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Model of neo-Malthusian population anticipating future changes in resources

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ABSTRACT

In this paper we develop a class of models to study a population and resource dynamical system in which the decision to give birth is based on a rational far-sighted cost–benefit analysis on what the future of the resource level will be. This leads to consider a system in which a time forward population/resource dynamical system is coupled with a time backward Bellman's equation (which models the choice of having a child). We construct, from a population model with food consumption, an example, to study the change in time of the fertility rate when a catastrophic change in resource is announced at a given moment, when a birth control policy is announced and we compare these two announcements in case nothing happens. Moreover, we provide, mathematical tools to theoretically and numerically study this complex coupling of time forward and time backward equations.

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1. Introduction

Basically, living organisms are born, consume resources (organisms), give birth and finally become resources, in a competitive environment. Therefore, the survival of a species depends on the ability to produce well fitted newborns and, obviously, on the level of available resources. The relationship between consumers and their resources is a core study in ecology and in demography. There exist numerous theoretical models, which deal with different cases of relationship between consumers and their resources (Freedman, 1980; Getz and Owen-Smith, 2011; May, 1973; van Opheusden et al., 2015; Vance, 1990; Volterra, 1928; Terry, 2014), where consumer is a predator and resource is a prey. The foundation of the mathematical modeling approach is based on the Lotka–Volterra equations (Volterra, 1928) of coupled predator–prey (or consumer–resource) dynamics. Moreover, in some works (for instance Anon, 2007 p277, Stanková et al., 2013; Stukalin and Schmidt, 2011), the authors have introduced the optimization of a gain functional, to optimize the number of prey and predators at, or during, a given time. This approach leads to adding an adjoint equation to the Lotka–Volterra system of equations (Bellman's equation Bellman, 1957).

Since there is a close correlation between economic and human population growth (Nielsen, 2016), application to human populations arises in demography and economics. In this context, the Lotka–Volterra equations therefore describe the demography of human populations (Basener et al., 2008). The same type of equations is suggested to model a human population and a resource is given in Anderies (2000, 2003), Basener et al. (2008),

Nagase and Uehara (2011), Roman et al. (2018) and Uehara et al. (2016) (close to Lotka–Volterra model). There has been much recent activity in the modeling of human civilizations using this formalism. In Brander and Taylor (1998), Brander and Taylor study the collapse of Easter Island. Robert Axtel, in Axtell et al. (2002), uses these models to study the collapse of the Kayenta Anasazi civilization. In Roman et al. (2018), authors propose a model to study the dynamics of Human/Environment interactions in the collapse of classic Maya. All of these models consider that the population undergoes a lack of resources without birth control (or with a fixed birth control that does not anticipate the lack of resources). In Puleston and Tuljapurkar (2008), the resources used are modeled by the food ratio which is a function of the size of the population and could be considered as a steady state of the resource equation.

In these models, individuals adapt their fertility rate to the current level of resources which is implicitly modeled by the choice of the birth/fertility rate and its variations with respect to the level of resources. Nevertheless, they do not anticipate their behavior with future variations in the amount of resources. Along with the question of population growth and its impact on the environment, arise the question of birth control and the anticipation of the fertility rate in the ecological debate (Obaid, 2001). More precisely, population growth is seen as the main detriment to the environment: some two billion people already lack food security and water supplies, and agricultural land is under increasing pressure. These figures alarm many people, who take it for granted that population growth will imply famine, economic backwardness, more pollution and a faster depletion of natural resources in the world (Collins, 2002). Consequently,

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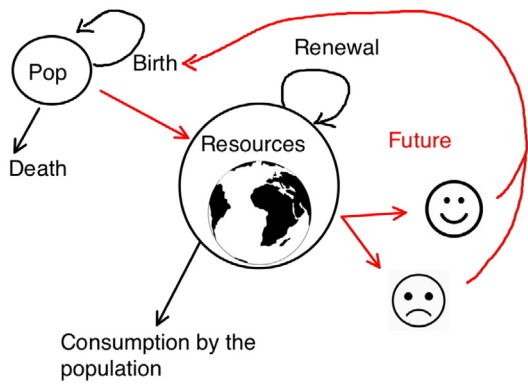


Fig. 1. Population/Resource coupling in an anticipation dynamics. The population changes due to death and birth. Resources change due to their own dynamics and their consumption by the population. If the population anticipates a problem of resource in the future, from a neo-Malthusian point of view, it does not give birth and vice versa, if the resources are sufficiently important, it gives birth.

the child can be considered as a cost for the environment (environmental cost¹) and the expected difficulties of life of the child in the future (due to the environmental problems) could be a reason for parents not to have children (personal cost). Both of these costs decrease with the level of resources and the value $V(t)$ of having a child depends on the predictions (see Fig. 1) on the future states of the resources which is given by the dynamic programming via Bellman equations (Bellman, 1957; Stukalin and Schmidt, 2011) (and, for instance, in Flaig et al., 2018, 2020 in epidemiological models).

In this paper, we develop a class of toy models to take into account the value of having a child due to resource level assessment, using backward/forward ordinary differential systems close to those developed in Flaig et al. (2018, 2020), Stanková et al. (2013) and Stukalin and Schmidt (2011). These models are developed in Section 2. In Section 3, we compare the behavior of a population which adapts its birth rate to the current level of resources and of the same population which anticipates the variation of resources (here food ratio). Finally, we conclude our work.²

2. Population change in time with anticipation and adaptive behavior

In the classical Lotka–Volterra equations (Volterra, 1928), the level of resources (represented by $Re(t)$ at time t) and the level of consumers (represented by $Pop(t)$ at time t) satisfy the following Ordinary Differential Equations, for $t \geq 0$,

$$\begin{cases} \frac{d}{dt} Pop(t) = G(Re(t), Pop(t))Pop(t) \\ \frac{d}{dt} Re(t) = \rho(Re(t)) - H(Re(t), Pop(t)) \\ Pop(0) = Pop_0 \geq 0, \quad Re(0) = R_0 \geq 0 \end{cases}, \quad (1)$$

where ρ is the functional gain in the absence of consumer, H the function governing the consumption of resources and G the growth function (birth minus death) in the population of consumers as a function of resources (Getz and Owen-Smith, 2011; Basener et al., 2008). The growth rate G could be decomposed into

¹ Environmental degradation, dwindling fisheries, shrinking forests, decreasing biodiversity.

² We give in Appendix A, mathematical proves of existence, uniqueness and numerical tools used to compute solutions.

a birth rate B and a death rate D (see Terry, 2014) and we focus on (1) of the form

$$\begin{cases} \frac{d}{dt} Pop(t) = (B(Re(t)) - D(Re(t)))Pop(t) \\ \frac{d}{dt} Re(t) = \rho(Re(t)) - H(Re(t), Pop(t)) \end{cases}, \quad (2)$$

with the initial data $Pop(0) = Pop_0 \geq 0$, $Re(0) = R_0 \geq 0$. In Puleston and Tuljapurkar (2008), the authors use a discrete time evolution equation for the population level equation and a resource level (food ratio) which is expressed directly as a function of the population level. This could be understood as if the resources in (1) are in a stable steady state, i.e.,

$$\frac{d}{dt} Re(t) = 0, \quad \rho(Re(t)) = H(Re(t), Pop(t)),$$

with ρ and H define, not only, as $\rho(Re) = Re(D - Re)$ and $H(Re, Pop) = D(1 - \frac{1-e^{-CPop}}{CPop})Re$ where C and D are two constants, i.e., $Re = D \frac{(1-e^{-CPop})}{CPop}$ (see Puleston and Tuljapurkar, 2008 for the equation of the food ratio). This behavior can be approximated in (1) by taking

$$\frac{d}{dt} Re(t) = \frac{1}{\epsilon} [\rho(Re(t)) - H(Re(t), Pop(t))],$$

with $\epsilon \ll 1$ (corresponding to a time scale difference: slow variation for population and rapid variation for resources (agriculture)) and corresponds to the following system of coupled population/resource time evolution equations

$$\begin{cases} \frac{d}{dt} Pop(t) = (B(Re(t)) - D(Re(t)))Pop(t) \\ 0 = \rho(Re(t)) - H(Re(t), Pop(t)) \end{cases}. \quad (3)$$

In Section 2.1, we complete the population and resources co-evolution model with equations describing decision-making process of individuals to have children.

2.1. Construction of anticipation models

At time t , the size of the population $Pop(t)$ and the level of resources $Re(t)$ are driven by a time evolution equation such as (2) (resp. (3)).

Now we consider that the decision to give birth is assumed to be based on a rational and far-sighted cost–benefit analysis on what the future will be. If the parents anticipate that, in the near future, there will be war or famine (due to overpopulation) they are not having children at present (for their own safety and for the environment). On the other hand, if the parents anticipate that the future will be safe, they can choose to have a child (see Fig. 1). Let γ be a probability/wish to have a child, then (2), becomes

$$\begin{cases} \frac{d}{dt} Pop(t) = (\alpha\gamma(t) - D(Re(t)))Pop(t) \\ \frac{d}{dt} Re(t) = \rho(Re(t)) - H(Re(t), Pop(t)) \end{cases}, \quad (4)$$

where α is the maximum birth rate. We notice that (3), respectively, becomes

$$\begin{cases} \frac{d}{dt} Pop(t) = (\alpha\gamma(t) - D(Re(t)))Pop(t) \\ 0 = \rho(Re(t)) - H(Re(t), Pop(t)) \end{cases}. \quad (5)$$

If we follow Stanková et al. (2013), Stukalin and Schmidt (2011), in a certain sense, by choosing this probability of having a child, the parents want to maximize a gain functional of the Bolza type (from current time 0 to time T where T is large enough)

$$\int_0^T [u(Re(s))Pop(s) - C\alpha\gamma(s)Pop(s)]e^{-\beta s} ds, \quad (6)$$

where u is a utility function depending on the resource level Re , C is a constant cost of having a child (related to the time (or money) parents have to spend raising a child: one of the reasons why some adults do not want children Gillespie, 2003)³ and β is a time discount factor (simplifying assumption modeling the forgetting process). This approach was used in Anon (2007) p277 to optimize the number of predators and prey at a given time by choosing the best hunting rate function of predators. The gain (or cost function) is similar to those proposed in Stanková et al. (2013) and Stukalin and Schmidt (2011) for the fishing optimization problem and in Flaig et al. (2018, 2020) for rational far-sighted cost-benefit analysis of vaccination in the case of epidemiology. Moreover in Stukalin and Schmidt (2011), the authors show how to obtain the adjoint equation (Bellman's equation Bellman, 1957) to solve the optimal control problem with a gain function close to (6). More precisely, optimized gain function

$$\tilde{V}(t, Pop) = \max_{\gamma} \int_t^T [u(Re(s)) - C\alpha\gamma(s)]Pop(s)e^{-\beta(s-t)}ds,$$

where $0 \leq \gamma(t) \leq 1$ for all t , satisfies the time backward equation (Stukalin and Schmidt, 2011; Bellman, 1957)

$$-\frac{\partial}{\partial t}\tilde{V}(t, Pop) = -\beta\tilde{V} + \left[\alpha \max\left(\frac{\partial}{\partial Pop}\tilde{V} - C, 0\right) + u(Re(t)) \right] Pop(t) - D(Re(t))Pop(t)\frac{\partial}{\partial Pop}\tilde{V},$$

and

$$\gamma(t) = Heaviside\left(\frac{\partial \tilde{V}}{\partial Pop} - C\right) = \begin{cases} 1, & \text{if } \frac{\partial \tilde{V}}{\partial Pop} - C > 0 \\ 0, & \text{if } \frac{\partial \tilde{V}}{\partial Pop} - C < 0 \end{cases}.$$

Therefore, by setting,

$$\tilde{V}(t, Pop) = V(t)Pop,$$

we have V which satisfies

$$-\frac{d}{dt}V = u(Re(t)) + \alpha\gamma(t)(V - C) - (\beta + D(Re(t)))V. \quad (7)$$

Hence, the value $V(t)$ (at time t) that the individual expects to have a child, depends on the variation of the level of resources and the immediate cost of raising a child. Note that the value of having a child depends on predictions about future resource states. In order to ease numerical methods and yet certainly as a realistic assumption, we use the concept of smoothed best response (Fudenberg and Levine, 1998) that uses logistic functions, i.e.

$$z \mapsto \frac{1}{(1 + e^{-T_e z})},$$

which is a smooth approximation of the Heaviside step function (with T_e which parametrizes the slope of the function at the origin). Moreover we choose the following form for the utility function (exponential)

$$u : z \mapsto 1 - e^{-a_u z + c_u},$$

where a_u and c_u are reals. The equations describing the decision making process by individuals are given in Eq. (7) and can be understood using the decision trees (Zwanziger et al., 2001; Hinman et al., 2004) which is a list of scenarios in which an individual is confronted with their probabilities, and individual and societal costs.

