

# ASYNCHRONOUS GROWTH AND COMPETITION IN A TWO-SEX AGE-STRUCTURED POPULATION MODEL

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ABSTRACT. Asynchronous exponential growth has been extensively studied in population dynamics. In this paper we find out the asymptotic behaviour in a non-linear age-dependent model which takes into account sexual reproduction interactions. The main feature of our model is that the non-linear process converges to a linear one as the solution becomes large, so that the population undergoes asynchronous growth. The steady states analysis and the corresponding stability analysis are completely made and are summarized in a bifurcation diagram according to the parameter  $R_0$ . Furthermore the effect of intraspecific competition is taken into account, leading to complex dynamics around steady states.

## 1. INTRODUCTION

The asymptotic behavior of solutions in models of structured population dynamics is in some cases very regular, specially when the equation of the system is linear. See e.g. the survey in the book [6] and the references there in. A typical regular dynamical behaviour is the so-called *asynchronous exponential growth* or *balanced exponential growth* which, in the classical linear age-dependent problem (Lotka-McKendrick equation), is determined by the existence of persistent solutions. These solutions are exponentially increasing or decreasing in time, namely  $e^{\alpha t}u(a)$  with  $u$  a function of age  $a$ . Moreover, all the solutions have the property that the total population size approaches exponential growth/decay in time but the age-profile, that is, the age-density normalized to total integral 1, converges to an asymptotic age-profile which is independent of the initial condition. See for instance the book [2] Chapters 1 and 2 or the book [5] Chapter 14.

Beyond linear systems, the property of balanced exponential growth can be found as well in non-linear systems where even persistent solutions can exist. An example of the latter are the homogeneous (of degree one) systems which can arise in epidemiological models and also in two-sex (pair-formation) models. See e.g. [1] where the authors undertake a stability analysis for the persistent solutions of an abstract homogeneous dynamical system with the help of a normalized system. See also the book [7] Chapter 5.

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*Key words and phrases.* Continuous age-structured population models; equilibria and stability analysis; asymptotic age-profile; renewal equation.

For a nice introduction to the subject of asynchronous exponential growth in linear and non-linear models see [8], where the authors study an abstract semilinear differential equation such that non-linear processes converge to linear processes as the solution becomes large.

In this paper we investigate a basic population model, which is neither linear nor homogeneous, describing the dynamics of a two-sex population. The system is instead asymptotically linear in the sense that it converges to a linear one as the population tends to infinity. We focus on the age-profile and the final goal is to find the asymptotic age-profile according to the parameters of the model and the initial condition. Furthermore, we consider the effect of intra-specific competition that modifies the previous scenario changing the bifurcation diagram and preventing the population from unlimited growth.

## 2. A BASIC MODEL

Our basic model concerns a two-sex population structured by the age of the individuals and such that the sex-ratio is constant and age-specific. Such framework accounts for different mechanisms that produce age-specific sex heterogeneity. We have in mind at least two mechanisms such as sequential hermaphroditism (i.e. individuals can switch from one sex to the other sex in only one direction once in a lifetime) as described in [3] and [4], and the case of different mortality between males and females. Precisely, we have

- i) *the case of hermaphroditism:*

here we assume that each individual during its lifetime undergoes a transition to the other sex so that the net process produces an appreciable age-specific deviation of the sex-ratio from 1 to 1. Thus calling  $\sigma(a)$  the probability of being male at age  $a$ , we have

$$p^m(a, t) = \sigma(a) p(a, t), \quad p^f(a, t) = (1 - \sigma(a)) p(a, t)$$

where  $p^m$ ,  $p^f$  and  $p$  respectively are the age-density of males, females and joint sex population.

- ii) *the case of different mortalities:*

if we assume that males and females have respective age-specific mortalities  $\mu^m(a)$  and  $\mu^f(a)$  then it is easy to see that the age-specific sex-ratio defined as the proportion of males ( $0 \leq \sigma(a) \leq 1$ ) has the following form

$$\sigma(a) = \frac{\Pi_m(a)\sigma_0}{\Pi_m(a)\sigma_0 + \Pi_f(a)(1 - \sigma_0)}$$

where

$$\Pi_m(a) := e^{-\int_0^a \mu_m(x) dx}, \quad \Pi_f(a) := e^{-\int_0^a \mu_f(x) dx}$$

are the respective probabilities of survival and  $\sigma_0$  is the sex-ratio at birth. Moreover, for the joint sex population we have the mortality

$$\mu_0(a) = \mu_m(a)\sigma(a) + \mu_f(a)(1 - \sigma(a)).$$

The evolution of our population is described by the following Gurtin-MacCamy type system

$$(1) \quad \begin{cases} p_t(a, t) + p_a(a, t) + \mu_0(a) p(a, t) = 0, & t > 0, \quad a \in (0, a_+) \\ p(0, t) = \Phi(S(t)) \int_0^{a_+} \beta(a) p(a, t) da, & t > 0, \\ p(a, 0) = p_0(a), & a \in [0, a_+]. \end{cases}$$

where  $p(a, t)$  is the age-density of the population at time  $t$ ,  $a_+$  is the maximum age and

