

# Stability of equilibria of a predator prey model of phenotype evolution

Sílvia Cuadrado

## Abstract

We consider a selection mutation predator prey model for the distribution of individuals with respect to an evolutionary trait. Local stability of the equilibria of this model is studied using the linearized stability principle and taking advantage of the (assumed) asymptotic stability of the equilibria of the resident population adopting an evolutionarily stable strategy.

*Keywords:* Asymptotic stability, Weinstein Aronszajn determinant, evolutionarily stable strategy.

*AMS Subject Classification:* 35B35, 47A10, 92D15.

## 1 Introduction

The evolutionary process of certain evolutionary traits can be modelled by selection mutation equations for the distribution of individuals with respect to the trait that can be either discrete (see, for instance [2]) or continuous (see for instance [9], [5], [21]).

These evolutionary traits can be either genotypical or phenotypical. In the continuous framework, the use of selection mutation equations in population genetics can be traced back to the works of Crow and Kimura ([14], [20]) for the frequency distribution of a continuum of alleles in order to explain the maintenance of variability due to the balance effect of selection and mutation. In [14] mutation was modelled by a convolution operator whereas in [20] it was approximated by a diffusion operator. Later on, Bürger and Bomze ([5]) have generalized Kimura's model considering general integral operators. They show, under certain hypotheses, existence and uniqueness of stationary distributions in  $L^1$  and, in some other cases, existence of equilibrium solutions that are Borel measures.

Selection mutation equations have also been used to model evolution of (pure) continuous phenotypic traits. The main ingredient for these models is a density of individuals with respect to some phenotypical evolutionary trait (the more natural

formulation of these equations in the space of measures is still being developed, see [1], [4], [13] for a formulation in the space of measures of pure selection models). Selection appears in the equations as some nonlinear terms that model the competition among individuals. Mutation is modelled either by means of a Laplacian operator ([9], [10], [21], [18]) or by an integral operator with a mutation kernel which is often linear ([6], [7], [11]) although it can also be nonlinear ([16]) (see also [24] where selection mutation equations considering both ways of modelling mutation are used to analyse experimental studies of in vitro viral evolution). Of particular interest for many of these works has been the study of the equilibria of these models for the density of individuals with respect to a phenotypic evolutionary trait and their relation with the evolutionarily stable strategies (ESS) of the underlying ecological models (that is, the models that we obtain when there is no mutation and all individuals have the same value of the evolutionary variable). The evolutionarily stable strategies are the stationary values of the evolutionary process and it is a concept that was first introduced by Maynard Smith and Price in the context of game theory (see [22]). In a few words, a strategy  $x$  (value of a phenotypic characteristic) is an ESS if a clonal population of individuals with strategy  $x$  cannot be invaded by another small clonal population of individuals with a different strategy  $y$ .

An example of a selection mutation equation for a phenotypical characteristic is the following predator prey model ([15]) for the distribution of individuals with respect to the index of activity of the predator during daytime  $x \in [0, 1]$

$$\left\{ \begin{array}{l} f'(t) = (a - \mu f(t) - \int_0^1 \frac{\beta(x)u(x,t)}{1 + \beta(x)hf(t)} dx) f(t), \\ \frac{\partial u(x,t)}{\partial t} = (1 - \varepsilon) \frac{\alpha\beta(x)f(t)u(x,t)}{1 + \beta(x)hf(t)} + \varepsilon \int_0^1 \gamma(x,y) \frac{\alpha\beta(y)f(t)u(y,t)}{1 + \beta(y)hf(t)} dy \\ - d(x)u(x,t), \end{array} \right. \quad (1)$$

where  $f(t)$  denotes the number of individuals of the prey population at time  $t$  (that follows a logistic growth law in absence of predators),  $u(x,t)$  denotes the density of predators at time  $t$  with respect to the trait,  $d(x)$  and  $\beta(x)$  are the searching efficiency and the mortality of the predator,  $\varepsilon$  is the probability of mutation and  $\gamma(x,y)$  is the density of probability that the trait of the mutant offspring of a predator with trait  $y$  is  $x$ .

In [15] we proved, under some hypotheses, existence of a family of equilibria  $(f_\varepsilon, u_\varepsilon)$  of System (1) that tend to concentrate, when the probability of mutation tends to zero at a certain value of the evolutionary trait that turns out to be the (unique) evolutionarily stable strategy of the finite dimensional predator prey model obtained when we consider in (1) that there is no mutation and all individuals have the same value of the evolutionary variable. The present work is devoted to study local stability of these equilibria.

More in general, selection mutation equations for the distribution of individuals with respect to a phenotypical trait give rise (in some cases) to equations for densities on the trait parameter space  $\Omega$ . That is, equations for  $\mathbb{R}^n$  valued densities in

the state space  $L^1(\Omega)$  which can be written in the form

$$\vec{z}_t = A_\varepsilon(F(\vec{z}))\vec{z} \quad (2)$$

where  $A_\varepsilon(E)$  is a (generally unbounded) linear operator,  $\varepsilon$  denotes the mutation rate and  $F$  is a function from the state space to  $\mathbb{R}^m$  which summarizes the environmental interaction variables (like predator density or food concentration for instance), in such a way that, given  $F(\vec{z})$ , the population problem becomes linear. If we assume for these equations that there is no mutation and all individuals have the same value of the evolutionary variable, we can consider the  $n$ -dimensional ordinary differential equations model

$$\vec{v}_t = A_0(x, F(\vec{v}\delta_x))\vec{v} \quad (3)$$

being the relationship between the operators  $A_\varepsilon(E)$  and  $A_0(x, E)$  that  $A_\varepsilon(E)$  tends (formally) as  $\varepsilon$  goes to 0 to a matrix multiplication operator generated by the matrix  $A_0(x, E)$ .

Assuming the existence of an (hyperbolic) asymptotically stable nontrivial steady state  $\vec{v}_x$  of (3) for some values of the parameter  $x$ , one of these values  $\hat{x}$  is called an evolutionarily stable strategy (ESS) if the linear equation  $\vec{w}_t = A_0(x, F(\vec{v}_{\hat{x}}\delta_{\hat{x}}))\vec{w}$ , is hyperbolically asymptotically stable for any value  $x \neq \hat{x}$  (see [23]).

A nontrivial stationary solution  $\vec{z}_\varepsilon$  of equation (2) is a positive eigenvector of eigenvalue 0 of the linear operator  $A_\varepsilon(F(\vec{z}_\varepsilon))$ . That is, the problem of finding non trivial stationary solutions of these equations is related to infinite dimensional versions of the Perron Frobenius theorem.

In [8] we studied local stability (for  $\varepsilon$  close to zero) of equilibria  $\vec{z}_\varepsilon$  of selection mutation equations of the form (2) taking advantage of the asymptotic stability of the corresponding ESS “ecological” equilibrium (that is, the equilibrium of (3) for the value  $\hat{x}$  of ESS of the parameter). The main feature for this kind of equations is that, in general, when the environment,  $F(\vec{z})$ , is finite dimensional, the linearized operator at the stationary solution is a degenerate perturbation of an operator with spectral bound equal to zero. Because of this, the computation of the spectrum of the linearization reduces to the computation of the zeroes of a characteristic equation given by the so called Weinstein-Aronszajn determinant (see [19] for a definition of this determinant).

However, this analysis is in general not easy due to the fact that the operator  $A_\varepsilon(F(\vec{z}_\varepsilon))$  tends, when  $\varepsilon$  goes to zero to a multiplication operator and therefore its dominant eigenvalue is not uniformly isolated with respect to  $\varepsilon$ . For the prey predator model (1), the two dimensionality of the model adds difficulties in order to apply the stability results of [8].

Linearizing System (2) at the steady state  $\vec{z}_\varepsilon$ , we obtain that the linearized operator (that will be denoted by  $\tilde{A}_\varepsilon + S_\varepsilon$ ) is a perturbation by a finite dimensional range operator of the operator that we have when in the model the nonlinearity is given by the equilibrium (denoted by  $\tilde{A}_\varepsilon$  and that in general has spectral bound zero but not for the predator prey model (1), which is one of the difficulties in order to apply some of the results of [8]). Computing the spectrum of  $\tilde{A}_\varepsilon + S_\varepsilon$  we have that  $\sigma(\tilde{A}_\varepsilon + S_\varepsilon) \subset \sigma(\tilde{A}_\varepsilon) \cup \{\lambda : \det(I + S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1}) = 0\}$ . That is, the

spectrum of the linearized operator is contained in the spectrum of the operator  $\tilde{A}_\varepsilon$  union the zeros of a characteristic equation given by the Weinstein-Aronszajn determinant associated with the operators  $\tilde{A}_\varepsilon$  and  $S_\varepsilon$ .

Linearizing the prey predator model (1) at the steady state  $(f_\varepsilon, u_\varepsilon)$ , we obtain that  $\sigma(\tilde{A}_\varepsilon) = \{a - \mu f_\varepsilon\} \cup \sigma(C_{\varepsilon, f_\varepsilon})$  where  $a - \mu f_\varepsilon$  is a positive real number and  $C_{\varepsilon, f_\varepsilon}$  is an operator with dominant eigenvalue zero. So, in order to see that the steady state of the predator prey model is asymptotically stable we first show that  $a - \mu f_\varepsilon$  and 0 are not in the spectrum of  $\tilde{A}_\varepsilon + S_\varepsilon$ . In order to prove that the characteristic equation given by the Weinstein-Aronszajn determinant does not vanish for  $\lambda$  with positive real part we take advantage of the asymptotical stability of the corresponding ESS “ecological” equilibrium to obtain that for all  $L_1 > 0$  there exists  $\varepsilon$  small enough such that  $\det(I + S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1}) \neq 0$  for  $\lambda \in \mathbb{C}$  s.t.  $\text{Re}\lambda > 0$ ,  $|\lambda| \geq L_1$ . Finally, we show that, for a particular case of the model (1) the set  $\{\lambda \in \mathbb{C} \text{ s.t. } \text{Re}\lambda > 0, |\lambda| < L_1\}$  for some  $L_1 > 0$  can be excluded from the spectrum of the linearized operator  $\tilde{A}_\varepsilon + S_\varepsilon$  obtaining then, for  $\varepsilon$  small, stability of the equilibrium.

