy does not over-rely on the use of pesticides, although this, in some sense, has already been observed above, we briefly study below the case in which no pesticides are sprayed (that is, $\delta_1 = \delta_2 = \delta_3 = 0$) and outline the success conditions.

It is seen that in this situation $\ln(1 - \delta_1) + rT = rT > 0$ and $\int_0^T z_{d_2}^*(s) ds = \mu/d_2$. Also, this time $x_r^*(t) = r/a$ for $t \ge 0$ (see (1.3.8) and (1.3.9)). We consequently obtain with the help of Theorems 1.3.1 and 1.3.2 the following result.

Theorem 1.3.3. Suppose that $\delta_1 = \delta_2 = \delta_3 = 0$. Then the following statements hold.

- 1. The resource and intermediate consumer-free periodic solution $(0, 0, z_{d_2}^*(t))$ is unstable.
- 2. The intermediate consumer-free periodic solution $(r/a, 0, z_{d_2}^*)$ is stable provided that

$$(k_1g_1(r/a) - d_1) T < g'_2(0)\mu/d_2,$$

respectively globally asymptotically stable provided that

$$(k_1 g_1(r/a) - d_1) T < c_{q_2} \mu/d_2.$$

3. The intermediate consumer-free periodic solution $(r/a, 0, z_{d_2}^*)$ is unstable provided that

$$(k_1g_1(r/a) - d_1)T > g'_2(0)\mu/d_2.$$

It is now easy to see that a voracious top predator can always stabilize the system, driving the intermediate consumer to extinction and the prey to the carrying capacity of the environment. Also, for μ large enough or T small enough, the global stability condition is always satisfied. Note that, for a significant part of the parameter space, the dynamical outcome does not depend upon the initial population sizes, which is perhaps not surprising, having in view that we study a model with predator-dependent functional responses, as opposed to a model with ratio-dependent functional responses. We may further particularize $g_i(x) = (a_i x)/(1 + b_i x)$, $i \in \{1, 2\}$, and obtain that $(r/a, 0, z_{d_2}^*)$ is stable provided that $T < (a_2 \mu(a + b_1 r)) / (d_2(k_1 a_1 r - d_1 a - d_1 b_1 r))$ and unstable provided that the reverse inequality holds, that is, a result similar to Theorem 3.1 in Zhang and Chen [139].

In the situations in which the intermediate consumer-free equilibrium is globally asymptotically stable, or at least the intermediate consumer population stabilizes below the economic injury level, it would be interesting from a practical point of view to give a general estimate of the time required for the intermediate consumer population to drop below the economic injury level. Unfortunately, we were not able to address this issue in this work.

1.3.7 Numerical simulations

We are now concerned with the numerical investigation of some situations not covered by our Theorems 1.3.1 and 1.3.2 which may lead to a chaotic behavior of the system. Following Klebanoff and Hastings [63] and Kuznetsov and Rinaldi [73], we rescale the variables using the formulas

$$x_1 = \frac{ax}{r}, \quad x_2 = \frac{ay}{rk_1}, \quad x_3 = \frac{az}{rk_1k_2}, \quad s = rt$$

and obtain the following scaled system

$$(SC) \begin{cases} x_1'(s) = x_1(s)[1 - x_1(s)] - \frac{m_1 x_1(s)}{1 + n_1 x_1(s)} x_2(s), & s \neq (n + l - 1)T_1, \ s \neq nT_1; \\ x_2'(s) = \frac{m_1 x_1(s)}{1 + n_1 x_1(t)} x_2(s) - \frac{m_2 x_2(s)}{1 + n_2 x_2(s)} x_3(s) & s \neq (n + l - 1)T_1, \ s \neq nT_1; \\ - D_1 x_2(s), \\ x_3'(s) = \frac{m_2 x_2(s)}{1 + n_2 x_2(t)} x_3(s) - D_2 x_3(s), & s \neq (n + l - 1)T_1, \ s \neq nT_1; \\ \Delta x_1(s) = -\delta_1 x_1(s), & s = (n + l - 1)T_1; \\ \Delta x_2(s) = -\delta_2 x_2(s), & s = (n + l - 1)T_1; \\ \Delta x_3(s) = -\delta_3 x_3(s), & s = (n + l - 1)T_1; \\ \Delta x_1(s) = 0, & s = nT_1; \\ \Delta x_2(s) = 0, & s = nT_1; \\ \Delta x_3(s) = \mu_1, & s = nT_1, \end{cases}$$
where

$$m_1 = \frac{a_1 k_1}{a}, \quad n_1 = \frac{b_1 r}{a}, \quad n_2 = \frac{r b_2 k_1}{a}, \quad D_1 = \frac{d_1}{r}, \quad D_2 = \frac{d_2}{r}, \quad T_1 = rT,$$
$$\mu_1 = \frac{a\mu}{rk_1k_2}.$$

It is easy to see that the corresponding unperturbed system (RSC)

$$\begin{cases} x_1'(s) = x_1(s)[1 - x_1(s)] - \frac{m_1 x_1(s)}{1 + n_1 x_1(s)} x_2(s), & s \neq (n+l-1)T_1, \ s \neq nT_1; \\ x_2'(s) = \frac{m_1 x_1(s)}{1 + n_1 x_1(t)} x_2(s) - \frac{m_2 x_2(s)}{1 + n_2 x_2(s)} x_3(s) & s \neq (n+l-1)T_1, \ s \neq nT_1; \\ -D_1 x_2(s), \\ x_3'(s) = \frac{m_2 x_2(s)}{1 + n_2 x_2(t)} x_3(s) - D_2 x_3(s), & s \neq (n+l-1)T_1, \ s \neq nT_1; \end{cases}$$

has at most five equilibria, namely

- 1. The trivial equilibrium O = (0, 0, 0).
- 2. The intermediate consumer and top predator-free equilibrium R = (1, 0, 0).
- 3. The top predator-free equilibrium

$$RC = (D_1/(m_1 - n_1D_1), (m_1 - n_1D_1 - D_1)/(m_1 - n_1D_1)^2, 0).$$

4. The positive equilibria

$$P_1 = (x_1^{P_1}, D_2/(m_2 - n_2 D_2), x_3^{P_1}), \quad P_2 = (x_1^{P_2}, D_2/(m_2 - n_2 D_2), x_3^{P_2}),$$

where

$$\begin{aligned} x_1^{Pi} &= \frac{n_1 - 1}{2n_1} + (-1)^i \frac{\sqrt{(n_1 + 1)^2 - 4\frac{m_1n_1D_2}{m_2 - n_2D_2}}}{2n_1} \\ x_3^{Pi} &= \frac{1}{m_2 - n_2D_2} \left(\frac{m_1x_1^{Pi}}{1 + n_1x_1^{Pi}} - D_1\right), \quad i \in \{1, 2\} \end{aligned}$$

Note that the first two equilibria exist irrespective of the values of the parameters which characterize the system, while several conditions need to be satisfied for the existence of the last three equilibria.

The dynamics of the unperturbed system (RSC) has been studied in detail by Klebanoff and Hastings in [63] and by Kuznetsov and Rinaldi in [73]. However, the behavior of the perturbed system (SC) is severely affected by our periodic forcing and the qualitative picture bears little resemblance, at least for significant forcing, to that of the unperturbed system.

From Theorem 1.3.1, it is easy to see that the intermediate consumer-free periodic solution is unstable provided that $m_2 < m_{2s}$, where

$$m_{2s} = \frac{\ln(1-\delta_2) + \int_0^{T_1} \frac{m_1(x_1)^*(s)}{1+n_1(x_1)^*(s)} ds - D_1 T_1}{\int_0^{T_1} (x_3)^*_{D_2}(s) ds}$$

and locally stable provided that the reverse inequality is satisfied.

For $m_1 = 2.4$, $n_1 = 3$, $m_2 = 0.02$, $n_2 = 0.4$, $D_1 = 0.4$, $D_2 = 0.01$, $\delta_1 = 0.1$, $\delta_2 = 0.3$, $\delta_3 = 0.05$, $\mu_1 = 0.25$, $T_1 = 10$, l = 0.5 (part of the values are close to the ones used by McCann and Yodzis in [99]) and $x_1(0) = 0.75$, $x_2(0) = 0.49$, $x_3(0) = 0.05$, it is seen that the intermediate consumer-free periodic solution is unstable and the stabilizing value is $m_{2s} = 0.098$. The unperturbed system has a top predator-free equilibrium, but no positive equilibria.

It is then seen that in this case the trajectory of the perturbed system tends to a periodic orbit of period T_1 . Apart from deciding the stability or instability of the intermediate consumer-free periodic solution, the parameter m_2 does not seem to otherwise influence the qualitative properties or the shape of the limiting set. The behavior of the trajectory is depicted in Figure 1.3.1.

A related behavior is captured in Figure 1.3.2 for $m_1 = 10$, $n_1 = 3$, $D_1 = 0.4$, $m_2 = 0.1$, $n_2 = 0.4$, $D_2 = 0.01$, $\delta_1 = 0.1$, $\delta_2 = 0.3$, $\delta_3 = 0.05$, $\mu_1 = 0.25$, $T_1 = 11$, l = 0.5and $x_1(0) = 0.75$, $x_2(0) = 0.49$, $x_3(0) = 0.05$. The intermediate consumer-free periodic solution is unstable and the stabilizing value is $m_{2s} = 1.329$. The unperturbed system has a top predator-free equilibrium and a positive equilibrium. In this case the trajectory of the perturbed system tends to a periodic orbit of period $3T_1$.

A typical example of chaotic behavior (strange attractor) is captured in Figure 1.3.3 for $m_1 = 10$, $n_1 = 3$, $D_1 = 0.4$, $m_2 = 0.1$, $n_2 = 0.4$, $D_2 = 0.01$, $\delta_1 = 0.1$, $\delta_2 = 0.3$, $\delta_3 = 0.05$, $\mu = 0.25$, $T_1 = 30$, l = 0.5 and $x_1(0) = 0.75$, $x_2(0) = 0.49$, $x_3(0) = 0.05$. The intermediate consumer-free periodic solution is unstable and the stabilizing value is $m_{2s} = 1.244$. Again, the unperturbed system has a top predator-free equilibrium and a positive equilibrium. The two dimensional plot x_2 vs. x_1 and the time series for x_1 , x_2 , x_3 also indicate that the trajectory has a chaotic behavior. A slight increase in m_2 Figure 1.3.1: $m_1 = 2.4$, $n_1 = 3$, $m_2 = 0.02$, $n_2 = 0.4$, $D_1 = 0.4$, $D_2 = 0.01$, $\delta_1 = 0.1$, $\delta_2 = 0.3$, $\delta_3 = 0.05$, $\mu_1 = 0.25$, $T_1 = 10$, l = 0.5. The trajectory approaches a periodic orbit of period T_1 . The unperturbed system admits a top predator-free equilibrium, but no positive equilibria.



 $(m_2 = 0.109)$ "stabilizes" the behavior of the system, and the trajectory tends again to a periodic solution of period T_1 .

A somewhat similar situation is captured in Figure 1.3.4 for $m_1 = 10$, $n_1 = 2$, $D_1 = 0.4$, $m_2 = 0.1$, $n_2 = 0.4$, $D_2 = 0.01$, $\delta_1 = 0.1$, $\delta_2 = 0.3$, $\delta_3 = 0.05$, $\mu = 0.25$, $T_1 = 10$, l = 0.5and $x_1(0) = 0.75$, $x_2(0) = 0.49$, $x_3(0) = 0.05$. The intermediate consumer-free periodic solution is unstable and the stabilizing value is $m_{2s} = 1.745$. The unperturbed system has a top predator-free equilibrium and two positive equilibria. A slight increase in m_2 $(m_2 = 0.1119)$ "stabilizes" the behavior of the system, and the trajectory tends again to a periodic solution of period T_1 . That is, m_2 does not have only the potential to stabilize the intermediate consumer-free periodic solution, but also the potential to mitigate the chaotic behavior of a trajectory for certain values significantly smaller than the stabilizing critical value, an increase of m_2 over these values ensuring that the trajectories of the system tend to certain periodic solutions. Figure 1.3.2: $m_1 = 10$, $n_1 = 3$, $D_1 = 0.4$, $m_2 = 0.1$, $n_2 = 0.4$, $D_2 = 0.01$, $\delta_1 = 0.1$, $\delta_2 = 0.3$, $\delta_3 = 0.05$, $\mu_1 = 0.25$, $T_1 = 11$, l = 0.5. The trajectory approaches a periodic orbit of period $3T_1$. The unperturbed system admits a top predator-free equilibrium and a positive equilibrium.



1.4 An impulsively perturbed predator-prey system with Beddington-DeAngelis functional response and time delay

1.4.1 A survey of models with Beddington-DeAngelis functional response

There is much significant evidence to suggest that predator dependence in the functional response occurs quite frequently in laboratory and natural systems (see, for instance, Jost and Ellner [62] or Skalski and Gilliam [121]) and due to large numbers of experiments and observations, the models with predator-dependent functional response stand as reasonable alternatives to the models with prey-dependent functional response. Arditi and Ginzburg [6] first proposed and investigated the following ratio-dependent predator-prey model:

$$\begin{cases} N' = N(a - bN) - \frac{cNP}{mP + N}, \\ P' = -dP + \frac{fNP}{mP + N}. \end{cases}$$

Note that the above model is a result of replacing the Holling type II prey-dependent functional response $\frac{N}{m+N}$ employed in (H) with a ratio-dependent one $\frac{N/P}{m+N/P}$.

The Beddington-DeAngelis functional response $F = \frac{\alpha N}{a+bN+cP}$ was originally introduced by Beddington [11] and DeAngelis et al [21], independently, and actually for different Figure 1.3.3: $m_1 = 10$, $n_1 = 3$, $D_1 = 0.4$, $m_2 = 0.1$, $n_2 = 0.4$, $D_2 = 0.01$, $\delta_1 = 0.1$, $\delta_2 = 0.3$, $\delta_3 = 0.05$, $\mu = 0.25$, $T_1 = 30$, l = 0.5. The trajectory is chaotic (bistability-like scenario). The unperturbed system admits a top predator-free equilibrium and a positive equilibrium.



reasons.

Consequently, a predator-prey model with Beddington-DeAngelis functional response can be obtained through a similar replacement of the Holling type II functional response, in the form:

(1.4.1)
$$\begin{cases} x' = x(r - \frac{x}{k}) - \frac{\alpha xy}{a + bx + cy} \\ y' = -dy + \frac{\beta xy}{a + bx + cy}. \end{cases}$$

Motivated by this system, many researchers proposed and studied models consisting of ordinary or functional differential equations incorporating Beddington-DeAngelis type functional responses. For instance, in his papers [56, 57], Hwang showed that the interior equilibrium of the above system is globally stable provided that it is locally asymptotically stable. Further, he obtained sufficient conditions for the uniqueness of limit cycles of the system. Inspired by the work of Beretta and Kuang [12], Liu and Yuan [91] considered the situation in which the numerical response term appearing in the predator equation of (1.4.1) contains a delay term τ , which can be regarded as a gestation period or reaction time of the predators. Further, incorporating a stage structure for the predator population, Liu and Beretta [86] proposed and studied the case in which a time delay τ Figure 1.3.4: $m_1 = 10$, $n_1 = 2$, $D_1 = 0.4$, $m_2 = 0.1$, $n_2 = 0.4$, $D_2 = 0.01$, $\delta_1 = 0.1$, $\delta_2 = 0.3$, $\delta_3 = 0.05$, $\mu = 0.25$, $T_1 = 10$, l = 0.5. The trajectory is chaotic (bistability-like scenario). The unperturbed system admits a top predator-free equilibrium and two positive equilibria.



appears in the response term of the immature predator equation as well as in the mature predator equation. Here, τ , dissimilar to the above delay, represents the time taken from birth to maturity. The stability of the interior equilibrium, the permanence of the system and conditions for the delay-induced stability switch were also considered in Gopalsamy [35] and Kuang [69]. Since biological and environmental parameters are naturally subject to fluctuation in time, in order to describe the model more accurately, Fan and Kuang [23] studied the dynamics of a nonautonomous, periodic (almost periodic) predator-prey system with Beddington-DeAngelis functional response by using the coincidence degree theory, as proposed by Gaines and Mawhin [26].

From the above-mentioned brief literature survey, it may be noted that the effect caused by the periodic impulsive perturbation of the prey population on the dynamics of the stage-structured predator-prey model with Beddington-DeAngelis functional response and time delay has not been modeled and analyzed. The aim of this section is to model and explain this phenomenon from a mathematical viewpoint. More precisely, hunting and harvesting usually occur seasonally or yearly, with fixed periodicity, and as a result the prey population decreases significantly over a short period of time. That is, hunting and harvesting can be modeled, up to some extent, as occurring in periodic pulses. As a result, the dynamics of the system is considerably affected in a way which is worth of further study.

This section is organized in the following manner. In Subsection 1.4.2, we propose the model to be studied and give certain preliminary boundedness and comparison results. In Subsection 1.4.3, we discuss the global attractivity of the predator-free positive periodic solution. Sufficient conditions for the permanence of the model are obtained in Subsection 1.4.4. In the final subsection, we present some numerical experiments to illustrate our results. A brief discussion of the biological significance of our findings is also provided. This section is based on the results obtained in Zhang, Georgescu and Chen [138].

1.4.2 The model and its simplification

In this section, we denote by x(t) the size of the prey population. Also, the predator population is divided into juvenile and mature classes, with the size of each class given by $y_j(t)$ and y(t), respectively. The model we shall study has the form: (BDA)

$$\begin{cases} x'(t) = x(t)g(x(t)) - \frac{bx(t)y(t)}{1 + k_1x(t) + k_2y(t)}, \\ y'(t) = \frac{\beta b e^{-d_j\tau}x(t-\tau)y(t-\tau)}{1 + k_1x(t-\tau) + k_2y(t-\tau)} - dy(t), \\ y'_j(t) = \frac{\beta bx(t)y(t)}{1 + k_1x(t) + k_2y(t)} - \frac{\beta b e^{-d_j\tau}x(t-\tau)y(t-\tau)}{1 + k_1x(t-\tau) + k_2y(t-\tau)} - d_jy_j(t) \end{cases} \quad t \neq kT, \\ \Delta x(t) = -\mu x(t), \qquad t = kT \end{cases}$$

with initial conditions

(1.4.2)
$$\begin{cases} (x(\cdot), y(\cdot), y_j(\cdot)) = (\varphi_1(\cdot), \varphi_2(\cdot), \varphi_3(\cdot)) \in \mathbf{C}_3^+, \varphi_i(0) > 0, i = 1, 2, 3, \\ \varphi_3(0) = \int_{-\tau}^0 e^{d_j \theta} \frac{\beta b \varphi_1(\theta) \varphi_2(\theta)}{1 + k_1 \varphi_1(\theta) + k_2 \varphi_2(\theta)} d\theta, \end{cases}$$

in which,

$$\mathbf{C}_3^+ \doteq C\Big([-\tau, 0], \mathbb{R}^3_+\Big),$$

where $\mathbb{R}^3_+ \doteq \{(z_1, z_2, z_3) : z_i \ge 0, i = 1, 2, 3\}$ and $\tau, T > 0$. Here, $\Delta x(t) = x(t^+) - x(t)$. To derive the mathematical model, the following assumptions are made:

(A1) In the absence of predation, the dynamics of the prey population follows the logistic law of growth with intrinsic growth rate r and carrying capacity $\frac{r}{c}$, i.e. xg(x) = x(r-cx).

- (A2) Juvenile predators are not able to hunt for prey and are raised by their parents because of their weakness. Moreover, they can not breed.
- (A3) The parameter τ represents a constant maturation time which, from a mathematical point of view, introduces a delay in our model. The product term $\frac{\beta b e^{-d_j \tau} x(t-\tau)y(t-\tau)}{1+k_1 x(t-\tau)+k_2 y(t-\tau)}$ represents the movement of the young predator population to the mature class.
- (A4) The prey population is subject to a perturbation which causes its proportional reduction, with reduction parameter μ ($0 \le \mu < 1$). This proportional reduction can be interpreted as hunting (or harvesting) with a constant hunting (or harvesting) effort.
- (A5) The positive constants b and k_1 represent the effects of capture rate and handling time, respectively, on the feeding rate; $\beta > 0$ is the birth rate of the predator and $k_2 \ge 0$ is a constant describing the magnitude of the interference among predators. The positive constants d and d_j denote the death rates of the mature predator population and immature predator population, respectively.

We now define the notion of solution of a delayed impulsive differential system which shall be used in the following.

Definition 1.4.1. A map $X: [-\tau, \infty) \to \mathbb{R}^n$ is said to be a solution of the impulsively perturbed Cauchy problem

(1.4.3)
$$\begin{cases} X'(t) = f(t, X(t), X(t - \tau)), & t \neq kT, k \in \mathbb{N}, \\ \Delta X(kT) = I_k(X(kT)), \\ X(0) = X_0, \end{cases}$$

if it satisfies the following conditions:

(H1) X(t) is continuous on [0, T] and on each interval $(kT, (k+1)T], k \in \mathbb{N}$. The points $\{kT\}, k \in \mathbb{N}$, are discontinuities of the first kind for f, f being continuous at the left of each point.

(H2) X(t) satisfies the former n equations of the system (1.4.3) on $[0,\infty)\setminus\{kT, k \in \mathbb{N}\}$ and satisfies the latter equations for every $t = kT, k \in \mathbb{N}$.

Under these circumstances, it can be shown that the positive solutions of (BDA) are ultimately bounded, fact which is accomplished in the following Lemma. **Lemma 1.4.1.** There exists a constant M > 0 such that $x(t) \leq M$, $y_j(t) \leq M$ and $y(t) \leq M$ for each positive solution $(x(t), y(t), y_j(t))$ of the system (BDA) and t large enough.

Proof. Let $N(t) = x(t) + \frac{1}{\beta} (y_j(t) + y(t))$. By a simple computation we have

$$D^+N|_{(\text{BDA})} = xg(x) - \frac{1}{\beta} (d_j y_j(t) + dy(t)), \ t \in (kT, (k+1)T].$$

Obviously, from (A1), it is easy to see that there exists a constant $\lambda > 0$ such that

 $D^+N|_{(\text{BDA})} + \overline{\delta}N < \lambda, \ t \in (kT, (k+1)T], \text{ for } k \text{ large enough},$

where $\overline{\delta} = \min\{d, d_j\}$. When t = kT, we get

$$N(kT^+) \le N(kT).$$

According to Lemma C.1.2, applied for $\tau_k = kT$, we obtain

$$N(t) < N(0)e^{-\overline{\delta}t} + \int_0^t \lambda e^{-\overline{\delta}(t-s)} ds \to \frac{\lambda}{\overline{\delta}} \quad \text{as } t \to \infty.$$

Let $M \doteq \max\{\frac{\lambda}{\delta}, \frac{\beta\lambda}{\delta}\}$. Therefore, by the definition of N(t), we derive that each positive solution of system (1.4.1) is uniformly ultimately bounded with ultimate boundedness constant M. This completes the proof.

Finally, we indicate an exponential estimation which shall be used in the following for proving asymptotic stability results.

Lemma 1.4.2. [40] Let \mathfrak{t}_0 be a real number and τ_0 be a nonnegative number. If $m : [\mathfrak{t}_0 - \tau_0, \infty) \to [0, \infty)$ satisfies

$$\dot{m}(t) \le -\rho m(t) + \varrho[\sup_{t-\tau_0 \le s \le t} m(s)] \text{ for } t \ge \mathfrak{t}_0,$$

and if $\rho > \rho > 0$, then there exist positive numbers ι and κ such that

$$m(t) \leq \iota e^{-\kappa(t-\mathfrak{t}_0)} \text{ for } t \geq \mathfrak{t}_0.$$

Before going into any detail, we need to simplify the model (BDA). Since

$$y_j(t) = \int_{t-\tau}^t e^{-d_j(t-\theta)} \frac{\beta b x(\theta) y(\theta)}{1 + k_1 x(\theta) + k_2 y(\theta)} d\theta,$$

i.e. $y_j(t)$ is completely determined by x(t), y(t), we may restrict ourselves to the following reduced model:

(R-BDA)
$$\begin{cases} x'(t) = x(t)g(x(t)) - \frac{bx(t)y(t)}{1 + k_1x(t) + k_2y(t)}, \\ y'(t) = \frac{\beta b e^{-d_j\tau}x(t-\tau)y(t-\tau)}{1 + k_1x(t-\tau) + k_2y(t-\tau)} - dy(t), \\ \Delta x(t) = -\mu x(t), \end{cases} \quad t = kT$$

1.4.3 The stability of the mature predator-free periodic solution

Consider the following case in which $y(t) \equiv 0$ in (R-BDA):

(1.4.4)
$$\begin{cases} x'(t) = x(t)(r - cx(t)), & t \neq kT, \\ \Delta x(t) = -\mu x(t), & t = kT. \end{cases}$$

Lemma 1.3.3 then easily leads to the following conclusion.

Lemma 1.4.3. Assume that $\mu < \mu^* = 1 - e^{-rT}$. Then the system (1.4.4) has a unique positive periodic solution $x^*(t)$ which is globally asymptotically stable, expressed as

$$x^*(t) = \frac{\frac{r}{c}(1 - \mu - e^{-rT})}{1 - \mu - e^{-rT} + \mu e^{-r(t - (n-1)T)}}, \quad t \in ((n-1)T, nT], \ n \in \mathbb{N}^*.$$

Consequently, the system (R-BDA) has a mature predator-free periodic solution $(x^*(t), 0)$. From (R-BDA), one notes that

$$\begin{cases} x'(t) \le x(t)(r - cx(t)), & t \ne kT, \\ \Delta x(t) = -\mu x(t), & t = kT. \end{cases}$$

Then, by using Lemma 1.4.3, we obtain that for each arbitrary small positive constant ε there exists a positive integer n_1 such that for all $t \ge n_1 T$,

$$x(t) \le x^*(t) + \varepsilon$$

As a consequence, for all $t \ge n_1 T + \tau$ we have

(1.4.5)
$$x(t-\tau) \le x^*(t-\tau) + \varepsilon \le \frac{\frac{r}{c} \left(1-\mu-e^{-rT}\right)}{\left(1-\mu\right) \left(1-e^{-rT}\right)} + \varepsilon = \eta + \varepsilon$$

Further, in view of (1.4.5) and the second equation of (R-BDA), we have that for all $t \ge n_1 T + \tau$,

(1.4.6)
$$y'(t) \le \frac{\beta b e^{-d_j \tau} (\eta + \varepsilon) y(t - \tau)}{1 + k_1 (\eta + \varepsilon)} - dy(t)$$

According to the above analysis, the following result is easily derived.

Theorem 1.4.1. Assume that $\mu < \mu^* = 1 - e^{-rT}$. If

$$R_1 = \frac{\beta b e^{-d_j \tau} \eta}{1 + k_1 \eta} < d,$$

then the mature predator-free periodic solution $(x^*(t), 0)$ is globally attractive.

Proof. Let $\varepsilon > 0$ be such that

$$\frac{\beta b e^{-d_j \tau} \left(\eta + \varepsilon\right)}{1 + k_1 \left(\eta + \varepsilon\right)} < d.$$

Consider the comparison equation

$$z'(t) = \frac{\beta b e^{-d_j \tau} (\eta + \varepsilon) z(t - \tau)}{1 + k_1 (\eta + \varepsilon)} - dz(t).$$

According to the conditions of Theorem 1.4.1 and with the help of Lemma 1.4.2, one obtains that

$$\lim_{t \to \infty} z(t) = 0.$$

Since $y(s) = z(s) = \varphi_2(s) > 0$ for all $s \in [\tau, 0]$, by a comparison argument, we have

$$\limsup_{t \to \infty} y(t) \le \limsup_{t \to \infty} z(t) = 0.$$

Using the positivity of y(t), we then obtain that $\lim_{t\to\infty} y(t) = 0$.

Therefore, for any sufficiently small $\epsilon_1(0 < \epsilon_1 < \frac{r}{b})$, there exists an integer $n_2 > n_1$ such that $y(t) < \epsilon_1$ for all $t > n_2T \ge n_1T + \tau$.

From the first equation of the system (R-BDA), we obtain

$$x(t)(r - \frac{b\epsilon_1}{1 + k_2\epsilon_1} - cx(t)) \le x'(t) < x(t)g(x(t)), \ t \ne kT.$$

From Lemmas C.1.1 and 1.4.3, there exists a $n_3(>n_2)$ such that $x_1(t) \leq x(t) \leq x_2(t)$ and $x_1(t) \to \tilde{x}(t), x_2(t) \to x^*(t)$ as $t > n_3T$, where $x_1(t)$ and $x_2(t)$ are, respectively, the solutions of

$$\begin{cases} x_1'(t) = x_1(t)(r - \frac{b\epsilon_1}{1 + k_2\epsilon_1} - cx_1(t)), & t \neq kT, \\ \Delta x_1(t) = -\mu x_1(t), & t = kT, \\ x_1(0^+) = x_0 \end{cases}$$

and

$$\begin{cases} x_2'(t) = x_2(t)g(x_2(t)), & t \neq kT, \\ \Delta x_2(t) = -\mu x_2(t), & t = kT, \\ x_2(0^+) = x_0, \end{cases}$$

while

$$\widetilde{x}(t) = \frac{\frac{r - \frac{b\epsilon_1}{1 + k_2\epsilon_1}}{c} (1 - \mu - e^{-(r - \frac{b\epsilon_1}{1 + k_2\epsilon_1})T})}{1 - \mu - e^{-(r - \frac{b\epsilon_1}{1 + k_2\epsilon_1})T} + \mu e^{-(r - \frac{b\epsilon_1}{1 + k_2\epsilon_1})(t - (n - 1)T)}}, \ (n - 1)T < t \le nT, \ n > n_3.$$

Therefore, for any $\varepsilon_1 > 0$ we have $\widetilde{x}(t) - \varepsilon_1 < x(t) < x^*(t) + \varepsilon_1$ for t large enough. For $\epsilon_1 \to 0$, we get $\widetilde{x}(t) \to x^*(t)$. Hence $x(t) \to x^*(t)$ as $t \to \infty$. This completes the proof. \Box

From the above, one may easily obtain the following result

Corollary 1.4.1. The mature predator-free periodic solution $(x^*(t), 0)$ of the system (R-BDA) is globally attractive provided that one of the following conditions holds:

(I) $R_0 \le d$, where $R_0 = \frac{\beta b e^{-d_j \tau}}{k_1}$;

(II) $R_0 > d$ and $\frac{r}{c} \leq \Theta(1 - e^{-rT})$, where $\Theta = \frac{d}{k_1(R_0 - d)}$.

(III) $R_0 > d$, $\frac{r}{c} > \Theta(1 - e^{-rT})$ and $\mu > \mu_*$, where $\mu_* = \frac{(1 - \Theta_r^c)(1 - e^{-rT})}{1 - \Theta_r^c(1 - e^{-rT})}$.