$$S(t) = \int_0^{a_+} \sigma(a) p(a, t) da$$

is the size of the male subpopulation. We assume that

$$\sigma(\cdot) \in L_+^\infty(0, a_+).$$

Moreover

$$\mu_0(\cdot) \in L_{loc,+}^1(0, a_+)$$

is the per capita mortality rate, which defines the survival probability as

$$\Pi_0(a) := e^{-\int_0^a \mu_0(x) dx}$$

with  $\Pi_0(a_+) = 0$ . Also, our initial condition is a biologically meaningful initial age distribution

$$p_0(\cdot) \in L_+^1(0, a_+).$$

Concerning the birth process (see the boundary condition above) is modeled by two terms:

$$\beta_0(\cdot) \in L_+^\infty(0, a_+)$$

which is the *age specific fertility rate*, and the function  $\phi: [0, \infty) \rightarrow [0, \infty)$  which accounts for the mechanism of encounters in sexual reproduction (i.e. interactions between the sub-populations of females and males). Actually this function gives the functional response to the search for a male and

$$\phi(S(t)) (1 - \sigma(a)) p(a, t) da$$

is the number of effective encounters per unit of time of females with age between  $a$  and  $a + da$  with any male. Regarding  $\phi(x)$  we suppose that

$$(2) \quad \begin{cases} \phi(x) & \text{is continuous and increasing,} \\ \phi(0) = 0 & \text{and} \quad \lim_{x \rightarrow \infty} \phi(x) = \phi_\infty, \end{cases}$$

where  $1/\phi_\infty$  represents the time to produce newborns before a new encounter. Moreover

$$(3) \quad R_0 := \phi_\infty \int_0^{a_+} \beta_0(a) (1 - \sigma(a)) \Pi_0(a) da$$

is the basic reproduction number in the sense that represents the number of newborns produced by an individual of the population during his lifespan with a complete availability of males. Then in (1) we have rescaled our functions setting

$$(4) \quad \Phi(x) = \frac{\phi(x)}{\phi_\infty}, \quad \beta(a) = \phi_\infty \beta_0(a)(1 - \sigma(a)) \leq \beta^+,$$

so that

$$R_0 := \int_0^{a_\dagger} \beta(a) \Pi_0(a) da.$$

A standard form for  $\phi$  may be a Holling type II functional response

$$(5) \quad \phi(x) = \frac{\gamma x}{1 + \tau x},$$

that has been used in [3] [4]. At this stage of the model we neglect the competition for the resources that we will introduce later in Section 5. Let us remark that in order to avoid degenerated cases we assume that both parameters  $\sigma(a)$  and  $\beta(a)$  are not zero a.e. on  $(0, a_\dagger)$ .

Existence of steady states to the model equation (1) can be easily established. Namely, it is clear that the origin (or *extinction equilibrium*) is a solution of (1). Moreover, there possibly exist non-trivial equilibria given by

$$(6) \quad p^*(a) = \frac{S^* \Pi_0(a)}{\int_0^{a_\dagger} \sigma(a) \Pi_0(a) da}$$

where  $S^*$  must satisfy the following non-linear equation:

$$(7) \quad R_0 \Phi(S^*) = 1.$$

Now it is not difficult to see that there exist at most a non-trivial equilibrium. More precisely, if  $R_0 \leq 1$  there is no non-trivial equilibrium whereas if  $R_0 > 1$  there exists a unique non-trivial equilibrium. The latter follows from the fact that the function  $\Phi$  is increasing and takes all the values between 0 and 1.

Notice that equation (7) also gives a bifurcation diagram which is plotted as the graph of the function  $S^* = \Phi^{-1}\left(\frac{1}{R_0}\right)$  in the plane  $(R_0, S^*)$ , (see Figure 1 where the particular case of (5) is discussed). In particular, one has that  $S^*$  tends to infinity as  $R_0 \rightarrow 1^+$ . In this model the (positive) parameter  $R_0$  plays a fundamental role as it is quite usual in population dynamics. Other bifurcation diagrams are possible according to other model parameters accounting for more specific biological features of the population, see e.g. the diagrams in [3] and [4].

### 3. ASYMPTOTIC BEHAVIOR

Based on the integral formulation of (1) we may derive some global result about the asymptotic behaviour of the solution. Namely we consider the two variables

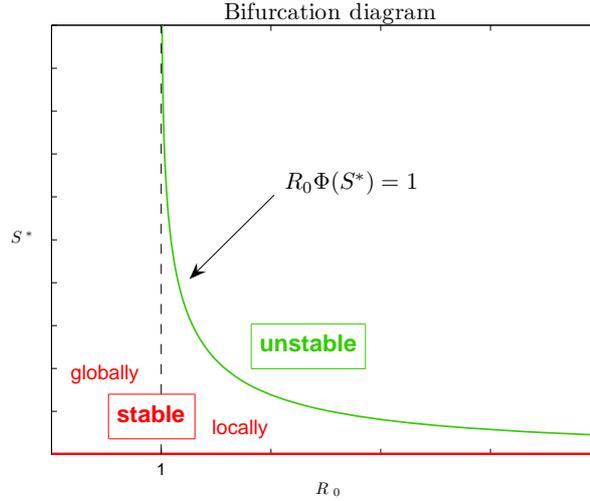


FIGURE 1. Bifurcation diagram for system (1) where the weighted population size at equilibrium  $S^*$  is plotted versus the parameter  $R_0 > 0$ , see Sections 2 and 3. There is a qualitative change at  $R_0 = 1$ , an unstable non-trivial equilibrium appears coming from infinity. The total population at equilibrium is given by  $P^* = S^* \frac{\int_0^{a_+} \Pi_0(a) da}{\int_0^{a_+} \sigma(a) \Pi_0(a) da}$ .

