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Abstract In this work, we model the time and age evolution of a partially clonal population, i.e., able to reproduce sexually and asexually, in an environment with unlimited resources. The population is divided in two subpopulations, sexual and asexual, whose densities follow a coupled system of McKendrick-Von Foerster equations of evolution. The transition from one subpopulation to another are driven by transition probabilities for newborns to be sexual (resp. asexual) when their parent(s) is(are) in the asexual (sexual) subpopulation. We study the optimization of the growth rate of the whole population, with respect to these transition probabilities. We prove, using a result of the variation of the first eigenvalue (Malthusian growth rate) for this problem, that the maximal eigenvalue is reached when the probabilities are exactly (in time) equal to zero or one. Moreover, depending on birth and death rates of both subpopulations (asexual and sexual), we show that the maximal growth rate is reached when the population newborns switch (completely) from sexual to asexual and then to asexual to sexual (periodically in time) or when a subpopulation disappears.

Keywords Bang-Bang control · Growth rate · Eigenvalue · McKendrick equation

Mathematics Subject Classification (2000) 65N25 · 35Q93 · 49J30

1 Introduction

Species that reproduce asexually (such as bacteria) or by parthenogenesis (female able to produce child without male and fertilization) produce clones at

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each generation, sexual beings produce half males and half females. At the specie scale, parthenogenesis is much more prolific and cost free (no sexual disease, no time lost in partner selection) than the sexual reproduction, and, at the individual scale this is the most selfish way to reproduce (female do not have to share their genetic material) and so costless than the sexual reproduction ([1] Ch. 1). Nevertheless, at the specie scale, variability of the genome of a specie and ability to find a solution when arise environmental changes (new diseases, new predators, climate...) gives a long time advantage to sexual reproduction. The dynamic balance between the long-time evolutive advantage of sexual function and its reproductive cost in the short-time is an enigma of sexuality [1,2].

Aphids are unusual organisms (partially clonal) which can both reproduce sexually and by parthenogenesis, which is determined by environmental conditions [3–6]. In [7], authors consider a time evolution model (using ODE) of Aphids population, they study the nonlinear dynamics but do not study the optimal growth rate and their optimisation with respect to the fecundation function in an environment with unlimited resources, i.e., when birth and death rates do not depend on the size of the population. In this case, the population grows exponentially in time and the problem of optimal growth rate becomes an eigenvalue optimization [8,9].

In this work, we first rewrite the model given in [7] to introduce transition probabilities for a parthenogenetic individual to give birth to a sexual one and for a sexual individual to give birth to a parthenogenetic one. Moreover, we add an age structure, using the partial differential equation of evolution introduced by McKendrick-Von Foerster [9], in Section 2. The population is divided in two subpopulations : the asexual subpopulation of density $n_A(t,a)$ at time t and age a and the sexual subpopulation of density $n_S(t,a)$ at time t and age a. In Section 3, we give first results on the dynamics of $(n_A,n_S)(t,a)$ and we show that the dynamic is time-exponential and is driven by an eigenvalue/eigenfunction. Then, in Section 4, we study the optimization of this eigenvalue (to improve the growth of the population) with respect to the probabilities to switch from a way to produce offsprings to another (which could be a measure to the ability of a population to invade (or replace) a less fitted population, i.e., with a smaller Malthusian growth rate, see [10–15]). In Section 5, we give an example of application to this work when the balance between death rates and birth rates changes and makes the asexual subpopulation have a better growth rate, i.e., best fitted than an alternation of sexual to asexual. We illustrate the work by giving numerical simulation in Section 6. Finally, in Section 7, we discuss and conclude this work.

2 Model

In [7], a population u splits into asexual (i.e. born by parthenogenesis) : x and sexual (i.e. born from females fertilized by males) y. Therefore, there are $y/2$ males and $x+y/2$ females, and so, the excess of females per male is $\psi := 2x/y$.

We notice that authors assume that the ratio of male offsprings over the female offsprings on the sexual population is 1:1 which is the case of most species [16]. In [16,17], Fisher develop an evolutionary model (mathematically formalized by [18]) that explains that, this approximatively 1:1, sex ratio of offsprings is an evolutionarily stable strategy. Therefore, we do not modify this point in this work. Then authors introduce a fecundation function, $h : \psi \mapsto 1 + g \tanh(\psi/g)$ where $g =$ the limit number of females fertilized per male -1[1]. The dynamics of population x and y are driven by the following system

$$\begin{cases} x'(t) = -\beta(u)x + \alpha(u)[x + y/2 - h(\psi)y/2], \\ y'(t) = -\beta(u)y + \alpha(u)[h(\psi)y/2], \end{cases} \tag{1}$$

where β is the death rate, α the birth rate and $u(t) = x(t) + y(t)$ is the total population. No sexual activity means that $h = 0$ and so, we have,

$$\begin{cases} x'(t) = -\beta(u)x + \alpha(u)[x + y/2], \\ y'(t) = -\beta(u)y. \end{cases}$$

Now, let $q = \frac{\tanh(\psi/g)}{\psi/g} \in [0, 1]$ and $p = h - \psi q \in [0, 1]$, then we can rewrite the system (1) as follows

$$\begin{cases} x'(t) = -\beta(u)x + \alpha(u)[(1 - q)x + (1 - p)y/2], \\ y'(t) = -\beta(u)y + \alpha(u)[qx + py/2]. \end{cases} \tag{2}$$

Therefore, we see that q is the probability for a parthenogenetic individual to give birth to a sexual one and p is the probability for a sexual individual to give birth to a sexual one. And so, the limit case $p = q = 0$ corresponds to the case where there is no sexual activity. In an environment with unlimited resources, the birth rate α and the death rate β do not depend on the size of the population and

$$\begin{pmatrix} x \\ y \end{pmatrix}' (t) = (-\beta I + \alpha M) \begin{pmatrix} x \\ y \end{pmatrix} (t), \tag{3}$$

with

$$M = \begin{pmatrix} 1 - q & (1 - p)/2 \\ q & p/2 \end{pmatrix}.$$

What would be the optimal growth rate of the population with respect to the probabilities (p, q) *(chosen in* $[0, 1]^2$*)?* Since $(p, q) \in [0, 1]^2$, solutions to the linear system (3) are given by

$$\begin{pmatrix} x \\ y \end{pmatrix} (t) = e^{(-\beta I + \alpha M)t} \begin{pmatrix} x \\ y \end{pmatrix} (0),$$