Remark 1.4.1. Considering the pulses-free case in the system (R-BDA), one notes from Liu and Beretta [86] that if $R = \frac{\beta b e^{-d_j \tau} \frac{r}{c}}{1+k_1 \frac{r}{c}} < d$ holds, then $\lim_{t\to\infty} (x(t), y(t)) = (\frac{r}{c}, 0)$. After adding the periodic impulsive perturbations of the prey population, we first consider for the new system the dynamics of the mature predator-free periodic solution $(x^*(t), 0)$ which corresponds to the trivial equilibrium $(\frac{r}{c}, 0)$ of the pulses-free system. It is easy to see that for $\mu \to 0$ one has that $\eta \to \frac{r}{c}$, so $R_1 \to R$ and we obtain the persistence result given in [86] from the above Theorem 1.4.1. Obviously, a similarity among R, μ^* and $R_i(i = 0, 1)$ is that these critical values are independent of the effect of k_2 , which is to introduce a self-limiting term into the predator equation.

Remark 1.4.2. The fraction $\frac{\beta b \eta_1}{1+k_1 \eta_1}$ approximates the mature predator's numerical response when (x(t), y(t)) is near the mature predator-free periodic solution $(x^*(t), 0)$, while $e^{-d_j\tau}$ is a correction term incorporating the "degree of stage structure" $d_j\tau$, named as such by Liu et al in [88], meant to describe the loss of juvenile predators due to through-stage mortality. In this regard, Theorem 1.4.1 can be interpreted as if few predators introduced into an environment stabilized at the periodic mature predator-free solution cannot reproduce fast enough, compensating through-stage mortality, as described by the degree of stage structure, then the mature predator-free periodic solution is globally asymptotically stable.

Remark 1.4.3. It is interesting to note that, as far as the effect of the delay τ is concerned, a large delay τ may always stabilize the predator-free equilibrium by bringing R_0 below d, as seen from (I) of Corollary 1.4.1. Also, from (II) of Corollary 1.4.1, it is seen that the systems with low resources $(\frac{r}{c} < \Theta(1 - e^{-rT}))$ are more likely to be stabilized to the mature predator-free periodic solution. Having also in view (III) of Corollary 1.4.1, it is seen that increasing the carrying capacity of the system may destabilize an otherwise stable mature predator-free periodic solution, which is certainly conceivable from a purely biological point of view.

Remark 1.4.4. Clearly, one notes that the global attractivity of juvenile and mature predator-free periodic solution $(x^*(t), 0, 0)$ of the system (BDA) is equivalent to the global attractivity of mature predator-free periodic solution $(x^*(t), 0)$ of the system (R-BDA). Its biological implication is that for certain harvesting and hunting rates, if the carrying capacity of the environment is below a certain determinable value, then the predator population vanishes in time.

1.4.4 A permanence result

Uniform persistence (or permanence), defined as such in Section 1.1, is an important property of systems arising in ecology, epidemics, population dynamics and not only. It is actually a concept which is important in itself, addressing the long-term survival of some or all components of a system. In this subsection, we focus our attention on the permanence of the system (R-BDA).

In the following, we first consider the single species model with delay described below:

(1.4.7)
$$v'(t) = \frac{a_1 v(t-\nu)}{a_2 + a_3 v(t-\nu)} - a_4 v(t),$$

where $a_i (i = 1, 2, 3, 4)$ and ν are positive constants. Obviously, v(t) is strictly positive if

(1.4.8)
$$v(t) = \widetilde{\varphi}(t) > 0 \text{ for } t \in [-\nu, 0].$$

The following Lemma is an application of Theorem 9.1 in [17, Chapter 4].

Lemma 1.4.4. The equation (1.4.7) has a unique positive equilibrium $v^* = \frac{a_1 - a_2 a_4}{a_3 a_4}$, which is absolutely globally asymptotically stable provided that $a_1 > a_2 a_4$.

Here, the absolute global asymptotic stability of v^* means that v^* is globally asymptotically stable for all $\nu > 0$. We now start investigating the permanence of the system

(R-BDA). Let $\varepsilon > 0$ be an arbitrary positive constant. Recalling (1.4.5), together with the second equation of (R-BDA), one notes that there exists a $n_4 > n_3$ such that for $t > n_4T$,

(1.4.9)
$$y'(t) \le \frac{\beta b e^{-d_j \tau} (\eta + \varepsilon) y(t - \tau)}{1 + k_1 (\eta + \varepsilon) + k_2 y(t - \tau)} - dy(t).$$

Hence from the above Lemma, combined with a comparison argument, one obtains that for an arbitrary small positive constant $\tilde{\varepsilon}$, there exists a $n_5 > n_4$ such that if

$$\frac{\beta b e^{-d_j \tau} (\eta + \varepsilon)}{(1 + k_1 (\eta + \varepsilon))d} > 1,$$

then

(1.4.10)
$$y(t) \le \frac{\beta b e^{-d_j \tau} (\eta + \varepsilon) - (1 + k_1 (\eta + \varepsilon))d}{dk_2} + \widetilde{\varepsilon} = \zeta(\varepsilon, \widetilde{\varepsilon})$$

for $t > n_5 T$. Consequently, we obtain that for $t > n_5 T$ and $t \neq kT$,

(1.4.11)
$$x'(t) \ge x(t)g(x(t)) - \frac{b\zeta(\varepsilon,\widetilde{\varepsilon})}{1 + k_1(\eta + \varepsilon) + k_2\zeta(\varepsilon,\widetilde{\varepsilon})}x(t)$$

Next let $r(\varepsilon, \tilde{\varepsilon}) = r - \frac{b\zeta(\varepsilon, \tilde{\varepsilon})}{1+k_1(\eta+\varepsilon)+k_2\zeta(\varepsilon, \tilde{\varepsilon})} > 0$. In view of Lemmas C.1.1 and 1.4.3, it follows that there exists a $n_6 > n_5$ such that for $\mu < 1 - e^{-r(\varepsilon, \tilde{\varepsilon})T}$ and $t \ge n_6T$,

(1.4.12)
$$x(t) \ge \frac{\frac{r(\varepsilon,\tilde{\varepsilon})}{c}(1-\mu-e^{-r(\varepsilon,\tilde{\varepsilon})T})}{1-\mu-e^{-r(\varepsilon,\tilde{\varepsilon})T}+\mu} = \vartheta(\varepsilon,\tilde{\varepsilon}).$$

In the following, we define

$$W(t) = y(t) + \beta b e^{-d_j \tau} \int_{t-\tau}^t \frac{x(s)y(s)}{1 + k_1 x(s) + k_2 y(s)} ds.$$

Then the derivative of W(t) with respect to the solutions of the system (R-BDA) is governed by

(1.4.13)
$$\frac{dW}{dt}\Big|_{(\mathrm{R}-\mathrm{BDA})} = \left(\frac{\beta b e^{-d_j \tau} x(t)}{1 + k_1 x(t) + k_2 y(t)} - d\right) y(t)$$
$$\geq \left(\frac{\beta b e^{-d_j \tau} \vartheta(\varepsilon, \widetilde{\varepsilon})}{1 + k_1 \vartheta(\varepsilon, \widetilde{\varepsilon}) + k_2 y(t)} - d\right) y(t).$$

If

(1.4.14)
$$\frac{\beta b e^{-d_j \tau} \vartheta(\varepsilon, \widetilde{\varepsilon})}{1 + k_1 \vartheta(\varepsilon, \widetilde{\varepsilon})} - d > 0,$$

we can choose sufficiently small y^* such that

(1.4.15)
$$\frac{\beta b e^{-d_j \tau} \vartheta(\varepsilon, \widetilde{\varepsilon})}{1 + k_1 \vartheta(\varepsilon, \widetilde{\varepsilon}) + k_2 y^*} - d > 0$$

We claim that for any $t_0 > 0$, it is impossible that $y(t) < y^*$ for all $t \ge t_0$. Suppose that the claim is not valid. Then there is a $t_0 > 0$ such that $y(t) < y^*$ for all $t \ge \max\{t_0, n_6T\}$. From (1.4.13), one notes there exists a $t_1 > \max\{t_0 + \tau, n_6T + \tau\}$ such that for $t \ge t_1$,

(1.4.16)
$$\frac{dW}{dt}\Big|_{(\text{R-BDA})} \ge \Big(\frac{\beta b e^{-d_j \tau} \vartheta(\varepsilon, \widetilde{\varepsilon})}{1 + k_1 \vartheta(\varepsilon, \widetilde{\varepsilon}) + k_2 y^*} - d\Big) y(t).$$

Set

$$y_l \doteq \min_{t \in [t_1, t_1 + \tau]} y(t).$$

We will show that $y(t) \ge y_l$ for all $t \ge t_1 > t_0$. Otherwise, there exists a $T_0 \ge 0$ such that $y(t) \ge y_l$ for $t_1 \le t \le t_1 + \tau + T_0$, and $y(t_1 + \tau + T_0) = y_l$. Hence, from the second equation of (R-BDA), we derive

$$y'(t_1 + \tau + T_0) \ge \left(\frac{\beta b e^{-d_j \tau} \vartheta(\varepsilon, \widetilde{\varepsilon})}{1 + k_1 \vartheta(\varepsilon, \widetilde{\varepsilon}) + k_2 y^*} - d\right) y_l$$

and so $y'(t_1 + \tau + T_0) > 0$. Consequently, y is locally increasing near $t_1 + \tau + T_0$ and cannot fall below y_l . Thus

$$(1.4.17) y(t) \ge y_l$$

for all $t \ge t_1$. As a consequence, (1.4.16) and (1.4.17) lead to

$$\frac{dW}{dt}\Big|_{(\text{R-BDA})} > \tilde{\delta} \text{ for some } \tilde{\delta} > 0 \text{ and } t \ge t_1,$$

which implies that $W(t) \to \infty$ as $t \to \infty$. This contradicts the boundedness of W(t). The claim that $y(t) \ge y_l$ is then proved.

By the above claim, we need to consider two cases. The first one is the case in which $y(t) \ge y^*$ for all large t, which yields the uniform persistence of the mature predator. Combined with (1.4.12), this means that our system (R-BDA) is uniformly persistent. Second, y(t) oscillates about y^* for all large t. Let us define

$$q = \min\left\{\frac{y^*}{2}, \ y^* e^{-d\tau}\right\}.$$

We want to show that $y(t) \ge q$ for all large t, which, as done above, will yield the uniform persistence of the system (R-BDA). Let $t^* > 0$ and $\tilde{\nu} > 0$ satisfy

$$y(t^*) = y(t^* + \widetilde{\nu}) = y^*$$

and

$$y(t) < y^*, t \in (t^*, t^* + \widetilde{\nu}).$$

It is seen that y(t) is uniformly equicontinuous since the positive solutions of (R-BDA) are ultimately bounded and y(t) is not affected by the impulsive perturbations. Thus there exists a \widetilde{T} ($0 < \widetilde{T} < \tau$, and \widetilde{T} is independent of the choice of t^*) such that

$$y(t) > \frac{y^*}{2}$$

for $t^* < t < t^* + \widetilde{T}$. If $\widetilde{\nu} \leq \widetilde{T}$, there is nothing to prove. Let us consider the case $\tau \geq \widetilde{\nu} > \widetilde{T}$. It follows that for $t^* + \widetilde{T} \leq t \leq t^* + \widetilde{\nu}$,

$$y'(t) \ge -dy(t)$$

Hence

$$y(t) \ge y^* e^{-d\tau}$$

for $t^* + \widetilde{T} \leq t \leq t^* + \widetilde{\nu} \leq t^* + \tau$, since $y(t^*) = y^*$. If $\widetilde{\nu} > \tau$, it is obvious that $y(t) \geq q$ for $t \in [t^*, t^* + \tau]$. Then, proceeding exactly as the for the derivation of (1.4.17), we see that $y(t) \geq q$ for $t \in [t^* + \tau, t^* + \widetilde{\nu}]$. Since this interval $[t^*, t^* + \widetilde{\nu}]$ is chosen in an arbitrary way (we only need t^* to be large), we conclude that $y(t) \geq q$ for all large t. Due to the above-mentioned analysis, we obtain the following result.

Theorem 1.4.2. The system (R-BDA) is permanent provided that

$$r(0,0) > 0, \quad \mu < 1 - e^{-r(0,0)T}, \quad R_1 > d, \quad \frac{\beta b e^{-d_j \tau} \vartheta(0,0)}{1 + k_1 \vartheta(0,0)} - d > 0.$$

After some further computations, we may consequently deduce the following result.

Corollary 1.4.2. The system (R-BDA) is permanent provided that one of the following conditions holds:

(I) $d < R_1, r \ge \frac{b}{k_2} + c\Theta, \mu < \overline{\mu}_1^*, where$

$$\overline{\mu}_1^* = (1 - e^{-r(0,0)T})(1 - \frac{c\Theta}{r(0,0)})$$
$$r(0,0) = \left(r - \frac{b}{k_2}\right) + \frac{bd}{R_1k_2}$$

(II) $d < R_1 < d^*$, $r < \frac{b}{k_2} + c\Theta$, $\mu < \overline{\mu}_1^*$, where

$$d^* = \frac{bd}{b + k_2 c\Theta - rk_2}.$$

Remark 1.4.5. From [86], we note that if $R = \frac{\beta b e^{-d_j \tau} \frac{r}{c}}{1+k_1 \frac{r}{c}} \ge d$ holds, then the corresponding pluses-free system is permanent. After adding periodic impulsive perturbations of the prey population, in order to keep the permanence of the new system (R-BDA) we have to fulfill a related condition, although there is still room for improvement in the estimations given in Corollary 1.4.2.

1.4.5 Numerical analysis and a discussion of the main results

To facilitate the interpretation of our mathematical results and to further establish the importance of the proportional impulsive part and of the delay term, we proceed to investigate further by using numerical simulations. A first example is indicated in Table 1.4.5, which illustrates the loss of permanence due to the effects of the impulsive perturbation. Let us also choose a set of parameters as follows:

pulses-free	r, β, k_1	С	b	d	k_2	d_j	τ	Permanence
system [86]	1	5/8	1.5	0.5	0.1	0.01	0.8	Yes
impulsive	r, β, k_1	c	b	d	k_2	d_j	au	R_1
system	1	5/8	1.5	0.5	0.1	0.01	0.8	$\approx 0.251 < d$
	Θ	T	μ_*	μ^*	η	R_0	μ	Permanence
	pprox 0.506	1	pprox 0.540	pprox 0.6321	pprox 0.203	≈ 1.488	0.6	No

Table 1.4.1: Comparing the impulsive system with the corresponding pulses-free system

• $r = 1.8, c = 0.2, \beta = 1, b = 0.1, d_j = 0.01, T = 0.3, \tau = 1, d = 0.15, k_1 = 0.5, k_2 = 0.1, \mu = 0.1.$

After a few computations, one gets that

• $r(0,0) \approx 1.756 > 0, \ 1 - e^{-r(0,0)T} = 0.409 > \mu, \ R_1 - d = 0.006 > 0, \ \frac{\beta b e^{-d_j \tau} \vartheta(0,0)}{1 + k_1 \vartheta(0,0)} - d \approx 0.002 > 0.$

Hence, by applying Theorem 1.4.2, it is shown that the system (BDA) with the above coefficients is permanent. However, when $\mu = 0.2$ and the other coefficients remain fixed, it follows that $R_1 = 0.147 < d$ and the corresponding impulsive system is not permanent, the mature predator-free periodic solution being globally asymptotically stable from Theorem 1.4.1. Similarly, when $\tau = 6$ and the other coefficients remain fixed, it follows that $R_1 = 0.149$ and the corresponding impulsive system loses again its permanence. As a consequence, from Table1.4.5 and the above-mentioned example, it is easy to see that the impulsive perturbation and the time delay play an important role in the dynamics of the system.

Obviously, from Corollary 1.4.2 we see that when the prey has a large intrinsic growth rate, the proportional reduction μ is small and the predators can breed quickly, then the prey population and predator population can coexist forever. The same happens if the carrying capacity is lower, provided that the breeding rate of the mature predators remains also lower than a certain value.

As far as the the impulsive control for the prey population is concerned, we show that the system tends to a state of "total extinction of the predator" if conditions in Theorem 1.4.1 are satisfied. However, from the point of view of protecting the predator population and subsistence hunting or harvesting, the aim is to keep both species at an acceptable level. In this regard, sufficient conditions guaranteeing the permanence of the system are also found in Theorem 1.4.2.

Chapter 2

Epidemiology: studying disease dynamics

2.1 Basic concepts of mathematical epidemiology

The latest decades witnessed a resurrection of infectious diseases which were once thought as being on their way to eradication, due to the apparition of antibiotic-resistant strains or to climate changes, which helped spreading the diseases to new geographical areas. Tuberculosis, malaria, dengue fever and yellow fever are just a few diseases which continue to persist despite of the efforts committed to their eradication and of the advances in modern medicine and hygiene.

New infectious diseases such as AIDS, SARS and hepatitis C have also emerged and are now major mortality causes throughout the world. Consequently, there is a rising interest in the mathematical modeling of infectious diseases, as mathematical models may provide accurate assessments, identify key threshold parameters and provide hints about possible eradication strategies. Further, mathematical models provide a convenient vehicle by the use of which various conceptual conjectures about the nature and transmission of the disease can be tested against real data. In this regard, comprehensive surveys of concepts, methods and results in the mathematical modeling of infectious diseases can be found in Anderson and May [4], Hethcote [46, 47], Capasso [15].

A very important factor which should be considered when attempting to formulate a mathematical model to describe the evolution of a disease is the time-space scale. For instance, the constant population assumption, which may be reasonable at the macro-scopic scale (to study the propagation of a disease in human or animal populations, that is) is clearly not an option at the microscopic scale (to study the propagation of a virus in the human body, when of concern are cell populations). Other considerations regarding the use of different functions to model the spread of the disease at the microscopic and macroscopic level also apply. Consequently, we have split the remaining part of this section into two parts, corresponding to issues arising at the macroscopic and microscopic scale, respectively.

2.1.1 Modeling for the macroscopic level

Compartmental models

To model the propagation of a disease in human (or animal) populations, it is often convenient to subdivide the population which is considered into a small number of epidemiological classes, or compartments, the resulting model being called a compartmental model. The classes which are usually considered are

- S The class of susceptibles, that is, the individuals which have not yet been exposed to infection and do not possess immunity.
- E The class of exposed, that is, the individuals which have been exposed to the disease, but are not yet capable of transmitting the disease, being still in the incubating stage, and do not possess immunity. This class is also called the latent class.
- *I* The class of infectives, that is, the individuals which are capable of transmitting the disease to susceptibles.
- R The class of removed, that is, the individuals which possess permanent or temporary immunity and may not contract or transmit the disease, or which have died.

Other classes may be added for increased accuracy. Specifically, the class A of asymptomatic individuals, the class H of hospitalized individuals and the class M of infants which possess passive (maternally transmitted) immunity are sometimes considered.

Especially for macroparasitic infections, the manifestation and severity of the disease is dependent upon the parasite load and consequently one may need to consider the so-called stage structure for the infection, that is, a succession of infection stages, with possibly different clinical symptoms and chances of survival. The corresponds models are called stage-structured models.

To model the effect of spatial spread without resorting to the use of partial differential equations, one may sometimes assume that the above classes are organized into interrelated, but formally separated, groups of different sizes. The models which are consequently obtained are called multipatch models.

A flowchart characterizing the general evolution of a disease within the boundaries of the so-called SEIRS model, named as such after the compartmental flow path, is given below. In the following, we shall briefly describe the concepts mentioned therein.



The sizes of each class at moment t are denoted by S(t), E(t), I(t), R(t), respectively, while N(t) denotes the total population size, that is N = S + E + I + R. If the time scale of the epidemic process is significantly faster than the demographic time scale (which is the case for many human diseases, one notable exception, however, being AIDS) and the disease-induced mortality is low, the population may be considered as being at equilibrium, that is, N may be assumed as being constant.

Regarding the transmission mechanism, the disease may be transmitted through horizontal incidence (that is, from infectives to susceptibles, the latter moving to the exposed class or to the infected class if the latent period is negligible) and through vertical incidence (that is, from infected mothers to newborns, the latter being born directly to the infected class). The per capita rate at which susceptible individuals acquire infection is sometimes called the force of infection and is generally understood as a function of the total number of infective individuals.

A typical form of horizontal incidence rate is the so-called standard incidence. To derive the standard incidence, let β be the average number of adequate contacts (i.e., which suffice for transmission) of an individual per unit time. Then the average number of adequate contacts of an infective individual with susceptibles per unit time is $\beta \frac{S}{N}$, so the incidence rate is $\beta \frac{SI}{N}$, hereinafter called the standard incidence rate.

The assumption that the average number of adequate contacts is independent of the total population size N is motivated by the fact that the daily activity pattern of humans is mostly independent of the community size. A more general situation is the case in which β is density-dependent, that is, $\beta = \beta(N)$, which gives rise to a density-dependent incidence rate $\beta(N)\frac{SI}{N}$. In this regard, Hesterbeek and Metz proposed in [45] a contact

rate of type

$$\beta(N) = \frac{bN}{1 + bN + \sqrt{1 + 2bN}}$$

Also, it is sometimes argued that $\beta(N)$ should be independent of N only for large N (that is, the saturation effect is reached only for large population sizes), while for small $N \beta(N)$ should be linear in N. Another reasonable requirement is that $\frac{\beta(N)}{N}$ be nonincreasing as a function of N.

To model vertical incidence, one usually assumes that a fixed proportion of the newborns of infective mothers are infected at birth. Consequently, the most common vertical transmission term is kI, understood as the product of the probability of the disease being transmitted at birth, the birth rate and the number of infected women.

Regarding the progression from one stage to another, if it is supposed, for instance, that a fixed fraction pE of the total number of exposed individuals leaves the class at any given time, it is seen that the waiting time in the exposed class are exponentially distributed (that is, the probability of a exposed individual still being in the exposed class t units of time afterwards is e^{-pt}) and the average time spent in this class is $\frac{1}{p}$. Similar interpretations hold with respect to the other classes. If it is assumed instead that an exposed individual spends a fixed time τ into the exposed class, then the associated model contains a delay differential part, with delay τ .

It is often found that the dynamics of a disease is governed by a threshold parameter R_0 , called the basic reproduction number (basic reproduction ratio, basic reproductive rate), defined as the average number of new infections caused by a single infective individual introduced into a totally susceptible population at equilibrium. In this regard, it is usually found out that if $R_0 < 1$, then the disease dies out, while if $R_0 > 1$, then the disease remains endemic. That is, R_0 is a threshold quantity which determines whether or not a disease is capable of invading a population.

A typical SEIR model with constant population size, vertical transmission, standard incidence rate and exponentially distributed waiting times is then

$$\begin{cases} S' = \mu N - \mu S - \beta \frac{SI}{N} - kI \\ E' = \beta \frac{SI}{N} - (\varepsilon + \mu)E \\ I' = \varepsilon E - (\gamma + \mu)I + kI \\ R' = \gamma I - \mu R. \end{cases}$$

For this model, the basic reproduction number R_0 is shown to be $R_0 = \frac{\beta\varepsilon}{(\mu+\varepsilon)(\mu+\gamma)-k\varepsilon}$ (see Li et al [83]).

2.1.2 Modeling for the microscopic level

To model the propagation of a viral disease at the cellular level, it is again useful to divide the cell population into a number of classes, or compartments, although this time the resulting partition has a different construction. The classes which are generally considered are

- X The class of susceptible cells.
- Y The class infected cells.
- V The class of viral cells.

An additional class of exposed cells might be considered, but there is no class of recovered cells considered separately anymore. Since X, Y are classes of body cells and V is a class of viral cells (of a different type, that is), a total constant population size is not to be expected.

The number of cells in each class will be denoted by x, y and v, respectively. The constant contact rate which has been found appropriate for human populations, based on the existence of a daily activity pattern, no longer applies. In this situation, under a homogeneous mixing assumption, it may be assumed that the contact rate of an infective cell depends on the size of the susceptible class x, which gives rise to the so-called mass action law, in which the horizontal incidence has the form βxy , that is, it is bilinear. In this situation, β does not have a direct epidemiological meaning.

Also, at cell level, there is no direct correspondent of the concept of vertical incidence. Still, the global dynamics of a virus propagation model is again governed by a basic reproduction number, defined as done for human populations, with a few obvious changes.

A typical virus propagation model is the following, introduced by Zeuzem et al. [136] and by Bonhoeffer et al. [13].

$$\begin{cases} x' = \lambda - dx - \beta xv \\ y' = \beta vx - ay \\ v' = ky - \mu v. \end{cases}$$

For this model, the basic reproduction number is shown to be $R_0 = \frac{\lambda \beta k}{a d u}$ (see Bonhoeffer et al. [13]). Note that certain shortcomings of this model have been pointed out by Min et al. [102].

2.2 The dynamics of a virus propagation model

We consider a compartmental model for the propagation of a virus in vivo, in the form

(VP)
$$\begin{cases} S' = n(S) - c(S)f(V), \\ E' = c(S)f(V) - c_1i(E), \\ I' = c_2i(E) - c_3p(I), \\ V' = c_4p(I) - r(V). \end{cases}$$

Here, S denotes the concentration of the cells in the susceptible (i.e., uninfected) class, E denotes the concentration of cells in the exposed (i.e., latent) class, I denotes the concentration of cells in the infected class, and V denotes the concentration of the virus itself.

The intrinsic growth rate of the susceptible class, which includes both production of new cells and natural mortality of cells, is given by n(S) with all the newly produced cells assumed to be susceptible. The movement of cells from the exposed class into the infected class and the production of free virus from infected cells are given by $c_2i(E)$ and $c_4p(I)$, respectively. By $c_1i(E)$ and $c_3p(I)$, we denote the removal of the exposed and infected classes, respectively, which include the mortality of cells in the above-mentioned classes.

It is assumed that the infection process is characterized by the incidence rate c(S)f(V), where c(S) denotes the contact function at concentration S and f(V) denotes the force of infection by virus at concentration V. We note that our incidence rate is sufficiently general to encompass many forms of commonly used incidence rate, including simple mass action. The removal rate of the virus is denoted by r(V). All functions c, f, i, p, r, n are allowed to be nonlinear and all constants c_1, c_2, c_3, c_4 are assumed to be positive.

We thereby assume that the major infection pathway is virus-to-cell, since the cell-tocell pathway is sometimes less documented and therefore less considered, particularly in diseases such as AIDS (see Perelson and Nelson [116]).

While this model has been studied in Bonhoeffer et al. [13], Korobeinikov [64], Nowak and May [107], and Perelson and Nelson [116], among others, for linear c, f, i, p, r, n,

it is perhaps important to account for a number of nonlinear features of the biological phenomena which are involved, especially for the nonlinearity of the incidence rate, which is influenced by the availability of susceptible cells and by the force of infection of viral cells. As the concentration of viral cells becomes higher, the simple mass action law βSV may not necessarily suffice. Moreover, the rate at which an infected cell or virus will die as a function of their concentrations is generally not known, and hence we make a further generalization by assuming that the removal rate is also nonlinear. For a detailed discussion on the virus dynamics of HIV, readers are referred to Perelson and Nelson [116].

We note that in (VP), for i(x) = x and p(x) = x, the constant $1/c_1$ represents the average time spent by a cell in the latent state, while $1/c_3$ represents the average lifetime of an infected cell. Also, $c_1 \ge c_2$ and $c_1 - c_2$ represents the mortality rate of the exposed cells, while c_4 relates to the production of virus from infected cells. See also the details on the mathematical modeling of infectious diseases given in the previous section.

As noted by Korobeinikov in [64], if there is no exposed class E and consequently c(S)f(V) represents the movement of cells from the susceptible class directly into the infected class, the (reduced three-dimensional) system (VP) is equivalent to a SEIR model with a constant population assumption. It is therefore expected that the dynamics of our model will share some features with the dynamics of a SEIR model. Some perspectives and results from the global stability theory for SEIR models would also be relevant for our discussion. See Korobeinikov and Maini [66], Li et al. [80], Li and Muldowney [81], and Li, Muldowney, and van den Driessche [82] for global stability results for SEIR models. However, in [80, 81, 82] the approach is essentially geometrical, using a stability criteria which extends the Poincaré–Bendixson theorem and ruling out periodic orbits, rather than constructing a Lyapunov functional.

A related investigation pertaining to the dynamics of infectious disease models which incorporated nonlinear incidence rates of a very general form has recently been performed by Korobeinikov and Maini in [67] by using the Lyapunov method. In [67], the local stability of the equilibria for SIRS and SEIRS models has been considered assuming that the incidence rate is given by an arbitrary function f(S, I, N), while the global stability of the equilibria for SIR and SEIR models has been considered assuming that the incidence rate is of the form f(I)g(S). However, apart from the incidence rate, the other functions which appear in the models considered in [67] are linear and a constant population assumption is used, while for our model full nonlinearity is assured and a constant population assumption would not be an option. Moreover, the analysis performed in [67] is done in a somewhat different manner, with a focus on the role of the concavity of the nonlinear incidence rate in the existence and stability of the endemic equilibrium.

Substantial results regarding the global dynamics of a three-dimensional HIV model have been obtained by De Leenheer and Smith [20] using a different approach; their result distinguishes whether or not the term -kVT, which models the loss of a free virus particle once it enters the target cell, can be absorbed into the general loss term $-\gamma V$. In [20], V is the concentration of free virus particles in the blood and T is the concentration of T cells. De Leenheer and Smith start with general assumptions on the function f which models T cell dynamics in a healthy individual and then specialize their results for two particular functions: $f_1(T) = \delta - \alpha T + pT(1 - T/T_{max})$ as used by Perelson and Nelson in [116] and $f_2(T) = \delta - \alpha T$ as used by Nowak and May in [107]. Certain linearity assumptions on some other functions appearing in the model are also made.

In the particular case in which the term -kVT is absorbed into the general loss term (as done in [116] and [107])) and $f = f_2$, the model used in [20] can be thought of as a reduced version of our model, with no exposed class and extra linearity assumptions. However, the proof of our global stability result uses in an unavoidable manner the monotonicity assumption on n, which corresponds to f in [20], and therefore it can accommodate the case $f = f_2$ only and not the case $f = f_1$. In particular, our model does not admit orbitally asymptotically stable periodic solutions, which are obtained in [20] for $f = f_1$; see [20, Theorem 1] for details.

The remaining part of this Section is organized as follows. We propose the model to be studied in Subsection 2.2.1 and discuss its well-posedness. In Subsection 2.2.2, we give results on the stability of the disease-free equilibrium and persistence of the system, while Subsections 2.2.3 and 2.2.4 contain discussions on the existence, uniqueness, and global stability of the endemic equilibrium. Finally, in Subsection 2.2.5, we give some remarks on the biological interpretation of our results, as well as on some further extensions of the model. This Section is based on the results obtained in Georgescu and Hsieh [28].

2.2.1 A compartmental model for the propagation of a virus in vivo

We assume that c, f, i, p, r are real locally Lipschitz functions defined at least on $[0, \infty)$ which satisfy

$$c(0) = f(0) = i(0) = p(0) = r(0) = 0,$$

$$c(t), f(t), i(t), p(t), r(t) > 0 \quad \text{for } t > 0$$

and that n is a real locally Lipschitz function defined at least on $[0, \infty)$ with n(0) > 0such that the equation n(S) = 0 has a single solution S_0 . We also assume that

(2.2.1)
$$(n(S) - n(S_0))(S - S_0) < 0 \quad \text{for } S \neq S_0,$$
$$(c(S) - c(S_0))(S - S_0) > 0 \quad \text{for } S \neq S_0$$

together with

(D)
$$\int_{0+}^{1} \frac{1}{\varphi(\tau)} d\tau = +\infty \quad \text{for all } \varphi \in \{c, f, i, p\}.$$

Note that (2.2.1) is satisfied if, for instance, n is strictly decreasing and c is strictly increasing. We also suppose that there are k_n , k_i , k_p , k_v , $\tilde{k}_n > 0$ such that

(G)
$$n(S) \le k_n - k_n S$$
 for $S \ge 0$, $i(E) \ge k_i E$ for $E \ge 0$, $p(I) \ge k_p I$ for $I \ge 0$,
 $r(V) \ge k_r V$ for $V \ge 0$.