$B(t) = p(0, t)$  (total birth rate at time  $t$ ) and  $S(t)$ , focusing on the integral system

$$(8) \quad \begin{cases} B(t) = \Phi(S(t)) \left( \int_0^t K(t-x)B(x) dx + F(t) \right), \\ S(t) = \int_0^t H(t-x)B(x) dx + G(t), \end{cases}$$

where the following definitions apply

$$K(a) := \beta(a)\Pi_0(a), \quad H(a) := \sigma(a)\Pi_0(a),$$

$$F(t) := \int_0^\infty K(a+t) \frac{p_0(a)}{\Pi_0(a)} da, \quad G(t) := \int_0^\infty H(a+t) \frac{p_0(a)}{\Pi_0(a)} da,$$

with all the functions extended by zero outside the interval  $[0, a_+]$  (we note also that both  $F(t)$  and  $G(t)$  vanish outside the interval  $[0, a_+]$ ). From (8) we can get the solution of the original system as (see e.g. [2] for further details)

$$(9) \quad p(a, t) = \begin{cases} p_0(a-t) \frac{\Pi_0(a)}{\Pi_0(a-t)} & a > t, \\ B(t-a)\Pi_0(a) & a \leq t. \end{cases}$$

First we have a global result concerning the extinction equilibrium

**Proposition 1.** *If  $R_0 < 1$  then the origin is globally asymptotically stable.*

*Proof.* First we note that  $B(t)$  is bounded. In fact from the first equation in (8) we have

$$\max_{s \in [0, t]} B(s) \leq R_0 \max_{s \in [0, t]} B(s) + \max_{s \in [0, a_\dagger]} F(s)$$

and, consequently

$$\sup_{t \geq 0} B(t) \leq \frac{\max_{s \in [0, a_\dagger]} F(s)}{1 - R_0} \leq \frac{\beta^+}{1 - R_0} \int_0^{a_\dagger} p_0(a) da.$$

Then, using this estimate and the form (9) of the solution, we have

$$\int_0^{a_\dagger} p(a, t) da \leq \left( a_\dagger + \frac{\beta^+}{1 - R_0} \right) \int_0^{a_\dagger} p_0(a) da$$

that shows that the solution is stable. Moreover we draw

$$\limsup_{t \rightarrow \infty} B(t) < +\infty,$$

and, considering the first equation in (8), which for  $t > a_\dagger$  is

$$B(t) = \Phi(S(t)) \int_0^{a_\dagger} K(t - x) B(x) dx,$$

we get

$$\limsup_{t \rightarrow \infty} B(t) \leq R_0 \limsup_{t \rightarrow \infty} B(t),$$

and, since  $R_0 < 1$ ,

$$\lim_{t \rightarrow \infty} B(t) = 0.$$

By (9) we finally get

$$\lim_{t \rightarrow \infty} \int_0^{a_\dagger} p(a, t) da = 0. \quad \square$$

The previous result concerns the case in which only the extinction equilibrium exists. However, in the case  $R_0 > 1$  we can still give an estimate of the attraction due to this equilibrium.

**Proposition 2.** *If  $R_0 > 1$  then for any initial condition  $p_0(\cdot) \in L^1_+(0, a_\dagger)$  such that*

$$(10) \quad p_0(a) \leq \delta p^*(a), \quad a.e. \quad \text{in} \quad [0, a_\dagger], \quad \delta < 1$$

*we have*

$$\lim_{t \rightarrow \infty} \int_0^{a_\dagger} |p(a, t)| da = 0.$$

*Proof.* From the second equation in (8) we have

$$S(0) = \int_0^\infty \sigma(a)p_0(a)da \leq \delta S^*$$

where we have used (6). Then we define

$$t_0 = \sup \left\{ T \mid S(t) \leq \tilde{\delta} S^*, \quad \text{for } t \in [0, T] \right\}$$

where we take  $\delta < \tilde{\delta} < 1$ . If  $t_0 < \infty$ , from (8) we also have for  $t \in [0, t_0]$

$$B(t) \leq \Phi(\tilde{\delta} S^*) \left( \max_{s \in [0, t_0]} B(s) \int_0^t \beta(a) \Pi_0(a) da + \frac{\delta S^*}{\int_0^{a^\dagger} \sigma(a) \Pi_0(a) da} \int_t^\infty \beta(a) \Pi_0(a) da \right)$$

that yields

$$\max_{s \in [0, t_0]} B(s) \leq R_0 \Phi(\tilde{\delta} S^*) \max \left\{ \max_{s \in [0, t_0]} B(s), \frac{\delta S^*}{\int_0^{a^\dagger} \sigma(a) \Pi_0(a) da} \right\}.$$