We modify the value equation by adding an altruism parameter χ which models a biased assessment of the value for the child

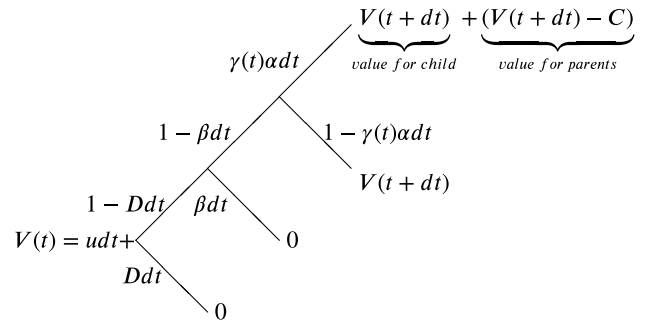


Fig. 2. Probability tree for individuals for Eq. (7). During a step time dt at time t , we evaluate $V(t)$ as $u(Re(t))dt$ (the utility of the resources during time dt) plus a value, depending on events happening to individuals and the value at time $t + dt$:

- when death happens (with probability Ddt) the value is zero
- when forgetting (with probability βdt) the value is zero
- if the parents do not have child (with probability $1 - \gamma\alpha dt$) the value is $V(t + dt)$
- if the parents want a child and have one (with probability $\gamma\alpha dt$) the value is $V(t + dt) + (V(t + dt) - C)$ (value to the child and value to parents minus the cost of raising the child).

Therefore, to evaluate the value at time t , we compute the mean of the value, which depends on the value at time $t + dt$:

$$V(t) = u(Re(t + dt))dt + \alpha\gamma(t)(V(t + dt) - C)dt + (1 - (D + \beta)dt)V(t + dt) + O(dt^2),$$

therefore by dividing by dt and passing to the limit in dt to zero we find (7).

when the decision to have a child is made⁴ (see Fig. 2 for the change in probability tree and Fig. 6 to see the variation in birth rate due to this parameter: when resources are low (resp. high) the birth rate can be higher or lower (resp. lower or higher) from one population to another) and the value when finally, the value function $V(t)$, for individual, from 'having a child' at time t follows the time backward equation

$$-\frac{d}{dt}V(t) = u(Re(t)) + \alpha\gamma(t)(\chi V(t) - C) - (D(Re(t)) + \beta)V(t), \quad V(T) = V_T, \quad (8)$$

where χ is an altruism parameter (we add χV to the value V when having the child), C the cost of having a child, β the time discount factor, u a utility function for available resources Re and

$$\gamma(t) = \frac{1}{(1 + e^{-T_e(\chi V(t) - C)})}, \quad (9)$$

with $T_e \in]0, \infty[$ the slope of the sigmoid and $\alpha \in]0, \infty[$ the maximal number of birth rate. Therefore, we can compute the individual and societal costs of a single case of 'having a child' as the net present value over lifetime of the expected cost of all scenarios (see Fig. 3).

The complete model of anticipation for (4) (resp. (5)) is then given by the coupled system of equations

$$\begin{cases} \frac{d}{dt}Pop(t) = (\alpha\gamma(t) - D(Re(t)))Pop(t) \\ \frac{d}{dt}Re(t) = \rho(Re(t)) - H(Pop(t), Re(t)) \\ -\frac{d}{dt}V(t) = u(Re(t)) + \alpha\gamma(t)(\chi V(t) - C) - (D(Re(t)) + \beta)V(t) \end{cases}, \quad (10)$$

(resp. $0 = \rho(Re(t)) - H(Pop(t), Re(t))$ for the resources equation in the adaptation model of (5)) with initial data $Pop(0) = Pop_0$, $Re(0) = Re_0 \geq 0$ and final data $V(T) = V_T$ (mathematical results are in Appendix A).

To model the change in the case where individuals adopt an adaptive behavior, i.e. do not anticipate the variation of the

³ Therefore $u(Re(s)) - C\alpha\gamma(s)$ is the individual's gain function.

⁴ We choose a linear evaluation: $V_{child} = \chi V$.

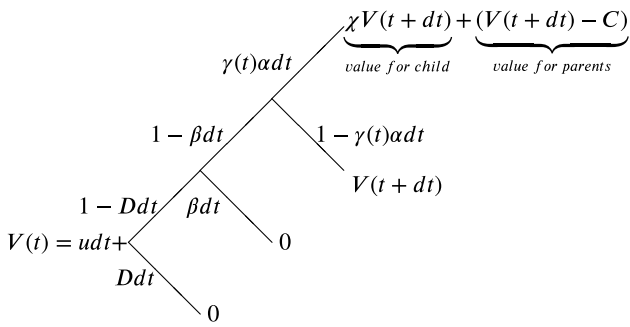


Fig. 3. Probability tree for individuals Eq. (8). During a step time dt at time t , we evaluate $V(t)$ as $u(Re(t))dt$ (the utility of the resources during time dt) plus a value, depending on events happening to individuals and the value at time $t + dt$:

- when death happens (with probability Ddt) the value is zero
- when forgetting (with probability βdt) the value is zero
- if the parents do not have child (with probability $1 - \gamma\alpha dt$) the value is $V(t + dt)$
- if the parents want a child and have one (with probability $\gamma\alpha dt$) the value is $\chi V(t + dt) + (V(t + dt) - C)$ (biased value to the child and value to parents minus the cost to raise the child).

Therefore, to evaluate the value at time t , we compute the mean of the value, which depends on the value at time $t + dt$:

$$V(t) = u(Re(t+dt))dt + \alpha\gamma(t)(\chi V(t+dt) - C)dt + (1 - (D + \beta)dt)V(t+dt) + O(dt^2),$$

therefore by dividing by dt and passing to the limit in dt to zero we find (8).

level of resources at an aggregate level, even if they evaluate the resources for their own survival, we set the value equation at its equilibrium ($\frac{d}{dt}V(t) = 0$):

$$\begin{cases} \frac{d}{dt}Pop_{ad}(t) = (\alpha\gamma_{ad}(t) - D(Re_{ad}(t)))Pop_{ad}(t) \\ \frac{d}{dt}Re_{ad}(t) = \rho(Re_{ad}(t)) - H(Pop_{ad}(t), Re_{ad}(t)) \\ 0 = u(Re_{ad}(t)) + \alpha\gamma_{ad}(t)(\chi V_{ad}(t) - C) - (D(Re_{ad}(t)) + \beta)V_{ad}(t) \end{cases}, \quad (11)$$

with $(0 = \rho(Re_{ad}(t)) - H(Pop_{ad}(t), Re_{ad}(t)))$ for the resources equation to the adaptive behavior of (5)

$$\gamma_{ad}(t) = \frac{1}{(1 + e^{-T_e(\chi V_{ad}(t) - C)})}, \quad (12)$$

and initial data $Pop(0) = Pop_0$, $Re(0) = Re_0 \geq 0$ (here dynamic is only time forward).

2.2. Discussion and parameters estimation

In this Section, we discuss the model and its parameters. The probability tree given in Fig. 3 shows that the first time event of 'having' a child depends on γ . We give its law in Section 2.2.1 and we give some examples when γ is fixed. Then we show, in the Sections 2.2.2–2.2.3, we explain how to understand and estimate parameters. In Section 2.2.4, we discuss about the model and its limits.

2.2.1. Choice and its related law

The personal choice to have a child, during $[t, t + dt]$, is modeled by $\gamma(t)\alpha dt$ which represents the probability of choosing to have a child (during $[t, t + dt]$). Therefore, the first time the event 'have a child' occurs follows a Cox process (Brigo and Mercurio, 2006 p763) X of intensity $\int_0^t \alpha\gamma(s)ds$, and its density is given by

$$f_X(t) = \begin{cases} 0, & t \leq 0 \\ \alpha\gamma(t)e^{-\int_0^t \alpha\gamma(s)ds}, & t > 0 \end{cases},$$

which is, when γ is constant over time, nothing more than an exponential law. In order to understand it in demographic terms (Hayford and Agadjanian, 2019), we give two examples, when γ is constant over time and when γ is a Heaviside step function.

1. Case $\gamma = 0$ means to stop or never have children and case $\gamma(t) = \gamma_0 > 0$, for all t , means that time between two events 'having a child' is, on average, $1/(\gamma_0\alpha)$ and so decay of γ_0 involves spacing two events 'having a child'.
2. When γ is a Heaviside step function

$$\gamma(t) = \begin{cases} 0, & t \leq \tau \\ \gamma_0, & t > \tau \end{cases},$$

then the first time the event 'have a child' happens follows an exponential law of parameter γ_0 translated, i.e. postponed, of time τ .

2.2.2. Time discount factor and its estimation

First, we study the dynamics of V in the case of constant resources (which is valid in a short time analysis), i.e.

$$\bar{u}, \quad D = \bar{D} \geq 0,$$

and so V satisfies

$$-\frac{d}{dt}V(t) = \bar{u} + \alpha\gamma(t)(\chi V(t) - C) - (\bar{D} + \beta)V(t).$$

Under assumption $\beta \gg \alpha\chi$ and \bar{D} , we have that V and so, the probability of having a child, γ converges to an equilibrium in a long time V_{eq} and γ_{eq} with

$$\gamma_{eq} \sim \frac{1}{1 + e^{-T_e(\frac{\chi\bar{u}}{\beta} - C)}},$$

and so χ , β , C and T_e are linked with the probability of having a child in a long time γ_{eq}

$$\left(\frac{\chi\bar{u}}{\beta} - C\right) \sim \frac{\log(\frac{\gamma_{eq}}{1-\gamma_{eq}})}{T_e}. \quad (13)$$

The value after having a child could be measured by the probability of wanting a child immediately after having a child (figure 1 Hayford and Agadjanian, 2019): γ_0 . The dynamics of γ when $\gamma(t=0) = \gamma_0$ is given by

$$\gamma(t) \sim \frac{\gamma_0 \left(\frac{\gamma_{eq}(1-\gamma_0)}{(1-\gamma_{eq})\gamma_0}\right)^{1-e^{-\beta t}}}{1 - \gamma_0 + \gamma_0 \left(\frac{\gamma_{eq}(1-\gamma_0)}{(1-\gamma_{eq})\gamma_0}\right)^{1-e^{-\beta t}}},$$

and so, at time $t_{1/2}$ such that

$$\log\left(\frac{\gamma}{1-\gamma}\right)(t_{1/2}) = \left[\log\left(\frac{\gamma_0}{1-\gamma_0}\right) + \log\left(\frac{\gamma_{eq}}{1-\gamma_{eq}}\right)\right]/2,$$

we have $e^{-\beta t_{1/2}} = 1/2$, i.e., $\beta \sim \frac{\log(2)}{t_{1/2}}$. The time discount factor β can be related to the time necessary to reach half of the equilibrium (of $\log(\frac{\gamma}{1-\gamma})$) in growth, i.e., in a sense, 'forgetting' the cost of having a child.

