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Bang-Bang growth rate optimization in a coupled

McKendrick model

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Abstract We study the optimization of the growth rate (a maximal eigenvalue) of a partially clonal population, which density follows a coupled system of McKendrick-VonFoerster equations of evolution (extend of the model given in [1]), with respect to probabilities of switching from sexual (resp. asexual) to asexual (resp. sexual) way of reproducing at the boundary condition, i.e. the newborn condition. The idea is to apply the result of the variation of the first eigenvalue (Malthusian growth rate) [2,3] for this problem.

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

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

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Introduction

Species that reproduce asexually (such as bacteria) or by parthenogenesis (female able to produce child without male and fertilization) produce clones at 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. 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 [4].

Aphids are unusual organisms (partially clonal) which can both reproduce sexually and by parthenogenesis, which is determined by environmental conditions. In [1], authors consider a time evolution model (using ODE) of Aphids population. 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 $\psi := 2x/y$. Then they 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 is driven by the following

¹ for aphids around 7

system

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

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

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

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 resource, we have the birth rate α and the death rate β which does not depend on the size of the population and

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

with

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

Authors of [1], do not study the optimal growth rate and their optimisation with respect to the fecundation function.

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

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

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

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

$$\lambda_{max}(p, 0) = \max(1, p/2), \quad \max_p(\lambda_{max}(p, 0)) = \lambda_{max}(p', 0) = 1, \quad \forall p' \in [0, 1],$$

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

and $\lambda_{max}(0, q) = \lambda_{max}(0, 0) = 1$. Therefore, the maximum of the eigenvalue (growth rate) is reached as $q = 0$, i.e., parthenogenetic gives only parthenogenetic whatever do the sexual population. Then we have

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

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 larger eigenvalue is given when $p = 0$ and $q = 0$ and so $h = 0$ which means that there is no more sex.

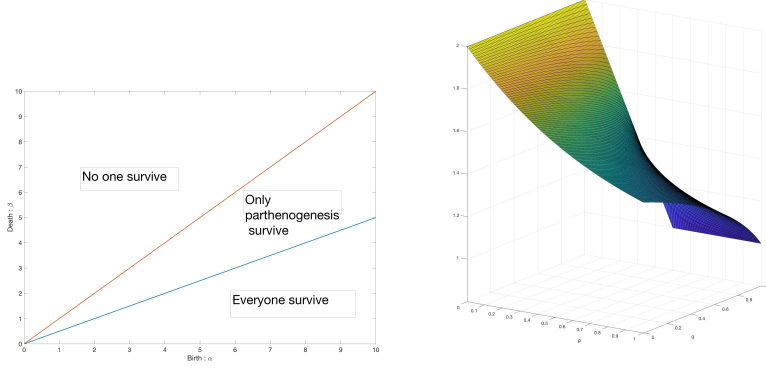


Fig. 1 Left : Survival of species depending on the birth rate α and the death rate β . Right : $(p, q) \mapsto \lambda_{max}(p, q)$.

The same question, in the case where α, β, p, q are T -periodic functions², since $\max Sp((-\beta(t)I + \alpha(t)M)) = -\beta(t) + \alpha(t)$ for all t , gives a same answer : the best way to reproduce is given by $q = 0$, i.e.,

$$y(t) = y(0)e^{\int_0^T (\alpha p/2 - \beta)(s)t/T}, \quad \text{and} \quad x(t) = (x(0) + o(1))e^{\int_0^T (\alpha - \beta)(s)t/T},$$

and so 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 both species in the model, we have to deal with the difference of birth and death rate of both sub-population. We add an age-structure in the model (McKendrick-VonFoerster model [5, 6, 2, 3, 7, 8]) for both population, at time t and age x , the density of asexual subpopulation $n_A(t, x)$ and the density of the sexual population $n_S(t, x)$ have their time

² seasonal variations

evolution driven by the systems of transport equation (with loss due to death term) :

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

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 and leads to the following boundary condition.

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

with

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

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 $p_{A \rightarrow A}(t)$ at time t , and to sexual female with probability $p_{A \rightarrow S}(t)$. 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 $p_{S \rightarrow A}(t)$ at time t to a parthenogenetic female and with probability $p_{S \rightarrow S}(t)$ to sexual female (5).

Since parthenogenesis is much more prolific and cost free than the sexual reproduction we assume that

$$B_A(x') > B_S(x'). \quad (6)$$

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

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

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

Remark 0.1 We consider an environment with unlimited resource. 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). Therefore, we expect that the population has an exponential growth or decay [9,6].

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). Proving that the optimal growth rate with respect to $p_{S \rightarrow A}, p_{A \rightarrow A} \in [0, 1]^{\mathbb{R}^+}$ is reached for $p_{S \rightarrow A}, p_{A \rightarrow A} \in \{0, 1\}^{\mathbb{R}^+}$ now much more complex than in the example above (2) where solutions are explicit and the eigenvalue is computable.