[1] for aphids around 7. [7]

and the growth rate is given by the maximal eigenvalue of $(-\beta I+\alpha M)$ which is $\alpha\lambda_{max}(p,q)-\beta$ where $\lambda_{max}(p,q)$ is the the maximal eigenvalue of M : $\lambda_{max}(p,q)=\frac{1-q+p/2+\sqrt{(1-q+p/2)^2-2(p-q)}}{2}$. Since we have

$$\frac{\partial}{\partial q}\lambda_{max}=-\frac{1}{2}+\frac{(q-p/2)}{\sqrt{(p/2-q)^2+(1-p)}}$$

and $\frac{\partial}{\partial p}\lambda_{max}=-\frac{1}{2}[\frac{\partial}{\partial q}\lambda_{max}]-\frac{1}{2\sqrt{(p/2-q)^2+(1-p)}}$, the maximum of λ_{max} is reached on the boundary of $[0,1]^2$. We notice that

$$\lambda_{max}(1,q)=\max(1-q,1/2),\quad \max_q(\lambda_{max}(1,q))=\lambda_{max}(1,0)=1,$$

$$\lambda_{max}(p,1)=\max(1,(1-p)/2),\quad \max_p(\frac{p/2+\sqrt{(p/2)^2-2(p-1)}}{2})=\sqrt{2}/2,$$

and $\lambda_{max}(0,q)=\lambda_{max}(0,0)=1$. For all $p'\in[0,1]$, we have,

$$\lambda_{max}(p,0)=\max(1,p/2),\quad \max_p(\lambda_{max}(p,0))=\lambda_{max}(p',0)=1.$$

Therefore, the maximum of the eigenvalue (growth rate) λ_{max} is reached as $q=0$, i.e., when parthenogenetic gives only parthenogenetic whatever do the sexual population. Then, we have

$$y(t)=y(0)e^{(\alpha p/2-\beta)t},\quad \textit{and}\quad x(t)=(x(0)+o(1))e^{(\alpha-\beta)t},$$

and so, the growth of a population which reproduces only by parthenogenesis is larger than every other choices of reproduction function. Moreover, we observe that the parthenogenesis/sexual population survival depends on the value of α and β (see fig. 1). In particular we notice that the maximum of the larger eigenvalue is reached when $p=0$ and $q=0$ (so $h=0$) which means that there is no more sex.

The same question, in the case where α,β,p,q are $T-$periodic functions modeling seasonal variations of the parameters, since we have

$$\max Sp((-\beta(t)I+\alpha(t)M))=-\beta(t)+\alpha(t),$$

for all t, gives the same answer : the best way to reproduce is given by $q=0$, i.e., $y(t)=y(0)e^{(\int_0^T(\alpha p/2-\beta)(s)t/T}$ and $x(t)=(x(0)+o(1))e^{(\int_0^T(\alpha-\beta)(s)t/T}$. Consequently we have again Figure 1 with $\int_0^T\alpha ds/T$ (resp. $\int_0^T\beta ds/T$) instead of α (resp. β). To include specificities of parthenogenetic and sexual subpopulations in the model, we have to deal with the differences of birth and death rates of both subpopulations. We add an age-structure in the model (McKendrick-Von Foerster model [9–13]) for both subpopulations, at time t and age x, the density of asexual subpopulation $n_A(t,x)$ and the density of the sexual population

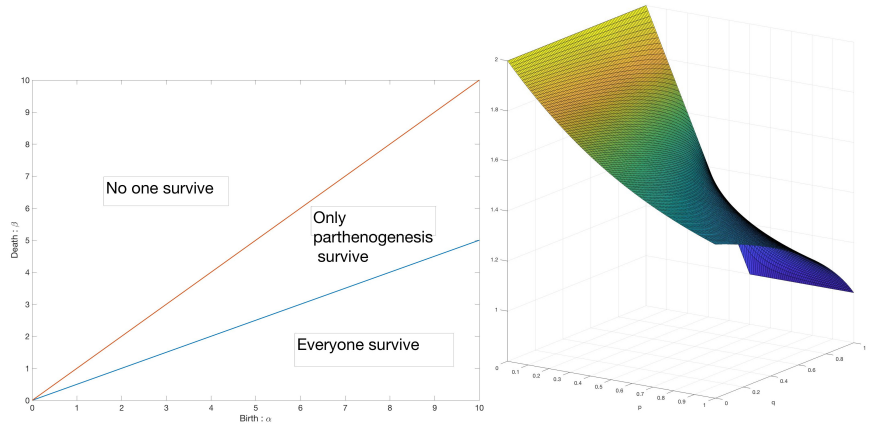

Fig. 1 Left : Survival of species depending on the birth rate α and the death rate β. Right : $(p, q) \mapsto \lambda_{max}(p, q)$.

$n_S(t, x)$ have their time evolution driven by the system of transport equations (with loss due to death term) :

$$\begin{cases} \frac{\partial}{\partial t} n_A(t,x) + \frac{\partial}{\partial x} n_A(t,x) + d(t) n_A(t,x) = 0, \\ \\ \frac{\partial}{\partial t} n_S(t,x) + \frac{\partial}{\partial x} n_S(t,x) + d(t) \chi_{x>x_0} n_S(t,x) = 0, \end{cases} \tag{4}$$

where $d(t)$ is the death rate (due to environment and time periodic due to seasonal variation). The only difference for death for both subpopulations is during the first stage development and we consider that, for age x less than x_0 a sexual individual is an egg which have a null death rate and the same death rate for individuals (not in an egg). Newborns appear at age 0 which leads to the following boundary condition,

$$\begin{cases} n_A(t, x=0) = \displaystyle\int_{x' \geq 0} p_{S\to A}(t) B_S(x') n_S(t,x')\, dx' \\ \qquad\qquad + \displaystyle\int_{x' \geq 0} p_{A\to A}(t) B_A(x') n_A(t,x')\, dx', \\ \\ n_S(t, x=0) = \displaystyle\int_{x' \geq 0} p_{S\to S}(t) B_S(x') n_S(t,x')\, dx' \\ \qquad\qquad + \displaystyle\int_{x' \geq 0} p_{A\to S}(t) B_A(x') n_A(t,x')\, dx'. \end{cases} \tag{5}$$

with

$$p_{A\to A}(t) + p_{A\to S}(t) = p_{S\to A}(t) + p_{S\to S}(t) = 1, \quad \forall t.$$

Parthenogenetic female can give birth, with a birth rate depending on the age x of the female : $B_A(x)$ to parthenogenetic female, with probability $p_{A\to A}(t)$ at time t, and to sexual female with probability $p_{A\to S}(t)$. Respectively, sexual

female can give birth, with a rate $B_S(x)$ (which is $< B_A(x)$) depending on the age x (in particular for eggs $B_S(x) = 0$ for $x \in [0, x_0]$), with probability $p_{S\to A}(t)$ at time t to a parthenogenetic female and with probability $p_{S\to S}(t)$ to sexual female (5). Since parthenogenesis is much more prolific and cost free than the sexual reproduction we assume that

$$B_A(x') > B_S(x'). \tag{6}$$

We set that for $T > 0$ (here $T = 365$ days)

$$t \mapsto d(t) \in L^\infty(\mathbb{R}) \quad T - periodic, \tag{7}$$

$$x \mapsto B_A(x), \quad (resp\ \ B_S(x)) \in L^\infty(\mathbb{R}) \text{ and vanishing for } x \text{ large enough.} \tag{8}$$

Remark 2.1 We consider an environment with unlimited resources. This means that we assume that the death rate and the birth rate do not depend on the population itself (only on time for death rate : season and more precisely for Aphids : temperature and only on age for birth rates (see [19] p17)). Therefore, we expect that the population has an exponential growth or decay [8,9].

