



CENTRO DE INVESTIGACIÓN EN MATEMÁTICAS.

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DOCTORADO EN CIENCIAS CON ORIENTACIÓN EN  
MATEMÁTICAS APLICADAS.

ANALYTICAL AND NUMERICAL STUDIES OF  
AGE-STRUCTURED PREDATOR-PREY MODELS

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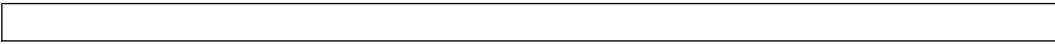
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# Summary

The study of predator-prey models is a very active research area and highly applicable area nowadays. Although classical models date back to the work of Thomas Robert Malthus (1798) and P. F. Verhulst (1837), the basic modeling ideas are still useful in our days. One highly generalized assumption in population models is the homogeneity of their individuals. However, the reality is quite different from this because in a population there are individuals with different characteristics. Furthermore, the natality and mortality coefficients usually depend on the individual's age. Then, in order to improve the modeling of population dynamics it is necessary to take into account the age structure or any other structure in the population which may be considered relevant. The consequences of doing this are an increase in the complexity of the model, the appearance of integro-differential equations and instability of the solutions.

In this work, we introduce a new gamma of age-structured predator-prey models and we study their solutions. These models have age structure in the prey population. The nonlinear analytical tools that we use are the Painlevé test (*P-test*) and the bifurcation theory. The main objective of this study is to propose suitable modeling terms based on *analytical modeling*. In order to do this, we assume general predation terms. This allows us to study a wide variety of models and also to find conditions in such a way that they satisfy the P-test requirements. Then, we look in the set of functions that fulfill those requirements and search for periodic solutions. This is important because the existence of periodic solutions is equivalent to having coexistence between the predator-prey species. When P-test or the integrability conditions are not satisfied we are able to provide characteristics of the solutions. Finally, we study the effect of general birth rate which is important because the initial set of equations change increasing the number of equations. We numerically find that such a birth rate can help to stabilize the model without modifying dramatically the behavior of the model.

# Introduction

The study of predator-prey models is a very active research area these days. This accounts for the large number of papers published yearly on the subject, for example a rapid search using Google Scholar reports 5,290 papers in 2012. When we introduce predator-prey models it is inevitable to mention the founders of population dynamics: T.R. Malthus (1798) and P.F. Verhulst (1837) who proposed linear population growth and the logistic equation, respectively. Later, Lotka [26] and Volterra's [45] work appeared on the competence phenomena between species. They proposed the model:

$$\frac{P(t)}{dt} = P(t)(a - bD(t)) \tag{1}$$

$$\frac{D(t)}{dt} = D(t)(cP(t) - d), \tag{2}$$

where  $P(t)$  is the prey population,  $D(t)$  is the predator population and  $a, b, c$  and  $d$  are positive constants. We can observe from equation (1) that in the absence of predators ( $D(t) = 0$ ) the prey population ( $P(t)$ ) grows in a Malthusian way. Also from equation (1) we note the term  $(a - bP(t))$  is the growth rate of the prey. Then, this rate is reduced by the presence of predators. When the prey population is zero the predator population  $D$  disappears, see equation (2). The term  $cD(t)P(t)$  in (2) is what we call the *Lotka-Volterra predation term*. This model considers that these populations are homogeneous. A further analysis of this model can be also be found in [29].

Clearly, there are different characteristics depending on age such as fertility and mortality rates in a population. Then, a more complete model is obtained by taking into account the age structure of the population. The idea of age structure in population dynamics can be traced back to Leslie (1945) [23]. He proposed a matrix model where different stages of a population were considered:

$$N_0(t + \Delta t) = b_0N_0(t) + b_1N_1(t) + \dots + b_nN_n(t) \tag{3}$$

$$N_1(t + \Delta t) = (1 - d_0)N_0(t) \tag{4}$$

$$N_2(t + \Delta t) = (1 - d_1)N_1(t) \tag{5}$$

$$\vdots \tag{6}$$

$$N_m(t + \Delta t) = (1 - d_{m-1})N_{m-1}(t) \tag{7}$$

$$\vdots \tag{8}$$

$$N_n(t + \Delta t) = (1 - d_{n-1})N_{n-1}(t). \tag{9}$$

There,  $N_i$  is the number of individuals of age in the interval  $[i - 1, i]$ ,  $i = 1, \dots, n$ . The birth rate of the population of  $i$  years is denoted by  $b_i$  and  $d_i$  is the death rate. This model is for one population. We observe that the offspring of each group of age contributes to the population of age zero in (3), the first equation of the model. The model can be written in matrix notation as,

$$\mathbf{N}(t + \Delta t) = A\mathbf{N}(t) \quad (10)$$

where  $A$  is a square matrix and the  $\mathbf{N}(t)$  is the vector,

$$\mathbf{N}(t) = \begin{bmatrix} N_0(t) \\ N_1(t) \\ \vdots \\ N_n(t) \end{bmatrix}. \quad (11)$$

Different models can be constructed using the ideas of Leslie. In particular, predator-prey models can be analyzed using these models. However, the model we study in our work has a discrete version proposed in [40]:

$$P_1(n + 1) = (1 - \mu)P_1(n) + \frac{cB(n)}{1 + kP_2(n)}, \quad (12)$$

$$B(n + 1) = -(\gamma - 2)B(n) + \beta A, \quad (13)$$

$$A(n + 1) = -(\gamma - 2)A(n) + e^\alpha \left( \frac{cB(n + 1)}{1 + kP_2(n + 1)} + \frac{(\mu - 2)cB(n)}{1 + kP_2(n)} \right), \quad (14)$$

$$P_2(n + 1) = bP_2(n) + dB(n)P_2(2) \lambda(1 - e^{-gP_2(n)}), \quad (15)$$

where  $P_1(t)$  is the total prey population,  $B(t)$  is the juvenile prey population, and the predator population is  $P_2(t)$ . All other letters represent positive constants. This predator-prey model considers the age structure in the prey. It is important to remark that this system also exhibits unbounded behavior.

On the other hand, we are interest in continuous models. The equations that describe this phenomenon are described in [17]:

$$\rho_\omega(\omega, t) + \rho_t(\omega, t) + \hat{\mu}\rho(\omega, t) = 0, \quad (16)$$

$$B(t) = \rho(0, t) = \int_0^\infty \beta(\omega, P(t))\rho(\omega, t)d\omega, \quad (17)$$

$$P(t) = \int_0^\infty \rho(\omega, t)d\omega \quad (18)$$

where  $\rho(\omega, t)$  indicates the number of individuals of age  $\omega$  at the time  $t$ , ( $\omega \geq 0$ ),  $t \geq 0$ ),  $P(t)$  is the total population,  $B(t)$  is the juvenile population,  $\beta(\omega, P(t))$



is the birth rate,  $\hat{\mu}$  is the mortality rate,  $\beta(\omega, P(t))$  is the reproductive rate at age  $\omega$  and population  $P(t)$ . All parameters and variables are supposed positive. Our work takes ideas from this work. Predator-prey models with age structure have been analyzed using different techniques [33, 5, 4, 14, 13, 11]. Cushing's book [11] is an excellent starting point of the topic of structured population dynamics. There, discrete and continuous models with age structure are described.

Our work is developed in the context of predator-prey population dynamics with age structure. We study models of two interacting populations: one is the predator population and the second is the prey population. Age structure is assumed in the prey population, which allows us to study predation only on the juvenile population. In addition, cannibalism can also be found in the interaction of certain populations [24]. An undesirable characteristic of population models with age structure is having unstable periodic solutions. These kinds of solutions do not correspond to the biological reality where prey and predator populations can coexist. Among the efforts to reach coexistence are the inclusion of diverse factors such as self-limitation of the prey, harvesting of the prey, and cannibalism of the younger prey, see for example [10, 25, 37].

A related model studied by Cushing in [9] is following model,

$$\frac{dP(t)}{dt} + \mu P(t) = bh(R(t), P(t)) \int_0^\infty \beta \frac{\beta(a)}{da} P(t-a) e^{-\mu a} da, \quad (19)$$

$$\frac{dR(t)}{dt} = rR(t) \left( 1 - \frac{R(t)}{K} \right) - g(R(t), P(t)), \quad (20)$$

where  $P$  is predator population,  $R$  the prey population,  $\mu$  the mortality rate,  $f$  the fecundity rate,  $h$  and  $g$  are the fecundity function and the predation function responses, respectively. In the model, we can see the use of delay differential system of equations, integro-differential equations, general predation function, etc.

As we mentioned, one drawback associated with these previous models is the presence of unbounded oscillations [17]. Therefore, a key feature sought in these models is the long term coexistence of species. The classical approach to finding criteria of mathematical coexistence is through asymptotic stability or global asymptotic stability of a unique equilibrium point or a periodic solution [46, 48]. One of the relevant aspect to consider is the predation of a population on only one age group [24]. Our results deal with these processes but using the Painlevé test. Applications of such tools have been done on predator-prey models, but the age structure has not been taken into account [33]. Besides that, Painlevé tools are usually used to find conditions of integrability.

This work can be understood as the further study of the model presented in [36] where there is a first modification of the way in which the newborns enter the

population and also there the self-limitation was considered:

$$\begin{aligned}
 \frac{dP(t)}{dt} &= -\mu_0 P(t) - \mu P^2 + \frac{B}{1 + kP_2} \\
 \frac{dB(t)}{dt} &= -\theta B(t) - \mu P(t)B(t) + \beta_0 A(t) \\
 \frac{dA(t)}{dt} &= -\theta A(t) - \mu D(t)A(t) + \frac{B}{1 + kP_2} \\
 \frac{dD(t)}{dt} &= -bD(t) + cB(t)D(t) - \lambda(1 - e^{-dP_2}).
 \end{aligned} \tag{21}$$

where  $P_2$  is the predator population and the term  $\lambda(1 - e^{-dP_2})$  represents the fishing on the predator.  $B(t)$  is the prey juvenile population and  $A(T)$  is an auxiliary variable. All other letters are positive constants. In [36] a numerical study with different modelling terms was carried out. Predator-prey coexistence was numerically found with self-limitation.

In our case, one of the techniques we use in this work is based on Painlevé analysis, which has its origin in the work of S.V. Kovalevskaya who was the first to consider the analytical theory of differential equations in physics problems [20]. A criteria to establish necessary conditions to have integrability is the Painlevé test or for short the *P-test*. Another technique used is the theory of bifurcation to analyze the nature of equilibrium and periodic solutions which are of biological interest. The initial model we consider is the following:

$$\begin{aligned}
 \frac{dP(t)}{dt} &= -\mu_o P(t) - \mu P^2 + F(P(t), B(t), A(t), D(t)), \\
 \frac{dB(t)}{dt} &= -\theta B(t) - \mu P(t)B(t) + \beta_0 A(t), \\
 \frac{dA(t)}{dt} &= -\theta A(t) - \mu D(t)A(t) + F(P(t), B(t), A(t), D(t)), \\
 \frac{dD(t)}{dt} &= -bD(t) + cB(t)D(t),
 \end{aligned} \tag{22}$$

where the variables have the same meaning as the previous model but  $D = P_2$ . Its construction is detailed en Chapter 2.

The objective of this thesis is to introduce a new gamma of age-structured population models and to analyze their solutions using the Painlevé analysis and techniques from bifurcation theory, which is what we have called *analytical modeling*. Part of this process will be carried out using the Painlevé test [1, 2, 3] to propose conditions in order to have integrability in the systems by considering solutions where only pole type singularities are allowed [8, 30, 41]. The modeling is also

part of this work, because one of the goals is to describe realistic behavior of both populations, which allows us to propose predation functions where coexistence or stable periodic solutions are difficult to achieve. We also carry out numerical analysis of all models including one with a more general birth rate in order to find important information about biological aspects such as coexistence of predator and prey populations.

### **Specific objectives**

The specific objectives are:

1. To establish functional conditions for juvenile survivors in order to obtain solutions where only pole type singularities are allowed.
2. To allow the predation function in the models to vary in such a way that it allows us more flexibility to succeed in the P-test.
3. To propose viable interaction population functions to achieve coexistence.
4. To study numerically how these previous functions modify the behavior of the system.
5. To search numerically for functions that exhibit periodic solution in the models.
6. To consider new parametrized birth functions in order to propose new age-structured models.



# Age-structured predator-prey models

## 1.1 Age-structured models

The model that we study in this work has evolved from the pioneer work of Gurtin and Mac Camy [17]. They introduced a theory of population dynamics with age dependence. The equations that describe this phenomenon are:

$$\rho_\omega(\omega, t) + \rho_t(\omega, t) + \hat{\mu}\rho(\omega, t) = 0, \quad (1.1)$$

$$B(t) = \rho(0, t) = \int_0^\infty \beta(\omega, P(t))\rho(\omega, t)d\omega, \quad (1.2)$$

$$P(t) = \int_0^\infty \rho(\omega, t)d\omega \quad (1.3)$$

where  $\rho(\omega, t)$  indicates the number of individuals of age  $\omega$  at the time  $t$ , ( $\omega \geq 0$ ),  $t \geq 0$ ),  $P(t)$  is the total population,  $B(t)$  is the juvenile population,  $\beta(\omega, P(t))$  is the birth rate,  $\hat{\mu}$  is the mortality rate,  $\beta(\omega, P(t))$  is the reproductive rate at age  $\omega$  and population  $P(t)$ . All parameters and variables are supposed positive. These equations involve one population, which could be either the predator or the prey.

Equation (16) describes the age structure in the population. The variation in the number of individuals with respect to the age ( $\rho_\omega(\omega, t)$ ) plus its variation with respect to the time  $\rho_t(\omega, t)$ , is proportional to the total number of individuals  $-\hat{\mu}\rho(\omega, t)$ . Equation (17) tells us that the juvenile population is due to the newborn population  $\rho(0, t)$  of age zero. Also, the new births are proportional to the product of the number of individuals times the birth rate. Equation (18) computes the total population by adding the population of all ages. The integral limits are given from zero to infinity, but it could be given up to a finite age.

In the following subsections, we apply this theory to construct a predator-prey model with age structure in the prey population which is the starting point of this thesis.

### 1.1.1 The McKendrick- von Foester equation

To deduce equation (16, we proceed as in [28]. Let us consider a population where  $\rho(\omega, t)$  is the number of individuals of age  $\omega$  at time  $t$ . The number of individuals in the age interval,  $\omega$  to  $\omega + \Delta\omega$ , is computed as follows:

$$P(t, \omega) = \int_{\omega}^{\omega+\Delta\omega} \rho(\psi, t) d\psi. \quad (1.4)$$

Assuming that there is no migration, then the change in this population is caused by the arrival of individuals who have reached age  $\omega$ , the outcome of individuals who become older than the age group  $\rho(\omega + \Delta\omega, t)$ . And finally, the natural death of the members occurred in this age group. Then, we obtain

$$\frac{d}{dt}P(t, \omega) = \rho(\omega, t) - \rho(\omega + \Delta\omega, t) - \hat{\mu}P(t) \quad (1.5)$$

and using equation (1.5), we find,

$$\int_{\omega}^{\omega+\Delta\omega} \frac{\partial}{\partial t} \rho(\psi, t) d\psi = \rho(\omega, t) - \rho(\omega + \Delta\omega, t) - \hat{\mu} \int_{\omega}^{\omega+\Delta\omega} \rho(\psi, t) d\psi \quad (1.6)$$

where  $\hat{\mu}$  is the mortality rate. Next, we divide the function by  $\Delta\omega$  and we take the limit as  $\Delta\omega$  tends to zero, we obtain,

$$\lim_{\Delta\omega \rightarrow 0} \left[ \frac{1}{\Delta\omega} \int_{\omega}^{\omega+\Delta\omega} \frac{\partial}{\partial t} \rho(\psi, t) d\psi + \hat{\mu} \frac{1}{\Delta\omega} \int_{\omega}^{\omega+\Delta\omega} \rho(\psi, t) d\psi + \frac{\rho(\omega + \Delta\omega, t) - \rho(\omega, t)}{\Delta\omega} \right] = 0.$$

The result is the so called McKendrick- von Foester equation.

$$\frac{\partial}{\partial t} \rho(\omega, t) + \hat{\mu} \rho(\omega, t) + \frac{\partial}{\partial \omega} \rho(\omega, t) = 0. \quad (1.7)$$

or for short:

$$\rho_t + \rho_{\omega} + \hat{\mu} \rho = 0. \quad (1.8)$$

A different construction of this equation that shows the relation between the Leslie's work [23] and the equation of MacKendrick can be found in [11].

### 1.1.2 A first model

In order to get a well defined model, it is necessary to have a specific birth rate of the population ( $\beta(\omega)$ ) and it is also necessary to define the mortality rate. Our birth rate selection is

$$\beta(\omega) = \beta_0 \omega e^{-\alpha \omega} \quad (1.9)$$

with  $\beta_0 > 0$  and  $\alpha \geq 0$ . This function is particularly suitable for biological aspects because it is zero for newborns and small for ages close to zero. This is because newborns usually do not reproduce at early stages. Another characteristic is that the birth rate increases with age up to a maximum for the young adults and it decreases to zero when age becomes advanced ( $\omega$  tends to infinity). In addition to this, if  $\alpha > 0$ , the birth rate suits well for many mammals. When  $\alpha = 0$  then  $\beta = \beta_0 \omega$  which may be appropriate for certain fish species, where fertility increases with age.

The mortality rate  $\hat{\mu}$  can depend on the age of the total population or it can depend on the number of individuals of another population, for example the predators. In our case we will consider  $\hat{\mu}$  to be independent of age.

Now, we construct a system of differential equations which includes the variables of the total population,  $P(t)$  and the population of newborns  $B(t)$ . In order to do this, we take equation (18)

$$\frac{d}{dt}P(t) = \int_0^\infty \frac{\partial}{\partial t} \rho(\omega, t) d\omega. \quad (1.10)$$

Then, we substitute the equation of MacKendrick (1.7) in (1.10),

$$\frac{d}{dt}P(t) = - \int_0^\infty \frac{\partial}{\partial \omega} \rho(\omega, t) d\omega - \hat{\mu} \int_0^\infty \rho(\omega, t) d\omega \quad . \quad (1.11)$$

Using the fundamental theorem of calculus and assuming that  $\rho(\omega, t) \rightarrow 0$  as  $\omega \rightarrow \infty$  we get,

$$\frac{dP(t)}{dt} = \rho(0, t) - \hat{\mu}P(t). \quad (1.12)$$

The equation for  $B(t)$  is obtained by multiplying equation (16) by  $\beta(\omega)$  and then we integrate it from zero to infinity,

$$\int_0^\infty \beta(\omega) \frac{\partial}{\partial \omega} \rho(\omega, t) d\omega + \frac{d}{dt} \int_0^\infty \beta(\omega) \rho(\omega, t) d\omega + \hat{\mu} \int_0^\infty \beta(\omega) \rho(\omega, t) d\omega = 0 \quad (1.13)$$

$$\int_0^\infty \beta(\omega) \frac{\partial}{\partial \omega} \rho(\omega, t) d\omega + \frac{d}{dt} B(t) + \hat{\mu} B(t) = 0. \quad (1.14)$$

This is an integro-differential equation. However, if we use integration by parts in the equation (1.14)

$$\int_0^{\infty} \beta(\omega) \frac{\partial}{\partial \omega} \rho(\omega, t) d\omega = \beta_0 \int_0^{\infty} \omega e^{-\alpha\omega} \frac{d}{d\omega} \rho(\omega, t) d\omega \quad (1.15)$$

$$= \beta_0 \omega e^{-\alpha\omega} \rho(\omega, t) \Big|_{\omega=0}^{\infty} - \beta_0 \int_0^{\infty} (1 - \alpha\omega) e^{-\alpha\omega} \rho(\omega, t) d\omega$$

$$= -\beta_0 \int_0^{\infty} e^{-\alpha\omega} \rho(\omega, t) d\omega + \beta_0 \int_0^{\infty} \alpha\omega e^{-\alpha\omega} \rho(\omega, t) d\omega$$

$$= -\beta_0 \int_0^{\infty} e^{-\alpha\omega} \rho(\omega, t) d\omega + \alpha B(t).$$

(1.16)

When we plug this integral in (1.14) we have the equation for the juvenile population,

$$\alpha B(t) - \beta_0 \int_0^{\infty} e^{-\alpha\omega} \rho(\omega, t) d\omega + \frac{d}{dt} B(t) + \hat{\mu} B(t) = 0. \quad (1.17)$$

Solving for  $\frac{d}{dt} B(t)$ ,

$$\frac{d}{dt} B(t) = \beta_0 \int_0^{\infty} e^{-\alpha\omega} \rho(\omega, t) d\omega - (\hat{\mu} + \alpha) B(t). \quad (1.18)$$

This is still an integro-differential equation but if we define an auxiliary function as,

$$A(t) = \int_0^{\infty} e^{-\alpha\omega} \rho(\omega, t) d\omega, \quad (1.19)$$

the equation for the juveniles is then,

$$\frac{d}{dt} B(t) = \beta_0 A(t) - (\hat{\mu} + \alpha) B(t). \quad (1.20)$$

We can say that this is an auxiliary variable produced by the selection of the birth rate.  $A(t)$  also satisfies the following differential equation,

$$\frac{d}{dt} A(t) = \rho(0, t) - (\hat{\mu} + \alpha) A(t). \quad (1.21)$$

In order to summarize this section we put together the equations for one age-



structured population:

$$\begin{aligned}\frac{dP}{dt} &= -\hat{\mu}P + \rho(0, t) \\ \frac{dB}{dt} &= -\theta B + \beta_0 A \\ \frac{dA}{dt} &= -\theta A + \rho(0, t)\end{aligned}\tag{1.22}$$

where  $b, c$ , and  $\theta = \alpha + \hat{\mu}$  are positive constants.