In section 1, we give first results on the dynamics of (n_A, n_S) solution to (4)-(5) and we show that the dynamic is time-exponential and is driven by an eigenvalue/eigenfunction. Then, in section 2, we study the optimization of this

eigenvalue (to improve the growth of population) with respect to the switching probabilities (which could be a measure the ability of a population to invade (or replace) a less fitted population, i.e., with a smaller Malthusian growth rate, see [10, 7, 8, 2, 3, 11–14]. Finally, in section 4, we discuss and conclude this work.

1 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 Equation. The proposition 1.1 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 the proposition 1.2 deals with the variation of the eigenvalue with respect to the probability transition $t \mapsto (p_{A \rightarrow A}(t), p_{S \rightarrow S}(t))$.

Proposition 1.1 *Under assumptions (7)-(8) and for all $n_A(0, \cdot), n_S(0, \cdot) \in L^1(\mathbb{R}_+, \mathbb{R}_+)$, there exists an unique $(n_A, n_S) \in L^\infty([0, T], (L^1(\mathbb{R}_+, \mathbb{R}_+))^2)$ solution to (4)-(5). 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 $\sim_{t \rightarrow \infty}$) 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

$$\left\{ \begin{array}{l} \left(\frac{\partial}{\partial t} + \frac{\partial}{\partial x} + \begin{pmatrix} d(t) & 0 \\ 0 & d(t)\chi_{x>x_0} \end{pmatrix} \right) \begin{pmatrix} N_A(t, x) \\ N_S(t, x) \end{pmatrix} + \lambda \begin{pmatrix} N_A(t, x) \\ N_S(t, x) \end{pmatrix} = 0, \\ \begin{pmatrix} N_A(t, 0) \\ N_S(t, 0) \end{pmatrix} = \int_{x' \geq 0} \begin{pmatrix} p_{A \rightarrow A}(t)B_A(x') & p_{S \rightarrow A}(t)B_S(x') \\ p_{A \rightarrow S}(t)B_A(x') & p_{S \rightarrow S}(t)B_S(x') \end{pmatrix} \begin{pmatrix} N_A(t, x') \\ N_S(t, x') \end{pmatrix} dx'. \end{array} \right. \quad (9)$$

Proof This is direct [6–8]. This a generalization of Floquet [15] results on linear periodic Ordinary Differential Equation, using the General relative Entropy.

□

The next result allow us to differentiate the eigenvalue λ (of the proposition 1.1) with respect to parameters of the model. We follow the same proof as in [2, 3].

Proposition 1.2 *There exists a positive solution $\left(\Phi_A(t, x) \Phi_S(t, x) \right) \in L^\infty([0, T], (L^\infty(\mathbb{R}_+, \mathbb{R}_+))^2)$ and T - periodic to the dual eigenproblem (of (9)) :*

$$\mathcal{L}^* \left(\Phi_A(t, x) \Phi_S(t, x) \right) = \lambda \left(\Phi_A(t, x) \Phi_S(t, x) \right), \quad (10)$$

which satisfies for all $t > 0$

$$\int \left(\Phi_A(t, x) \Phi_S(t, x) \right) \begin{pmatrix} N_A(t, x) \\ N_S(t, x) \end{pmatrix} dx = 1, \quad (11)$$

where

$$\begin{aligned} \mathcal{L}^* : \left(\Phi_A(t, x) \ \Phi_S(t, x) \right) &\mapsto \frac{\partial}{\partial t} \left(\Phi_A(t, x) \ \Phi_S(t, x) \right) \\ &+ \frac{\partial}{\partial x} \left(\Phi_A(t, x) \ \Phi_S(t, x) \right) - \left(\Phi_A(t, x) \ \Phi_S(t, x) \right) \begin{pmatrix} d(t) & 0 \\ 0 & d(t)\chi_{x>x_0} \end{pmatrix} \\ &+ \left(\Phi_A(t, 0) \ \Phi_S(t, 0) \right) \begin{pmatrix} p_{A \rightarrow A}(t)B_A(x) & p_{S \rightarrow A}(t)B_S(x) \\ p_{A \rightarrow S}(t)B_A(x) & p_{S \rightarrow S}(t)B_S(x) \end{pmatrix}. \end{aligned} \quad (12)$$

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

$$\frac{\partial}{\partial p_j^A} \lambda = \iint_{\mathbb{R}_+ \times [0, T]} (\Phi_A(t, 0) - \Phi_S(t, 0)) B_A(x) N_A(t, x) \chi_{I_j}(t) dx dt / T, \quad (13)$$

and

$$\frac{\partial}{\partial p_j^S} \lambda = - \iint_{\mathbb{R}_+ \times [0, T]} (\Phi_A(t, 0) - \Phi_S(t, 0)) B_S(x) N_S(t, x) \chi_{I_j}(t) dx dt / T. \quad (14)$$