The set of growth conditions (G) will be used to establish, in our general setting, the global existence of the solution for the Cauchy problem associated with the system (VP). We note that these conditions may be dropped if the global existence property is known or the a priori boundedness of the solutions may be established by other methods. We shall indicate in Subsection 2.2.5 how to remove conditions (G) at the expense of other conditions on the behavior of c, f, i, p near $+\infty$ if f/r is nonincreasing on $(0, \infty)$.

First, it can be easily shown that a solution of the system (VP) which starts in $[0, \infty)^4$ remains there on its whole interval of existence. To this purpose, we note that the vector (R_1, R_2, R_3, R_4) points inside $Q = [0, \infty)^4$ at all points of ∂Q , where R_1, R_2, R_3 , and R_4 are the right-hand sides appearing in (VP), and hence Nagumo's tangency conditions are satisfied. See Pavel [109] for details.

From our assumptions, it is clear that the system (VP) has a unique saturated (i.e., nonextendable) solution for any initial data (S(0), E(0), I(0), V(0)). Using (G), it is

possible to prove that all saturated solutions are global. To this aim, note that

$$\left(S + E + \frac{c_1}{2c_2}I + \frac{c_1c_3}{4c_2c_4}V\right)' \le \tilde{k}_n - k_n S - \frac{c_1k_i}{2}E - \frac{c_1c_3}{4c_2}k_p I - \frac{c_1c_3}{4c_2c_4}k_r V,$$

it follows that there is $\delta = \delta(k_n, k_i, k_p, k_r, c_1, c_2, c_3, c_4) > 0$ small enough such that

$$\left(S + E + \frac{c_1}{2c_2}I + \frac{c_1c_3}{4c_2c_4}V\right)' + \delta\left(S + E + \frac{c_1}{2c_2}I + \frac{c_1c_3}{4c_2c_4}V\right) \le \tilde{k}_n,$$

which implies that

$$S + E + \frac{c_1}{2c_2}I + \frac{c_1c_3}{4c_2c_4}V - \frac{k_n}{\delta}$$

$$\leq \left(S(0) + E(0) + \frac{c_1}{2c_2}I(0) + \frac{c_1c_3}{4c_2c_4}V(0) - \frac{\tilde{k}_n}{\delta}\right)e^{-\delta t} \quad \text{for } t \ge 0,$$

and therefore S, E, I, V are bounded on their maximal interval of existence. It follows that the functions S(t), E(t), I(t), V(t) are defined on $[0, \infty)$, and so the Cauchy problem with nonnegative initial data is well-posed for the system (VP). Moreover, if we denote

$$F = \left\{ (S, E, I, V) \in [0, \infty)^4; S + E + \frac{c_1}{2c_2}I + \frac{c_1c_3}{4c_2c_4}V \le \frac{\tilde{k}_n}{\delta} \right\},$$

it follows that F is a feasible region for the system (VP). Of course, the feasible region determined above is neither minimal nor unique, and the parameter δ above is obviously not uniquely determined. We shall simply choose

(2.2.2)
$$\delta = \min\left(k_n, \frac{c_1}{2}k_i, \frac{c_3}{2}k_p, k_r\right).$$

If S is small, then S' = n(S) - c(S)F(V) > 0 if V stays in a bounded set, since n(0) > 0and $\lim_{S\to 0} c(S) = 0$, and we may infer that for any S(0) > 0 there is $\varepsilon_{S(0)} > 0$ such that $S(t) \ge \varepsilon_{S(0)}$ for all t > 0. This means that all solutions which start with positive S(0)do not reach any point with S = 0 in future time. If S(0) = 0, then S' > 0 in a vicinity of 0 and, again, S(t) raises over a certain minimum value (of course, the case in which S(0) = 0 does not make much biological sense). Also, it can be seen that the only w-limit point of (VP) on the boundary of F is the disease-free equilibrium $(S_0, 0, 0, 0)$ and the only points on the boundary of $[0, \infty)^4$ which can be attained in finite time are situated on [OS, the positive S-semiaxis containing the origin.

2.2.2 The stability of the disease-free equilibrium

Since the equation n(S) = 0 has a single solution S_0 and f(0) = i(0) = p(0) = r(0) = 0, it is easy to see that the system (VP) admits a unique disease-free equilibrium $(S_0, 0, 0, 0)$. We now turn our attention to the study of its stability.

Consider the Lyapunov functional

$$U_1(S, E, I, V) = \int_{S_0}^{S} \frac{c(\tau) - c(S_0)}{c(\tau)} d\tau + E + \frac{c_1}{c_2}I + \frac{c_1c_3}{c_2c_4}V.$$

Since $(c(S) - c(S_0))(S - S_0) > 0$ for $S \neq S_0$, it is seen that U_1 increases whenever any of $|S - S_0|$, E, I, V increases and $U_1(S, E, I, V) \ge 0$ for all $S, E, I, V \ge 0$, while $U_1(S, E, I, V) = 0$ if and only if $(S, E, I, V) = (S_0, 0, 0, 0)$.

We now compute the time derivative of U_1 along the solutions of (VP). It is seen that

$$\dot{U}_{1} = \left(1 - \frac{c(S_{0})}{c(S)}\right) (n(S) - c(S)f(V)) + (c(S)f(V) - c_{1}i(E)) + \frac{c_{1}}{c_{2}}(c_{2}i(E) - c_{3}p(I)) + \frac{c_{1}c_{3}}{c_{2}c_{4}}(c_{4}p(I) - r(V)),$$

and since $n(S_0) = 0$, we can deduce that

(2.2.3)
$$\dot{U}_1(S, E, I, V) = \left(1 - \frac{c(S_0)}{c(S)}\right) (n(S) - n(S_0)) + \left[c(S_0)f(V) - \frac{c_1c_3}{c_2c_4}r(V)\right].$$

Due to (2.2.1), it is easily seen that

(2.2.4)
$$\left(1 - \frac{c(S_0)}{c(S)}\right)(n(S) - n(S_0)) < 0 \text{ for } S \neq S_0,$$

and the first term in the right-hand side of (2.2.3) is negative. It is then seen that the stability of the disease-free equilibrium is related to the sign of the remaining term in the right-hand side of (2.2.3).

Theorem 2.2.1. Suppose that there is a number $V_R > 0$ such that

(2.2.5)
$$c(S_0)\frac{f(V)}{r(V)}\frac{c_2c_4}{c_1c_3} \le 1 \quad \text{for } V \in (0, V_R),$$

and let $m = U_1(S_0, 0, 0, V_R)$. Then the disease-free equilibrium $(S_0, 0, 0, 0)$ is locally asymptotically stable and its domain of attraction includes the set

$$M_m = \left\{ (S, E, I, V) \in (0, \infty) \times [0, \infty)^3; U_1(S, E, I, V) < m \right\}.$$

Proof. From (2.2.3), (2.2.4), and (2.2.5), it is seen that $U_1(S, E, I, V) \leq 0$ for $0 \leq V < V_R$, with equality if and only if $S = S_0$ and either V = 0 or the equality in (2.2.5) holds.

Let us denote $\tilde{M} = \{(S, E, I, V) \in (0, \infty) \times [0, \infty)^3, 0 \le V < V_R\}$ and take k < m arbitrary. Since for all $V \ge V_R$ one has $U_1(S, E, I, V) \ge U_1(S_0, 0, 0, V_R)$, it is seen that $M_k \subset \tilde{M}$. Consequently, $U_1(S, E, I, V) \le 0$ on M_k , with equality if and only if $S = S_0$ and the equality in (2.2.5) holds.

We now find the invariant subsets \tilde{P} within the set

$$P = \{ (S, E, I, V) \in M_k; U_1(S, E, I, V) = 0 \}.$$

Since $S = S_0$ on \tilde{P} and consequently $S' = -c(S_0)f(V)$, it is seen that V = 0 and one similarly deduces that E = I = 0; that is, the only invariant subset of P is the singleton $\tilde{P} = \{(S_0, 0, 0, 0)\}$. From LaSalle's invariance principle (see Appendix A or LaSalle [77]) and the fact that k < m was arbitrary, the conclusion follows.

Consider the Lyapunov function

$$U_2(S, E, I, V) = E + \frac{c_1}{c_2}I + \frac{c_1c_3}{c_2c_4}V.$$

Similar to the derivation of (2.2.3), the time derivative of U_2 along the solutions of (VP) is given by

(2.2.6)
$$\dot{U}_2(S, E, I, V) = c(S)f(V) - \frac{c_1c_3}{c_2c_4}r(V).$$

Obviously, if (VP) is uniformly persistent, then the disease remains endemic and stability for the disease-free equilibrium is excluded. In this regard, we have already observed that if (2.2.5) is satisfied on some interval $(0, V_R)$, then the disease-free equilibrium is locally asymptotically stable. If, on the other hand, the opposite of (2.2.5) is satisfied on some interval $(0, V_R)$, then the system (VP) is uniformly persistent in the sense mentioned above.

Theorem 2.2.2. Assume that there is a number $V_R > 0$ such that

(2.2.7)
$$c(S^0)\frac{f(V)}{r(V)}\frac{c_2c_4}{c_1c_3} > 1 \quad for \ V \in (0, V_R).$$

Then (VP) is uniformly persistent and the disease-free equilibrium $(S_0, 0, 0, 0)$ is unstable, with the positive semiaxis [OS as its stable manifold. **Proof.** From (2.2.6), (2.2.7), and the continuity of the function c at S_0 , it follows that $U_2 > 0$ on a small vicinity of $(S_0, 0, 0, 0)$, except for the points with V = 0. It then follows that any solution which starts in that vicinity remains away from $(S_0, 0, 0, 0)$, except for those starting on the positive semiaxis $[OS, which tend to (S_0, 0, 0, 0) while remaining on <math>[OS]$. It may now be obtained, as in Proposition 3.3 in Li et al. [80], that the system (VP) is uniformly persistent. This amounts to observing that $(S_0, 0, 0, 0)$ is the unique compact invariant set on the boundary of our feasible domain (so it is isolated) and its stable manifold is the positive semiaxis [OS, which is contained in the boundary of the feasible domain. Then the use of Theorem 4.1 in Hofbauer and So [49], together with the remark that a flow and its time one map have the same maximal compact invariant set and the same stable set in a region, concludes the proof.

It now remains to indicate some situations in which (2.2.5) or (2.2.7) are satisfied. Suppose for the moment that f/r is nonincreasing on $(0, \infty)$ and define a basic reproduction number R_0 of the system (VP) by

(2.2.8)
$$R_0 = c(S_0) \frac{c_2 c_4}{c_1 c_3} \lim_{V \to 0} \frac{f(V)}{r(V)}$$

(note that the limit $\lim_{V\to 0} \frac{f(V)}{r(V)}$ does indeed exist, since f/r is monotone on $(0,\infty)$).

If $R_0 \leq 1$, then (2.2.5) is satisfied on $[0, \infty)$, while if $R_0 > 1$, then (2.2.7) is satisfied for V in a vicinity of 0. Also, it may be seen that $\lim_{V_R\to\infty} U_1(S_0, 0, 0, V_R) = +\infty$. One then obtains the following result, which establishes that R_0 is the threshold parameter for the stability of the disease-free equilibrium.

Theorem 2.2.3. Suppose that f/r is nonincreasing on $(0, \infty)$.

- 1. If $R_0 \leq 1$, then the disease-free equilibrium $(S_0, 0, 0, 0)$ is globally asymptotically stable.
- 2. If $R_0 > 1$, then (VP) is uniformly persistent and the disease-free equilibrium $(S_0, 0, 0, 0)$ is unstable, with the positive semiaxis [OS as its stable manifold.

In fact, if f/r is nonincreasing on $(0, \infty)$, more can be said for the case $R_0 > 1$, and it will be shown in Subsections 2.2.3 and 2.2.4 that, in this situation, the system (VP) admits a positive endemic equilibrium, which is globally asymptotically stable. We also note that if the functions f and r are of class C^1 and the limit $\lim_{V\to 0} \frac{f'(V)}{r'(V)}$ exists, then by the L'Hôpital theorem

$$R_0 = c(S_0) \frac{c_2 c_4}{c_1 c_3} \lim_{V \to 0} \frac{f'(V)}{r'(V)},$$

which is in agreement with the definition of the basic reproduction number given by van den Driessche and Watmough in [126] for a large class of compartmental models, including the present model. We do not need, however, to assume C^1 regularity for the functional coefficients throughout our proofs. We also note that, since no C^1 regularity is assumed, local stability analysis based on Jacobian matrices would fail.

2.2.3 The existence of the endemic equilibrium

We now try to establish some sufficient conditions for the existence of the endemic equilibrium (S^*, E^*, I^*, V^*) . Since it would be somehow unrealistic to attempt to solve the system (EQ) in its greatest generality, we impose some additional conditions on our functional coefficients. Let us suppose the following:

(2.2.9) f/r is nonincreasing on $(0, \infty)$,

(2.2.10)

c, f, i, p are strictly increasing on $[0, \infty)$ and n is strictly decreasing on $[0, \infty)$,

(2.2.11)

$$\lim_{x \to \infty} i(x) = \lim_{x \to \infty} p(x) = +\infty.$$

Necessarily, $S^*, E^*, I^*, V^* > 0$, and the following equilibrium relations are satisfied:

(EQ)
$$n(S^*) = c(S^*)f(V^*), \quad c(S^*)f(V^*) = c_1i(E^*), \quad c_2i(E^*) = c_3p(I^*),$$

 $c_4p(I^*) = r(V^*).$

To solve the equilibrium system (EQ), note first that from the last three equalities in (EQ) one obtains

$$c(S^*)f(V^*) = \frac{c_1c_3}{c_2c_4}r(V^*).$$

Let us define

$$F_1(S,V) = n(S) - c(S)f(V), \quad F_2(S,V) = c(S)f(V) - \frac{c_1c_3}{c_2c_4}r(V).$$

Since $S \mapsto F_1(S, V)$ is strictly decreasing and $F_1(0, V) \cdot F_1(S_0, V) < 0$ for all V, the equation $F_1(S, V) = 0$ can be uniquely solved with respect to S as a function of V for all V. That is, there is a function $S = \psi_1(V)$ which satisfies

(2.2.12)
$$\frac{n(\psi_1(V))}{c(\psi_1(V))} = f(V).$$

Since n/c is strictly decreasing and f is strictly increasing, it follows that ψ_1 is strictly decreasing. Note also that due to (2.2.12), $\lim_{V\to\infty} \psi_1(V) = 0$.

Similarly, $S \mapsto F_2(S, V)$ is strictly increasing and $F_2(0, V) < 0$ for all V. However, in this instance it is not necessarily true that $F_2(S_0, V) > 0$, and hence the same approach we used to solve the equation $F_2(S, V) = 0$ would not work. However, for our purpose we do not actually need the global solvability of the equation $F_2(S, V) = 0$, since we are searching for a unique endemic equilibrium and consequently for a single V^* . In some situations, local solvability may suffice.

To gain insight, suppose for the moment that the equation $F_2(S, V) = 0$ may also be uniquely solved with respect to S as a function of V (locally for V). That is, there is a function $S = \psi_2(V)$ which satisfies

$$c(\psi_2(V)) = \frac{c_1 c_3}{c_2 c_4} \frac{r(V)}{f(V)}.$$

Since c is strictly increasing, it follows that ψ_2 is strictly increasing.

Since ψ_1 is strictly decreasing, ψ_2 is strictly increasing and $\lim_{V\to\infty} \psi_1(V) = 0$, the curves defined by $S = \psi_1(V)$ and $S = \psi_2(V)$ have a common point (S^*, V^*) with $S^* > 0$ and $V^* > 0$ if and only if $\psi_1(0) > \psi_2(0)$, or equivalently, $c(\psi_1(0)) > c(\psi_2(0))$. Since $\psi_1(0) = S_0$ and $c(\psi_2(0)) = \frac{c_{1c_3}}{c_{2c_4}} \lim_{V\to 0} \frac{r(V)}{f(V)}$, the existence condition is $c(S_0) > \frac{c_{1c_3}}{c_{2c_4}} \lim_{V\to 0} \frac{r(V)}{f(V)}$. Using the basic reproduction number of the system (VP) as defined in (2.2.8) (note again that f/r is monotone), this condition may be rewritten as $R_0 > 1$.

Up to now, we have shown that if the equation $F_2(S, V) = 0$ is solvable with respect to S as a function of V, then the necessary and sufficient condition for the existence of positive (S^*, V^*) is that $R_0 > 1$. In this case, we have

$$F_2(S,V) = \frac{c_1 c_3}{c_2 c_4} r(V) \left[c(S) \frac{c_2 c_4}{c_1 c_3} \frac{f(V)}{r(V)} - 1 \right];$$

and $F_2(S_0, V)$ is positive for V in a vicinity of 0. Since we have already noted that $F_2(0, V) < 0$ for all V, it follows that the equation $F_2(S, V) = 0$ is solvable with respect to S as a function of V (locally for V) if $R_0 > 1$, which is precisely what we needed. That

is, we have shown that the existence of positive (S^*, V^*) is equivalent to the validity of condition $R_0 > 1$.

Also, if i, p are strictly increasing on $[0, \infty)$ and $\lim_{x\to\infty} i(x) = \lim_{x\to\infty} p(x) = +\infty$, then the equations $i(E) = \frac{1}{c_1}n(S^*)$ and $p(I) = \frac{c_2}{c_3c_1}n(S^*)$ will have unique positive solutions E^* , I^* , respectively. In view of the above, we can summarize our discussion with the following result.

Theorem 2.2.4. Assume that conditions (2.2.9), (2.2.10), and (2.2.11) are satisfied. Then there is a unique positive endemic equilibrium (S^*, E^*, I^*, V^*) of (VP) if and only if $R_0 > 1$, where R_0 is the basic reproduction number for the system (VP), as defined in (2.2.8).

We note that conditions (2.2.9), (2.2.10), and (2.2.11) (combined with $R_0 > 1$) are sufficient for the existence of the endemic equilibrium but not necessary. Actually, if one assumes that the removal rate r(V) of the virus is influenced by treatment which is administered if an increase of the virus load over a certain value is observed, while the force of infection f(V) is not, it is easy to think of a function f/r which is not monotone, for instance. In this situation, the disease-free equilibrium may coexist with multiple positive endemic equilibria. It is perhaps also worth noting that the stability of the equilibria depends essentially on the behavior of the function f/r and depends on the contact function c only through the basic reproduction number R_0 .

2.2.4 The stability of the endemic equilibrium

In this subsection we assume that the system (VP) admits a positive endemic equilibrium (S^*, E^*, I^*, V^*) and study its stability. However, we do not assume that (2.2.9), (2.2.10), and (2.2.11) are satisfied and establish our results under somewhat weaker hypotheses. This is consistent with the remark that conditions (2.2.9), (2.2.10), and (2.2.11) are sufficient for the existence of the endemic equilibrium but not necessary. For our purpose, apart from the existence of the endemic equilibrium, we assume that

(P)

$$(c(S) - c(S^*)) (S - S^*) > 0 \quad \text{for } S \neq S^*, S \ge 0,$$

$$(f(V) - f(V^*)) (V - V^*) > 0 \quad \text{for } V \neq V^*, V \ge 0,$$

$$(i(E) - i(E^*)) (E - E^*) > 0 \quad \text{for } E \neq E^*, E \ge 0,$$

$$(p(I) - p(I^*)) (I - I^*) > 0 \quad \text{for } I \neq I^*, I \ge 0$$

and

(N)
$$(n(S) - n(S^*))(S - S^*) \le 0$$
 for all $S \ge 0$.

Note that conditions (P) and (N) are satisfied if (2.2.10) holds. However, nonmonotone functions c, f, i, p, n can also satisfy (P) and (N).

We consider the Lyapunov function

$$U_{3}(S, E, I, V) = \int_{S^{*}}^{S} \frac{c(\tau) - c(S^{*})}{c(\tau)} d\tau + \int_{E^{*}}^{E} \frac{i(\tau) - i(E^{*})}{i(\tau)} d\tau + \frac{c_{1}}{c_{2}} \int_{I^{*}}^{I} \frac{p(\tau) - p(I^{*})}{p(\tau)} d\tau + \frac{c_{1}c_{3}}{c_{2}c_{4}} \int_{V^{*}}^{V} \frac{f(\tau) - f(V^{*})}{f(\tau)} d\tau.$$

Due to the sign conditions (P), it is seen that U_3 increases whenever any of $|S - S^*|$, $|E - E^*|$, $|I - I^*|$, $|V - V^*|$ increases and $U_3(S, E, I, V) \ge 0$ for all $S, E, I, V \ge 0$, while $U_3(S, E, I, V) = 0$ if and only if $(S, E, I, V) = (S^*, E^*, I^*, V^*)$. We note that if any of S, E, I, V tends to 0, then $U_3(S, E, I, V)$ tends to ∞ due to the divergence condition (D). It then follows that all level sets of U_3 have no limit points on the boundary of $(0, \infty)^4$.

We now compute the time derivative of U_3 along the solutions of (VP).

Lemma 2.2.1. The time derivative of U_3 with respect to the solutions of (VP) is

$$\begin{aligned} U_3(S, E, I, V) \\ &= (n(S) - n(S^*)) \left(1 - \frac{c(S^*)}{c(S)} \right) + c(S^*)r(V) \left(\frac{f(V^*)}{f(V)} - 1 \right) \left(\frac{f(V^*)}{r(V^*)} - \frac{f(V)}{r(V)} \right) \\ &- c_1 i(E^*) \left[\frac{c(S^*)}{c(S)} + \frac{i(E^*)}{i(E)} \frac{c(S)}{c(S^*)} \frac{f(V)}{f(V^*)} + \frac{i(E)}{i(E^*)} \frac{p(I^*)}{p(I)} + \frac{f(V^*)}{f(V)} \frac{p(I)}{p(I^*)} - 4 \right]. \end{aligned}$$

If the inequality

(2.2.13)
$$c(S^*)r(V)\left(\frac{f(V^*)}{f(V)} - 1\right)\left(\frac{f(V^*)}{r(V^*)} - \frac{f(V)}{r(V)}\right) \le 0$$

holds true for V in some given interval (V_L, V_R) , then $U_3(S, E, I, V) \leq 0$ for $V \in (V_L, V_R)$, with equality if and only if

$$S = S^*$$
 and $\frac{i(E)}{i(E^*)} = \frac{f(V)}{f(V^*)} = \frac{p(I)}{p(I^*)}$

Proof. It is seen that

$$\begin{split} \dot{U}_3 &= \left(1 - \frac{c(S^*)}{c(S)}\right) (n(S) - c(S)f(V)) + \left(1 - \frac{i(E^*)}{i(E)}\right) (c(S)f(V) - c_1i(E)) \\ &+ \frac{c_1}{c_2} \left(1 - \frac{p(I^*)}{p(I)}\right) (c_2i(E) - c_3p(I)) + \frac{c_1c_3}{c_2c_4} \left(1 - \frac{f(V^*)}{f(V)}\right) (c_4p(I) - r(V)) \\ &= n(S) \left(1 - \frac{c(S^*)}{c(S)}\right) + c(S^*)f(V) - \frac{i(E^*)}{i(E)}c(S)f(V) + c_1i(E^*) - c_1\frac{p(I^*)}{p(I)}i(E) \\ &+ \frac{c_1c_3}{c_2}p(I^*) - \frac{c_1c_3}{c_2c_4}r(V) - \frac{c_1c_3}{c_2}\frac{f(V^*)}{f(V)}p(I) + \frac{c_1c_3}{c_2c_4}\frac{f(V^*)}{f(V)}r(V). \end{split}$$

Using the equilibrium relations (EQ), it follows that

$$\begin{split} \dot{U}_{3} &= n(S) \left(1 - \frac{c(S^{*})}{c(S)} \right) + c(S^{*})f(V) - c_{1}i(E^{*})\frac{i(E^{*})}{i(E)}\frac{c(S)}{c(S^{*})}\frac{f(V)}{f(V^{*})} + c_{1}i(E^{*}) \\ &- c_{1}i(E^{*})\frac{i(E)}{i(E^{*})}\frac{p(I^{*})}{p(I)} + c_{1}i(E^{*}) - c_{1}i(E^{*})\frac{r(V)}{r(V^{*})} - c_{1}i(E^{*})\frac{f(V^{*})}{f(V)}\frac{p(I)}{p(I^{*})} \\ &+ c_{1}i(E^{*})\frac{f(V^{*})}{f(V)}\frac{r(V)}{r(V^{*})} \\ &= n(S) \left(1 - \frac{c(S^{*})}{c(S)} \right) + c(S^{*})f(V) + c_{1}i(E^{*}) \left(\frac{f(V^{*})}{f(V)}\frac{r(V)}{r(V^{*})} - \frac{r(V^{*})}{r(V)} \right) \\ &- c_{1}i(E^{*}) \left[\frac{i(E^{*})}{i(E)}\frac{c(S)}{c(S^{*})}\frac{f(V)}{f(V^{*})} + \frac{i(E)}{i(E^{*})}\frac{p(I^{*})}{p(I)} + \frac{f(V^{*})}{f(V)}\frac{p(I)}{p(I^{*})} - 2 \right] \\ &= n(S) \left(1 - \frac{c(S^{*})}{c(S)} \right) + c_{1}i(E^{*})\frac{f(V)}{f(V^{*})} + c_{1}i(E^{*}) \left(\frac{f(V^{*})}{r(V)}\frac{r(V)}{r(V^{*})} - \frac{r(V)}{r(V^{*})} \right) \\ &- c_{1}i(E^{*}) \left[\frac{c(S^{*})}{c(S)} + \frac{i(E^{*})}{i(E)}\frac{c(S)}{c(S^{*})}\frac{f(V)}{f(V^{*})} + \frac{i(E)}{i(E^{*})}\frac{p(I^{*})}{p(I)} + \frac{f(V^{*})}{f(V)}\frac{p(I)}{p(I^{*})} - 4 \right] \\ &+ c_{1}i(E^{*})\frac{c(S^{*})}{c(S)} - 2c_{1}i(E^{*}). \end{split}$$

This implies that

$$\dot{U}_{3} = (n(S) - c_{1}i(E^{*})) \left(1 - \frac{c(S^{*})}{c(S)}\right) + c_{1}i(E^{*}) \left(\frac{f(V^{*})}{f(V)} \frac{r(V)}{r(V^{*})} - \frac{r(V)}{r(V^{*})} + \frac{f(V)}{f(V^{*})} - 1\right) - c_{1}i(E^{*}) \left[\frac{c(S^{*})}{c(S)} + \frac{i(E^{*})}{i(E)} \frac{c(S)}{c(S^{*})} \frac{f(V)}{f(V^{*})} + \frac{i(E)}{i(E^{*})} \frac{p(I^{*})}{p(I)} + \frac{f(V^{*})}{f(V)} \frac{p(I)}{p(I^{*})} - 4\right],$$

and since $c_1i(E^*) = n(S^*)$, it follows that

 $\dot{U}_3(S, E, I, V)$
$$= (n(S) - n(S^*)) \left(1 - \frac{c(S^*)}{c(S)}\right) + c_1 i(E^*) \left(\frac{f(V^*)}{f(V)} - 1\right) \left(\frac{r(V)}{r(V^*)} - \frac{f(V)}{f(V^*)}\right) - c_1 i(E^*) \left[\frac{c(S^*)}{c(S)} + \frac{i(E^*)}{i(E)} \frac{c(S)}{c(S^*)} \frac{f(V)}{f(V^*)} + \frac{i(E)}{i(E^*)} \frac{p(I^*)}{p(I)} + \frac{f(V^*)}{f(V)} \frac{p(I)}{p(I^*)} - 4\right].$$

Using the relation $c_1i(E^*) = c(S^*)f(V^*)$, one gets the required conclusion. Now, from the sign condition (N) it is seen that

$$(n(S) - n(S^*))\left(1 - \frac{c(S^*)}{c(S)}\right) \le 0 \quad \text{for } S \ge 0,$$

with equality if and only if $S = S^*$, and from the AM-GM inequality (which says that the algebraic mean is not smaller than the geometric mean) it is seen that

$$\frac{c(S^*)}{c(S)} + \frac{i(E^*)}{i(E)}\frac{c(S)}{c(S^*)}\frac{f(V)}{f(V^*)} + \frac{i(E)}{i(E^*)}\frac{p(I^*)}{p(I)} + \frac{f(V^*)}{f(V)}\frac{p(I)}{p(I^*)} \ge 4$$

with equality if and only if

(2.2.14)
$$\frac{c(S^*)}{c(S)} = \frac{i(E^*)}{i(E)} \frac{c(S)}{c(S^*)} \frac{f(V)}{f(V^*)} = \frac{i(E)}{i(E^*)} \frac{p(I^*)}{p(I)} = \frac{f(V^*)}{f(V)} \frac{p(I)}{p(I^*)} = 1.$$

It then follows that if the inequality

$$c(S^*)r(V)\left(\frac{f(V^*)}{f(V)} - 1\right)\left(\frac{f(V^*)}{r(V^*)} - \frac{f(V)}{r(V)}\right) \le 0$$

holds true for $v \in (V_L, V_R)$, then $U_3(S, E, I, V) \leq 0$. For the equality case, we note that $c(S^*) = c(S)$ if and only if $S = S^*$, and substituting this into (2.2.14) one obtains that

$$\frac{i(E)}{i(E^*)} = \frac{f(V)}{f(V^*)} = \frac{p(I)}{p(I^*)}.$$

It is now obvious that the stability of the endemic equilibrium (S^*, E^*, I^*, V^*) is related to the validity of the inequality (2.2.13). Subsequently, we estimate the size of the domain of attraction associated with (S^*, E^*, I^*, V^*) .

Theorem 2.2.5. Assume that the sign conditions (P) and (N) are satisfied and there are V_L and V_R such that

(2.2.15)
$$\frac{f(V)}{r(V)} \le \frac{f(V^*)}{r(V^*)} \quad \text{for } V^* \le V < V_R,$$
$$\frac{f(V)}{r(V)} \ge \frac{f(V^*)}{r(V^*)} \quad \text{for } V_L < V \le V^*.$$

Define $m = \min(U_3(S^*, E^*, I^*, V_L), U_3(S^*, E^*, I^*, V_R))$. Then (S^*, E^*, I^*, V^*) is locally asymptotically stable and its domain of attraction includes the set

$$M_m = \{ (S, E, I, V) \in (0, \infty)^4; U_3(S, E, I, V) < m \}.$$

Proof. Denote

$$\tilde{M} = \{(S, E, I, V) \in (0, \infty)^4; V_L < V < V_R\}$$

From (2.2.15), it follows that (2.2.13) is satisfied for $V \in (V_L, V_R)$, and using Lemma 2.2.1 one may infer that $U_3(S, E, I, V) \leq 0$ on \tilde{M} , with equality if and only if

$$S = S^*$$
 and $\frac{i(E)}{i(E^*)} = \frac{f(V)}{f(V^*)} = \frac{p(I)}{p(I^*)}$

Take an arbitrary k < m. Since U_3 increases whenever any of $|S - S^*|$, $|E - E^*|$, $|I - I^*|$, $|V - V^*|$ increases, it follows easily that, for all V outside (V_L, V_R) , one has $U_3(S, E, I, V) \ge m$ for all S, E, I > 0. Consequently $M_k \subset \tilde{M}$. Moreover, as noted previously, M_k is a bounded set which has no limit points on the boundary of \tilde{M} .