This set of equations were deduced following Gurtin and MacCamy's theory (16)-(18). They assumed that the term  $\rho(0, t)$  is equal to the baby population  $B(t)$ . However, a significant change is made in this work by taking this term as a general function that depends on the other population variables,

$$\rho(0, t) = F(P(t), B(t), A(t), D(t)).\tag{1.23}$$

Finally, this model stands for one population which we will set as the prey population. Our beginning model is for a predator-prey interaction. We assume that the predator population,  $D$ , behaves according to a Lotka-Volterra type equation, but feeding only on the newborns. The complete model is then,

$$\begin{aligned}\frac{dP}{dt} &= -\hat{\mu}P(t) + F(P(t), B(t), A(t), D(t)) \\ \frac{dB}{dt} &= -\theta B(t) + \beta_0 A(t) \\ \frac{dA}{dt} &= -\theta A(t) + F(P(t), B(t), A(t), D(t)) \\ \frac{dD}{dt} &= -bD(t) + cB(t)D(t)\end{aligned}\tag{1.24}$$

where the coefficients  $b$  and  $c$  are positive. We will refer this model as our *basic model without self-limitation*.

### 1.1.3 Self-limitation of the prey population

A second aspect in which we are interested is the limitation in the prey caused by the growth of the prey population. This can understood as a lack of food resources or overpopulation in the prey population. The effect of such self-limitation is modeled in our system by considering that the mortality function depends linearly on the total prey population, that is,

$$\hat{\mu} = \mu_0 + \mu P\tag{1.25}$$

with  $\mu_0$  and  $\mu$  are positive constants. If we incorporate (1.25) to the system, the resulting equations become:

$$\begin{aligned}\frac{dP(t)}{dt} &= -\mu_0 P(t) - \mu P^2 + F(P(t), B(t), A(t), D(t)) \\ \frac{dB(t)}{dt} &= -\theta B(t) - \mu P(t)B(t) + \beta_0 A(t) \\ \frac{dA(t)}{dt} &= -\theta A(t) - \mu D(t)A(t) + F(P(t), B(t), A(t), D(t)) \\ \frac{dD(t)}{dt} &= -bD(t) + cB(t)D(t).\end{aligned}\tag{1.26}$$

With this model we begin our study and search of new models based the *analytical modeling*.

# Aspects of nonlinear analysis

## 2.1 Introduction

The objective of this chapter is to provide an introduction to the nonlinear tools that we have used to achieve our objectives. The first one is the Painlevé test [30, 32] which is an algorithm based on the theory of nonlinear differential equations in the complex plane. The second one is the bifurcation theory, centered in bifurcation of equilibria and Hopf bifurcations. For the numerical analysis we use AUTO, the software developed by Doedel [12], which is a powerful tool for the continuation of asymptotic solutions such as equilibrium points and periodic solutions.

## 2.2 The Painlevé Property

To begin with, we give a historic overview of the Painlevé analysis. Later, we explain in detail the Painlevé test. In [7] we can find a panoramic review of the Painlevé property in different areas. The historic references are taken from [43].

### 2.2.1 The work of Sofia Kovalevskaya and Paul Painlevé

Kovalevskaya was the first one to use a method based on the complex variable theory to study a physical problem [20]. She was interested in the motion of a heavy top about a fixed point. The system consisted of the following six first-order,

nonlinear differential equations:

$$\begin{aligned}
 A \frac{dp}{dt} &= (B - C)qr - \beta z_0 + \gamma y_0 \\
 B \frac{dq}{dt} &= (C - A)pr - \gamma x_0 + \alpha z_0 \\
 C \frac{dr}{dt} &= (A - B)pq - \alpha y_0 + \beta x_0 \\
 \frac{d\alpha}{dt} &= \beta r - \gamma q \\
 \frac{d\beta}{dt} &= \gamma p - \alpha r \\
 \frac{d\gamma}{dt} &= \alpha q - \beta p
 \end{aligned} \tag{2.1}$$

where  $p, q, r$  are the components of angular velocity and  $\alpha, \beta, \gamma$ , are the direction cosines describing the orientation of the top. The rest of the variables are parameters. Kovalevskaya searched for solutions in the complex plane allowing that functions have singularities of only pole type. She won the Bordin prize of the Paris Academy of Science in 1888 because she found a first integral using this method:

$$I = (p^2 - q^2 - \frac{x_0}{C}\alpha) + (2pq - \frac{x_0}{C}\beta). \tag{2.2}$$

Her work was considered a special case where analytic theory could be used. Meanwhile, Paul Painlevé (1863-1933), was a French mathematician who was interested in the classification of second-order differential equations of the form,

$$\frac{d^2t}{dx^2} = F\left(\frac{dy}{dx}, y, x\right) \tag{2.3}$$

where  $F$  is an analytic function in  $x$  and a rational function in  $y$  and  $dy/dx$ . He and his coworkers found 50 types of equations whose only movable singularities were poles. They also found six new functions defined as solutions of nonlinear ordinary differential equations which could not be written in terms of known functions such as polynomial, trigonometric functions, etc. They are called Painlevé transcendents [43].

### 2.2.2 Revival of Painlevé ideas

The current research on Painlevé's ideas is due to several papers, in particular Ablowitz, Ramani and Segur (ARS) [2]. They noted that reductions of partial differential equations of soliton type gave rise to ordinary differential equations

whose movable singularities were exclusively poles. They conjectured that “ All reductions of complete integrable partial differential equations are of Painlevé type, perhaps only after a change of variables”. ARS proposed an algorithm known as the Painlevé test which gives conditions such that an ordinary differential equation to be of Painlevé type. This is the tool we amply use in this work and it needs to be described later on this chapter. Since then, a lot of research has been carried out applying the P-test to different models in the physical and non physical areas. An important fact was the extension of the P-test to partial differential equations by Weiss, Tabor and Carnevale [47].

### 2.2.3 Definitions and conventions

Here we introduce basic definitions in the context of ordinary differential equations in the complex plane in order to describe efficiently the Painlevé algorithm. In the following, we will consider an ordinary differential equation of the form,

$$w'(z) = F[z, w(z)] \quad (2.4)$$

where we assume that the function  $F(z, w(z))$  is an analytic function,  $w(z)$  is vector value in  $\mathbb{C}^n$ ,  $z$  is a complex variable, and  $F(z, w(z))$  is a holomorphic mapping of  $\mathbb{C}^{n+1}$  to  $\mathbb{C}^n$

**Definition 2.2.1.** A *singularity* is a point at which the solution of an ordinary differential equation is not holomorphic or analytic.

*Example 2.2.2.* Let us assume that the function  $F(z) = \frac{1}{z}$  is a solution of a given ordinary differential equation. It has a singularity at  $z = 0$ .

**Definition 2.2.3.** Singularities can be either **fixed** given by the ordinary differential equation or movable which means that it depends on the initial conditions.

*Example 2.2.4.* The equation  $w' = 1 + w^2$  is satisfied by the function  $w = \tan(z - z_0)$ . It has singularities in  $z = z_0 + \frac{1}{2}(2n + 1)\pi$  which are movable because  $z_0$  is arbitrary.

*Example 2.2.5.* The equation  $zw''(z) = [w(z)]^2$  has fixed singularities which are  $z = 0$  and  $z = \infty$ .

**Definition 2.2.6.** A *critical point* is a singularity at which branching takes place.

*Example 2.2.7.* For the complex function  $f(z) = \log(z)$  shows the branching.

**Definition 2.2.8.** A differential equation is said to have the **Painlevé property** if its general solution has no movable critical points.

This previous definition is equivalent to find conditions for the solution  $\omega(z)$  of (2.4), which can be written as the following Laurent series,

$$\omega(z) = \sum_{i=1}^k \alpha_{-i}(z - z_0)^{-i} + \sum_{i=0}^{\infty} \alpha_i(z - z_0)^i. \quad (2.5)$$

where  $z_0$  is an arbitrary point in the complex plane. For an ordinary differential equation to be of P-type, it is necessary that it has no movable branch points i.e. logarithmic or algebraic.

### 2.2.4 The ARS Painlevé test or P-test

In this subsection, we describe the Painlevé test or P-test as it is presented in [2]. We make the following assumptions:

1. We will consider a  $n$ -th order system of an ordinary differential equation of the form

$$\frac{dw_j}{dz} = F_j(z; w_1, w_2, \dots, w_n), \quad j = 1, \dots, n, \quad (2.6)$$

where the function  $F_j$  is analytic in  $z$  and rational in its other arguments.

2. We assume that the dominant behavior of the function in a sufficiently small neighborhood of a movable singularity is algebraic:

$$w_j \sim \alpha_j(z - z_0)^{p_j} \quad z \rightarrow z_0. \quad (2.7)$$

These assumptions do not exclude logarithmic branch points. An ordinary differential equation still admits movable essential singularities and the P-test does not identify essential singularities.

#### 2.2.4.1 First step of the Painlevé test

Substitute

$$w_j \sim \alpha_j(z - z_0)^{p_j}, \quad j = 1, \dots, n, \quad (2.8)$$

into (2.6) and determine the  $\mathbf{p} = \{p_j\}_{j=1}^n$  for which there are two or more terms in the system of equations such that in each equation they balance. It also depends on the choice of the  $\alpha_i$ 's, and the rest of terms in the equation can be ignored when  $z \rightarrow z_0$  because they do not have the higher negative power  $p_j$  and they are “dominated” by the *leading order terms*.

**Definition 2.2.9.** For such a choice of  $p_j$ , the terms which balance are called the *leading order term or dominant terms*

The choices of  $\{p_j\}_{i_1}^n$  might be several. If any of the  $p_j$  is not an integer, and if (2.8) is asymptotic near  $z_0$  then it represents the dominant behavior in the neighborhood of a movable algebraic branch point of order  $p$ . It means that the system (2.6) is not of Painlevé type or *P-type*. To prove that (2.8) is asymptotic, define the new variable  $v = w^{1/p}$  and rewrite the system (2.6) in terms of  $v$ . By construction,  $v$  vanishes at  $z_0$  and  $\frac{dv}{dz}$  is finite. We have to show that  $v(z)$  is analytic.

The P-test stops unless the only possible  $p_j$  are integers.

If all possible  $p$ 's are integers, then for each  $p$ , (2.8) may represent the first term in the Laurent series, valid in a deleted neighborhood of a movable pole. Then, the solution of the system (2.6) is

$$w(z) = (z - z_0)^p \sum_{j=0}^{\infty} (z - z_0)^j, \quad |z - z_0| < R. \quad (2.9)$$

If there are  $n-1$  arbitrary coefficients  $\{a_j\}$ , then there are  $n$  constants of integration of the system of ordinary differential equations because  $z_0$  is already arbitrary.

**Definition 2.2.10.** The power at which these arbitrary constants enter are called the *resonances*.

**Remark**  $z_0$  is an arbitrary constant in the series (2.9). This constant is determined by the initial condition. For example, in the equation  $\frac{dx}{dz} = x$ , its general solution is  $x(z) = e^{-z_0} e^z = ce^z$ ,  $z_0$  (or  $c$ ) an arbitrary constant. If the initial condition is  $x(z_0) = x_0$  then the solution is  $x(z) = x_0 e^{z-z_0}$ .

#### 2.2.4.2 An example of the P-test application

In this section we present an example of the first step of the Painlevé test. It was taken from the book [8]. Let us consider the Lorenz model:

$$\begin{aligned} \frac{dx}{dt} &= \sigma(x - y), \\ \frac{dy}{dt} &= rx - y - xz, \\ \frac{dz}{dt} &= xy - bz, \end{aligned} \quad (2.10)$$

where  $\sigma$ ,  $r$  and  $b$  are the coefficients of the system.

**First step. Find the dominant behavior** We look for solutions of pole type by proposing as possible solutions the following ansatz for the system variables  $x$ ,  $y$  and  $z$ ,

$$x \sim x_0 \chi^{p_1}, \quad (2.11)$$

$$y \sim y_0 \chi^{p_2}, \quad (2.12)$$

$$z \sim z_0 \chi^{p_3}, \quad (2.13)$$

where we assume that  $(x_0, y_0, z_0) \neq (0, 0, 0)$ ,  $\chi = t - t_0$  and the  $p_j$ , are to be determined. Observe that system (2.10) corresponds to the system (2.6) and that the variables  $x$ ,  $y$  and  $z$  are the  $w_j$  for  $j = 1, 2, 3$ , respectively. Also, the coefficients  $x_0$ ,  $y_0$ ,  $z_0$  are the  $\alpha_j$  for  $j = 1, 2, 3$ , respectively. The simbol  $\sim$  means that we are interested in the asymptotic behavior when  $t \rightarrow t_0$ . Then, we substitute in the system (2.10). We require that at least one  $p_j$ ,  $j = 1, 2, 3$  to be a negative integer.

$$\frac{d(x_0 \chi^{p_1})}{dt} = p_1 x_0 \chi^{p_1-1} = \sigma(x_0 \chi^{p_1} - y_0 \chi^{p_2}), \quad (2.14)$$

$$\frac{d(y_0 \chi^{p_2})}{dt} = p_2 y_0 \chi^{p_2-1} = r x_0 \chi^{p_1} - y_0 \chi^{p_2} - (x_0 \chi^{p_1})(z_0 \chi^{p_3}), \quad (2.15)$$

$$\frac{d(z_0 \chi^{p_3})}{dt} = p_3 z_0 \chi^{p_3-1} = x_0 \chi^{p_1} y_0 \chi^{p_2} - b z_0 \chi^{p_3}. \quad (2.16)$$

Let us focus on the equation one (2.14) of the last system. There are three terms and their corresponding powers are:  $p_1 - 1$ ,  $p_1$  and  $p_2$ .  $p_1 - 1$  dominates to  $p_1$  because is more negative and in fact they can not equal. Then, this power has to balance with the power  $p_2$  and their corresponding dominant terms are  $\frac{dx}{dt}$  and the  $-\sigma y$  in the first equation. It is easy to see that we obtain the following system of linear equations when we balance the more dominant powers in equations (2.14-2.16):

$$p_1 - 1 = p_2, \quad (2.17)$$

$$p_2 - 1 = p_1 + p_3, \quad (2.18)$$

$$p_3 - 1 = p_1 + p_2. \quad (2.19)$$

Then, by solving for the  $p_i$  we get  $(p_1, p_2, p_3) = (-1, -2, -2)$ . It is possible to have more than one set of values for the  $p_i$ 's satisfying this system and such values of  $p_i$ 's must also be considered. The system obtained for the coefficients is,

$$-p_1 x_0 + \sigma y_0 = 0,$$

$$-p_2 y_0 - x_0 z_0 = 0,$$

$$-p_3 z_0 + x_0 y_0 = 0,$$



and its solution is  $(x_0, y_0, z_0) = (2i, -2i\sigma^{-1}, 2\sigma^{-1})$ ,  $i^2 = -1$ . By substituting the exponents  $(p_1, p_2, p_3) = (-1, -2, -3)$  and the coefficients  $(x_0, y_0, z_0) = (2i, -2i\sigma^{-1}, 2\sigma^{-1})$ , in the Laurent series we obtain:

$$x(t) = \sum_{j=-1}^{p_1} \alpha_j(t-t_0)^j + \sum_{j=0}^{\infty} \alpha_i(t-t_0)^i =$$

$$y(t) = \sum_{j=-1}^{p_2} \beta_j(t-t_0)^j + \sum_{j=0}^{\infty} \beta_i(t-t_0)^i =$$

$$z(t) = \sum_{j=-1}^{p_3} \alpha_j(t-t_0)^j + \sum_{j=0}^{\infty} \gamma_i(t-t_0)^i =$$

$$= 2i(t-t_0)^{-1} + \sum_{i=0}^{\infty} \alpha_i(t-t_0)^i \quad (2.20)$$

$$= -2i\sigma^{-1}(t-t_0)^{-2} + \sum_{i=-1}^{\infty} \beta_i(t-t_0)^i \quad (2.21)$$

$$= 2\sigma^{-1}(t-t_0)^{-3} + \sum_{i=-2}^{\infty} \gamma_i(t-t_0)^i \quad (2.22)$$

where  $t_0$  is an arbitrary point in the complex plane. At this point we have finished the application of the first step of the P-test to the Lorenz model.

### 2.2.4.3 Second step of the Painlevé test

Let us go back to the general system of ordinary differential equations (2.6). At this stage of the P-test we have found the exponents and coefficients of the dominant terms, i.e. the  $(p_j, \alpha_j)$ . In the second step, we will construct a simplified system retaining only the leading terms. Then, we substitute the simplified equations

$$w_j = \alpha_j(z-z_0)^{p_j} + \kappa_j(z-z_0)^{p_j-r}, \quad j = 1, \dots, n \quad (2.23)$$

with the same  $r$  for every  $w_j$ . Using the leading order in  $\beta = (\beta_1, \beta_2, \dots, \beta_n)^T$ , we can obtain the system of equations:

$$[Q(r)] = 0 \quad (2.24)$$

where  $[Q]$  is an  $n \times n$  matrix, whose elements depend on  $r$ . The resonances are the nonnegative roots of

$$\det[Q(r)] = 0. \quad (2.25)$$

This equation corresponds to the “ indicial equation” in the method of Frobenius for finding solutions of a linear ordinary differential equation near a regular singular point. The aspects that must be remembered when performing this step are:

- i) The value  $r = -1$  represents the arbitrariness of  $z_0$ . Then  $-1$  is always a root.
- ii) If any  $\alpha_j$  results arbitrary in the first step then zero is also a root. The converse is not always true. If we apply the change of variables  $\omega = f(\text{Ln}(z-z_0))/(z-z_0)$  and we obtain as a result the analyticity of the solutions then we have a logarithmic branch point in the original equation.
- iii) If a root  $r$  of the indicial equation is  $\text{Re}(r) < 0$  then, it must be ignored because the dominant term was already found.
- iv) Any root  $\text{Re}(r) > 0$  means that the ordinary differential equation is not of P-type.
- v) If the roots  $\det Q(j)$ , besides  $-1$  and  $0$ , are positive then there are no algebraic branch points.
- vi) If  $\det Q(r)$  has  $n-1$  distinct roots and they are non-negative then it is possible to represent the solution by the Laurent series.

#### 2.2.4.4 Example of the second step of the P-test

We recall the example of the Lorenz model (2.10). Then, according to the algorithm described in the second step, we have to find the location  $r$  at which arbitrary coefficients may be in the Laurent series. This can be directly done substituting,

$$X \sim x_0 \chi^{p_1} + \kappa_1 \chi^{r+p_1}, \quad (2.26)$$

$$Y \sim y_0 \chi^{p_2} + \kappa_2 \chi^{r+p_2}, \quad (2.27)$$

$$Z \sim z_0 \chi^{p_3} + \kappa_3 \chi^{r+p_3}, \quad (2.28)$$

in the system formed by the dominant terms of system (2.10):

$$\begin{aligned} \frac{dx}{dt} &= -\sigma y, \\ \frac{dy}{dt} &= -xz, \\ \frac{dz}{dt} &= xy. \end{aligned} \quad (2.29)$$

The matrix corresponding to an arbitrary coefficient is obtained by considering the linear part in the variables  $(\kappa_1, \kappa_2, \kappa_3)$  which stands for the arbitrary coefficients  $\kappa_j$ ,

$$\mathbf{P}_r \begin{pmatrix} \kappa_1 \\ \kappa_2 \\ \kappa_3 \end{pmatrix} = \begin{pmatrix} -r + p_1 & \sigma & 0 \\ z_0 & -r + p_2 & -x_0 \\ y_0 & x_0 & -r - p_3 \end{pmatrix} \begin{pmatrix} \kappa_1 \\ \kappa_2 \\ \kappa_3 \end{pmatrix} = \quad (2.30)$$

$$\begin{pmatrix} -r + 1 & \sigma & 0 \\ 2\sigma_{-1} & -r + 2 & -2i \\ -2i\sigma^{-1} & 2i & -r + 2 \end{pmatrix} \begin{pmatrix} \kappa_1 \\ \kappa_2 \\ \kappa_3 \end{pmatrix} \quad (2.31)$$

and equation

$$\det \mathbf{P}_r = -(r + 1)(r - 2)(r - 4) = 0 \quad (2.32)$$

is the so called the *indicial equation* and its roots are the Fuchs indices.