We are expecting that the best way (to give an optimal growth rate) is to switch from sexual to asexual when it is profitable to do so (and so a Bang-Bang principle). In Section 3 we study the dynamics of (n_A, n_S) solution to (4)-(5). Then in Section 4 we prove that the optimal growth rate of (n_A, n_S) with respect to $(p_{S\to A}, p_{A\to A}) \in [0,1]^{\mathbb{R}_+}$ is reached for $p_{S\to A}, p_{A\to A} \in \{0,1\}^{\mathbb{R}_+}$. We give a theoretical result, in Section 5, showing that under some conditions on the death rate, the sexual subpopulation could disappear. We illustrate this work by a numerical example in Section 6 and we conclude in Section 7.

3 First Mathematical Results

We have the following results on the dynamic (and more precisely on the long time behavior) of this system of Partial Differential Equations. Proposition 3.1 cares about the long time behavior of the solution and we prove that it is characterized by a time exponential growth rate (positive : growth, negative : decay) which corresponds to the larger (in real part) eigenvalue. Whereas Proposition 3.2 deals with the variation of the eigenvalue with respect to the probability transition $t \mapsto (p_{A\to A}(t), p_{S\to S}(t))$.

Proposition 3.1 *Under assumptions (7)-(8) and for all initial data* $n_A(0,.)$, $n_S(0,.) \in L^1(\mathbb{R}_+, \mathbb{R}_+)$*, there exists an unique solution to (4)-(5) :*

$$(n_A, n_S) \in L^\infty([0,T], (L^1(\mathbb{R}_+, \mathbb{R}_+))^2).$$

Moreover, we have $(n_A(t,x), n_S(t,x))$ *behaves as*
$Cst\ e^{\lambda t}(N_A(t,x), N_S(t,x))$*, (as* $\sim_{t\to\infty}$*) where* $Cst \geq 0$*,* $\lambda \in \mathbb{R}$ *and*

$(N_A(t,x), N_S(t,x))$ are $T-$ periodic $L^\infty([0,T],(L^1(\mathbb{R}_+,\mathbb{R}_+))^2)$ solutions to the following eigenproblem

$$\begin{cases} (\frac{\partial}{\partial t}+\frac{\partial}{\partial x}+\begin{pmatrix} d(t) & 0 \\ 0 & d(t)\chi_{x>x_0}\end{pmatrix})\begin{pmatrix} N_A(t,x) \\ N_S(t,x)\end{pmatrix}+\lambda\begin{pmatrix} N_A(t,x) \\ N_S(t,x)\end{pmatrix}=0, \\ \\ \begin{pmatrix} N_A(t,0) \\ N_S(t,0)\end{pmatrix}=\int_{x'\geq 0}\begin{pmatrix} p_{A\to A}(t)B_A(x') & p_{S\to A}(t)B_S(x') \\ p_{A\to S}(t)B_A(x') & p_{S\to S}(t)B_S(x')\end{pmatrix} \\ \qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad \begin{pmatrix} N_A(t,x') \\ N_S(t,x')\end{pmatrix}\,dx'. \end{cases} \tag{9}$$

Proof The proof of existence and uniqueness of (n_A, n_S) solution to (4)-(5) (transport equation with a nonlocal boundary condition) is similar to the proves given in [20] (chapter IV, using Semigroup theory), [21] and [9] (chapter III, using Banach Picard fixed point theorem and bound given by an energy methods : the General Relative Entropy [8] and [9] chapter III.3 and III.9.5 for the periodic case). The existence of the eigenelements $\lambda, (N_A(t,x), N_S(t,x))$ is also a generalization of the Floquet result [22], and the proof is similar to [8] p1256-1259. The asymptotic behavior is a direct application of the General Relative Entropy ([8] p1256-1259 and [9,12,13]) which gives a general form of energy : let H any positive regular convex function, and define the entropy by

$$\mathcal{H}_t := \Big[\int_{[0,\infty[} H(\frac{n_A(t,a)e^{-\lambda t}}{N_A(t,a)})N_A(t,a)\Phi_A(t,a)da + \int_{[0,\infty[} H(\frac{n_S(t,a)e^{-\lambda t}}{N_S(t,a)})N_S(t,a)\Phi_S(t,a)da\Big],$$

where (Φ_A, Φ_S) is solution to a dual eigenproblem (10) then we have

$$\begin{aligned}\frac{d}{dt}\mathcal{H}_t &= \Phi_A(t,0)N_A(t,0)\Big[H(\int\frac{n_A(t,a)e^{-\lambda t}}{N_A(t,a)}d\nu_1(a)+\int\frac{n_S(t,a)e^{-\lambda t}}{N_S(t,a)}d\nu_2(a)) \\ &\quad -\int H(\frac{n_A(t,a)e^{-\lambda t}}{N_A(t,a)})d\nu_1(a)-\int H(\frac{n_S(t,a)e^{-\lambda t}}{N_S(t,a)})d\nu_2(a)\Big] \\ &\quad +\Phi_S(t,0)N_S(t,0)\Big[H(\int\frac{n_A(t,a)e^{-\lambda t}}{N_A(t,a)}d\mu_1(a)+\int\frac{n_S(t,a)e^{-\lambda t}}{N_S(t,a)}d\mu_2(a)) \\ &\quad -\int H(\frac{n_A(t,a)e^{-\lambda t}}{N_A(t,a)})d\mu_1(a)-\int H(\frac{n_S(t,a)e^{-\lambda t}}{N_S(t,a)})d\mu_2(a)\Big],\end{aligned}$$

with $d\nu_1$, $d\nu_2$, $d\mu_1$ and $d\mu_2$ positive measures satisfying $d\nu_1+d\nu_2$ and $d\mu_1+d\mu_2$, are probability measures. Therefore using Jensen inequality, we find that $\frac{d}{dt}\mathcal{H}_t \leq 0$ (decay of Entropy). This decay result implies uniform bound of $\frac{n_A(t,a)e^{-\lambda t}}{N_A(t,a)}$ (resp. $\frac{n_S(t,a)e^{-\lambda t}}{N_S(t,a)}$) and convergence (in L^p norm, for $H: z\mapsto |z|^p$) to a constant (due to the equality case in the Jensen inequality) [8]. □

The next result allows us to differentiate the eigenvalue λ (of Proposition 3.1) with respect to parameters of the model.