## 2 The model

Our aim is to study local stability of the equilibria of the prey predator model introduced in [15]

$$\left\{ \begin{array}{l} f'(t) = (a - \mu f(t) - \int_0^1 \frac{\beta(x)u(x,t)}{1 + \beta(x)hf(t)} dx) f(t), \\ \frac{\partial u(x,t)}{\partial t} = (1 - \varepsilon) \frac{\alpha\beta(x)f(t)u(x,t)}{1 + \beta(x)hf(t)} + \varepsilon \int_0^1 \gamma(x,y) \frac{\alpha\beta(y)f(t)u(y,t)}{1 + \beta(y)hf(t)} dy \\ - d(x)u(x,t), \end{array} \right. \quad (4)$$

where  $f(t)$  denotes the number of individuals of the prey population at time  $t$  and  $u(x,t)$  denotes the density of predators at time  $t$  with respect to the trait  $x \in [0, 1]$  that denotes the index of activity of the predator during daytime.

$a$  and  $\mu$  are fixed positive numbers denoting the intrinsic growth rate and the competition coefficient of the prey population and  $\alpha$  is the proportion of energy that the predator obtains from prey consumption.

$d(x)$  and  $\beta(x)$  are increasing bounded functions such that  $\beta(0) = 0$  and  $d(0) > 0$  denoting the searching efficiency and the mortality of the predator respectively. Finally,  $\varepsilon$  denotes the probability of mutation which is given by the density of probability  $\gamma(x, y)$  that we assume that it is a strictly positive continuous function satisfying  $\int_0^1 \gamma(x, y) dx = 1$  for all  $y$ .

In [15] we also considered the finite dimensional model

$$\begin{cases} f'(t) &= (a - \mu f(t) - \frac{\beta(x)u(t)}{1 + \beta(x)hf(t)})f(t), \\ u'(t) &= (\alpha \frac{\beta(x)f(t)}{1 + \beta(x)hf(t)} - d(x))u(t), \end{cases} \quad (5)$$

where  $f(t)$  and  $u(t)$  are the number of individuals of the prey and predator population respectively and  $x$  plays the role of a parameter. Under the hypotheses

- for fixed, not too small  $f$ , the function  $x \rightarrow \lambda(f, x) = \frac{\alpha\beta(x)f}{1+\beta(x)hf} - d(x)$  has a unique non degenerate critical point which is an absolute maximum that will be denoted by  $x(f)$ ,
- there exists  $\hat{f} > 0$  such that  $\lambda(\hat{f}, x(\hat{f})) = 0$  (we denoted  $x(\hat{f}) =: \hat{x}$ ),
- $ah\beta(\hat{x}) \leq \mu < a\beta(\hat{x})\frac{\alpha-d(\hat{x})h}{d(\hat{x})}$ ,

we showed existence of an hyperbolic and asymptotically stable equilibrium point  $(\hat{f}, \hat{u})$  corresponding to the unique value of ESS of the parameter  $\hat{x}$ . Under these hypotheses we also proved existence of a family equilibria  $(f_\varepsilon, u_\varepsilon)$  of System (4) that tend to concentrate, when the probability of mutation tends to zero, at the evolutionarily stable value (ESS) of the “corresponding” finite dimensional model (5) and moreover, that the total population at equilibrium of System (4) tends to the equilibrium of System (5) for the value of ESS of the parameter.

### 3 Stability

In [8] we studied, under some hypotheses, local stability of the equilibria  $\vec{z}_\varepsilon$  (for  $\varepsilon$  close to 0) of a nonlinear equation of the form

$$\vec{z}_t = A_\varepsilon(F(\vec{z}))\vec{z} \quad (6)$$

in the space  $X$  of  $L^1$ -  $\mathbb{R}^n$  valued functions defined on a domain  $\Omega$  of  $\mathbb{R}^N$ .  $F$  was a function from the state space  $X$  to a  $m$ - dimensional space, which we assumed linear and continuous. Since (6) has semilinear structure and the spectral mapping property holds in  $L^1$ , by the principle of linearized stability  $\vec{z}_\varepsilon$  will be locally exponentially asymptotically stable if the spectrum of the linearization of (6) at  $\vec{z}_\varepsilon$  lies in  $\{\text{Re}\lambda < \alpha\}$  for some  $\alpha < 0$ . Linearizing, we obtained

$$\begin{aligned} \vec{v}_t &= A_\varepsilon(F(\vec{z}_\varepsilon))\vec{v} + DA_\varepsilon(F(\vec{z}_\varepsilon))F(\vec{v})\vec{z}_\varepsilon \\ &=: \tilde{A}_\varepsilon\vec{v} + S_\varepsilon\vec{v}. \end{aligned} \quad (7)$$

On the other hand, we considered the  $n$ -dimensional ordinary differential equations system

$$\vec{v}_t = A_0(x, F(\vec{v}\delta_x))\vec{v}, \quad (8)$$

being the relationship between the operators  $A_\varepsilon(E)$  and  $A_0(x, E)$  that  $A_\varepsilon(E)$  tends (formally) as  $\varepsilon$  goes to 0 to a matrix multiplication operator generated by the matrix  $A_0(x, E)$ .

Assuming the existence of an (hyperbolic) asymptotically stable nontrivial steady state  $\vec{v}_x$  of (8) for some values of the parameter  $x$ , one of these values  $\hat{x}$  is called an ESS if the linear equation

$$\vec{w}_t = A_0(x, F(\vec{v}_{\hat{x}}\delta_{\hat{x}}))\vec{w},$$

is hyperbolically asymptotically stable for any value  $x \neq \hat{x}$ .

Denoting by  $\hat{x}$  a value of ESS of (8) and by  $\vec{v}_{\hat{x}}$  the corresponding equilibrium and linearizing, we obtained

$$\begin{aligned} \vec{w}' &= A_0(\hat{x}, F(\vec{v}_{\hat{x}}\delta_{\hat{x}}))\vec{w} + (D_2 A_0(\hat{x}, F(\vec{v}_{\hat{x}}\delta_{\hat{x}}))F(\vec{w}\delta_{\hat{x}}))\vec{v}_{\hat{x}} \\ &=: \hat{A}_0\vec{w} + \hat{S}_0\vec{w}. \end{aligned}$$

The main result of [8] is summarized in the following

**Theorem 3.1.** *Let  $\vec{z}_\varepsilon$  be a (nontrivial) positive equilibrium solution of the nonlinear equation  $\vec{z}_t = A_\varepsilon(F(\vec{z}))\vec{z}$  where  $F$  is a linear function from the state space  $X$  to a  $m$ -dimensional space and such that, for fixed  $E = F(\vec{z})$ ,  $A_\varepsilon(E)$  is the generator of a  $C^0$  positive semigroup on  $X$ . Let  $\tilde{A}_\varepsilon + S_\varepsilon$  be the linearized operator at the equilibrium  $\vec{z}_\varepsilon$  and let  $\omega_\varepsilon(\lambda) := \det(I + S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1})$  and  $\omega_0(\lambda) := \det(I + \hat{S}_0(\hat{A}_0 - \lambda I)^{-1})$ . Let us denote by  $D := \{\lambda \in \mathbb{C} \text{ such that } \operatorname{Re} \lambda \geq 0, \lambda \neq 0\}$ . Let us assume that  $\omega_\varepsilon(\lambda)$  and  $\omega_0(\lambda)$  are holomorphic functions for all  $\lambda \in D$ , that  $\omega_0(\lambda)$  does not vanish for  $\lambda \in D$  and that*

$$\omega_\varepsilon(\lambda) \xrightarrow{\varepsilon \rightarrow 0} \omega_0(\lambda)$$

*uniformly on  $\lambda$  in compact sets contained in  $D$ .*

*Let us also assume that there exists a constant  $L_2 > 0$  such that if  $|\lambda| > L_2$  then  $\|S_\varepsilon R(\lambda, \tilde{A}_\varepsilon)|_{R(S_\varepsilon)}\| < \frac{1}{2}$ .*

*Then, for all  $L_1 > 0$  there exists  $\varepsilon_0$  small enough such that  $\omega_\varepsilon(\lambda)$  does not vanish for  $\varepsilon < \varepsilon_0$  and  $\lambda \in \{\lambda \in \mathbb{C} \text{ such that } \operatorname{Re} \lambda \geq 0, |\lambda| \geq L_1\}$ .*

*Moreover, if  $m = 1$  let us assume that 0 is a strictly dominant eigenvalue of  $\tilde{A}_\varepsilon = A_\varepsilon(F(\vec{z}_\varepsilon))$  with algebraic multiplicity 1. Let  $P_\varepsilon$  be the projection corresponding to the eigenvalue 0 of  $\tilde{A}_\varepsilon$ . Finally, let us assume that  $F(P_\varepsilon D A_\varepsilon(E_\varepsilon)\vec{z}_\varepsilon) \neq 0$  and that  $\liminf_{(\varepsilon, \lambda) \in D \rightarrow (0^+, 0)} \lambda F(\tilde{A}_\varepsilon - \lambda I)^{-1} D A_\varepsilon(E_\varepsilon)\vec{z}_\varepsilon \neq 0$ . Then, for  $\varepsilon$  small enough, the equilibrium solution  $\vec{z}_\varepsilon$  is uniformly asymptotically stable.*

### 3.1 Linearization

System (4) can be written in the form  $\vec{z}_t = A_\varepsilon(F(\vec{z}))\vec{z}$  where

$$\begin{aligned} F : \quad \mathbb{R} \times L^1(0, 1) &\longrightarrow \mathbb{R} \\ (f, u) &\longrightarrow f, \end{aligned}$$

$$A_\varepsilon(f) = \begin{pmatrix} a - \mu f & -\int_0^1 \frac{\beta(x)f}{1+\beta(x)hf} \cdot dx \\ 0 & -d(x) + (1-\varepsilon)\alpha \frac{\beta(x)f}{1+\beta(x)hf} + \varepsilon \int_0^1 \alpha \gamma(x,y) \frac{\beta(y)f}{1+\beta(y)hf} \cdot dy \end{pmatrix}.$$

Our aim in this section would be to apply Theorem 3.1 to study the stability of the equilibria  $(f_\varepsilon, u_\varepsilon)$  of the prey predator System (4). A direct application of Theorem 3.1 however is not possible since 0 is not a strictly dominant eigenvalue of the operator

$$\tilde{A}_\varepsilon := A_\varepsilon(f_\varepsilon) = \begin{pmatrix} a - \mu f_\varepsilon & -\int_0^1 \frac{\beta(x)f_\varepsilon}{(1+\beta(x)hf_\varepsilon)} \cdot dx \\ 0 & -d(x) + (1-\varepsilon)\alpha \frac{\beta(x)f_\varepsilon}{1+\beta(x)hf_\varepsilon} \\ & + \varepsilon \int_0^1 \alpha \gamma(x,y) \frac{\beta(y)f_\varepsilon}{1+\beta(y)hf_\varepsilon} \cdot dy \end{pmatrix} \quad (9)$$

and therefore the hypothesis that  $\omega_\varepsilon(\lambda)$  is an holomorphic function for all  $\lambda \in D$  does not hold. Nevertheless, proving some extra results, we will still be able to use Theorem 3.1 to study the stability, for  $\varepsilon$  small enough, of the equilibria  $(f_\varepsilon, u_\varepsilon)$  of System (4).