An equivalent way to obtain this solution is to substitute equation (2.20- 2.22) in the system of equations (2.10) and to write as a linear equations system for the coefficients of the Laurent series. Then, a recursive relation for the  $r$ -th coefficient  $(x_r, y_r, z_r)$  of the Laurent series, using matrix notation, is obtained,

$$\mathbf{P}_r(x_r, y_r, z_r)^T + \mathbf{Q}_r = 0 \quad (2.33)$$

or explicitly

$$\begin{pmatrix} -r + 1 & \sigma & 0 \\ 2\sigma_{-1} & -r + 2 & -2i \\ -2i\sigma^{-1} & 2i & -r + 2 \end{pmatrix} \begin{pmatrix} x_r \\ y_r \\ z_r \end{pmatrix} + \begin{pmatrix} -\sigma x_{r-1} \\ \sum_{k=1}^{r-1} x_k z_{r-k} + r x_{r-1} - y_{r-1} \\ \sum_{k=1}^{r-1} x_k y_{r-k} - b z_{r-1} \end{pmatrix} = 0 \quad (2.34)$$

in which the  $\mathbf{P}_j$  is a square matrix depending only on the index  $r$  and the leading  $p_i$ ,  $x_0$ ,  $y_0$ ,  $z_0$  found in the first step (dominant terms). This represents a linear system for each  $r$ . The problem of finding arbitrary coefficients of the Laurent series translates into a linear algebra problem of finding multiple solutions of singular matrix. In order to allow arbitrary coefficients the matrix  $\mathbf{P}_j$  must be singular and its roots have to be positive integers. Solving the indicial equation is equivalent to allowing arbitrary coefficients of the Laurent series. However, the vector must be in the range of matrix  $\mathbf{P}_r$  otherwise there will not be an  $r$  that solves equation (2.33).

### 2.2.4.5 Third step. The compatibility condition

As we mentioned, the problem of representing a solution by the Laurent series turns into a linear algebra problem. This condition requires the vector in equation (2.33) to be in the range of the matrix  $\mathbf{P}_j$ . This is accomplished by computing the recursive relations to form the Laurent series up to the location of the arbitrary coefficients.

## 2.3 Integrability and the Painlevé property

We have described the Painlevé property and the P-Test. The first related to *integrability* and the second to test necessary conditions to achieve this property. However, what it is not clear is what meant by integrability. The ideas associated with integrability usually are globally soluble. Even though the Painlevé consists of a local analysis. It also implies that solutions of the system exhibits global regular behavior, i.e. its solutions are sensitive to initial conditions. On the other hand, a non-integrable system generally implies that its solutions behave in an irregular way (sensitive to initial conditions) diverging from the average at an exponential rate. As a conclusion of the ideas discussed in [49] about integrability we can say there is not definition of integrability suitable for all problems. For example, if we use the definition of integrability by quadratures the equation  $\dot{x} = x^2 + t$  can not be integrated by quadratures, but it admits a linearization that expresses the solution in terms of Airy function. Then, it is integrable in such a sense.

When we think of an Hamilton system with  $n$ -degree of freedom then the existence of  $n$ -independent integrals in involution is what we call Liouville integrability. For a system of ordinary differential equations, integrability is the existence of  $n - 1$  independent analytic integrals. These are two definitions of integrability which are compatible because an integral of an Hamiltonian system is generally not integrable as an ordinary differential system.

We can also have the notion of integrability in partial differential equations. For example the existence of conservation laws which implies that the flow of the equations is constrained by an infinite set of symmetries. And this idea led to the discovery of the Inverse Scattering Transform (IST) which integrates the KdV equation. We can say that the IST is the analogue to the Arnol'd Liouville integrability for the infinite dimensional case. This method was found when researchers were looking for an infinite set of conservation laws. However, the nonexistence of such conservation laws does no preclude integrability.

This Painlevé test is one of the most powerful methods to identify integrable systems despite the kind of integrability we are looking for. It has been useful to find integral of equations, leads to Lax Pair, Bäcklund transformation, etc. This method has also shown that can reveal geometric properties and the algebraic structure that underlies many integrable equations.

We use this method to restrict our search of possible solutions of the systems that we study in such a way they only have singularities of pole type. The underlying idea is that we will obtain solutions with this property. This could lead to obtain regular solutions more easily. Another desirable characteristic we search is periodicity.

## 2.4 Bifurcation theory

Here we give a review of some aspects of bifurcation theory, starting with the implicit function theorem and some of the bifurcation results on which we base our numerical bifurcation study. This section follows the book [42].

Let us consider the problem of the following form,

$$f(\lambda, x) = 0 \tag{2.35}$$

where  $f$  is an operator on  $\mathbb{R} \times B_1$  into  $B_2$ , with  $B_1$  and  $B_2$  Banach spaces. One might think this equation as an ordinary differential system of equations.  $\lambda$  is the parameter we are interested in varying. Then, we seek conditions on  $f$  such that when a solution  $(\bar{\lambda}, \bar{x})$  of (2.35) lies on a curve of solutions or bifurcation diagram  $(\lambda, x(\lambda))$  at least in a neighborhood of  $\bar{\lambda}$ . It might also be required that  $(\bar{\lambda}, \bar{x})$  lies on several curves.

**Definition 2.4.1.** *Let us assume that  $\Gamma : (\lambda, x(\lambda))$ , is a curve of solutions of (2.35) and  $(\lambda_0, x_0) \equiv (\lambda_0, x(\lambda_0))$  be an interior point on this curve, with the property that every neighborhood of  $(\lambda_0, x_0)$  in  $\mathbb{R} \times B$  contains solutions of (2.35) which are not on  $\Gamma$ . Then,  $(\lambda_0, x_0)$  is called a **bifurcation point** with respect to  $\Gamma$ .*

There are several questions in bifurcation theory. Among them we can mention: given a curve  $\Gamma$  of solutions of (2.35), what are the conditions to have a bifurcation point? Given this curve, can it be continued? Does secondary bifurcation occur? These questions can be solved by the systematic use of the implicit function theorem.

### 2.4.1 The implicit function theorem

In order to state the main bifurcation theorems, we review some important definitions and notations. If  $a \in \Omega$  the derivative of  $f$  at  $a$ , written  $f'(a)$  or  $df_a$ , is the  $n \times m$  matrix

$$df_a = \frac{\partial f_i(a)}{\partial x_j} \tag{2.36}$$

where  $f = (f_1, f_2, \dots, f_n)$ . Hence,  $df_a \in B(\mathbb{R}^m, \mathbb{R}^n)$  where  $B(\mathbb{R}^m, \mathbb{R}^n)$  represents the set of bounded linear maps  $\mathbb{R}^m \rightarrow \mathbb{R}^n$ . Let  $\Omega$  be an open subset of  $\mathbb{R}^m$ , and suppose that  $f \in C^1(\Omega, \mathbb{R}^n)$ , where  $C^1$  is the set of functions having one continuous derivative. More generally,  $C^k(B_1, B_2)$  is the space of continuous functions having  $k$  continuous derivatives with  $k \in \mathbb{Z}^+$  which are defined on  $B_1$  and take values on  $B_2$ . We are going to consider functions defined on product spaces. Let

$B_1, B_2$  and  $B_3$  be Banach spaces and let  $U$  be open in  $B_1 \times B_2$ . If  $f : U \rightarrow B_3$ , and  $u = (u_1, u_2) \in U$ , we let  $U_1$  be the cross section,  $U_1 = \{x_1 \in B_1 : (x_1, u_2) \in U\}$ . We say that  $f$  is differentiable with respect to the  $x_1$  variable at  $(u_1, u_2)$  if the function  $g(x_1) = f(x_1, u_2)$  is differentiable with respect to  $x_1$  at  $u_1$ . When this holds, we write  $dg_u = D_1f(u_1, u_2)$ ;  $dg_u$  is a linear map from  $U_1$  into  $B_3$ .  $f$  is said differentiable with respect to  $x_1$  on  $U$ , if it is differentiable with respect to  $x_1$  at each  $u \in U$ . The usual properties for partial derivatives hold in this general context. In particular, if  $f$  is differentiable at  $u = (u_1, u_2) \in U$ , then  $f$  is differentiable with respect to both  $x_1$  and  $x_2$  at  $u$  and for all  $(\xi_1, \xi_2) \in B_1 \times B_2$ ,

$$df_u(\xi_1, \xi_2) = D_1f(u) \cdot \xi_1 + D_2f(u) \cdot \xi_2 \quad (2.37)$$

Now, we are ready to state the implicit function theorem.

**Theorem 2.4.2.** (*Implicit function theorem*) Let  $f \in C(U, B)$  where  $U$  is an open set in  $\Lambda \times B_1$  and  $B, B_1$  and  $\Lambda$  are Banach spaces. Assume that

1.  $f(\lambda_0, u_0) = 0$  for some  $(\lambda_0, u_0) \in U$
2.  $D_2f : (\lambda, u) \rightarrow D_2f(\lambda, u)$  is continuous in a neighborhood of  $(\lambda_0, u_0)$ ,  $D_2$  is the derivative of  $f$  with respect to  $u$ ) and
3.  $D_2f(\lambda_0, u_0)$  is nonsingular (has a bounded inverse)

Then there exists a continuous curve  $u = u(\lambda)$  defined in a neighborhood  $N$  of  $\lambda_0$ , such that  $u(\lambda_0) = u_0$  and  $f(\lambda, u(\lambda)) = 0$  in  $N$ . These  $u = u(\lambda)$  are the only solutions of  $f(\lambda, u)$  in  $N$ . Finally, if  $f \in C^k(U, B)$ , then  $u \in C^k(N, B)$ .

Thus, according to the implicit function theorem, we can expect bifurcation at  $(\lambda_0, u_0)$  if  $D_2f(\lambda_0, u_0)$  is singular. On the other hand, even if  $D_2f(\lambda_0, u_0)$  is singular,  $(\lambda_0, u_0)$  need not be a bifurcation point.

*Example 2.4.3.* Let us consider the function  $G(\lambda, x) = \lambda - x^3$ . It has a bifurcation point at  $(0, 0)$  and in fact  $G(0, 0) = G_x(0, 0)$ . The key point in order that  $(0, 0)$  be bifurcation point is the change of sign of  $G_x = 2x$  at  $x = 0$ .

## 2.4.2 Bifurcation from a single eigenvalue

Since our main focus is on the finite dimensional case (actually in  $\mathbb{R}^4$ ), we will present the following bifurcation theorem in this setting. Let us consider the function  $f$  and for simplicity, we assume that  $f(\lambda, 0) = 0$  for all  $\lambda \in \mathbb{R}$ . Using Taylor's theorem, we can write,

$$f(\lambda, u) = L_0u + (\lambda - \lambda_0)L_1u + r(\lambda, u) \quad (2.38)$$

where  $L_0 = D_2f(\lambda_0, 0)$  and  $L_1 = D_1D_2f(\lambda_0, 0)$  are  $n \times n$  matrices, and  $r \in C_2$  satisfies

$$r(\lambda, 0) \equiv 0, \quad D_2r(\lambda_0, 0) = D_1D_2r(\lambda_0, 0) = 0. \quad (2.39)$$

**Theorem 2.4.4.** (*Bifurcation from a single eigenvalue*) Let  $U$  be an open set of  $\mathbb{R} \times \mathbb{R}^4$  and let  $f \in C^2(U, \mathbb{R}^4)$  be given by

$$f(\lambda, u) = D_2(\lambda_0, 0)(u) + (\lambda - \lambda_0)D_1D_2f(\lambda_0, 0)(u) + r(\lambda, u)$$

where  $r \in C^2(\mathbb{R}^5)$  satisfies

$$r(\lambda, 0) = 0, \quad D_2r(\lambda_0, 0) = D_1D_2r(\lambda_0, 0) = 0.$$

Assume that the kernel of  $D_2(\lambda_0, 0)$  is spanned by  $u_0$ , and that  $D_1D_2f(\lambda_0, 0)u_0$  is not in the range of  $D_2(\lambda_0, 0)$ .

Then there is a  $\delta > 0$  and a  $C^1$ -curve  $\Gamma(s) = (\lambda, \phi) : (-\delta, \delta) \rightarrow \mathbb{R} \times \{u_0\}^\perp$  such that

1.  $\lambda(0) = \lambda_0$
2.  $\phi(0) = 0$
3.  $f(\lambda(s), s(u_0, +\phi(s))) = 0$  for  $|s| < \delta$ .

Furthermore, there is a neighborhood of  $(\lambda_0, 0)$  such that any zero of  $f$  either lies on this curve or is of the form  $(\lambda, 0)$ .

Thus  $(\lambda_0, 0)$  is a bifurcation point for  $f$ . Note that we get some information about the direction of bifurcation ( $du/ds = u_0$ ) at  $s = 0$ . Furthermore, if we use the notation  $N(T)$  and  $R(T)$  to denote, respectively, the kernel and the range of an operator  $T$ , then the conditions

$$N(D_2(\lambda_0, 0)) = \text{span}\{u_0\}, \text{ and } D_1D_2f(\lambda_0, 0)u_0 \notin R(L_0)$$

are equivalent to the fact that  $\mu = 0$  is a simple root of

$$\det(D_2(\lambda_0, 0) + \mu D_1D_2f(\lambda_0, 0));$$

hence, in particular,  $\det(D_2(\lambda_0, 0) + (\lambda - \lambda_0)D_1D_2f(\lambda_0, 0))$  changes sign at  $\lambda = \lambda_0$ .

### 2.4.3 Stability of equilibrium branches

Let us now investigate the conditions for an equilibrium solution (of a system of the form  $\frac{du}{dt} = f(u)$ ) to be stable. Suppose that  $\bar{u}$  is a solution and we make a perturbation of the form  $\bar{u} + \epsilon$ , then we consider the initial value problem

$$\frac{du}{dt} = f(u), \quad u(0) = \bar{u} + \epsilon$$

We want to determine whether this solution tends to  $\bar{u}$  as  $t \rightarrow \infty$ , or even if it stays close to  $\bar{u}$  for all  $t > 0$ . If we consider the linearized problem

$$\frac{dv}{dt} = df_{\bar{u}}(v)$$

then if the spectrum of  $df_{\bar{u}}$  lies in the left-half complex plane, the solution  $v$  decays exponentially to zero as  $t \rightarrow \infty$ . In this case, we say that  $\bar{u}$  is stable. On the other hand, if the spectrum contains points in the right-half plane, we say that  $\bar{u}$  is unstable. We are interested here in the stability properties of bifurcation solutions.

Let us consider the equations

$$\frac{du}{dt} = f(\lambda, u)$$

where  $f(\lambda, 0) = 0$ , for all  $\lambda$  and suppose that we have the following situation. For  $\lambda < \bar{\lambda}$ , the spectrum  $\sigma(D_2f(\lambda, 0))$  lies in the left-half plane,  $Re z < 0, z \in \mathbb{C}$  while for  $\lambda > \bar{\lambda}$ ,  $\sigma(D_2f(\lambda, 0))$  intersects  $Re z > 0, z \in \mathbb{C}$ . Then at  $\lambda = \bar{\lambda}$  at least one point of the spectrum crosses the imaginary axis, that is, a point of the form  $ir$  with  $r$  real is in  $\sigma(D_2f(\lambda, 0))$ . Now, if  $r = 0$ , in general, the trivial solution bifurcates into new equilibrium solutions, while if  $r \neq 0$  it bifurcates into periodic solutions. The latter occurs with a so-called Hopf's bifurcation.

**Definition 2.4.5.** Let  $X$  and  $Y$  be Banach spaces and let  $L_0$  and  $K \in B(X, Y)$ . We say that  $\mu \in \mathbb{C}$  is a ***K-simple eigenvalue*** of  $L_0$  (with eigenfunction  $u_0$ ) if the following three conditions hold:

1.  $\dim Ker(L_0 - \mu K) = \text{codim}R(L_0 - \mu K) = 1$
2.  $u_0$  spans  $Ker(L_0 - \mu K)$
3.  $Ku_0 \notin R(L_0 - \mu K)$

The terminology comes from the case where  $X = Y$ ,  $K = I$ , and  $L_0$  is a compact operator. The importance of this notation comes from the next lemma, which implies that *K-simple eigenvalues* “continue” along the bifurcating branches.



**Lemma 2.4.6.** *Let  $\mu_0$  be a  $K$ -simple eigenvalue of  $L_0$ , with eigenfunction  $u_0$ . Then, there exists  $\rho > 0$  such that if  $\|L - L_0\| > \rho$ ,  $L$  has a unique  $K$ -simple eigenvalue  $\eta(L) \in \mathbb{Z}$ . Also  $\eta(L_0) = \mu_0$ ,  $w(L_0) = u_0$  and the mapping  $L \rightarrow (\eta(L), w(L))$  is smooth.*

Let the hypotheses of Theorem 2.4.4 hold. Then,  $D_2f(\lambda_0, 0)$  has 0 as a single eigenvalue of  $D_1D_2f(\lambda_0, 0)$ . Let  $\lambda(s)$  and  $u(s) \equiv s(u_0 + \phi(s))$  be the bifurcating curve as provided by this theorem. We will use the notation of Theorem 2.4.4 and use the notation  $f'(s) = D_2f(\lambda(s), u(s))$ . Now suppose that  $X \subset Y$ , the inclusion  $i : X \rightarrow Y$  is continuous, 0 is an  $i$ -simple eigenvalue of  $D_2f(\lambda_0, 0)$ . Then by Lemma 2.4.6, there exist functions

$$\lambda \rightarrow (\gamma(\lambda), \nu(\lambda)), \quad s \rightarrow (\eta(s), w(s)) \quad (2.40)$$

defined on a neighborhood of  $\lambda_0$  and 0, respectively, into  $\mathbb{R} \times X$ , such that

$$(\gamma(\lambda_0), \nu(\lambda_0)) = (0, u_0) = (\eta(0), w(0)), \nu(\lambda) - u_0 \in Z, w(s) - u_0 \in \mathbb{Z}$$

and these neighborhoods,

$$D_2f(\lambda, 0)\nu(\lambda) = \gamma(\lambda)\nu(\lambda), \quad (2.41)$$

$$f'(s)w(s) = \eta(s)w(s). \quad (2.42)$$

The following theorem is used to determine the stability of the bifurcating solution.

**Theorem 2.4.7.** *Let the hypotheses of the Theorem 2.4.4 hold, and let  $\gamma$  and  $\eta$  be defined as above. Then  $\gamma'(\lambda_0) \neq 0$  and if  $\eta(s) \neq 0$  for  $s$  near 0,*

$$\lim_{s \rightarrow 0} \frac{s\lambda'(s)\gamma'(\lambda_0)}{\eta(s)} = -1.$$

## 2.4.4 Hopf Bifurcation

Consider the bifurcation of a periodic orbit from the equilibrium position of an autonomous differential equation, the so called Hopf bifurcation. This type of bifurcation is one of the most elementary ones and is important in the theory of nonlinear oscillations.

Suppose that

$$\frac{du}{dt} = A(\lambda)u + f(\lambda, u)$$

where  $u \in \mathbb{R}^n$ ,  $\lambda \in \mathbb{R}$ ,  $A(\lambda)$  is an  $n \times n$  matrix.  $A(\lambda), f(\lambda, u)$  have continuous derivatives up through order one,  $D_{\lambda u}f(\lambda, u)$  is continuous for  $|\lambda| < \lambda_0$  and  $u \in \mathbb{R}^n$ ,  $f(\lambda, 0) = 0$ ,  $D_u f(\lambda, 0) = 0$  for  $|\lambda| < \lambda_0$  and

$$A(\lambda) = \begin{pmatrix} B(\lambda) & 0 \\ 0 & C(\lambda) \end{pmatrix}$$

$$B(\lambda) = \begin{pmatrix} \lambda & \beta(\lambda) \\ -\beta(\lambda) & \lambda \end{pmatrix} \quad \beta(0) = 1$$

$$(e^{C(\lambda)2\pi} - I)^{-1} \quad \text{exists for } |\lambda| < \lambda_0.$$

**Theorem 2.4.8.** *Under the above hypotheses, there are constants  $a_0 > 0$ ,  $\lambda_0, \delta_0$ , functions  $\lambda(a) \in \mathbb{R}$ ,  $\lambda(0) = 0$ ,  $w(0) = 2\pi$  and a  $w(a)$ -periodic function  $u^*(a)$  with all functions having continuous first derivatives up through order one for  $|\lambda| < \lambda_0$ , such that  $u^*(a)$  is a solution of (2.4.4) with*

$$u^*(a)(t) = \begin{pmatrix} a \cos(w(a)t) \\ -a \sin(w(a)t) \\ 0 \\ \vdots \\ 0 \end{pmatrix} + o(|a|)$$

as  $|a| \rightarrow 0$ . Furthermore, for  $|\lambda| < \lambda_0$ ,  $|w - 2\pi| < \delta_0$ , every  $w$ -periodic solution  $u$  of equation (2.4.4) with  $u(t) < \delta_0$  must be given by  $u^*(a)$  except for a translation in phase.