For instance, in Hayford and Agadjanian (2019), the authors study the desire of women (in Sub-Saharan) childbearing and by identifying, in figure 1 (Hayford and Agadjanian, 2019), the probability that a woman want to delay childbearing, as $1 - \gamma$ we can plot the time $t \mapsto \log(\frac{\gamma}{1-\gamma})(time)$ (see Fig. 4) and we notice that, $\beta \sim \frac{\log(2)}{t_{1/2}}$ leads to $\beta \in [10\%, 20\%]$.

2.2.3. Adaptive equation and its link with classical time evolution equations

Since individuals evaluate the resources for their own survival: the time evolution Eq. (2) is, in fact, the adaptive Eq. (11)–(12).

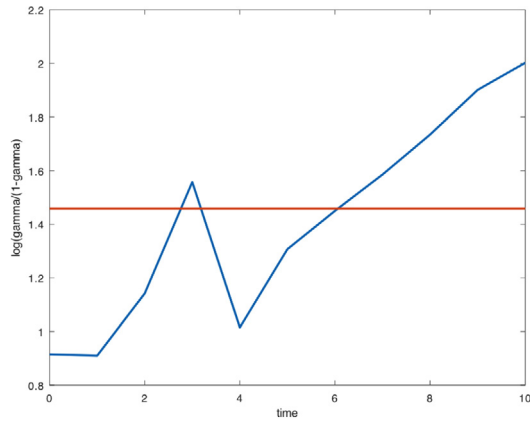


Fig. 4. In blue: $\log(\frac{\gamma}{1-\gamma})$ where $1-\gamma$ is given by the probability than a woman want to delay childbearing in Fig. 1. Hayford and Agadjanian (2019). In red, the constant line $[\log(\frac{\gamma_0}{1-\gamma_0}) + \log(\frac{\gamma_{eq}}{1-\gamma_{eq}})]/2$ which cuts the blue line in different points (around 3 years and around 7 years).

By identifying (11)–(12) and (2) we have $\alpha\gamma_{ad}$ is equal to the birth rate function $Re \mapsto B(Re)$, i.e. for well-chosen parameters (C, χ, T_e, α and function u) we should have for all $Re: \gamma_{Re}$ solution to

$$\begin{cases} 0 = u(Re) + \alpha\gamma_{Re}(\chi V_{Re} - C) - (D(Re) + \beta)V_{Re} \\ \gamma_{Re} = \frac{1}{(1+e^{-T_e(\chi V_{Re}-C)})} \end{cases}, \quad (14)$$

satisfies $\alpha\gamma_{Re} = B(Re)$. Therefore, (2) and (11)–(12) have the same solutions.

2.2.4. Discussion

Since we do not model the variation of age in (1), it is impossible to model the change of childbearing with respect to age nor the ‘peak’ around year three in Fig. 4. To cope with these two effects, it is necessary to introduce age of individuals and age of the last birth. It might be possible to introduce age structure using Kermack–McKendrick (Kermack and McKendrick, 1991) that models continuous aging of population or a discrete age model (with a vector of population such as Puleston and Tuljapurkar, 2008) for the population time evolution equation and adapt the value equation (time backward) with these age structure. Nevertheless, this could increase complexity of the model and make it less readable. The choice of a linear relationship between the value given to the child and the value, through the ‘altruism’ parameter, is done to add more complex behavior without being too complex: this could be improved in the future with a more complex relationship.

3. Adaptive versus anticipation over an example

In this Section, we adapt a model given in Puleston and Tuljapurkar (2008) of time evolution of the population with food consumption (Section 3.1) where the size of the population is represented by a vector structured by age with a discrete time to a continuous time model with a single age group. Then, in Section 3.2, we give the anticipation model and compare with the dynamics of the adaptive model. This is an application of the construction of adaptive and anticipation model from equation type (3).⁵

⁵ We give an example of construction of adaptive and anticipation model from equation type (2) in appendix Appendix B.

3.1. Basic model: an adaptive behavior

At time t the size of the population is given by $Pop(t)$, the consumption is represented by the food ratio $E(t)$ and is computed by the food produced over the food consumed:

$$E(t) = (YA_m) \frac{(1 - e^{-HkPop(t)\hat{\phi}/A_m})}{JPop(t)\hat{\rho}},$$

where A_m is the maximum area in active cultivation, H the hours worked per day, $\hat{\phi}$ part of the population that produces food, k a constant that converts hour of labour to area, Y the caloric yield per area cultivated and J the calorie requirement (per individual) modulated by a consumption rate (variable with age of individuals) $\hat{\rho}$ (see Puleston and Tuljapurkar, 2008 for more details). The survival probability of the population depends on the food ratio

$$p : E \mapsto p(E),$$

that we take as a piecewise linear function close to the curves given in figure 3 (Puleston and Tuljapurkar, 2008) (ages 5 or 65) and we see in Fig. 5, the death rate, i.e.

$$D(E) = 1 - p(E).$$

The fertility rate, named m in Puleston and Tuljapurkar (2008), is also an increasing function of the food ratio

$$B : E \mapsto B(E) \in [0, .135].$$

We notice that the birth rate (and the death rate) is depending on food ratio, i.e., the birth rate is ‘adapted’ to the level of this variable. The food ratio depends on the maximum area cultivated A_m and a sudden change in this value could be related to one of the expected difficulties predicted by neo-malthusianists: the depletion of natural resources in the world (Collins, 2002). Finally, a low food ratio is an indicator of a famine or an overpopulation. Therefore, we choose this variable as the key variable, for parents, to decide whether or not to have a child in order to optimize the well-being of the population (particularly their child) in the future.

The size of the population follows the main ordinary differential equation

$$\begin{cases} \frac{d}{dt} Pop(t) = (B(E(t)) - D(E(t)))Pop(t), \\ E(t) = \frac{YHk}{J} \frac{(1 - e^{-HkPop(t)\hat{\phi}/A_m})}{HkPop(t)\hat{\rho}/A_m}. \end{cases} \quad (15)$$

Since individuals value resources for their own survival: the time evolution Eq. (15) is, in fact, the adaptive equation: the fertility rate $t \mapsto B(E(t))$ is computed as $t \mapsto .135\gamma(t)$ where $.135$ is the maximal fertility rate and γ is the probability/wish to have a child (adaptive behavior)

$$\begin{cases} \frac{d}{dt} Pop(t) = (.135\gamma(t) - D(E(t)))Pop(t) \\ E(t) = \frac{YHk}{J} \frac{(1 - e^{-HkPop(t)\hat{\phi}/A_m})}{HkPop(t)\hat{\rho}/A_m} \\ 0 = u(E(t)) + .135\gamma(t)(\chi V(t) - C) - (D(E(t)) + \beta)V(t) \end{cases}, \quad (16)$$

with

$$\gamma(t) = \frac{1}{(1 + e^{-T_e(\chi V(t)-C)})}, \quad (17)$$

and so by identifying (16)–(17) and (15) we choose parameters (see Table 1) to have, for all $E \in [0, 1]$: $.135\gamma_E$ is close to $m(E)$ where γ_E satisfies

$$\begin{cases} 0 = u(E) + .135\gamma_E(\chi V_E - C) - (D(E) + \beta)V_E \\ \gamma_E = \frac{1}{(1 + e^{-T_e(\chi V_E - C)})} \end{cases}. \quad (18)$$

For well chosen parameters (see Table 1) we have $.135\gamma$ close to m given in figure 4. Puleston and Tuljapurkar (2008) (see Fig. 5).

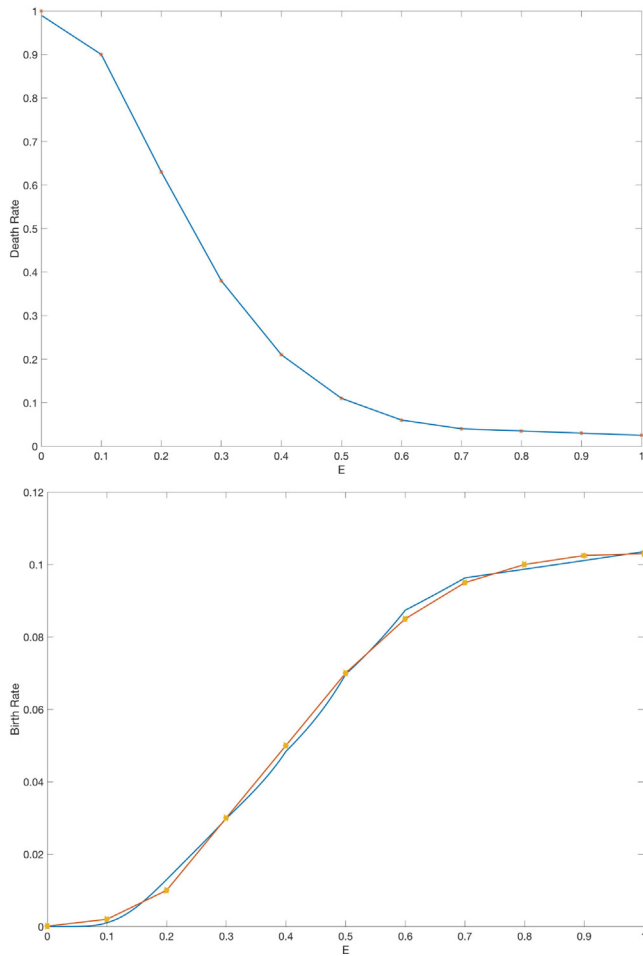


Fig. 5. Up: In blue the curve of death rate, i.e. one minus the survival probability, given in Puleston and Tuljapurkar (2008). Down: Plot of $E \mapsto m(E)$ (plain line, m is the name of the fertility rate in Puleston and Tuljapurkar, 2008) and $.135\gamma(E)$ (dashed line) solution to (18) with parameters given in Table 1.

Table 1

Parameters definition.		
Definition	Variable	Value
Max. food	J	2,785 Kcal/day
Agricultural potential	Y	13,100 Kcal/ha/day
Total arable land	A_m	1000 ha
Labor contribution	H	5 h/indiv./day
Conversion from time	k	0.0944
To annual area cultivated		ha-days/h/yr
Average effective		
Workers/person	$\hat{\phi}$	0.723
Average age structure		
Weighted consumption	$\hat{\rho}$	0.827
Parameters of	$(a_u; c_u)$	(15.5347; 3.4672)
The utility function		
Slope of the γ sigmoid	Te	3.1826
Cost	C	0.6102
Altruism factor	χ	0.1659
Discount time factor	β	15/100

3.1.1. Remark on parameters and sensitivity of fertility rate to personal cost and altruism

The evaluation of the cost parameter C , the altruism factor χ and the parameters of the utility function is not easy and depends on countries, age, social category, religion (Pearce et al., 2015)... We notice that childfree movement (Gillespie, 2003), claiming that having children is not costless in particular for women who

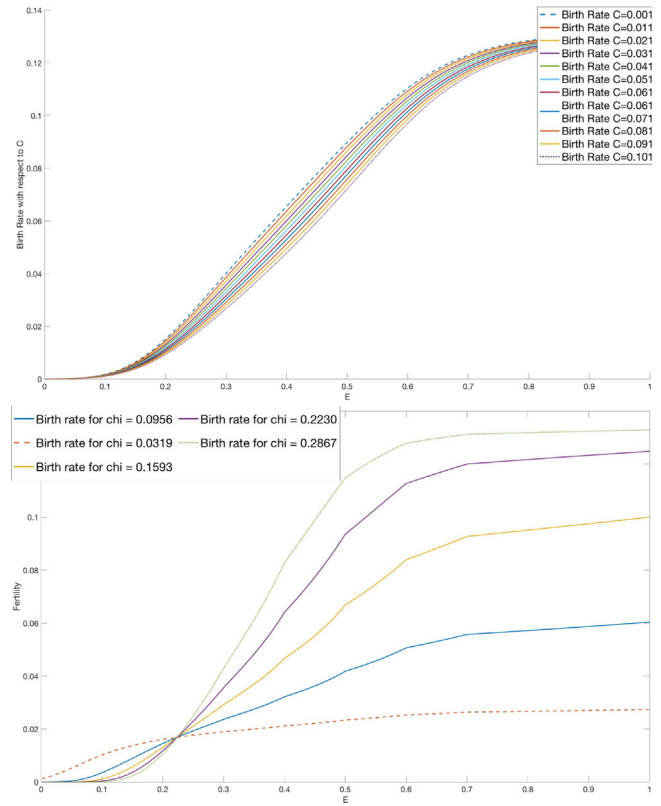


Fig. 6. Variation of $.135\gamma \mapsto .135\gamma(E)$ solution to (18) with respect to C and χ . Down, we set parameters in Table 1 (except C) and we plot $\gamma \mapsto .135\gamma(E)$ for $C = 0.001 \rightarrow 0.101$. The birth rate is decreasing with respect to C . Up, we set parameters in Table 1 (except χ) and we plot $\gamma \mapsto .135\gamma(E)$ for $\chi = 0.0319 \rightarrow 0.2867$.

lose their freedom and career to raise their(s) child(ren) (Maier, 2008), surely have an impact on the parameters of cost and altruism.