The linearized system for the prey predator model (4) at the equilibrium  $(f_\varepsilon, u_\varepsilon)$  (considering  $f(t) = f_\varepsilon + \bar{f}$ ,  $u(x,t) = u_\varepsilon + \bar{u}(x,t)$ , using that  $(f_\varepsilon, u_\varepsilon)$  is a steady state, Taylor's formula and eliminating higher order terms) is

$$\begin{pmatrix} \bar{f}' \\ \frac{\partial \bar{u}}{\partial t} \end{pmatrix} = (\tilde{A}_\varepsilon + S_\varepsilon) \begin{pmatrix} \bar{f} \\ \bar{u} \end{pmatrix}$$

where  $\tilde{A}_\varepsilon$  was defined by (9) and

$$S_\varepsilon = \begin{pmatrix} -\mu f_\varepsilon - \int_0^1 \frac{\beta(x)u_\varepsilon(x)}{(1+\beta(x)hf_\varepsilon)^2} dx & 0 \\ (1-\varepsilon)\alpha \frac{\beta(x)u_\varepsilon(x)}{(1+\beta(x)hf_\varepsilon)^2} + \varepsilon \int_0^1 \alpha \gamma(x,y) \frac{\beta(y)u_\varepsilon(y)}{(1+\beta(y)hf_\varepsilon)^2} dy & 0 \end{pmatrix}. \quad (10)$$

Let us note that

$$\sigma(\tilde{A}_\varepsilon) = \{a - \mu f_\varepsilon\} \cup \sigma(C_{\varepsilon, f_\varepsilon}),$$

where we have denoted

$$C_{\varepsilon, f_\varepsilon} := -d(x) + (1-\varepsilon)\alpha \frac{\beta(x)f_\varepsilon}{1+\beta(x)hf_\varepsilon} + \varepsilon \int_0^1 \alpha \gamma(x,y) \frac{\beta(y)f_\varepsilon}{1+\beta(y)hf_\varepsilon} \cdot dy. \quad (11)$$

In [15] we proved that zero is the dominant eigenvalue of the operator  $C_{\varepsilon, f_\varepsilon}$ . Since  $a - \mu f_\varepsilon > 0$ , the hypothesis of Theorem 3.1 saying that  $\omega_\varepsilon(\lambda) = \det(I + S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1})$  is holomorphic for all  $\lambda$  such that  $\text{Re } \lambda \geq 0$ ,  $\lambda \neq 0$  does not hold. However,

this hypothesis was only used (see [8]) because if it holds then,  $\sigma(\tilde{A}_\varepsilon)$  does not contain values with positive real part and since (see [8])

$$\sigma(\tilde{A}_\varepsilon + S_\varepsilon) \subset \sigma(\tilde{A}_\varepsilon) \cup \{\lambda \text{ s.t. } \det(I + S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1}) = 0\},$$

we only had to show that  $\det(I + S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1}) \neq 0$  for  $\lambda$  such that  $\operatorname{Re} \lambda \geq 0$ ,  $\lambda \neq 0$  and that  $0 \notin \sigma(\tilde{A}_\varepsilon + S_\varepsilon)$ . The determinant  $\det(I + S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1})$  is called the Weinstein-Aronszajn determinant associated with the operators  $\tilde{A}_\varepsilon$  and  $S_\varepsilon$ . The Weinstein-Aronszajn determinant is defined in general for the sum of a closed operator  $A$  and an operator  $S$  which is relatively degenerate with respect to  $A$  (see [19]).

From now on, let us denote

$$D_\varepsilon := \{\lambda \in \mathbb{C} \text{ s.t. } \operatorname{Re} \lambda \geq 0, \quad \lambda \neq 0, \quad \lambda \neq a - \mu f_\varepsilon\}.$$

Then, in the prey predator model (4), in order to obtain stability of  $(f_\varepsilon, u_\varepsilon)$  we will have to show that  $\omega_\varepsilon(\lambda) := \det(I + S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1}) \neq 0$  for  $\lambda \in D_\varepsilon$ , that  $0 \notin \sigma(\tilde{A}_\varepsilon + S_\varepsilon)$  and moreover, that  $a - \mu f_\varepsilon \notin \sigma(\tilde{A}_\varepsilon + S_\varepsilon)$ .

On the other hand, linearizing the finite dimensional prey predator model (5) when  $x = \hat{x}$  (ESS value) at the equilibrium point  $(\hat{f}, \hat{u})$  (which, recall, is the unique equilibrium point corresponding to the value of ESS of the parameter) and eliminating higher order terms we obtain the linear system

$$\begin{pmatrix} \bar{f} \\ \bar{u} \end{pmatrix}' = \hat{A}_0 \begin{pmatrix} \bar{f} \\ \bar{u} \end{pmatrix} + \hat{S}_0 \begin{pmatrix} \bar{f} \\ \bar{u} \end{pmatrix},$$

where

$$\hat{A}_0 := \begin{pmatrix} a - \mu \hat{f} & -\frac{\beta(\hat{x})\hat{f}}{1+\beta(\hat{x})h\hat{f}} \\ 0 & 0 \end{pmatrix} \quad \hat{S}_0 := \begin{pmatrix} -\mu \hat{f} - \frac{\beta(\hat{x})\hat{u}}{(1+\beta(\hat{x})h\hat{f})^2} & 0 \\ \frac{\alpha\beta(\hat{x})\hat{u}}{(1+\beta(\hat{x})h\hat{f})^2} & 0 \end{pmatrix}.$$

Let us define  $\omega_0(\lambda) := \det(I + \hat{S}_0(\hat{A}_0 - \lambda I)^{-1})$  for  $\lambda \notin \sigma(\hat{A}_0)$  (i.e. for  $\lambda$  such that  $\lambda \neq 0$  and  $\lambda \neq a - \mu \hat{f}$ ).

Let us denote

$$D_0 := \{\lambda \in \mathbb{C} \text{ s.t. } \operatorname{Re} \lambda \geq 0, \quad \lambda \neq 0, \quad \lambda \neq a - \mu \hat{f}\}.$$

Since the equilibrium point  $(\hat{f}, \hat{u})$  is hyperbolic and asymptotically stable

$$\omega_0(\lambda) = \det(I + \hat{S}_0(\hat{A}_0 - \lambda I)^{-1}) \neq 0$$

for  $\lambda \in D_0$ , that is,

$$1 + \left( -\mu \hat{f} - \frac{\beta(\hat{x})\hat{u}}{(1+\beta(\hat{x})h\hat{f})^2} \right) \left( \frac{1}{(a-\mu\hat{f}-\lambda)} \right) + \frac{\alpha\beta(\hat{x})\hat{u}}{(1+\beta(\hat{x})h\hat{f})^2} \left( \frac{\frac{\beta(\hat{x})\hat{f}}{1+\beta(\hat{x})h\hat{f}}}{(a-\mu\hat{f}-\lambda)(-\lambda)} \right) \neq 0$$

for  $\lambda \in D_0$ .



Our aim is to use the fact that  $\omega_0(\lambda) \neq 0$  for  $\lambda \in D_0$  to prove that, for  $\varepsilon$  small,  $\omega_\varepsilon(\lambda) \neq 0$  for  $\lambda \in D_0 \cap D_\varepsilon$ . Therefore one of the hypotheses that we have to prove is that  $\omega_\varepsilon(\lambda) \xrightarrow{\varepsilon \rightarrow 0} \omega_0(\lambda)$  uniformly on  $\lambda$  in compact sets contained in  $D_0 \cap D_\varepsilon$ . In order to show it, let us consider the following operators in  $\mathbb{R} \times M$  (where  $M$  is the space of Radon measures),

$$\tilde{A}_0 = \begin{pmatrix} a - \mu \hat{f} & - \int_0^1 \frac{\beta(x) \hat{f}}{1 + \beta(x) h \hat{f}} \cdot dx \\ 0 & \frac{\alpha \beta(x) \hat{f}}{1 + \beta(x) h \hat{f}} - d(x) \end{pmatrix}, \quad S_0 = \begin{pmatrix} -\mu \hat{f} - \frac{\beta(\hat{x}) \hat{u}}{(1 + \beta(\hat{x}) h \hat{f})^2} & 0 \\ \frac{\alpha \beta(x) \hat{u}}{(1 + \beta(x) h \hat{f})^2} \delta_{\hat{x}} & 0 \end{pmatrix}. \quad (12)$$

We can define  $g_0(\lambda) := \det(I + S_0(\tilde{A}_0 - \lambda I)^{-1})|_{R(S_0)}$ . Since the operator  $(\tilde{A}_0 - \lambda I)^{-1}$  can be computed explicitly

$$(\tilde{A}_0 - \lambda I)^{-1} = \begin{pmatrix} \frac{1}{(a - \mu \hat{f} - \lambda)} & \frac{1}{(a - \mu \hat{f} - \lambda)} \int_0^1 \frac{\beta(x) \hat{f}}{1 + \beta(x) h \hat{f}} \frac{1}{\frac{\alpha \beta(x) \hat{f}}{1 + \beta(x) h \hat{f}} - d(x) - \lambda} \cdot dx \\ 0 & \frac{1}{\frac{\alpha \beta(x) \hat{f}}{1 + \beta(x) h \hat{f}} - d(x) - \lambda} \end{pmatrix}$$

and the range of  $S_0$  is one dimensional and generated by

$$\begin{pmatrix} -\mu \hat{f} - \frac{\beta(\hat{x}) \hat{u}}{(1 + \beta(\hat{x}) h \hat{f})^2} \\ \frac{\alpha \beta(x) \hat{u}}{(1 + \beta(x) h \hat{f})^2} \delta_{\hat{x}} \end{pmatrix},$$

$g_0(\lambda)$  can be computed explicitly and we obtain that  $g_0(\lambda) = \omega_0(\lambda)$  and therefore  $g_0(\lambda) \neq 0$  for  $\lambda \in D_0$ .