This theorem sets conditions in order that a system of ordinary differential equations has a bifurcation point that leads to a periodic solution. It will help us to find periodic solutions.

### 2.4.5 Numerical Continuation of solutions of autonomous systems

In this section, we describe the numerical analysis of systems of the form

$$\frac{du(t)}{dt} = f(\lambda, u(t)) \quad u, f \in \mathbb{R}^n \tag{2.43}$$

where  $\lambda$  denotes one (or several) parameters. Our goal is to describe the capabilities of AUTO, which is a software for continuation and bifurcation problems in ordinary differential equations. AUTO was originally developed by Eusebius Doedel.

AUTO requires the following data: the Jacobian of  $f$ ,  $\frac{\partial f}{\partial \lambda}$  and an equilibrium solution for some fixed values of  $U$  and  $\lambda$ . Then the program has the following capabilities:

1. The calculation of branches of equilibrium points.
2. The finding of the bifurcation points of the above branches.
3. The finding of Hopf bifurcation points.
4. The calculation of branches of periodic solutions.
5. The calculation of stability of the solution branches. For periodic solutions this process is achieved by solving a boundary value problem.
6. The use of adapting meshes and stepsizes along the branches of periodic solutions.
7. The capacity to restart the calculation at certain points.
8. The storing of calculations in files, allowing the use of different plotting programs.

### 2.4.6 Continuation of fixed points

In equation (2.43), we have one more unknown variable than equations, and generically such problems have families of solutions. A continuation method consists of a procedure in which a known solution to Equation (2.43) is used to discover new solutions. We can proceed iteratively; known solutions lead to new solutions which are then added to our collection of known solutions, leading to more solutions, etc. There are various classes of such methods and in this section we will restrict our attention to the class of predictor-corrector methods. These are the methods used in AUTO. In predictor-corrector methods one uses some set of known solutions to equation (2.43) to generate a new point  $x$ . The new point  $x$  is only a guess, and typically does not lie on the bifurcation diagram, so one then corrects it to within a given tolerance, perhaps using Newton's method, to a point  $x$  on the bifurcation diagram.

Bifurcation diagrams are often more complex than single curves. For example, two curves in a bifurcation diagram may intersect. Such an intersection point is called a bifurcation point, and there exists a whole menagerie of different types of bifurcation points. For example, a simple bifurcation is one in which two solution

curves with the same general properties intersect, while a Hopf bifurcation is one in which a branch of steady state solutions intersects a branch of periodic solutions.

The parameter continuation methods in AUTO may be used to compute very complex bifurcation diagrams. The algorithms include the ability to detect and switch branches at bifurcations of various types. For example, one may perform the following calculation:

- Continue a given solution until you reach the third simple bifurcation.
- Go onto a bifurcating branch and continue until reaching a Hopf bifurcation.
- Continue the branch of periodic solutions until a certain value is reached.

This type of modality is very common in AUTO and very complex bifurcation diagrams can result, with many bifurcation points and branch switches. Therefore, the main goal of using an interface for AUTO (such as Python) is to facilitate the control of the continuation algorithm and the construction of bifurcation diagrams, whether it be for the beginning or advanced user.

### 2.4.7 Continuation of periodic solutions

The calculation of branches of equilibrium solutions is basically an algebraic problem, which consists of the bifurcation analysis of  $f(\lambda, u(t)) = 0$ . This can be accomplished numerically using arclength continuation and branch switching techniques [19]. Furthermore, the continuation of periodic solutions can be treated in the same framework. Let us review the basic features of these techniques.

Consider the operator equation

$$G(\lambda, u(t)) = 0, \tag{2.44}$$

where  $G : H_1 \rightarrow H_2$  is a nonlinear map between the two Hilbert spaces  $H_1$  and  $H_2$ . If there exists a parametrized branch of solutions  $(u(t)(s), \lambda(s))$ , then under appropriate smoothness assumptions the result that the derivative of  $G$  always has a nullspace along the branch. Assume now that we have a solution of (2.44) denoted by  $w_0$  and also assume that the kernel of  $G'(w_0)$  is spanned by the vector  $w'_0$ . Thus the kernel is one dimensional. Let  $w_0^*$  be the adjoint element such that  $w_0'^* w'_0 = 1$ . Then the augmented problem

$$G(w) = 0 \quad w_0'^*(w - w_0) - s \tag{2.45}$$

has the solution  $w = w_0$  when  $s = 0$ . Further the derivative  $(G'(w_0, w_0'^*))$  is nonsingular. Hence, the implicit function theorem guarantees the existence of a branch of solutions  $w(s)$  for small  $s$ .

If  $G(w) = 0$  represents a differential equation, then of course the equation must be discretized first. Further for numerical purposes it is often more convenient to use the approximation  $w'_0 \approx \frac{w(s)-w_0}{s}$ . In addition, we solve (2.45) for only one value of  $s$ , say  $s = \Delta s$ , then (2.45) becomes

$$G(w) = 0 \quad \frac{w - w_0^*(w - w_0)}{\Delta s} - \Delta s = 0. \quad (2.46)$$

Essentially the same procedure can be used to switch branches at a bifurcation point after the direction of the bifurcating branch has been computed.

Now consider the problem of determining branches of periodic solutions to the autonomous system (2.43). First note that not only the periodic solution  $u$  but also its period  $P$  changes along such branch. To fix the period, one must map linearly  $(0, P)$  into  $(0, 2\pi)$ . This transforms the differential equation into

$$\frac{du(t)}{dt} = \frac{P}{2\pi} f(\lambda, u(t)) \quad (2.47)$$

where the unknown period appears explicitly and where  $2\pi$ -periodic solutions are to be determined, that is we impose the condition  $u(0) = u(2\pi)$ . Suppose that  $(\lambda_0, P_0, u_0(t))$  defines a known periodic solution. The objective is to set up the equations for finding a solution nearby on the branch. A remaining difficulty is the inherent non-uniqueness of  $u$  due to the fact that a periodic solution can be translated freely in time. For numerical computation the new solution  $u$  must be anchored. To achieve this, we need to simply fix one of the components of  $u$  at  $t = 0$ . However, the resulting set of equations has an isolated solution only under conditions that are not required for the underlying problem itself. For theoretical purposes a better choice is the orthogonality condition  $(u(0) - u_0(0))^T f(u_0(0), \lambda) = 0$ , which ensures that  $u(0)$  on the orbit to be determined occupies a similar position to  $u_0(0)$  on the known orbit.



# Nonlinear juvenile predation population dynamics<sup>1</sup>

## 3.1 Introduction

As we already mentioned, age structure in predator-prey models has been extensively studied in the literature (see for example [15, 17, 24]). Unstable periodic solutions are frequently found in these models although they do not correspond to biological nature where prey and predator populations can coexist. Among the efforts to reach coexistence, the inclusion of diverse factors, such as self limitation of the prey, harvesting of prey and cannibalism of the younger prey, should be included [36, 25].

One of the successful tools to analyze biological models has been the Painlevé property, which has its origin in the work of S.V. Kovalevskaya who was the first to consider the analytical theory of differential equations but to physical problems [20]. Paul Painlevé took these ideas and classified ordinary differential equations of second order according to the type of singularities of their solutions [30]. Since then, the property has been used to construct symmetries, to find explicit solutions, to detect control parameters and so on [27, 44].

Basically, a system of ordinary differential equations has the Painlevé property if its general solution has no movable critical singular points. Equivalently, we might say that the only singularities of the system of ordinary differential equations are poles. Ablowitz, Ramani and Segur [2] described an algorithm named P-test, which allows one to determine in three steps if an ODE has the property: finding a) the dominant behavior, b) the resonances and c) the constants of integration. It is important to remark that this algorithm does not identify essential singularities.

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<sup>1</sup>This chapter is based on F.J. Solis, R.A. Ku, Nonlinear juvenile predation population dynamics, *Mathematical and Computer Modeling* 54 (2011) 1687-1692

The necessary conditions for a system to have the Painlevé property are established only.

The goal of this chapter is to use the Painlevé property in age-structured predator-prey models as a modeling tool in order to provide candidates to stabilize such models and to discover essential biological factors. The main idea is to analyze a general form of the term that models the incorporation of the newborn prey into the dynamics. Finally, to verify coexistence between predator and prey, we will use standard techniques in bifurcation analysis.

## 3.2 The model

In this section we develop an age-structured model that was already presented in chapter one, but for the sake of self-contentedness we deduce here again. Let  $\rho(\omega, t)$  be the number of prey individuals of age  $\omega$  at the time  $t$ . The total prey population can be defined as

$$P(t) = \int_0^{\infty} \rho(\omega, t) d\omega.$$

From the conservation law

$$\frac{d}{dt} \int_w^{w+\Delta w} \rho(\psi, t) d\psi = -\mu \int_w^{w+\Delta w} \rho(\psi, t) d\psi + \rho(w, t) - \rho(w + \Delta w, t),$$

dividing by  $\Delta w$  and taking the limit as  $\Delta w$  tends to zero, we obtain the equation of evolution

$$\rho_{\omega}(\omega, t) + \rho_t(\omega, t) + \mu\rho(\omega, t) = 0. \quad (3.1)$$

We suppose that the birth rate of the population is, at time  $t$ , given by a law of births of the type:

$$B(t) = \int_0^{\infty} \beta(\omega)\rho(\omega, t) d\omega,$$

where  $\beta(\omega) = \beta_0\omega e^{-\alpha\omega}$  is the reproductive rate of individuals of age  $\omega$ . Defining

$$A(t) = \int_0^{\infty} e^{-\alpha\omega}\rho(\omega, t) d\omega$$



and from the evolution equation (3.1), we obtain the following three equations:

$$\begin{aligned}\frac{dP(t)}{dt} &= -\mu(P)P + \rho(0, t), \\ \frac{dB(t)}{dt} &= -(\mu(P) + \alpha)B(t) + \beta_0A(t) \\ \frac{dA(t)}{dt} &= -(\mu(P) + \alpha)A(t) + \rho(0, t).\end{aligned}$$

Assuming that the predator population,  $D$ , which feeds only on the newborn prey, behaves according to a Lotka-Volterra type equation, we get

$$\frac{dD}{dt} = -bD + cBD.$$

Moreover, if we consider  $\mu(P) = \mu_0 + \epsilon P$ , which represents the self-limitation of the prey, and substitute it in the model we obtain:

$$\frac{dP(t)}{dt} = -\mu_0P(t) - \epsilon P^2(t) + \rho(0, t) \quad (3.2)$$

$$\frac{dB(t)}{dt} = -\theta B(t) - \epsilon P(t)B(t) + \beta_0A(t), \quad (3.3)$$

$$\frac{dA(t)}{dt} = -\theta A(t) - \epsilon P(t)A(t) + \rho(0, t) \quad (3.4)$$

$$\frac{dD(t)}{dt} = -bD(t) + cB(t)D(t), \quad (3.5)$$

where  $\mu_0, \epsilon, \eta, \theta = \alpha + \mu_0, \beta_0, b$  and  $c$  are positive parameters. We will consider a general form of the function  $\rho(0, t)$  depending on  $P, B, A$  and  $D$  as,

$$\rho(0, t) = F(P(t), B(t), A(t), D(t)). \quad (3.6)$$

Then, we will consider two models. In the first one, the juvenile predation term is given by the general function (3.6) and the complete system is:

$$\frac{dP(t)}{dt} = -\mu_0P(t) - \epsilon P^2(t) + F(P(t), B(t), A(t), D(t)) \quad (3.7)$$

$$\frac{dB(t)}{dt} = -\theta B(t) - \epsilon P(t)B(t) + \beta_0A(t), \quad (3.8)$$

$$\frac{dA(t)}{dt} = -\theta A(t) - \epsilon P(t)A(t) + F(P(t), B(t), A(t), D(t)) \quad (3.9)$$

$$\frac{dD(t)}{dt} = -bD(t) + cB(t)D(t), \quad (3.10)$$

where  $\mu_0, \epsilon, \eta, \theta = \alpha + \mu_0, \beta_0, b$  and  $c$  are positive parameters. In the second one, we will consider a particular  $\rho(0, t)$  as a benchmark, given by,

$$\rho(0, t) = \frac{B^m(t)(1 - \rho B(t) - \sigma P^L(t) - \tau A^M(t))}{1 + \eta D(t)}, \quad (3.11)$$

where  $\rho, \sigma, \tau$  are positive parameters and  $m, L$  and  $M$  are positive integers. The complete system is then:

$$\frac{dP(t)}{dt} = -\mu_0 P(t) - \epsilon P^2(t) + F(P(t), B(t), A(t), D(t)) \quad (3.12)$$

$$\frac{dB(t)}{dt} = -\theta B(t) - \epsilon P(t)B(t) + \beta_0 A(t), \quad (3.13)$$

$$\frac{dA(t)}{dt} = -\theta A(t) - \epsilon P(t)A(t) + F(P(t), B(t), A(t), D(t)) \quad (3.14)$$

$$\frac{dD(t)}{dt} = -bD(t) + cB(t)D(t). \quad (3.15)$$

This particular function (3.11) is a generalization of the function  $\rho(0, t) = B(t)(1 + \eta D(t))^{-1}$ . We can observe that this function models the juvenile predation on the newborns  $B(t)$ . When the predator populations  $D(t)$  is small then the juvenile predation is large. On the contrary, if the  $D(t)$  is large the predation is low because exists more competence among predator themselves. The general version of it (3.11) models the predation also but also takes into account the competence between the babies  $B(t)$ , the adult populations  $P(t)$  and also the auxiliary variable  $A(t)$ . This variable in particular represents a part of the population.

In the following three sections we will present theorems which result from the application of the Painlevé test. It is important to remark that the P-test was established in the complex domain. However, we applied it to a differential system of equations in  $\mathbb{R}$  which is valid because  $\mathbb{R} \subset \mathbb{C}$ .

### 3.3 No contribution of $F$

In this section, we make the assumption that the function  $\rho(0, t)$  depends on  $P, B, A$  and  $D$ , ie.  $\rho(0, t) = F(P(t), B(t), A(t), D(t))$  and also that is a rational function. This allows us write the  $F$  function in its Laurent series:

$$F(P, B, A, D) = \sum_{i=1}^{k_5} \hat{f}_{-i}(t - t_0)^{-i} + \sum_{i=0}^{\infty} \hat{f}_i(t - t_0)^i.$$

When the function  $F$  does not contribute to the dominant terms in the first step of P-test (Chapter 2) we obtain the following theorem.

**Theorem 3.3.1.** *Let us consider the system of differential equations (3.2)-(3.5). If the function  $F(P, B, A, P)$  does not provide dominant terms in the P-test then the system does not have the Painlevé property and the only solutions without movable critical points are of the form:*

$$P(t) = \frac{1}{\epsilon} \xi^{-1} + \sum_{i=0}^{\infty} \alpha_i \xi^i, \quad (3.16)$$

$$B(t) = \frac{-k_4}{c} \xi^{-1} + \sum_{i=0}^{\infty} \beta_i \xi^i, \quad (3.17)$$

$$A(t) = \gamma_{-i} \xi^{-1} + \sum_{i=0}^{\infty} \gamma_i \xi^i, \quad (3.18)$$

$$D(t) = \sum_{i=1}^{k_4} \delta_{-i} \xi^{-i} + \sum_{i=0}^{\infty} \delta_i \xi^i, \quad (3.19)$$

$k_4$  is an arbitrary positive integer and  $\xi = t - t_0$  where  $t_0$ ,  $\gamma_{-1}$  and  $\delta_{-k_4}$  are arbitrary constants.

*Proof.* We apply the P-test as described in Ablowitz ([2]).

Step 1. We start by writing down the ansatz

$$P(t) = \alpha_{-k_1} \xi^{-k_1}, \quad (3.20)$$

$$B(t) = \beta_{-k_2} \xi^{-k_2} \quad (3.21)$$

$$A(t) = \gamma_{-k_3} \xi^{-k_3} \quad (3.22)$$

$$D(t) = \delta_{-k_4} \xi^{-k_4}, \quad (3.23)$$

$$F(t) = f_{-k_5} \xi^{-k_5}, \quad (3.24)$$

and substitute in (3.2)- (3.5):

$$-k_1 \alpha_{-k_1} \xi^{-k_1-1} = -\mu_0 \alpha_{-k_1} \xi^{-k_1} - \epsilon \alpha_{-k_1}^2 \xi^{-2k_1} + f_{-k_5} \xi^{-k_5} \quad (3.25)$$

$$-k_2 \beta_{-k_2} \xi^{-k_2-1} = -\theta \beta_{-k_2} \xi^{-k_2} - \epsilon \alpha_{-k_1} \beta_{-k_2} \xi^{-k_1-k_2} + \lambda \gamma_{-k_3} \xi^{-k_3} \quad (3.26)$$

$$-k_3 \gamma_{-k_3} \xi^{-k_3-1} = -\theta \gamma_{-k_3} \xi^{-k_3} - \epsilon \alpha_{-k_1} \gamma_{-k_3} \xi^{-k_1-k_3} + f_{-k_5} \xi^{-k_5} \quad (3.27)$$

$$-k_4 \delta_{-k_4} \xi^{-k_4-1} = -b \delta_{-k_4} \xi^{-k_4} + c \beta_{-k_2} \xi^{-k_2} \delta_{-k_4} \xi^{-k_4}. \quad (3.28)$$

The fact that the function  $F$  does not contribute to the dominant terms implies that  $k_5 < k_1 - 1$  and  $k_5 < k_3 - 1$ . The dominant terms are those which can be equal in each equation (3.25-3.28). Let us recall that the  $k_i$ 's must be integer positive numbers in order to succeed the P-test. This is accomplished with the set  $k_1 = 1$ ,

$k_2 = 1$ ,  $k_3 = 1$  and  $k_4$  is an arbitrary positive integer. The corresponding dominant terms are then  $\dot{P}$  and  $-\varepsilon P^2$  in first equation of (3.2),  $\dot{B}$  and  $-\varepsilon PB$  in second equation of (3.3),  $\dot{A}$  and  $-\varepsilon PA$  in third equation of (3.4)  $\dot{D}$  and  $cBD$  in fourth equation of (3.5).

Step 2. To find the resonances,  $r$ , we use the coefficients and the exponents already found in step one to form the equations:

$$P = \frac{1}{\varepsilon}(t - t_0)^{-1} + \kappa_1(t - t_0)^{r-1}, \quad (3.29)$$

$$B = \frac{k_4}{c}(t - t_0)^{-1} + \kappa_2(t - t_0)^{r-1}, \quad (3.30)$$

$$A = \gamma_{-1}(t - t_0)^{-1} + \kappa_3(t - t_0)^{r-1}, \quad (3.31)$$

$$D = \delta_{-k_4}(t - t_0)^{-k_4} + \kappa_4(t - t_0)^{r-k_4}, \quad (3.32)$$

Then, we substitute them in system (3.2)-(3.5).

$$\begin{aligned} \eta\delta_{-k_4}(r+1)\kappa_1 &= 0 \\ -\varepsilon\frac{k_4}{c}\kappa_1 + r\kappa_2 &= 0 \\ \eta\varepsilon\delta_{-k_4}\gamma_{-1}\kappa_1 + b\kappa_2 + \eta\delta_{-k_4}r\kappa_3 &= 0 \\ -c\delta_{-k_4}\kappa_2 + r\kappa_4 &= 0, \end{aligned}$$

We take the linear part in  $\kappa_1$ ,  $\kappa_2$ ,  $\kappa_3$  and  $\kappa_4$  to form the resonance matrix

$$\mathbf{Q}(\mathbf{r}) = \begin{pmatrix} \eta\delta_{-k_4}(r+1) & 0 & 0 & 0 \\ -\frac{\varepsilon k_4}{c} & r & 0 & 0 \\ \eta\varepsilon\delta_{-k_4}\gamma_{-1} & 0 & \eta\delta_{-k_4}r & 0 \\ 0 & -c\delta_{-k_4} & 0 & r \end{pmatrix}, \quad (3.33)$$

since  $F$  does not provide leading terms. In order to have resonances, we must have  $\det Q(r) = r^3(r+1) = 0$ , which exhibits a root  $r = 0$  of multiplicity three and  $r = -1$  of multiplicity one. Any root equal to zero must come from an arbitrary coefficient in order to pass the test. We already have two arbitrary coefficients given by  $\gamma_{-1}$  and  $\delta_{-1}$ . In general, we can not find a third coefficient because  $\beta_{-1} = -k_4/c$  is restricted since  $k_4$  has to be a positive arbitrary integer. Therefore the system does not pass the Painlevé test and (3.16-3.19) does not represent the general solution.  $\square$

**Remark** Let us notice that the leading coefficient of the solution for the prey population is given by  $\alpha_{-1} = 1/\varepsilon$ . Therefore, self-limitation in the prey population is an important biological factor. Otherwise, the solutions will be unbounded. In an analogous way, we notice the importance of the predation factor since the leading coefficient of the juvenile population,  $B$ , is  $k_4/c$ .