We use a genetic algorithm to find parameters such that $.135\gamma$ is sufficiently close to the fertility rate m given in Puleston and Tuljapurkar (2008), i.e. a prehistoric population and therefore, these parameters must be re-evaluated for another fertility rate data (see Fig. 5).

In order to see the sensitivity of the fertility rate to these parameters, we plot, in Fig. 6, the variation of $.135\gamma$ solution to (18) with respect to the personal cost C (with other parameters fixed in Table 1) and the altruism factor χ (with other parameters fixed in Table 1). We notice that, as the personal cost increases, $.135\gamma$ decreases and therefore the equilibrium \hat{E} also increases. The variation with respect to the altruism factor is more complicated. Note that the shape of $.135\gamma$ changes from nearly linear to sigmoid and is increasing with respect to χ when E is large enough ($E > \hat{E}$, with $V(\hat{E}) = 0$) and decreasing with respect to χ when E is small enough ($E < \hat{E}$). Since the death rate function $E \mapsto (1 - p(E))$ intersects the curves in the first case (E large enough), \hat{E} decreases with respect to χ .

3.1.2. First simulation

We have directly that $(Pop(t), E(t))$ reaches a stable equilibrium when t goes to infinity (due to the growth of $p + m$ with respect to E and decreasing of E with respect to Pop), and this equilibrium (\hat{Pop}, \hat{E}) satisfies

$$B(\hat{E}) = D(\hat{E}), \quad \hat{E} = \frac{YHk(1 - e^{-Hk\hat{Pop}\hat{\phi}/A_m})}{J - Hk\hat{Pop}\hat{\rho}/A_m}$$

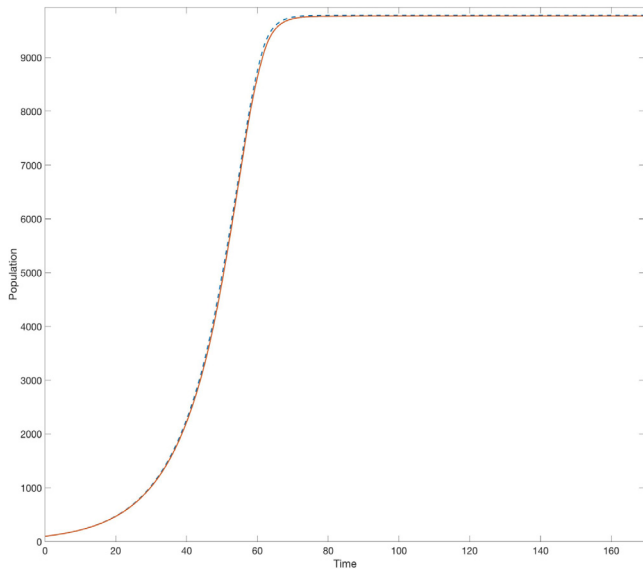


Fig. 7. Numerical solution of (15) with parameter given in Table 1. Time change of the population size $time \mapsto Pop(time)$. Plain line: solution to Eqs. (15) and dashed line: solution to (16)–(17).

which is (0.5606; 9786) for the parameters given in Table 1 (same as parameters give in table 1 Puleston and Tuljapurkar, 2008) (see Fig. 7 for a numerical simulation of (16)–(17). The equilibrium found in Puleston and Tuljapurkar (2008) is (0.680; 4752). The difference with (Puleston and Tuljapurkar, 2008) is due to the approximation of the death rate, fertility rate and loss of age structure: indeed, by taking only one age group, we choose a fertility rate of one age group that overestimates the fertility rate of the whole population, the same goes for the death rate which underestimates the death rate of the whole population. To find an equilibrium close to that given in Puleston and Tuljapurkar (2008), it might be possible to modify average effective workers/person parameter $\hat{\phi}$ and average age structure weighted consumption $\hat{\rho}$ to take into account the simplification to an age class. However we have chosen to keep parameters as given in Puleston and Tuljapurkar (2008), to be more consistent with the original model and its functions definitions.

3.2. The anticipation model and simulations

Now we add the anticipation, following (10), with the backward equation of the value

$$\begin{cases} \frac{d}{dt}Pop(t) = (.135\gamma(t) - D(E(t)))Pop(t) \\ E(t) = (YA_m) \frac{(1 - e^{-HKPop(t)\hat{\phi}/Am})}{JPop(t)\hat{\rho}} \\ -\frac{d}{dt}V(t) = u(E(t)) + .135\gamma(t)(\chi V(t) - C) \\ \quad - (D(E(t)) + \beta)V(t) \end{cases}, \quad (19)$$

and $\gamma(t) = \frac{1}{1 + e^{-\chi V(t) - C}}$ with parameters given in Table 1. We give three numerical simulations to analyze the difference in behavior between an adaptive and an anticipating individual. In the first case ('nothing change'), we compare both models when there is no change in the future: no change in the agriculture parameter such as the area of arable land, the agricultural potential... and no birth rate policy. In the second case ('agriculture catastrophe'), we see what is changed by announcing that at a given time the total arable land has its area will be divided by two. In the third case ('birth control policy'), we see the effect of announcing of a birth control policy that would be modeled by fixing the birth rate at a certain value at a given time.

3.2.1. Case 1. nothing change

Since the adaptive model corresponds to an equilibrium for the value equation in the anticipation model, equilibria of the adaptive model (16) are the same as the anticipation model (19). The stability of steady states can be studied as in classical (forward) way by keeping the backward/forward structure.

Theorem 1 (Stability). *The only steady state of (16) (resp. (19)): (\hat{Pop}, \hat{E}) is locally stable for both model.*

The proof is direct for the adaptive model (due to the growth of $\gamma + p$ with respect to E and the decay of E with respect to Pop). For the adaptation model, we have to deal with the Jacobian at (\hat{Pop}, \hat{V})

$$Jac = \begin{pmatrix} 0 & J_{12} \\ J_{21} & J_{22} \end{pmatrix},$$

with $J_{12} = .135 \frac{\partial}{\partial V} \gamma Pop > 0$, $J_{21} = (u'(E) + p'(E)V) \frac{\partial E}{\partial Pop} < 0$ and $J_{22} = .135 \frac{\partial}{\partial V} (\gamma(\chi V(t) - C)) - (1 - p(E) + \beta) < 0$ (by numerical computation). Since $det(Jac) > 0$ and $tr(Jac) < 0$, eigenvalues are negative and the steady state is locally asymptotically stable.

Therefore, we do not expect much difference between the two models when the resource condition (here, for instance, A_m : area of arable land) does not change (see Fig. 8) during of temporal evolution.

3.2.2. Case 2. agriculture catastrophe

Nevertheless, differences between anticipation and adaptive behavior appear when adding information such as ecological catastrophe (modeled here by a decay in very short time of the total area of arable land).

To illustrate a difference in behavior, we assume that the area of arable land is divided by two at a given time:

$$A_m = \begin{cases} 1000, & \text{for } t \in [0, 500] \\ 500, & \text{for } t \geq 500 \end{cases},$$

where $t = 500$ is chosen to compare behavior of adaptive and adaptation when population has reached its equilibrium before area change happens. The information of area decay is known by the population.

We see, in Fig. 9, that the food ratio only changes for a relatively short time (time 500 to time 510) due to the short evolution over time of the area of arable land and the high death rate during this period to reach a new steady state in population and food ratio.

Note that in the adaptive model (the classical model), individuals do not change their birth rate before the loss of area of arable land $t = 500$.

In the adaptation model, we see, in Fig. 9, that after time 490 (therefore before any change of the arable land area), the birth rate decreases due to the anticipation of the decay of the food ratio E . True or not, the information of the decay of the area of arable land has an impact on the behavior on the fertility rate and therefore on the dynamics of the population before the moment it could (or not) occur (neo-Malthusian behavior).

3.2.3. Case 3. birth control policy

Here we illustrate an another difference in behavior in the case of a birth control announcement that would be applied after a given time.

We assume that at time $t = 470$ is announced that the birth rate will be limited to 0.0420 (which corresponds to half of the case 1. at equilibrium) thirty years after the announcement, i.e. at time $t = 500$.

We observe, in Fig. 10, that between time $t = 470$ and $t = 500$ the birth rate increases due to the fact that individuals anticipate

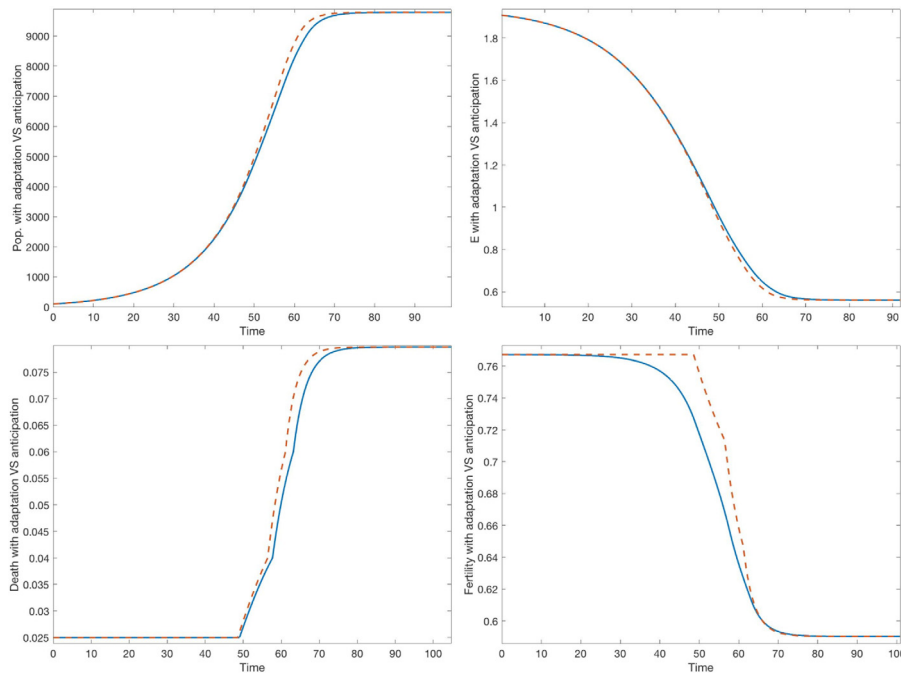


Fig. 8. Anticipation VS Adaptation case 1. In blue (plain line) we see time evolution of the population that adapts its behavior and in red (dashed line) time evolution of the population that anticipates. There is a small difference on the fertility rate due to the adaptation to the variation of the food ratio E . Population, food ratio and death rate are similar.

an increase in the food ratio under the effect of limitation of the birth rate after time $t = 500$.