**Proposition 1.** *Let  $\omega_\varepsilon(\lambda) := \det(I + S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1})$  where  $\tilde{A}_\varepsilon$  and  $S_\varepsilon$  are defined by (9) and (10) respectively and  $g_0(\lambda) := \det(I + S_0(\tilde{A}_0 - \lambda I)^{-1})$  where  $\tilde{A}_0$  and  $S_0$  are defined in (12). Then*

$$\omega_\varepsilon(\lambda) \xrightarrow{\varepsilon \rightarrow 0} g_0(\lambda) (= \omega_0(\lambda))$$

*uniformly on  $\lambda$  in compact sets contained in  $D_0 \cap D_\varepsilon$ .*

*Proof.* It is enough showing that

$$\|(S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1})|_{R(S_\varepsilon)} - (S_\varepsilon(\tilde{A}_0 - \lambda I)^{-1})|_{R(S_\varepsilon)}\| \xrightarrow{\varepsilon \rightarrow 0} 0 \quad (13)$$

and that

$$\|(S_\varepsilon(\tilde{A}_0 - \lambda I)^{-1})|_{R(S_\varepsilon)} - (S_0(\tilde{A}_0 - \lambda I)^{-1})|_{R(S_0)}\| \xrightarrow{\varepsilon \rightarrow 0} 0. \quad (14)$$

Let us denote by  $B_\varepsilon := \tilde{A}_\varepsilon - \tilde{A}_0$ . Then

$$\begin{aligned} (\tilde{A}_\varepsilon - \lambda I)^{-1} &= R(\lambda, \tilde{A}_\varepsilon) = R(\lambda, (\tilde{A}_0 + B_\varepsilon)) \\ &= R(\lambda, \tilde{A}_0)(I - B_\varepsilon R(\lambda, \tilde{A}_0))^{-1} \\ &= R(\lambda, \tilde{A}_0) \sum_{n=0}^{\infty} (B_\varepsilon R(\lambda, \tilde{A}_0))^n \end{aligned}$$

where in the last equality we have used that, as  $\|B_\varepsilon\| \xrightarrow{\varepsilon \rightarrow 0} 0$ , for  $\varepsilon$  small enough  $\|B_\varepsilon R(\lambda, \tilde{A}_0)\| < 1$ . Hence, for  $\varepsilon$  small enough

$$\begin{aligned}
& \| (S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1}) - (S_\varepsilon(\tilde{A}_0 - \lambda I)^{-1}) \| \\
&= \| S_\varepsilon R(\lambda, \tilde{A}_0) \sum_{i=0}^{\infty} (B_\varepsilon R(\lambda, \tilde{A}_0))^i - S_\varepsilon R(\lambda, \tilde{A}_0) \| \\
&= \| S_\varepsilon R(\lambda, \tilde{A}_0) \sum_{n=1}^{\infty} (B_\varepsilon R(\lambda, \tilde{A}_0))^n \| \\
&\leq \| S_\varepsilon \| \| R(\lambda, \tilde{A}_0) \| \frac{\| B_\varepsilon R(\lambda, \tilde{A}_0) \|}{1 - \| B_\varepsilon R(\lambda, \tilde{A}_0) \|}.
\end{aligned}$$

As  $R(\lambda, \tilde{A}_0)$  and  $S_\varepsilon$  are bounded operators (uniformly with respect to  $\varepsilon$ ) and  $\|B_\varepsilon\| \xrightarrow{\varepsilon \rightarrow 0} 0$  we obtain that  $\| (S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1}) - (S_\varepsilon(\tilde{A}_0 - \lambda I)^{-1}) \| \xrightarrow{\varepsilon \rightarrow 0} 0$ . Therefore (13) holds.

In order to prove (14) let us compute  $S_\varepsilon R(\lambda, \tilde{A}_0)$  in the basis of the range of  $S_\varepsilon$  which is

$$\left( \begin{array}{c} -\mu f_\varepsilon - \int_0^1 \frac{\beta(x)u_\varepsilon}{(1+\beta(x)hf_\varepsilon)^2} dx \\ (1-\varepsilon)\alpha \frac{\beta(x)u_\varepsilon}{1+\beta(x)hf_\varepsilon} + \varepsilon \int_0^1 \alpha \gamma(x,y) \frac{\beta(y)u_\varepsilon}{1+\beta(y)hf_\varepsilon} dy \end{array} \right).$$

Then

$$\begin{aligned}
S_\varepsilon R(\lambda, A_0)|_{R(S_\varepsilon)} &= \frac{1}{(a-\mu\hat{f}-\lambda)} \left( -\mu f_\varepsilon - \int_0^1 \frac{\beta(x)u_\varepsilon}{(1+\beta(x)hf_\varepsilon)^2} dx \right) \\
&+ \frac{1}{(a-\mu\hat{f}-\lambda)} \int_0^1 \frac{\beta(x)\hat{f}}{1+\beta(x)h\hat{f}} \left( \frac{(1-\varepsilon)\alpha \frac{\beta(x)u_\varepsilon}{(1+\beta(x)hf_\varepsilon)^2} + \varepsilon \int_0^1 \alpha \gamma(x,y) \frac{\beta(y)u_\varepsilon}{(1+\beta(y)hf_\varepsilon)^2} dy}{\frac{\alpha\beta(x)\hat{f}}{1+\beta(x)h\hat{f}} - d(x)-\lambda} \right) dx.
\end{aligned}$$

In Theorem 3.5 in [15] we obtained the convergence results  $f_\varepsilon \xrightarrow{\varepsilon \rightarrow 0} \hat{f}$ ,  $u_\varepsilon \xrightarrow{\varepsilon \rightarrow 0} \hat{u}\delta_{\hat{x}}$  in the weak star topology,  $\int_0^\infty u_\varepsilon \xrightarrow{\varepsilon \rightarrow 0} \hat{u}$  and  $\int_{I^c} u_\varepsilon \xrightarrow{\varepsilon \rightarrow 0} 0$  for any subinterval of  $[0, 1]$ ,  $I$ , containing  $\hat{x}$ , which imply

$$\begin{aligned}
S_\varepsilon R(\lambda, \tilde{A}_0)|_{R(S_\varepsilon)} &\xrightarrow{\varepsilon \rightarrow 0} S_0 R(\lambda, \tilde{A}_0)|_{R(S_0)} \\
&= \left( \frac{1}{(a-\mu\hat{f}-\lambda)} \right) \left( -\mu\hat{f} - \frac{\beta(\hat{x})\hat{u}}{(1+\beta(\hat{x})h\hat{f})^2} \right) + \frac{\alpha\beta(\hat{x})\hat{u}}{(1+\beta(\hat{x})h\hat{f})^2} \left( \frac{\frac{\beta(\hat{x})\hat{f}}{1+\beta(\hat{x})h\hat{f}}}{(a-\mu\hat{f}-\lambda)(-\lambda)} \right).
\end{aligned}$$

□

Now we will prove that for  $\varepsilon$  small  $\omega_\varepsilon(a - \mu\hat{f}) \neq 0$ . In order to show it we will use the following technical/auxiliary lemma.

**Lemma 3.2.** *Let  $f_0(\lambda)$  be a meromorphic function. Let  $\lambda_0$  be a simple pole of  $f_0$ . Let  $f_\varepsilon(\lambda)$  be a family of meromorphic functions. Let us assume that for every  $\varepsilon$  small enough,  $\lambda_\varepsilon$  is a simple pole of  $f_\varepsilon$ . Moreover, let us assume that  $\lambda_\varepsilon \xrightarrow{\varepsilon \rightarrow 0} \lambda_0$  and that*

$$f_\varepsilon(\lambda) \xrightarrow{\varepsilon \rightarrow 0} f_0(\lambda)$$

*uniformly on compact sets that do not contain  $\lambda_0$ . Then  $f_\varepsilon(\lambda_0) \neq 0$  for  $\varepsilon$  small enough.*