Proposition 3.2 *There exists a positive and $T-$ periodic solution $\Phi := (\Phi_A\ \Phi_S) \in L^\infty([0,T],(L^\infty(\mathbb{R}_+,\mathbb{R}_+))^2)$ to the dual eigenproblem (of (9))*

$$\mathcal{L}^*\Phi = \lambda\Phi, \tag{10}$$

which satisfies for all $t>0$

$$\int \Phi(t,x)N(t,x)dx = 1, \tag{11}$$

where $N(t,x) = \begin{pmatrix} N_A(t,x) \\ N_S(t,x)\end{pmatrix}$, *and*

$$(\mathcal{L}^*\Phi)(t,x) := \frac{\partial}{\partial t}\Phi(t,x) + \frac{\partial}{\partial x}\Phi(t,x) - \Phi(t,x)\begin{pmatrix} d(t) & 0 \\ 0 & d(t)\chi_{x>x_0}\end{pmatrix} + \Phi(t,0)\begin{pmatrix} p_{A\to A}(t)B_A(x) & p_{S\to A}(t)B_S(x) \\ p_{A\to S}(t)B_A(x) & p_{S\to S}(t)B_S(x)\end{pmatrix}.$$

Moreover, if we assume that $p_{A\to A}(t) = \sum_j p_j^A\chi_{I_j}(t)$, $p_{S\to S}(t) = \sum_j p_j^S\chi_{I_j}(t)$, where $(I_J)_j$ is a partition of $[0,T]$ and $(p_j)_j$ is a sequence of real numbers (in $[0,1]$)

$$\begin{cases} \frac{\partial}{\partial p_j^A}\lambda = \iint_{\mathbb{R}_+\times[0,T]}(\Phi_A(t,0)-\Phi_S(t,0))B_A(x)N_A(t,x)\chi_{I_j}(t)\frac{dxdt}{T}, \\ \frac{\partial}{\partial p_j^S}\lambda = -\iint_{\mathbb{R}_+\times[0,T]}(\Phi_A(t,0)-\Phi_S(t,0))B_S(x)N_S(t,x)\chi_{I_j}(t)\frac{dxdt}{T}. \end{cases}$$

Proof The existence of the eigenelements $\lambda, (\Phi_A(t,x),\Phi_S(t,x))$ is similar to [8] p1256-1259 (see also [8,9]). Now, for the differentiation result, we follow the same proof as [10,11] : we have by integration of (10) and condition (11) $\int \mathcal{L}^*\Phi(t,x)N(t,x)dx = \lambda\int\Phi(t,x)N(t,x)dx = \lambda$, and so, by differentiating with respect to any parameter u we find that

$$\frac{\partial}{\partial u}\lambda = \int\frac{\partial}{\partial u}\Big[\mathcal{L}^*\Phi(t,x)N(t,x)\Big]dx = \int\Big[(\frac{\partial}{\partial u}\mathcal{L}^*)\Phi(t,x)N(t,x)\Big]dx + \int\Big[\mathcal{L}^*\frac{\partial}{\partial u}\Phi(t,x)N(t,x)\Big]dx + \int\Big[\mathcal{L}^*\Phi(t,x)\frac{\partial}{\partial u}N(t,x)\Big]dx.$$

Since we have $\int\Big[\mathcal{L}^*\Phi(t,x)\frac{\partial}{\partial u}N(t,x)\Big]dx = \lambda\int\Big[\Phi(t,x)\frac{\partial}{\partial u}N(t,x)\Big]dx$, and

$$\int\Big[\mathcal{L}^*\frac{\partial}{\partial u}\Phi(t,x)N(t,x)\Big]dx = \int\Big[\frac{\partial}{\partial u}\Phi(t,x)\mathcal{L}N(t,x)\Big]dx = \lambda\int\Big[\frac{\partial}{\partial u}\Phi(t,x)N(t,x)\Big]dx,$$

we obtain $\int \left[\mathcal{L}^* \frac{\partial}{\partial u}\Phi N\right]dx + \int \left[\mathcal{L}^*\Phi \frac{\partial}{\partial u}N\right]dx = \lambda \frac{\partial}{\partial u}\int \Phi N dx = 0$. Therefore, we have

$$\frac{\partial}{\partial p_j^A}\lambda = \iint \frac{\partial}{\partial p_j^A}\mathcal{L}^*\Phi(t,x)N(t,x)\frac{dxdt}{T} = \iint \Phi(t,0)B_A(x)$$
$$\begin{pmatrix} 1 & 0 \\ -1 & 0 \end{pmatrix} N(t,x)\chi_{I_j}\frac{dxdt}{T} = \iint (\Phi_A(t,0) - \Phi_S(t,0))B_A(x)N_A(t,x)\chi_{I_j}\frac{dxdt}{T},$$

and the same calculus holds for $\frac{\partial}{\partial p_j^S}\lambda$. □

Moreover the solution to the dual eigenproblem (10)-(11) is regular with respect to age and time.

Lemma 3.1 *Let* $\begin{pmatrix}\Phi_A & \Phi_S\end{pmatrix}$ *solution to the dual eigenproblem (10)-(11) then* $\Psi(t) := \Phi(t,0) = \begin{pmatrix}\Phi_A(t,0) & \Phi_S(t,0)\end{pmatrix}$*, satisfies* $\Psi(t) = \int_0^\infty \Psi(t+y)d\mu_\lambda^t(y)$*, with* $d\mu_\lambda^t(y) := B(t,y)e^{-\int_0^y D(t,z)dz}$ *where*

$$D(t,x) = \begin{pmatrix} d(t+x)+\lambda & 0 \\ 0 & d(t+x)\chi_{x>x_0}+\lambda \end{pmatrix},$$

$$B(t,x) = \begin{pmatrix} p_{A\to A}(t+x)B_A(x) & p_{S\to A}(t+x)B_S(x) \\ p_{A\to S}(t+x)B_A(x) & p_{S\to S}(t+x)B_S(x) \end{pmatrix}.$$

Finally, we have $\Psi \in C^0(\mathbb{R}_+)$ *and* $\Psi(t) = \lim_{n\to\infty} \iiint_{\mathbb{R}_+^n} \prod_{i=1}^n d\mu_\lambda^{t+\sum_{j=1}^{i-1}x_j}(x_i)$.

Proof We have, for all t,

$$-\frac{d}{dx}\Phi(t+x,x) + \Phi(t+x,x)D(t,x) - \Phi(t+x,0)B(t,x) = 0.$$

Therefore, we find

$$-\frac{d}{dx}(\Phi(t+x,x)e^{-\int_0^x D(t,y)dy}) - \left[\Phi(t+x,0)B(t,x)e^{-\int_0^x D(t,y)dy}\right] = 0.$$

Thus, integrating with respect to x, we find

$$\Phi(t+x,x) = \int_x^\infty \Phi(t+y,0)B(t,y)e^{-\int_x^y B(t,z)dz}dy.$$

Applying in $x = 0$ we finally obtain $\Psi(t) = \int_0^\infty \Psi(t+y)d\mu_\lambda^t(y)$, and regularity comes directly from this integral equation (convolution form). □