*Example 3.3.2.* In order to complete this section, we present an example of a function  $F$ . Let us consider the function  $F = B/(1 + \eta D)$ . By taking the coefficients and the exponents of the dominant terms we see that

$$\begin{aligned} P(t) &= 1/\varepsilon\xi^{-1}, \\ B(t) &= k_4/c\xi^{-1} \\ A(t) &= \gamma_{-1}\xi^{-1} \\ D(t) &= \delta_{-k_4}\xi^{-k_4}, \end{aligned}$$

Because  $k_4$  is arbitrary we can assume that  $k_4 = 1$  then the order of the function  $F$  is  $F \sim f\xi^0$ . This means that the function  $F$  does not contribute to the dominant terms in the P-test. This particular case was previously studied in [36].

So far, we have shown that a necessary condition to pass the P-test is the contribution of leading terms from  $\rho(0, t)$ . Thus, the nonlinearity of this function is an essential feature. Next, we make use of the specific form of the function  $\rho(0, t)$  in the following result.

### 3.4 Contribution of $F$

In this case, we use a specific function  $F(P(t), B(t), A(t), D(t))$ :

$$F(P, B, A, D) = \frac{B^m(1 - \rho B - \sigma P^L - \tau A^M)}{1 + \eta D}, \quad (3.34)$$

where  $\rho, \sigma, \tau, k$  are positive parameters and  $m, L$  and  $M$  are positive integers.

$$\frac{dP(t)}{dt} = -\mu_o P(t) - \mu P^2 + \frac{B^m(1 - \rho B - \sigma P^L - \tau A^M)}{1 + \eta D} \quad (3.35)$$

$$\frac{dB(t)}{dt} = -\theta B(t) - \mu P(t)B(t) + \beta_0 A(t) \quad (3.36)$$

$$\frac{dA(t)}{dt} = -\theta A(t) - \mu D(t)A(t) + \frac{B^m(1 - \rho B - \sigma P^L - \tau A^M)}{1 + \eta D} \quad (3.37)$$

$$\frac{dD(t)}{dt} = -bD(t) + cB(t)D(t) \quad (3.38)$$

where  $\mu_0, \epsilon, \eta, \theta = \alpha + \mu_0, \beta_0, b$  and  $c$  are positive parameters.

This function is a general version of the predation term used in [36] where a predation term of the form  $F = B/(1 + \eta D)$  was considered. This function represents

the juvenile population  $B$  contributes to the adult population  $P$  in a proportional way. However, there is competence between the other groups of the population named  $P$ ,  $B$  or  $A$ . Because we are assuming a predation process, the variable  $D$  is also included with a saturation effect.

The question is, whether under these general conditions the system (3.35)-(3.38) will pass the P-test. The answer is given in the following theorem.

**Theorem 3.4.1.** *Let us consider the system (3.35)-(3.38). Assume that the function  $F$  (3.34) contributes with at least one of the dominant terms in the P-test.*

- *If  $k_4$  is a positive integer, then the system has logarithmic branch points.*
- *If  $k_4$  is a non-integer rational number, then the system has a branch point of order  $-k_4$ .*

*In both cases, the system does not have the Painlevé property.*

*Proof.* Again, we apply the P-test.

Step 1. In an analogous way, as in the proof of Theorem (3.3.1) we substitute the ansatz (3.20-3.23) in the system (3.35)-(3.38) to obtain:

$$-k_1\alpha_{-k_1}\xi^{-k_1-1} = -\mu_0\alpha_{-k_1}\xi^{-k_1} - \varepsilon\alpha_{-k_1}^2\xi^{-2k_1} \quad (3.39)$$

$$+ \frac{(\beta_{-k_2}\xi^{-k_2})^m(1 - \rho(\beta_{-k_2}\xi^{-k_2}) - \sigma(\alpha_{-k_1}\xi^{-k_1})^L - \tau(\gamma_{-k_3}\xi^{-k_3})^M)}{1 + \eta(\delta_{-k_4}\xi^{-k_4})}$$

$$-k_2\beta_{-k_2}\xi^{-k_2-1} = -\theta\beta_{-k_2}\xi^{-k_2} - \varepsilon\alpha_{-k_1}\beta_{-k_2}\xi^{-k_1-k_2} + \lambda\gamma_{-k_3}\xi^{-k_3} \quad (3.40)$$

$$-k_3\gamma_{-k_3}\xi^{-k_3-1} = -\theta\gamma_{-k_3}\xi^{-k_3} - \varepsilon\alpha_{-k_1}\gamma_{-k_3}\xi^{-k_1-k_3}$$

$$+ \frac{(\beta_{-k_2}\xi^{-k_2})^m(1 - \rho(\beta_{-k_2}\xi^{-k_2}) - \sigma(\alpha_{-k_1}\xi^{-k_1})^L - \tau(\gamma_{-k_3}\xi^{-k_3})^M)}{1 + \eta(\delta_{-k_4}\xi^{-k_4})} \quad (3.41)$$

$$-k_4\delta_{-k_4}\xi^{-k_4-1} = -b\delta_{-k_4}\xi^{-k_4} + c\beta_{-k_2}\xi^{-k_2}\delta_{-k_4}\xi^{-k_4}. \quad (3.42)$$

We found that the exponents  $k_1 = 1, k_2 = 1, k_3 = 1$  balance at least two dominant terms in equations (3.36) and (3.38). These equations do not contain the function  $F$ . For equation (3.36) dominant terms are,  $B$  and  $-\varepsilon PB$ . The dominant terms for equation (3.38) are  $\dot{D}$  and  $-\varepsilon PB$ . Also, from these equations we have that  $\alpha_{-1} = \frac{1}{\varepsilon}, \beta_{-1} = -\frac{k_4}{c}$ . The coefficients  $\gamma_{-1}$  and  $\delta_{-k_4}$  have to be determined using equations (3.35) and (3.37). For equations (3.35) and (3.37), the dominant terms depends on the function  $F$ . There are several cases to analyze because the function  $F$  has parameters which have to be determined. Finally, the first step is achieved when  $k_4 + 2 = m + 1 \acute{o} m + L \acute{o} m + M$ , where at least two of  $m + 1, m + L, m + M$  are equal and the third one equal or lesser.

Step 2. The matrix of resonances is the same as that obtained in (3.33) but with  $F(P, B, A, D) \neq 0$ . To find the values of the resonances, we have to find the roots of the polynomial,

$$\begin{aligned} \det[Q(r)] &= \\ &= \det \begin{pmatrix} \eta\delta_{-k_4}(r+1) + \frac{\partial F}{\partial \kappa_1}(0) & \frac{\partial F}{\partial \kappa_2}(0) & \frac{\partial F}{\partial \kappa_3}(0) & 0 \\ -\frac{\varepsilon k_4}{c} & r & 0 & 0 \\ \eta\varepsilon\delta_{-k_4}\gamma_{-1} + \frac{\partial F}{\partial \kappa_1}(0) & \frac{\partial F}{\partial \kappa_2}(0) & \eta\delta_{-k_4}r + \frac{\partial F}{\partial \kappa_3}(0) & 0 \\ 0 & -c\delta_{-k_4} & 0 & r \end{pmatrix} \quad (3.43) \\ &= \eta\delta_{-k_4}r^2 \left[ r^2\eta\delta_{-k_4} + r \left( \eta\delta_{-k_4} + \xi^{k_1} \frac{\partial F}{\partial P}(X_1) + \xi^{k_3} \frac{\partial F}{\partial A}(X_1) \right) \right. \\ &\quad \left. + \xi^{k_2} \frac{\partial F}{\partial B}(X_1) \frac{\varepsilon k_4}{c} + \xi^{k_3} \frac{\partial F}{\partial A}(X_1)(1 - \varepsilon\gamma_{-k_3}) \right], \end{aligned}$$

where  $X_1 = (\alpha_{-k_1}\xi^{-k_1}, \beta_{-k_2}\xi^{-k_2}, \gamma_{-k_3}\xi^{-k_3}, \delta_{-k_4}\xi^{-k_4})$ . Thus,  $r = 0$  is always a double root which should correspond to two arbitrary constants. However, it is shown in Step 1, that there is only one arbitrary constant.

In order to show that solutions exhibit logarithmic branch points, we make the following transformation in (3.2)- (3.5)

$$P = \frac{f(\ln \xi)}{\xi}, \quad B = \frac{g(\ln \xi)}{\xi}, \quad A = \frac{\varphi(\ln \xi)}{\xi}, \quad D = \frac{\psi(\ln \xi)}{\xi}. \quad (3.44)$$

The functions  $f, g, \varphi$ , and  $\psi$  are analytic and therefore the system has logarithmic branch points. To show that the system exhibits logarithmic branches, let us suppose that at least two dominant terms are provided by (3.34) in (3.35-3.38). Then  $k_1 = 1, k_2 = 1, k_3 = 1$  and  $k_4 + 2 = m + 1$  or  $m + L$  or  $m + M$ , where at least two of  $m + 1, m + L$  and  $m + M$  are equal and bigger or equal than the third one. If  $k_4$  is an integer, we find logarithmic branch points as before. If  $k_4$  is not an integer, then we define a new variable

$$\Delta = D^{-\frac{1}{k_4}},$$

and substitute  $\Delta$  in (3.34).  $\Delta$  is analytic and as a result, the system has a branch point of order  $-k_4$ . In both cases, the system does not have the Painlevé property.  $\square$

*Example 3.4.2.* In order to complete this section, we present an example of a function  $F$ . When we select the parameters  $m = 2$ ,  $L = 1$ ,  $M = 0$  and  $\tau = 0$

$$F = \frac{B^2(1 - \rho B - \sigma P)}{1 + \eta D} \quad (3.45)$$

When  $k_4 = 1$  the solutions of the system (3.35-3.38) corresponds to the case is a positive rational number and it has a logarithmic branch. When  $k_4$  is a non-integer rational number the solutions have a branch point of order  $-k_4$ . This function is a more general function that the one studied in [36].

The previous theorems have shown that the system has failed the Painlevé test. However, they have exhibited the complexity of the solutions.

### 3.5 Conditions on $F$ to succeed the P-test

A natural question to ask is if we can find functions  $F(P, B, A, D) = \rho(0, t)$  for which the system (3.2)-(3.5) has the Painlevé property. In order to answer this question, let us suppose that the function  $F(P, B, A, D)$  can be written as

$$F(P, B, A, D) = \sum_{i=1}^{k_5} f_{-i} \xi^{-i} + \sum_{i=0}^{\infty} f_i \xi^i. \quad (3.46)$$

Then, taking the equation (3.7-3.10) and the ansatz (3.20-3.23) with the following values  $k_1 = 1$ ,  $k_2 = 1$ ,  $k_3 = 2$ ,  $k_4$  an arbitrary positive integer,  $\alpha_{-1} = 2/\varepsilon$ ,  $\beta_{-1} = -k_4/c$ ,  $\gamma_{-1} = -k_4/(\beta_0 c)$  and  $\delta_{-k_4}$  is an arbitrary constant. All these conditions are found by applying the P-test. Furthermore, we define  $X_2 = (\alpha_{-1} \xi^{-1}, \beta_{-1} \xi^{-1}, \gamma_{-2} \xi^{-2}, \delta_{-k_4} \xi^{-k_4})$ , and  $h = c/\varepsilon k_4$ , Under these conditions we obtain the following theorem.

**Theorem 3.5.1.** *Let us assume that the function  $F(P, B, A, D)$  is a rational function in the variables  $P, B, A, D$ , with a pole of order two in the variable  $t$  and the polynomial*

$$r^2 - r \left( \frac{\frac{\partial F}{\partial P}(X_2)}{\xi^{-k_1}} - 3 \right) - \left( \frac{\frac{\partial F}{\partial A}(X_2)}{\xi^{-k_3} \beta_0 h} + \frac{\frac{\partial F}{\partial B}(X_2)}{\beta_0 \xi^{-k_2}} \right) \quad (3.47)$$

*has two integer positive roots. Then, the system passes the first two steps of the P-test.*



### 3.5. CONDITIONS ON $F$ TO SUCCEED THE P-TEST

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*Proof.* Step 1. This step is completed for the values of  $k_i$ , ( $i = 1, 2, 3, 4$ ),  $\alpha_{-1}$ ,  $\beta_{-1}$ ,  $\gamma_{-2}$  and  $\delta_{-k_4}$  already given and with dominant terms given by  $\dot{P}$ ,  $-\varepsilon P^2$  and  $F(P, B, A, D)$  in (3.35)  $\dot{B}$ ,  $-\varepsilon PB$  and  $\beta_0 A$  in (3.36),  $\dot{A}$  and  $-\varepsilon PA$  in (3.37)  $\dot{D}$  and  $cBD$  in (3.38).

Step 2. As before, we make the substitution of the ansatz (3.29-3.32) with the new values along with (3.46) in the dominant terms of each equation. The resonances are the roots of the polynomial,

$$r(r+1) \left( r^2 - r \left( \frac{F_P(X_2)}{\xi^{-k_1}} - 3 \right) - \left( \frac{F_A(X_2)}{\xi^{-k_3} \beta_0 h} + \frac{F_B(X_2)}{\beta_0 \xi^{-k_2}} \right) \right) = 0. \quad (3.48)$$

The roots  $r = -1$  and  $r = 0$  correspond to the arbitrariness of  $t_0$  and  $\delta_{-k_4}$ , respectively. Finally, since  $r^2 - r \left( \frac{F_P(X_2)}{\xi^{-k_1}} - 3 \right) - \left( \frac{F_A(X_2)}{\xi^{-k_3} \beta_0 h} + \frac{F_B(X_2)}{\beta_0 \xi^{-k_2}} \right)$  has two positive integer roots, we find four resonances. Thus, the second step of the test has been accomplished.

Step 3. This is a compatibility test and it depends on a particular form of  $F$ .  $\square$

The last theorem shows how the term  $F(P, B, A, D)$  should be in order to pass the P-test. This is an important issue because the success of the P-test may indicate integrability. There are practical aspects that we can deduce from Theorem 3. If  $F$  is a polynomial, we can instantly assure that the system does not have the regularity required in its solutions. Moreover, we can find a great diversity of examples that satisfy the above conditions. We can achieve this task by setting  $F = P^{q_1} B^{q_2} A^{q_3}$ , where  $q_1 = 3 + m_1 + m_2$ ,  $q_2 = 2 - q_1 - 2q_3$  and  $q_3 = m_1 + m_2 + z$  with any two natural numbers  $m_1$  and  $m_2$  and  $z \in \mathbb{Z}$  arbitrary.

*Example 3.5.2.* As an example consider the following  $F = \frac{P^6 B^8}{A^6}$ . With this term, the system of equations (3.2)-(3.5) fulfills the conditions required by Theorem 3.5.1 and passes the P-test. Notice the specific nonlinearity of the example. So, we can discard traditional modeling terms for the function  $F$  that may include the law of mass action, logistic terms and saturation terms of the form  $\frac{B}{1+kD^s}$ .

An important fact to mention is that one of the conditions required to pass the P-test is that the  $F(P, B, A, D)$  be independent of the predator variable. This leads to a biological inconsistency because the prey is not longer affected by the predator, which might suggest that the system presents intrinsic unstable behavior and that the action of the predator should be modeled in a different way.

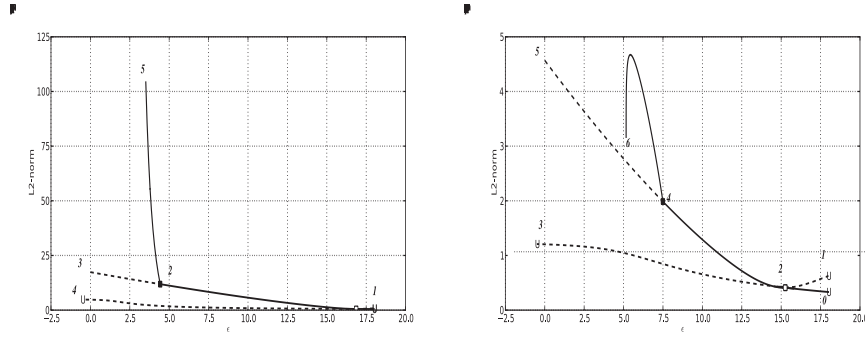


Figure 3.1: a)  $\mu = 1, b = 0.8, \rho = 0.2, m = 1$  and b)  $\mu = 0.8, b = 1.0, \rho = 0.8, m = 2$

### 3.6 Numerical Results

In order to illustrate coexistence between predator and prey, we apply standard bifurcation analysis to the ordinary differential equations system given by (3.2)-(3.5). In Figure 3.1, we show two bifurcation diagrams using AUTO (see [12]) with common values given by  $L = M = \eta = 1, \sigma = \tau = 0, \theta = 0.7, \beta_0 = 10$  and  $c = 2$ , and  $m = 1$  in 3.1 a) and  $m = 2$  in 3.1 b). The branch labeled as 2-5 in the first diagram is periodic and stable (4-6) in the second one. Here solid lines denote stability. Note that the system has three solution branches, one periodic and the other two, equilibrium branches. Also, observe that the period of the periodic solution in Figure 1 b) tends to infinity when  $\epsilon \rightarrow 0$ , while the other two branches become unstable. This fact strengthens the idea that self-limitation of the prey is an important factor to stabilize the system. Theorems 3.1 and 3.2 show that a necessary condition to pass the P-test is that the coefficient of the dominant term of the prey is given by  $\alpha_{-1} = 1/\epsilon$ . A similar behavior of the system is obtained when the coefficients  $\tau, \sigma$  and  $\rho$  vary. In all of these cases, there exist critical values of these parameters for which there is always a branch of periodic solutions. It is important to remark that the period of the solutions tend to infinity when these critical values tend to zero. If we increase the value of  $L$  or  $M$  then the critical values also increase. Numerical experiments show a specific way to choose the parameter  $\epsilon$  in to order to obtain periodic solutions. All these numerical results support the necessity that the function  $F$  contributes to the dominant terms in Step 1 of the P-test as in Theorem 3.2

## 3.7 Conclusions

In this chapter we have presented a new series of age-structure models in order to show the importance of the self-limitation in order to obtain solutions without movable critical points. The practical aspect of these models is to include the theoretical possibility that an effective strategy for the prey may result if predators can not interact with a particular class of prey. Moreover, aside from theoretical aspects, only small amount of experimental work has been carried out that includes different biological factors of self-limitation. We have shown that the Painlevé analysis plays an important role in modeling. We have discovered the necessary conditions which are required in the system in order to pass the P-test. These conditions require special nonlinearities that discard traditional interaction terms like the law of mass action, logistic terms, etc. All these necessary conditions depend on the the form of the term that models the number of newborn prey. If new nonlinearities are allowed in the model, potentially more realistic, then predation can be remodeled, since a traditional Lotka-Volterra equation for the predators population was assumed. We have shown numerically the coexistence between predator and prey by presenting several examples. The self-limitation is an essential biological factor to establish coexistence.



# Generic predation in age structure predator-prey models<sup>1</sup>

## 4.1 Introduction

In Chapter three, we tested two different versions of system (1.26) for integrability. The results were, two cases where the system did not pass the P-test and a third one where we established integrability conditions. The key idea in the last case was to allow the predation term  $F$  to be a general function and we looked for conditions to succeed the P-test. However, these conditions were restrictive and coexistence between predator-prey was found in one case where the P-test failed. Now, in this chapter we generalize the Lotka-Volterra predation term in the fourth equation of the system (1.26) and we search for conditions to pass the P-test. This led us to a modeling strategy that we called analytical modeling.