*Proof.* Developping  $f_0$  by its Laurent series at  $\lambda_0$  we can write

$$f_0(\lambda) = \frac{a_{-1}}{\lambda - \lambda_0} + h_0(\lambda)$$

where  $h_0(\lambda)$  is an holomorphic function and  $a_{-1} = \frac{1}{2\pi i} \int_C f_0(\xi) d\xi \neq 0$  where  $C$  is a positively oriented small circle enclosing  $\lambda_0$  but excluding other poles of  $f_0$ . In the same way

$$f_\varepsilon(\lambda) = \frac{(b_{-1})_\varepsilon}{\lambda - \lambda_\varepsilon} + h_\varepsilon(\lambda)$$

where  $h_\varepsilon(\lambda)$  is an holomorphic function and  $(b_{-1})_\varepsilon = \frac{1}{2\pi i} \int_C f_\varepsilon(\xi) d\xi$ , and where we have used that, since  $\lambda_\varepsilon \xrightarrow{\varepsilon \rightarrow 0} \lambda_0$ , for  $\varepsilon$  small enough  $C$  also encloses  $\lambda_\varepsilon$ . Therefore

$$\frac{(b_{-1})_\varepsilon}{\lambda - \lambda_\varepsilon} \xrightarrow{\varepsilon \rightarrow 0} \frac{a_{-1}}{\lambda - \lambda_0}$$

uniformly on compact sets that do not contain  $\lambda_0$ . This implies that  $h_\varepsilon(\lambda) \xrightarrow{\varepsilon \rightarrow 0} h_0(\lambda)$  uniformly on compact sets that do not contain  $\lambda_0$ . Since

$$h_\varepsilon(\lambda_0) = \frac{1}{2\pi i} \int_C \frac{h_\varepsilon(\xi)}{\xi - \lambda_0} d\xi \xrightarrow{\varepsilon \rightarrow 0} \frac{1}{2\pi i} \int_C \frac{h_0(\xi)}{\xi - \lambda_0} d\xi = h_0(\lambda_0),$$

we have that  $h_\varepsilon(\lambda) \xrightarrow{\varepsilon \rightarrow 0} h_0(\lambda)$  uniformly on compact sets in  $\mathbb{C}$ . Then

$$(\lambda - \lambda_\varepsilon)f_\varepsilon(\lambda) = (b_{-1})_\varepsilon + (\lambda - \lambda_\varepsilon)h_\varepsilon(\lambda) \xrightarrow{\varepsilon \rightarrow 0} a_{-1} + (\lambda - \lambda_0)h_0(\lambda) = (\lambda - \lambda_0)f_0(\lambda)$$

uniformly on compact sets in  $\mathbb{C}$ . Applying Rouché's theorem we obtain that, for  $\varepsilon$  small enough,  $(\lambda - \lambda_\varepsilon)f_\varepsilon(\lambda)$  does not vanish at  $\lambda_0$  and therefore that  $f_\varepsilon(\lambda_0) \neq 0$ .  $\square$

**Remark 1.** In fact we have proved that, for  $\varepsilon$  small enough there exists  $\delta > 0$  such that  $f_\varepsilon(\lambda) \neq 0$  for  $\lambda$  such that  $|\lambda - \lambda_0| < \delta$ .

**Proposition 2.** Let  $(\hat{f}, \hat{u})$  be the equilibrium point of the ordinary differential equations prey predator model (5) for the value  $\hat{x}$  of ESS. Let  $\omega_\varepsilon = \det(I + S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1})$  where  $\tilde{A}_\varepsilon$  and  $S_\varepsilon$  are the operators defined in (9) and (10) respectively. Then for  $\varepsilon$  small there exists  $\delta > 0$  such that  $\omega_\varepsilon(\lambda) \neq 0$  for  $\lambda$  such that  $|\lambda - (a - \mu\hat{f})| < \delta$ .

*Proof.* An application of Proposition 1, Lemma 3.2, Remark 1 and the fact that  $a - \mu\hat{f}$  is an eigenvalue of  $A_0$ .  $\square$

As we mentioned before, since System (4) does not satisfy the hypothesis that 0 is a dominant eigenvalue of  $\tilde{A}_\varepsilon$  a direct application of Theorem 3.1 in order to prove local stability of the equilibrium  $(f_\varepsilon, u_\varepsilon)$  is not possible. With the results proved so far we can now state the theorem saying that the conclusion of the first part of Theorem 3.1 holds for System (4).

**Theorem 3.3.** Let  $\omega_\varepsilon(\lambda) := \det(I + S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1})$  where  $\tilde{A}_\varepsilon$  and  $S_\varepsilon$  are defined by (9) and (10) respectively. Then for all  $L_1 > 0$  there exists  $\varepsilon$  small enough such that  $\omega_\varepsilon(\lambda)$  does not vanish for  $\lambda \in \{\lambda \in D_\varepsilon \text{ s.t. } \operatorname{Re} \lambda \geq 0, L_1 \leq |\lambda|\}$ .

*Proof.*  $\tilde{A}_\varepsilon$  is a bounded operator. Then, since  $\sup_\varepsilon \|\tilde{A}_\varepsilon\|$  and  $\sup_\varepsilon \|S_\varepsilon\|$  are bounded, for  $|\lambda| > 2\|\tilde{A}_\varepsilon\|$

$$\|S_\varepsilon R(\lambda, \tilde{A}_\varepsilon)\| = \|S_\varepsilon \lambda^{-1} \sum_{n=0}^{\infty} (\lambda^{-1} \tilde{A}_\varepsilon)^n\| \leq \frac{\|S_\varepsilon\|}{\lambda - \|\tilde{A}_\varepsilon\|} \leq \frac{2\|S_\varepsilon\|}{|\lambda|}$$

and therefore there exists  $L_2 > 0$  such that if  $|\lambda| > L_2$  then  $\|S_\varepsilon R(\lambda, \tilde{A}_\varepsilon)\| < \frac{1}{2}$ . This implies that  $|\omega_\varepsilon(\lambda)| > 0$  if  $|\lambda| > L_2$ . Indeed, denoting by  $P(\mu)$  the characteristic polynomial of  $S_\varepsilon R(\lambda, \tilde{A}_\varepsilon)|_{R(S_\varepsilon)}$  we have that any zero  $\mu_i$  of  $P(\mu)$  satisfies  $|\mu_i| < \frac{1}{2}$  and then  $|\omega_\varepsilon(\lambda)| = |\det((I + S_\varepsilon R(\lambda, \tilde{A}_\varepsilon))|_{R(S_\varepsilon)})| = |P(-1)| = |(-1)^l \prod_{i=1}^l (-1 - \mu_i)| > \frac{1}{2^l}$  if  $|\lambda| > L_2$  (where  $l = \dim \operatorname{Range} S_\varepsilon$ ).

Let us now consider the set  $D_1 := \{\lambda \in D_0 \text{ s.t. } L_1 \leq |\lambda|\} \cap \{\lambda \in \mathbb{C} \text{ s.t. } |\lambda - (a - \mu \hat{f})| \geq \delta\}$  for any  $L_1 \in (0, L_2)$ . Since  $a - \mu f_\varepsilon \xrightarrow{\varepsilon \rightarrow 0} a - \mu \hat{f}$ , by Proposition 1 and applying Rouché's theorem we have that for  $\varepsilon$  small  $\omega_\varepsilon(\lambda)$  does not vanish for  $\lambda \in D_1$ . By Proposition 2 we obtain that, in fact, for  $\varepsilon$  small enough  $\omega_\varepsilon(\lambda)$  does not vanish for  $\lambda \in \{\lambda \in D_\varepsilon \text{ s.t. } \operatorname{Re} \lambda \geq 0, L_1 \leq |\lambda|\}$ .  $\square$

Let us recall that, in order to prove stability of the equilibrium  $(f_\varepsilon, u_\varepsilon)$  of the prey predator model (4) we have to show that  $\omega_\varepsilon(\lambda) = \det(I + S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1}) \neq 0$  for  $\lambda \in D_\varepsilon := \{\lambda \in \mathbb{C} \text{ s.t. } \operatorname{Re} \lambda \geq 0, \lambda \neq 0, \lambda \neq a - \mu f_\varepsilon\}$ , that  $0 \notin \sigma(\tilde{A}_\varepsilon + S_\varepsilon)$  and moreover, that  $a - \mu f_\varepsilon \notin \sigma(\tilde{A}_\varepsilon + S_\varepsilon)$ .

By Theorem 3.3 what is left to show is that  $0 \notin \sigma(\tilde{A}_\varepsilon + S_\varepsilon)$ , that  $a - \mu f_\varepsilon \notin \sigma(\tilde{A}_\varepsilon + S_\varepsilon)$  and that, for  $\varepsilon$  small,  $\omega_\varepsilon(\lambda) \neq 0$  for  $\lambda \in \{\lambda \in D_\varepsilon \text{ s.t. } \operatorname{Re} \lambda \geq 0, |\lambda| < L_1\}$  for some  $L_1 > 0$ .

**Proposition 3.** Let  $\tilde{A}_\varepsilon, S_\varepsilon$  be the operators given by (9) and (10) respectively. Then  $0 \notin \sigma(\tilde{A}_\varepsilon + S_\varepsilon)$ .

*Proof.* 0 is a simple eigenvalue of  $\tilde{A}_\varepsilon$  with corresponding eigenfunction  $(f_\varepsilon, u_\varepsilon)$ . By the Weinstein Aronszajn formula (see [19]), if we show that 0 is a pole of order 1 of  $\omega_\varepsilon(\lambda) = \det((I + S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1})|_{R(S_\varepsilon)})$ , we will obtain that  $0 \notin \sigma(\tilde{A}_\varepsilon + S_\varepsilon)$ . The range of  $S_\varepsilon$  is one dimensional and a basis is

$$DA_\varepsilon(E_\varepsilon) \begin{pmatrix} f_\varepsilon \\ u_\varepsilon \end{pmatrix} = \begin{pmatrix} -\mu f_\varepsilon - \int_0^1 \frac{\beta(x)u_\varepsilon}{(1+\beta(x)hf_\varepsilon)^2} dx \\ (1-\varepsilon)\alpha \frac{\beta(x)u_\varepsilon}{(1+\beta(x)hf_\varepsilon)^2} + \varepsilon \int_0^1 \alpha \gamma(x, y) \frac{\beta(y)u_\varepsilon}{(1+\beta(y)hf_\varepsilon)^2} dy \end{pmatrix}.$$

More in general, considering the linearized operator  $\tilde{A}_\varepsilon + S_\varepsilon$  at the equilibrium  $\vec{z}_\varepsilon$  of a nonlinear equation  $\vec{z}_t = A_\varepsilon(F(\vec{z}))\vec{z}$  where  $F$  is a linear function from the state space to a one dimensional space, we showed in Proposition 1 in [8] that 0 is a pole of order 1 of  $\omega_\varepsilon(\lambda) = \det((I + S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1})|_{R(S_\varepsilon)})$  (and therefore  $0 \notin \sigma(\tilde{A}_\varepsilon + S_\varepsilon)$ )

if and only if the following two conditions

$$DA_\varepsilon(E_\varepsilon) \begin{pmatrix} f_\varepsilon \\ u_\varepsilon \end{pmatrix} \notin \text{Range}(\tilde{A}_\varepsilon) \quad (15)$$

$$F \begin{pmatrix} f_\varepsilon \\ u_\varepsilon \end{pmatrix} \neq 0 \quad (16)$$

hold.