Since

$$(11) \quad R_0 \Phi(\tilde{\delta} S^*) < 1$$

we have

$$(12) \quad \max_{s \in [0, t_0]} B(s) < \frac{\delta S^*}{\int_0^{a^\dagger} \sigma(a) \Pi_0(a) da}.$$

Then, plugging this inequality into the second of (8) we get

$$\tilde{\delta} S^* = S(t_0) = \int_0^{t_0} H(a) B(t_0 - a) da + G(t_0) \leq \delta S^*,$$

which is a contradiction, showing that  $t_0 = \infty$ . From this and (12) we have

$$\sup_{t \geq 0} S(t) \leq \tilde{\delta} S^*, \quad \sup_{t \geq 0} B(t) < +\infty$$

and, from the first equation in (8), we may derive

$$\limsup_{t \rightarrow \infty} B(t) \leq R_0 \Phi(\tilde{\delta} S^*) \limsup_{t \rightarrow \infty} B(t),$$

that, by (11) implies  $\lim_{t \rightarrow \infty} B(t) = 0$ . □

On the other hand we have also a symmetrical condition under which the non-trivial steady state repels the solution that goes to infinity.

**Proposition 3.** *If  $R_0 > 1$  then for any initial condition  $p_0(\cdot) \in L^1_+(0, a_+)$  such that*

$$(13) \quad p_0(a) \geq \delta p^*(a), \quad \text{a.e. in } [0, a_+], \quad \delta > 1$$

we have

$$\lim_{t \rightarrow \infty} \int_0^{a_+} |p(a, t)| da = +\infty.$$

*Proof.* the argument to prove this result follows the one used in the proof of Proposition 1, with reversed inequalities. However, in this case we need to preliminarily prove that  $B(t)$  is strictly positive. Actually we first prove that

$$B(t) > 0 \quad \text{for } t \in [0, a_+].$$

In fact, since  $S(0) \geq \delta S^* > 0$  we have

$$B(0) = \Phi(S(0))F(0) > R_0\Phi(S(0)) \frac{\delta S^*}{\int_0^{a_+} \sigma(a)\Pi_0(a)da} > 0$$

and, supposing that there exists  $t_0 \in [0, a_+]$  such that

$$B(t_0) = 0, \quad B(t) > 0 \quad \text{for } t \in [0, t_0),$$

we have

$$0 \geq \int_0^{t_0} K(t_0 - a)B(a)da + \frac{\delta S^*}{\int_0^{a_+} \sigma(a)\Pi_0(a)da} \int_{t_0}^{a_+} K(a)da$$

which yields the wrong conclusion

$$K(a) = 0 \quad \text{for } a \in [0, a_+].$$

Repeating this argument for  $t_0 > a_+$ , we conclude that  $B(t) > 0$  for all  $t$ .

Let now

$$t_0 = \sup \left\{ T \mid S(t) \geq \tilde{\delta} S^*, \quad \text{for } t \in [0, T] \right\}$$

with  $1 < \tilde{\delta} < \delta$ . If  $t_0 < +\infty$  we have

$$\min_{s \in [0, t_0]} B(s) \geq R_0\Phi(\tilde{\delta} S^*) \min \left\{ \min_{s \in [0, t_0]} B(s), \frac{\delta S^*}{\int_0^{a_+} \sigma(a)\Pi_0(a)da} \right\}.$$

Since  $\min_{s \in [0, t_0]} B(s) > 0$  and  $R_0\Phi(\tilde{\delta} S^*) > 1$  we draw

$$(14) \quad B(t) \geq \frac{\delta S^*}{\int_0^{a_+} \sigma(a)\Pi_0(a)da} \quad \text{for } t \leq t_0$$

then from the second equation in (8)

$$\tilde{\delta}S^* = S(t_0) \geq \delta S^*$$

which is absurd. Then  $S(t) \geq \tilde{\delta}S^*$  for all  $t \geq 0$  so that (14) holds for all  $t \geq 0$  and  $\liminf_{t \rightarrow +\infty} B(t) > 0$ . From the first equation in (8) we get

$$\liminf_{t \rightarrow +\infty} B(t) \geq R_0 \Phi(\tilde{\delta}S^*) \liminf_{t \rightarrow +\infty} B(t)$$

and, consequently

$$\lim_{t \rightarrow +\infty} B(t) = +\infty,$$

which implies the thesis.  $\square$

The previous propositions soon imply the following consequence

**Corollary 4.** *Let  $R_0 > 1$ , then the trivial equilibrium is asymptotically stable and the non-trivial one is unstable.*

*Proof.* Though the condition required in Proposition 2 is not in general satisfied by the initial datum  $p_0(a)$  however, applying Gronwall inequality to the first equation in (8) we have

$$B(t) \leq \beta^+ e^{\beta^+ a_\dagger} |p_0|_{L^1} \quad \text{for } t \in [0, a_\dagger]$$

so that

$$p(a, a_\dagger) = B(a_\dagger - a) \Pi_0(a) \leq \beta^+ e^{\beta^+ a_\dagger} |p_0|_{L^1} \Pi_0(a).$$

Then, calling  $\tilde{p}(a, t)$  the solution of the problem with initial datum  $\tilde{p}_0(a) = p(a, a_\dagger)$ , since for  $t > a_\dagger$  we have

$$p(a, t) = \tilde{p}(a, t - a_\dagger),$$

we can apply Proposition 2 to  $\tilde{p}(a, t)$  and conclude that the origin is asymptotically stable.