Proof Existence of a solution is given in [6, 9]. Now, following the same proof as [2, 3], we have

$$\int \mathcal{L}^* \left(\Phi_A(t, x) \ \Phi_S(t, x) \right) = \lambda \int \left(\Phi_A(t, x) \ \Phi_S(t, x) \right) \begin{pmatrix} N_A(t, x) \\ N_S(t, x) \end{pmatrix} dx = \lambda,$$

and so, by differentiating with respect to any parameter u we find that

$$\begin{aligned}
\frac{\partial}{\partial u} \lambda &= \int \frac{\partial}{\partial u} \left[\mathcal{L}^* \left(\Phi_A(t, x) \Phi_S(t, x) \right) \begin{pmatrix} N_A(t, x) \\ N_S(t, x) \end{pmatrix} \right] dx \\
&= \int \left[\left(\frac{\partial}{\partial u} \mathcal{L}^* \right) \left(\Phi_A(t, x) \Phi_S(t, x) \right) \begin{pmatrix} N_A(t, x) \\ N_S(t, x) \end{pmatrix} \right] dx \\
&\quad + \int \left[\mathcal{L}^* \frac{\partial}{\partial u} \left(\Phi_A(t, x) \Phi_S(t, x) \right) \begin{pmatrix} N_A(t, x) \\ N_S(t, x) \end{pmatrix} \right] dx \\
&\quad + \int \left[\mathcal{L}^* \left(\Phi_A(t, x) \Phi_S(t, x) \right) \frac{\partial}{\partial u} \begin{pmatrix} N_A(t, x) \\ N_S(t, x) \end{pmatrix} \right] dx.
\end{aligned}$$

Since we have

$$\begin{aligned}
&\int \left[\mathcal{L}^* \frac{\partial}{\partial u} \left(\Phi_A(t, x) \Phi_S(t, x) \right) \begin{pmatrix} N_A(t, x) \\ N_S(t, x) \end{pmatrix} \right] dx \\
&= \int \left[\frac{\partial}{\partial u} \left(\Phi_A(t, x) \Phi_S(t, x) \right) \mathcal{L} \begin{pmatrix} N_A(t, x) \\ N_S(t, x) \end{pmatrix} \right] dx \\
&= \lambda \int \left[\frac{\partial}{\partial u} \left(\Phi_A(t, x) \Phi_S(t, x) \right) \begin{pmatrix} N_A(t, x) \\ N_S(t, x) \end{pmatrix} \right] dx,
\end{aligned}$$

and

$$\begin{aligned}
&\int \left[\mathcal{L}^* \left(\Phi_A(t, x) \Phi_S(t, x) \right) \frac{\partial}{\partial u} \begin{pmatrix} N_A(t, x) \\ N_S(t, x) \end{pmatrix} \right] dx \\
&= \lambda \int \left[\left(\Phi_A(t, x) \Phi_S(t, x) \right) \frac{\partial}{\partial u} \begin{pmatrix} N_A(t, x) \\ N_S(t, x) \end{pmatrix} \right] dx,
\end{aligned}$$

we obtain that

$$\begin{aligned}
& \int \left[\mathcal{L}^* \frac{\partial}{\partial u} \left(\Phi_A(t, x) \Phi_S(t, x) \right) \begin{pmatrix} N_A(t, x) \\ N_S(t, x) \end{pmatrix} \right] dx \\
& \quad + \int \left[\mathcal{L}^* \left(\Phi_A(t, x) \Phi_S(t, x) \right) \frac{\partial}{\partial u} \begin{pmatrix} N_A(t, x) \\ N_S(t, x) \end{pmatrix} \right] dx \\
& \quad = \lambda \frac{\partial}{\partial u} \int \left(\Phi_A(t, x) \Phi_S(t, x) \right) \begin{pmatrix} N_A(t, x) \\ N_S(t, x) \end{pmatrix} dx = 0.
\end{aligned}$$

Therefore, we have

$$\begin{aligned}
\frac{\partial}{\partial p_j^A} \lambda &= \iint \frac{\partial}{\partial p_j^A} \mathcal{L}^* \left(\Phi_A(t, x) \Phi_S(t, x) \right) \begin{pmatrix} N_A(t, x) \\ N_S(t, x) \end{pmatrix} dx dt / T \\
&= \iint \left(\Phi_A(t, 0) \Phi_S(t, 0) \right) B_A(x) \begin{pmatrix} 1 & 0 \\ -1 & 0 \end{pmatrix} \begin{pmatrix} N_A(t, x) \\ N_S(t, x) \end{pmatrix} \chi_{I_j} dx dt / T \\
&= \iint (\Phi_A(t, 0) - \Phi_S(t, 0)) B_A(x) N_A(t, x) \chi_{I_j}(t) dx dt / T, \quad (15)
\end{aligned}$$

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

2 Optimization and survival analysis

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

$$\lambda_{max} := \sup_{p_{A \rightarrow A}, p_{S \rightarrow S} \in [0, 1]^{\mathbb{R}_+}} \lambda(p_{A \rightarrow A}, p_{S \rightarrow S}), \quad (16)$$

and more generally to evaluate $(p_{A \rightarrow A}, p_{S \rightarrow S}) \mapsto \lambda(p_{A \rightarrow A}, p_{S \rightarrow S})$. Indeed, the eigenvalue gives the growth rate of the population, and so, that can be used

as a fitness characterization of the population [10,7,8,2,3,11], 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 [16], from asexual to sexual gives the best exponential growth rate?