Since for the predator prey model (4) we have  $F \begin{pmatrix} f_\varepsilon \\ u_\varepsilon \end{pmatrix} = f_\varepsilon$ , condition (16) holds. Let us now show that (15) also holds. Since  $N(\tilde{A}_\varepsilon^*) = \text{Range}(\tilde{A}_\varepsilon)^\perp$ , where  $\tilde{A}_\varepsilon^*$  denotes the adjoint operator of  $\tilde{A}_\varepsilon$ ,  $N(\tilde{A}_\varepsilon^*)$  denotes the kernel of the operator  $\tilde{A}_\varepsilon^*$  and  $\perp$  denotes orthogonal (in the dual space sense), condition (15) is equivalent to

$$\left\langle \begin{pmatrix} f_\varepsilon^* \\ u_\varepsilon^* \end{pmatrix}, DA_\varepsilon(E_\varepsilon) \begin{pmatrix} f_\varepsilon \\ u_\varepsilon \end{pmatrix} \right\rangle \neq 0, \quad (17)$$

where  $\begin{pmatrix} f_\varepsilon^* \\ u_\varepsilon^* \end{pmatrix}$  is the eigenfunction of eigenvalue 0 of  $\tilde{A}_\varepsilon^*$ .

For the predator prey model (4) condition (17) is

$$\begin{aligned} & -\mu f_\varepsilon f_\varepsilon^* - f_\varepsilon^* \int_0^1 \frac{\beta(x)u_\varepsilon}{(1+\beta(x)hf_\varepsilon)^2} + (1-\varepsilon)\alpha \int_0^1 \frac{\beta(x)u_\varepsilon u_\varepsilon^*}{(1+\beta(x)hf_\varepsilon)^2} dx \\ & + \varepsilon \int_0^1 u_\varepsilon^*(x) \int_0^1 \alpha \gamma(x, y) \frac{\beta(y)u_\varepsilon(y)}{(1+\beta(x)hf_\varepsilon)^2} dy dx \neq 0. \end{aligned}$$

Computing  $\tilde{A}_\varepsilon^*$  we obtain

$$\tilde{A}_\varepsilon^* = \begin{pmatrix} a - \mu f_\varepsilon & 0 \\ \frac{-\beta(x)f_\varepsilon}{1+\beta(x)hf_\varepsilon} & -d(x) + (1-\varepsilon)\alpha \frac{\beta(x)f_\varepsilon}{1+\beta(x)hf_\varepsilon} \\ & + \varepsilon \alpha \frac{\beta(x)f_\varepsilon}{1+\beta(x)hf_\varepsilon} \int_0^1 \gamma(y, x) \cdot dy \end{pmatrix}.$$

Since  $\tilde{A}_\varepsilon^* \begin{pmatrix} f_\varepsilon^* \\ u_\varepsilon^* \end{pmatrix} = 0$  we obtain that  $f_\varepsilon^* = 0$  and  $u_\varepsilon^*$  satisfies

$$\begin{aligned} & (-d(x) + (1-\varepsilon)\alpha \frac{\beta(x)f_\varepsilon}{1+\beta(x)hf_\varepsilon}) u_\varepsilon^* \\ & + \varepsilon \alpha \frac{\beta(x)f_\varepsilon}{1+\beta(x)hf_\varepsilon} \int_0^1 \gamma(y, x) u_\varepsilon^*(y) dy = 0. \end{aligned}$$

The operator  $-d(x) + (1-\varepsilon)\alpha \frac{\beta(x)f_\varepsilon}{1+\beta(x)hf_\varepsilon} + \varepsilon \alpha \frac{\beta(x)f_\varepsilon}{1+\beta(x)hf_\varepsilon} \int_0^1 \gamma(y, x) \cdot dy$  is the adjoint operator of  $C_{\varepsilon, f_\varepsilon}$  (defined in (11)). Since the operator  $C_{\varepsilon, f_\varepsilon}$  generates a positive irreducible semigroup and its spectral bound  $s(C_{\varepsilon, f_\varepsilon})$  is a pole of the resolvent (see [15]) Theorem 8.17 in [12] gives that  $u_\varepsilon^*$  is strictly positive (and also that  $u_\varepsilon$  is strictly positive) and therefore

$$\left\langle \begin{pmatrix} f_\varepsilon^* \\ u_\varepsilon^* \end{pmatrix}, DA_\varepsilon(E_\varepsilon) \begin{pmatrix} f_\varepsilon \\ u_\varepsilon \end{pmatrix} \right\rangle > 0.$$

□

**Proposition 4.** *Let  $\tilde{A}_\varepsilon$ ,  $S_\varepsilon$  be the operators given by (9) and (10) respectively. Then  $a - \mu f_\varepsilon \notin \sigma(\tilde{A}_\varepsilon + S_\varepsilon)$ .*

*Proof.*  $a - \mu f_\varepsilon$  is a simple eigenvalue of  $\tilde{A}_\varepsilon$  with corresponding eigenfunction  $\begin{pmatrix} 1 \\ 0 \end{pmatrix}$ .

By the Weinstein-Aronszajn formula, if we show that  $a - \mu f_\varepsilon$  is a pole of order 1 of  $\omega_\varepsilon(\lambda) = \det((I + S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1})|_{R(S_\varepsilon)})$  we will obtain that  $a - \mu f_\varepsilon \notin \sigma(\tilde{A}_\varepsilon + S_\varepsilon)$ .

Let us recall that the range of  $S_\varepsilon$  is  $DA_\varepsilon(E_\varepsilon) \begin{pmatrix} f_\varepsilon \\ u_\varepsilon \end{pmatrix}$ .

Since  $a - \mu f_\varepsilon$  is a simple pole of  $R(\lambda, \tilde{A}_\varepsilon)$  by the Laurent series at  $\lambda = a - \mu f_\varepsilon$  we have

$$\begin{aligned} & (I + S_\varepsilon(\tilde{A}_\varepsilon - \lambda I)^{-1})DA_\varepsilon(E_\varepsilon) \begin{pmatrix} f_\varepsilon \\ u_\varepsilon \end{pmatrix} \\ &= DA_\varepsilon(E_\varepsilon) \begin{pmatrix} f_\varepsilon \\ u_\varepsilon \end{pmatrix} + S_\varepsilon \frac{1}{(\lambda - (a - \mu f_\varepsilon))} P_\varepsilon DA_\varepsilon(E_\varepsilon) \begin{pmatrix} f_\varepsilon \\ u_\varepsilon \end{pmatrix} \\ &+ S_\varepsilon \sum_{n=0}^{\infty} \frac{1}{2\pi i} (\lambda - (a - \mu f_\varepsilon))^n \int_\Gamma - \frac{(\tilde{A}_\varepsilon - \lambda I)^{-1} DA_\varepsilon(E_\varepsilon) \begin{pmatrix} f_\varepsilon \\ u_\varepsilon \end{pmatrix}}{(\lambda - (a - \mu f_\varepsilon))^{n+1}} d\lambda, \end{aligned}$$

where  $\Gamma$  is a positively-oriented small circle enclosing  $\lambda = a - \mu f_\varepsilon$  but excluding other eigenvalues of  $\tilde{A}_\varepsilon$  and  $P_\varepsilon$  is the spectral projection corresponding to the spectral set  $\{a - \mu f_\varepsilon\}$ .

$\omega_\varepsilon(\lambda)$  will have a pole of first order in  $a - \mu f_\varepsilon$  if  $S_\varepsilon P_\varepsilon DA_\varepsilon(E_\varepsilon) \begin{pmatrix} f_\varepsilon \\ u_\varepsilon \end{pmatrix} \neq 0$ . Since the eigenvector corresponding to the eigenvalue  $a - \mu f_\varepsilon$  of the operator  $\tilde{A}_\varepsilon$  is of the form  $\begin{pmatrix} 1 \\ 0 \end{pmatrix}$  we have  $P_\varepsilon DA_\varepsilon(E_\varepsilon) \begin{pmatrix} f_\varepsilon \\ u_\varepsilon \end{pmatrix} = \begin{pmatrix} -\mu f_\varepsilon - \int_0^1 \frac{\beta(x)u_\varepsilon}{(1 + \beta(x)hf_\varepsilon)^2} \\ 0 \end{pmatrix}$ .

Finally, since the equilibrium  $(f_\varepsilon, u_\varepsilon)$  is strictly positive we have  $S_\varepsilon P_\varepsilon DA_\varepsilon(E_\varepsilon) \begin{pmatrix} f_\varepsilon \\ u_\varepsilon \end{pmatrix} \neq 0$  and the proof is complete. □

Summarizing, with all the results we proved so far for the prey predator model, the only thing that remains to prove in order to show that the equilibrium  $(f_\varepsilon, u_\varepsilon)$  is uniformly asymptotically stable is to exclude, for  $\varepsilon$  small and for some  $L_1 > 0$  the set  $\{\lambda \in \mathbb{C} \text{ such that } \operatorname{Re} \lambda \geq 0, |\lambda| < L_1, \lambda \neq 0, a - \mu f_\varepsilon\}$  from the spectrum of the operator  $\tilde{A}_\varepsilon + S_\varepsilon$ . In [8] we proved that this is equivalent to show that

$$\liminf_{(\varepsilon, \lambda)_{\lambda \in D} \rightarrow (0^+, 0)} \lambda F(\tilde{A}_\varepsilon - \lambda I)^{-1} DA_\varepsilon(E_\varepsilon) \begin{pmatrix} f_\varepsilon \\ u_\varepsilon \end{pmatrix} \neq 0. \quad (18)$$

For System (4) we can compute

$$F((\tilde{A}_\varepsilon - \lambda I)^{-1} DA_\varepsilon(E_\varepsilon) \begin{pmatrix} f_\varepsilon \\ u_\varepsilon \end{pmatrix})$$

$$\begin{aligned}
&= \text{first component of } (\tilde{A}_\varepsilon - \lambda I)^{-1} D A_\varepsilon(E_\varepsilon) \begin{pmatrix} f_\varepsilon \\ u_\varepsilon \end{pmatrix} \\
&+ \frac{1}{a - \mu f_\varepsilon - \lambda} \left( -\mu f_\varepsilon - \int_0^1 \frac{\beta(x) u_\varepsilon(x)}{(1 + \beta(x) h f_\varepsilon)^2} dx \right) \\
&\quad \frac{1}{a - \mu f_\varepsilon - \lambda} \int_0^1 \frac{\beta(x) f_\varepsilon}{1 + \beta(x) h f_\varepsilon} R(\lambda, C_{\varepsilon, f_\varepsilon}) \\
&((1 - \varepsilon) \alpha \frac{\beta(x) u_\varepsilon(x)}{(1 + \beta(x) h f_\varepsilon)^2} + \varepsilon \int_0^1 \alpha \gamma(x, y) \frac{\beta(y) u_\varepsilon(y)}{(1 + \beta(y) h f_\varepsilon)^2} dy) dx.
\end{aligned}$$