Concerning the non-trivial equilibrium  $p^*(a)$  we take  $p_0(a) = (1 + \eta)p^*(a)$  with  $\eta > 0$  small enough in order to have  $p_0(a)$  as close as we want to  $p^*(a)$  and, applying Proposition 3 we see that with any such initial datum the solution is going to infinity, proving instability of  $p^*(a)$ .  $\square$

We can also estimate how the solution growth to infinity

**Corollary 5.** *If  $R_0 > 1$  and the assumptions of Proposition 3 are fulfilled, then we have*

$$(15) \quad B(t) > ce^{\omega t}$$

where  $c$  and  $\omega$  are suitable positive constants.

*Proof.* We start from the inequalities for  $t \geq 0$

$$B(t) > 0, \quad S(t) \geq \tilde{\delta}S^*,$$

established in the proof of Proposition 3. Then, setting

$$B_n = \min_{t \in [na_+, (n+1)a_+]} B(t), \quad n = 0, 1, \dots$$

we have from (8)

$$B_n \geq R_0 \Phi(\tilde{\delta}S^*) \min \{B_n, B_{n-1}\}$$

and consequently, since  $R_0 \Phi(\tilde{\delta}S^*) > 1$  and  $B_n > 0$ ,

$$B_n > R_0 \Phi(\tilde{\delta}S^*) B_{n-1}, \quad n = 0, 1, \dots$$

By induction we draw

$$B_n > \left( R_0 \Phi(\tilde{\delta}S^*) \right)^n B_0.$$

Then, if  $t \in [na_+, (n+1)a_+]$

$$B(t) > \left( R_0 \Phi(\tilde{\delta}S^*) \right)^{-1} \left( R_0 \Phi(\tilde{\delta}S^*) \right)^{\frac{1}{a_+} t}$$

and we have (15) with suitable  $c$  and  $\omega$ . □

#### 4. AGE-PROFILE

In this section we reformulate the original non-linear problem (1) introducing the age-profile (or the per capita age-density of the population) as a new state variable

$$w(a, t) = \frac{p(a, t)}{P(t)}$$

and the total population

$$P(t) = \int_0^{a_+} p(a, t) da > 0.$$

Notice that this description is possible for initial data  $p_0(a)$  that are not trivial, i.e. those data for which  $P(t)$  does not vanish in a finite time. Namely, we will assume in the sequel that the initial condition  $p_0(\cdot) \in L^1_+(0, a_+)$  for system (1) is such that for all  $t \geq 0$  the functions

$$\sigma(a+t)p_0(a) \text{ and } \beta_0(a+t)p_0(a) \text{ are not zero a.e. on } (0, a_+).$$

Actually this conditions guarantee that the initial population is endowed with males and fertile females, otherwise the population goes to extinction. See e.g. [5] Chapter 14.

From the original system (1) and noticing that  $p(a_{\dagger}, t) = 0$  (see (9)), it is possible to write a non-linear system for the age-profile and the total population jointly:

$$(16) \quad \begin{cases} w_t(a, t) + w_a(a, t) + (\mu_0(a) + M(t))w(a, t) = 0 \\ w(0, t) = \Phi(S(t)) \int_0^{a_{\dagger}} \beta(a) w(a, t) da \\ \int_0^{a_{\dagger}} w(a, t) da = 1 \\ \frac{d}{dt}P(t) = M(t) P(t) \end{cases}$$

where

$$M(t) := \int_0^{a_{\dagger}} (\Phi(S(t))\beta(a) - \mu_0(a))w(a, t) da$$

and

$$S(t) := P(t) \int_0^{a_{\dagger}} \sigma(a) w(a, t) da.$$

System (16) is a combination of a partial differential equation and an ordinary differential equation. In order to have an initial-boundary value problem an initial condition should be provided  $(w(a, 0), P(0)) = (w_0(a), P_0)$  satisfying the compatibility condition

$$\int_0^{a_{\dagger}} w_0(a) da = 1.$$

Moreover, we note that the joint state variables take values in an invariant subset of the positive cone  $L_+^1(0, a_{\dagger}) \times \mathbb{R}_+$ . Once we know the solution of (16), the solution of system (1) can be recovered by the formula

$$p(a, t) = P(t) w(a, t).$$

Now is a routine to check that the number of equilibria of (16) is exactly the same as the number of non-trivial equilibria of (1) and that they are just related through a normalization. So, according to equation (7), if  $R_0 \leq 1$  there is no equilibrium of (16) whereas if  $R_0 > 1$  there exists a unique (non-trivial) equilibrium given by

$$(17) \quad w_0^*(a) = \frac{\Pi_0(a)}{\int_0^{a_{\dagger}} \Pi_0(a) da}, \quad P^* = S^* \frac{\int_0^{a_{\dagger}} \Pi_0(a) da}{\int_0^{a_{\dagger}} \sigma(a) \Pi_0(a) da}$$

where  $S^*$  is the solution of (7). These are the stationary age-profile and the total population at equilibrium respectively.