Consequently, the effect of announcing a birth control policy to a population that anticipates change of resources may have a counter effect just before the application of the policy.

4. Conclusion

In this work we have given a construction scheme to model the anticipation behavior in a dynamic population and resource model. This construction leads to a coupling of a forward-in-time system of equations which models the interaction between population and resources and a backward-in-time equation which models the valuation of the value of childbearing. On an example using a simple dynamic on the time evolution of population, we show the construction of the anticipation model and we apply it on different scenarios. In a catastrophic scenario of a loss of arable area (announcement), we see that an adaptive population, i.e., that evaluates the value but does not anticipate its variations, does not adapt their fertility rate to the loss. Whereas in the anticipation model, the evolution of the fertility rate shows an anticipation of the loss. Since, the coupling is not classic in analysis we have given general tools to prove the existence, the uniqueness and the numerical analysis in appendix. To go further, it should be interesting to adapt the construction to an age structured model such as the model given in [Puleston and Tuljapurkar \(2008\)](#) (or a Kermack–McKendrick [Kermack and McKendrick, 1991](#) partial differential equation model) and to adjust parameters to more recent population fertility rate. Moreover, we consider that C and χ are constant in time, an inflation of these parameters could have a non-zero impact on the evolution of the birth rate over time.

CRediT authorship contribution statement

Philippe Michel: Conceptualization, Methodology, Software.

Appendix A

There are several and interesting mathematical problems arising in (10). Due to the coupling of time forward (for Pop and Re) and time backward (for V), the existence and uniqueness of a solution to (10) is not a trivial application of the Cauchy–Lipshitz theorem. Moreover, numerical approximation scheme of this problem is not easy. Trying to inverse time in the third equation (in V) and using a shooting method to find $V(0)$ such that $V(T) = V_T$ fails due to the fact that the equation in V is unstable for positive time, i.e. a small variation of $V(0)$ implies a large variation of $V(T)$. A direct Banach–Picard fixed point algorithm fails also. In this Section, we first give results on the existence and the uniqueness of solution. Moreover, we explain the reason of the convergence of a relaxed Banach–Picard scheme to the solution (the method has been used in previous works [Flaig et al., 2018, 2020](#) but not explained).

A.1. Mathematical results

In this Section, we give two main results. The first theorem concerns the existence and uniqueness of a solution to (10) and the second gives an approximation scheme which converges to the solution. In both theorems we use the function f defined as follows

$$f : (\gamma, Re) \in C([0, T], [0, 1]^2) \mapsto f(\gamma, Re) \in C([0, T], [0, 1]^2), \quad (20)$$

with

$$f : (\gamma, \tilde{Re}) \mapsto \left(\frac{1}{(1 + e^{-T_e(\chi V - C)})}, Re \right) \quad (21)$$

where (V, Re) is solution to

$$\begin{cases} \frac{d}{dt} Pop(t) = (\alpha\gamma(t) - D(\tilde{Re}(t)))Pop(t), & t \geq 0, \\ \frac{d}{dt} Re(t) = \rho(Re(t)) - H(Pop(t), Re(t)), \\ -\frac{d}{dt} V(t) = u(Re(t)) + \alpha \frac{(\chi V(t) - C)}{(1 + e^{-T_e(\chi V(t) - C)})} \\ - (D(Re(t)) + \beta)V(t), \end{cases} \quad (22)$$

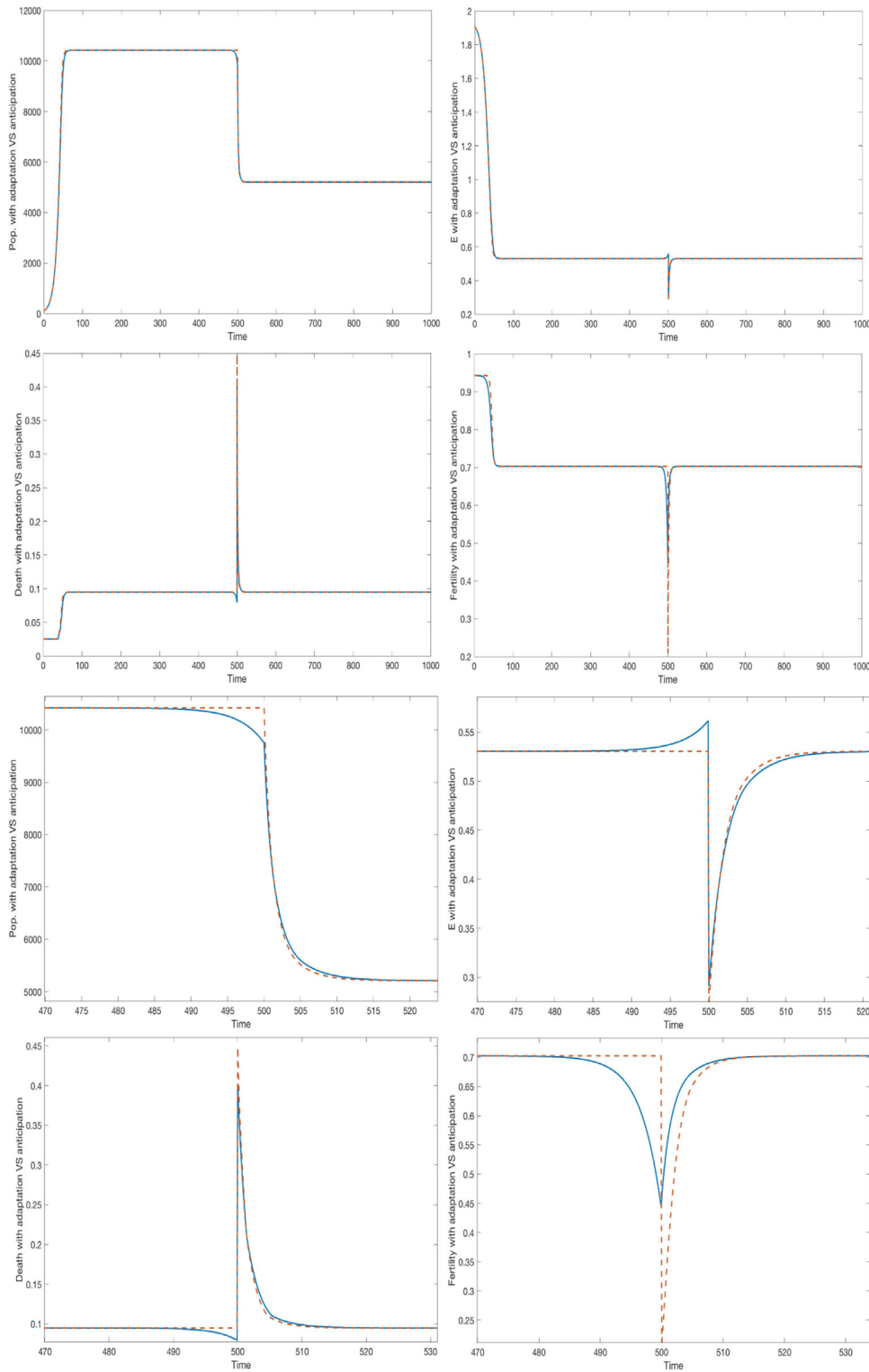


Fig. 9. Anticipation VS Adaptation case 2. In blue (plain line) we see time evolution of the population that adapts its behavior and in red (dashed line) time evolution of the population that anticipates. In the four up plots: we show simulations on time interval 0..1000. Note the effect of the change of area at time $t = 500$: the population changes from an equilibrium to an another with a large death rate and a decay of fertility. In the four down plots we magnify the change around time $t = 500$ in order to observe more precisely the difference of behavior.

with initial data $Pop(0) = Pop_0 \in]0, \infty[$, $Re(0) = Re_0 \in]0, 1]$, $V(T) = V_T$.

Theorem 2. Assuming that

$$D, \rho \in C^1(\mathbb{R}) \text{ and } H \in C^1(\mathbb{R}^2), \tag{23}$$

with

$$\rho(1) = \rho(0) = H(Pop, 0) = 0, \text{ and } D(0) > \alpha > D(1), \tag{24}$$

and

$$D' < 0 \text{ and } \frac{\partial}{\partial Pop} H < 0. \tag{25}$$

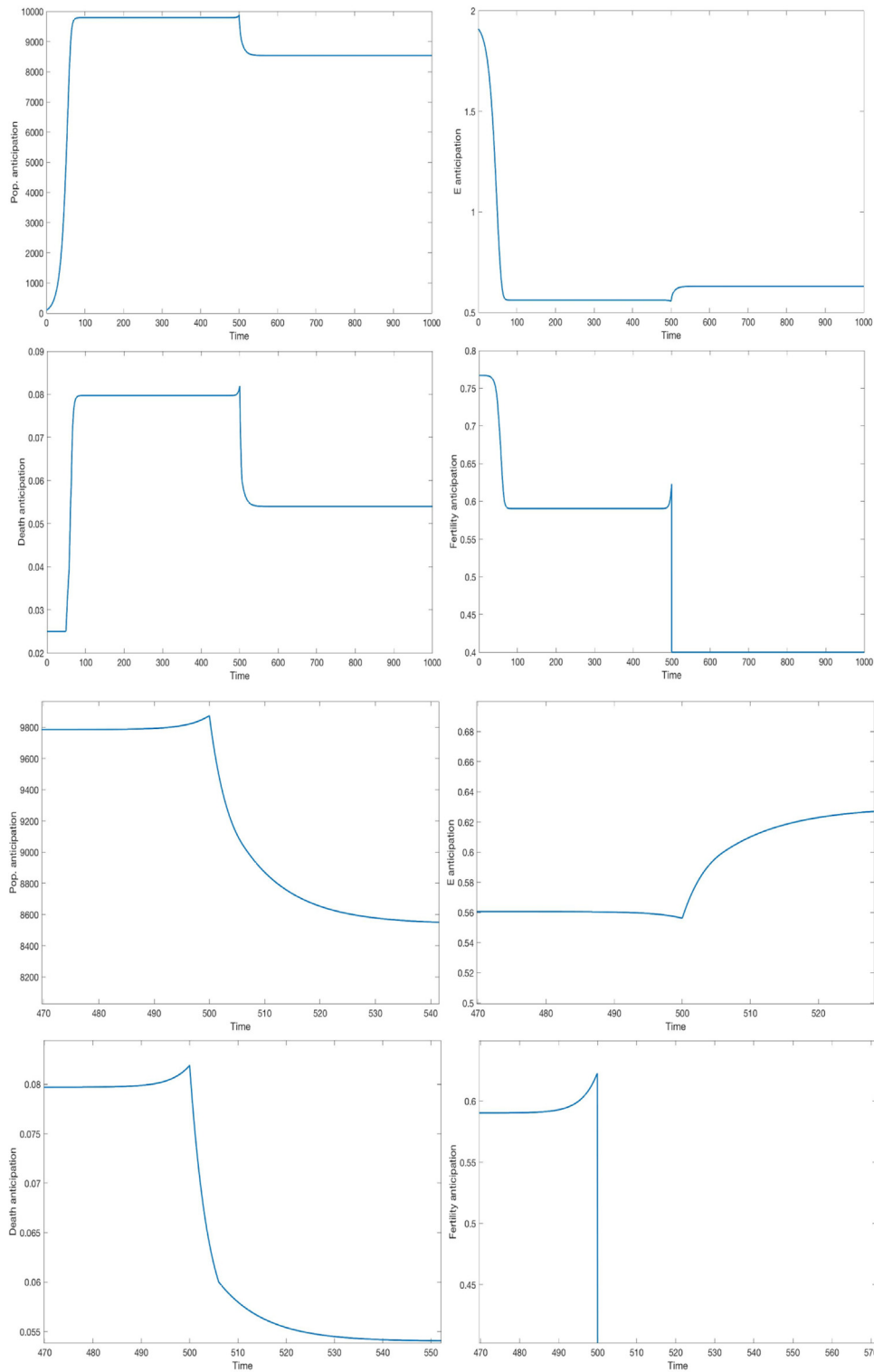


Fig. 10. Anticipation of a birth control policy. In the four up plots: we show simulations on time interval 0..1000. Note the effect of the change of area at time $t = 500$: the population moves from one equilibrium to an another with a decrease in fertility (except a peak around time $t = 500$). In the four down plots we magnify the change around time $t = 500$ to observe the fertility and the behavior of anticipating population.