We now find the invariant subsets \tilde{N} within the set

$$N = \{ (S, E, I, V) \in M_k; U_3(S, E, I, V) \le 0 \}.$$

Since $S = S^*$ on \tilde{N} and consequently $S' = n(S^*) - c(S^*)f(V)$, it follows that $S' = c(S^*)(f(V^*) - f(V))$, and so S' = 0 if and only if $V = V^*$. From $\frac{i(E)}{i(E^*)} = \frac{p(I)}{p(I^*)} = 1$ we then deduce that $E = E^*$ and $I = I^*$ by using the sign condition (P).

Therefore, using LaSalle's invariance principle (see Appendix A or LaSalle [77]) one obtains that any trajectory which starts in M_k tends to (S^*, E^*, I^*, V^*) as $t \to \infty$. Then the endemic equilibrium (S^*, E^*, I^*, V^*) is locally asymptotically stable and the set M_k belongs to its domain of attraction. Since k was arbitrary and less than m, one obtains the required conclusion.

We now continue with a few considerations on the inequalities (2.2.15). Since

$$\lim_{V_L \to 0} U_3(S^*, E^*, I^*, V_L) = \lim_{V_R \to \infty} U_3(S^*, E^*, I^*, V_R) = +\infty,$$

one obtains that if the following inequalities are satisfied,

(2.2.16)
$$\frac{f(V)}{r(V)} \le \frac{f(V^*)}{r(V^*)} \quad \text{for } V^* \le V,$$
$$\frac{f(V)}{r(V)} \ge \frac{f(V^*)}{r(V^*)} \quad \text{for } 0 < V \le V^*.$$

then (S^*, E^*, I^*, V^*) is globally asymptotically stable in $(0, \infty)^4$.

Regarding the inequalities (2.2.16) (or (2.2.15)), it is easy to see that they are verified if the function f/r is nonincreasing on $(0, \infty)$ (or on (V_L, V_R)); however, this monotonicity property is only sufficient and not necessary. If r(V) = kV, for some k, then the above monotonicity property is satisfied for three common incidence rates, namely $c_1(S)f_1(V) = \beta_1 SV$, $c_2(S)f_2(V) = \beta_2 S^p V^q$, where $0 < q \leq 1$, and $c_3(S)f_3(V) = \beta_3 SV/(1 + a_1V)$.

We also remark that the inequalities (2.2.16) alone imply the uniqueness of the endemic equilibrium (S^*, E^*, I^*, V^*) . To show this, suppose that there is another endemic equilibrium $(S_1^*, E_1^*, I_1^*, V_1^*)$. Apart from (EQ), one then has

(EQ')
$$n(S_1^*) = c(S_1^*)f(V_1^*), \quad c(S_1^*)f(V_1^*) = c_1i(E_1^*), \quad c_2i(E_1^*) = c_3p(I_1^*),$$

 $c_4p(I_1^*) = r(V_1^*).$

It follows that

(2.2.17)
$$c(S^*) - c(S_1^*) = \frac{c_1 c_3}{c_2 c_4} \left(\frac{r(V^*)}{f(V^*)} - \frac{r(V_1^*)}{f(V_1^*)} \right),$$

(2.2.18)
$$n(S^*) - n(S_1^*) = \frac{c_1 c_3}{c_2 c_4} \left(r(V^*) - r(V_1^*) \right)$$

and therefore

$$(c(S^*) - c(S_1^*)) (V^* - V_1^*) \ge 0.$$

If $V^* > V_1^*$, then, from (2.2.17), $c(S^*) \ge c(S_1^*)$ and $S^* \ge S_1^*$, which implies $n(S^*) \le n(S_1^*)$. Consequently, from (2.2.18), $r(V^*) \le r(V_1^*)$, which is a contradiction. The case $V^* < V_1^*$ is dismissed in a similar manner, subsequently $V^* = V_1^*$ and from (2.2.17), $S = S_1^*$. Substituting these equalities into (EQ) and (EQ') we obtain that $i(E^*) = i(E_1^*)$ and $p(I^*) = p(I_1^*)$, and hence $E^* = E_1^*$ and $I^* = I_1^*$; that is, the endemic equilibrium is uniquely determined. However, we should point out that inequalities (2.2.16) ensure the uniqueness of the endemic equilibrium only and not necessarily its existence.

2.2.5 Discussions and concluding remarks

The earlier analysis clearly indicates the importance of the quantity

$$c(S_0)\frac{f(V)}{r(V)}\frac{c_2c_4}{c_1c_3}$$

in the discussion on the local stability of the disease-free equilibrium and the persistence of the system. Moreover, under the monotonicity condition on f(V)/r(V), we obtain that the basic reproduction number is given by

(2.2.19)
$$R_0 = c(S_0) \frac{c_2 c_4}{c_1 c_3} \lim_{V \to 0} \frac{f(V)}{r(V)}$$

We will now give a biological interpretation of this result. From (VP), it is obvious that the terms in the numerator denote the growth in the concentrations of the infected cells, E and I, and of the virus V. The terms in the denominator, on the other hand, denote the removal (or decrease in concentration) of these three same classes. Therefore, the ratio of the two can be considered as a measurement of the combined "productivity", perhaps more aptly, the basic reproductive ratio of the infected classes in the system. The fact that the stability of the disease-free equilibrium and the persistence of the system depend on whether this quantity is less than one or not (Theorems 2.2.1 and 2.2.2) further confirms our assertion.

The quantity f(V)/r(V) is also important for our results. It can be interpreted as the efficiency of the virus, that is, the ratio of its infectivity to its removal, as a function of the virus concentration. Theorems 2.2.3, 2.2.4, and 2.2.5 require f(V)/r(V) to be a nonincreasing function of V. Some recent studies (see, e.g., [114, 115]) let f(V) =r(V) = V, an assumption which is supported by some clinical data. We note that in this case f(V)/r(V) = 1, and hence our condition of nonincreasing ratio f(V)/r(V), which generalizes to the models with nonlinear f(V) and r(V), is satisfied. For HIV, it has been observed that the productivity of the virus, f(V), increases as the virus concentration increases. Our analysis is valid if the increase in removal of the virus r(V) as virus concentration increases is at least to the same level as the increase in f(V). Further studies are needed to verify whether our assertion holds.

On the other hand, if the function f/r is indeed increasing on $(0, \infty)$, then U_1 and U_3 are not necessarily global Lyapunov functionals and therefore do not create their own boundedness structure for the solutions of (VP). To obtain the global existence of the solutions, the growth conditions (G) (see Subsection 2.2.2) need to be imposed. If f/r is nonincreasing on $(0, \infty)$, however, the boundedness structures created by the level sets of U_1 and U_3 render the growth conditions unnecessary.

Suppose that f/r is nonincreasing on $(0, \infty)$ and $R_0 > 1$. Assume that the following conditions are satisfied:

(B)
$$\lim_{y \to \infty} \left(y - \varphi(x) \int_x^y \frac{1}{\varphi(\tau)} d\tau \right) = +\infty \quad \text{for all } x > 0 \text{ and } \varphi \in \{c, f, i, p\}$$

Note that (B) is satisfied for a function φ such that $\lim_{y\to\infty}\varphi(y) = +\infty$, since in this situation

$$\lim_{y \to \infty} \frac{\int_x^y \frac{1}{\varphi(\tau)} d\tau}{y} = \lim_{y \to \infty} \frac{1}{\varphi(y)} = 0 \quad \text{for } \varphi \in \{c, f, i, p\}.$$

However, condition (B) is also satisfied for $\varphi(x) = x^p/(1 + ax^p), 0 (this is, for instance, the case when <math>\varphi(V) = f(V) = V^p/(1 + aV^p)$ is a nonlinear force of infection with saturation), which does not tend to $+\infty$ as $x \to +\infty$.

Regarding conditions (D), since the only points on the boundary of $[0, \infty)^4$ which can be reached in finite time are situated on [OS and the only w-limit point of (VP) on the boundary of $[0, \infty)^4$ is the disease-free equilibrium $(S_0, 0, 0, 0)$, a less restrictive condition than (D) would suffice to avoid these situations, namely

(D')
$$\int_{0+}^{1} \frac{1}{\varphi(\tau)} d\tau = +\infty \quad \text{for some } \varphi \in \{f, i, p\}$$

Then, by the results in the previous Subsection, there is a unique positive endemic equilibrium which verifies relations (EQ). Take $(S(0), E(0), I(0), V(0)) \in (0, \infty)^4$. Then $U_3 \leq 0$ for all t, and it follows that (S(t), E(t), I(t), V(t)) stays in a level set of U_3 on its whole interval of existence. Since the level sets of U_3 are bounded due to (B), it follows that the saturated solution which starts in (S(0), E(0), I(0), V(0)) exists on $[0, \infty)$. The growth conditions (G), which were used to obtain global existence, therefore become unnecessary and the proof proceeds in the same manner. Then, as in Subsection 2.2.2, all solutions which start in $[0, \infty)^4$ tend to (S^*, E^*, I^*, V^*) , except for those which start on [OS and tend to $(S_0, 0, 0, 0)$ as $t \to \infty$. The growth conditions become unnecessary for the proof of the uniform persistence result as well, since the system (VP) admits an endemic equilibrium and it is obviously uniformly persistent.

If $R_0 \leq 1$, the reasoning is quite similar, with U_1 in place of U_3 , and it is obtained again that all the saturated solutions are global and the stability result remains valid. We then summarize our discussion in the following result.

Theorem 2.2.6. Suppose that f/r is nonincreasing on $(0, \infty)$ and conditions (2.2.10), (2.2.11), (B), and (D') are satisfied.

- 1. If $R_0 \leq 1$, then the disease-free equilibrium $(S_0, 0, 0, 0)$ is globally asymptotically stable.
- 2. If $R_0 > 1$, then the system (VP) admits a unique positive endemic equilibrium which

is globally asymptotically stable. The disease-free equilibrium $(S_0, 0, 0, 0)$ is unstable, with the positive semiaxis [OS as its stable manifold.

Obviously, in the second statement the stable manifold of the endemic equilibrium actually excludes [OS].

As an example to illustrate the usefulness of our results, it is easy to see that a system which fits into our framework is

(RS)
$$\begin{cases} S' = b - mS - \beta S \frac{V^p}{1 + aV^p} \\ E' = \beta S \frac{V^p}{1 + a_1 V^p} - c_1 E, \\ I' = c_2 E - c_3 I, \\ V' = c_4 I - kV^{\gamma} \end{cases}$$

for $b, m, \beta, k > 0$, $a \ge 0$, and $0 . In this situation, <math>c(S) = \beta S$, $f(V) = V^p/(1 + aV^p)$, i(E) = E, p(I) = I, $r(V) = V^{\gamma}$, n(S) = b - mS.

It follows that $f/r = 1/((1 + a_1 V^p)V^{\gamma-p})$ is nonincreasing on $(0, \infty)$,

$$\lim_{E \to \infty} E = \lim_{I \to \infty} I = \lim_{V \to \infty} kV^{\gamma} = +\infty,$$

and $\lim_{V\to\infty} V^p/(1+aV^p) = +\infty$ if a = 0, while if a > 0, then

$$\lim_{V \to \infty} \left(V - \frac{x^p}{1 + ax^p} \int_x^V \frac{1 + a\tau^p}{\tau^p} d\tau \right) = +\infty \quad \text{for all } x > 0.$$

Also, $\int_{0+\frac{1}{E}}^{1} dE = +\infty$. Note that if a = 0 and $p \in (0,1)$, then $f(V) = V^p$ is not Lipschitzian on $[0,\infty)$ due to its behavior near 0. However, our solutions which start with V > 0 do not reach points for which V = 0 in finite time. Hence the uniqueness property is not impaired. The same remark applies to the function r. We can therefore apply the results in the previous Subsections and obtain the following result.

- **Theorem 2.2.7.** 1. If $p < \gamma$, the basic reproduction number R_0 of the system (RS) is $+\infty$. The system (RS) admits a positive endemic equilibrium which is globally asymptotically stable. The disease-free equilibrium $(S_0, 0, 0, 0)$ is unstable, with the positive semiaxis [OS as its stable manifold.
 - 2. If $p = \gamma$, the basic reproduction number R_0 of the system (RS) is

$$R_0 = \frac{\beta b}{m} \frac{c_2 c_4}{c_1 c_3} \frac{1}{k}.$$

In this case, if $R_0 \leq 1$, then the disease-free equilibrium $(S_0, 0, 0, 0)$ is globally asymptotically stable, while if $R_0 > 1$, the system (RS) admits a positive endemic equilibrium which is globally asymptotically stable. The disease-free equilibrium $(S_0, 0, 0, 0)$ is unstable, with the positive semiaxis [OS as its stable manifold.

Again, the "global" stable manifold of the endemic equilibrium is understood to exclude [OS. Note that for $p = \gamma = 1$ and a = 0 we obtain the results given in Korobeinikov [64].

As a final remark, we note that similar analysis can be extended to a system of the form

(SE)
$$\begin{cases} S' = n(S) - c(S)f(V), \\ E' = c(S)f(V) - c_1i(E), \\ I'_1 = c_2i(E) - k_1p_1(I_1), \\ I'_j = \tilde{k}_{j-1}p_{j-1}(I_{j-1}) - k_jp_j(I_j), \quad 2 \le j \le n, \\ V' = \tilde{k}_n p_n(I_n) - r(V). \end{cases}$$

The associated Lyapunov functionals are in this case

$$U_1(S, E, I_1, \dots, I_n) = \int_{S_0}^{S} \frac{c(\tau) - c(S_0)}{c(\tau)} d\tau + E + \frac{c_1}{c_2} \sum_{i=1}^n \left(\prod_{j=1}^{i-1} \frac{k_j}{\tilde{k}_j}\right) I_i + \frac{c_1}{c_2} \prod_{j=1}^n \frac{k_j}{\tilde{k}_j} V_i$$
$$U_2(S, E, I_1, \dots, I_n) = E + \frac{c_1}{c_2} \sum_{i=1}^n \left(\prod_{j=1}^{i-1} \frac{k_j}{\tilde{k}_j}\right) I_i + \frac{c_1}{c_2} \prod_{j=1}^n \frac{k_j}{\tilde{k}_j} V_i$$

and

$$U_{3}(S, E, I_{1}, \dots, I_{n}) = \int_{S^{*}}^{S} \frac{c(\tau) - c(S^{*})}{c(\tau)} d\tau + \int_{E^{*}}^{E} \frac{i(\tau) - i(E^{*})}{i(\tau)} d\tau + \frac{c_{1}}{c_{2}} \sum_{i=1}^{n} \left(\prod_{j=1}^{i-1} \frac{k_{j}}{\tilde{k}_{j}} \right) \int_{I_{i}^{*}}^{I_{i}} \frac{p_{i}(\tau) - p_{i}(I_{i}^{*})}{p_{i}(\tau)} d\tau + \frac{c_{1}}{c_{2}} \left(\prod_{j=1}^{n} \frac{k_{j}}{\tilde{k}_{j}} \right) \int_{V^{*}}^{V} \frac{c(\tau) - c(V^{*})}{c(\tau)} d\tau,$$

with the convention $\prod_{j=1}^{0} \frac{k_j}{k_j} = 1$.

Again, related asymptotic stability can be obtained as in previous Subsections, and the size of the domain of attraction depends essentially on the behavior of the function f/r. If the function f/r is nonincreasing on $(0, \infty)$, the threshold parameter R_0 is given by

$$R_{0} = c(S_{0})\frac{c_{2}}{c_{1}} \left(\prod_{j=1}^{n} \frac{\tilde{k}_{j}}{k_{j}}\right) \lim_{V \to 0} \frac{f(V)}{r(V)}.$$

The first Lyapunov functional of type $\sum_{i=1}^{n} d_i \left(x_i - x_i^* - x_i^* \ln \frac{x_i}{x_i^*}\right)$, to which our functional U_3 reduces when c, f, i, p are linear functions, has been used by Volterra in [128] to treat a two-dimensional predator-prey model which describes the interaction between sharks and predated fish in the Adriatic Sea. (See also Goh [34].) In [42], Harrison constructed a Lyapunov functional of this type for a two-dimensional predator-prey model which accounted for very general numerical and functional responses of the predator. The computation of the derivatives is straightforward and hence omitted for brevity.

Chapter 3

Ecoepidemiology: managing pest populations by inflicting a disease in the pest

3.1 Basic concepts of integrated pest management

Although synthetic pesticides were first seen as a miraculous way of solving all pestrelated issues, it has been quickly noticed that the heavy use of pesticides creates in the long run more problems that it solves. In some situations, chemicals become increasingly ineffective, as many pests quickly develop new generations which are resistant to various chemical agents. Also, when pesticides are used to control a given pest, its natural predators may be killed as well as a side effect, which may actually cause in the long run an increase in the size of the pest population, rather than the expected reduction. If the pest is living out of reach or just hiding, then pesticides may simply have no effect on the pest population. Finally, many pesticides are known to cause environmental problems and actually damage human health. Consequently, sophisticated and multifaceted ecosystem-based strategies have been constructed in order to minimize the use of hazardous chemicals.

Integrated pest management (IPM) is an ecological approach which represents a synthesis of techniques of various natures to control pests (mechanical, chemical, biological and not only), with an accent on those which are potentially less damaging to the environment. Further, techniques specifically suited to the target pests are preferred, in order to avoid harmful effects on non-target organisms. Specifically, natural predators, parasites or pathogens of pests may be used, together with genetically-engineered pestresistant varieties of crops, mechanical methods of pest control such as traps or insect barriers and habitat manipulation. In this approach, pesticides are used only as a last resort, when deemed an absolute necessity. For a historical perspective on the evolution of IPM definitions, see Bajwa and Kogan [9].

The purpose of IPM is often to drive the size of the pest population under certain economically significant levels, not to eradicate it totally, as the latter can be impossible, cost-ineffective or potentially damaging to the environment. In this regard, the economic injury level (EIL), as defined in Stern et al. [125], is the lowest population density of a pest that will cause economic damage, or the amount of pest injury which will justify the cost of using controls. Another related type of injury level which can be of interest in certain situations is called the aesthetic injury level (AIL) and is defined in the same manner, but based on aesthetic rather than economic considerations. Finally, a relevant parameter is also the action threshold, representing the pest density at which control measures should be implemented in order to prevent the pest populations to reach the economic (or aesthetic) injury level. See Stern et al. [125], Pedigo and Higley [112], Pedigo et al. [113], Pedigo [111] for further details.

Chemical control relies mainly on the use of synthetic pesticides to suppress pests. Biological pesticides, derived from plants or microorganisms, such as *Bacillus Thuringiensis* are also of use in chemical control.

Biological control is defined as the reduction of pest populations by using their natural enemies (see Hoffmann and Frodsham [50]). To use biological controls in an effective manner, detailed knowledge of the pest and of its natural enemies is needed, the practical details of implementing the biological control being then decided accordingly. An approach to control insect pests, for instance, is to release parasitoids or pathogens. While the first are generally species which develop within or on the host and ultimately kill it, the latter are viruses, fungi or bacteria which kill or incapacitate the host by causing a disease, or otherwise affect the biological processes within the host. Another approach to biological control is to release pests which are infected in laboratories, with the purpose of creating and maintaining a disease in the target pest population, on the grounds that infective pests usually cause less environmental damage. This is the approach to biological control which we use in the present section. Among the advantages of using biological controls, we mention that they are of much less environmental concern, lower cost and might be more effective if applied correctly. Also, they are self-regulating up to some extent.

3.2 Pest regulation by means of impulsive controls

3.2.1 Biological controls and proper incidence rates

Regarding disease transmission, in many papers on epidemiological models treating disease dynamics in animal populations, use is made of an incidence rate of infection which is bilinear in both the susceptible and the infective fraction of the total number of individuals. However, the assumption of homogeneous mixing, which motivates the mass action law behind the use of the bilinear incidence rate, may not be accurate under certain conditions. This is the case, for instance, when the concentration of infective pests is very high and saturation may occur or if multiple exposure to the disease vector or multiple contacts are required for disease transmission.

Also, many classical models using bilinear incidence rates exhibit threshold dynamics, that is, if the so-called basic reproduction number R_0 (that is, the average number of new infections produced by a single infective individual introduced in a totally susceptible population) is greater than 1, then the disease remains endemic and the endemic equilibrium is globally asymptotically stable, while if R_0 is lower than 1, then the disease dies out, the endemic equilibrium loses its stability and and the disease-free equilibrium becomes globally asymptotically stable. In this setting, the dynamics of the system is unaffected by the relative sizes of the initial populations. However, it has been observed that many diseases exhibit yearly variations in a periodic fashion and that for some diseases the persistence of the infective populations depends on their initial sizes. See Wang [129] for a more detailed discussion regarding this matter, which also outlines the fact that the nonlinearity of the force of infection may appear as a result of intervention policies.

Liu, Hethcote and Levin [89] studied a SEIRS model with nonlinear incidence rates of type $\lambda I^p S^q$, $0 , <math>0 < q \leq 1$, where I denotes the size of the infective population and S denotes the size of the susceptible population, and observed that while the choice of a $q \neq 1$ does not have a decisive impact on the qualitative behavior of the system, the choice of a $p \neq 1$ modifies the phase portrait of the system in an obvious manner. In the latter case, the meaning of the basic reproduction number understood as a threshold parameter for the stability of the system vanishes completely, since the disease remains endemic and the system always approaches a unique endemic equilibrium irrespective of q.

An incidence rate of type g(I)S has been proposed by Capasso and Serio in [16], with

 $g(I) = kI/(1 + \alpha I)$. This incidence rate includes behavioral change and crowding effect for infectives. A general incidence rate of type g(I)S with $g(I) = kI^p/(1 + \alpha I^q)$ has been employed by Liu, Levin and Iwasa in [90]; see also Hethcote and van den Driessche [48]. Particular incidence rates of type $g(I)S = kI^2S/(1 + \alpha I^2)$, $g(I)S = KIS/(1 + \alpha I^2)$ have been used in Ruan and Wang [120], respectively in Xiao and Ruan [133].

Models with general nonlinear incidence rates of type g(I)h(S) and respectively f(I, S)have been treated in Korobeinikov and Maini [67], respectively in Korobeinikov [65], and it has again been observed that the dependence on I plays a more prominent role in the stability of the endemic equilibrium than the dependence on S. Consequently, we shall use in the following a general incidence rate of type g(I)S to model disease transmission, under a few biologically feasible conditions on the nonlinear force of infection g.

A central problem in IPM strategies is to choose the appropriate moment to use each type of control. To account for the fact that pesticides cannot be sprayed continuously, we use a model in which both the biological and chemical controls are employed in an impulsive and periodic fashion, with the same period but not simultaneously. The choice of using impulsive controls is, in our opinion, justified since for certain pesticides the effect follows shortly after application and also since the size of the infected pest population grows immediately after the release of infective individuals. Therefore, such changes can be modeled as immediate jumps in the population sizes. In this regard, a general account of the theory of impulsive ordinary differential equations can be found in Bainov and Simeonov [8].

Our purpose is then to construct a model of pest control using both biological controls (periodic release of pests which are infected in laboratories) and chemical controls (pesticide spraying). The remaining part of this section is organized as follows: in Subsection 3.2.2, we formulate the main biological assumptions and subsequently employ them to construct our impulsive control model. In Subsection 3.2.3, we study the stability of the susceptible pest-eradication periodic solution, while the permanence of the system is discussed in Subsection 3.2.4. This section is based on the results obtained in Georgescu and Moroşanu [31].

3.2.2 The impulsive control model and some preliminaries

In the following, we denote by S the size of the susceptible pest population, by I the size of the infective pest population, and suppose that all pests are either susceptible

or infective. To formulate our mathematical model, we rely on the following biological assumptions.

- (A1) The intrinsic growth rate of the susceptible pest population in the absence of infection is given by the nonlinear function Sn(S), where n satisfies certain assumptions outlined below.
- (A2) The infective pests neither recover nor reproduce.
- (A3) The infective pests neither damage crops nor contribute to the total size of the environment-supported population.
- (A4) The incidence rate of the infection is nonlinear in I and given by g(I)S, where g satisfies certain assumptions outlined below.
- (A5) Infected pests are released in an impulsive and periodic fashion, in a fixed amount μ each time.
- (A6) Pesticides are sprayed in an impulsive and periodic fashion, with the same period as the action of releasing infective pests but at different moments. As a result, fixed proportions p_1 and p_2 of susceptible pests, respectively infective pests, are killed each time.

On the basis of the above assumptions, we may formulate the following impulsively controlled model which characterizes the behavior of the system under consideration.

$$(\text{IPM}) \begin{cases} I'(t) = g(I(t))S(t) - wI(t), & t \neq (n+l-1)T, t \neq nT; \\ S'(t) = S(t)n(S(t)) - g(I(t))S(t), & t \neq (n+l-1)T, t \neq nT; \\ \Delta I(t) = -\delta_2 I(t), & t = (n+l-1)T; \\ \Delta S(t) = -\delta_1 S(t), & t = (n+l-1)T; \\ \Delta I(t) = \mu, & t = nT; \\ \Delta S(t) = 0, & t = nT. \end{cases}$$

Here, T > 0, 0 < l < 1, $\Delta \varphi(t) = \varphi(t+) - \varphi(t)$ for $\varphi \in \{S, I\}$, $0 \le \delta_1, \delta_2 < 1$, $n \in \mathbb{N}^*$. The functions n and g satisfy the following hypotheses indicated below.

(N) n is decreasing on $[0,\infty)$, $\lim_{S\to\infty} n(S) < -w$, $S \mapsto Sn(S)$ is locally Lipschitz on $(0,\infty)$.

(G) g(0) = 0, g is increasing and globally Lipschitz on $[0, \infty)$.

Note that the hypothesis (G) is verified for three commonly used forces of infection, namely for $g_1(x) = ax$, $g_2(x) = \frac{ax}{1+mx}$, $g_3(x) = k(1-e^{-ax})$, as they are strictly increasing on $[0, \infty)$ and are globally Lipschitz functions since their derivatives are uniformly bounded on $[0, \infty)$. Also, hypothesis (N) is satisfied if the intrinsic growth rate of the susceptible population Sn(S) is given by the logistic growth law (Sn(S) = rS(1 - S/K)) or by Gompertz's growth law $(Sn(S) = rS \ln(K/S))$. In what follows, let us denote n(0) = r. Let us also observe that, in view of (G), $g(x) \leq Lx$ for $x \geq 0$, where by L we denote the Lipschitz constant of g.

Models related to this one have been studied by Zhang, Chen and Georgescu in [137], where the intrinsic growth rate of the susceptible population is of logistic type, which corresponds to n(S) = 1 - S/K, but a particular incidence rate of type Ih(S) is used rather than of type g(I)S, and by Liu, Chen and Zhang in [84], where an impulsively controlled system which models the dynamics of a prey-dependent consumption model is studied by similar methods. See also Song and Xiang [124] where an IPM strategy for a two-prey one-predator model with stage structure for predator is described, or Liu, Zhi and Chen [85], where the impulsive controllability of a predator-prey system with Ivlev functional response is studied. Note that, from a formal point of view, the abovementioned predator-prey models are related to our model, although they are not, strictly speaking, disease dynamics models.

It is also to be noted that our model can accomodate some situations in which the infective pest population contributes to the growth of the total population size towards the carrying capacity of the environment, that is, when (A3) is only partially satisfied. Precisely, if the second equation in our model is substituted by

$$S'(t) = S(t)\left(1 - \frac{S(t) + I(t)}{K}\right) - g(I)S,$$

then this equation can be rearranged as

$$S'(t) = S(t)\left(1 - \frac{S}{K}\right) - \left(g(I) + \frac{I}{K}\right)S,$$

which again fits our framework. Moreover, the decreases in the number of susceptible and respectively of infective pests in the third and fourth equation of (IPM) can also be achieved through selective catching rather than by pesticide poisoning only. Under these assumptions, it is seen that the Cauchy problem for the system (IPM) has a unique positive and global solution for positive initial data (I(0), S(0)), while if the initial data is strictly positive, then the corresponding solution is also unique, strictly positive and global, that is, the Cauchy problem for (IPM) with positive initial data is biologically well-posed.

First, using the results given in Appendix C, it is seen that all solutions of (IPM) are bounded.

Lemma 3.2.1. There is M > 0 such that $S(t) \leq M$, $I(t) \leq M$ for $t \geq 0$.

Proof. Let us define $u : \mathbb{R}^*_+ \to \mathbb{R}_+$ by

$$u(t) = S(t) + I(t), \quad t > 0.$$

Then

(3.2.1)
$$\frac{du}{dt} + wu = S(n(S) + w), \quad t > 0, t \neq (n+l-1)T, t \neq nT.$$

Since $\lim_{S\to\infty} n(S) < -w$, it follows that the right-hand side of (3.2.1) is bounded from above and consequently there is C > 0 such that

$$D^+u + wu \le C$$
, $t > 0, t \ne (n+l-1)T, t \ne nT$.

One also sees that

$$u((n+l-1)T+) \le (1-\delta)u((n+l-1)T)$$

and

$$u(nT+) = u(nT) + \mu,$$

where $\delta = \min(\delta_1, \delta_2)$. It the follows from Lemma C.1.2 that

$$(3.2.2) \quad u(t) \le u(0+) \left[\prod_{0 < (n+l-1)T < t} (1-\delta) \right] e^{-wt} + C \int_0^t \left[\prod_{s \le (n+l-1)T < t} (1-\delta) \right] e^{-w(t-s)} ds + \sum_{0 < nT < t} \mu e^{-w(t-nT)}, \quad t > 0,$$

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(3.2.3)
$$u(t) \le u(0+)e^{-wt} + \frac{C(1-e^{-wt})}{w} + \mu \frac{e^{wT}}{e^{wT}-1}, \quad t > 0,$$

and since the limit of the right-hand side of (3.2.3) as $t \to \infty$ is $C/w + \mu e^{wT}/(e^{wT} - 1)$, it easily follows that u is bounded on $[0, \infty)$. We now describe some properties of the subsystem

(RS)
$$\begin{cases} I'(t) = -wI(t), & t \neq nT, (n+l-1)T; \\ \Delta I(t) = -\delta_2 I(t), & t = (n+l-1)T; \\ \Delta I(t) = \mu, & t = nT; \\ I(0+) = I_0, \end{cases}$$

which describes the dynamics of the susceptible pest eradication state. It will be seen that the system formed with the first three equations of (RS) has a periodic solution to which all solutions of (RS) tend as $t \to \infty$. We shall label this periodic solution with I_w^* , rather than, say, with $I_{w,\delta_2,\mu}^*$, as systems of type (RS) occur throughout this section for different w's but always with the same δ_2 and μ so there is no danger of confusion. Lemma 1.3.3 then easily leads to the following conclusion.