## 4.2 Analytical modeling

The classical approach to finding criteria of mathematical coexistence is through asymptotic stability or the global asymptotic stability of a unique equilibrium point or periodic solution [46, 48]. However, from a biological point of view a more realistic criterion will be to allow the system itself to define their interaction by imposing that solutions behave in a predetermined generic form. This process is what we will refer to as *analytical modeling*. In order to introduce analytical modeling in this work, we will use two well known techniques in all the branches of nonlinear science. The first one is known as the Painlevé test and the second one is the

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<sup>1</sup>This chapter is based on F.J. Solis and R.A. Ku-Carrillo, *Generic predation in age structure predator-prey models* Applied Mathematics and Computation

bifurcation theory, both of them described in Chapter 2.

Our general procedure is the following. First, we derive a general predator-prey model with age structure. Then, we apply the P-test and describe the necessary conditions to pass it. These conditions relate to the dominant terms of the system, the power of such terms and the value of the coefficients of the leading order terms. Next, we propose functions compatible with the given conditions and we also look for biological compatibility. In particular, we select functions that have biological relevance. Finally, we carry a numerical bifurcation analysis of the model using the software AUTO by Doedel [12], where we find the values of the parameters for stable equilibrium solutions and stable periodic solutions.

As a practical purpose of this chapter, it is worthy to mention that there are biological control methods to prevent the spread of pests by introducing natural predators as we do it in this work. There are numerous examples of full or partial success. The idea is to control by finding stable periodic solutions of the populations involved. This type of control has received considerable attention because of its potential practical benefits [35, 31].

This chapter is organized as follows. In Section 4.3, we propose a general predator-prey model with age structure that we will study. In Section 4.4 we introduce the analytical modeling where we include numerical simulations and interpret the biological implications of the results. Finally, conclusions are given in section 4.5.

### 4.3 Age-structured predator-prey models

The aim of this section is to derive predator-prey population models with age distribution that will be subject to analytical modeling in the following section. Since our main goal in this work is to understand predation effects, we will propose a generic predation in order to obtain viable interactions and also where biological coexistence may be achieved.

Let us recall our starting model described in the previous chapter:

$$\begin{aligned}
 \frac{dP(t)}{dt} &= -\mu_o P(t) - \mu P^2 + F(P(t), B(t), A(t), D(t)) \\
 \frac{dB(t)}{dt} &= -\theta B(t) - \mu P(t)B(t) + \beta_0 A(t) \\
 \frac{dA(t)}{dt} &= -\theta A(t) - \mu D(t)A(t) + F(P(t), B(t), A(t), D(t)) \\
 \frac{dD(t)}{dt} &= -bD(t) + cB(t)D(t)
 \end{aligned} \tag{4.1}$$

where  $\mu_0, \epsilon, \eta, \theta = \alpha + \mu_0, \beta_0, b$  and  $c$  are positive parameters.

There are two important choices to make in the model. The first one is selecting the incoming of offspring into the prey population,  $F(t) = \rho(0, t)$ , and the second is how to postulate the quantitative growth of the predation process. In Chapter 3 [37], we investigated a predator-prey model where  $F(t) = \rho(0, t)$  is a general function depending on the prey, the offspring prey and the predator populations, with the assumption that predators followed an interaction given by the classical Lotka-Volterra evolution. Here, we again select a general function  $\rho(0, t)$  which we denote as  $F(P, B, A, D)$  where  $D$  denotes the predator density and we model the predator interactions by a general term given by  $G(P, B, A, D)$ . Thus, the system of equations that we will study is:

$$\begin{aligned} \frac{dP(t)}{dt} &= -\mu_0 P(t) - \epsilon P(t)^2 + F(P(t), B(t), A(t), D(t)) \\ \frac{dB(t)}{dt} &= -\theta B(t) - \epsilon P(t)B(t) + \beta_0 A(t) \\ \frac{dA(t)}{dt} &= -\theta A(t) - \epsilon P(t)A(t) + F(P(t), B(t), A(t), D(t)) \\ \frac{dD(t)}{dt} &= -bD(t) + G(P(t), B(t), A(t), D(t)), \end{aligned} \quad (4.2)$$

where  $\theta = \alpha + \mu_0$ . A detailed construction of a simplified version of this model can be found in [37, 38].

## 4.4 Analytical modeling process

We divide this section in two parts. In the first one, we will analyze the different functional forms that the function  $G$  may take in system (4.2) in order to obtain real solutions where only poles as singularities are allowed. Systems with this characteristic are said to possess the Painlevé property. In the second one, we will select among the successful functions  $G$  from the previous step, those that guarantee periodic solutions to system (4.2).

Painlevé analysis has proved to be one of the most successful and widely applied tools in nonlinear theory. This analysis reveals a deep interrelation between the integrability of soliton equations and the integrability of certain reductions to ordinary differential equations. One may use different methods to check whether a nonlinear system passes the Painlevé test. We will make use of an algorithm named P-test. Such a test is divided in three parts. In the first one, the system is solved only for the dominant behavior, then the second step consists of finding the resonances (also called indices), here the whole system is solved by proposing solutions as truncated Laurent series of the form:

$$\begin{aligned}
 P(t) &= \sum_{i=1}^{k_1} \alpha_{-i,1}(t-t_0)^{-i} + \sum_{i=0}^{\infty} \alpha_{i,j}(t-t_0)^i, \\
 B(t) &= \sum_{i=1}^{k_2} \alpha_{-i,2}(t-t_0)^{-i} + \sum_{i=0}^{\infty} \alpha_{i,2}(t-t_0)^i, \\
 A(t) &= \sum_{i=1}^{k_3} \alpha_{-i,3}(t-t_0)^{-i} + \sum_{i=0}^{\infty} \alpha_{i,3}(t-t_0)^i, \\
 D(t) &= \sum_{i=1}^{k_4} \alpha_{-i,4}(t-t_0)^{-i} + \sum_{i=0}^{\infty} \alpha_{i,4}(t-t_0)^i,
 \end{aligned} \tag{4.3}$$

and the functions  $F$  and  $G$  are assumed of the form:

$$\begin{aligned}
 F(P, B, A, D) &= \sum_{i=1}^{k_5} \hat{f}_{-i}(t-t_0)^{-i} + \sum_{i=0}^{\infty} \hat{f}_i(t-t_0)^i \\
 G(P, B, A, D) &= \sum_{i=1}^{k_6} \hat{g}_{-i}(t-t_0)^{-i} + \sum_{i=0}^{\infty} \hat{g}_i(t-t_0)^i,
 \end{aligned} \tag{4.4}$$

where  $t_0$  is arbitrary. Since our system is formed by four nonlinear differential equations then we must ensure that four resonances are possible. The third step in the P-test consists of verifying the compatibility of the resonances and it is important because it tells us if the series (4.3) can represent a general solution. In order to accomplish this step it is necessary to have the function  $F(P, B, A, D)$  explicitly and not only its general representation. Since we are dealing with general functions  $F$  and  $G$  we only focus on the first two steps.

Let us recall that the role of the predation term  $\rho(0, t) = F(P, B, A, D)$  was already analyzed in [38] with a Lotka Volterra interaction for predators. There, it was shown that if the function  $F$  does not contribute to the dominant terms (first step in the P-test) then the system (4.2) does not pass the P-Test. However, by considering a general predator interaction term  $G$ , we have found different classes of models which are organized based on the dominant terms considered in the P-test. We obtain four cases where the P-test is successful. In the first case, the function  $F$  is not a dominant term, which is a more general result than the one given in [38]. In cases two and three, the function  $F$  is a dominant term and also the self-limitation has to be included. Finally, in case four  $F$  is dominant and the system does not have self-limitation. All the cases are presented in Tables 4.1, 4.2 and 4.3 where  $k_{1,2,3} > 0$ ,  $k_4 < 0$  and  $k_5 = k_3 - 1$  in case 4.



Table 4.1: Dominant terms

Equations	Leading order terms			
	1	2	3	4
Case 1	$(P', \varepsilon P^2)$	$(B', -\varepsilon PB)$	$(A', \varepsilon PA)$	$(D', G)$
Case 2	$(P', \varepsilon P^2)$	$(B', -\varepsilon PB)$	$(A', \varepsilon PA, F)$	$(D', G)$
Case 3	$(P', \varepsilon P^2)$	$(B', -\varepsilon PB, \lambda A)$	$(A', \varepsilon PA, F)$	$(D', G)$
Case 4	$(P', F)$	$(B', \beta_0 A)$	$(A', F)$	$(D', G)$

Table 4.2: Exponents of dominant terms

Equations	Leading order exponents				
	$k_1$	$k_2$	$k_3$	$k_4$	$k_5$
Case 1	-1	-1	-1	$k_6 + 1$	$> -2$
Case 2	-1	-1	$\geq 0$	$k_6 + 1$	-2
Case 3	-1	$k_3 - 1$	$\leq 0$	$k_6 + 1$	$> -2$
Case 4	$\geq 0$	$\geq 1$	$k_1$	$k_6 + 1$	$k_3 - 1 < 2k_1$ ,

Table 4.3: Coefficients of leading order terms

Equations	Leading order coefficients			
	$\alpha_{k_1,1}$	$\alpha_{k_2,2}$	$\alpha_{k_3,3}$	$\alpha_{k_4,4}$
Case 1	$1/\varepsilon$	arbitrary	arbitrary	$g_{k_6}/k_4$
Case 2	$1/\varepsilon$	arbitrary	$\frac{f_{k_5}}{k_3-1}$	$g_{k_6}/k_4$
Case 3	$1/\varepsilon$	$\frac{\beta_0 \alpha_{k_3,3}}{k_2+1}$	$\frac{f_{k_5}}{k_3+1}$	$g_{k_6}/k_4$
Case 4	$f_{k_5}/k_1$	$\beta_0 \alpha_{k_3,3}/k_2$	$f_{k_5}/k_3$	$g_{k_6}/k_4$

#### 4.4.1 Case 1: No contributions of leading terms to $F$

In this first case, we discover that  $F$  is not necessary as a leading term in order to pass the P-test as it was a requirement in [38], which shows the importance of taking a general interaction for predators. By taking  $k_1 = k_2 = k_3 = -1$ ,  $k_4 = k_6 + 1 \in \mathbb{Z}$ ,  $k_5 > -2$ ,  $\alpha_{k_1,1} = 1/\varepsilon$ ,  $\alpha_{k_4,4} = \hat{g}_{k_6}/k_4$  with  $\alpha_{k_2,2}$  and  $\alpha_{k_3,3}$  arbitrary constants in (4.3) and defining  $\xi = t - t_0$  and  $X_1 = (\varepsilon^{-1}\xi^{-1}, \alpha_{k_2,3}\xi^{-1}, \alpha_{k_3,3}\xi^{-1}, \hat{g}_{k_6}/k_4\xi^{k_4})$ , we obtain the following theorem.

**Theorem 4.4.1.** *Consider system (4.2). Let us assume that the functions  $F$  and  $G$  are rational functions in the variables  $P, B, A$  and  $D$ .  $F$  with a pole of order greater than two in the variable  $\xi$ . If  $\xi^{-1}\frac{\partial G}{\partial D}(X_1) - k_4 \in \mathbb{Z}^+$  then all solutions of system (4.2) are of the form (4.3).*

*Proof.* As described in [3], the first step in the P-test is accomplished by solving the system with the most dominant terms, which are  $(P', \varepsilon P^2)$ ,  $(B', -\varepsilon PB)$ ,  $(A', \varepsilon PA)$  and  $(D', G)$  corresponding to equations 1, 2, 3, and 4 of system (4.2), respectively. Notice that  $F$  does not appear as a leading term in any of these equations. For step two, the matrix of resonances, for this case is:

$$\mathbf{Q}_1(r) = \begin{pmatrix} r+1 & 0 & 0 & 0 \\ \varepsilon\alpha_{k_2,2} & r & 0 & 0 \\ \varepsilon\alpha_{k_3,3} & 0 & r & 0 \\ \xi^{-1}\frac{\partial G}{\partial P}(X_1) & \xi^{-1}\frac{\partial G}{\partial P}(X_1) & \xi^{-1}\frac{\partial G}{\partial P}(X_1) & \xi^{-1}\frac{\partial G}{\partial D}(X_1) - r - k_4 \end{pmatrix}$$

The resonances,  $r$ , are the roots of  $\det \mathbf{Q}_1(r) = 0$ , which are  $r_1 = -1$  corresponding to the arbitrariness of  $t_0$ , and  $r_{2,3} = 0$  of multiplicity two corresponding to the arbitrariness of  $\alpha_{k_2,2}$  and  $\alpha_{k_3,3}$ . Since the last root must be a nonnegative integer, we must assume that  $r_4 = \xi^{-1}\frac{\partial G}{\partial D}(X) - k_4 \in \mathbb{Z}^+$ .  $\square$

The exclusion of the term  $F$  as a dominant term implies that a possible solution with poles should come from others terms instead of  $F$ . It is worthy to mention that  $\varepsilon$  has to be different than zero in order to have this result. We conjecture that self-limitation is an important factor to obtain integrability. On the other hand, the term  $F$  describes the income of the prey offspring in the system which in this case has to be lesser than the order of the self-interaction among prey. This result excludes the case where the predator interaction is of the The Lotka-Volterra, since it can be shown that this particular example does not provide the positive resonance required by the P-test. On the other hand functions that satisfy the conditions to accomplish the second part of the P-test can be easily found.

Now to complete the first case, we will state the conditions in order to have co-existence by finding conditions for the system (4.2) to have periodic solutions. First,

we need to find explicit candidates for the functions  $F$  and  $G$ . An heuristic method to find suitable predation terms  $F$  and  $G$  is the following. Choose particular fixed values for the exponents  $k_1, k_2, k_3, k_5$  and  $k_6$  that satisfy Theorem (4.4.1). Next, we test different functions  $F$  and  $G$ , formed by algebraic combinations of the system variables  $P, B, A$  and  $D$  such that their leading orders match. Of course, there is an enormous amount of possible combinations, however by imposing biological restrictions we can obtain viable candidates, for example that  $F$  must contain the predator variable  $D$  and so on.

We carried on a classical bifurcation numerical analysis of the model using the software AUTO by Doedel [12]. We were particularly interested in finding periodic solutions so different functions  $F$  and  $G$  were tested. One example is given by  $F = f_1BP/D$  and  $G = g_1B^2/D$ , which makes the system (4.2) posses periodic solutions and also to pass the P-test. Figure 1a exhibits equilibrium and periodic solution branches. Figure 4.1a shows a bifurcation diagram where the varying parameter is  $f_1$ , the coefficient of  $F$ . There is only one branch of equilibrium solutions, label 1. Its stability is shown as a continuous curve and its instability as a dotted curve. Squares represent Hopf bifurcation points (HB) such as labels 2 and 9. From the HB point, label 2, an unstable periodic solution branch is computed with an increasing period. There the total amount of individual increases when the parameter also  $f_1$  increases. This shows that species coexistence is possible for a small range in the parameter regime which indicates the difficulty of finding a viable system. There is a second branch of periodic solutions, HB labeled 9, but it is biologically irrelevant. In Figure 4.1b, a periodic solutions is shown using only the variables  $P, B$  and  $D$  which are the prey population, juvenile prey population and predator population, respectively. We can observe that an increase in juvenile individual leads to a take off in the prey population. For the predator population, an increment is observed up to a maximum with a subsequent decline. The modeling term used for  $G$  in the example shows a strong predation only on the youngsters with a saturation term for the predators.

### 4.4.2 Case 2 and 3: The importance of self-limitation

It is well documented that self-limitation is an essential biological factor to establish coexistence. In our case, the self-limitation coefficient appears as a leading term in three of the four general cases with successful P-tests. Its contribution is independent of the functional form of  $F$ , which is how the offspring enters in the prey population. We found two general cases (case 2 and case 3) with successful P-test, where two terms are essential, namely  $F$  and self-limitation. As before, we define  $\xi = t - t_0$  and  $X_2 = (\varepsilon^{-1}\xi^{-1}, \alpha_{k_2,3}\xi^{-1}, \alpha_{k_3,3}\xi^{-1}, \hat{g}_{k_6}/k_4\xi^{k_4})$ .

For case 2, we choose  $k_1 = k_2 = -1, k_3 \geq 0, k_4 = k_6 + 1 \in \mathbb{Z}, k_5 = k_3 - 1 >$

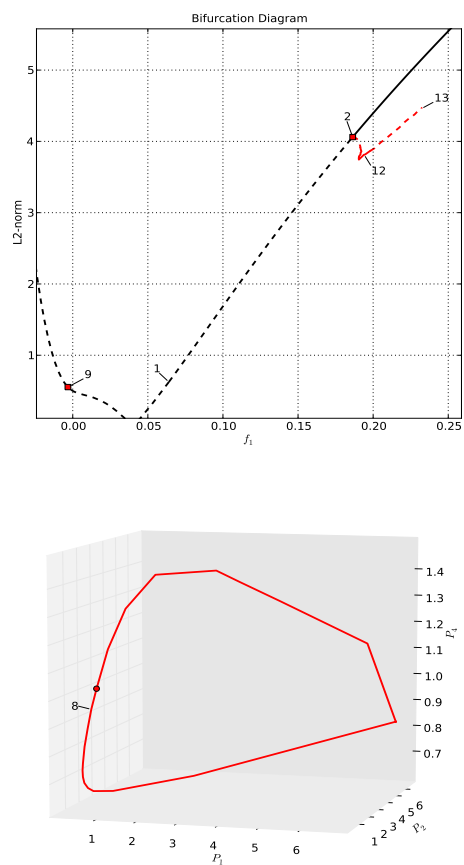


Figure 4.1: a) Bifurcation diagram with a periodic branch and  $F = PB/D$ ,  $G = B^2/D$ , b) Periodic solution for  $P, B, D$

$-2$ ,  $\alpha_{k_1,1} = 1/\varepsilon$ ,  $\alpha_{k_4,4} = \hat{g}_{k_6}/k_4$ ,  $\alpha_{k_3,3} = \hat{f}_{k_5}/(k_3 - 1)$  with  $\alpha_{k_2,2}$  being an arbitrary constant.

For case 3, we choose  $k_1 = -1$ ,  $k_2 = k_3 - 1$ ,  $k_3 \leq 0$ ,  $k_4 = k_6 + 1$ ,  $k_5 = k_3 - 1 > -2$ ,  $\alpha_{k_1,1} = 1/\varepsilon$ ,  $\alpha_{k_2,2} = \frac{\beta_0 \alpha_{k_3,3}}{k_2+1}$ ,  $\alpha_{k_3,3} = \frac{\hat{f}_{k_5}}{k_3+1}$  and  $\alpha_{k_4,4} = \hat{g}_{k_6}/k_4$ .

Let

$$\mathbf{Q}_2(\mathbf{r}) = \begin{pmatrix} r+1 & 0 & 0 & 0 \\ \varepsilon \alpha_{k_2,2} & r & 0 & 0 \\ \frac{\varepsilon \hat{f}_{k_5}}{k_3-1} - F_P^* & -F_B^* & k_3 + r + 1 - F_A^* & -F_D^* \\ G_P^* & G_B^* & G_A^* & G_D^* - r - k_4 \end{pmatrix} \quad (4.5)$$

and

$$\mathbf{Q}_3(\mathbf{r}) = \begin{pmatrix} r+1 & 0 & 0 & 0 \\ \frac{\varepsilon \beta_0 \alpha_{k_3,3}}{k_2+1} & k_2 + r + 1 & -\beta_0 & 0 \\ -\frac{\varepsilon \hat{f}}{k_3+1} + F_P^* & F_B^* & -(k_3 + r + 1) + F_A^* & F_D^* \\ G_P^* & G_B^* & G_A^* & G_D^* - r - k_4 \end{pmatrix} \quad (4.6)$$

where we have used the notation  $H_Z^*$  as  $\frac{\partial H}{\partial Z}(X_2)$ . Under these conditions we obtain the following theorem.