4 Optimization and Survival Analysis

In this part we focus on the optimization of the eigenvalue with respect to the probability transitions $t \mapsto (p_{A\to A}(t), p_{S\to S}(t))$, i.e. to find

$$\lambda_{max} := \sup_{(p_{A\to A}, p_{S\to S})\in[0,1]^{\mathbb{R}+}} \lambda(p_{A\to A}, p_{S\to S}),$$

and more generally to evaluate $(p_{A\to A}, p_{S\to S}) \mapsto \lambda(p_{A\to A}, p_{S\to S})$. Indeed, the eigenvalue λ gives the growth rate of the population, and so, that can be used as a fitness characterization of the population [10–15], the larger is λ the more invasive is a population and a negative λ implies the extinction of the population. Therefore, questions are :

1. Do switching, i.e. bang-bang [23], form asexual to sexual gives the best exponential growth rate?

$$\lambda_{max} := \sup_{p_{A\to A}, p_{S\to S}} \lambda(p_{A\to A}, p_{S\to S}) = \lambda(p^{switch}_{A\to A}, p^{switch}_{S\to S})?$$

2. What happens to population if there is no more switch, i.e., when $p_{A\to A}$ and $p_{S\to S}$ are constant functions equal to zero or one?
   (a) $\lambda_{max} := \lambda(0,1)$, which means that the parthenogenetic subpopulation disappears,
   (b) $\lambda_{max} := \lambda(1,0)$ which means that the sexual subpopulation disappears, or
   (c) $\lambda_{max} := \lambda(1,1)$ which means that subpopulations are no more mixed and so there are two separated populations.

Theorem 4.1 *[Sex Bang-Bang Optimization] The maximum of the eigenvalue is reached for (almost) a couple of probabilities satisfying*

$$(p_{A\to A}(t), p_{S\to S})(t) \in \{0,1\}, \quad \forall t \in [0,T].$$

More precisely, there exists $(a_j)_j$ *and* $(b_j)_j$ *in* $[0,T]$ *s.t.*

$$p_{A\to A}(t) = \sum_j \chi_{[a_j,b_j]}(t), \quad p_{S\to S}(t) = 1 - \sum_j \chi_{[a_j,b_j]}(t),$$

with $\Phi^A(a_j,0) = \Phi^S(a_j,0), \quad \Phi^A(b_j,0) = \Phi^S(b_j,0)$, *where* (Φ^A, Φ^S) *is solution to the dual eigenproblem (10)-(11).*

The proof is subdivided in two parts. Using the same argument as in proposition 3.2 (more general [10,11]), we prove that we can construct a sequence that increases the eigenvalue. Then, we prove that its limit is the "best one".

Increasing sequence Let, for all $\tau \geq 0$,

$$p^\tau_{A\to A}(t) := \frac{e^{\int_0^\tau [(\Phi^\tau_A{}'(t,0) - \Phi^\tau_S{}'(t,0))]d\tau'}}{1 + e^{\int_0^\tau [(\Phi^\tau_A{}'(t,0) - \Phi^\tau_S{}'(t,0))]d\tau'}},$$

$$p^\tau_{S\to S}(t) := \frac{e^{-\int_0^\tau [(\Phi^\tau_A{}'(t,0) - \Phi^\tau_S{}'(t,0))]d\tau'}}{1 + e^{-\int_0^\tau [(\Phi^\tau_A{}'(t,0) - \Phi^\tau_S{}'(t,0))]d\tau'}},$$

with $\Phi^\tau(t,x) = \left(\Phi^\tau_A(t,x)\ \Phi^\tau_S(t,x)\right)$ solution to the dual eigenproblem $\mathcal{L}^*\Phi^\tau = \lambda^\tau \Phi^\tau$ where

$$\begin{aligned}\mathcal{L}^*\left(\Phi^\tau_A\ \Phi^\tau_S\right)(t,x) = &\frac{\partial}{\partial t}\left(\Phi^\tau_A(t,x)\ \Phi^\tau_S(t,x)\right) + \frac{\partial}{\partial x}\left(\Phi^\tau_A(t,x)\ \Phi^\tau_S(t,x)\right)\\ &- \left(\Phi^\tau_A(t,x)\ \Phi^\tau_S(t,x)\right)\begin{pmatrix} d(t) & 0\\ 0 & d(t)\chi_{x>x_0}\end{pmatrix}\\ &+ \left(\Phi^\tau_A(t,0)\ \Phi^\tau_S(t,0)\right)\begin{pmatrix} p^\tau_{A\to A}(t)B_A(x) & p^\tau_{S\to A}(t)B_S(x)\\ p^\tau_{A\to S}(t)B_A(x) & p^\tau_{S\to S}(t)B_S(x)\end{pmatrix}.\end{aligned}$$

Using the same argument as in proposition 3.2, we have

$$\begin{aligned}\frac{d}{d\tau}\lambda^\tau = &\iint p^\tau_{A\to A}(t)(1 - p^\tau_{A\to A}(t))(\Phi^\tau_A(t,0) - \Phi^\tau_S(t,0))^2 B_A(x)N_A(t,x)dxdt\\ + &\iint p^\tau_{S\to S}(t)(1 - p^\tau_{S\to S}(t))(\Phi^\tau_A(t,0) - \Phi^\tau_S(t,0))^2 B_S(x)N_S(t,x)dxdt \geq 0.\end{aligned}$$

Since $(p^\tau_{A\to A}, p^\tau_{S\to S}, \Phi^\tau_A, \Phi^\tau_S)$ are uniformly bounded, using Banach Aologlu theorem, we can extract a weak* convergent subsequence as $\tau \to \infty$. Therefore, at the limit, we have

$$\begin{aligned}0 = &\iint p^\infty_{A\to A}(t)(1 - p^\infty_{A\to A}(t))(\Phi^\infty_A(t,0) - \Phi^\infty_S(t,0))^2 B_A(x)N_A(t,x)dxdt\\ &+ \iint p^\infty_{S\to S}(t)(1 - p^\infty_{S\to S}(t))(\Phi^\infty_A(t,0) - \Phi^\infty_S(t,0))^2 B_S(x)N_S(t,x)dxdt.\end{aligned}$$

Finally, we have

- $p^\infty_{A\to A}$,(resp. $p^\infty_{S\to S}$) belongs $\{0,1\}$,
  or
- $\int B_A(x)N_A(t,x) = 0$, (resp. $\int B_S(x)N_S(t,x) = 0$),
  or
- $\Phi^\infty_A(t,0) = \Phi^\infty_S(t,0)$.