Lemma 3.2.2. The system constructed with the first three equations in (RS) has a positive T-periodic solution I_w^* . With this notation, the following properties are satisfied.

- 1. $\lim_{t \to \infty} |I(t) I_w^*(t)| = 0 \text{ for all solutions } I(t) \text{ of } (RS) \text{ starting with strictly positive } I_0.$
- 2. $\sup_{t\geq 0} |I_{w_1}^*(t) I_{w_2}^*(t)| \leq f_2(w_1, w_2; T, \mu, \delta_2), \text{ with } \lim_{w_2 \to w_1} f_2(w_1, w_2; T, \mu, \delta_2) = 0.$

3.2.3 The extinction of the susceptible pest population

In this subsection, we study the situation in which the susceptible pest population tends to extinction. This situation occurs if a certain condition on the total action of the nonlinear force of infection in a period near the infective pest-only equilibrium is satisfied.

Theorem 3.2.1. The susceptible pest-eradication solution $(I_w^*(t), 0)$ is globally asymptotically stable provided that

(3.2.4)
$$\int_0^T g(I_w^*(s))ds > rT + \ln(1 - \delta_1)$$

Proof. In order to justify the use of (3.2.4), we first study the local stability of $(I_w^*(t), 0)$ by using small amplitude perturbation methods.

Let us denote

(3.2.5)
$$\begin{cases} I(t) = v(t) + I_w^*(t), \\ S(t) = u(t) \end{cases}$$

in which u and v are understood to be small amplitude perturbations. Substituting (3.2.5) into the first two equations of (IPM), one obtains

(3.2.6)
$$\begin{cases} v'(t) = g(v(t) + I_w^*(t))u(t) - wv(t) \\ u'(t) = u(t)n(u(t)) - g(v(t) + I_w^*(t))u(t). \end{cases}$$

The corresponding linearization of (3.2.6) at (0,0) is

(3.2.7)
$$\begin{cases} v'(t) = g(I_w^*(t))u(t) - wv(t) \\ u'(t) = ru(t) - g(I_w^*(t))u(t) \end{cases}$$

and so a fundamental matrix of (3.2.7) is

(3.2.8)
$$\Phi_L(t) = \begin{pmatrix} e^{-wt} & \int_0^t e^{-w(t-s)} e^{\int_0^s (r-g(I_w^*(\tau)))d\tau} g(I_w^*(s))ds \\ 0 & e^{\int_0^t [r-g(I_w^*(s))]ds} \end{pmatrix}.$$

The linearization of the jump conditions at (n+l-1)T reads as

(3.2.9)
$$\begin{cases} \Delta v = -\delta_2 v(t), & t = (n+l-1)T; \\ \Delta u = -\delta_1 u(t), \end{cases}$$

while the linearization of the jump conditions at nT reads as

(3.2.10)
$$\begin{cases} \Delta v = 0, \quad t = nT; \\ \Delta u = 0. \end{cases}$$

Consequently, the local stability of the susceptible pest-eradication solution $(I_w^*(t), 0)$ can be analyzed by studying the eigenvalues of the monodromy matrix

$$M_1 = \begin{pmatrix} 1 - \delta_1 & 0\\ 0 & 1 - \delta_2 \end{pmatrix} \Phi_L(T)$$

As the eigenvalues of M_1 are

$$\lambda_1 = (1 - \delta_2)e^{-wT}, \quad \lambda_2 = (1 - \delta_1)e^{\int_0^T [r - g(I_w^*(s))]ds}$$

and $0 < \lambda_1 < 1$, it follows by Lemma C.2.1 that $(I_w^*(t), 0)$ is locally asymptotically stable provided that

$$(1-\delta_1)e^{\int_0^T [r-g(I_w^*(s))]ds} < 1$$

that is, condition (3.2.4) holds.

We now prove that $(I_w^*(t), 0)$ is actually globally asymptotically stable provided that condition (3.2.4) is satisfied. We first show that $S(t) \to 0$ as $t \to \infty$. To this purpose, choose $\varepsilon_1 > 0$ such that

(3.2.11)
$$\int_{0}^{T} g(I_{w}^{*}(s) - \varepsilon_{1}) ds > rT + \ln(1 - \delta_{1})$$

(note that such a choice is feasible, as $|g(I_w^*(s) - \varepsilon_1) - g(I_w^*(s))| \le L\varepsilon_1$). Let us also denote

$$\xi = (1 - \delta_1)e^{rT - \int_0^T g(I_w^*(s) - \varepsilon_1)ds}$$

and observe that $0 < \xi < 1$.

It is seen that

$$I'(t) = g(I(t))S(t) - wI(t) \ge -wI(t)$$

and so, by Lemma C.1.1, $I(t) \geq \tilde{I}(t)$, where $\tilde{I}(t)$ is the solution of (RS) with the same initial data at 0+ as *I*. As any such solution becomes close to $I_w^*(t)$ as $t \to \infty$, by Lemma 3.2.2, there is some $T_1 > 0$ such that $I(t) \geq I_w^*(t) - \varepsilon_1$ for $t \geq T_1$. For the sake of simplicity, we suppose that $I(t) > I_w^*(t) - \varepsilon_1$ for all t > 0.

One then obtains that

$$S'(t) = S(t)n(S(t)) - S(t)g(I(t))$$

$$\leq S(t) [n(S(t)) - g(I_w^*(t) - \varepsilon_1)], \quad t \neq (n+l-1)T$$

and it consequently follows that

$$\frac{S'(t)}{S(t)} \le n(S(t)) - g(I_w^*(t) - \varepsilon_1), \quad t \ne (n+l-1)T.$$

By integrating the above inequality on ((n+l-1)T, (n+l)T], one obtains

$$\ln S((n+l)T) - \ln S((n+l-1)T+) \le \int_{(n+l-1)T}^{(n+l)T} \left[n(S(s)) - g(I_w^*(s) - \varepsilon_1) \right] ds$$

and so

$$\ln S((n+l)T) - \ln S((n+l-1)T) - \ln(1-\delta_1) \le \int_{(n+l-1)T}^{(n+l)T} \left[r - g(I_w^*(s) - \varepsilon_1)\right] ds.$$

It then follows that

$$S((n+l)T) \le S((n+l-1)T)\xi$$

and consequently

$$S((n+l)T) \le S(lT)\xi^n$$

which implies that $S((n+l)T) \to 0$ as $n \to \infty$. Also,

$$\frac{S'(t)}{S(t)} = n(S(t)) - g(I(t)) \le r$$

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$$S(t) \le S((n+l-1)T+)e^{r(t-(n+l-1)T)}, \quad t \in ((n+l-1)T, (n+l)T]$$

which implies that

$$S(t) \le (1 - \delta_1)S((n + l - 1)T)e^{rT}, \quad t \in ((n + l - 1)T, (n + l)T]$$

and consequently $S(t) \to 0$ as $t \to \infty$. We now prove that $I(t) \to I_w^*(t)$ as $t \to \infty$. To this purpose, let $0 < \varepsilon_2 < w/L$. Since $S(t) \to 0$ as $t \to \infty$, there is $T_2 > 0$ such that $S(t) < \varepsilon_2$ for $t \ge T_2$. For the sake of simplicity, we suppose that $S(t) < \varepsilon_2$ for all t > 0. Since

$$I'(t) = g(I(t))S(t) - wI(t), \quad t \neq (n+l-1)T, t \neq nT$$

and $g(x) \leq Lx$ for $x \geq 0$, it follows that

$$-wI(t) \le I'(t) \le -(w - \varepsilon_2 L)I(t) \quad t \ne (n+l-1)T, t \ne nT.$$

By Lemma C.1.1, it follows that

$$\tilde{I}_1(t) \le I(t) \le \tilde{I}_2(t),$$

where \tilde{I}_1 and \tilde{I}_2 are the solution of (RS) with the same initial data at 0+ as I, respectively the solution of (RS) with w changed into $w - \varepsilon_2 L$ and the same initial data. As these solutions become close to $I_w^*(t)$, respectively to $I_{w-\varepsilon_2 L}^*(t)$, it follows that, for t large enough,

$$I_w^*(t) - \varepsilon_2 < I(t) < I_{w-\varepsilon_2L}^*(t) + \varepsilon_2$$

and the conclusion now follows from Lemma 3.2.2.

Note that from (3.2.4) it follows that the susceptible pest eradication solution is globally asymptotically stable whenever $\delta_1 > 1 - e^{-rT}$, that is, the global asymptotic stability of this solution can be achieved by controlling δ_1 alone, which is a natural result (repeatedly removing enough many susceptible individuals will make the susceptible pest eradication solution globally asymptotically stable). The same result can be achieved provided that T is small enough, but depending on the value of δ_1 , that is, for $T < (1/r) \ln(1/(1-\delta_1))$.

It is noted that $\lim_{\mu\to\infty} \int_0^T g(I_w^*(s))ds = +\infty$ for large classes of functions g, so the impulsive control is also successful provided that μ is large enough. The impulsive control is then, theoretically speaking, always successful, provided that it is applied often enough (T is small), enough many susceptible pests die due to pesticide spraying (δ_1 is large) or if enough many infective pests are released periodically (μ is large). However, in practical contexts, μ cannot be arbitrarily large, and T can be limited by other coordinates of human activity, as not enough active time can be sometimes dedicated to pesticide spraying alone. Still, as noted in Section 3.1, the purpose of the IPM is actually to drive the size of the susceptible pest population below the EIL or the AIL (the infective pests do not count here, as they are assumed not to damage crops), rather than to eradicate the pests completely, so the controls may be successful even if (3.2.4) is not satisfied, provided that the size of the susceptible pest population stabilizes under the EIL (or AIL).

It is perhaps also worth noting that if $g(x) = \beta x$ for $x \ge 0$, then (3.2.4) reduces to

(3.2.12)
$$\mu > \frac{w \left(rT + \ln(1 - \delta_1) \right) \left(1 - e^{-wT} (1 - \delta_2) \right)}{\beta \left(1 - \delta_2 e^{-wT} - e^{-wT} (1 - \delta_2) \right)}.$$

Combined with a similar rewrite of (3.2.13) in the next subsection, this establishes the existence of a threshold parameter for the stability of the system, denoted μ_c and equal to the right-hand side of (3.2.12). That is, if $\mu > \mu_c$ then the susceptible pest-eradication solution is globally asymptotically stable, while if $\mu < \mu_c$, then susceptible pest-eradication solution loses its stability and (IPM) becomes uniformly persistent.

Similarly, for $g(x) = \beta x$, (3.2.4) also reduces to

$$\frac{1}{T}\int_0^T I^*(s)ds > \frac{r+(1/T)\ln(1-\delta_1)}{\beta}$$

By rewriting (3.2.13) in a similar manner, one obtains the existence of a second threshold parameter I_C , the so-called "epidemic threshold", defined as $I_C = \frac{r+(1/T)\ln(1-\delta_1)}{\beta}$. That is, if the average of I^* is greater than I_C , then the susceptible pest-eradication periodic solution is globally stable, while if the average of I^* is less than I_C , then the system (IPM) is uniformly persistent.

3.2.4 The permanence of the system

In this subsection, we study the permanence of the system and prove that the system (IPM) is permanent provided that the reverse of (3.2.4) holds.

Theorem 3.2.2. The system (IPM) is permanent provided that

(3.2.13)
$$\int_0^T g(I_w^*(s)) ds < rT + \ln(1 - \delta_1).$$

Proof. It has already been shown that, given $\varepsilon > 0$, one may find $T_{\varepsilon} > 0$ such that $I(t) > I_w^*(t) - \varepsilon$ for all $t > T_{\varepsilon}$. Now, it is enough to choose $\varepsilon < \frac{\mu e^{-wT}(1-\delta_2)}{1-e^{-wT}(1-\delta_2)}$ and observe that in this situation one has

$$I(t) > \frac{\mu e^{-wT}(1-\delta_2)}{1-e^{-wT}(1-\delta_2)} - \varepsilon \text{ for all } t > T_{\varepsilon}.$$

For the sake of simplicity, let us suppose that the above estimation is satisfied for all t > 0.

Also, we know that I and S are bounded, by Lemma 3.2.1. It now remains to prove that $S(t) \ge m_1$ for some $m_1 > 0$ and t large enough.

First, let $m_3 > 0$ and $\varepsilon_1 > 0$ be small enough, so that

(3.2.14)
$$m_3 < \frac{w}{L}, \quad n(m_3)T + \ln(1-\delta_1) > \int_0^T g(I_{w-m_3L}^*(t) + \varepsilon_1)dt.$$

As a first step, we now show that one cannot have $S(t) < m_3$ for all t > 0.

We argue by contradiction. Suppose that $S(t) < m_3$ for all t > 0. Then

$$I'(t) = g(I(t))S(t) - wI(t) \le -(w - Lm_3)I(t), \quad t \ne (n + l - 1)T, t \ne nT.$$

By Lemma C.1.1, it follows that $I(t) \leq \tilde{I}_1(t)$, where $\tilde{I}_1(t)$ is the solution of (RS) with the same initial data at 0+ as I and w changed into $w - Lm_3$. As this solution becomes close to $I^*_{w-Lm_3}(t)$ as $t \to \infty$, it follows that there is $T_1 > 0$ such that $I(t) \leq I^*_{w-Lm_3} + \varepsilon_1$ for $t \geq T_1$.

Let n large enough, so that $(n+l-1)T > T_1$. One then gets

(3.2.15)
$$S'(t) \ge S(t) \left[n(m_3) - g(I_{w-m_3L}^*(t) + \varepsilon_1) \right], \quad t \ne (n+l-1)T, t \ne nT, t \ge T_1.$$

By integrating the above inequality on ((n+l-1)T, (n+l)T], one obtains

$$\ln S((n+l)T) - \ln S((n+l-1)T+) \ge n(m_3)T - \int_{(n+l-1)T}^{(n+l)T} g(I_{w-m_3L}^*(t) + \varepsilon_1)dt$$

and so

$$\ln S((n+l)T) - \ln S((n+l-1)T) - \ln(1-\delta_1) \ge n(m_3)T - \int_{(n+l-1)T}^{(n+l)T} g(I_{w-m_3L}^*(t) + \varepsilon_1) dt.$$

Let us denote

(3.2.16)
$$\eta = (1 - \delta_1) e^{n(m_3)T - \int_{(n+l-1)T}^{(n+l)T} g(I_{w-m_3L}^*(t) + \varepsilon_1) dt}$$

and observe that, by (3.2.14), $\eta > 1$. It then follows that

$$S((n+l)T) \ge S((n+l-1)T)\eta$$

and consequently

$$(3.2.17) S((n+l)T) \ge S(lT)\eta^n$$

which implies that $S((n+l)T) \to \infty$ as $n \to \infty$, which contradicts the boundedness of S. It is then seen that one cannot have $S(t) < m_3$ for all t > 0 and consequently there is $t_1 > 0$ such that $S(t_1) \ge m_3$.

If $S(t_1) \ge m_3$ for all $t \ge t_1$, then (IPM) is persistent and there is nothing left to prove. Otherwise, $S(t) < m_3$ for some $t \ge t_1$. Let us denote

$$t^* = \inf \{t > t_1; S(t) < m_3\}.$$

To continue our investigation, we need to distinguish whether or not $t^* = (n+l-1)T$ for some n, so that we could discuss the value of $S(t^*)$. Note that the discussion has to be made in terms of whether or not t = (n+l-1)T for some n and not in terms of whether or not t = nT for some n, as the jumps of S occur only at t = (n+l-1)T.

Case A, $t^* = (n_1 + l - 1)T$ for some $n_1 \in \mathbb{N}^*$.

In this situation, $S(t) \ge m_3$ for $t \in [t_1, t^*]$ and therefore

$$S(t^*+) = (1 - \delta_1)S(t^*) \ge (1 - \delta_1)m_3.$$

Also,

$$S(t^*+) \le m_3.$$

Choose $n_2, n_3 \in \mathbb{N}^*$ so that

(3.2.18)
$$(n_2 - 1)T > \frac{1}{-w + Lm_3} \ln \frac{\varepsilon_1}{M + \frac{\mu}{1 - e^{-(w - Lm_3)}}}$$

(3.2.19) $(1-\delta_1)^{n_2} e^{n_2 \eta_1 T} \eta^{n_3} > 1,$

where η is given by (3.2.16) and η_1 is defined as

$$\eta_1 = n(m_3) - LM < 0.$$

Note that n_2 , n_3 do not depend on t^* .

We now show that there should be $t_2 \in (t^*, t^* + n_2T + n_3T]$ such that $S(t_2) > m_3$. Suppose that this is not the case. Then $I(t) \leq \tilde{I}(t)$ on $(t^*, t^* + n_2T + n_3T]$, where \tilde{I} is the solution of (RS) with the same initial data at t^* as I and w changed into $w - Lm_3$.

It is seen that

(3.2.20)

$$\tilde{I}(t) = \begin{cases} e^{-(w-m_3L)(t-n_1T)} \left[\tilde{I}(n_1T+) - \frac{\mu}{1-(1-\delta_2)e^{-(w-m_3L)T}} \right] & (1-\delta_2)^{n-(n_1+1)} + I_{w-m_3L}^*(t), \\ & t \in ((n-1)T, (n+l-1)T]; \\ e^{-(w-m_3L)(t-n_1T)} \left[\tilde{I}(n_1T+) - \frac{\mu}{1-(1-\delta_2)e^{-(w-m_3L)T}} \right] & (1-\delta_2)^{n-n_1} + I_{w-m_3L}^*(t), \\ & t \in ((n+l-1)T, nT], \end{cases}$$

for $n \ge n_1 + 1$. By the above relations, it follows that

(3.2.21)
$$\left| \tilde{I}(t) - I_{w-m_3L}^*(t) \right| < e^{-(w-m_3L)(t-n_1T)} \left| \tilde{I}(n_1T+) - \frac{\mu}{1 - (1-\delta_2)e^{-(w-m_3L)T}} \right|$$

for t > (n+l-1)T, $n \ge n_1 + 1$.

Also, since

$$\tilde{I}(n_1T+) = e^{-(w-m_3L)(n_1T-t^*)}\tilde{I}(t^*+) + \mu_3$$

one has that

(3.2.22)
$$\begin{aligned} \left| \tilde{I}(n_1T+) - \frac{\mu}{1 - (1 - \delta_2)e^{-(w - m_3L)T}} \right| \\ &= \left| e^{-(w - m_3L)(1 - l)T} I(t^*+) + \mu - \frac{\mu}{1 - (1 - \delta_2)e^{-(w - m_3L)T}} \right| \\ &\leq M + \frac{\mu}{1 - e^{-(w - m_3L)T}}, \end{aligned}$$

for t > (n+l-1)T and $n \ge n_1 + 1$.

For $t \ge n_1 T + (n_2 - 1)T$, it follows that

(3.2.23)
$$\left| \tilde{I}(t) - I_{w-m_3L}^*(t) \right| \le e^{-(w-m_3L)(n_2-1)T} \left(M + \frac{\mu}{1 - e^{-(w-m_3L)T}} \right),$$

by (3.2.18), (3.2.21) and (3.2.22). By (3.2.23), it is then seen that

$$I(t) \le I_{w-m_3L}^*(t) + \varepsilon_1$$
, for $n_1T + (n_2 - 1)T \le t \le t^* + n_2T + n_3T$

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and therefore (3.2.15) holds for $n_1T + (n_2 - 1)T \le t \le t^* + n_2T + n_3T$. As a result, by the same argument used for the derivation of (3.2.17), we deduce that

(3.2.24)
$$S(t^* + n_2T + n_3T) \ge S(t^* + n_2T)\eta^{n_3},$$

where η is given by (3.2.16).

Since $g(I(t)) \leq LI(t) \leq LM$, one obtains that

(3.2.25)
$$\begin{cases} S'(t) \ge S(t) [n(m_3) - LM], & t \ne (n+l-1)T; \\ S(t+) = (1-\delta_1)S(t), & t = (n+l-1)T, \end{cases}$$

for $t \in [t^*, t^* + n_2 T]$. Integrating (3.2.25) over $(t^*, t^* + n_2 T]$, one obtains that

(3.2.26)
$$S(t^* + n_2 T) \ge m_3 (1 - \delta_1)^{n_2} e^{n_2 \eta_1 T}$$

By (3.2.24) and (3.2.26), one may deduce that

$$S(t^* + n_2T + n_3T) \ge m_3(1 - \delta_1)^{n_2} e^{n_2\eta_1T} \eta^{n_3}$$

By (3.2.19), one obtains that $S(t^* + n_2T + n_3T) > m_3$, which is a contradiction, as it was supposed that $S(t) \leq m_3$ on $(t^*, t^* + n_2T + n_3T]$. It then follows that there is $t_1 \in (t^*, t^* + n_2T + n_3T]$ for which $S(t_1) > m_3$. Let us denote $\tilde{t}_1^* = \inf_{t > t^*} \{S(t) > m_3\}$. Obviously, $\tilde{t}_1^* \leq t^* + n_2T + n_3T$. Also, $S(t) \leq m_3$ for $t \in (t^*, \tilde{t}_1^*)$, while $S(\tilde{t}_1^*) \geq m_3$.

As in the derivation of (3.2.26), one may find that

$$S(t) \ge m_3(1-\delta_1)^{n_2+n_3} e^{(n_2+n_3)\eta_1 T}, \quad t \in (t^*, \tilde{t}_1^*)$$

as $\tilde{t}_1^* \leq (n_2 + n_3)T$. Consequently, if we denote,

$$m'_{3} = m_{3}(1 - \delta_{1})^{n_{2} + n_{3}} e^{(n_{2} + n_{3})\eta_{1}T}$$

we see that $S(t) \ge m'_3$ for $t \in (t^*, \tilde{t}_1^*)$ and so m'_3 may be taken as a persistency constant for S on (t^*, \tilde{t}_1^*) . As $S(\tilde{t}_1^*) \ge m_3$, our argument may be continued in the same manner.

Case B $t^* \neq (n+l-1)T$ for all $n \in \mathbb{N}^*$.

In this situation, S is continuous at t^* and $S(t) \ge m_3$ for $t \in [t_1, t^*]$, while $S(t^*) = m_3$, as t^* is not a jump point for S. Suppose that $t^* \in ((n_2 + l - 1)T, (n_2 + l)T)$ for some $n_2 \in \mathbb{N}^*$.

If $S(t) \leq m_3$ on the whole interval $(t^*, (n_2 + l)T]$, then one may continue exactly as in Case A; we omit the details. If there is $t_0 \in (t^*, (n_2 + l)T)$ such that $S(t) > m_3$, then let us denote $\tilde{t}_2^* = \inf_{t>t^*} \{S(t) > m_3\}$. Obviously, $\tilde{t}_2^* \in (t^*, (n_2 + l)T], S(t) \le m_3$ for $t \in (t^*, \tilde{t}_2^*)$ and $S(\tilde{t}_2^*) = m_3$ by continuity. We now study the persistency constant of S on (t^*, \tilde{t}_2^*) .

Since $S(t) \leq m_3$ on (t^*, \tilde{t}_2^*) , it is seen that

(3.2.27)
$$\begin{cases} S'(t) \ge S(t) [n(m_3) - LM], & t \ne (n+l-1)T; \\ S(t+) = (1-\delta_1)S(t), & t = (n+l-1)T, \end{cases}$$

for $t \in (t^*, \tilde{t}_2^*)$. Integrating (3.2.27), we obtain that

$$S(t) \ge S(t^*)e^{\eta_1(t-t^*)} \ge m_3 e^{\eta_1 T}$$

and so, if we denote

$$m'_4 = m_3 e^{\eta_1 T}$$

we see that $S(t) \ge m'_4$ for $t \in (t^*, \tilde{t}^*_2)$ and so m'_4 may be taken as a persistency constant for S on (t^*, \tilde{t}^*_2) As $S(\tilde{t}^*_2) = m_3$, our argument may be continued in the same manner. \Box

We now give an approximative interpretation of (3.2.13). Let us suppose that (I(t), S(t))approaches the trivial solution $(I^*, 0)$. Then, as the incidence rate of the infection is of the form g(I)S, the integral $\int_0^T g(I^*(t))dt$ approximates the (per-susceptible) loss of susceptible pests in a period due to their movement in the infective class, while since the production of newborn susceptible pests is given by Sn(S) and n(0) = r, rT approximates the total (per-susceptible) gain of susceptible pests in a period. A correction term $-\ln(1-\delta_1)$ should also be added to account for the loss of susceptible pests due to pesticide spraying. If (3.2.13) is satisfied, then this inequality prevents (I, S) from being arbitrarily close to $(I_w^*(t), 0)$, as there is a net gain of susceptibles near $(I_w^*(t), 0)$, while the opposite of (3.2.13) makes $(I_w^*(t), 0)$ globally asymptotically stable, since there is a net loss of susceptibles near $(I_w^*(t), 0)$.

3.3 The bifurcation of nontrivial periodic solutions

3.3.1 Related results

We now attempt to treat the situation in which

$$\int_0^T g(I_w^*(s)) ds = rT + \ln(1 - \delta_1),$$

not covered by our previous analysis, and prove a bifurcation result for this situation. In this regard, an unified approach to deal with the existence of nontrivial periodic solutions for a large class of two dimensional systems of differential equations which are impulsively perturbed in a periodic fashion by means of possibly nonlinear controls has been laid out in Lakmeche and Arino [74]. Their method consists in reformulating the problem as a fixed point problem for an operator defined *ad-hoc* which incorporates the effects of the impulsive perturbations, and solve the latter using the method of bifurcation theory; specifically, a certain projection method is employed. They also apply their general method to the study of the existence of nontrivial periodic solutions for a concrete problem arising from the chemoterapeutic treatment of tumors. Their concrete model contains nonlinearities of logistic type and linear impulses and has been originally introduced by Panetta in [108].

Consequently, this section employs the method introduced in [74] together with some of the notations therein, although our model is structurally different from Panetta's, in the sense that it is not a competitive model, like the one in [108] (it is actually neither competitive nor cooperative). Notably, we obtain the bifurcation of nontrivial periodic solutions for general nontrivial infection rates and employ two distinct types of impulsive controls, corresponding to the use of a biological and a chemical control, respectively. See also Lakmeche and Arino [75], where the bifurcation of nontrivial periodic solutions for a Kolmogorov-like system arising from heterogeneous tumor therapy by several drugs with instantaneous effects administered one at a time is studied by the same method. The approach devised by Lakmeche and Arino is also employed, among others, by Lu, Chi and Chen in [92] for a predator-pest model subject to pulsed use of insecticides and by the same authors in [93] for a SIR epidemic model with horizontal and vertical transmission which is subject to pulse vaccination.

The remaining part of this Section is organized as follows. In Subsection 3.3.2, we introduce a few definitions and notations and reformulate our problem as a fixed point problem. In Subsection 3.3.3, we study the onset of nontrivial periodic solutions by means of bifurcation theory. It is to be noted that some more technical computations necessary in the above are given in the Appendix D. This Section is based on the results obtained in Georgescu et al. [32].

3.3.2 Definition and notations. The fixed point problem

It has been shown in the previous section that the susceptible pest-eradication periodic solution $(I^*, 0)$ is globally asymptotically stable provided that

$$\int_0^T g(I^*(t))dt > rT + \ln(1 - \delta_1),$$

while if the opposite inequality is satisfied, then the susceptible pest-eradication solution, called also in the following the trivial periodic solution, loses its stability and the system (IPM) becomes uniformly persistent. In the following, we shall mainly study this loss of stability and prove that it is due to the onset of nontrivial periodic solutions obtained via a supercritical bifurcation.

We shall denote by $\Phi(t; X_0)$ the solution of the (unperturbed) system formed with the first two equations in (IPM) for the initial data $X_0 = (x_0^1, x_0^2)$; also, $\Phi = (\Phi_1, \Phi_2)$. We define $I_1, I_2 : \mathbb{R}^2 \to \mathbb{R}^2$ by

$$I_1(x_1, x_2) = ((1 - \delta_2)x_1, (1 - \delta_1)x_2), \quad I_2(x_1, x_2) = (x_1 + \mu, x_2)$$

and $F_1, F_2 : \mathbb{R}^2 \to \mathbb{R}$ by

$$F_1(x_1, x_2) = g(x_1)x_2 - wx_1, \quad F_2(x_1, x_2) = x_2n(x_2) - g(x_1)x_2.$$

also, $F : \mathbb{R}^2 \to \mathbb{R}^2$,

$$F(x_1, x_2) = (F_1(x_1, x_2), F_2(x_1, x_2))$$

First, we reduce the problem of finding a periodic solution of (IPM) to a fixed point problem. To this purpose, let us define $\Psi : [0, \infty) \times \mathbb{R}^2 \to \mathbb{R}^2$ by

$$\Psi(T, \mathbf{X}_0) = I_2(\Phi((1-l)T; I_1(\Phi(lT; \mathbf{X}_0))));$$

also

$$\Psi(T, X_0) = (\Psi_1(T; X_0), \Psi_2(T; X_0)).$$

Then X is a periodic solution of period T for (IPM) if and only if its initial data $X(0) = X_0$ is a fixed point for Ψ . Consequently, to study the existence of nontrivial periodic solutions for (IPM), we need to study the existence of nontrivial fixed points of Ψ .