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

2. What happens to population if there is no more switch?

$$\lambda(1, 1)? \quad \lambda(0, 1)? \quad \lambda(1, 0)?$$

Theorem 2.1 [*Sex Bang-Bang optimization*] *The maximum of the eigenvalue is reached for (almost) a couple of probabilities satisfying*

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

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

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

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 1.2 (more general [2,3]), 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 $\tau \geq 0$,

$$p_{A \rightarrow A}^\tau(t) := \frac{e^{\int_0^\tau [(\Phi_A^{\tau'}(t,0) - \Phi_S^{\tau'}(t,0))] d\tau'}}{1 + e^{\int_0^\tau [(\Phi_A^{\tau'}(t,0) - \Phi_S^{\tau'}(t,0))] d\tau'}},$$

$$p_{S \rightarrow S}^\tau(t) := \frac{e^{-\int_0^\tau [(\Phi_A^{\tau'}(t,0) - \Phi_S^{\tau'}(t,0))] d\tau'}}{1 + e^{-\int_0^\tau [(\Phi_A^{\tau'}(t,0) - \Phi_S^{\tau'}(t,0))] d\tau'}},$$

with $\begin{pmatrix} \Phi_A^\tau(t, x) & \Phi_S^\tau(t, x) \end{pmatrix}$ solution to the dual eigenproblem

$$\mathcal{L}^* \begin{pmatrix} \Phi_A^\tau(t, x) & \Phi_S^\tau(t, x) \end{pmatrix} = \lambda^\tau \begin{pmatrix} \Phi_A^\tau(t, x) & \Phi_S^\tau(t, x) \end{pmatrix},$$

where

$$\begin{aligned} \mathcal{L}^* : \begin{pmatrix} \Phi_A^\tau(t, x) & \Phi_S^\tau(t, x) \end{pmatrix} &\mapsto \frac{\partial}{\partial t} \begin{pmatrix} \Phi_A^\tau(t, x) & \Phi_S^\tau(t, x) \end{pmatrix} + \frac{\partial}{\partial x} \begin{pmatrix} \Phi_A^\tau(t, x) & \Phi_S^\tau(t, x) \end{pmatrix} \\ &- \begin{pmatrix} \Phi_A^\tau(t, x) & \Phi_S^\tau(t, x) \end{pmatrix} \begin{pmatrix} d(t) & 0 \\ 0 & d(t)\chi_{x>x_0} \end{pmatrix} \\ &+ \begin{pmatrix} \Phi_A^\tau(t, 0) & \Phi_S^\tau(t, 0) \end{pmatrix} \begin{pmatrix} p_{A \rightarrow A}^\tau(t) B_A(x) & p_{S \rightarrow A}^\tau(t) B_S(x) \\ p_{A \rightarrow S}^\tau(t) B_A(x) & p_{S \rightarrow S}^\tau(t) B_S(x) \end{pmatrix}. \end{aligned}$$

Using the same argument as in proposition 1.2, we have

$$\begin{aligned} \frac{d}{d\tau} \lambda^\tau &= \iint p_{A \rightarrow A}^\tau(t) (1 - p_{A \rightarrow A}^\tau(t)) (\Phi_A^\tau(t, 0) - \Phi_S^\tau(t, 0))^2 B_A(x) N_A(t, x) dx dt \\ &+ \iint p_{S \rightarrow S}^\tau(t) (1 - p_{S \rightarrow S}^\tau(t)) (\Phi_A^\tau(t, 0) - \Phi_S^\tau(t, 0))^2 B_S(x) N_S(t, x) dx dt \geq 0. \end{aligned}$$

Since $(p_{A \rightarrow A}^\tau, p_{S \rightarrow S}^\tau, \Phi_A^\tau, \Phi_S^\tau)$ are uniformly bounded, using Banach Aologlu theorem, we can extract a weak* convergent subsequence as $\tau \rightarrow \infty$. Therefore,

at the limit, we have

$$\begin{aligned} 0 &= \iint p_{A \rightarrow A}^\infty(t) (1 - p_{A \rightarrow A}^\infty(t)) (\Phi_A^\infty(t, 0) - \Phi_S^\infty(t, 0))^2 B_A(x) N_A(t, x) dx dt \\ &+ \iint p_{S \rightarrow S}^\infty(t) (1 - p_{S \rightarrow S}^\infty(t)) (\Phi_A^\infty(t, 0) - \Phi_S^\infty(t, 0))^2 B_S(x) N_S(t, x) dx dt. \end{aligned}$$

Finally, we have

- $p_{A \rightarrow A}^\infty$, (resp. $p_{S \rightarrow S}^\infty$) belongs $\{0, 1\}$,
- or
- $\int B_A(x)N_A(t, x) = 0$, (resp. $\int B_S(x)N_S(t, x) = 0$),
- or
- $\Phi_A^\infty(t, 0) = \Phi_S^\infty(t, 0)$.