Then, there exists a unique solution to (10).⁶

We approach this solution can be by the following algorithm: let $u_0 = 0$, and define by induction

$$u_{n+1} = (1 - \epsilon)u_n + \epsilon f(u_n), \quad (26)$$

⁶ C^1 assumptions could be replaced by Lipschitz, $D' < 0$ by D decreasing and $\frac{\partial}{\partial Pop} H < 0$ by H decreasing with respect to Pop .

with $\epsilon \in]0, 1[$ small enough. More precisely, we have the following convergence result.

Theorem 3. Under assumptions (23)–(25) then $u = (\gamma, Re)$ the solution to (10) is a locally asymptotically stable state to the equation

$$\frac{d}{ds} U(s, t) = f(U(s, \cdot))(t) - U(s, t), \quad \forall t \in [0, T], s \geq 0. \quad (27)$$

Remark 1. Indeed, an Euler approximation of (27) is given by

$$\begin{aligned} U_{n+1}(t) &= U_n(t) + \epsilon[f(U(n, \cdot))(t) - U(n, t)] \\ &= \epsilon f(U(n, \cdot))(t) + (1 - \epsilon)U(n, t), \end{aligned}$$

where ϵ is the time step, i.e., the relaxed algorithm (26). Another scheme, given by a semi-implicit Euler approximation of (27) could be

$$U_{n+1}(t) = (U_n(t) + \epsilon f(U(n, \cdot))(t)) / (1 + \epsilon),$$

where ϵ is the time step.

A.2. Proof of existence and uniqueness

We first give the existence result which comes directly from the compactness of the operator f and the Schauder fixed point theorem (see Istratescu, 1981). Then we prove uniqueness using the decay of f and Ordinary Differential Equations tools (upper/lower solutions).

Existence. This is a direct application of Schauder fixed point theorem (see Istratescu, 1981). Indeed, for all (γ, \bar{R}_e) which belongs to $C([0, T], [0, 1]^2)$, (V, Re, Pop) is the solution to the Ordinary Differential system of Eqs. (22) which existence and uniqueness is a consequence to the Cauchy Lipschitz theorem (see Coddington and Levinson, 1955). Moreover (V, Re, Pop) are regular functions, i.e. $(Pop, Re) \in C^1([0, T], [0, 1])$ and V is a $C^1([0, T], [0, 1]^2)$. Now, using that

$$x \mapsto \frac{1}{1 + e^{-T_e(\chi x - C)}} \in C^1(\mathbb{R}, \mathbb{R}),$$

then $f(\gamma, Re)$ is bounded in $C^1([0, T], [0, 1]^2)$. Therefore f is compact on the convex set $C([0, T], [0, 1]^2)$ and so, using Schauder theorem (see Istratescu, 1981), there exists a fixed point to f .

Uniqueness. Let (γ_1, Re_1) and (γ_2, Re_2) be two solutions to the fixed point $(\gamma, Re) = f(\gamma, Re)$, i.e., solutions to (10) then

$$\begin{cases} \frac{d}{dt} Pop_i(t) = (\alpha \gamma_i(t) - D(Re_i(t))) Pop_i(t), \\ \frac{d}{dt} Re_i(t) = \rho(Re_i(t)) - H(Pop_i(t), Re_i(t)), \\ \frac{d}{dt} V_i(t) = -u(Re_i(t)) - \alpha \frac{(\chi V_i(t) - C)}{(1 + e^{-T_e(\chi V_i(t) - C)})} \\ \quad + (D(Re_i(t)) + \beta)V_i(t), \end{cases}$$

with the initial data $Pop_i(0) = Pop_0 \in]0, \infty[$, $Re_i(0) = Re_0 \in]0, 1[$, $V_i(0) = V_i^0$ and $V_i^0 = (C - \log(1/\gamma_i(0) - 1)/T_e)/\chi$. If $V_1^0 = V_2^0$, by Cauchy Lipschitz theorem $\gamma_1 = \gamma_2$. We suppose that $\gamma_1(0) > \gamma_2(0)$ (and so $V_1(0) > V_2(0)$), then we have $\frac{d}{dt} Pop_1(0) > \frac{d}{dt} Pop_2(0)$ and so

$$Pop_1(t) > Pop_2(t),$$

in a neighborhood of $t = 0$. Then, using assumption (25), we have

$$Re_1(t) < Re_2(t),$$

and so we have

$$D(Re_1(t)) - u(Re_1(t)) > D(Re_2(t)) - u(Re_2(t)),$$

which implies that $V_1(t) > V_2(t)$ and so $\gamma_1(t) > \gamma_2(t)$ in a neighborhood of 0. Therefore $\Omega = \{s \in [0, T] \text{ s.t. } \gamma_1(t) > \gamma_2(t) \forall t \in [0, s]\}$ is a nonempty set. On $\bar{\Omega} \setminus \{0\}$, we have by comparison principle $Pop_1 > Pop_2$ and $Re_1 < Re_2$ and so $\Omega = \bar{\Omega} = [0, T]$: which is impossible since $V_1(T) = V_2(T) = V_T$ and so $\gamma_1(T) = \gamma_2(T)$. \square

A.3. Proof of convergence result

The most difficult is to prove the convergence of the algorithm (26). Indeed, since f is not a contractant operator, the Banach fixed point theorem (see Istratescu, 1981) cannot be used directly. Nevertheless, we can prove that f is decreasing (antitone, see Sommariva and Vianello, 2000), its differential df is a strongly negative (see Dautray and Lions, 1990) and compact operator and so we can construct a dynamical system which converges to the solution. The algorithm (26) can be seen as a numerical approximation of this dynamical system.

By differentiation of $V = f(U) - U$ with respect to s we have directly that $V = f(U) - U$, where f is defined by (21)–(22) and U solution to (27) satisfies

$$\frac{d}{ds} V(s, t) = df_{U(s, \cdot)} V(s, \cdot)(t) - V(s, t), \quad \forall t \in [0, T], s \geq 0. \quad (28)$$

We show that $df_{U(s, \cdot)}$ is a strongly negative (see Dautray and Lions, 1990) and compact operator (uniformly along a trajectory U).

Lemma 4. Let f defined by (21)–(22) then $df_{U(s, \cdot)}$ an integral operator with the following properties:

1. $df_{U(s, \cdot)} : h \mapsto df_{U(s, \cdot)}(h)$ is a linear, regular (continuous) and strongly negative operator, i.e., $-df_{U(s, \cdot)}$ is strongly positive (see Dautray and Lions, 1990),
2. $df_U : h \in C^0([0, T] \times \mathbb{R}_+) \mapsto df_{U(s, \cdot)}(h) \in C^0([0, T] \times \mathbb{R}_+)$ is a compact operator,
3. $\inf_{U \in \{U(s, \cdot), s \geq 0\}} df_U, \sup_{U \in \{U(s, \cdot), s \geq 0\}} df_U$ are linear, regular (continuous) and strongly negative operator.

And finally we prove that, for all dynamical system of this form (with a strongly negative (see Dautray and Lions, 1990) and compact operator), we have the convergence of the solution to 0 exponentially.

Lemma 5. Let $\epsilon(s, t)$ solution to

$$\frac{d}{ds} \epsilon(s, t) = -(\mathcal{K}_t + I)\epsilon(s, t),$$

where \mathcal{K}_t is a compact strongly positive operator on the function set $C^0([0, T], [0, 1]^2)$ then we have

1. the spectral radius of \mathcal{K}_t , named $\rho(t)$, is a single eigenvalue, there exists $N(\cdot, t) \geq 0$ eigenfunction associated to this eigenvalue
2. there are no other eigenvalue of modulus $\rho(t)$

More precisely there exists (ρ, N, ϕ) , with $\rho > 1$, solution to

$$\begin{cases} -\frac{d}{ds} \Phi(s, t) = \mathcal{L}_t^* \Phi(s, t) + \rho(t)\Phi(s, t), \\ \frac{d}{ds} N(s, t) = \mathcal{L}_t N(s, t) + \rho(t)N(s, t), \end{cases} \quad (29)$$

with $\mathcal{L}_t = -(\mathcal{K}_t + I)$ and \mathcal{L}_t^* its dual operator. Moreover, we have the convergence of ϵ to 0 and

$$\int |\epsilon(s, t)| \Phi(s, t) dt = O(e^{-s}). \quad (30)$$

Therefore we have proved that U solution to (27) satisfies

$$f(U) - U \rightarrow_{s \rightarrow \infty} 0,$$

in $C^0([0, \infty[, L^1([0, T]))$.

Proof of Lemma 4. Let γ, Re and ϵ_1, ϵ_2 then compute

(Pop, Re, V) , with the input functions (γ, Re) and $(Pop_\epsilon, Re_\epsilon, V_\epsilon)$ with the input functions $(\gamma + \epsilon_1, Re + \epsilon_2)$. We have, at first order,

$$Pop_\epsilon(t) = Pop(t) + \epsilon_{Pop}(t), \quad Re_\epsilon(t) = Re(t) + \epsilon_{Re}(t),$$

$$V_\epsilon(t) = V(t) + \epsilon_V(t),$$

with

$$\frac{d}{dt}\epsilon_{Pop}(t) = (\alpha\gamma(t) - D(Re(t)))\epsilon_{Pop}(t) + \alpha\epsilon_1(t)Pop(t) - D'(Re(t))\epsilon_2(t),$$

with $\epsilon_{Pop}(0) = 0$, i.e., by integration

$$\epsilon_{Pop}(t) = \int_0^t e^{\int_s^t (\alpha\gamma(w) - D(Re(w)))dw} [\alpha\epsilon_1(s)Pop(s) - D'(Re(s))\epsilon_2(s)]ds.$$

Moreover, we have

$$\frac{d}{dt}\epsilon_{Re}(t) = [\rho'(Re) - \frac{\partial}{\partial Re}H(Re, Pop)]\epsilon_{Re}(t) - \frac{\partial}{\partial Pop}H(Re, Pop)\epsilon_{Pop}(t),$$

with $\epsilon_{Re}(0) = 0$, i.e., by integration we have

$$\epsilon_{Re}(t) = \int_0^t e^{\int_s^t [\rho'(Re) - \frac{\partial}{\partial Re}H(Re, Pop)](w)dw} [-\frac{\partial}{\partial Pop}H(Re, Pop)]\epsilon_{Pop}(s)ds,$$

and finally

$$\epsilon_{Re}(t') = \int_0^{t'} 1_{s \leq t'} \int_q^{t'} e^{\int_s^{t'} [\rho'(Re) - \frac{\partial}{\partial Re}H(Re, Pop)](w)dw} [-\frac{\partial}{\partial Pop}H(Re, Pop)](e^{\int_q^s (\alpha\gamma(w) - D(Re(w)))dw} ds [\alpha\epsilon_1(q)Pop(q) - D'(Re(q))\epsilon_2(q)]dq).$$