First, we note that

$$D_X \Psi(T, X) = D_X \Phi((1-l)T; I_1(\Phi(lT; X))) \begin{pmatrix} 1 - \delta_2 & 0 \\ 0 & 1 - \delta_1 \end{pmatrix} D_X \Phi(lT; X).$$

Let us denote $X_0 = (x_0, 0)$ the starting point for the trivial periodic solution $(I^*, 0)$, where $x_0 = I^*(0+), I^*(0+)$ being given by

(3.3.1)
$$I^*(0+) = \frac{\mu}{1 - e^{-wT}(1 - \delta_2)}$$

We are interested in the bifurcation of nontrivial periodic solutions near $(I^*, 0)$. To this purpose, we need to find $D_X \Phi(t; X_0)$, which can be computed by (formally) deriving the first two equations in (IPM) (see Appendix D). One then obtains that

$$D_X \Psi(T, X_0) = \begin{pmatrix} d_{11} & d_{12} \\ 0 & d_{22} \end{pmatrix}$$

with

$$\begin{cases} d_{11} = (1 - \delta_2)e^{-wT}, \quad d_{11} \in (0, 1); \\ d_{12} = e^{-wT} \left[(1 - \delta_2) \int_0^{lT} g(I^*(s))e^{(r+w)s - \int_0^s g(I^*(\tau))d\tau} ds \right] \\ + (1 - \delta_1) \int_{lT}^T g(I^*(s))e^{(r+w)s - \int_0^s g(I^*(\tau))d\tau} ds \right]; \\ d_{22} = (1 - \delta_1)e^{rT - \int_0^T g(I^*(s))ds}, \quad d_{22} > 0. \end{cases}$$

It is known that $(I^*, 0)$, the trivial periodic solution starting from X_0 , is exponentially stable if and only if the spectral radius $\rho(D_X\Psi(T, X_0))$ is less than 1 (see Iooss [58]). From the above, it follows that the trivial periodic solution $(I^*, 0)$ is exponentially stable if and only if

$$(1-\delta_1)e^{rT-\int_0^T g(I^*(s))ds} < 1.$$

3.3.3 The bifurcation of nontrivial periodic solutions

We now study the bifurcation of nontrivial periodic solutions near $(I^*, 0)$. To this purpose, let us denote

$$au = T + \overline{\tau}, \quad X = X_0 + \overline{X}.$$

To find a nontrivial periodic solution of period τ with initial data X, we need to solve the fixed point problem $X = \Psi(\tau, X)$, that is,

$$X_0 + \overline{X} = \Psi(T + \overline{\tau}, X_0 + \overline{X}).$$

Let us define

$$N(\overline{\tau},\overline{X}) = X_0 + \overline{X} - \Psi(T + \overline{\tau}, X_0 + \overline{X}); \quad N(\overline{\tau},\overline{X}) = (N_1(\overline{\tau},\overline{X}), N_2(\overline{\tau},\overline{X})).$$

Using the newly defined function N, it then remains to solve the equation $N(\overline{\tau}, \overline{X}) = 0$. Let us denote

$$D_X N(0, (0, 0)) = \begin{pmatrix} a'_0 & b'_0 \\ c'_0 & d'_0 \end{pmatrix}.$$

Since

$$D_X N(0, (0, 0)) = I_2 - D_X \Psi(T, X_0),$$

it follows that

$$a'_0 = 1 - d_{11}, \quad b'_0 = -d_{12}, \quad c'_0 = -d_{21}, \quad d'_0 = 1 - d_{22}$$

and consequently

(3.3.2)
$$a'_{0} = 1 - (1 - \delta_{2})e^{-wT}$$

(3.3.3)
$$b'_{0} = -e^{-wT} \left[(1 - \delta_{2}) \int_{0}^{lT} g(I^{*}(s))e^{(r+w)s - \int_{0}^{s} g(I^{*}(\tau))d\tau} ds + (1 - \delta_{1}) \int_{lT}^{T} g(I^{*}(s))e^{(r+w)s - \int_{0}^{s} g(I^{*}(\tau))d\tau} ds \right];$$

(3.3.4)
$$c'_{t} = 0;$$

(3.3.4) $c'_0 = 0;$ (3.3.5) $d'_0 = 1 - (1 - \delta_1) e^{rT - \int_0^T g(I^*(s)) ds}.$

A necessary condition for the bifurcation of nontrivial periodic solutions near $(I^*, 0)$ is

 $\det \left[D_X N(0, (0, 0)) \right] = 0$

and since $D_X N(0, (0, 0))$ is upper triangular and $a'_0 = 1 - (1 - \delta_2)e^{-wT} \neq 0$, it consequently follows that $d'_0 = 0$, that is,

(3.3.6)
$$(1 - \delta_1)e^{rT - \int_0^T g(I^*(s))ds} = 1.$$

It is seen that

 $\dim(\text{Ker}\,[D_X N(0,(0,0))]) = 1,$

and a basis in Ker $[D_X N(0, (0, 0))]$ is $(-\frac{b'_0}{a'_0}, 1)$. Then the equation $N(\overline{\tau}, \overline{X}) = 0$ is equivalent to

$$\begin{cases} N_1(\overline{\tau}, \alpha Y_0 + zE_0) = 0;\\ N_2(\overline{\tau}, \alpha Y_0 + zE_0) = 0, \end{cases}$$

where

$$E_0 = (1,0), \quad Y_0 = (-\frac{b'_0}{a'_0},1)$$

and $\overline{X} = \alpha Y_0 + zE_0$ represents the direct sum decomposition of \overline{X} using the projections onto Ker $[D_X N(0, (0, 0))]$ and Im $[D_X N(0, (0, 0))]$. See Chow and Hale [18, Section 2.4] for details.

Let us denote

(3.3.7)
$$f_1(\overline{\tau}, \alpha, z) = N_1(\overline{\tau}, \alpha Y_0 + zE_0);$$

(3.3.8)
$$f_2(\overline{\tau}, \alpha, z) = N_2(\overline{\tau}, \alpha Y_0 + zE_0).$$

First, we see that

$$\frac{\partial f_1}{\partial z}(0,0,0) = \frac{\partial N_1}{\partial x_1}(0,(0,0)) = a'_0 \neq 0.$$

By the implicit function theorem, one may locally solve the equation $f_1(\overline{\tau}, \alpha, z) = 0$ near (0, 0, 0) with respect to z as a function of $\overline{\tau}$ and α and find $z = z(\overline{\tau}, \alpha)$ such that z(0, 0) = 0 and

$$f_1(\overline{\tau}, \alpha, z(\overline{\tau}, \alpha)) = N_1(\overline{\tau}, \alpha Y_0 + z(\overline{\tau}, \alpha)E_0) = 0.$$

Moreover, the first order partial derivatives $\frac{\partial z}{\partial \alpha}(0,0)$ and $\frac{\partial z}{\partial \overline{\tau}}(0,0)$ are given by

$$\begin{cases} \frac{\partial z}{\partial \alpha}(0,0) = 0\\ \frac{\partial z}{\partial \overline{\tau}}(0,0) = -\frac{w}{a'_0}I^*(T) \end{cases}$$

(see Appendix D).

It now remains to study the solvability of the equation

(3.3.9)
$$f_2(\overline{\tau}, \alpha, z(\overline{\tau}, \alpha)) = 0,$$

that is,

$$(3.3.10) N_2(\overline{\tau}, \alpha Y_0 + z(\overline{\tau}, \alpha)E_0) = 0.$$

The equation (3.3.10) is called the determining equation and the number of its solutions equals the number of periodic solutions of (IPM). We now proceed to solving (3.3.10) (or, equivalently, (3.3.9)). Let us denote

(3.3.11)
$$f(\overline{\tau}, \alpha) = f_2(\overline{\tau}, \alpha, z(\overline{\tau}, \alpha)).$$

First, it is easy to see that

$$f(0,0) = N(0,(0,0)) = 0$$

To determine the number of solutions of (3.3.10), we first determine the Taylor expansion of f around (0,0). To this goal, we compute the first order partial derivatives $\frac{\partial f}{\partial \tau}(0,0)$ and $\frac{\partial f}{\partial \alpha}(0,0)$ and observe that

$$\frac{\partial f}{\partial \overline{\tau}}(0,0) = \frac{\partial f}{\partial \alpha}(0,0) = 0.$$

For the proof of this fact, see Appendix D.

It now becomes necessary to compute the second order partial derivatives $\frac{\partial^2 f}{\partial \alpha^2}(0,0)$, $\frac{\partial^2 f}{\partial \overline{\tau}^2}(0,0)$, $\frac{\partial^2 f}{\partial \overline{\tau}^2}(0,0)$. It is seen that

$$A = \frac{\partial^2 f}{\partial \alpha^2}(0,0) = 0$$
$$B = \frac{\partial^2 f}{\partial \alpha \partial \overline{\tau}}(0,0) < 0$$
$$C = \frac{\partial^2 f}{\partial \overline{\tau}^2}(0,0) > 0.$$

We need now find a nontrivial solution of the equation $f(\overline{\tau}, \alpha) = 0$ near (0, 0). By expanding f into a second order Taylor series, one obtains that

$$f(\overline{\tau},\alpha) = B\alpha\overline{\tau} + C\frac{\alpha^2}{2} + o(\overline{\tau},\alpha)(\overline{\tau}^2 + \alpha^2).$$

By denoting $\overline{\tau} = k\alpha$ $(k = k(\alpha))$, it is seen that

$$Bk + C\frac{k^{2}}{2} + o(\alpha, k\alpha)(1 + k^{2}) = 0,$$

equation which is solvable with respect to k as a function of α , since B < 0 and C > 0. Moreover, $k \approx -\frac{2B}{C}$, that is, k is positive.

From the above, one sees that there is a supercritical bifurcation of a nontrivial periodic solution near a period T which satisfies the sufficient condition for bifurcation given in (3.3.6). Note that, as it appears via a supercritical bifurcation, the nontrivial periodic solution is stable. More precisely, one obtains the following result, in which X_0 , Y_0 , E_0 , $z, \overline{\tau}$ are as indicated above.

Theorem 3.3.1. Suppose that the impulsive period T satisfies condition (3.3.6). Then there is $\varepsilon > 0$ such that for all $0 < \alpha < \varepsilon$ there is a stable positive nontrivial periodic solution of (IPM) with period $T + \overline{\tau}(\alpha)$ which starts in $X_0 + \alpha Y_0 + z(\overline{\tau}(\alpha), \alpha)E_0$.

3.3.4 Conclusions

Let us briefly comment upon the threshold condition (3.3.6), which may be reformulated as

$$\int_0^T g(I^*(s))ds - \ln(1 - \delta_1) = rT.$$

Using the interpretation given in the previous section, the threshold condition represents just the fact that the total (per-susceptible) loss of susceptible pests in a period balances the total (per-susceptible) gain of newborn susceptible pests in a period. In this regard, it has been shown in Subsection 3.2.3 that $(I^*, 0)$ is globally asymptotically stable provided that

$$\int_0^T g(I^*(s))ds - \ln(1 - \delta_1) > rT,$$

while if the opposite inequality is satisfied, then $(I^*, 0)$ loses its stability and (IPM) becomes uniformly persistent.

In the case in which g is a linear force of infection, $g(I) = \beta I$, then the threshold condition can be reformulated as

$$\frac{1}{T} \int_0^T I^*(s) ds = \frac{r + (1/T) \ln(1 - \delta_1)}{\beta}.$$

It is then seen from the above and Theorem 3.3.1 that nontrivial periodic solutions (I, S) appear when the average of the susceptible pest-eradication periodic solution over a period reaches the epidemic threshold I_C . In concrete terms, a nontrivial periodic solution coresponds to the onset of a persistent susceptible pest population, while a nontrivial periodic solution with small amplitude, below the economic injury level, indicates that the pest management strategy remains successful. As mentioned above, if the average of I^* is greater than I_C , then the susceptible pest-eradication periodic solution is globally stable, while if the average of I^* is less than I_C , then the system (IPM) is uniformly persistent.

Let us also define, for a general g,

$$R_0^S = \frac{rT}{\int_0^T g(I^*(s))ds - \ln(1 - \delta_1)}$$

as being a "basic reproduction number"-like quantity with respect to the susceptible pest population. Note that this is a "mirror image" of what usually a basic reproduction number means, since the survival of the susceptible pest population is usually unquestioned, the main problem being whether or not the infection becomes endemic. In the usual situation, the alternative endings are, roughly, an infection-free state and an endemic state, in which the infective pest population persists, at a certain level, alongside the susceptible pest population.

Here, the situation is somewhat different. The long-term survival of the infective pest population is unquestionable, due to the pulsed supply of infectives at t = nT and what is at stake is the survival of the susceptible pest population, the alternative endings being a susceptible-free state and an endemic state.

With this notation, the threshold condition can simply be rewritten as $R_0^S = 1$. If $R_0^S < 1$, then the newborn susceptibles are not produced fast enough and the system tends to the susceptible pest-eradication periodic solution, while if $R_0^S > 1$, then the system becomes uniformly persistent, as seen in the previous section.

Appendix A

Stability results

A.1 Definitions and notations

Throughout this Appendix, we shall introduce a few notions and results regarding the stability of autonomous differential systems which will ultimately lead to the formulation of LaSalle invariance principle.

Let us consider the autonomous system

(AS)
$$x' = f(x),$$

where $f : G^* \to \mathbb{R}^n$ is locally Lipschitz continuous on the open set $G^* \subset \mathbb{R}^n$. Given $x_0 \in \mathbb{R}^n$, it is seen that the solution of (AS) with initial data x_0 at t = 0, denoted $\pi(\cdot; x_0)$, is uniquely determined on its maximal interval of existence $(\alpha, \omega), \alpha < 0 < \omega$.

The set $\gamma^+(x_0) = \{\pi(t; x_0); t \in [0, \omega)\}$ is then called the positive orbit of π , while the associated positive limit set of π (the ω -limit set $\omega(x_0)$) is defined as

$$\omega(x_0) = \{ p \in \mathbb{R}^n; \exists (t_n)_{n \ge 0} \subset [0, \omega) \text{ such that } t_n \to \omega \text{ and } \pi(t_n; x_0) \to p \text{ as } n \to \infty \}.$$

Similarly, the set $\gamma^{-}(x_0) = \{\pi(t; x_0); t \in (\alpha, 0]\}$ is called the negative orbit of π , while the associated negative limit set of π (the α -limit set $\alpha(x_0)$) is defined as

$$\alpha(x_0) = \left\{ p \in \mathbb{R}^n; \exists (t_n)_{n \ge 0} \subset (\alpha, 0] \text{ such that } t_n \to \alpha \text{ and } \pi(t_n; x_0) \to p \text{ as } n \to \infty \right\}.$$

A set $S \subset G^*$ is called positively (negatively) invariant if any positive (negative) orbit starting in S remains there for its whole interval of existence, that is, given $x_0 \in S$, it follows that $\pi(t; x_0) \in S$ for all $t \in [0, \omega)$ and $\pi(t; x_0) \in S$ for all $t \in (\alpha, 0]$, respectively. If S is both positively and negatively invariant, then it is called weakly invariant. If S, in addition to being weakly invariant, has the property that all trajectories $\pi(\cdot; x_0)$ starting in $x_0 \in S$ are defined on the whole \mathbb{R} , then it is called invariant. If a singleton $\{x\}$ is invariant (which implies that $\pi(t, x) = x$ for all $t \in \mathbb{R}$), then x is called an equilibrium point. A solution $\pi = \pi(\cdot, x_0)$ of (AS) is called positively (negatively) precompact with respect to G^* if it is bounded and does not have positive (negative) limit points on the boundary of G^* . If π is both positively and negatively precompact, then it is called precompact.

We now introduce the notion of a Lyapunov functional associated to an autonomous differential system. A function $V: G^* \to \mathbb{R}$ is called a Lyapunov functional for (AS) on $G \subset G^*$ if it is continuous and $V(x) \leq 0$ for all $x \in G$, where

$$\dot{V}(x) = \liminf_{t \to 0} \frac{V(\pi(t;x)) - V(x)}{t}$$

A.2 LaSalle invariance principle

We shall denote

$$E = \left\{ x \in \overline{G} \cap G^*; V = 0 \right\};$$

$$M^* = \text{The largest weakly invariant set in } E;$$

$$M = \text{The largest invariant set in } E.$$

With these notations, one may state the LaSalle invariance principle as follows.

Theorem A.2.1. Let V be a Lyapunov functional for (AS) on G and let $\pi(t; x_0)$ be a solution of (AS) with initial data x_0 which stays in G for $t \in [0, \omega)$. Then

$$\omega(x_0) \cap G^* \subset M^* \cap V^{-1}(c) \quad for \ some \ c \in \mathbb{R}.$$

If $\pi(\cdot; x_0)$ is positively precompact, then

$$\pi(t; x_0) \to M \cap V^{-1}(c) \text{ as } t \to \infty..$$

Corollary A.2.1. Under the hypotheses above, it follows that $\omega(x_0)$ is contained in the set $\left\{x \in \overline{G} \cap G^*; \dot{V}(x) = 0\right\}$. Also, if $\pi(\cdot; x_0)$ is positively precompact and $M \cap V^{-1}(c)$ consists of isolated points, then $\pi(t; x_0)$ approaches an equilibrium point for $t \to \infty$.

For related stability results, see also LaSalle [77].

Appendix B

Compound matrices

B.1 Definitions and notations

In this Appendix, we shall define a few notions regarding the theory of compound matrices and indicate their applications to the stability of periodic trajectories for systems of ordinary differential equations.

Let $C \in M_{m,n}(\mathbb{R})$ be a $m \times n$ real matrix. Given $1 \leq i_1 < i_2 < \ldots i_k \leq m$ and $1 \leq j_1 < j_2 \ldots < j_k \leq n$, we shall denote by $M_{i_1,i_2,\ldots,i_k}^{j_1,j_2,\ldots,j_k}$ the minor of C determined by rows i_1, i_2, \ldots, i_k and columns j_1, j_2, \ldots, j_k . The k-th multiplicative compound $C^{(k)}$ of $C, 1 \leq k \leq \min(m, n)$ is then the $\binom{m}{k} \times \binom{n}{k}$ matrix with entries $M_{i_1,i_2,\ldots,i_k}^{j_1,j_2,\ldots,j_k}$ considered in lexicographic order. The term "multiplicative compound" is used since it may be shown that, given $C_1 \in M_{m_1,n_1}(\mathbb{R})$ and $C_2 \in M_{n_1,n_2}(\mathbb{R})$, one has that

$$(C_1 C_2)^{(k)} = C_1^{(k)} C_2^{(k)}$$

The matrix $C^{[k]}$ is also sometimes called the k-th exterior power of C.

For m = n, the k-th additive compound of C, $1 \le k \le n$ is then the $\binom{n}{k} \times \binom{n}{k}$ matrix defined as

$$C^{[k]} = D\left[(I + hC)^{(k)} \right] \Big|_{h=0},$$

where D denotes (component-wise) derivation with respect to h. The term "additive compound" is used here since it may be shown that, given $C_1, C_2 \in M_{n,n}(\mathbb{R})$, one has that

$$(C_1 + C_2)^{[k]} = C_1^{[k]} + C_2^{[k]}$$

An explicit formula for computing the entries of $C^{[k]}$ is as follows. Let $1 \leq i_1 < i_2 < \ldots i_k \leq n$ and $1 \leq j_1 < j_2 \ldots < j_k \leq n$, corresponding to the entry $(C^{[k]})_{ij}$ (that is, (i_1, i_2, \ldots, i_k) is the *i*-th multiindex in the lexicographic ordering and $(j_1, j_2 \ldots, j_k)$ is the
j-th one, respectively). Let us denote $(i) = (i_1, i_2, \ldots, i_k)$ and $(j) = (j_1, j_2, \ldots, j_k)$. Then

$$\left(C^{[k]}\right)_{ij} = \begin{cases} c_{i_1j_1} + c_{i_2j_2} + \dots + c_{i_kj_k} & \text{if } (i) = (j) \\ (-1)^{k_1 + k_2} c_{i_{k_1}j_{k_2}} & \text{if exactly one entry } i_{k_1} \text{ in } (i) \text{ does not} \\ & \text{appear in } (j) \text{ and exactly one entry} \\ & j_{k_2} \text{ in } j \text{ does not appear in } (j) \\ 0 & \text{otherwise.} \end{cases}$$

For instance, if n = 3, k = 2 and $C = (c_{ij})_{1 \le i,j \le 3}$, then the second additive compound of C is given by the formula

$$C^{[2]} = \begin{pmatrix} c_{11} + c_{22} & c_{23} & -c_{13} \\ c_{32} & c_{11} + c_{33} & c_{12} \\ -c_{31} & c_{21} & c_{22} + c_{33} \end{pmatrix}.$$

B.2 Applications to stability theory

Let us now consider the autonomous differential system

(B.2.1)
$$x' = f(x), \quad f : \mathcal{D} \subset \mathbb{R}^n \to \mathbb{R}^n,$$

Of great interest in the study of orbital stability of periodic solutions is the following result of Muldowney [103, Theorem 4.2], which converts a somewhat nonstandard problem associated to an autonomous dynamical system (the orbital stability of a periodic solution) into a more standard one, but associated to a nonautonomous system.

Theorem B.2.1. A sufficient condition for a periodic trajectory $\gamma = \{p(t); 0 \le t \le T\}$ of (B.2.1) to be orbitally asymptotically stable is that the nonautonomous linear system

$$Z' = J^{[2]}_{(B.2.1)}(p(t))Z$$

be asymptotically stable.

Here, $J_{(B,2,1)}^{[2]}$ is the second additive compound of the Jacobian matrix of (B.2.1). For other notions or applications of k-th additive and multiplicative compound matrices of dimension n, see Muldowney [103].

Appendix C

Impulsive differential equations

C.1 Comparison results

In this Appendix, we shall list a few definitions and notations together with several auxiliary results relating to comparison methods and Floquet theory for impulsively perturbed systems of ordinary differential equations. Let us consider the following differential system on \mathbb{R}^N

$$(C.1.1) X' = \mathfrak{f}(t, X)$$

for a continuous function \mathfrak{f} which is locally Lipschitz in the second variable. Let $0 < \mathcal{L} < 1$ and let also \mathcal{V}_0 be the set of functions $V : \mathbb{R}_+ \times \mathbb{R}^N_+ \to \mathbb{R}_+$ which are locally Lipschitz in the second variable, continuous on $((n + \mathcal{L} - 1)T, nT] \times \mathbb{R}^N_+$ and on $(nT, (n + \mathcal{L})T] \times \mathbb{R}^N_+$ and for which the limits

$$\lim_{(t,y)\to((n+\mathcal{L}-1)T+,x)} V(t,y) = V((n+\mathcal{L}-1)T+,x) \quad \text{and} \quad \lim_{(t,y)\to(nT+,x)} V(t,y) = V(nT+,x)$$

exist and are finite for $x \in \mathbb{R}^N_+$ and $n \in \mathbb{N}^*$.

For $V \in \mathcal{V}_0$, we define the upper right Dini derivative of V with respect to the system (C.1.1) at $(t, x) \in ((n + \mathcal{L} - 1)T, nT) \times \mathbb{R}^N_+$ or $(nT, (n + \mathcal{L})T) \times \mathbb{R}^N_+$ by

$$D^{+}V(t,x) = \limsup_{h \downarrow 0} \frac{1}{h} \left[V(t+h, x+h\mathfrak{f}(t,x)) - V(t,x) \right].$$

We now indicate a comparison result for solutions of impulsive differential inequalities. We suppose that $h : \mathbb{R}_+ \times \mathbb{R}_+ \to \mathbb{R}$ satisfies the following hypotheses.

(H) h is continuous on $((n + \mathcal{L} - 1)T, nT] \times \mathbb{R}_+$ and on $(nT, (n + \mathcal{L})T] \times \mathbb{R}_+$ and the limits

$$\lim_{(t,y)\to((n+\mathcal{L}-1)T+,x)} h(t,y) = h((n+\mathcal{L}-1)T+,x), \text{ and } \lim_{(t,y)\to(nT+,x)} h(t,y) = h(nT+,x)$$

exist and are finite for $x \in \mathbb{R}_+$ and $n \in \mathbb{N}^*$.

Lemma C.1.1. ([8]) Let $V \in \mathcal{V}_0$ and assume that

(C.1.2)
$$\begin{cases} D^+V(t, X(t)) \le h(t, V(t, X(t))), & t \ne (n + \mathcal{L} - 1)T, nT; \\ V(t, X(t+)) \le \Psi_n^{(1)}(V(t, X(t))), & t = (n + \mathcal{L} - 1)T; \\ V(t, X(t+) \le \Psi_n^{(2)}(V(t, X(t))), & t = nT, \end{cases}$$

where $h : \mathbb{R}_+ \times \mathbb{R}_+ \to \mathbb{R}$ satisfies (H) and $\Psi_n^{(1)}, \Psi_n^{(2)} : \mathbb{R}_+ \to \mathbb{R}_+$ are nondecreasing for all $n \in \mathbb{N}^*$. Let R(t) be the maximal solution of the impulsive Cauchy problem

(C.1.3)
$$\begin{cases} u'(t) = h(t, u(t)), & t \neq (n + \mathcal{L} - 1)T, \ nT; \\ u(t+) = \Psi_n^{(1)}(u(t)), & t = (n + \mathcal{L} - 1)T; \\ u(t+) = \Psi_n^{(2)}(u(t)), & t = nT; \\ u(0+) = u_0 \end{cases}$$

defined on $[0,\infty)$. Then $V(0+,X_0) \leq u_0$ implies that $V(t,X(t)) \leq R(t)$ for all $t \geq 0$, where $X(t) = X(t,0,X_0)$ is an arbitrary solution of (C.1.1).

Proof. For $t \in [0, \mathcal{L}T]$, we have by the classical comparison theorem for ordinary differential equations that $V(t, X(t)) \leq R(t)$. Since $\Psi_1^{(1)}$ nondecreasing and $V(\mathcal{L}T, X(\mathcal{L}T)) \leq R(\mathcal{L}T)$, we obtain

$$V(\mathcal{L}T^+, X(\mathcal{L}T^+)) \le \Psi_1^{(1)}(V(\mathcal{L}T, X(\mathcal{L}T)))$$
$$\le \Psi_1^{(1)}(R(\mathcal{L}T)) = R(\mathcal{L}T^+).$$

For $t \in (\mathcal{L}T, T]$, it follows, using again the classical comparison theorem, that $V(t, X(t)) \leq R(t)$. Since $\Psi_1^{(2)}$ is nondecreasing and $V(T, X(T)) \leq R(T)$, we get

$$V(T^+, X(T^+)) \le \Psi_1^{(2)}(V(T, X(T)))$$
$$\le \Psi_1^{(2)}(R(T)) = R(T^+).$$

Thus, for $t \in [0, T]$, it follows $V(t, X(t)) \leq R(t)$. Repeating this argument, we finally arrive at the desired result. This completes the proof.

Note that under appropriate regularity conditions the Cauchy problem (C.1.3) has a unique solution and in that case R becomes the unique solution of (C.1.3). We now indicate a result which provides estimations for the solution of a system of differential inequalities. In this regard, let J be an interval in \mathbb{R} . Let us define

 $PC(J, \mathbb{R}) \doteq \{u : J \to \mathbb{R} : u \text{ is continuous at } t \in J, t \neq \tau_k, \text{ for some } (\tau_k)_{k \geq 1}, \text{ continuous}$ from the left at $t \in J$, and has discontinuities of the first kind at the points $\tau_k \in J, k \in \mathbb{N}\}$ and

$$PC^{1}(J,\mathbb{R}) \doteq \left\{ u \in PC(J,\mathbb{R}) : u \text{ is continuously differentiable at } t \in J, t \neq \tau_{k}; \\ u'(\tau_{k}^{+}) \text{ and } u'(\tau_{k}^{-}) \text{ exist}, k \in \mathbb{N} \right\}.$$

Under these circumstances, one may obtain the following boundedness result

Lemma C.1.2. ([8]) Let the function $u \in PC^1(\mathbb{R}_+, \mathbb{R})$ satisfy the inequalities

(C.1.4)
$$\begin{cases} \frac{du}{dt} \le (\ge)p(t)u(t) + f(t), & t \ne \tau_k, \ t > 0; \\ u(\tau_k +) \le (\ge)d_k u(\tau_k) + h_k, & k \ge 0; \\ u(0+) \le (\ge)u_0, \end{cases}$$

where $p, f \in PC(\mathbb{R}_+, \mathbb{R})$ and $d_k \geq 0$, h_k and u_0 are constants and $(\tau_k)_{k\geq 0}$ is a strictly increasing sequence of positive real numbers. Then, for t > 0,

$$u(t) \leq (\geq) u_0 \left(\prod_{0 < \tau_k < t} d_k\right) e^{\int_0^t p(s)ds} + \int_0^t \left(\prod_{0 \leq \tau_k < t} d_k\right) e^{\int_s^t p(\tau)d\tau} f(s)ds$$
$$+ \sum_{0 < \tau_k < t} \left(\prod_{\tau_k < \tau_j < t} d_j\right) e^{\int_{\tau_k}^t p(\tau)d\tau} h_k.$$

For other results on impulsive differential equations, see Bainov and Simeonov [8] or Lakhsmikantham et al [76].

C.2 Floquet theory

We now introduce a few basic results regarding the Floquet theory of impulsive systems of ordinary differential equations. Let us consider the system

(C.2.1)
$$\begin{aligned} X'(t) &= A(t)X(t), \quad t \neq \tau_k, \ t \in \mathbb{R}; \\ \Delta X &= B_k X, \qquad t = \tau_k, \ \tau_k < \tau_{k+1}, \ k \in \mathbb{Z}. \end{aligned}$$

under the following hypotheses.

(H1) $A(\cdot) \in PC(\mathbb{R}, M_n(\mathbb{R}))$ and there is T > 0 such that A(t+T) = A(t) for all $t \ge 0$.

(H2) $B_k \in M_n(\mathbb{R}), \det(I_n + B_k) \neq 0 \text{ for } k \in \mathbb{Z}.$

(H3) There is $q \in \mathbb{N}^*$ such that $B_{k+q} = B_k$, $\tau_{k+q} = \tau_k + T$ for $k \in \mathbb{Z}$.

Let $\Phi(t)$ be a fundamental matrix of (C.2.1). Then there is a unique nonsingular matrix $M \in M_n(\mathbb{R})$ such that $\Phi(t+T) = \Phi(t)M$ for all $t \in \mathbb{R}$, which is called the monodromy matrix of (C.2.1) corresponding to Φ . Actually, all monodromy matrices of (C.2.1) are similar and consequently they have the same eigenvalues $\lambda_1, \lambda_2, \ldots, \lambda_n$, which are called the Floquet multipliers of (C.2.1). Under these hypotheses, the following result holds.

Lemma C.2.1. ([8]) Suppose that conditions (H1)-(H3) hold. Then

- 1. The system (C.2.1) is stable if and only if all Floquet multipliers λ_k , $1 \le k \le n$ satisfy $|\lambda_k| \le 1$ and if $|\lambda_k| = 1$, then to λ_k there corresponds a simple elementary divisor.
- 2. The system (C.2.1) is asymptotically stable if and only if all Floquet multipliers $\lambda_k, 1 \leq k \leq n \text{ satisfy } |\lambda_k| < 1.$
- 3. The system (C.2.1) is unstable if there is a Floquet multiplier λ_k such that $|\lambda_k| > 1$.