The best. Now, using lemma 3.1, we have $(\Phi_A^\infty(t,0),\Phi_S^\infty(t,0))$ is continuous and T- periodic, therefore, the set $\{t\ :\ \Phi_A^\infty(t,0)=\Phi_S^\infty(t,0)\}=\cup_j I_j^0$ is a countable union of intervals (the same holds for $\{t\ :\ \Phi_A^\infty(t,0)>\Phi_S^\infty(t,0)\}=\cup_j I_j^+$ and $\{t\ :\ \Phi_A^\infty(t,0)<\Phi_S^\infty(t,0)\}=\cup_j I_j^-$). We have

$$p_{A\to A}^\infty(t)=\sum_j \chi_{I_j^0}(t)p_{A\to A}^\infty(t)+\sum_j \chi_{I_j^+}(t)p_{A\to A}^\infty(t)+\sum_j \chi_{I_j^-}(t)p_{A\to A}^\infty(t),$$

and the same for $p_{S\to S}^\infty(t)$. We notice that, for all piecewise constant functions $p_{A\to A}^{\infty,J}$ and $p_{A\to A}^{\infty,J}$, defined as follows

$$p_{A\to A}^{\infty,J}(t)=\sum_j \chi_{I_j^0}(t)p_j^0+\sum_j \chi_{I_j^+}(t)p_j^+ +\sum_j \chi_{I_j^-}(t)p_j^-,$$

$$p_{A\to A}^{\infty,J}(t)=\sum_j \chi_{I_j^0}(t)q_j^0+\sum_j \chi_{I_j^+}(t)q_j^+ +\sum_j \chi_{I_j^-}(t)q_j^-.$$

We have directly that $\frac{\partial}{\partial p_j^0}[\mathcal{L}^*(\Phi)]=\frac{\partial}{\partial p_j^0}[\lambda\Phi]$, and so, we obtain that

$$(\frac{\partial}{\partial p_j^0}\mathcal{L}^*)(\Phi)+\mathcal{L}^*(\frac{\partial}{\partial p_j^0}\Phi)=(\frac{\partial}{\partial p_j^0}\lambda)\Phi+(\frac{\partial}{\partial p_j^0}\Phi)\lambda.$$

Since we have $(\frac{\partial}{\partial p_j^0}\mathcal{L}^*)(\Phi)=0$ and $(\frac{\partial}{\partial p_j^0}\lambda)=0$, we find $\mathcal{L}^*(\frac{\partial}{\partial p_j^0}\Phi)=(\frac{\partial}{\partial p_j^0}\lambda)\Phi$. Noticing that the first eigenvalue of $\mathcal{L}^*$ has its eigenspace of dimension 1 (Perron Frobenius extension [9]), there exists a constant C so that $\frac{\partial}{\partial p_j^0}\Phi=C\Phi$. This implies that $(\Phi^A(t,0)-\Phi^S(t,0))=0$ for all $p_j^0\in[0,1]$. We, thus, can choose $p_j^0\in\{0,1\}$. Since, this result holds for all $p_{A\to A}^{\infty,J}$, we can approximate $p_{A\to A}^\infty$ by a sequence of $(p_{A\to A}^{\infty,J})_J$ and $p_{A\to A}^\infty(t)$ can be chosen in $\{0,1\}$ for all t.

End of proof. To prove that $\Phi^A(a_j,0)=\Phi^S(a_j,0),\quad \Phi^A(b_j,0)=\Phi^S(b_j,0)$, when $p_{A\to A}(t)=\sum_j\chi_{[a_j,b_j]}(t),\quad p_{S\to S}(t)=1-\sum_j\chi_{[a_j,b_j]}(t)$, it is sufficient to derivate λ with respect to a_i (resp. b_i). We find that

$$\frac{d}{da_i}\lambda=(\Phi_A(a_i,0)-\Phi_S(a_i,0))\int B_A(x)N_A(a_i,x)dx.$$

Therefore, to be optimal, it needs to have $(\Phi_A(a_i,0)-\Phi_S(a_i,0))=0$ or no newborn at time a_i. The same holds for b_i. When there is no newborn for asexual population, we can choose $p_{A\to A}=1$ without changing anything (and the same for $p_{S\to S}$ when there is no newborn for sexual population). Therefore, the only case where switches appear are given by $(\Phi_A(a_i,0)-\Phi_S(a_i,0))=0$. □

We show in Sections 4.1 and 4.2 that assumption

$$\int_{x\geq 0} B_A(x)e^{-x\int_0^T d(s)/Tds}<1, \tag{12}$$

implies that a only parthenogenetic female population has a negative Malthusian growth rate, i.e., extinguishes and assumption

$$\int_{x'>x_0} B_S(x')e^{-\int_0^T d(s)ds/Tx'}\,dx' \max_t e^{\int_t^{t+x_0} d(w)dw} < 1, \tag{13}$$

implies the extinction of the only sexual female population. Therefore, under assumptions (12)-(13) we have $\lambda(1,1) = \max(\lambda(0,1), \lambda(1,0)) < 0$. Nevertheless, it suffices that the condition[2]

$$\int_{x'>x_0} B_S(x')e^{-\int_{T-x_0'}^T d|s>x_0 ds/Tx'}\,dx' \max_t e^{\int_t^{t+x_0} d|w>x_0 dw} \int_{x\geq 0} B_A(x)e^{-x\int_0^{T-x_0'} d|s>x_0/T ds}dx > 1,$$

is satisfied, for almost a $x_0' > x_0$, to find a, mixing way of reproducing, survival strategy, i.e., we have $\lambda_{max} > 0$. Therefore, we have the following inequality $\lambda_{max} \geq \lambda(p_{A\to A}^{winter\ switch}, p_{S\to S}^{winter\ switch}) \geq 0$.

4.1 Only Parthenogenetic Female. No Sex

Assuming that

$$p_{A\to A}^{\infty} = 1, \quad p_{S\to S}^{\infty} = 0, \tag{14}$$

is satisfied. Then, after a living time of the individuals of the sexual population (since there is no newborn), the sexual population (able to reproduce) vanishes. Therefore, we only have to look for n_A solution to the McKendrick Von-Foerster equation

$$\begin{cases} \frac{\partial}{\partial t}n_A(t,x) + \frac{\partial}{\partial x}n_A(t,x) + d(t)n_A(t,x) = 0, \\ n_A(t,x=0) = \int_{x'\geq 0} B_A(x')n_A(t,x')\,dx'. \end{cases} \tag{15}$$

Using Proposition 3.2, to study the dynamics of n_A solution to (15), it is sufficient (see lemma 4.1) to study the eigenproblem (9), which becomes under the assumption (14)

$$\begin{cases} \frac{\partial}{\partial t}N_A(t,x) + \frac{\partial}{\partial x}N_A(t,x) + d(t)n_A(t,x) = -\lambda_A N_A(t,x), \\ N_A(t,x=0) = \int_{x'\geq 0} B_A(x')N_A(t,x')\,dx'. \end{cases} \tag{16}$$

and leads to a condition on λ_A :

$$1 = \int_{x\geq 0} B_A(x)e^{\int_0^x(-\lambda_A - \int_0^T d(s)ds/T)dx}. \tag{17}$$

We have then the following result on the survival of the parthenogenetic population :

[2] for the survival (and more precisely the growth) of the asexual population during Spring to Autumn

Proposition 4.1 *Assuming that*

$$\int_{x\geq 0} B_A(x)e^{-x\int_0^T d(s)/Tds} < 1 \quad (\geq 1). \tag{18}$$

then $\lambda_A < 0$ (resp. $\lambda_A \geq 0$), i.e., parthenogenetic population disappears (resp. survives) in long time with a Malthusian exponential growth rate : λ_A.