Note that no solution corresponds to the trivial solution of (1) because if  $P^* = 0$  then the second condition in (16) would give  $w_0^*(a) \equiv 0$  and the third condition would not be satisfied.

Since we know from the previous section that non-trivial equilibrium is unstable, we have to check asymptotic states such those we obtain going to the limit

with  $\lim_{t \rightarrow +\infty} P(t) = +\infty$ . In fact, this formal limit performed in (16), and taking into account  $\lim_{t \rightarrow +\infty} \Phi(S(t)) = 1$ , leads to the following equation

$$(18) \quad \begin{cases} w_t(a, t) + w_a(a, t) + \mu_0(a)w(a, t) \\ \quad + w(a, t) \int_0^{a^\dagger} (\beta(s) - \mu_0(s)) w(s, t) ds = 0 \\ w(0, t) = \int_0^{a^\dagger} \beta(a) w(a, t) da \\ \int_0^{a^\dagger} w(a, t) da = 1 \end{cases}$$

which has a steady solution

$$(19) \quad w_\infty^*(a) = \frac{e^{-\alpha^* a} \Pi_0(a)}{\int_0^{a^\dagger} e^{-\alpha^* x} \Pi_0(x) dx}$$

where  $\alpha^*$  is the only real solution of the equation (the intrinsic Malthusian parameter of the limiting system)

$$\int_0^{a^\dagger} \beta(a) \Pi_0(a) e^{-\lambda a} da = 1.$$

Now, in order to assure the convergence of the solution of (16) to (19), we need an additional hypothesis on  $\Phi(x)$ , namely,

$$(20) \quad \int_1^\infty \frac{1 - \Phi(x)}{x} dx < \infty,$$

which means that the function  $1 - \Phi(x)$  must have a sufficiently fast decay (see also e.g. [8]). For instance, the function considered in (5), corresponding to a Holling type II functional response, fulfills this further condition (20). Next theorem is concerned with the convergence of the age-profile to (19)

**Theorem 6.** *Let  $R_0 > 1$  and suppose that  $p_0(a)$  satisfies condition (13) of Proposition 3. Then, if  $\Phi(x)$  fulfills (20), we have*

$$(21) \quad \lim_{t \rightarrow \infty} \int_0^{a^\dagger} |w(a, t) - w_\infty^*(a)| da = 0.$$

*Proof.* We first go back to the first equation of system (8) and note that it can be viewed as a time-dependent linear renewal equation

$$B(t) = \int_0^t K(t, s) B(t - s) ds + F(t)$$

with

$$K(t, s) = \Phi(S(t)) \beta(a) \Pi_0(a)$$

which converges to  $K(a) = \beta(a)\Pi_0(a)$  in the following sense

$$(22) \quad |K(t, \cdot) - K(\cdot)|_{L^\infty} \leq \beta^+ (1 - \Phi(t)) \rightarrow 0 \text{ as } t \rightarrow +\infty,$$

and, moreover is rapidly converging, that is

$$(23) \quad \int_0^\infty |K(t, \cdot) - K(\cdot)|_{L^\infty} dt < +\infty.$$

To see this we use the bound (15) derived for  $B(t)$  at the end of the proof of Proposition 3. In fact (15) implies, for  $t$  sufficiently large

$$S(t) = \int_0^{a_\dagger} B(t-s)\Pi_0(s)ds > ce^{\omega t},$$

with some constant  $c > 0$ , and consequently, for some constant  $C > 0$

$$\Phi(S(t)) > \Phi(Ce^{\omega t}) \text{ for } t \geq 0.$$

Thus

$$\begin{aligned} \int_0^\infty |K(t, \cdot) - K(\cdot)|_{L^\infty} dt &\leq \beta^+ \int_0^\infty (1 - \Phi(S(t))) dt \\ &\leq \beta^+ \int_0^\infty (1 - \Phi(Ce^{\omega t})) dt = \frac{\beta^+}{\omega} \int_1^\infty \left( \frac{1 - \Phi(x)}{x} \right) dx < +\infty. \end{aligned}$$

as we claimed.

Now we are able to use a result in [2] where it is proved that (22) and (23) imply

$$(24) \quad B(t) = b_0 e^{\alpha^* t} (1 + \Omega(t))$$

where

$$\lim_{t \rightarrow +\infty} \Omega(t) = 0$$

and

$$b_0 = \frac{\widehat{K}(\alpha^*) + \widehat{g}(\alpha^*)}{\int_0^{a_\dagger} e^{-\alpha^* s} s K(s)} > 0$$

with

$$g(t) = (1 - \Phi(S(t))) \int_0^t K(s)B(t-s)ds$$

which is positive and absolutely Laplace transformable thanks to assumption (20).