Appendix D

Partial derivatives of Φ , z and f

D.1 The first order partial derivatives of Φ_1, Φ_2

By (formally) deriving

$$\frac{d}{dt}\left(\Phi(t;X_0)\right) = F(\Phi(t;X_0)),$$

one obtains

$$\frac{d}{dt}\left[D_X\Phi(t;X_0)\right] = D_XF(\Phi(t;X_0))D_X\Phi(t;X_0).$$

Also, it is clear that

$$\Phi(t; X_0) = (\Phi_1(t; X_0), 0).$$

We then deduce

$$\frac{d}{dt} \begin{pmatrix} \frac{\partial \Phi_1}{\partial x_1} & \frac{\partial \Phi_1}{\partial x_2} \\ \frac{\partial \Phi_2}{\partial x_1} & \frac{\partial \Phi_2}{\partial x_2} \end{pmatrix} (t; X_0) = \begin{pmatrix} -w & g(\Phi_1(t; X_0)) \\ 0 & r - g(\Phi_1(t; X_0)) \end{pmatrix} \begin{pmatrix} \frac{\partial \Phi_1}{\partial x_1} & \frac{\partial \Phi_1}{\partial x_2} \\ \frac{\partial \Phi_2}{\partial x_1} & \frac{\partial \Phi_2}{\partial x_2} \end{pmatrix} (t; X_0),$$

the initial condition being

(D.1.1)
$$D_X \Phi(0; X_0) = I_2$$

Here, I_2 is the identity matrix in $M_2(\mathbb{R})$. It follows that

$$\frac{d}{dt}\left(\frac{\partial\Phi_2}{\partial x_1}(t;X_0)\right) = \left(r - g(\Phi_1(t;X_0))\right)\frac{\partial\Phi_2}{\partial x_1}(t;X_0)$$

and then

$$\frac{\partial \Phi_2}{\partial x_1}(t;X_0) = e^{\int_0^t (r - g(\Phi_1(s;X_0)))ds} \frac{\partial \Phi_2}{\partial x_1}(0;X_0),$$

which implies, using (D.1.1), that

(D.1.2)
$$\frac{\partial \Phi_2}{\partial x_1}(t; X_0) = 0 \quad \text{for } t \ge 0.$$

One then gets

(D.1.3)
$$\begin{cases} \frac{d}{dt} \left(\frac{\partial \Phi_1}{\partial x_1}(t; X_0) \right) = -w \frac{\partial \Phi_1}{\partial x_1}(t; X_0) \\ \frac{d}{dt} \left(\frac{\partial \Phi_1}{\partial x_2}(t; X_0) \right) = -w \frac{\partial \Phi_1}{\partial x_2}(t; X_0) + g(\Phi_1(t; X_0)) \frac{\partial \Phi_2}{\partial x_2}(t; X_0) \\ \frac{d}{dt} \left(\frac{\partial \Phi_2}{\partial x_2}(t; X_0) \right) = (r - g(\Phi_1(t; X_0))) \frac{\partial \Phi_2}{\partial x_2}(t; X_0), \end{cases}$$

from which we deduce, using (D.1.1), that

$$\begin{cases} \frac{\partial \Phi_1}{\partial x_1}(t;X_0) = e^{-wt} \\ \frac{\partial \Phi_1}{\partial x_2}(t;X_0) = e^{-wt} \int_0^t g(\Phi_1(s;X_0))e^{(r+w)s - \int_0^s g(\Phi_1(\tau;X_0))d\tau} ds \\ \frac{\partial \Phi_2}{\partial x_2}(t;X_0) = e^{rt - \int_0^t g(\Phi_1(s;X_0))ds}. \end{cases}$$

Also, from (D.1.2), it follows that

$$D_X \Psi(T, X_0) = \begin{pmatrix} d_{11} & d_{12} \\ 0 & d_{22} \end{pmatrix},$$

with d_{11} , d_{12} , d_{22} being given by

(D.1.4)
$$d_{11} = (1 - \delta_2) \frac{\partial \Phi_1}{\partial x_1} ((1 - l)T; I_1(\Phi(lT; X_0))) \frac{\partial \Phi_1}{\partial x_1} (lT; X_0)$$

(D.1.5)
$$d_{12} = (1 - \delta_2) \frac{\partial \Phi_1}{\partial x_1} ((1 - l)T; I_1(\Phi(lT; X_0))) \frac{\partial \Phi_1}{\partial x_2} (lT; X_0) + (1 - \delta_1) \frac{\partial \Phi_1}{\partial x_2} ((1 - l)T; I_1(\Phi(lT; X_0))) \frac{\partial \Phi_2}{\partial x_2} (lT; X_0) (D.1.6)
$$d_{22} = (1 - \delta_1) \frac{\partial \Phi_2}{\partial x_2} ((1 - l)T; I_1(\Phi(lT; X_0))) \frac{\partial \Phi_2}{\partial x_2} (lT; X_0).$$$$

Consequently,

$$\begin{aligned} \text{(D.1.7)} \\ d_{11} &= (1 - \delta_2)e^{-wT}, \\ \text{(D.1.8)} \\ d_{12} &= (1 - \delta_2)e^{-w(1-l)T}e^{-wlT}\int_0^{lT}g(I^*(s))e^{(r+w)s - \int_0^s g(I^*(\tau))d\tau}ds \\ &+ (1 - \delta_1)e^{-w(1-l)T}\int_0^{(1-l)T}g(\Phi_1(s;I_1(\Phi(lT;X_0))))e^{(r+w)s - \int_0^s g(\Phi_1(\tau;I_1(\Phi(lT;X_0))))d\tau}ds \\ &\cdot e^{rlT - \int_0^{lT}g(I^*(s))ds} \\ &= (1 - \delta_2)e^{-wT}\int_0^Tg(I^*(s))e^{(r+w)s - \int_0^s g(I^*(\tau))d\tau}ds \\ &+ (1 - \delta_1)e^{-w(1-l)T}\int_0^{(1-l)T}g(I^*(s + lT))e^{(r+w)s - \int_0^s g(I^*(\tau + lT))d\tau}ds \cdot e^{rlT - \int_0^{lT}g(I^*(s))ds} \\ &= e^{-wT}\left[(1 - \delta_2)\int_0^{lT}g(I^*(s))e^{(r+w)s - \int_0^s g(I^*(\tau))d\tau}ds \right] \end{aligned}$$

+
$$(1 - \delta_1) \int_{lT}^{T} g(I^*(s)) e^{(r+w)s - \int_0^s g(I^*(\tau))d\tau} ds \bigg];$$

(D.1.9)

$$d_{22} = (1 - \delta_1) e^{r(1-l)T - \int_0^{(1-l)T} g(\Phi_1(s; I_1(\Phi(lT; X_0)))) ds} e^{rlT - \int_0^{lT} g(I^*(s)) ds}$$

$$= (1 - \delta_1) e^{rT - \int_0^{(1-l)T} g(I^*(s+lT)) ds - \int_0^{lT} g(I^*(s)) ds}$$

$$= (1 - \delta_1) e^{rT - \int_0^T g(I^*(s)) ds}$$

D.2 The partial derivatives of z at (0,0)

From the implicit function theorem, it follows that

$$\frac{\partial N_1}{\partial x_1}(0,(0,0))\left(-\frac{b_0'}{a_0'}\right) + \frac{\partial N_1}{\partial x_2}(0,(0,0)) + \frac{\partial N_1}{\partial x_1}(0,(0,0))\frac{\partial z}{\partial \alpha}(0,0) = 0$$

and consequently

$$a_0'\left(-\frac{b_0'}{a_0'}\right) + b_0' + a_0'\frac{\partial z}{\partial \alpha}(0,0) = 0,$$

from which we obtain that

$$\frac{\partial z}{\partial \alpha}(0,0) = 0.$$

The computations required for finding $\frac{\partial z}{\partial \overline{\tau}}(0,0)$ are somewhat more complicated, as $\frac{\partial N}{\partial \overline{\tau}}(0,(0,0))$ is not known beforehand, unlike $\frac{\partial N}{\partial x_1}(0,(0,0))$ and $\frac{\partial N}{\partial x_2}(0,(0,0))$. Again, by the implicit function theorem, it follows from (3.3.7) that

$$\begin{aligned} \frac{\partial z}{\partial \overline{\tau}}(0,0) &= \frac{\partial \Phi_1}{\partial \overline{\tau}}((1-l)T; I_1(\Phi(lT;X_0)))(1-l) \\ &+ \frac{\partial \Phi_1}{\partial x_1}((1-l)T; I_1(\Phi(lT;X_0)))(1-\delta_2) \left(\frac{\partial \Phi_1}{\partial \overline{\tau}}(lT;X_0) \cdot l + \frac{\partial \Phi_1}{\partial x_1}(lT;X_0)\frac{\partial z}{\partial \overline{\tau}}(0,0)\right) \\ &+ \frac{\partial \Phi_1}{\partial x_2}((1-l)T; I_1(\Phi(lT;X_0)))(1-\delta_1) \left(\frac{\partial \Phi_2}{\partial \overline{\tau}}(lT;X_0) \cdot l + \frac{\partial \Phi_2}{\partial x_1}(lT;X_0)\frac{\partial z}{\partial \overline{\tau}}(0,0)\right). \end{aligned}$$

Since

(D.2.1)
$$\frac{\partial \Phi_2}{\partial x_1}(lT; X_0) = 0,$$

(D.2.2)
$$\frac{\partial \Phi_2}{\partial \overline{\tau}}(lT; X_0) = 0,$$

it follows that

$$\frac{\partial z}{\partial \overline{\tau}}(0,0) = \frac{\partial \Phi_1}{\partial \overline{\tau}}((1-l)T; I_1(\Phi(lT;X_0)))(1-l)
+ \frac{\partial \Phi_1}{\partial x_1}((1-l)T; I_1(\Phi(lT;X_0)))(1-\delta_2) \left(\frac{\partial \Phi_1}{\partial \overline{\tau}}(lT;X_0) \cdot l + \frac{\partial \Phi_1}{\partial x_1}(lT;X_0)\frac{\partial z}{\partial \overline{\tau}}(0,0)\right)$$

and consequently

$$\frac{\partial z}{\partial \overline{\tau}}(0,0) \left(1 - \frac{\partial \Phi_1}{\partial x_1}((1-l)T; I_1(\Phi(lT;X_0)))(1-\delta_2)\frac{\partial \Phi_1}{\partial x_1}(lT;X_0)\right) \\
= \frac{\partial \Phi_1}{\partial \overline{\tau}}((1-l)T; I_1(\Phi(lT;X_0)))(1-l) + \frac{\partial \Phi_1}{\partial x_1}((1-l)T; I_1(\Phi(lT;X_0)))(1-\delta_2)\frac{\partial \Phi_1}{\partial \overline{\tau}}(lT;X_0) \cdot l$$

From (3.3.2), it follows that

$$\frac{\partial z}{\partial \overline{\tau}}(0,0) = \frac{1}{a_0'} \left[\frac{\partial \Phi_1}{\partial \overline{\tau}} ((1-l)T; I_1(\Phi(lT;X_0)))(1-l) + \frac{\partial \Phi_1}{\partial x_1} ((1-l)T; I_1(\Phi(lT;X_0)))(1-\delta_2) \frac{\partial \Phi_1}{\partial \overline{\tau}} (lT;X_0) \cdot l \right].$$

Consequently, one may obtain that

$$\begin{aligned} \frac{\partial z}{\partial \overline{\tau}}(0,0) &= \frac{1}{a'_0} \left[-wI^*(T)(1-l) + (1-\delta_2)e^{-w(1-l)T}(-wI^*(lT)) \cdot l \right] \\ &= -\frac{w}{a'_0} \left[I^*(T)(1-l) + e^{-w(1-l)T}I^*(lT+) \cdot l \right] \\ &= -\frac{w}{a'_0} \left[I^*(T)(1-l) + I^*(T) \cdot l \right] \\ &= -\frac{w}{a'_0} I^*(T) \end{aligned}$$

D.3 The first order partial derivatives of f at (0,0)

It is easy to see that

$$\begin{split} \frac{\partial f}{\partial \alpha}(\overline{\tau},\alpha) &= \frac{\partial}{\partial \alpha} \left[\alpha - \Psi_2(T+\overline{\tau},X_0+\alpha Y_0+z(\overline{\tau},\alpha)E_0) \right] \\ &= 1 - \frac{\partial}{\partial \alpha} \left[\Phi_2((1-l)(T+\overline{\tau});I_1(\Phi(l(T+\overline{\tau});X_0+\alpha Y_0+z(\overline{\tau},\alpha)E_0)))) \right] \\ &= 1 - \frac{\partial \Phi_2}{\partial x_1}((1-l)(T+\overline{\tau});I_1(\Phi(l(T+\overline{\tau});X_0+\alpha Y_0+z(\overline{\tau},\alpha)E_0))) \\ &\quad \cdot (1-\delta_2) \left(\frac{\partial \Phi_1}{\partial x_1}(l(T+\overline{\tau});X_0+\alpha Y_0+z(\overline{\tau},\alpha)E_0) \left(-\frac{b'_0}{a'_0} + \frac{\partial z}{\partial \alpha}(\overline{\tau},\alpha) \right) \right) \\ &\quad + \frac{\partial \Phi_1}{\partial x_2}(l(T+\overline{\tau});X_0+\alpha Y_0+z(\overline{\tau},\alpha)E_0) \right) \\ &\quad - \frac{\partial \Phi_2}{\partial x_2}((1-l)(T+\overline{\tau});I_1(\Phi(l(T+\overline{\tau});X_0+\alpha Y_0+z(\overline{\tau},\alpha)E_0)))) \\ &\quad \cdot (1-\delta_1) \left(\frac{\partial \Phi_2}{\partial x_1}(l(T+\overline{\tau});X_0+\alpha Y_0+z(\overline{\tau},\alpha)E_0) \left(-\frac{b'_0}{a'_0} + \frac{\partial z}{\partial \alpha}(\overline{\tau},\alpha) \right) \right) \\ &\quad + \frac{\partial \Phi_2}{\partial x_2}(l(T+\overline{\tau});X_0+\alpha Y_0+z(\overline{\tau},\alpha)E_0) \left(-\frac{b'_0}{a'_0} + \frac{\partial z}{\partial \alpha}(\overline{\tau},\alpha) \right) \\ &\quad + \frac{\partial \Phi_2}{\partial x_2}(l(T+\overline{\tau});X_0+\alpha Y_0+z(\overline{\tau},\alpha)E_0) \right). \end{split}$$

It then follows that

$$\frac{\partial f}{\partial \alpha}(0,0) = 1 - \frac{\partial \Phi_2}{\partial x_1}((1-l)T; I_1(\Phi(lT;X_0)))(1-\delta_2) \left(\frac{\partial \Phi_1}{\partial x_1}(lT;X_0) \left(-\frac{b'_0}{a'_0} + \frac{\partial z}{\partial \alpha}(0,0)\right) + \frac{\partial \Phi_1}{\partial x_2}(lT;X_0)\right) \\
- \frac{\partial \Phi_2}{\partial x_2}((1-l)T; I_1(\Phi(lT;X_0)))(1-\delta_1) \left(\frac{\partial \Phi_2}{\partial x_1}(lT;X_0) \left(-\frac{b'_0}{a'_0} + \frac{\partial z}{\partial \alpha}(0,0)\right) + \frac{\partial \Phi_2}{\partial x_2}(lT;X_0)\right)$$

From (D.2.1) and

(D.3.1)
$$\frac{\partial \Phi_2}{\partial x_1}((1-l)T; I_1(\Phi(lT; X_0))) = 0,$$

it is seen that

$$\frac{\partial f}{\partial \alpha}(0,0) = 1 - \frac{\partial \Phi_2}{\partial x_2}((1-l)T; I_1(\Phi(lT;X_0)))(1-\delta_1)\frac{\partial \Phi_2}{\partial x_2}(lT;X_0)$$
$$= d'_0$$
$$= 0.$$

It is also seen that

$$\begin{split} \frac{\partial f}{\partial \overline{\tau}}(\overline{\tau},\alpha) &= \frac{\partial}{\partial \overline{\tau}} \left[\alpha - \Psi_2(T+\overline{\tau},X_0+\alpha Y_0+z(\overline{\tau},\alpha)E_0) \right] \\ &= -\frac{\partial}{\partial \overline{\tau}} \left[\Phi_2((1-l)(T+\overline{\tau});I_1(\Phi(l(T+\overline{\tau});X_0+\alpha Y_0+z(\overline{\tau},\alpha)E_0)))) \right] \\ &= -\frac{\partial \Phi_2}{\partial \overline{\tau}} \left((1-l)(T+\overline{\tau});I_1(\Phi(l(T+\overline{\tau});X_0+\alpha Y_0+z(\overline{\tau},\alpha)E_0)))(1-l) \right) \\ &- \frac{\partial \Phi_2}{\partial x_1} \left((1-l)(T+\overline{\tau});I_1(\Phi(l(T+\overline{\tau});X_0+\alpha Y_0+z(\overline{\tau},\alpha)E_0))) \right) \\ &\cdot \left(1-\delta_2 \right) \left(\frac{\partial \Phi_1}{\partial \overline{\tau}} (l(T+\overline{\tau});X_0+\alpha Y_0+z(\overline{\tau},\alpha)E_0) \frac{\partial z}{\partial \overline{\tau}}(\overline{\tau},\alpha) \right) \\ &+ \frac{\partial \Phi_2}{\partial x_2} \left((1-l)(T+\overline{\tau});I_1(\Phi(l(T+\overline{\tau});X_0+\alpha Y_0+z(\overline{\tau},\alpha)E_0))) \right) \\ &\cdot \left(1-\delta_1 \right) \left(\frac{\partial \Phi_2}{\partial \overline{\tau}} (l(T+\overline{\tau});X_0+\alpha Y_0+z(\overline{\tau},\alpha)E_0) \cdot l \\ &+ \frac{\partial \Phi_2}{\partial x_1} (l(T+\overline{\tau});X_0+\alpha Y_0+z(\overline{\tau},\alpha)E_0) \cdot l \\ &+ \frac{\partial \Phi_2}{\partial x_1} (l(T+\overline{\tau});X_0+\alpha Y_0+z(\overline{\tau},\alpha)E_0) \right). \end{split}$$

It then follows that

$$\begin{split} \frac{\partial f}{\partial \overline{\tau}}(0,0) &= -\frac{\partial \Phi_2}{\partial \overline{\tau}}((1-l)T; I_1(\Phi(lT;X_0)))(1-l) \\ &- \frac{\partial \Phi_2}{\partial x_1}((1-l)T; I_1(\Phi(lT;X_0))) \\ &\cdot (1-\delta_2) \left(\frac{\partial \Phi_1}{\partial \overline{\tau}}(lT;X_0) \cdot l + \frac{\partial \Phi_1}{\partial x_1}(lT;X_0)\frac{\partial z}{\partial \overline{\tau}}(0,0)\right) \\ &- \frac{\partial \Phi_2}{\partial x_2}((1-l)T; I_1(\Phi(lT;X_0))) \\ &\cdot (1-\delta_1) \left(\frac{\partial \Phi_2}{\partial \overline{\tau}}(lT;X_0) \cdot l + \frac{\partial \Phi_2}{\partial x_1}(lT;X_0)\frac{\partial z}{\partial \overline{\tau}}(0,0)\right). \end{split}$$

From (D.2.1),(D.2.2),(D.3.1) and

(D.3.2)
$$\frac{\partial \Phi_2}{\partial \overline{\tau}}((1-l)T; I_1(\Phi(lT; X_0))) = 0.$$

it consequently follows that

$$\frac{\partial f}{\partial \overline{\tau}}(0,0) = 0$$

D.4 The second order partial derivatives of Φ_2

Again, by formally deriving

$$\frac{d}{dt}\left(\Phi(t;X_0)\right) = F(\Phi(t;X_0)),$$

one may obtain $\frac{\partial^2 \Phi_2}{\partial x_1^2}(t; X_0)$, $\frac{\partial^2 \Phi_2}{\partial x_2^2}(t; X_0)$, $\frac{\partial^2 \Phi_2}{\partial x_1 \partial x_2}(t; X_0)$ as the solutions of certain initial value problems. One sees that

$$\frac{d}{dt}\left(\frac{\partial^2 \Phi_2}{\partial x_1^2}(t;X_0)\right) = (r - g(\Phi_1(t;X_0)))\frac{\partial^2 \Phi_2}{\partial x_1^2}(t;X_0) - g'(\Phi_1(t;X_0))\frac{\partial \Phi_1}{\partial x_1}(t;X_0)\frac{\partial \Phi_2}{\partial x_1}(t;X_0)$$

and since

$$\frac{\partial \Phi_2}{\partial x_1}(t; X_0) = 0 \quad \text{for } t \ge 0,$$

it follows that

$$\frac{d}{dt}\left(\frac{\partial^2 \Phi_2}{\partial x_1^2}(t;X_0)\right) = (r - g(\Phi_1(t;X_0)))\frac{\partial^2 \Phi_2}{\partial x_1^2}(t;X_0)$$

and consequently

$$\frac{\partial^2 \Phi_2}{\partial x_1^2}(t; X_0) = e^{rt - \int_0^t g(\Phi_1(s; X_0)) ds} \frac{\partial^2 \Phi_2}{\partial x_1^2}(0; X_0).$$

Since $\frac{\partial^2 \Phi_2}{\partial x_1^2}(0; X_0) = 0$, this implies that

$$\frac{\partial^2 \Phi_2}{\partial x_1^2}(t; X_0) = 0 \quad \text{ for } t \ge 0.$$

Also,

$$\frac{d}{dt} \left(\frac{\partial^2 \Phi_2}{\partial x_2^2}(t; X_0) \right)$$

= $(r - g(\Phi_1(t; X_0))) \frac{\partial^2 \Phi_2}{\partial x_2^2}(t; X_0) - g'(\Phi_1(t; X_0)) \frac{\partial \Phi_1}{\partial x_2}(t; X_0) \frac{\partial \Phi_2}{\partial x_2}(t; X_0)$

and since

$$\frac{\partial^2 \Phi_2}{\partial x_2^2}(0; X_0) = 0,$$

one may deduce that

$$\begin{aligned} &(\mathrm{D}.4.1) \\ &\frac{\partial^2 \Phi_2}{\partial x_2^2}(t;X_0) \\ &= -e^{rt - \int_0^t g(\Phi_1(s;X_0))ds} \int_0^t g'(\Phi_1(s;X_0)) \frac{\partial \Phi_1}{\partial x_2}(s;X_0) \frac{\partial \Phi_2}{\partial x_2}(s;X_0) e^{-(rs - \int_0^s g(\Phi_1(\tau;X_0))d\tau)} ds \\ &= -e^{rt - \int_0^t g(\Phi_1(s;X_0))ds} \int_0^t g'(\Phi_1(s;X_0)) \frac{\partial \Phi_1}{\partial x_2}(s;X_0) ds. \end{aligned}$$

Similarly,

$$\frac{d}{dt} \left(\frac{\partial^2 \Phi_2}{\partial x_1 \partial x_2}(t; X_0) \right)
= (r - g(\Phi_1(t; X_0))) \frac{\partial^2 \Phi_2}{\partial x_1 \partial x_2}(t; X_0) - g'(\Phi_1(t; X_0)) \frac{\partial \Phi_1}{\partial x_1}(t; X_0) \frac{\partial \Phi_2}{\partial x_2}(t; X_0)$$

and since

$$\frac{\partial^2 \Phi_2}{\partial x_1 \partial x_2}(0; X_0) = 0,$$

one obtains that

$$\begin{aligned} (\mathrm{D}.4.2) \\ & \frac{\partial^2 \Phi_2}{\partial x_1 \partial x_2}(t; X_0) \\ & = -e^{rt - \int_0^t g(\Phi_1(s; X_0)) ds} \int_0^t g'(\Phi_1(s; X_0)) \frac{\partial \Phi_1}{\partial x_1}(s; X_0) \frac{\partial \Phi_2}{\partial x_2}(s; X_0) e^{-(rs - \int_0^s g(\Phi_1(\tau; X_0)) d\tau)} ds \\ & = -e^{rt - \int_0^t g(\Phi_1(s; X_0)) ds} \int_0^t g'(\Phi_1(s; X_0)) \frac{\partial \Phi_1}{\partial x_1}(s; X_0) ds. \end{aligned}$$

D.5 The second order partial derivatives of f

One remarks that

(D.5.1)
$$\frac{\partial^2 \Phi_2}{\partial x_1 \partial \overline{\tau}} ((1-l)T; I_1(\Phi(lT; X_0)) = 0$$

(D.5.2)
$$\frac{\partial^2 \Phi_2}{\partial x_1^2} ((1-l)T; I_1(\Phi(lT; X_0)) = 0$$

(D.5.3)
$$\frac{\partial^2 \Phi_2}{\partial x_1^2} (lT; X_0) = 0$$

By (D.5.1)-(D.5.3), combined with (D.2.1)-(D.3.2), it follows that

$$\frac{\partial^2 f}{\partial \tau^2}(0,0) = -\frac{\partial^2 \Phi_2}{\partial \tau^2}((1-l)T; I_1(\Phi(lT;X_0)))(1-l)^2.$$

Since

(D.5.4)
$$\frac{\partial^2 \Phi}{\partial \overline{\tau}^2}((1-l)T; I_1(\Phi(lT; X_0))) = 0,$$

it is then concluded that

$$\frac{\partial^2 f}{\partial \overline{\tau}^2}(0,0) = 0.$$

We then compute $\frac{\partial^2 f}{\partial \alpha^2}(0,0)$. By (D.2.1) and (D.3.1), it follows that

$$\begin{split} \frac{\partial^2 f}{\partial \alpha^2}(0,0) &= -\frac{\partial}{\partial \alpha} \left[\frac{\partial \Phi_2}{\partial x_1} ((1-l)(T+\overline{\tau}); I_1(\Phi(l(T+\overline{\tau}); X_0 + \alpha Y_0 + z(\overline{\tau}, \alpha)E_0)))) \right] \Big|_{(\overline{\tau},\alpha)=(0,0)} \\ & \cdot (1-\delta_2) \left(\frac{\partial \Phi_1}{\partial x_1} (lT; X_0) \left(-\frac{b'_0}{a'_0} + \frac{\partial z}{\partial \alpha}(0,0) \right) + \frac{\partial \Phi_1}{\partial x_2} (lT; X_0) \right) \\ & - \frac{\partial}{\partial \alpha} \left[\frac{\partial \Phi_2}{\partial x_2} ((1-l)(T+\overline{\tau}); I_1(\Phi(l(T+\overline{\tau}); X_0 + \alpha Y_0 + z(\overline{\tau}, \alpha)E_0)))) \right] \Big|_{(\overline{\tau},\alpha)=(0,0)} \\ & \cdot (1-\delta_1) \left(\frac{\partial \Phi_2}{\partial x_1} (lT; X_0) \left(-\frac{b'_0}{a'_0} + \frac{\partial z}{\partial \alpha}(0,0) \right) + \frac{\partial \Phi_2}{\partial x_2} (lT; X_0) \right) \\ & - \frac{\partial \Phi_2}{\partial x_2} ((1-l)T; I_1(\Phi(lT; X_0))) \\ & \cdot \frac{\partial}{\partial \alpha} \left[(1-\delta_1) \left(\frac{\partial \Phi_2}{\partial x_1} (l(T+\overline{\tau}); X_0 + \alpha Y_0 + z(\overline{\tau}, \alpha)E_0) \left(-\frac{b'_0}{a'_0} + \frac{\partial z}{\partial \alpha}(\overline{\tau}, \alpha) \right) \right) \\ & + \frac{\partial \Phi_2}{\partial x_2} (l(T+\overline{\tau}); X_0 + \alpha Y_0 + z(\overline{\tau}, \alpha)E_0) \right) \right] \Big|_{(\overline{\tau},\alpha)=(0,0)}. \end{split}$$

Using again (D.5.2) and (D.2), it follows that

$$\begin{split} \frac{\partial^2 f}{\partial \alpha^2}(0,0) &= -2 \frac{\partial^2 \Phi_2}{\partial x_1 \partial x_2} ((1-l)T; I_1(\Phi(lT;X_0)))(1-\delta_1)(1-\delta_2) \\ &\quad \cdot \left(\frac{\partial \Phi_1}{\partial x_1}(lT;X_0) \left(-\frac{b'_0}{a'_0}\right) + \frac{\partial \Phi_1}{\partial x_2}(lT;X_0)\right) \frac{\partial \Phi_2}{\partial x_2}(lT;X_0) \\ &\quad - \frac{\partial^2 \Phi_2}{\partial x_2^2} ((1-l)T; I_1(\Phi(lT;X_0)))(1-\delta_1)^2 \left(\frac{\partial \Phi_2}{\partial x_2}(lT;X_0)\right)^2 \\ &\quad - \frac{\partial \Phi_2}{\partial x_2} ((1-l)T; I_1(\Phi(lT;X_0)))(1-\delta_1) \\ &\quad \cdot \left[2 \frac{\partial^2 \Phi_2}{\partial x_2 \partial x_1}(lT;X_0) \left(-\frac{b'_0}{a'_0}\right) + \frac{\partial^2 \Phi_2}{\partial x_2^2}(lT;X_0)\right]. \end{split}$$

Consequently, from (D.4.1), (D.4.2), (3.3.2) and (3.3.3) one easily gets that

$$\frac{\partial^2 f}{\partial \alpha^2}(0,0) > 0.$$

From (D.2.1),(D.2.2) and (D.3.1), one may see that

$$\begin{split} \frac{\partial^2 f}{\partial \alpha \partial \overline{\tau}}(0,0) &= -\frac{\partial}{\partial \alpha} \left[\frac{\partial \Phi_2}{\partial \overline{\tau}} ((1-l)(T+\overline{\tau}); I_1(\Phi(l(T+\overline{\tau}); X_0 + \alpha Y_0 + z(\overline{\tau}, \alpha)E_0)))) \right] \Big|_{(\overline{\tau},\alpha)=(0,0)} \cdot (1-l) \\ &- \frac{\partial}{\partial \alpha} \left[\frac{\partial \Phi_2}{\partial x_1} ((1-l)(T+\overline{\tau}); I_1(\Phi(l(T+\overline{\tau}); X_0 + \alpha Y_0 + z(\overline{\tau}, \alpha)E_0)))) \right] \Big|_{(\overline{\tau},\alpha)=(0,0)} \\ &\cdot (1-\delta_2) \left(\frac{\partial \Phi_1}{\partial \overline{\tau}} (lT; X_0) \cdot l + \frac{\partial \Phi_1}{\partial x_1} (lT; X_0) \frac{\partial z}{\partial \overline{\tau}} (0, 0) \right) \\ &- \frac{\partial \Phi_2}{\partial x_2} ((1-l)T; I_1(\Phi(lT; X_0))) \\ &\cdot (1-\delta_1) \frac{\partial}{\partial \alpha} \left[\frac{\partial \Phi_2}{\partial \overline{\tau}} (l(T+\overline{\tau}); X_0 + \alpha Y_0 + z(\overline{\tau}, \alpha)E_0) \cdot l \\ &+ \frac{\partial \Phi_2}{\partial x_1} (l(T+\overline{\tau}); X_0 + \alpha Y_0 + z(\overline{\tau}, \alpha)E_0) \frac{\partial z}{\partial \overline{\tau}} (\overline{\tau}, \alpha) \right] \Big|_{(\overline{\tau},\alpha)=(0,0)} . \end{split}$$

Using again (D.5.1) and (D.5.3), one sees that

$$\begin{aligned} \frac{\partial^2 f}{\partial \alpha \partial \overline{\tau}}(0,0) &= -\frac{\partial^2 \Phi_2}{\partial x_2 \partial \overline{\tau}} ((1-l)T; I_1(\Phi(lT;X_0))))(1-\delta_1) \frac{\partial \Phi_2}{\partial x_2} (lT;X_0)(1-l) \\ &- \frac{\partial^2 \Phi_2}{\partial x_2 \partial x_1} ((1-l)T; I_1(\Phi(lT;X_0))))(1-\delta_1) \frac{\partial \Phi_2}{\partial x_2} (lT;X_0) \\ &\cdot (1-\delta_2) \left(\frac{\partial \Phi_1}{\partial \overline{\tau}} (lT;X_0) \cdot l + \frac{\partial \Phi_1}{\partial x_1} (lT;X_0) \frac{\partial z}{\partial \overline{\tau}} (0,0) \right) \\ &- \frac{\partial \Phi_2}{\partial x_2} ((1-l)T; I_1(\Phi(lT;X_0))) \\ &\cdot (1-\delta_1) \left(\frac{\partial^2 \Phi_2}{\partial x_2 \partial \overline{\tau}} (lT;X_0) \cdot l + \frac{\partial^2 \Phi_2}{\partial x_2 \partial x_1} (lT;X_0) \frac{\partial z}{\partial \overline{\tau}} (0,0) \right). \end{aligned}$$