Now, for ϵ_V , we have

$$-\frac{d}{dt}\epsilon_V(t) = [u'(Re(t)) - D'(Re(t))V(t)]\epsilon_{Re}(t) - (\mu + \beta + \alpha P'(V))\epsilon_V(t),$$

with $\epsilon_V(T) = 0$ and $P(V) := \frac{(\chi V(t) - C)}{(1 + e^{-Te(\chi V(t) - C)})}$. Therefore, by integration, we obtain

$$\epsilon_V(t) = \int_t^T [u'(Re(s)) - D'(Re(s))V(s)]\epsilon_{Re}(s) e^{-\int_t^s (D(Re(w)) + \beta + \alpha P'(V(w)))dw} ds.$$

Finally, we find

$$\begin{aligned} \epsilon_V(t') &= \int_{t'}^T [u'(Re(t)) - D'(Re)V(t)] \\ &e^{-\int_{t'}^t (D(Re(w)) + \beta + \alpha P'(V))dw} \\ &\int_0^t e^{\int_s^t [\rho'(Re) - \frac{\partial}{\partial Re}H(Re, Pop)](w)dw} \\ &[-\frac{\partial}{\partial Pop}H(Re, Pop)](s) \\ &\int_0^s e^{\int_q^s (\alpha\gamma(w) - D(Re(w)))dw} [\alpha\epsilon_1(q)Pop(q) \\ &- D'(Re(q))\epsilon_2(q)]dq ds dt, \end{aligned}$$

which could be written, using Fubini, in the following form

$$\begin{aligned} \epsilon_V(t') &= \int_0^T \int_{t'}^T \int_q^t [u'(Re(t)) - D'(Re)V(t)] \\ &[-\frac{\partial}{\partial Pop}H(Re, Pop)](s) \\ &e^{-\int_t^t (D(Re(w)) + \beta + \alpha P'(V))dw} e^{\int_s^t [\rho'(Re) - \frac{\partial}{\partial Re}H(Re, Pop)](w)dw} \\ &e^{\int_q^s (\alpha\gamma(w) - D(Re(w)))dw} ds dt [\alpha\epsilon_1(q)Pop(q) \end{aligned}$$

$$-D'(Re(q))\epsilon_2(q)]dq.$$

Therefore, we have

$$\begin{pmatrix} \epsilon_V(t') \\ \epsilon_{Re}(t') \end{pmatrix} = \int_0^T Q(s, t') \begin{pmatrix} \epsilon_1(s) \\ \epsilon_2(s) \end{pmatrix} ds,$$

with

$$Q(s, t') = \begin{pmatrix} Q_{11}(s, t') & Q_{12}(s, t') \\ Q_{21}(s, t') & Q_{22}(s, t') \end{pmatrix}.$$

$$Q_{11}(q, t') = C_f'(V(t'))\alpha Pop(q)$$

$$\begin{aligned} &\int_{t'}^T \int_q^t [u'(Re(t)) - D'(Re)V(t)] \\ &[-\frac{\partial}{\partial Pop}H(Re, Pop)](s) \\ &e^{-\int_{t'}^t (D(Re(w)) + \beta + \alpha P'(V))dw} \\ &e^{\int_s^t [\rho'(Re) - \frac{\partial}{\partial Re}H(Re, Pop)](w)dw} \\ &e^{\int_q^s (\alpha\gamma(w) - D(Re(w)))dw} ds dt, \end{aligned}$$

$$Q_{12}(q, t') = C_f'(V(t'))$$

$$\begin{aligned} &\int_{t'}^T \int_q^t [u'(Re(t)) - D'(Re)V(t)] \\ &[-\frac{\partial}{\partial Pop}H(Re, Pop)](s) \\ &e^{-\int_{t'}^t (D(Re(w)) + \beta + \alpha P'(V))dw} \\ &e^{\int_s^t [\rho'(Re) - \frac{\partial}{\partial Re}H(Re, Pop)](w)dw} \\ &e^{\int_q^s (\alpha\gamma(w) - D(Re(w)))dw} ds dt (-D'(Re(q))), \end{aligned}$$

$$Q_{21}(q, t') = \alpha Pop(q) 1_{q \leq t'}$$

$$\begin{aligned} &\int_q^{t'} e^{\int_s^{t'} [\rho'(Re) - \frac{\partial}{\partial Re}H(Re, Pop)](w)dw} \\ &[-\frac{\partial}{\partial Pop}H(Re, Pop)] \\ &e^{\int_q^s (\alpha\gamma(w) - D(Re(w)))dw} ds, \end{aligned}$$

and

$$\begin{aligned} Q_{22}(q, t') &= [-D'(Re(q))] 1_{q \leq t'} \int_q^{t'} \\ &e^{\int_s^{t'} [\rho'(Re) - \frac{\partial}{\partial Re}H(Re, Pop)](w)dw} \\ &[-\frac{\partial}{\partial Pop}H(Re, Pop)] \\ &e^{\int_q^s (\alpha\gamma(w) - D(Re(w)))dw} ds, \end{aligned}$$

where $C_f(V) := \frac{1}{(1 + e^{-Te(\chi V(t) - C)})}$. We notice that $Q_{ij} < 0$ for all i, j and using assumptions (23) and (25) we have that $\inf_{q, t', i, j}$

$Q_{ij}(q, t') < 0$. Therefore, $-df_U$ is a strongly positive operator (and the same holds for sup and inf of $-df_U$). Since df_U is an integral operator with Q continuous with respect to q and C^1 with respect to t' we have compactness of this operator on $C^0([0, T] \times \mathbb{R}_+)$. \square

Proof of Lemma 5. Using Krein Rutmann theorem (Dautray and Lions, 1990), we have existence of (ρ_t, N_t, ϕ_t) solution to (29). By computation, we find

$$\begin{aligned} & \frac{d}{ds} \int \epsilon(s, t) e^{\int_0^s \rho(s') ds'} \Phi(s, t) dt \\ &= \int \mathcal{L} \epsilon(s, \cdot)(t) e^{\int_0^s \rho(s') ds'} \Phi(s, t) dt \\ &+ \int \epsilon(s, t) e^{\int_0^s \rho(s') ds'} \left[\frac{d}{ds} \Phi(s, t) + \rho(s) \Phi(s, t) \right] dt, \end{aligned}$$

and so we have the conservation law

$$\begin{aligned} & \frac{d}{ds} \int \epsilon(s, t) e^{\int_0^s \rho(s') ds'} \Phi(s, t) dt = \int \epsilon(s, t) e^{\int_0^s \rho(s') ds'} \\ & [\mathcal{L}^* \Phi(s, t) + \frac{d}{ds} \Phi(s, t) + \rho(s) \Phi(s, t)] dt = 0. \end{aligned}$$

Let $\epsilon_+(s, t) := \max(\epsilon(s, t), 0)$ and $\epsilon_-(s, t) := \max(-\epsilon(s, t), 0)$ then we have

$$\begin{aligned} & \frac{d}{ds} \int \epsilon_+(s, t) e^{\int_0^s \rho(s') ds'} \Phi(s, t) dt = \int \epsilon(s, t) \\ & e^{\int_0^s \rho(s') ds'} \\ & [\mathcal{L}^*(\text{sgn}_+(\epsilon(s, \cdot)) \Phi(s, \cdot)) \\ & + \left(\frac{d}{ds} \Phi(s, t) + \rho(s) \Phi(s, t) \right) \text{sgn}_+(\epsilon(s, t))] dt. \end{aligned}$$

Using (29), we find

$$\begin{aligned} & \frac{d}{ds} \int \epsilon_+(s, t) e^{\int_0^s \rho(s') ds'} \Phi(s, t) dt = \int \epsilon(s, t) \\ & e^{\int_0^s \rho(s') ds'} [\mathcal{L}^*(\text{sgn}_+(\epsilon(s, \cdot)) \Phi(s, \cdot)) \\ & - \mathcal{L}^*(\Phi(s, \cdot) \text{sgn}_+(\epsilon(s, t)))(t)] dt. \end{aligned}$$

The same computation holds for ϵ_- and we find

$$\begin{aligned} & \frac{d}{ds} \int \epsilon_-(s, t) e^{\int_0^s \rho(s') ds'} \Phi(s, t) dt = \int \epsilon(s, t) e^{\int_0^s \rho(s') ds'} \\ & [\mathcal{L}^*(\text{sgn}_-(\epsilon(s, \cdot)) \Phi(s, \cdot)) - \mathcal{L}^*(\Phi(s, \cdot) \text{sgn}_-(\epsilon(s, t)))(t)] dt. \end{aligned}$$

Now using that $\mathcal{L}_t = -(\mathcal{K} + I)$ and $\mathcal{L}_t^* = -(\mathcal{K}^* + I)$, we have

$$\begin{aligned} & \frac{d}{ds} \int \epsilon_+(s, t) e^{\int_0^s \rho(s') ds'} \Phi(s, t) dt = \int \epsilon(s, t) e^{\int_0^s \rho(s') ds'} \\ & [\mathcal{K}^*(\text{sgn}_+(\epsilon(s, \cdot)) \Phi(s, \cdot)) - \mathcal{K}^*(\Phi(s, \cdot) \text{sgn}_+(\epsilon(s, t)))(t)] dt, \end{aligned}$$

and

$$\begin{aligned} & \frac{d}{ds} \int \epsilon_-(s, t) e^{\int_0^s \rho(s') ds'} \Phi(s, t) dt = - \int \epsilon(s, t) e^{\int_0^s \rho(s') ds'} \\ & [\mathcal{K}^*(\text{sgn}_-(\epsilon(s, \cdot)) \Phi(s, \cdot)) - \mathcal{K}^*(\Phi(s, \cdot) \text{sgn}_-(\epsilon(s, t)))(t)] dt. \end{aligned}$$

Therefore, using that $|\epsilon(s, t)| = \epsilon_+ + \epsilon_-$ we obtain

$$\begin{aligned} & \frac{d}{ds} \int |\epsilon(s, t)| e^{\int_0^s \rho(s') ds'} \Phi(s, t) dt = - \int \epsilon(s, t) \\ & e^{\int_0^s \rho(s') ds'} \mathcal{K}^*(\Phi(s, \cdot)) dt \\ & + \int |\epsilon(s, t)| e^{\int_0^s \rho(s') ds'} \mathcal{K}^*(\Phi(s, \cdot)) dt. \end{aligned}$$

Using that

$$\frac{d}{ds} \Phi + (\rho - 1) \Phi = \mathcal{K}^* \Phi,$$

we have

$$\frac{d}{ds} \int |\epsilon(s, t)| e^{\int_0^s \rho(s') ds'} \Phi(s, t) dt = -(\rho - 1) \int \epsilon(s, t)$$

$$\begin{aligned} & e^{\int_0^s \rho(s') ds'} \Phi dt + (\rho - 1) \int |\epsilon(s, t)| e^{\int_0^s \rho(s') ds'} \Phi dt \\ & - \int [|\epsilon(s, t)| - |\epsilon(s, t)|] e^{\int_0^s \rho(s') ds'} \frac{d}{ds} \Phi dt, \end{aligned}$$

and so we find

$$\begin{aligned} & \frac{d}{ds} \int |\epsilon(s, t)| e^{\int_0^s \rho(s') ds'} \Phi(s, t) dt = -(\rho - 1) \int \epsilon(s, t) \\ & e^{\int_0^s \rho(s') ds'} \Phi dt + (\rho - 1) \int |\epsilon(s, t)| e^{\int_0^s \rho(s') ds'} \Phi dt \\ & + 2 \int \epsilon_-(s, t) e^{\int_0^s \rho(s') ds'} \frac{d}{ds} \Phi dt. \end{aligned}$$