Lemma 4.1 *Solution (λ_A, N_A) to the eigenproblem (16) is given by*

$$N_A(t,x) = e^{-\int_0^t (d(s)-\int_0^T d(w)dw/T)ds} e^{\int_0^x (-\lambda_A - \int_0^T d(s)ds/T)dx}$$

where λ_A satisfies (17).

Proof We search a solution of the form $N_A(t,x) = f(t)g(x)$. Therefore we have

$$\begin{cases} f'(t)/f(t) + g'(x)/g(x) + (d(t) - \int_0^T d(s)ds) = -\lambda_A - \int_0^T d(s)ds, \\ g(0) = \int_{x'\geq 0} B_A(x')g(x')\,dx'. \end{cases}$$

and so, we have $f'(t) = -f(t)(d(t) - \int_0^T d(s)ds/T)$, $g'(x) = g(x)(-\lambda_A - \int_0^T d(s)ds/T)$. Finally, the boundary condition implies that (17) is satisfied. □

4.2 Only Sex. No Parthenogenesis

Assuming that

$$p^{\infty}_{A\to A} = 0, \quad p^{\infty}_{S\to S} = 1, \tag{19}$$

is satisfied. Then, after a living time of the individuals of the asexual population (since there is no newborn), the asexual population vanishes. Therefore, we only have to look for n_S solution to the McKendrick-Von Foerster equation

$$\begin{cases} \frac{\partial}{\partial t} n_S(t,x) + \frac{\partial}{\partial x} n_S(t,x) + d(t)\chi_{x>x_0} n_S(t,x) = 0, \\ n_S(t,x=0) = \int_{x'\geq 0} B_S(t,x')n_S(t,x')\,dx' \end{cases} \tag{20}$$

Using proposition 3.2, to study the dynamics of n_S solution to (20), it is sufficient (see lemma 4.1) to study the eigenproblem (9), which becomes under the assumption (19)

$$\begin{cases} \frac{\partial}{\partial t} N_S(t,x) + \frac{\partial}{\partial x} N_S(t,x) + d(t)\chi_{x>x_0} N_S(t,x) = -\lambda_S N_S(t,x), \\ N_S(t,x=0) = \int_{x'\geq x_0} B_S(t,x')N_S(t,x')\,dx' \end{cases} \tag{21}$$

where $N_S(T,.) = N_S(0,.)$.

Proposition 4.2 *Assuming that*

$$\int_{x'>x_0} B_S(x')e^{-\int_0^T d(s)ds/Tx'}\,dx' \max_t e^{\int_t^{t+x_0} d(w)dw} < 1,$$
$$(resp \quad \int_{x'>x_0} B_S(x')e^{-\int_0^T d(s)ds/Tx'}\,dx' \min_t e^{\int_t^{t+x_0} d(w)dw} > 1), \quad (22)$$

then $\lambda_S < 0$ (resp. $\lambda_S \geq 0$), i.e., sexual population disappears in long time (resp. survive) with a Malthusian growth rate : λ_S.

Proof Here, the term $d(t)\chi_{x>x_0}$ leads to some difficulties. We write the problem on $[0, x_0]$ and on $[x_0, \infty]$. We define

$$N_S(t,x) = \begin{cases} N_S^0(t,x), & x \in [0,x_0], \\ N_S^1(t,x), & x \in [x_0,\infty], \end{cases}$$

which satisfy

$$\begin{cases} \frac{\partial}{\partial t}N_S^0(t,x) + \frac{\partial}{\partial x}N_S^0(t,x) = -\lambda_S N_S^0(t,x), \quad x \leq x_0, \\ \frac{\partial}{\partial t}N_S^1(t,x) + \frac{\partial}{\partial x}N_S^1(t,x) + d(t)N_S^1(t,x) = -\lambda_S N_S^1(t,x), \quad x \geq x_0, \\ N_S^1(t,x_0) = N_S^0(t,x_0), \quad N_S^0(t,x=0) = \int_{x'\geq x_0} B_S(t,x')N_S^1(t,x')\,dx'. \end{cases}$$

We let

$$M_S^1(t,x) := N_S^1(t,x)e^{\int_0^t (d(w) - \int_0^T d(s)ds/T)dw}. \quad (23)$$

Then, we have

$$M_S^1(t,x) = \underbrace{\int_{x'\geq x_0} B_S(x')M_S^1(t-x,x')\,dx' e^{\int_{t-x}^{t+x_0-x}(d(w)-\int_0^T d(s)ds/T)dw}}_{:=J(t-x)} e^{\lambda_S x_0} e^{(-\lambda_S - \int_0^T d(s)ds/T)(x-x_0)}.$$

Now, using the boundary condition and equation (23) we find that J satisfies $J(t) = \int_{x'\geq x_0} J(t-x')d\mu_{\lambda_S}(x')U(t)$, where $U(t) = e^{\int_t^{t+x_0} d(w)dw}$ (independent of λ_S) and $d\mu_{\lambda_S}(x') = B_S(x')e^{(-\lambda_S - \int_0^T d(s)ds/T)x'}\,dx'$. Consequently, assuming that (22) is satisfied, $J \neq 0$ and $\lambda_S \geq 0$ (resp. $\lambda_S \leq 0$), we find that

$$\sup_t J(t) < \sup_t J(t), \quad (resp. \quad \inf_t J(t) > \inf_t J(t)),$$

which is absurd, therefore, $\lambda_S < 0$ (resp. $\lambda_S > 0$). □

5 Environment Change

Since parthenogenesis is much more prolific and cost free (no sexual disease, no time lost in partner selection) than sexual reproduction, when the death rate does not depend on time, we have a better Malthusian growth rate for the asexual population than for the sexual population. For Aphids, eggs produced (by sexual reproduction) have the ability to survive to winter [3–6]. When the death rate due to winter is large enough, it suffices to produce only parthenogenetic female between the end of winter and to change before the next winter to sexual female that produce eggs (which are not sensible to the death rate that eliminate the whole population) to survive and improve growth rate. However, in our model, the end of winter, i.e., the increase of temperature, means the end of sex as soon as a mutant, which reproduces exclusively by parthenogenesis, appears. We notice that, there exists a threshold death rate, under which the parthenogenetic strategy is better.

Proposition 5.1 *Assuming that*

$$\int_0^\infty B_S(y+x_0)e^{-d\,y}dy < \int_0^\infty B_A(y)e^{-d\,y}dy, \tag{24}$$

(verified as $B_S(.+x_0) < B_A(.)$) and $d(t) = d$, then $p_{A\to A} = 1$, $p_{S\to S} = 0$, is the best choice to have the best growth rate.