We now determine the sign of $\frac{\partial^2 f}{\partial \alpha \partial \overline{\tau}}(0,0)$. It is seen that

$$\begin{aligned} &-\frac{\partial^2 \Phi_2}{\partial x_2 \partial x_1} ((1-l)T; I_1(\Phi(lT; X_0))))(1-\delta_1) \frac{\partial \Phi_2}{\partial x_2} (lT; X_0) \\ &= e^{r(1-l)T - \int_0^{(1-l)T} g(\Phi_1(s; I_1(\Phi(lT; X_0)))) ds} \cdot \left(\int_0^{(1-l)T} g'(\Phi_1(s; I_1(\Phi(lT; X_0)))) e^{-ws} ds \right) \\ &\cdot (1-\delta_1) e^{rlT - \int_0^{lT} g(\Phi_1(s; X_0)) ds} \\ &= e^{rT - \int_0^{(1-l)T} g(I^*(s+lT)) ds - \int_0^{lT} g(I^*(s)) ds} (1-\delta_1) \left(\int_0^{(1-l)T} g'(I^*(s+lT)) e^{-ws} ds \right) \\ &= e^{rT - \int_0^T g(I^*(s)) ds} (1-\delta_1) \left(\int_0^{(1-l)T} g'(I^*(s+lT)) e^{-ws} ds \right). \end{aligned}$$

Since

$$\int_0^T g(I^*(s))ds = rT + \ln(1 - \delta_1),$$

it follows that

$$-\frac{\partial^2 \Phi_2}{\partial x_2 \partial x_1} ((1-l)T; I_1(\Phi(lT; X_0))))(1-\delta_1) \frac{\partial \Phi_2}{\partial x_2} (lT; X_0)$$
$$= \int_0^{(1-l)T} g'(I^*(s+lT)) e^{-ws} ds.$$

Similarly,

$$\begin{aligned} &-\frac{\partial^2 \Phi_2}{\partial x_2 \partial \overline{\tau}} ((1-l)T; I_1(\Phi(lT; X_0))))(1-\delta_1) \frac{\partial \Phi_2}{\partial x_2} (lT; X_0)(1-l) \\ &= -\left(r - g(\Phi_1((1-l)T; I_1(\Phi(lT; X_0))))\right) \frac{\partial \Phi_2}{\partial x_2} ((1-l)T; I_1(\Phi(lT; X_0))) \\ &\cdot (1-\delta_1) \frac{\partial \Phi_2}{\partial x_2} (lT; X_0)(1-l) \\ &= -(r - g(I^*(T)))(1-d_0')(1-l) \\ &= -(r - g(I^*(T)))(1-l). \end{aligned}$$

Also,

$$(1 - \delta_2) \left(\frac{\partial \Phi_1}{\partial \overline{\tau}} (lT; X_0) \cdot l + \frac{\partial \Phi_1}{\partial x_1} (lT; X_0) \frac{\partial z}{\partial \overline{\tau}} (0, 0) \right)$$

= $(1 - \delta_2) \left(-wI^*(lT) \cdot l + e^{-wlT} \left(\left(-\frac{1}{a'_0} \right) wI^*(T) \right) \right)$
= $-w(1 - \delta_2)e^{-wlT} \left(I^*(0+) \cdot l + \frac{1}{a'_0} I^*(T) \right).$

It is seen that

$$-\frac{\partial \Phi_2}{\partial x_2}((1-l)T; I_1(\Phi(lT; X_0)))(1-\delta_1) \left[\frac{\partial^2 \Phi_2}{\partial x_2 \partial \overline{\tau}}(lT; X_0) \cdot l + \frac{\partial^2 \Phi_2}{\partial x_2 \partial x_1}(lT; X_0) \frac{\partial z}{\partial \overline{\tau}}(0, 0) \right]$$

$$= -\frac{\partial \Phi_2}{\partial x_2}((1-l)T; I_1(\Phi(lT; X_0)))(1-\delta_1)$$

$$\left[(r-g(\Phi_1(lT; X_0))) \frac{\partial \Phi_2}{\partial x_2}(lT; X_0) \cdot l - \left(\frac{\partial \Phi_2}{\partial x_2}(lT; X_0) \int_0^{lT} g'(I^*(s)) e^{-ws} ds \right) \frac{\partial z}{\partial \overline{\tau}}(0, 0) \right].$$

Since $d'_0 = 0$, it follows that

$$-\frac{\partial \Phi_2}{\partial x_2}((1-l)T; I_1(\Phi(lT; X_0)))(1-\delta_1) \left[\frac{\partial^2 \Phi_2}{\partial x_2 \partial \overline{\tau}}(lT; X_0) \cdot l + \frac{\partial^2 \Phi_2}{\partial x_2 \partial x_1}(lT; X_0) \frac{\partial z}{\partial \overline{\tau}}(0, 0) \right]$$

= $-(r - g(I^*(lT))) \cdot l + \left(\int_0^{lT} g'(I^*(s))e^{-ws}ds \right) \left(-\frac{1}{a'_0}wI^*(T) \right)$
= $-\left[(r - g(I^*(lT))) \cdot l + \frac{w}{a'_0} \left(\int_0^{lT} g'(I^*(s))e^{-ws}ds \right) I^*(T) \right]$

It is consequently deduced that

$$\begin{split} \frac{\partial^2 f}{\partial \alpha \partial \overline{\tau}}(0,0) &= -(r - g(I^*(T)))(1-l) \\ &+ \left(\int_0^{(1-l)T} g'(I^*(s+lT))e^{-ws}ds \right) \left(-w(1-\delta_2)e^{-wlT} \left(I^*(0+) \cdot l + \frac{1}{a'_0}I^*(T) \right) \right) \\ &- \left[(r - g(I^*(lT))) \cdot l + \frac{w}{a'_0} \left(\int_0^{lT} g'(I^*(s))e^{-ws}ds \right) I^*(T) \right] \\ &= - \left[r - lg(I^*(lT)) - (1-l)g(I^*(T)) \right] \\ &- w \left(\int_0^{(1-l)T} g'(I^*(s+lT))e^{-w(s+lT)}ds \right) (1-\delta_2) \left(I^*(0+) \cdot l + \frac{1}{a'_0}I^*(T) \right) \\ &- \frac{w}{a'_0} \left(\int_0^{lT} g'(I^*(s))e^{-ws}ds \right) I^*(T), \end{split}$$

which implies

(D.5.5)
$$\frac{\partial^2 f}{\partial \alpha \partial \overline{\tau}}(0,0) = -\left[r - lg(I^*(lT)) - (1-l)g(I^*(T))\right] - w\left(\int_{lT}^{T} g'(I^*(s))e^{-ws}ds\right)(1-\delta_2)\left(I^*(0+)l + \frac{1}{a'_0}I^*(T)\right) - \frac{w}{a'_0}\left(\int_{0}^{lT} g'(I^*(s))e^{-ws}ds\right)I^*(T).$$

We note that

$$rT - \int_0^T g(I^*(s))ds = -\ln(1-\delta_1) > 0$$

and also, since I^* is decreasing on (0, T],

$$\begin{split} \int_0^T g(I^*(s)) ds &= \int_0^{lT} g(I^*(s)) ds + \int_{lT}^T g(I^*(s)) ds \\ &> lTg(I^*(lT)) + (1-l)Tg(I^*(T)). \end{split}$$

Consequently, the first term in the right-hand side of (D.5.5) is negative. Since g is increasing and I^* is positive, the other terms are negative as well and consequently

$$\frac{\partial^2 f}{\partial \alpha \partial \tau}(0,0) < 0.$$

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Bibliography

- P. A. Abrams, The fallacies of "ratio-dependent" predation, Ecology, 75 (1994), 1842– 1850.
- [2] A. Abrams, L.R. Ginzburg, *The nature of predation: prey dependent, ratio dependent or neither?*, Trends Ecol. Evol., 15 (2000), 337–341.
- [3] W. G. Aiello, H. I. Freedman, A time-delay model of single species growth with stage structure, Math. Biosci., 101 (1990), 139–153.
- [4] R. Anderson, R. May, Infectious Diseases of Humans: Dynamics and Control, Oxford University Press, Oxford, 1991.
- [5] N. Apreutesei, Necessary optimality conditions for a Lotka-Volterra three species system, Math. Modelling Nat. Phenomena, 1 (2006), 123-135.
- [6] R. Arditi, L. R. Ginzburg, Coupling in predator-prey dynamics: ratio-dependence, J. Theor. Biol., 139 (1989), 311–326.
- [7] R. Arditi, J. Michalski, Nonlinear food web models and their response to increased basal productivity, in Food Webs : Integration of Patterns and Dynamics, G. A. Polis and K. O. Winemiller, eds., Chapman and Hall, New York, 1996, 122–133.
- [8] D. Bainov, P. Simeonov, Impulsive differential equations: periodic solutions and applications, Longman, John Wiley, New York, NY, 1993.
- [9] W. I. Bajwa, M. Kogan, Compendium of IPM definitions, available online at http://ippc.orst.edu/IPMdefinitions/, 1997.
- [10] J. Bascompte, C. J. Melián, E. Sala, Interaction strength combinations and the overfishing of a marine food web, Proc. Natl. Acad. Sci. USA, 102 (2005), 5443–5447.
- [11] J. R. Beddington, Mutual interference between parasites or predators and its effect on searching efficiency, J. Anim. Ecol., 51 (1975), 331–340.
- [12] E. Beretta, Y. Kuang, Global analysis in some ratio-dependent predator-prey systems, Nonlinear Anal., 32 (1998), 381–408.
- [13] S. Bonhoeffer, R. M. May, G. M. Shaw, and M. A. Nowak, Virus dynamics and drug therapy, Proc. Nat. Acad. Sci. U.S.A., 94 (1997), 6971–6976.
- [14] G. Butler, H. I. Freedman, P. Waltman, Uniformly persistent systems, Proc. Amer. Math. Soc., 96 (1986), 425–430.
- [15] V. Capasso, Mathematical Structures of Epidemic Systems, Lecture Notes in Biomath., Vol. 97, Springer, Heidelberg, 1993.

- [16] V. Capasso, G. Serio, A generalization of Kermack-McKendrick deterministic epidemic model, Math. Biosci., 42 (1978), 43–61.
- [17] F. Chen, Periodicity in a ratio-dependent predator-prey system, J. Appl. Math., 2 (2005), 153–169.
- [18] S. N. Chow, J. Hale, Methods of bifurcation theory, Springer Verlag, New York, NY, 1982.
- [19] P. H. Crowley, E. C. Martin, Functional responses and interferences within and between year classes of a dragonfly population, J. North Amer. Benth. Soc., 8 (1989), 211–221.
- [20] P. De Leenheer and H. L. Smith, Virus dynamics: A global analysis, SIAM J. Appl. Math., 63 (2003), 1313–1327.
- [21] D. L. DeAngelis, R. A. Goldstein, R. V. O'Neill, A model for trophic interaction, Ecology, 56 (1975), 881–892.
- [22] B. Deng, S. Jessie, G. Ledder, A. Rand, S. Srodulski, Biological control does not imply paradox - a case against ratio-dependent models, Math. Biosci., 208 (2007), 26–32.
- [23] M. Fan, Y. Kuang, Dynamics of a nonautonomous predator-prey system with the Beddington-DeAngelis functional response, J. Math. Anal. Appl., 295 (2004), 15–39.
- [24] A. Fonda, Uniformly persistent dynamical systems, Proc. Amer. Math. Soc., 104 (1998), 111–116.
- [25] H. I. Freedman, S. Ruan, M. Tang, Uniform persistence near a closed positively invariant set, J. Dynam. Differential Equations, 6 (1994), 583–600.
- [26] R.E. Gaines, R.M. Mawhin, Coincidence Degree and Nonlinear Differential Equations, Springer-Verlag, Berlin (1977).
- [27] P. Georgescu, Y.-H. Hsieh, Global dynamics of a predator-prey model with stage structure for predator, SIAM J. Appl. Math., 67 (2006), 1379–1395.
- [28] P. Georgescu, Y.-H. Hsieh, Global stability for a virus dynamics model with nonlinear incidence of infection and removal, SIAM J. Appl. Math., 67 (2006), 337–353.
- [29] P. Georgescu, G. Moroşanu, Impulsive perturbations of a three-trophic prey-dependent food chain system, to appear in Math. Comput. Modelling.
- [30] P. Georgescu, G. Moroşanu, Global stability for a stage-structured predator-prey model, Math. Sci. Res. J., 10 (2006), 214–226.
- [31] P. Georgescu, G. Moroşanu, Pest regulation by means of impulsive controls, Appl. Math. Comput., 190 (2007), 790–803.

- [32] P. Georgescu, H. Zhang and L. Chen, Bifurcation of nontrivial periodic solutions for an impulsively controlled pest management model, preprint.
- [33] M. E. Gilpin, Spiral chaos in a predator-prey model, Am. Naturalist, 107 (1979), 306–308.
- [34] B. S. Goh, Global stability in many species systems, Am. Naturalist, 111 (1977), pp. 135–143.
- [35] K. Gopalsamy, Stability and Oscillations in Delay Differential Equations of Population Dynamics, Kluwer Academic Publishers, Boston (1991).
- [36] S. A. Gourley, Y. Kuang, A stage structured predator-prey model and its dependence on maturation delay and death rate, J. Math. Biol., 49 (2004), 188–200.
- [37] S. C. Gurney, R. M. Nisbet, S. P. Blythe, The systematic formulation of models of stage-structured populations, Lecture Notes in Biomath. 68, Springer, Berlin, 1986, 474–494.
- [38] A.P. Gutierrez, The physiological basis of ratio-dependent predator-prey theory: a metabolic pool model of Nicholson's blowflies as an example, Ecology, 73 (1992), 1552–1563.
- [39] N. G. Hairston, F. E. Smith, L. B. Slobodkin, Community structure, population control and competition, Am. Naturalist, 94 (1960), 421–425.
- [40] A. Halanay, Differential equations: stability, oscillations, time lags, Academic Press, New York (1966).
- [41] G. W. Harrison, Comparing predator-prey models to Luckinbill's experiment with Didinium and Paramecium, Ecology, 76 (1995), 357–374.
- [42] G. W. Harrison, Global stability of predator-prey interactions, J. Math. Biol., 8 (1979), 159–171.
- [43] M. P. Hassell and G. C. Varley, New inductive population model for insect parasites and its bearing on biological control, Nature, 223 (1969), 1133–1136.
- [44] A. Hastings, T. Powell, Chaos in a three-species food chain, Ecology, 72 (1991), 896– 903.
- [45] J. A. P. Hesterbeek, J. A. Metz, The saturating contact rate in marriage and epidemic models, J. Math. Biol., 31 (1993), 529-539.
- [46] H. W. Hethcote, One thousand and one epidemic models. In: S.A. Levin, Editor, Frontiers in Mathematical Biology, Springer, New York, 1994.
- [47] H. W. Hethcote, The mathematics of infectious diseases, SIAM Rev., 42 (2000), 579–653.

- [48] H. W. Hethcote, P. van den Driessche, Some epidemiological models with nonlinear incidence, J. Math. Biol., 29 (1991), 271–287.
- [49] J. Hofbauer, J. W. H. So, Uniform persistence and repellors for maps, Proc. Amer. Math. Soc., 107 (1989), 1137–1142.
- [50] M. P. Hoffmann, A. C. Frodsham, Natural Enemies of Vegetable Insect Pests, Cooperative Extension, Cornell University, Ithaca, NY, (1993).
- [51] C. S. Holling, The components of predation as revealed by a study of small mammal predation of the European pine sawfly, Canad. Entomol., 91 (1959), 293–320.
- [52] C. S. Holling, The functional response of predators to prey density and its role in mimicry and population regulation, Mem. Entomol. Soc. Canada, 45 (1965), 1–60.
- [53] Y.-H. Hsieh, J. Y. Lee, H. L. Chang, SARS epidemiology modeling, Emerg. Infect. Dis., 10 (2004), 1165-1167.
- [54] S.-B. Hsu, T.-W. Hwang, Y. Kuang, A ratio-dependent food chain model and its applications to biological control, Math. Biosci., 181 (2003), 55–83.
- [55] C. Huisman, R. J. DeBoer, A formal derivation of the Beddington functional response, J. Theor. Biol., 185 (1997), 389–400.
- [56] Z. W. Hwang, Global analysis of the predator-prey system with Beddington-DeAngelis functional response, J. Math. Anal. Appl., 281 (2003), 395–401.
- [57] Z. W. Hwang, Uniqueness of limit cycles of the predator-prey system with Beddington-DeAngelis functional response, J. Math. Anal. Appl., 290 (2004), 113– 122.
- [58] G. Iooss, Bifurcation of maps and applications, Elsevier, North-Holland, New York, NY, 1979.
- [59] V. S. Ivlev, *Experimental ecology of the feeding of fishes*, Yale University Press, New Haven (1961).
- [60] J. Jiao, L. Chen and W. Long, Pulse fishing policy for a stage-structured model with state-dependent harvesting, J. Biol. Sys., 15 (2007), 409–416.
- [61] C. Jost, O. Arino, R. Arditi, About deterministic extinction in ratio-dependent predator-prey models, Bull. Math. Biol., 61 (1999), 19–32.
- [62] C. Jost, S. Ellner, Testing for predator dependence in predator-prey dynamics: a nonparametric approach, Proc. Royal Soc. London Ser. B, 267 (2000), 1611–1620.
- [63] A. Klebanoff, A. Hastings, Chaos in three species food chains, J. Math. Biol., 32 (1993), 427–451.
- [64] A. Korobeinikov, Global properties of basic virus dynamics models, Bull. Math. Biol., 66 (2004), 879–883.

- [65] A. Korobeinikov, Lyapunov functions and global stability for SIR and SIRS epidemiological models with non-linear transmission, Bull. Math. Biol., 30 (2006), 615–626.
- [66] A. Korobeinikov, P. K. Maini, A Lyapunov function and global properties for SIR and SEIR epidemiological models with nonlinear incidence, Math. Biosci. Eng., 1 (2004), 57–60.
- [67] A. Korobeinikov, P. K. Maini, Non-linear incidence and stability of infectious disease models, Math. Med. Biol., 22 (2005), 113–128.
- [68] Y. Kuang, Basic properties of mathematical population models, J. Biomath., 17 (2002), 129–142.
- [69] Y. Kuang, Delay Differential Equations with Applications in Population Dynamics, Springer, New York (1993).
- [70] Y. Kuang, Global stability of Gause-type predator-prey systems, J. Math. Biol., 28 (1990), 463–474.
- [71] Y. Kuang, Rich dynamics of Gause-type ratio-dependent predator-prey system, Fields Inst. Commun., 21 (1999), 325–337.
- [72] Y. Kuang, E. Beretta, Global qualitative analysis of a ratio-dependent predator-prey system, J. Math. Biol., 36 (1998), 389–406.
- [73] Y. A. Kuznetsov, S. Rinaldi, Remarks on food chain dynamics, Math. Biosci., 134 (1996), 1–33.
- [74] A. Lakmeche, O. Arino, Bifurcation of nontrivial periodic solutions of impulsive differential equations arising chemoterapeutic treatment, Dyn. Contin. Discrete Impuls. Syst. Ser. A Math. Anal., 7 (2000), 265–287.
- [75] A. Lakmeche, O. Arino, Nonlinear mathematical model of pulsed-therapy of heterogeneous tumors, Nonlinear Anal. Real World Appl., 2 (2001), 455–465.
- [76] V. Lakshmikantham, D.D. Bainov, P.S. Simeonov, Theory Of Impulsive Differential Equations, World Scientific, Singapore, 1989.
- [77] J. P. LaSalle, *The stability of dynamical systems*, Regional Conference Series in Applied Mathematics, SIAM, Philadelphia, PA, 1976.
- [78] P. H. Leslie, Some further notes on the use of matrices in population mathematics, Biometrika, 35 (1948), 213–245.
- [79] P. Leslie, J. Gower, The properties of a stochastic model for two competing species, Biometrika, 45 (1958), 316–330.
- [80] M. Y. Li, J. R. Graef, L. K. Wang, and J. Karsai, Global dynamics of a SEIR model with a varying total population size, Math. Biosci., 160 (1999), 191–213.

- [81] M. Y. Li, J. S. Muldowney, Global stability for the SEIR model in epidemiology, Math. Biosci., 125 (2005), 155–164.
- [82] M. Y. Li, J. S. Muldowney, and P. van den Driessche, Global stability for SEIRS models in epidemiology, Can. Appl. Math. Q., 7 (1999), 409–425.
- [83] M. Y. Li, H. L. Smith, L. Wang, Global Dynamics of an Seir Epidemic Model with Vertical Transmission, SIAM J. Appl. Math., 62 (2001), 58-69.
- [84] B. Liu, L. Chen, Y. Zhang, The dynamics of a prey-dependent consumption model concerning impulsive control strategy, Appl. Math. Comput., 169 (2005), 305–320.
- [85] B. Liu, Y. Zhi, L. Chen, The dynamics of a predator-prey model with Ivlev's functional response concerning integrated pest management, Acta Math. Appl. Sin. Engl. Ser., 20 (2004), 133–146.
- [86] S. Liu, E. Beretta, A stage-structured predator-prey model of Beddington-DeAngelis type, SIAM J. Appl. Math., 66 (2006), 1101–1129.
- [87] S. Liu, L. Chen, R. Agarwal, Recent progress on stage-structured population dynamics, Math. Comput. Modelling, 36 (2002), 1319–1360.
- [88] S. Liu, L. Chen, G. Luo and Y. Jiang, Asymptotic behavior of competitive Lotka-Volterra system with stage structure, J. Math. Anal. Appl., 271 (2002), 124–138.
- [89] W. M. Liu, H. W. Hethcote, S. A. Levin, Dynamical behavior of epidemiological models with nonlinear incidence rates, J. Math. Biol., 25 (1987), 359–380.
- [90] W. M. Liu, S. A. Levin, Y. Iwasa, Influence of nonlinear incidence rates on the behavior of SIRS epidemiological models, J. Math. Biol., 23 (1986), 187–204.
- [91] Z. Liu, R. Yuan, Stability and bifurcation in a delayed predator-prey system with Beddington-DeAngelis functional response, J. Math. Anal. Appl., 296 (2004), 521– 537.
- [92] Z. Lu, X. Chi, L. Chen, Impulsive control strategies in biological control of pesticide, Theor. Pop. Biol., 64 (2003), 39–47.
- [93] Z. Lu, X. Chi, L. Chen, The effect of constant and pulse vaccination of a SIR epidemic model with horizontal and vertical transmission, Math. Comput. Modelling, 36 (2002), 1039–1057.
- [94] R. F. Luck, Evaluation of natural enemies for biological control: a behavior approach, Trends Ecol. Evol., 5 (1990), 196–199.
- [95] L. S. Luckinbill, Coexistence in laboratory populations of Paramecium aurelia and its predator Didinium nasutum, Ecology, 54 (1973), 1320–1327.
- [96] A. Margheri, C. Rebelo, Some examples of persistence in epidemiological models, J. Math. Biol., 46 (2003), 564–570.

- [97] R. M. May, Stability and complexity in model ecosystems, Princeton University Press, Princeton, New Jersey, 1973.
- [98] K. McCann, A. Hastings, G. R. Huxel, Weak trophic interactions and the balance of nature, Nature, 395 (1998), 794–798.
- [99] K. McCann, P. Yodzis, Bifurcation structure of a three-species food chain model, Theor. Pop. Biol., 48 (1995), 93–125.
- [100] K. McCann, P. Yodzis, Biological conditions for chaos in a three-species food chain, Ecology, 75 (1994), 561–564.
- [101] X. Meng, Z. Song, L. Chen, A new mathematical model for optimal control strategies of integrated pest management, J. Biol. Sys., 15 (2007), 219–234.
- [102] L. Min, Y. Su, Y. Kuang Global dynamics of a basic virus infection model with application to HBV infection, preprint.
- [103] J. S. Muldowney, Compound matrices and ordinary differential equations, Rocky Mountain J. Math., 20 (1990), 857–872.
- [104] R. M. Nisbet, W. S. C. Gurney, *Modeling fluctuating populations*, Wiley-Interscience, Chichester (1982).
- [105] R. M. Nisbet, W. S. C. Gurney, Stage-structured models of uniform larval competition, Lecture Notes in Biomath. 54, Springer, Berlin, 1984, 97–113.
- [106] R. M. Nisbet, W. S. C. Gurney, J. A. J. Metz, Stage-structured models applied in evolutionary ecology, in Applied Mathematical Ecology, S.A. Levin, T.G. Hallam and L.J. Gross, eds., Springer, Berlin, 1989, 428–449.
- [107] M. A. Nowak and R. M. May, Virus Dynamics: Mathematical Principles of Immunology and Virology, Oxford University Press, New York, 2000.
- [108] J. C. Panetta, A mathematical model of periodically pulsed chemotherapy: tumor recurrence and metastasis in a competition environment, Bull. Math. Biol., 58 (1996), 425–447.
- [109] N. H. Pavel, Differential equations, flow invariance and applications, Pitman Research Notes in Mathematics 113, Pitman, London, 1984.
- [110] E. C. Pielou, Introduction to Mathematical Ecology, Wiley-Interscience, New York, NY, 1969.
- [111] L. P. Pedigo, Entomology and Pest Management (second edition), Prentice Hall Pub., Englewood Cliffs, NJ, 1996.
- [112] L. P. Pedigo, L. G. Higley, The economic injury level concept and environmental quality: a new perspective, Am. Entomologist, 38 (1992), 12–21.

- [113] L. P. Pedigo, S. H. Hutchins, L. G. Higley, Economic injury levels in theory and practice, Annu. Rev. Entomol., 31 (1986), 341–368.
- [114] A. S. Perelson, A. U. Neumann, M. Markowitz, J. M. Leonard, and D. D. Ho, HIV-1 dynamics in vivo: Virion clearance rate, infected cell life-span, and viral generation time, Science, 271 (1996), 1582–1586.
- [115] A. S. Perelson, Modelling viral and immune system dynamics, Nat. Rev. Immunol., 2 (2002), 28–36.
- [116] A. S. Perelson and P. W. Nelson, Mathematical analysis of HIV-1 dynamics in vivo, SIAM Rev., 41 (1999), 3–44.
- [117] F. J. Richards, A flexible growth function for empirical use, J. Exp. Bot., 10 (1959), 290–300.
- [118] M. L. Rosenzweig, Exploitation in three trophic levels, Am. Naturalist, 107 (1973), 275–294.
- [119] M. R. Rosenzweig, Paradox of enrichment: destabilization of exploitation systems in ecological time, Science, 171 (1969), 385–387.
- [120] S. Ruan, W. Wang, Dynamical behavior of an epidemic model with a nonlinear incidence rate, J. Differential Equations, 188 (2003), 135–163.
- [121] G. T. Skalski and J. F. Gilliam, Functional responses with predator interference: viable alternatives to Holling type II model, Ecology, 82 (2001), 3083–3092.
- [122] H. L. Smith, A classification theorem for three dimensional competitive systems, J. Differential Equations, 70 (1987), 325–332.
- [123] H. L. Smith, Monotone dynamical systems: An introduction to the theory of competitive and cooperative systems, Mathematical Surveys and Monographs 41, AMS, Providence, RI, 1995.
- [124] Z. Song, Z. Xiang, The prey-dependent consumption two-prey one-predator models with stage structure for the predator and impulsive effects, to appear in J. Theor. Biol.
- [125] V. M. Stern, R. F. Smith, R. van den Bosch, K. S. Hagen, The integrated control concept, Hilgardia, 29 (1959), 81–101.
- [126] P. van den Driessche, J. Watmough, Reproduction numbers and sub-threshold endemic equilibria for compartmental models of disease transmission, Math. Biosci., 180 (2002), 29–48.
- [127] P. Verhulst, Notice sur la loi que la population suit dans son accroisement, Corr. Math. Phys., 10 (1838), 113–121.

- [128] V. Volterra, Leçons sur la Theorie Mathematique de la Lutte pour la Vie, Gauthier-Villars, Paris, 1931.
- [129] W. Wang, Epidemic models with nonlinear infection forces, Math. Biosci. Eng., 3 (2006), 267–279.
- [130] W. Wang, Global dynamics of a population model with stage structure for predator, in Advanced Topics in Biomathematics, Proceedings of the International Conference on Mathematical Biology, L. Chen et al, eds., World Scientific Publishing Co., Pte. Ltd., 1997, 253–257.
- [131] W. Wang, L. Chen, A predator-prey system with stage structure for predator, Comput. Math. Appl., 33 (1997), 83-91.
- [132] W. Wang, G. Mulone, F. Salemi, V. Salone, Permanence and stability of a stagestructured predator-prey model, J. Math. Anal. Appl., 262 (2001), 499–528.
- [133] D. Xiao, S. Ruan, *Global analysis of an epidemic model with nonmonotone incidence rate*, to appear in Math. Biosci.
- [134] Y. N. Xiao, L. Chen, Global stability of a predator-prey system with stage structure for predator, Acta Math. Sin. (Engl. Ser.), 20 (2004), 63–70.
- [135] P. Yodzis, Predator-prey theory and management of multispecies fisheries, Ecol. Appl., 4 (1994), 51–58.
- [136] S. Zeuzem, R.A. de Man, P. Honkoop, W.K. Roth, S.W. Schalm and J.M. Schmidt, Dynamics of hepatitis B virus infection in vivo, J. Hepatol., 27 (1997), 431–436.
- [137] H. Zhang, L. Chen and P. Georgescu, Impulsive control strategies for pest control, J. Biol. Sys., 15 (2007), 235–260.
- [138] H. Zhang, P. Georgescu and L. Chen, On the impulsive controllability and bifurcation of a predator-pest model of integrated pest management with Beddington-DeAngelis functional response for the predator, to appear in Int. J. Biomath..
- [139] S. Zhang, L. Chen, A Holling II functional response food chain model with impulsive perturbations, Chaos Solitons Fractals, 24 (2005), 1269–1278.
- [140] S. Zhang, L. Chen, A study of predator-prey models with the Beddington-DeAngelis functional response and impulsive effect, Chaos Solitons Fractals, 27 (2006), 237–248.
- [141] S. Zhang, L. Chen, Chaos in three species food chain system with impulsive perturbations, Chaos Solitons Fractals, 24 (2005), 73–83.
- [142] S. Zhang, L. Dong, L. Chen, The study of predator-prey system with defensive ability of prey and impulsive perturbation on the predator, Chaos Solitons Fractals, 23 (2005), 631–643.

- [143] S. Zhang, D. Tan, L. Chen, Dynamic complexities of a food chain model with impulsive perturbations and Beddington-DeAngelis functional response, Chaos Solitons Fractals, 27 (2006), 768–777.
- [144] S. Zhang, F. Wang, L. Chen, A food chain model with impulsive perturbations and Holling type IV functional response, Chaos Solitons Fractals, 26 (2005), 855–866.
- [145] X. Zhang, L. Chen, A. U. Neumann, The stage-structured predator-prey model and optimal harvesting policy, Math. Biosci., 168 (2000), 201–210.
- [146] Y. Zhang, L. Chen, B. Liu, The periodic Holling II predator-prey model with impulsive effect, J. Syst. Sci. Complex., 17 (2004), 555–566.
- [147] H.-R. Zhu, H. L. Smith, Stable periodic orbits for a class of three-dimensional competitive systems, J. Differential Equations, 110 (1994), 143–156.