The best. Now, using lemma 5.1, 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 an denumerable union of intervals (and 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

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

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

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

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

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

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

Since we have

$$\left(\frac{\partial}{\partial p_j^0} \mathcal{L}^*\right)(\Phi) = 0 \quad \text{and} \quad \left(\frac{\partial}{\partial p_j^0} \lambda\right) = 0,$$

we find that $\mathcal{L}^*\left(\frac{\partial}{\partial p_j^0} \Phi\right) = \left(\frac{\partial}{\partial p_j^0} \lambda\right) \Phi$. Noticing that the first eigenvalue of \mathcal{L}^* has its eigenspace of dimension 1 (Perron Frobenius extension [6]), 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 results holds for all $p_{A \rightarrow A}^{\infty, J}$, we can approximate $p_{A \rightarrow A}^{\infty}$ by a sequence of $(p_{A \rightarrow A}^{\infty, J})_J$ and $p_{A \rightarrow A}^{\infty}(t)$ 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

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

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 $p_{A \rightarrow A} = 1$ without changing anything (and the same for $p_{S \rightarrow S}$ 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 2.1 and 2.2 that assumption

$$\int_{x \geq 0} B_A(x) e^{-x \int_0^T d(s)/T ds} < 1, \quad (17)$$

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

$$\int_{x' > x_0} B_S(x') e^{-\int_0^T d(s) ds / T x'} dx' \max_t e^{\int_t^{t+x_0} d(w) dw} < 1, \quad (18)$$

implies the extinction of the only sexual female population. Therefore, under assumptions (17)-(18)

$$\lambda(1, 1) = \max(\lambda(0, 1), \lambda(1, 0)) < 0.$$

Nevertheless, it suffices that the condition³

$$\int_{x' > x_0} B_S(x') e^{-\int_{T-x'_0}^T d|s > x_0 ds / T x'} dx' \max_t e^{\int_t^{t+x_0} d|w > x_0 dw} \int_{x \geq 0} B_A(x) e^{-x \int_0^{T-x'_0} d|s > x_0 / T ds} dx > 1, \quad (19)$$

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 $\lambda_{max} \geq \lambda(p_{A \rightarrow A}^{winter\ switch}, p_{S \rightarrow S}^{winter\ switch}) \geq 0$.

2.1 Only parthenogenetic female. No sex

Assuming that

$$p_{A \rightarrow A}^\infty = 1, \quad p_{S \rightarrow S}^\infty = 0, \quad (20)$$

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

$$\begin{cases} \frac{\partial}{\partial t} n_A(t, x) + \frac{\partial}{\partial x} n_A(t, x) + d(t) n_A(t, x) = 0, \\ n_A(t, x = 0) = \int_{x' \geq 0} B_A(x') n_A(t, x') dx'. \end{cases} \quad (21)$$

³ for the survival (and more precisely the growth) of the asexual population during Spring to Autumn

Using proposition 1.2, to study the dynamics of n_A solution to (21), it is sufficient (see lemma 2.1) to study the eigenproblem (9), which becomes under the assumption (20)

$$\begin{cases} \frac{\partial}{\partial t} N_A(t, x) + \frac{\partial}{\partial x} N_A(t, x) + d(t)n_A(t, x) = -\lambda_A N_A(t, x), \\ N_A(t, x = 0) = \int_{x' \geq 0} B_A(x') N_A(t, x') dx'. \end{cases} \quad (22)$$

and leads to a condition on λ_A :

$$1 = \int_{x \geq 0} B_A(x) e^{\int_0^x (-\lambda_A - \int_0^T d(s) ds / T) dx}. \quad (23)$$

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

Proposition 2.1 *Assuming that*

$$\int_{x \geq 0} B_A(x) e^{-x \int_0^T d(s) / T ds} < 1 \quad (\geq 1). \quad (24)$$

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 2.1 *Solution (λ_A, N_A) to the eigenproblem (22) 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 (23).

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 (23) is satisfied. \square

2.2 Only sex. No parthenogenesis.

Assuming that

$$p_{A \rightarrow A}^\infty = 0, \quad p_{S \rightarrow S}^\infty = 1, \quad (25)$$

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

$$\begin{cases} \frac{\partial}{\partial t} n_S(t, x) + \frac{\partial}{\partial x} n_S(t, x) + d(t)\chi_{x > x_0} n_S(t, x) = 0, \\ n_S(t, x = 0) = \int_{x' \geq 0} B_S(t, x') n_S(t, x') dx' \end{cases} \quad (26)$$

Using proposition 1.2, to study the dynamics of n_S solution to (26), it is sufficient (see lemma 2.1) to study the eigenproblem (9), which becomes under the assumption (25)

$$\begin{cases} \frac{\partial}{\partial t} N_S(t, x) + \frac{\partial}{\partial x} N_S(t, x) + d(t)\chi_{x > x_0} N_S(t, x) = -\lambda_S N_S(t, x), \\ N_S(t, x = 0) = \int_{x' \geq x_0} B_S(t, x') N_S(t, x') dx' \end{cases} \quad (27)$$