**Theorem 4.4.2.** *Consider the system (4.2). Let us assume that the functions  $F$  and  $G$  are rational functions in the variables  $P, B, A$  and  $D$ .  $F$  with a pole of order  $k_3 - 1$ .*

*case 2. If all zeros of the second degree polynomial  $\frac{\det \mathbf{Q}_2(\mathbf{r})}{r(r+1)}$  are different positive integers then all solutions of system (4.2) are of the form (4.3).*

*case 3. If all zeros of the third degree polynomial  $\frac{\det \mathbf{Q}_3(\mathbf{r})}{(r+1)}$  are positive integers then all solutions of system (4.2) are of the form (4.3).*

*Proof.* This proof is analogous to proof of Theorem 4.4.1. The first step of the P-Test is accomplished by solving the system for the most dominant terms, which are:

case 2,  $(P', \varepsilon P^2)$ ,  $(B', -\varepsilon PB)$ ,  $(A', \varepsilon PA, F)$  and  $(D', G)$

case 3,  $(P', \varepsilon P^2)$ ,  $(B', -\varepsilon PB, \beta_0 A)$ ,  $(A', \varepsilon PA, F)$  and  $(D', G)$

corresponding to equations 1, 2, 3 and 4 of the system (4.2), respectively. Notice, that  $F$  does appear as a leading order term in both cases. For step two, the resonance matrices are (4.5) and (4.6). The resonances,  $r$ , are the roots of  $\det \mathbf{Q}_2(r) = 0$  and  $\det \mathbf{Q}_3(r) = 0$  for case 2 and case 3, respectively. Such roots are  $r_1 = -1$  (case 2 and case 3) corresponding to the arbitrariness of  $t_0$ , and  $r_2 = 0$  (only case 3) corresponding to the arbitrariness  $\alpha_{k_3,3}$ . Since the last root must be a nonnegative integer, the roots of  $\frac{\det \mathbf{Q}_2(\mathbf{r})}{r(r+1)} = 0$  and  $\frac{\det \mathbf{Q}_3(\mathbf{r})}{(r+1)} = 0$  must be different and are  $\in \mathbb{Z}^+$ .  $\square$

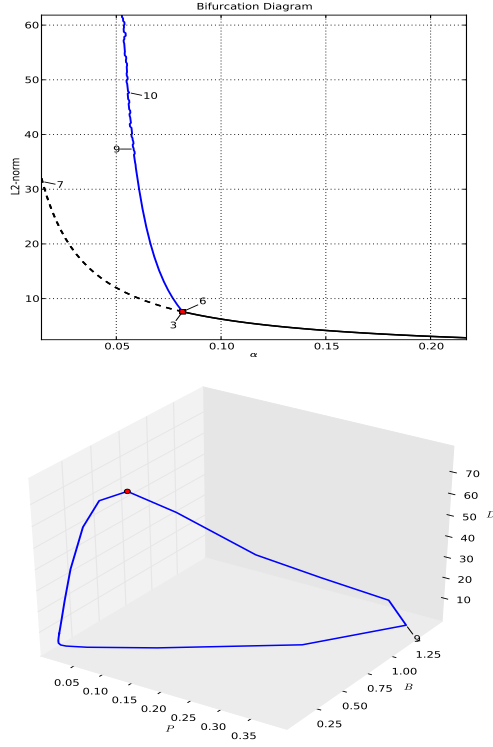


Figure 4.2: Bifurcation diagram of model 4.2 a) Bifurcation diagram with a periodic branch and  $F = f_1 \frac{B}{1+D}$ ,  $G = f_2 \frac{BD}{1+A}$ , b) Periodic solution for  $P, B, D$

Theorem 4.4.2 also highlights the importance of the self-limitation because the coefficient  $\varepsilon$  also appears in the resonance matrices (4.5) and (4.6). The viability of solutions of type (4.3) rely strongly on this parameter. Cases 2 and 3 are generalizations of Theorem 3 from [38], where the system (4.2) passes the P-Test considering  $G = -cBD$  as a Lotka-Volterra interaction term.

Among the possible choices of mechanisms of new incoming of individuals into the system  $F$  and the predation term  $G$ , we show as an example a particular combination that guarantees coexistence between the species, namely  $F = f_1 \frac{B}{1+D}$  and  $G = f_2 \frac{BD}{1+A}$ . It is important to remark on the similarity between these terms and the original ones proposed in [37]. There, the system (4.2) was studied with  $F = \frac{B}{1+\eta P^4}$  and  $G = BD$ , where  $\eta$  is a positive constant. The new function  $G$  suggested by our method can be described as a modified Lotka-Volterra predation term. The term  $cBD$  was by substituted by a saturation term of the form  $f_2 \frac{BD}{1+A}$ . The biological interpretation of this term is that resources for the predator, other than the prey population, are limited.

Figure 4.2a shows a bifurcation diagram for case 2 varying the parameter  $\alpha$  which is one of the constants in the natality rate  $\beta$ . Again, the lines depict equilibrium solutions where solid lines represent stability and the dashed lines represent instability. The branch labels 7, 3 show unstable equilibrium points. From this figure, we observe that the  $L_2$  norm tends to zero as  $\alpha$  grows. This fact is biologically consistent because  $\alpha$  controls the maximum value of the natality function  $\beta$ . The bifurcation point label 6 is a HB point and the line labeled as 9 and 10 is a stable periodic solution branch. We found again a narrow existence interval of coexistence between species. Figure 2b shows a typical periodic solution in the space  $(P, B, D)$  where the HB point is depicted as a red point. From this graph we note that the adult prey population and the predator population grow at the same time while the predator population remains at a low steady level. The predator population starts growing after the prey population, both adult and juvenile, has reached a peak. So far analytical modeling has led us to predation terms were coexistence between the predator and the prey exists.

### 4.4.3 Case 4: No self-limitation and coexistence

Two natural questions arise. Is it possible that the system passes the P-Test without self-limitation? Also, would be this enough to have coexistence of both species? The answer to both questions is positive and significant because we have widely discussed the requirement of self-limitation to have periodic solutions. This is a consequence of taking generic functional forms for  $F$  and  $G$ .

By taking  $k_1 \geq 0$ ,  $k_2 \geq 1$ ,  $k_3 = k_1$ ,  $k_4 = k_6 + 1$ ,  $k_5 = k_3 - 1 = 2k_1$ ,  $\alpha_{k_1,1} = \hat{f}_{k_5}/k_1$ ,  $\alpha_{k_2,2} = \beta_0 \alpha_{k_3,3}/k_2$ ,  $\alpha_{k_3,3} = \hat{f}_{k_5}/k_3$ ,  $\alpha_{k_4,4} = \hat{g}_{k_6}/k_4$  in (4.3) and defining  $\xi = t - t_0$  and  $X_3 = (\hat{f}_{k_5}/k_1 \xi^{k_1}, \alpha_{k_2,2} \xi^{k_2}, \alpha_{k_3,3} \xi^{k_3}, \hat{g}_{k_6}/k_4 \xi^{k_4})$  we obtain the following theorem.

**Theorem 4.4.3.** *Consider system (4.2). Let us assume that the functions  $F$  and  $G$  are rational functions in the variables  $P, B, A$  and  $D$ .  $F$  with a pole of order less than  $2k_1$  in the variable  $\xi$ . If the third degree polynomial  $\frac{\det \mathbf{Q}_4(r)}{r+1}$  has different positive roots, then all solutions of system (4.2) are of the form (4.3).*

*Proof.* The proof is similar to proofs of Theorems (4.4.1) and (4.4.2). In this case the resonance matrix is:

$$\mathbf{Q}_4(\mathbf{r}) = \begin{pmatrix} -k_1 - r & 0 & k_3 + r & 0 \\ 0 & k_2 + r & -k_3 + r & 0 \\ F_P^* & F_B^* & -(k_3 + r) + F_A^* & F_D^* \\ G_P^* & G_B^* & G_A^* & G_D^* - r - k_4 \end{pmatrix} \quad (4.7)$$

□

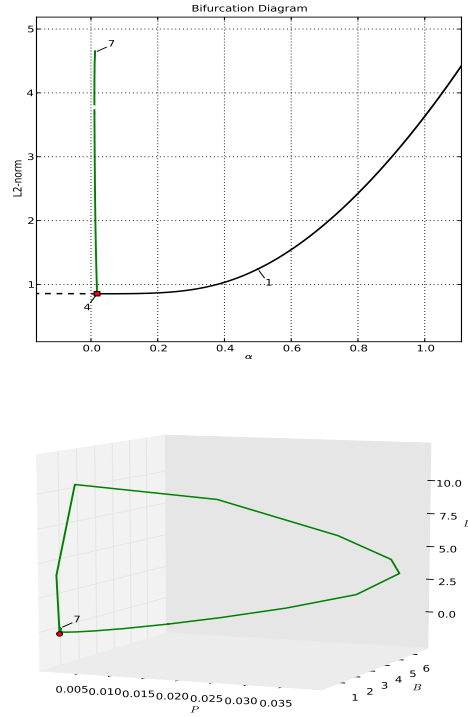


Figure 4.3: Bifurcation diagram of model 4.2 a) Bifurcation diagram with a periodic branch and  $F = P/D$ ,  $G = D^3/B$ , b) Periodic solution for  $P, B, D$

The first fact we want to remark is that we found that the some of the exponents  $k_i$  are strictly positive, which indicates analytical solutions, which allows one to use predation terms of the saturation type. The only power which admits a negative value is  $k_4$ . So, we have that the predator population  $D$  has a pole-type behavior.

Following the procedure described above, we select functions  $F$  and  $G$  fulfilling Theorem 4.4.3 conditions. A numerical study reveals that in order to obtain coexistence they all must share the same functional structure. Examples of functions  $F$  are given by  $f_1 \frac{PD}{1+P}$ ,  $f_1 \frac{PD}{1+B}$  and  $f_1 \frac{PD}{1+A}$  with a function  $G$  of the form  $G = D/B$ . This last functional term means that predation has to be carried out in adults and it exhibits saturations effects due to a portion of the prey population namely  $P, B$  or  $A$ . Biologically, the predation term points out that predator population feeds from adult prey population. However, an adverse effect is caused by the juvenile population because  $F$  is reduced when  $B$  grows. This might suggest that this juvenile population is toxic to prey population. Figure 4.3a illustrates this scenario using a bifurcation diagram were lines have the same meaning as in previous sections. A stable equilibrium solution branch is shown, which becomes unstable at a HB point,



label 4. From this point a stable periodic solution branch is computed where the  $L_2$  norm abruptly increases while the  $\alpha$  decreases, label 7. Coexistence is stable in almost the whole branch although, the existence interval of the periodic solution is small. As an example, a periodic solution is presented in Figure 4.3b. As predicted from the modeling terms  $F$  and  $G$ , the juvenile prey population grows proportionally to the adult population. One final remark is that the predator population  $D$  grows with adult prey population  $P$  steadily, but a steep descent occurs when the prey population is small.

## 4.5 Conclusions

In this chapter we have proposed an analytical way of modeling in the context of predator-prey modeling. This is based on the P-test giving conditions to obtain solutions where the only singularities are poles. An important assumption was made considering general predation functions  $F$  and  $G$  depending only on the system variables  $P$ ,  $B$ ,  $A$ , and  $D$ . Four general cases were found to pass the first two steps of the P-test. They establish the required conditions leading to special nonlinearities that discard traditional interactional terms like the law of mass action, logistic terms, etc. In all these cases, we exhibited examples with predation functions where coexistence between the predator population, juvenile and adult, and the predator population was achieved. The analytical modeling procedure also unveiled the importance of self-limitation on the prey because it was found in three of the four cases where the P-test was successful. Another relevant case with coexistence was also obtained even though self-limitation is not used in the modeling.



# Age-structured predator-prey models with varying prey birth rates <sup>1</sup>

## 5.1 Introduction

So far we have been modeling the interactions between two species capturing essential features of the interactions being modeled. Simulations also have reflected those aspects of real-life behavior. There are still many open questions that we would like to address. At each stage, we have required some type of validation concerning the new features being added and the extent to which the numbers predicted by the model compare with real data.

In this chapter, we focus on developing age structure models where birth rates can be varied. Such an analysis will help our understanding of the effects of several factors and management actions since there is a clearer link from these factors to vital rates than to abundance. Before attempting to model the vital-rate changes, we needed to address the critical lack of age-structure information. To do this, we propose a parametrized birth rate which includes the one presented in previous chapters as a particular case.

## 5.2 Birth rate analysis

Population models are commonly used to study the dynamics of animal populations. Such models are characterized by an explicit representation of age structure. This is desirable for animals which have delayed maturation, have long life spans, and for which aging methods are well established. The building blocks for demographic

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<sup>1</sup>This chapter is based on Solis, F.J. and Ku-Carrillo, R.A., Computers and Mathematics with Applications

models are age-specific birth rates and survival rates

The birth rate is usually the dominant factor in determining the rate of population growth. It depends on both the level of fertility and the age structure of the population. It is expected that this rate will be small for newborns and old individuals and large for young adults. We make the assumption that the birth rate dependence is only on age.

Mathematically, a birthrate denoted by  $\beta(\omega)$ , is a function defined only for non-negative ages, that is  $\omega \geq 0$ . Furthermore, it is a positive bounded function with compact support since the birthrate for old individuals are 0. That is,  $\beta(\omega) = 0$ , for  $\omega > A_1$  and  $\beta(\omega) < A_2$  for all  $w$  for some constants  $A_1$  and  $A_2$ .

There are several functional forms of the function  $\beta$  that have been introduced in the literature. For example, in Chapter 3 we have introduced an appropriate reproductive rate of the prey population given by

$$\beta(\omega) = \beta_0 \omega e^{-\alpha \omega} \quad (5.1)$$

with  $\beta_0 > 0$  and  $\alpha \geq 0$ . Let us recall that if  $\alpha > 0$  the birth function behaves in a way that is appropriate for many mammals and if  $\alpha = 0$  then  $\beta = \beta_0 \omega$  has been used for certain fish species. We can observe in this case that when the age  $\omega$  is zero or it tends to infinity, the corresponding  $\beta$  is zero too. Also, it is easy to check that it reaches a global maximum at the age  $\omega = \frac{1}{\alpha}$  equal to  $\beta = \frac{\beta_0}{\alpha} e^{-1}$ . All these facts fit the biology of populations properly, that is, the young and very old population do not reproduce and there is naturally a better age interval to reproduce.

In this chapter, we propose a parametrized birth rate which includes (5.1) as a particular case. This new rate is given by

$$\beta(\omega, m) = \beta_0 \omega^m e^{-\alpha \omega} \quad (5.2)$$

where  $m$  is a natural number. Notice that the new rate has mathematically and biologically all required properties. See Figure 5.1 where we plot the graph of  $\beta(\omega, m)$  for some specific values of  $m$ . It is important to clarify that the new birth rate also will allow us to obtain a differential system instead of an integro-differential system as we will discuss next.

### 5.3 Age-structured models

In this section we develop age-structure models that includes our new proposed birth rate function as well as self-limitation of the prey and generic predation interactions. Earlier versions of these new models were discussed in previous chapters. In those models, a basic assumption was made by considering that the birth rate  $\beta$  is

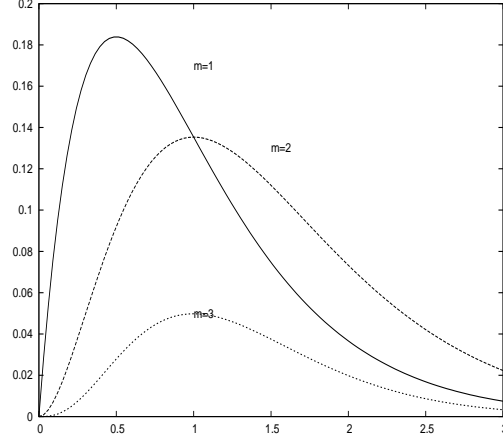


Figure 5.1: Graphs of the birth rate  $\beta(\omega, m)$  for different values of  $m$ .

equal to (5.1). The role of this natality rate is important because it allows us to have the following system of differential equations (instead of an integro-differential system):

$$\begin{aligned}
 \frac{dP_1}{dt} &= -\mu_0 P_1 - \varepsilon P_1^2 + F(P_1, P_2, P_3, P_4) \\
 \frac{dP_2}{dt} &= -\theta P_2 - \varepsilon P_1 P_2 + \beta_0 P_3 \\
 \frac{dP_3}{dt} &= -\theta P_3 - \varepsilon P_1 P_3 + F(P_1, P_2, P_3, P_4) \\
 \frac{dP_4}{dt} &= -b P_4 + G(P_1, P_2, P_3, P_4),
 \end{aligned} \tag{5.3}$$

where  $P_1, P_2, P_3$  and  $P_4$  represent a time  $t$ , the total population of the prey, the juvenile population, and auxiliary variable and the total predator population, respectively. The functions  $F(P_1, P_2, P_3, P_4)$  and  $G(P_1, P_2, P_3, P_4)$  are general predation functions. All other coefficients are positive constants.

Next, we will construct age-structured models based on the birth rate (5.2). Let us consider that the prey population of age  $\omega$  at the time  $t$  is denoted by  $\rho(\omega, t)$ . The total population is the sum over the ages,

$$P_1(t) = \int_0^\infty \rho(\omega, t) d\omega. \tag{5.4}$$

We also consider an age structure by using the McKendrick equation,

$$\rho_\omega(\omega, t) + \rho_t(\omega, t) + \mu\rho(\omega, t) = 0. \tag{5.5}$$

Now, let us find differential equations for the total population,  $P_1(t)$  and the population of newborns  $P_2(t)$ . In order to do this, we integrate (5.5) from zero to infinity obtaining:

$$\frac{dP_1(t)}{dt} = -\mu(P_1)P_1 + \rho(0, t). \quad (5.6)$$

The juvenile population is calculated as  $P_2(t) = \int_0^\infty \beta(w, m)\rho(w, t) dw$ . Its corresponding differential equation is obtained if we multiply (5.5) by  $\beta_0 w^m e^{-\alpha w}$ , which is the new birth rate. Then, we integrate again and use integration by parts,

$$\frac{dP_2(t)}{dt} = -(\mu(P_1) + \alpha)P_2(t) + \beta_0 m \int_0^\infty w^{m-1} e^{-\alpha w} \rho(w, t) dw. \quad (5.7)$$

This integro-differential equation can be transformed to an ordinary differential equation defining the variable  $P_3(t)$ ,

$$P_3(t) = \int_0^\infty w^{m-1} e^{-\alpha w} \rho(w, t) dw. \quad (5.8)$$

This new variable  $P_3$  also satisfies the following differential equation obtained derivating (5.8) with respect to  $t$  to get,

$$\frac{dP_3(t)}{dt} = -(\mu + \alpha)P_3 + (m - 1) \int_0^\infty w^{m-2} e^{-\alpha w} \rho(w, t) dw. \quad (5.9)$$

Again, we get a integro-differential equation but the procedure described above can be use by defining,

$$P_j(t) = \int_0^\infty w^{m+2-j} e^{-\alpha w} \rho(w, t) dw \text{ for } j = 2, \dots, m + 2 \quad (5.10)$$

In general, for  $j = 2, \dots, m + 1$  we obtain

$$\frac{dP_j(t)}{dt} = -(\mu + \alpha)P_j + (m + 2 - j) \int_0^\infty w^{m+1-j} e^{-\alpha w} \rho(w, t) dw \quad (5.11)$$

which by definition can be written as

$$\frac{dP_j(t)}{dt} = -(\mu + \alpha)P_j + (m + 2 - j)P_{j+1}. \quad (5.12)$$

Finally, for  $j = m + 2$  we get

$$\frac{dP_{m+2}(t)}{dt} = -(\mu + \alpha)P_{m+2} + \rho(0, t). \quad (5.13)$$

Since we have discovered that an essential mechanism to achieve coexistence is the self-limitation of the prey, we will assume that  $\mu = \mu_0 + \epsilon P_1$ . Thus, by substituting it in the model we obtain the following prey age-structured model.

$$\begin{aligned}\frac{dP_1(t)}{dt} &= -\mu_0 P_1 - \epsilon P_1^2 + \rho(0, t) \\ \frac{dP_2(t)}{dt} &= -\theta P_2 - \epsilon P_1 P_2 + m\beta_0 P_3 \\ \frac{dP_3(t)}{dt} &= -\theta P_3 - \epsilon P_1 P_3 + (m-1)P_4 \\ &\vdots \\ \frac{dP_{m+2}(t)}{dt} &= -\theta P_{m+2} - \epsilon P_1 P_{m+2} + \rho(0, t)\end{aligned}$$

where  $\mu_0, \epsilon, \eta, \theta = \alpha + \mu_0, \beta_0, b$  and  $c$  are positive parameters.

There are two important choices to make in the model. The first one is selecting the incoming of offspring into the prey population,  $\rho(0, t)$ , and the second is how to postulate the quantitative growth of the predation process. In [37, 38], we proposed general predation functions suggested by the Painlevé analysis, which we will use in this work. We will denote by  $P_{m+3}$  the predator population and its interaction given  $\frac{dP_{m+3}(t)}{dt} = -bP_{m+3} + G(P_1, \dots, P_{m+2}, P_{m+3})$ . We make the assumption that  $\rho(0, t)$  depends only on  $P_j(t)$  for  $j = 1, 2, \dots, m+3$ . Therefore  $\rho(0, t) = F(P_1, \dots, P_{m+2}, P_{m+3})$  for some suitable functions  $F$ . So our final models take the form:

$$\begin{aligned}\frac{dP_1(t)}{dt} &= -\mu_0 P_1 - \epsilon P_1^2 + F(P_1, \dots, P_{m+2}, P_{m+3}) \\ \frac{dP_2(t)}{dt} &= -\theta P_2 - \epsilon P_1 P_2 + m\beta_0 P_3 \\ \frac{dP_3(t)}{dt} &= -\theta P_3 - \epsilon P_1 P_3 + (m-1)P_4 \\ &\vdots \\ \frac{dP_{m+2}(t)}{dt} &= -\theta P_{m+2} - \epsilon P_1 P_{m+2} + F(P_1, \dots, P_{m+2}, P_{m+3}) \\ \frac{dP_{m+3}(t)}{dt} &= -bP_{m+3} + G(P_1, \dots, P_{m+2}, P_{m+3}).\end{aligned}\tag{5.14}$$

## 5.4 Numerical results

In this section we focus on the numerical analysis of system (5.14) by choosing appropriate functions for  $F$  and  $G$ . Our goal is to analyze how the birth rate modifies the behavior of system (5.14), that is to investigate the effect of varying the power  $m$  in the birth rate. In order to do this, we will select some choices of the parameter  $m$ . We divide our analysis into several cases that have been analyzed in previous chapters.