Finally, since (24) imply (for  $t > a_\dagger$ )

$$w(a, t) = \frac{B(t-a)\Pi_0(a)}{\int_0^{a_\dagger} B(t-a)\Pi_0(a)da} = \frac{e^{-\alpha^* a} (1 + \Omega(t-a)) \Pi_0(a)}{\int_0^{a_\dagger} e^{-\alpha^* a} (1 + \Omega(t-a)) \Pi_0(a)da}$$

we have (21). □

Concerning the latter results, it is worth to mention that in [8] the authors give a result (Theorem 2.6), using the theory of semigroups on dual Banach spaces, which cannot be applied directly to our model in order to study the asymptotic age-profile. However, if in addition to the assumptions of the previous Theorem 6 we assume that  $\sigma(a) \geq \underline{\sigma} > 0$  a.e. on  $(0, a_{\dagger})$  then we arrive to the same conclusion as in Example 3.8 of [8] with the functions

$$F(\phi) := \left( \Phi \left( \int_0^{a_{\dagger}} \sigma(a) |\phi(a)| da \right) - 1 \right) \int_0^{a_{\dagger}} \beta(a) \phi(a) da \cdot \delta_0,$$

where  $\delta_0$  is the Dirac delta concentrated at the origin, and  $f(r) := (1 - \Phi(\underline{\sigma}r)) |\beta(\cdot)|_{L^\infty}$ .

## 5. COMPETITION EFFECTS

We now take into account competition effects that may arise at high population densities and modify the long term behavior of the basic model. So, we investigate the following non-linear equation which is a modification of system (1)

$$(25) \quad \begin{cases} p_t(a, t) + p_a(a, t) + \mu_0(a) p(a, t) = 0 \\ p(0, t) = \Phi(S(t)) \Psi(P(t)) \int_0^{a_{\dagger}} \beta(a) p(a, t) da, \end{cases}$$

where

$$P(t) = \int_0^{\infty} p(a, t) da$$

is the total population and  $\Psi: [0, \infty) \rightarrow [0, 1]$  introduces the effect of competition for limited resources, producing a reduction of fertility due to population crowding. Regarding the latter we suppose that

$$(26) \quad \begin{cases} \Psi \text{ is continuous and decreasing,} \\ \Psi(0) = 1 \text{ and } \lim_{x \rightarrow \infty} \Psi(x) = 0. \end{cases}$$

The other terms  $\mu_0(a)$ ,  $\beta(a)$ ,  $\sigma(a)$ ,  $\Phi(x)$  and  $S(t)$  are like in the basic model (1). A standard prototype for the function  $\Psi(x)$  is for instance

$$(27) \quad \Psi(x) = \frac{1}{1 + (x/k)^\theta}$$

where the parameter  $\theta > 0$  accounts for the different impact of competition (see Figure 3 for an example of the functions defined in (5) and (27)).

Now, proceeding as in Section 2, non-trivial equilibria are given by

$$p^*(a) = p^*(0) \Pi_0(a)$$

where  $p^*(0)$  is related to the two variables

$$S^* := p^*(0) \int_0^{a_{\dagger}} \sigma(a) \Pi_0(a) da \quad \text{and} \quad P^* := p^*(0) \int_0^{a_{\dagger}} \Pi_0(a) da$$

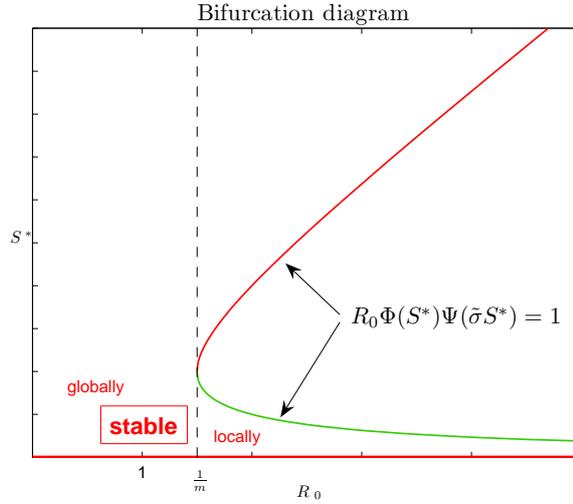


FIGURE 2. New bifurcation diagram when competition effects are included. The weighted population size at equilibrium  $S^*$  is plotted versus  $R_0 > 0$  assuming that  $0 \leq \Phi(x) \Psi(\tilde{\sigma}x) \leq M$  is unimodal (with maximum value  $M < 1$ , see (29)). Two non-trivial equilibria exist for  $R_0 > \frac{1}{M}$ .

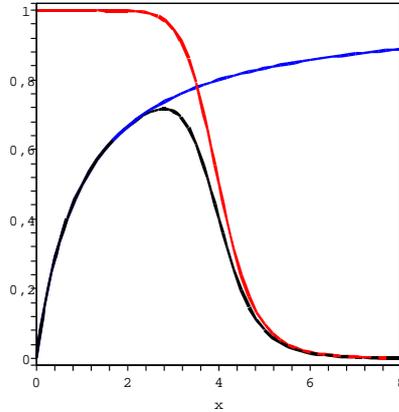


FIGURE 3. From top to bottom, the picture shows the functions  $\Psi(\tilde{\sigma}x)$ ,  $\Phi(x)$  and the function  $\Phi(x) \times \Psi(\tilde{\sigma}x)$  which is unimodal.

which regarded as positive independent variables must satisfy the following non-linear equations:

$$(28) \quad R_0 \Phi(S^*) \Psi(P^*) = 1, \quad P^* = S^* \frac{\int_0^{a^\dagger} \Pi_0(a) da}{\int_0^{a^\dagger} \sigma(a) \Pi_0(a) da},$$

with  $R_0$  still defined in (3). Once we know the solutions of (28) we get the steady states  $p^*(\cdot)$ .