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

Proposition 2.2 *Assuming that*

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

$$(resp \int_{x' > x_0} B_S(x') e^{-\int_0^T d(s) ds / T x'} dx' \min_t e^{\int_t^{t+x_0} d(w) dw} > 1), \quad (28)$$

then $\lambda_S < 0$ (resp. $\lambda_S \geq 0$), i.e., sexued 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

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

We let

$$M_S^1(t, x) := N_S^1(t, x) e^{\int_0^t (d(w) - \int_0^T d(s) ds / T) dw}. \quad (29)$$

Then, we have

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

Now, using the boundary condition and the equation (29) 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 (28) is satisfied, $J \neq 0$ and $\lambda_S \geq 0$ (resp. $\lambda_S \leq 0$), we find that

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

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

3 Environment change and numerical simulations

Since parthenogenesis is much more prolific and cost free (no sexual disease, no time lost in partner selection) than the 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 [17–20]. Therefore, for numerical simulations, we consider that the death rate depends on time $t \mapsto d(t)$ is time periodic (annual) and $d|_{\text{Winter}} \geq d|_{\text{Summer, Spring, Autumn}}$, moreover we consider that death rate for eggs (sexual population of age $x \in [0, x_0]$ [17]) is null and we chose for birth and death rate as in the figure 2.

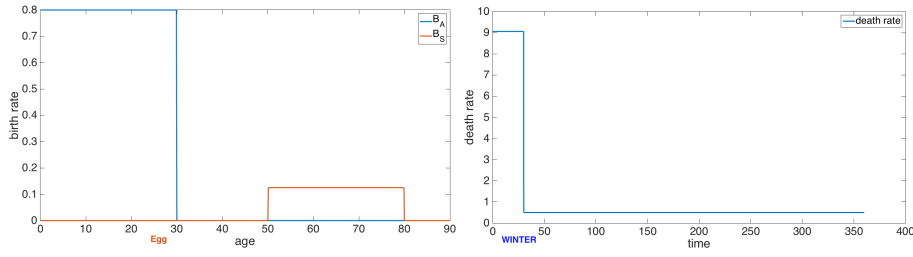


Fig. 2 Rates. Right : death rate on a time period. Left : birth rates (asexual in blue, sexual in red). From 0 to 50 days there is no birth (egg time) for sexual population. The birth rate for asexual population is higher than for the sexual population after egg time. During winter, the death rate is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

Consequently, the end of winter, i.e., the increase of temperature, means the end of sex as soon as a mutant that reproduce exclusively by parthenogenesis appears. 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). We observe, in figure 3, annual growth rates ($e^{\lambda T}$) of two populations : the first one obtained by the optimal mixing reproducing strategy finding in section 2 and the second only parthenogenetic, with respect to the death rate induced by winter. We notice that, there exists a threshold death rate, under which the parthenogenetic strategy is better.

Proposition 3.1 *Assuming that*⁴

$$\int_0^\infty B_S(y + x_0)e^{-d y} dy < \int_0^\infty B_A(y)e^{-d y} dy, \quad (30)$$

and

$$d(t) = d,$$

⁴ verified as $B_S(\cdot + x_0) < B_A(\cdot)$

then

$$p_{A \rightarrow A} = 1, \quad p_{S \rightarrow S} = 0,$$

is the best choice to have the best growth rate.

Proof We notice that solution to the dual eigenproblem (10)-(11) as $p_{A \rightarrow A} = 1$, $p_{S \rightarrow S} = 0$ are satisfied is given by

$$\begin{aligned} \Phi_A(x) &= \int_x^\infty B_A(y) e^{-(d+\lambda)(y-x)} dx, \\ (\Phi_S(x) e^{-d \int_0^x \chi_{y>x_0} dy - \lambda x}) &= \int_x^\infty B_S(y) e^{-d \int_x^y \chi_{z>x_0} dz - \lambda(y-x)} dy. \end{aligned}$$

Using (30) 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 1.2, λ is increasing with respect to $p_{A \rightarrow A}$ and decreasing with respect to $p_{S \rightarrow S}$. \square

Numerical simulations. For (in days) $T = 365$, we set

- $Age_{max} = 90$,
- $Age_{max \text{ reproduction}} = 30$,
- $egg_{state} = 50$,
- $B_A(x) = .8 \chi_{a \in [0, Age_{max \text{ reproduction}]}$,
- $B_S = .125 \chi_{a \in [egg_{state}, egg_{state} + Age_{max \text{ reproduction}]}$,
- $d(t) = 10 \chi_{t < 30} + .5 \chi_{30 \leq t < 365}$ and T periodic.