In the first case we choose  $F = fP_2/(1 + P_{m+3})$  and  $G = gP_2P_{m+3}$ . This case has been analyzed in [37] for  $m = 1$ . In the second case we select  $F = fP_1P_{m+3}/(1 + P_2)$  and  $G = gP_{m+3}/P_2$ , in the third case  $F = fP_2/(1 + P_{m+3})$  and  $G = gP_2P_{m+3}/(1 + P_3)$ , and finally, in the fourth case  $F = fP_1P_2/(\sigma + P_{m+3})$  and  $G = gP_2^2/(\sigma + P_{m+3})$ . All of these combinations have presented periodic branches for the case  $m = 1$ .

### 5.4.1 Case 1. $F = fP_2/(1 + P_{m+3})$ and $G = gP_2P_{m+3}$

This combination of functions  $G$  and  $F$  correspond to a juvenile predation interaction of the Lotka-Volterra type and a saturation term, respectively. The function  $F$  was first obtained in [37] as the following approximation assuming that predator population  $P_{m+2}$  is small:

$$F(P_2, P_{m+3}) = cP_2(t) - \mu_0 P_2(t)P_{m+3}(t) = \frac{P_2(t)}{1 + \mu_0 P_{m+3}(t)} + O(P_{m+3}^2(t)) \quad (5.15)$$

where we take  $F$  as the following proportional truncated form assuming that  $\mu_0 = c$ ,

$$F(P_2, P_{m+3}) = \frac{f_1 P_2(t)}{1 + P_{m+3}(t)}. \quad (5.16)$$

The choice of function  $G$ , the Lotka-Volterra predation term, was made by considering the simplest case for predation interaction. System (5.14) with this selection of functions  $F$  and  $G$  with  $m = 1$  and fixed coefficients was proposed as a viable solution for coexistence between the species. Thus, it is an important case to analyze by modifying the prey birth rate.

We will fix every parameter except  $\alpha$ , with values  $\mu = 0.77125$ ,  $\varepsilon = 0.01$ ,  $f_1 = 3.5416$ ,  $\alpha = 0.47075$ ,  $\beta_0 = 0.46875$ ,  $b = 0.03$  and  $d = 0.10$ . As we vary  $\alpha$ , we find that there are eleven solution branches for every value of  $\alpha$  and every value of  $m$ . Of those branches, only five are of biological interest. Four of them correspond to equilibrium branches and the other one is a periodic branch. The stability of



equilibria varies with the parameter  $\alpha$ . But what is of paramount importance is the fact that for  $m = 1$  such periodic branch is unstable but for  $m > 1$  it is stable. Following the stable periodic branch solution ( $m > 1$ ), the period increases up to infinity. In biological terms these results are important since by varying the birth rate we are able to obtain coexistence from an unstable system. These facts can be seen more clearly in Figures 5.2-5.4 where we plot the parameter  $\alpha$  against the norm of the solution. For stationary solutions we use the Euclidean norm and for periodic solutions we use the norm

$$\sqrt{\frac{1}{T} \int_0^T \sum_{j=1}^{m+3} P_j^2(t) dt}$$

where  $T$  is the period of the solution. Branches of stable solutions periodic and stationary are represented solid lines. A dotted curve means that the solution is unstable for those values of  $\alpha$ .

#### 5.4.2 Case 2. $F = fP_1P_{m+3}/(1 + P_2)$ and $G = gP_{m+3}/P_2$

In this case we study the case for social prey which becomes aggressive towards the predators when their number is large enough, but becomes susceptible for small numbers, for example *Syncerus caffer*. Thus we choose  $G$  proportional to  $P_{m+3}/P_2$ . For  $F$  we select the truncated form  $F = fP_1P_{m+3}/(1 + P_2)$  analogous to (5.16). This time the calculation of the continuation of equilibrium points and periodic solutions become more complicated. We again fix the values of all the parameters and vary  $\alpha$ . The values are the same as in the previous case, except that  $\varepsilon = 0$  meaning that self-limitation is not considered. We find that there is only one branch of equilibrium solutions and one branch of periodic solutions for every value of  $\alpha$  and only for  $m = 1, 2$  and for every particular initial condition. The periodic branch is stable and its period also increases to infinity. Notice that even for the case  $m = 1$ , coexistence is established. In Figure 5.5 we can observe these facts in detail. What is remarkable in this case is that self-limitation is not necessary to achieve coexistence.

#### 5.4.3 Case 3. $F = fP_2/(1 + P_{m+3})$ and $G = gP_2P_{m+3}/(1 + P_3)$

In this case, we choose  $G$  proportional to  $P_2P_{m+3}/(1 + P_3)$ . For  $F$  we select the truncated form  $F = fP_2/(1 + P_{m+3})$  analogous to (5.16). The values of the constants are the same as in Case 1. As in Case 2, there is only one branch of equilibrium solutions and one branch of periodic solutions at least for the cases  $m = 1, 2, 3$

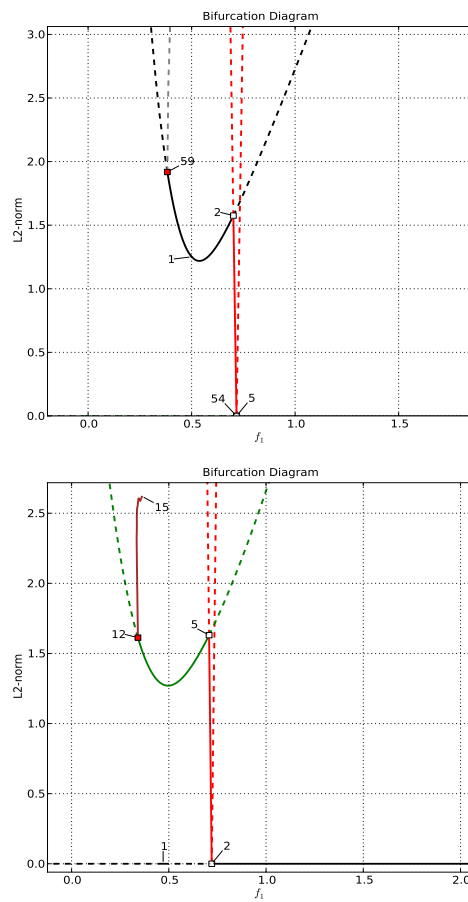


Figure 5.2: Case 1.  $F = fP_2/(1 + P_{m+3})$  and  $G = gP_2P_{m+3}$ , a)  $m = 1$ , b)  $m = 2$

5.4. NUMERICAL RESULTS

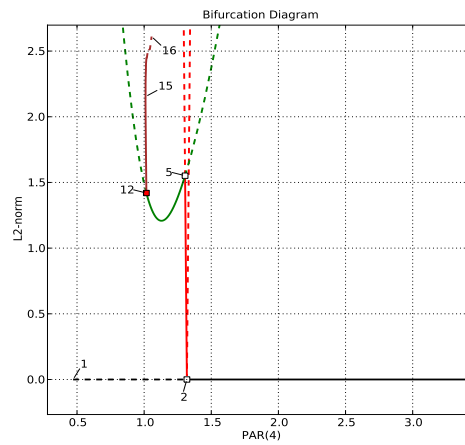
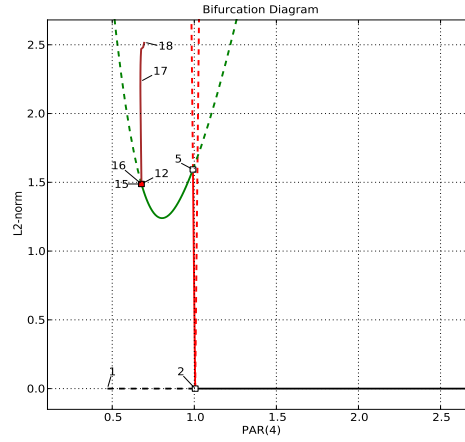


Figure 5.3: Case 1.  $F = fP_2/(1 + P_{m+3})$  and  $G = gP_2P_{m+3}$ , a)  $m = 3$ , b)  $m = 4$

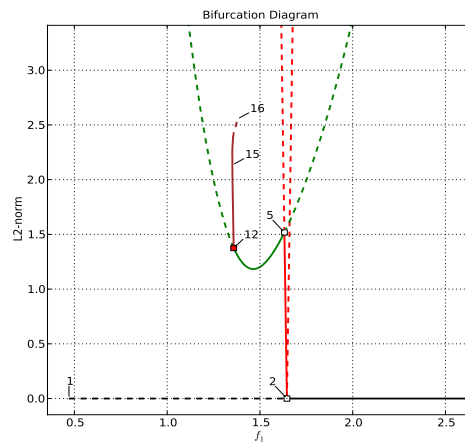


Figure 5.4: Case 1.  $F = fP_2/(1 + P_{m+3})$  and  $G = gP_2P_{m+3}$ ,  $m = 5$ .

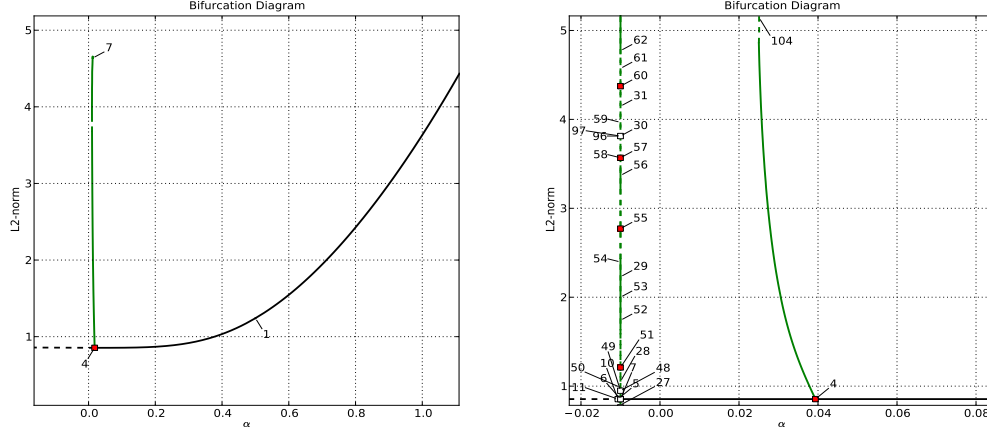


Figure 5.5: Case 2.  $F = fP_1P_{m+3}/(1 + P_2)$  and  $G = gP_{m+3}/P_2$ , a)  $m = 1$  b)  $m = 2$

Bigger values of  $m$  were not analyzed. The periodic branch is stable and its period increases faster to infinity than those for cases 1 and 2. In this case  $m$  acts as a perturbation parameter for the Hopf bifurcation points. See Figures 5.6 and 5.7.

**5.4.4 Case 4.**  $F = fP_1P_2/(\sigma + P_{m+3})$  and  $G = gP_2^2/(\sigma + P_{m+3})$

This case is presented only for theoretical purposes in order to illustrate the possibilities in the selection of the predator interaction and the fraction of juveniles that survive predation. We assumed that  $\sigma \approx 0$  and we vary the parameter  $f_1$  instead of the parameter  $\alpha$ . The qualitative behavior is the same as the previous case. The only difference is the variation of the equilibrium branch.

5.4. NUMERICAL RESULTS

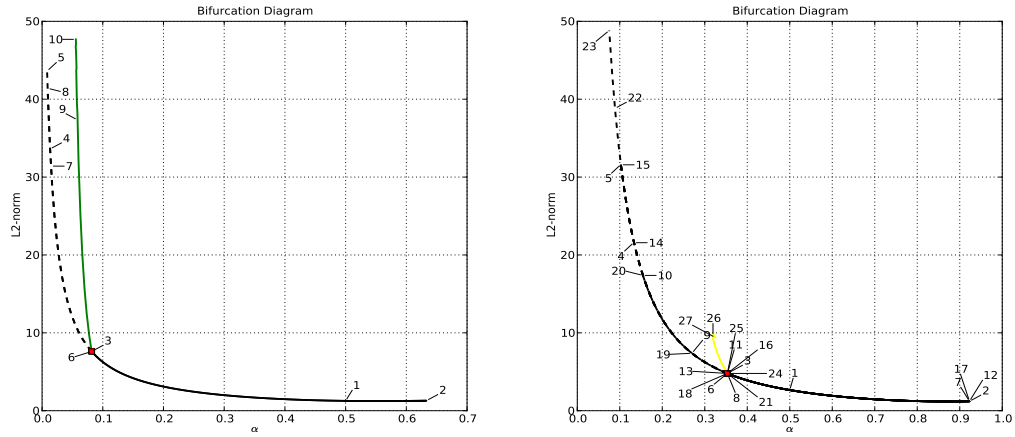


Figure 5.6: Case 3.  $F = fP_2/(1 + P_{m+3})$  and  $G = gP_2P_{m+3}/(1 + P_3)$ , a)  $m = 1$   
 b)  $m = 2$

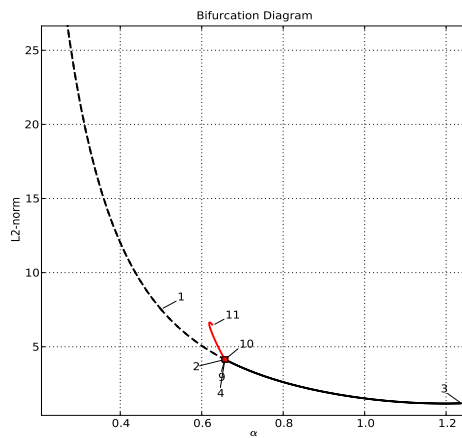


Figure 5.7: Case 3.  $F = fP_2/(1 + P_{m+3})$  and  $G = gP_2P_{m+3}/(1 + P_3)$ ,  $m = 3$

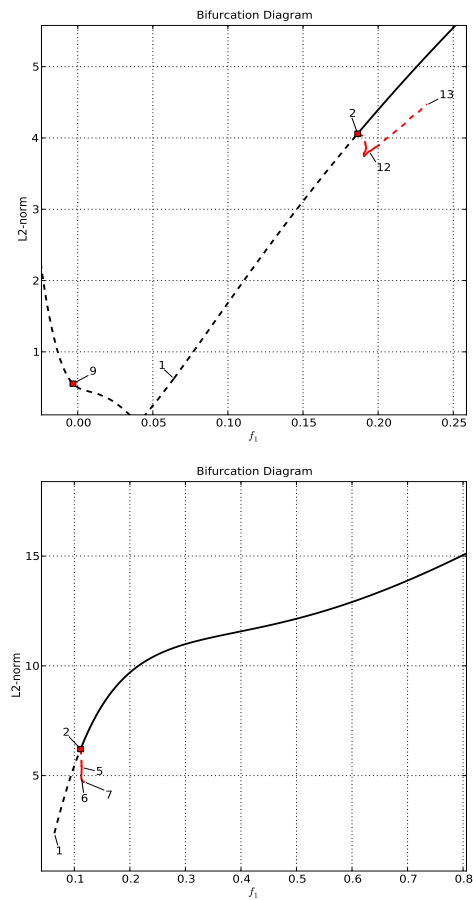


Figure 5.8: Case 4.  $F = fP_1P_2/(\sigma + P_{m+3})$  and  $G = gP_2^2/(\sigma + P_{m+3})$ , a)  $m = 1$   
 b)  $m = 2$

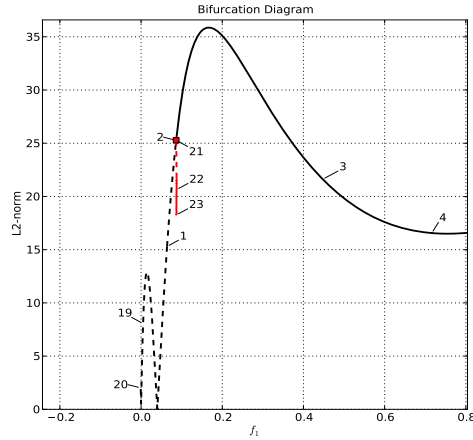


Figure 5.9: Case 4.  $F = fP_1P_2/(\sigma + P_{m+3})$  and  $G = gP_2^2/(\sigma + P_{m+3})$ ,  $m = 3$

## 5.5 Conclusions

In this chapter we have presented a new series of age-structured models to show the importance of the birth rate in order to obtain coexistence. We have shown that by changing the rate of birth we can obtain periodic solutions for more simple models. The qualitative and quantitative mathematical properties and biological and ecological consequences have been addressed. We are planning to analyze different functional forms of the birth rate in the near future.

*CHAPTER 5. AGE-STRUCTURED PREDATOR-PREY MODELS WITH  
VARYING PREY BIRTH RATES*<sup>8</sup>

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## Conclusions

The most important contribution of this thesis to the study of age-structured predator-prey models is what we called the *analytical modeling*. What we mean by this is that integrability conditions can be used to suggest modeling terms. In particular, we were interested in setting conditions in such a way the system of ordinary differential equations which models a predator-prey interaction have singularities of pole type only. This led us to find predation functions that allowed the predator-prey model to succeed the P-test, i.e. the singularities of the predator-prey model can be only of pole type. This provides a methodology to introduce a new gamma of predator-prey models which already satisfied the required regularity. The idea of *analytical modeling* is a generalization of the widely applied process of finding conditions under the parameters to have a first integral. However, a major difference is achieved when the P-test is used to determine modeling terms. Theorem 3.5.1 set the conditions in order the model (3.7)-(3.10) passes the first two steps of the P-test. However, the allowed predation functions  $F$  were biologically irrelevant.

A second contribution was accomplished applying this general methodology. We considered general predation functions  $F$  and  $G$  depending only on the system variables  $P$ ,  $B$ ,  $A$ , and  $D$ . By this mean, we were able to analyze a more general model or a set of predator-prey models. Four general cases were found to pass the first two steps of the P-test. Then, we established the required conditions under the modeling terms that led us to special nonlinearities that discard traditional interaction terms like the law of mass action, logistic terms, etc. In all these cases, we presented examples with predation functions where coexistence between the predator population, juvenile and adult, and the prey population was achieved.

In Chapter 3, we study a specific predation function (3.46) which includes a variety of models. This function is a generalization of the predation functions used in [36]. Our results described the characteristics of the solutions where the existence of algebraic or logarithmic branches were proved in Theorem 3.4.1. This is our third contribution. This was made using the Painlevé analysis and the bifurcation

analysis. We carried out a numerical study which exhibited periodic solutions even though the integrability conditions were not satisfied.

It is well documented the importance of self-limitation as a strategy to stabilize a model. In fact, the Painlevé analysis also showed the importance of the self-limitation of the prey (parameter  $\varepsilon$ ) as described in section 4.4.2. With this in mind, we can say that another contribution of the described methodology is that we were able to find a model where the self-limitation is not longer necessary to find periodic solutions. This modeling term was suggested by the P-test also. In section 4.4.3 we showed an example and Theorem 4.4.3 gives the required conditions. This improves the results of [36, 37] where a number of modeling strategies were applied to obtain the coexistence of the species.

The last contribution is that the variation of the birth rate of the prey in Chapter 5 provided a wide variety of age-structured predator-prey models. This rate is more general than one used in Chapters 3 and 4. And also this rate includes the birth rate used in previous studies [36, 37, 38]. However, the analysis was numerical but the bifurcation results gave us evidence that the variation of the birth rate can lead to coexistence of the predator and prey populations. Furthermore, it was shown that the variation of such parameter usually does not modify the structure of periodic solutions.

Finally, we would mention several directions of future work which can be developed on this topic. Age structure can be associated to both populations: predator and prey instead of only one population. Other approach which could be used is to study the predator and the prey populations from the partial differential equations. Let us recall that our work was done considering a set of ordinary differential equations obtained from the partial differential equations. An important work could be also to establish analytical results concerning the general birth rate studied in Chapter 5. All of these research topics are important and challenging. They will be part of forthcoming study.

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