So, in this case, condition (18) is

$$\begin{aligned}
&\liminf_{(\varepsilon, \lambda)_{\lambda \in D} \rightarrow (0^+, 0)} \lambda \left( \frac{1}{a - \mu f_\varepsilon - \lambda} \int_0^1 \frac{\beta(x) f_\varepsilon}{1 + \beta(x) h f_\varepsilon} R(\lambda, C_{\varepsilon, f_\varepsilon}) \right. \\
&\left. ((1 - \varepsilon) \alpha \frac{\beta(x) u_\varepsilon(x)}{(1 + \beta(x) h f_\varepsilon)^2} + \varepsilon \int_0^1 \alpha \gamma(x, y) \frac{\beta(y) u_\varepsilon(y)}{(1 + \beta(y) h f_\varepsilon)^2} dy) dx \right) \neq 0. \quad (19)
\end{aligned}$$

Since  $C_{\varepsilon, f_\varepsilon}$  tends to a multiplication operator (with continuous spectrum), the resolvent operator tends to be singular at 0 when  $\varepsilon \xrightarrow{\varepsilon \rightarrow 0} 0$ . Therefore we have an undetermined limit of the form  $0 \cdot \infty$ , which makes it difficult to prove the previous inequality. However, if we make the assumption of “house of cards model” considered by Bürger and Bomze in [5], then the limit can be computed.

### 3.2 Particular case

Let us consider the predator prey model

$$\left\{ \begin{array}{l} f'(t) = (a - \mu f(t) - \int_0^1 \frac{\beta(x) u(x, t)}{1 + \beta(x) h f(t)} dx) f(t), \\ \frac{\partial u(x, t)}{\partial t} = (1 - \varepsilon) \frac{\alpha \beta(x) f(t) u(x, t)}{1 + \beta(x) h f(t)} + \varepsilon \gamma(x) \int_0^1 \frac{\alpha \beta(y) f(t) u(y, t)}{1 + \beta(y) h f(t)} dy \\ -d(x) u(x, t), \end{array} \right. \quad (20)$$

where we have made the “house of cards model” assumption, that is we have assumed that the mutation kernel is independent of the parents trait. Let  $(f_\varepsilon, u_\varepsilon(x))$  denote the family of stationary solutions of System (20) and

$$\begin{aligned}
C_{\varepsilon, f_\varepsilon} v &= -d(x) v + (1 - \varepsilon) \frac{\alpha \beta(x) f_\varepsilon v}{1 + \beta(x) h f_\varepsilon} + \varepsilon \gamma(x) \int_0^1 \frac{\alpha \beta(y) f_\varepsilon v(y)}{1 + \beta(y) h f_\varepsilon} dy \\
&=: -\tilde{a}_\varepsilon(x) v + \varepsilon \gamma(x) L_\varepsilon v
\end{aligned}$$

where  $\tilde{a}_\varepsilon(x) = d(x) - (1 - \varepsilon) \frac{\alpha\beta(x)f_\varepsilon}{1 + \beta(x)hf_\varepsilon}$ ,  $L_\varepsilon v = \int_0^1 \frac{\alpha\beta(y)f_\varepsilon v(y)}{1 + \beta(y)hf_\varepsilon} dy$ . The resolvent operator of  $C_{\varepsilon, f_\varepsilon}$  can be computed explicitly (see [8] for more details)

$$\begin{aligned} (\tilde{C}_{\varepsilon, f_\varepsilon} - \lambda I)^{-1} g &= \frac{1}{\varepsilon\lambda} \left( L_\varepsilon(\tilde{a}_\varepsilon(\tilde{a}_\varepsilon + \lambda))^{-1} \gamma \right)^{-1} \left( -(\tilde{a}_\varepsilon + \lambda)^{-1} g \right. \\ &\quad \left. + \varepsilon(L_\varepsilon((\tilde{a}_\varepsilon + \lambda)^{-1} \gamma)(\tilde{a}_\varepsilon + \lambda)^{-1} g \right. \\ &\quad \left. - L_\varepsilon((\tilde{a}_\varepsilon + \lambda)^{-1} g)(\tilde{a}_\varepsilon + \lambda)^{-1} \gamma) \right) \end{aligned}$$

which allows us to compute limit (18) explicitly

$$\begin{aligned} &\liminf_{(\varepsilon, \lambda)_{\lambda \in D \rightarrow (0^+, 0)}} \lambda F(\tilde{A}_\varepsilon - \lambda I)^{-1} D A_\varepsilon(E_\varepsilon) \begin{pmatrix} f_\varepsilon \\ u_\varepsilon \end{pmatrix} \\ &= \liminf_{(\varepsilon, \lambda)_{\lambda \in D \rightarrow (0^+, 0)}} \frac{\int_0^1 \frac{-\beta(x)f_\varepsilon k_\varepsilon(x)}{\varepsilon(1+\beta(x)hf_\varepsilon)(a-\mu f_\varepsilon-\lambda)(\tilde{a}_\varepsilon(x)+\lambda)} dx}{\int_0^1 \frac{\alpha\gamma(x)\beta(x)f_\varepsilon}{1+\beta(x)hf_\varepsilon} \frac{1}{\tilde{a}_\varepsilon(x)(\tilde{a}_\varepsilon(x)+\lambda)} dx} \\ &\quad + \frac{\varepsilon \int_0^1 \frac{\alpha\beta(x)f_\varepsilon\gamma(y)}{(1+\beta(x)hf_\varepsilon)(\tilde{a}_\varepsilon(x)+\lambda)} dx \int_0^1 \frac{\beta(x)f_\varepsilon k_\varepsilon(x)}{\varepsilon(1+\beta(x)hf_\varepsilon)(a-\mu f_\varepsilon-\lambda)(\tilde{a}_\varepsilon(x)+\lambda)} dx}{\int_0^1 \frac{\alpha\gamma(x)\beta(x)f_\varepsilon}{1+\beta(x)hf_\varepsilon} \frac{1}{\tilde{a}_\varepsilon(x)(\tilde{a}_\varepsilon(x)+\lambda)} dx} \\ &\quad - \frac{\varepsilon \int_0^1 \frac{\beta(x)f_\varepsilon k_\varepsilon(x)}{\varepsilon(1+\beta(x)hf_\varepsilon)(a-\mu f_\varepsilon-\lambda)(\tilde{a}_\varepsilon(x)+\lambda)} dx \int_0^1 \frac{\alpha\beta(x)f_\varepsilon\gamma(y)}{(1+\beta(x)hf_\varepsilon)(\tilde{a}_\varepsilon(x)+\lambda)} dx}{\int_0^1 \frac{\alpha\gamma(x)\beta(x)f_\varepsilon}{1+\beta(x)hf_\varepsilon} \frac{1}{\tilde{a}_\varepsilon(x)(\tilde{a}_\varepsilon(x)+\lambda)} dx} \end{aligned}$$

where we have denoted  $k_\varepsilon(x) := (1 - \varepsilon)\alpha \frac{\beta(x)u_\varepsilon(x)}{(1+\beta(x)hf_\varepsilon)^2} + \varepsilon\gamma(x) \int_0^1 \frac{\alpha\beta(y)u_\varepsilon(y)}{(1+\beta(x)hf_\varepsilon)^2} dy$  for simplicity in the notation.

From the equilibria equations we have that  $u_\varepsilon = \frac{\varepsilon\gamma(x)\alpha(a-\mu f_\varepsilon)f_\varepsilon}{\tilde{a}_\varepsilon(x)}$ .

Substituting it in  $k_\varepsilon(x)$  and noting that the last two terms in the previous limit simplify we have

$$\begin{aligned} &\liminf_{(\varepsilon, \lambda)_{\lambda \in D \rightarrow (0^+, 0)}} \lambda F(\tilde{A}_\varepsilon - \lambda I)^{-1} D A_\varepsilon(E_\varepsilon) \begin{pmatrix} f_\varepsilon \\ u_\varepsilon \end{pmatrix} \\ &= \liminf_{(\varepsilon, \lambda)_{\lambda \in D \rightarrow (0^+, 0)}} \frac{1}{\int_0^1 \frac{\alpha\gamma(x)\beta(x)f_\varepsilon}{1+\beta(x)hf_\varepsilon} \frac{1}{\tilde{a}_\varepsilon(x)(\tilde{a}_\varepsilon(x)+\lambda)} dx} \\ &\quad \left( \frac{(a-\mu f_\varepsilon)f_\varepsilon}{(a-\mu f_\varepsilon-\lambda)} \int_0^1 \frac{-\alpha\beta(x)f_\varepsilon}{(1+\beta(x)hf_\varepsilon)(\tilde{a}_\varepsilon(x)+\lambda)} \left( (1-\varepsilon) \frac{\alpha\beta(x)\gamma(x)}{\tilde{a}_\varepsilon(x)(1+\beta(x)hf_\varepsilon)^2} \right. \right. \\ &\quad \left. \left. + \varepsilon\gamma(x) \int_0^1 \frac{\alpha\beta(x)\gamma(x)}{\tilde{a}_\varepsilon(x)(1+\beta(x)hf_\varepsilon)^2} dy \right) dx \right). \end{aligned}$$

Let us recall the following lemma stated in [8]

**Lemma 3.4.** *a) Let  $h(x)$  be continuous in  $\hat{x} \in [a, b]$  and such that  $h(\hat{x}) = 0$  and  $|h(x)| \leq M$  for  $x \in [a, b]$ . Let  $g_\varepsilon(x)$  be a family of positive functions,*



indexed by  $\varepsilon$  in a subset of  $\mathbb{C}^n$  with 0 in its closure, with integral uniformly bounded and such that  $\int_{I^c} g_\varepsilon(x) dx \xrightarrow{\varepsilon \rightarrow 0} 0$  for any (open) interval  $I \subset [a, b]$  centered at  $\hat{x}$  (in particular if  $g_\varepsilon(x)$  tend uniformly in  $x \in I^c$  to 0 as  $\varepsilon \rightarrow 0$ ).