Regarding equations (28), multiple situations can occur depending on the explicit form of the functions  $\Phi$  and  $\Psi$ . Nevertheless, defining

$$(29) \quad \tilde{\sigma} := \frac{\int_0^{a^\dagger} \Pi_0(a) da}{\int_0^{a^\dagger} \sigma(a) \Pi_0(a) da} > 0 \quad \text{and} \quad M := \max_{x>0} \{\Phi(x) \Psi(\tilde{\sigma}x)\} < 1$$

one has that if  $R_0 < \frac{1}{M}$  there is no non-trivial equilibrium, if  $R_0 = \frac{1}{M}$  there exist at least a non-trivial equilibrium, and if  $R_0 > \frac{1}{M}$  there exist at least two non-trivial equilibria. The latter follows from the fact that the function  $x \rightarrow \Phi(x) \Psi(\tilde{\sigma}x)$  takes all the values between 0 and  $M$  at least twice.

We now focus on the simple case in which this function is unimodal so that, for  $R_0 > \frac{1}{M}$  we have exactly two non-trivial states as illustrated in the bifurcation diagram in Figure 2. In fact the action of competition reduces males availability and rises the threshold for  $R_0$ , from 1 to  $\frac{1}{M} > 1$ , in order to non-trivial states to exist and allow the population not to go extinct.

Concerning stability of these states, we soon remark that, by the same argument as in Proposition 1 we can prove

**Proposition 7.** *If  $R_0 < \frac{1}{M}$  then the extinction equilibrium  $p^* \equiv 0$  is globally asymptotically stable.*

And, with an argument similar to the one used in the proof of Proposition 2, we also have

**Proposition 8.** *If  $R_0 > \frac{1}{M}$  then the extinction equilibrium is asymptotically stable.*

In order to analyze the stability of the non-trivial states we consider the characteristic equation arising from linearization at such states and we obtain

$$(30) \quad 1 = \widehat{K}_0(\lambda) + R_0 S^* \left[ \Phi'(S^*) \Psi(\tilde{\sigma} S^*) \widehat{K}_1(\lambda) + \tilde{\sigma} \Phi(S^*) \Psi'(\tilde{\sigma} S^*) \widehat{K}_2(\lambda) \right],$$

where  $\widehat{K}_0(\lambda)$ ,  $\widehat{K}_1(\lambda)$ ,  $\widehat{K}_2(\lambda)$  are the Laplace transforms of the respective kernels

$$K_0(a) = \frac{\beta(a) \Pi_0(a)}{R_0}, \quad K_1(a) = \frac{\sigma(a) \Pi_0(a)}{\int_0^{a^\dagger} \sigma(a) \Pi_0(a) da}, \quad K_2(a) = \frac{\Pi_0(a)}{\int_0^{a^\dagger} \Pi_0(a) da}$$

Such characteristic equation will be systematically analyzed numerically in a forthcoming paper as in [9], in order to discuss the effect of the interplay between the increasing growth rate of the basic model and the reduction operated by the logistic term introduced by function  $\Psi$ .

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## REFERENCES

- [1] Iannelli, M., Martcheva, M.: Homogeneous dynamical systems and the age-structured SIR model with proportionate mixing incidence, *Evolution equations: applications to physics, industry, life sciences and economics* (Levico Terme, 2000), 227–251, *Progr. Nonlinear Differential Equations Appl.*, 55, Birkhäuser, Basel, 2003.
- [2] Iannelli, M.: *Mathematical Theory of Age-Structured Population Dynamics*, Applied Mathematics Monograph C.N.R. vol. 7, Giardini editori e stampatori, Pisa 1995.
- [3] Calsina, À., Ripoll, J.: A general structured model for a sequential hermaphrodite population, *Math. Biosci.* 208(2) (2008), 393–418.
- [4] Calsina, À., Ripoll, J.: Evolution of age-dependent sex-reversal under adaptive dynamics, *J. Math. Biol.* (2009).
- [5] Thieme, H.R.: *Mathematics in Population Biology*, Princeton Series in Theoretical and Computational Biology, Princeton University Press, Princeton and Oxford, 2003.
- [6] Rudnicki, R. (editor): *Mathematical Modelling of Population Dynamics*, Polish Academy of Sciences, Institute of Mathematics, Banach Center Publ. 63, Warszawa 2004.
- [7] Iannelli, M., Martcheva, M., Milner, F.A.: *Gender-Structured Population Modeling: Mathematical Methods, Numerics, and Simulations*, *Frontiers in Applied Mathematics* 31, SIAM, Philadelphia, 2005.
- [8] Gyllenberg, M., Webb, G.F.: Asynchronous exponential growth of semigroups of nonlinear operators, *J. Math. Anal. Appl.* 167(2) (1992), 443–467.
- [9] D. Breda, C. Cusulin, M. Iannelli, S. Maset and R. Vermiglio: Stability analysis of age-structured population equations by pseudospectral differencing methods, *J. Math. Biol.* 54 (2007), 701–720.

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