Proof We notice that solution to the dual eigenproblem (10)-(11), as we have $p_{A\to A} = 1$, $p_{S\to S} = 0$, is given by $\Phi_A(x) = \int_x^\infty B_A(y)e^{-(d+\lambda)(y-x)}dx$, and $(\Phi_S(x)e^{-d\int_0^x \chi_{y>x_0}dy-\lambda x}) = \int_x^\infty B_S(y)e^{-d\int_x^y \chi_{z>x_0}dz-\lambda(y-x)}dy$. Using (24) we have directly that $\int_0^\infty B_S(y+x_0)e^{-d\,y}dy < \int_0^\infty B_A(y)e^{-d\,y}dy$. Therefore, we have $\Phi_S(0) = \int_0^\infty B_S(y)e^{-d\int_0^y \chi_{z>x_0}dz-\lambda y}dy < \Phi_A(0)$, and so, using proposition 3.2, λ is increasing with respect to $p_{A\to A}$ and decreasing with respect to $p_{S\to S}$. □

6 Numerical Simulations

For numerical simulations, we consider that death rate depends on time (with annual, i.e., 365 days, periodicity) $t \mapsto d(t)$ and death rate is higher in winter : $d|_{Winter} \geq d|_{Summer,Spring,Autumn}$ [3–6]. We consider that death rate for eggs (sexual population of age $x \in [0, x_0]$ [3], for *U. cirsii* aphids) is null and we chose for birth and death rate as in Figure 2.

We can notice that asexual birth rate is higher (see [3], for pea aphids : in ten days a female can give birth to 80 clones) than for the sexual (for *E. betulae* aphids, see [6], in twenty days, population is multiplied by approximatively 1.5). Parameters are chosen to take in account the difference between asexual and sexual birth rates and the difference during winter and for other seasons for death rates, but are not fitted for a peculiar aphid specie (see table 1).

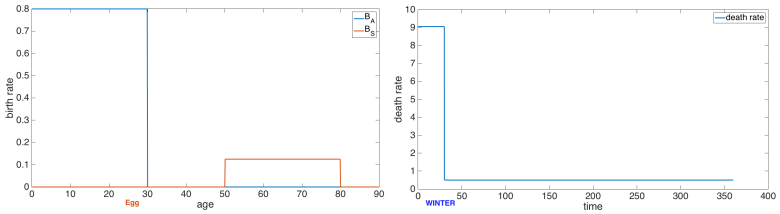

Fig. 2 Rates. Right : death rate on a time period. Left : birth rates (asexual in blue, sexual in red). From 0 to 50 days there is no birth (egg time) for sexual population. The birth rate for asexual population is higher than for the sexual population after egg time. During winter, the death rate is higher than the death rate during other seasons.

Table 1 Parameters and functions definition.

Definition	Variable	Value
Maximal age of an Aphid	Age_{max}	90 (days)
Maximal age to reproduce	Age_{rep}	30 (days)
Time in egg state	egg_{state}	50 (days)
Definition	Function	Value
Birth rate for asexual	B_A	$.8\chi_{a\in[0,Age_{ep}]}$
Birth rate for sexual	B_S	$.125\chi_{a\in[egg_{state},egg_{state}+Age_{rep}]}$
Death rate	d	$10\chi_{t<30} + .5\chi_{30\leq t<365}$

We search for the best bang-bang strategy, i.e.,

$$\max_{p_{A\to A}(t)=\chi_{[x_a,x_b]},\quad p_{S\to S}(t)=1-p_{A\to A}(t)} \lambda(p_{A\to A}, p_{S\to S}).$$

We observe in figure 3 that for x_b to large, i.e., when the sexual population appears to late before winter, the population disappears (zero multiplicative growth). The same happens if the asexual population arise too late (x_a too large). Maximum is reached for $x_a = 21$ and $x_b \in [5, 30]$ days. We see, on figure 4, that sexual population n_S vanishes except before winter and asexual population n_A increases exponentially between the end of winter to the end of autumn and then disappears just before winter.

7 Conclusions

In this work, we have proposed a Partial Differential Equations model to study the time evolution of a population that uses both sexual and asexual way of reproducing in an environment with unlimited resources. Then, we show that the bang-bang strategy (switch from parthenogenesis to sex and from sex to parthenogenesis) is the best in order to optimize the growth rate of the population. Moreover, even in the case of both type of subpopulation can extinguish (if they do not cooperate), a mixing strategy (a cooperation), i.e. sexual can produce asexual and asexual can produce sexual, may implies survival of the

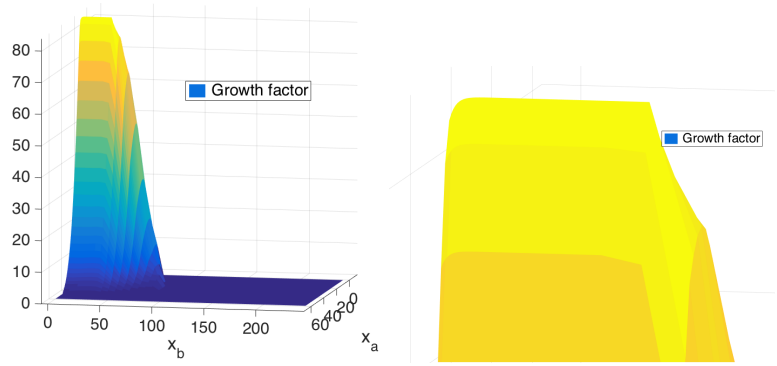

Fig. 3 Computation of $(x_a, x_b) \mapsto e^{T\lambda}$, as $p_{A\to A} = \chi_{[x_a,x_b]}$, $\quad p_{S\to S} = 1 - p_{A\to A}$. At the right, we show the decay as x_b is near 0 (zoom of the highest part of left figure).

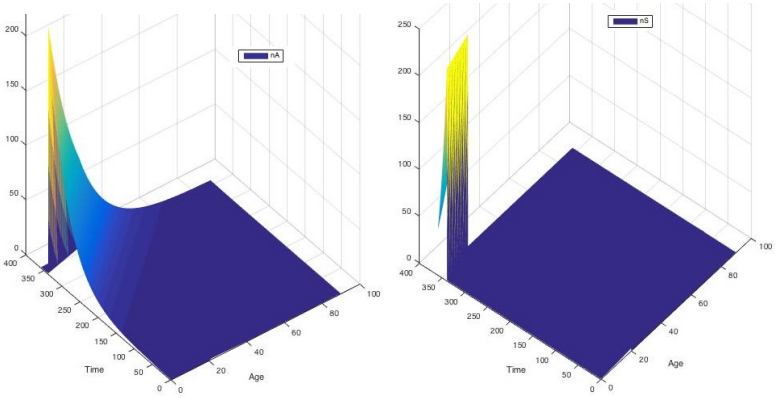

Fig. 4 Computation of n_A (left figure) and n_S (right figure) with respect to age and time. In particular, in dark blue, we have the extinction of the population.

population. Nevertheless, environment variations imply adaptation of species to these variations. Consequently, if the death rate that penalize the asexual population (which has a higher birth rate than the sexual one) decreases, at some point, the asexual population becomes the best (in a growth rate) way to reproduce. Thus, a mutant, that has lost sex, can invade the population. It could be interesting to develop the research of an optimal strategy by taking in account the growth rate and its variations due to random variations of the environment.

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