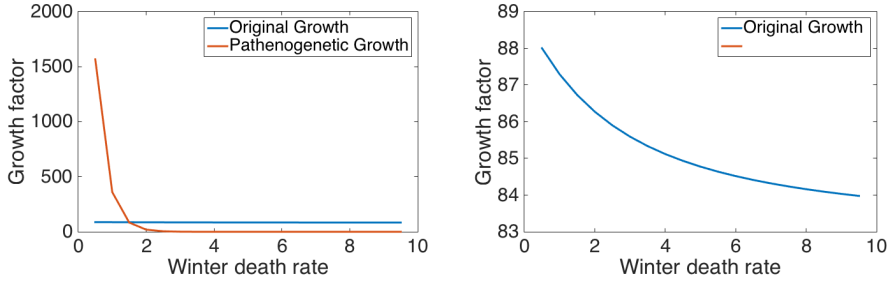


Fig. 3 Computation of $e^{T\lambda}$, i.e. the growth of a population after a year with respect to Winter death rate. We simulate (5) for (in days) $T = 365$, $Age_{max} = 90$, $Age_{max} reproduction = 30$, $eggstate = 50$, $B_A(x) = .8\chi_{a \in [0, Age_{max} reproduction]}$, $B_S = .125\chi_{a \in [eggstate, eggstate + Age_{max} reproduction]}$, $d(t) = Winter\ death\ rate\ \chi_{t < 30} + .5\chi_{30 \leq t < 365}$ and T periodic. Even if it seems to be constant (at the right), the growth rate of the mixed reproducing strategy (in blue) is slowly decreasing (at the left).

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

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

We observe in figure 4 that for x_b too large, i.e., when the sexual population appears too late before winter, the population disappears (zero multiplicative growth). The same happens if the asexual population arises too late (x_a too large). Maximum is reached for $x_a = 21$ and $x_b \in [5, 30]$ days. We see, on figure 5, that the 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.

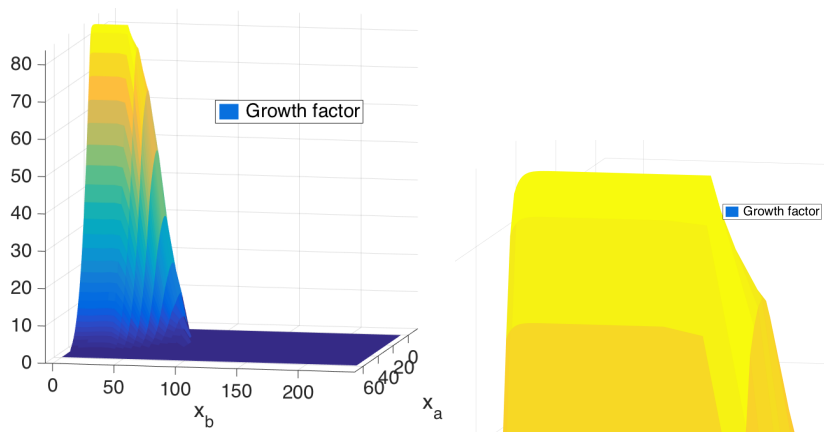


Fig. 4 Computation of $(x_a, x_b) \mapsto e^{T\lambda}$, as $p_{A \rightarrow A} = \chi_{[x_a, x_b]}$, $p_{S \rightarrow S} = 1 - p_{A \rightarrow A}$. At the right, we show the decay as x_b is near 0 (zoom of the highest part of left figure).

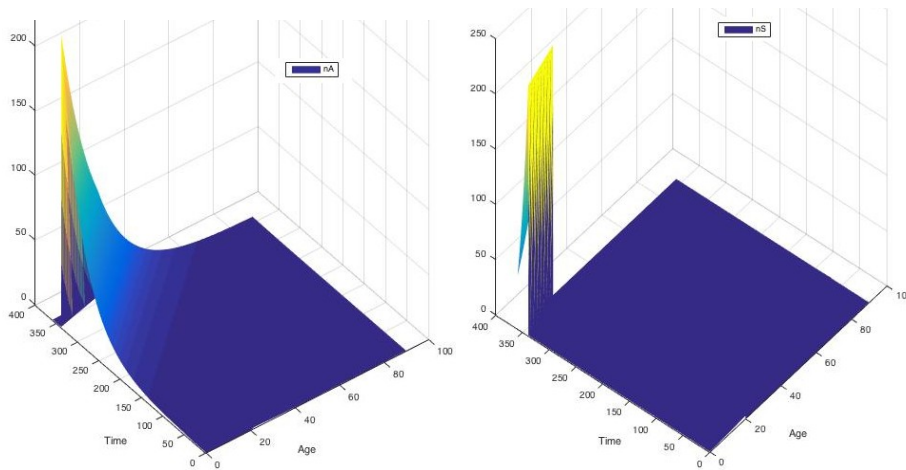


Fig. 5 Computation of n_A (left figure) and n_S (right figure) with respect to age and time. In particular, in dark blue, we have the extinction of the population.

4 Conclusion and perspectives

In this work, we have proposed a partial differential equation model to study the time evolution of a population that uses both sexual and asexual way of reproducing in an unlimited resource environment. 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 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.

5 Annex : Dual eigenproblem

In this part, we focus on the solution to the dual eigenproblem (10)-(11) and show that the solution is regular.