Then  $\int_a^b h(x) f_\varepsilon(x) dx \xrightarrow{\varepsilon \rightarrow 0} 0$ .

b) If we substitute the hypothesis  $h(\hat{x}) = 0$  by  $h_\varepsilon(x) \xrightarrow{\varepsilon \rightarrow 0} h(x)$  uniformly and  $\int_a^b g_\varepsilon(x) dx = 1$  for all  $\varepsilon$ , then the conclusion is  $\int_a^b h_\varepsilon(x) g_\varepsilon(x) dx \xrightarrow{\varepsilon \rightarrow 0} h(\hat{x})$ .

With a similar argument as in [8], applying the lemma with

$$g_\varepsilon(x) = \frac{\frac{\alpha\beta(x)f_\varepsilon\gamma(x)}{\tilde{a}_\varepsilon(x)(\tilde{a}_\varepsilon(x)+\lambda)(1+\beta(x)hf_\varepsilon)}}{\int_0^1 \frac{\alpha\beta(x)f_\varepsilon\gamma(x)}{\tilde{a}_\varepsilon(x)(\tilde{a}_\varepsilon(x)+\lambda)(1+\beta(x)hf_\varepsilon)} dx}$$

$$h_\varepsilon(x) = -(1-\varepsilon) \frac{\alpha\beta(x)}{(1+\beta(x)hf_\varepsilon)^2} + \varepsilon \tilde{a}_\varepsilon(x) \int_0^1 \frac{\alpha\beta(x)\gamma(y)}{\tilde{a}_\varepsilon(x)(1+\beta(x)hf_\varepsilon)^2} dx$$

we obtain

$$\liminf_{(\varepsilon, \lambda)_{\lambda \in D} \rightarrow (0^+, 0)} \lambda F(\tilde{A}_\varepsilon - \lambda I)^{-1} D A_\varepsilon(E_\varepsilon) \begin{pmatrix} f_\varepsilon \\ u_\varepsilon \end{pmatrix} = -\frac{\alpha\beta(\hat{x})f_0}{(1+\beta(\hat{x})f_0)^2}$$

which is a nonvanishing limit.

## 4 Concluding remarks

Selection mutation equations are models for structured populations with respect to evolutionary traits. Some aspects of the adaptive dynamics can be understood by studying the relationship between the steady states of these selection mutation equations and the evolutionarily stable strategies of the underlying ecological models.

In [15] a predator prey model for the evolution of a phenotypical trait (namely the index of activity of the predator during daytime) was studied obtaining, under some hypotheses, existence of a family of equilibria that tend to concentrate, when the probability of mutation goes to zero, at the evolutionarily stable value of the “corresponding” finite dimensional predator prey model.

The present paper is devoted to study the stability of these equilibria. The main mathematical tools are the principle of linearized stability and the fact that, since the environment (the nonlinearity) is finite dimensional (in fact one dimensional) the linearized operator at the steady state,  $\tilde{A}_\varepsilon + S_\varepsilon$ , turns out to be a degenerate perturbation of an operator ( $\tilde{A}_\varepsilon$ ) satisfying  $\sigma(\tilde{A}_\varepsilon) = \{a - \mu f_\varepsilon\} \cup \{\sigma(C_{\varepsilon, f_\varepsilon})\}$ , where  $a - \mu f_\varepsilon > 0$  and  $C_{\varepsilon, f_\varepsilon}$  is an operator with spectral bound equal to zero.

Since we prove that  $0 \notin \sigma(\tilde{A}_\varepsilon + S_\varepsilon)$  (Proposition 3) and  $a - \mu f_\varepsilon \notin \sigma(\tilde{A}_\varepsilon + S_\varepsilon)$  (Proposition 4), the analysis of the stability reduces to the computation of the zeroes of the characteristic equation given by the Weinstein-Aronszajn determinant associated to  $\tilde{A}_\varepsilon$  and  $S_\varepsilon$ , that we have denoted by  $\omega_\varepsilon(\lambda)$ .

Taking advantage of the asymptotic stability of the equilibrium of the corresponding finite dimensional model at the ESS value we show that, for all  $L_1 > 0$ ,  $\omega_\varepsilon(\lambda)$  does not vanish for  $\{\lambda \in \mathbb{C} \text{ such that } \operatorname{Re} \lambda \geq 0, |\lambda| \geq L_1, \lambda \neq 0, a - \mu f_\varepsilon\}$  (Theorem 3.3). Finally, in section 3.2 we show, under the assumption of the “house of cards model”, that  $\omega_\varepsilon(\lambda)$  does not vanish for  $\{\lambda \in \mathbb{C} \text{ such that } \operatorname{Re} \lambda \geq 0, |\lambda| < L_1, \lambda \neq 0, a - \mu f_\varepsilon\}$  obtaining then, stability of the steady state.

## Acknowledgements

The author would like to thank Prof. À. Calsina for his helpful comments and suggestions. This work was partially supported by MTM2008-06349-C03-03.

## References

- [1] A.S. Ackleh, B.G. Fitzpatrick and H. Thieme, *Rate distributions and survival of the fittest: a formulation on the space of measures*, Discrete Continuous. Dynam. Systems. Ser. B., **5** (2005), 917–928.
- [2] A.S. Ackleh and S. Hu, *Comparison between Stochastic and Deterministic Selection-Mutation Models*, Math. Biosci. Eng., **4** (2007), 133–157.
- [3] W. Arendt, A. Grabosch, G. Greiner, U. Groh, H.P. Lotz, U. Moustakas, R. Nagel, F. Neubrander and U. Schlotterbeck, “One-parameter semigroups of positive operators” Lecture Notes in Mathematics, 1184, Springer-Verlag, Berlin, 1986.
- [4] I. Bomze, *Cross entropy minimization in uninhabitable states of complex populations*, J. Math. Biol., **30** (1991), 73–87.
- [5] R. Bürger and I.M. Bomze, *Stationary distributions under mutation-selection balance: structure and properties*, Adv. in Appl. Probab., **28** (1996), 227–251.
- [6] À. Calsina and S. Cuadrado, *Small mutation rate and evolutionarily stable strategies in infinite dimensional adaptive dynamics*, J. Math. Biol., **48** (2004), 135–159.
- [7] À. Calsina and S. Cuadrado, *Stationary solutions of a selection mutation model: the pure mutation case*, Math. Models. Meth. Appl. Sci., **15** (2005), 1091–1117.
- [8] À. Calsina and S. Cuadrado, *Asymptotic stability of equilibria of selection-mutation equations*, J. Math. Biol., **54** (2007), 489–511.
- [9] À. Calsina and C. Perelló, *Equations for biological evolution*, Proc. Roy. Soc. Edinburgh Sect. A, **125** (1995), 939–958.

- [10] À. Calsina, C. Perelló and J. Saldaña, *Non-local reaction-diffusion equations modelling predator-prey coevolution*, Publ. Mat., **38** (1994), 315–325.
- [11] J.A. Carrillo, S. Cuadrado and B. Perthame, *Adaptive dynamics via Hamilton Jacobi approach and entropy methods for a juvenile-adult model*, Math. Biosci., **205** (2007), 137–161.
- [12] Ph. Clément, H.J.A.M. Heijmans, S. Angenent, C.J. van Duijn and B. de Pagter, “One-parameter semigroups” CWI Monographs, 5. North-Holland Publishing Co., Amsterdam, 1987.
- [13] R. Cressman and J. Hofbauer, *Measure dynamics on a one-dimensional continuous trait space: theoretical foundations for adaptive dynamics*, Theor. Popul. Biol., **67** (2005), 47–59.
- [14] J.F. Crow and M. Kimura, *The theory of genetic loads*, in Proc XIth Int. Congr. Genetics, (1964) 495–505.
- [15] S. Cuadrado, *Equilibria of a predator prey model of phenotype evolution*, J. Math. Anal. Appl., **354** (2009), 286–294.
- [16] O. Diekmann, P.E. Jabin, S. Mischler and B. Perthame, *The dynamics of adaptation : an illuminating example and a Hamilton-Jacobi approach*, Theor. Popul. Biol., **67** (2005), 257–271.
- [17] S.A.H. Geritz, É. Kisdi, G. Meszéna and J.A.J. Metz, *Evolutionary singular strategies and the adaptive growth and branching of the evolutionary tree*, Evol. Ecol., **12** (1998), 35–57.
- [18] I. Gudelj, C.D. Coman and R.E. Beardmore, *Classifying the role of trade-offs in the evolutionary diversity of pathogens*, Proc. R. Soc. Lond. Ser. A Math. Phys. Eng. Sci., **462** (2006), 97–116.
- [19] T. Kato, “Perturbation theory for Linear Operators” Springer-Verlag New York, Inc., New York, 1966.
- [20] M. Kimura, *A stochastic model concerning the maintenance of genetic variability in quantitative characters*, Proc. Natl. Acad. Sci. U.S.A, **54** (1965), 731–736.
- [21] P. Magal and G.F. Webb, *Mutation, selection and recombination in a model of phenotype evolution*, Discrete Continuous Dynam. Systems, **6** (2000), 221–236.
- [22] J. Maynard-Smith and G.R. Price, *The logic of animal conflict*, Nature, **246** (1973), 15–18.
- [23] J.A.J. Metz, S.A.H. Geritz, G. Mészéna, F.J.A. Jacobs and J.S. van Heerwaarden, *Adaptive dynamics, a geometrical study of the consequences of nearly faithful reproduction*, in Stochastic and spatial structures of dynamical systems (Amsterdam, 1995), 183–231, Konink. Nederl. Akad. Wetensch. Verh. Afd. Natuurk. Eerste Reeks, 45, North-Holland, Amsterdam, 1996.

- [24] J. Saldaña, S.F. Elena and R.V. Solé, *Coinfection and superinfection in RNA populations: a selection-mutation model*, Math. Biosci., **183** (2003), 135–160.