Lemma 5.1 *Let $\left(\Phi_A \ \Phi_S \right)$ solution to the dual eigenproblem (10)-(11) then*

$$\Phi(t) := \left(\Phi_A(t, 0) \ \Phi_S(t, 0) \right), \quad (31)$$

satisfies

$$\Phi(t) = \int_0^\infty \Phi(t+y) d\mu_\lambda^t(y), \quad (32)$$

with

$$d\mu_\lambda^t(y) := \left(\begin{array}{l} p_{A \rightarrow A}(t+y)B_A(y)e^{-\int_0^y d(t+z)-\lambda dz} p_{S \rightarrow A}(t+y)B_S(y)e^{-\int_0^y (d(t+z)\chi_{z>x_0}+\lambda)dz} \\ p_{A \rightarrow S}(t+y)B_A(y)e^{-\int_0^y d(t+z)-\lambda dz} p_{S \rightarrow S}(t+y)B_S(y)e^{-\int_0^y (d(t+z)\chi_{z>x_0}+\lambda)dz} \end{array} \right) dy. \quad (33)$$

And finally, we have $\Phi \in C^0(\mathbb{R}_+)$ and

$$\Phi(t) = \lim_{n \rightarrow \infty} \iiint_{\mathbb{R}_+^n} \prod_{i=1}^n d\mu_\lambda^{t+\sum_{j=1}^{i-1} x_j}(x_i).$$

Proof We have, for all t ,

$$\begin{aligned} & -\frac{d}{dx} \left(\Phi_A(t+x, x) \Phi_S(t+x, x) \right) \\ & + \left(\Phi_A(t+x, x) \Phi_S(t+x, x) \right) \begin{pmatrix} d(t+x) & 0 \\ 0 & d(t+x)\chi_{x>x_0} \end{pmatrix} \\ & - \left(\Phi_A(t+x, 0) \Phi_S(t+x, 0) \right) \begin{pmatrix} p_{A \rightarrow A}(t+x)B_A(x) & p_{S \rightarrow A}(t+x)B_S(x) \\ p_{A \rightarrow S}(t+x)B_A(x) & p_{S \rightarrow S}(t+x)B_S(x) \end{pmatrix} \\ & = -\lambda \left(\Phi_A(t+x, x) \Phi_S(t+x, x) \right). \end{aligned}$$

Therefore, we find that

$$\begin{aligned}
& -\frac{d}{dx} \left(\left(\Phi_A(t+x, x) \Phi_S(t+x, x) \right) e^{-\int_0^x \begin{pmatrix} d(t+y) - \lambda & 0 \\ 0 & d(t+y)\chi_{y>x_0} - \lambda \end{pmatrix} dy} \right) \\
& - \left[\left(\Phi_A(t+x, 0) \Phi_S(t+x, 0) \right) \begin{pmatrix} p_{A \rightarrow A}(t+x)B_A(x) & p_{S \rightarrow A}(t+x)B_S(x) \\ p_{A \rightarrow S}(t+x)B_A(x) & p_{S \rightarrow S}(t+x)B_S(x) \end{pmatrix} \right. \\
& \left. e^{-\int_0^x \begin{pmatrix} d(t+y) + \lambda & 0 \\ 0 & d(t+y)\chi_{y>x_0} + \lambda \end{pmatrix} dy} \right] = 0.
\end{aligned}$$

Thus, integrating with respect to x , we find that

$$\begin{aligned}
\left(\Phi_A(t+x, x) \Phi_S(t+x, x) \right) &= \int_x^\infty \left(\Phi_A(t+y, 0) \Phi_S(t+y, 0) \right) \\
& \begin{pmatrix} p_{A \rightarrow A}(t+y)B_A(y) & p_{S \rightarrow A}(t+y)B_S(y) \\ p_{A \rightarrow S}(t+y)B_A(y) & p_{S \rightarrow S}(t+y)B_S(y) \end{pmatrix} \\
& e^{-\int_x^y \begin{pmatrix} d(t+z) + \lambda & 0 \\ 0 & d(t+z)\chi_{z>x_0} + \lambda \end{pmatrix} dz} dy.
\end{aligned}$$

Applying in $x = 0$ we finally obtain that

$$\begin{aligned} \left(\begin{array}{c} \Phi_A(t, 0) \Phi_S(t, 0) \end{array} \right) &= \int_0^\infty \left(\begin{array}{c} \Phi_A(t + y, 0) \Phi_S(t + y, 0) \\ p_{A \rightarrow A}(t + y) B_A(y) \ p_{S \rightarrow A}(t + y) B_S(y) \\ p_{A \rightarrow S}(t + y) B_A(y) \ p_{S \rightarrow S}(t + y) B_S(y) \end{array} \right) \\ &\quad e^{-\int_0^y \left(\begin{array}{cc} d(t + z) + \lambda & 0 \\ 0 & d(t + z) \chi_{z > x_0} + \lambda \end{array} \right) dz} dy, \end{aligned}$$

and (32) holds for Φ defined by equation (31) and $d\mu_\lambda^t$ defined by (33). Regularity comes directly from the integral equation (convolution form) (32).

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