Noticing that

$$-\frac{d}{ds} \Phi = (\rho - 1) \left[Id - \frac{\mathcal{K}^*}{\rho - 1} \right] \Phi,$$

where $[Id - \frac{\mathcal{K}^*}{\rho - 1}] \geq 0$ and $[Id - \frac{\mathcal{K}^*}{\rho - 1}] > 0$ whenever $\Phi \neq Cts\Psi$ with

$$\left[Id - \frac{\mathcal{K}^*}{\rho - 1} \right] \Psi = 0,$$

(using Krein Rutmann), we have

$$-\frac{d}{ds} \Phi \geq 0,$$

since $\Phi \geq 0$. Finally, we have

$$\begin{aligned} & \frac{d}{ds} \int |\epsilon(s, t)| e^{\int_0^s \rho(s') ds'} \Phi(s, t) dt \leq \\ & -(\rho - 1) \int \epsilon(0, t) \Phi(0, t) dt \\ & + (\rho - 1) \int |\epsilon(s, t)| e^{\int_0^s \rho(s') ds'} \Phi dt, \end{aligned}$$

and, using Gronwall inequality, we obtain

$$\begin{aligned} & \int |\epsilon(s, t)| \Phi(s, t) dt \leq -(\rho - 1) \int \epsilon(0, t) \Phi(0, t) dt e^{-s} \\ & + e^{-s} \int_0^s e^{-\int_0^{s'} (\rho(s'') - 1) ds''} ds', \end{aligned}$$

and (30) is satisfied. \square

Appendix B. An example of predator-prey model with anti-cipation

We follow here the work of J. Terry in Terry (2014), in which, the growth rate of predators is decomposed into a birth rate B and a death rate D . At time t , predators $P(t)$ and preys $N(t)$ follow the master system of equations

$$\begin{cases} \frac{d}{dt} N(t) = \underbrace{rN(1 - N/K)}_{\text{logistic growth}} - \underbrace{P(t)F(N(t))}_{\text{hunt}} \\ \frac{d}{dt} P(t) = P(t) \left[\underbrace{B(F(N(t)))}_{\text{birth rate}} - \underbrace{D(F(N(t)))}_{\text{death rate}} \right], \end{cases} \quad (31)$$

with F (Holling type II) defined as (a, b positive constants)

$$F(N) = \frac{aN}{1 + bN}.$$

Paper gives as example,

$$B(F(N)) = \begin{cases} 0, & 0 \leq F(N) \leq \phi_1 \\ \beta, & F(N) \geq \phi_2 \\ \beta \cos^2\left(\frac{\pi}{2}\left(1 + \frac{F(N) - \phi_1}{\phi_2 - \phi_1}\right)\right), & \text{else} \end{cases}, \quad (32)$$

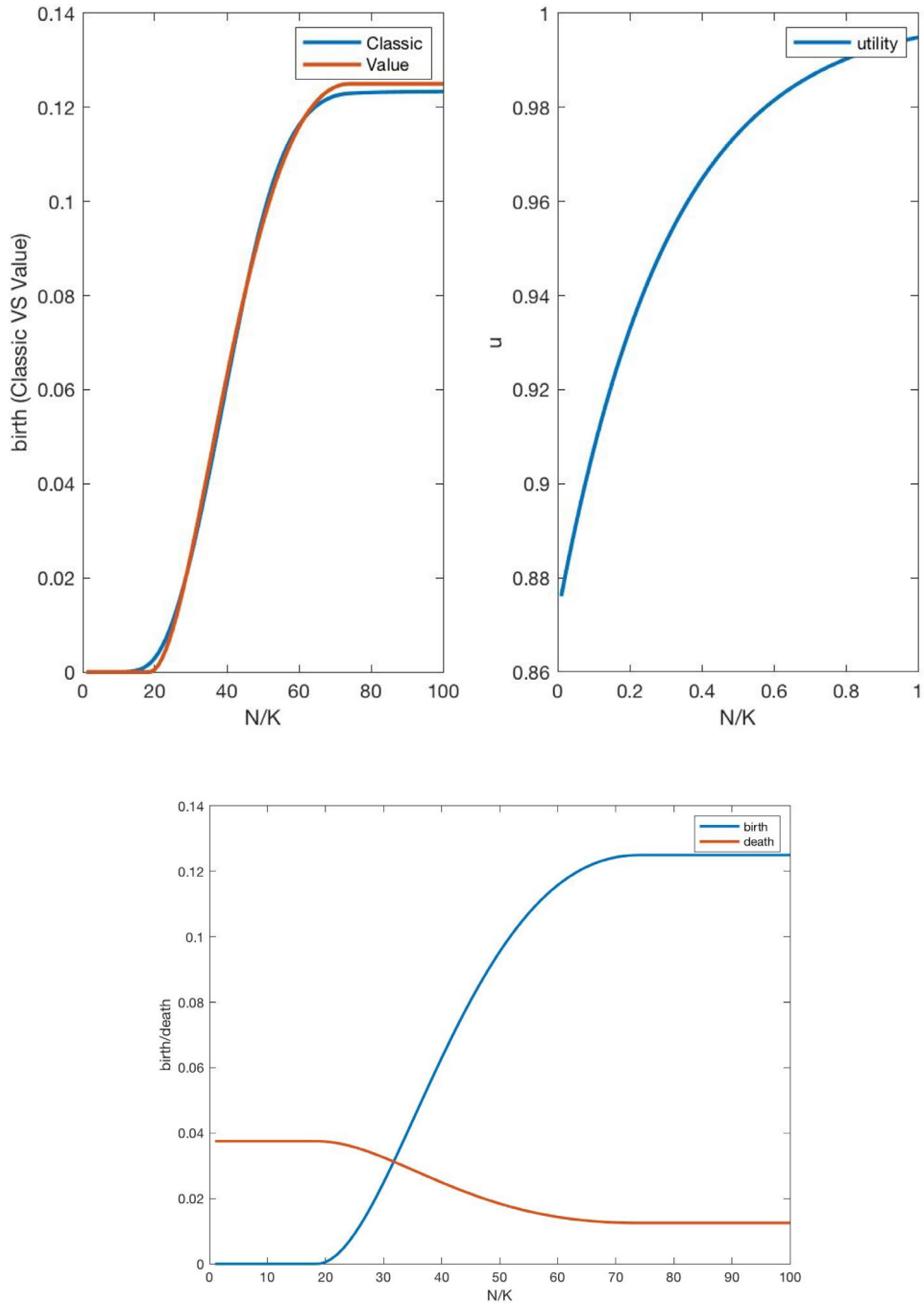


Fig. 11. Down. Birth and Death rate with respect to N/K . Up. For parameters $[Te, C, \chi, a_u, c_u] = [3.4862, 3.3665, 0.6019, 6.9439, 0.8421]$ well chosen and $discount_{factor} = 15/100$ we have the birth rate B and $N \mapsto \beta\gamma_N$ solution to $0 = u(N) + \beta\gamma_N(\chi V_N - C) - (D(F(N)) + discount_{factor})V_N$, with $\gamma_N = \frac{1}{1+e^{-\chi(V_N-C)}}$ are equal ($B = \beta\gamma_N$).

and

$$D(F(N)) = \begin{cases} d_M, & 0 \leq F(N) \leq \theta_1 \\ d_m, & F(N) \geq \theta_2, \\ d_m + (d_M - d_m) \cos^2\left(\frac{\pi}{2} \left(\frac{F(N) - \theta_1}{\theta_2 - \theta_1}\right)\right), & \text{else} \end{cases}, \quad (33)$$

with $\theta_1, \theta_2, \phi_1, \phi_2, \beta$ (maximal birth rate), d_M (maximal death rate) and d_m (minimal death rate) positive constants. Following

the construction of Section 2.1, we have

$$\begin{cases} \frac{d}{dt} N(t) = \underbrace{rN(1 - N/K)}_{\text{logistic growth}} - \underbrace{P(t)F(N(t))}_{\text{hunt}} \\ \frac{d}{dt} P(t) = P(t) \left[\underbrace{\beta\gamma(t)}_{\text{birth}} - \underbrace{D(F(N(t)))}_{\text{death rate}} \right] \\ -\frac{d}{dt} V(t) = u(N(t)) + \beta\gamma(t)(\chi V(t) - C) - (D(F(N(t))) + discount_{factor})V(t) \end{cases}, \quad (34)$$

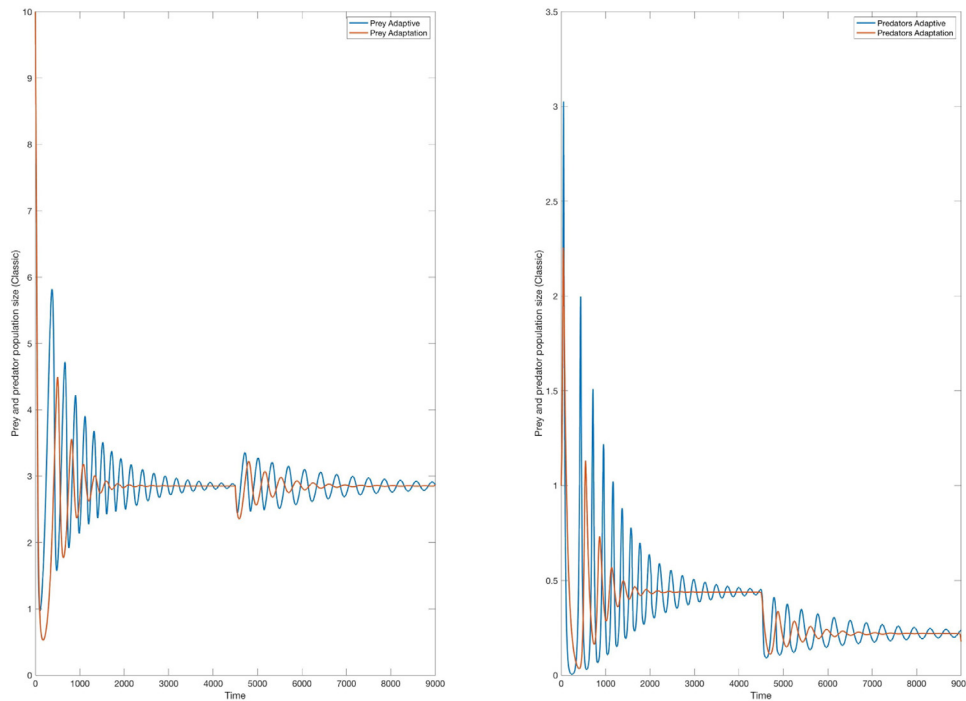


Fig. 12. Comparing adaptive and anticipation when the growth rate for prey changes brutally (at time $t = 4500$) for $r = .0125$ to $r = 0.0063$ (demographic catastrophe): at left preys, at right predators, in blue adaptive and in red adaptation.

and

$$\gamma(t) = \frac{1}{1 + e^{-Te(\chi V(t) - C)}}$$

for the anticipation model and

$$\begin{cases} \frac{d}{dt} N(t) = \underbrace{rN(1 - N/K)}_{\text{logistic growth}} - \underbrace{P(t)F(N(t))}_{\text{hunt}} \\ \frac{d}{dt} P(t) = P(t) \left[\underbrace{\beta\gamma(t)}_{\text{birth}} - \underbrace{D(F(N(t)))}_{\text{death rate}} \right] \\ 0 = u(N(t)) + \beta\gamma(t)(\chi V(t) - C) - (D(F(N(t))) + \text{discount}_{\text{factor}})V(t) \end{cases}, \quad (35)$$

and

$$\gamma(t) = \frac{1}{1 + e^{-Te(\chi V(t) - C)}}$$

for the adaptive model. The author studies the existence, uniqueness and stability of steady states depending of values of $\theta_1, \theta_2, \phi_1, \phi_2, \beta, d_M, d_m, r, K, a$ et b . For $\phi_1 = \theta_1 = .05, \phi_2 = \theta_2 = .1250, \beta = .15, d_M = .0375, d_m = .0125, r = .0125, K = 9, a = .0250$ et $b = .1$, there exists a locally asymptotically stable non-trivial steady state. The birth and the death rates are given in Fig. 11, we notice that for parameters $[Te, C, \chi, a_u, c_u]$ well chosen, the birth rate B can be approximated by $\beta\gamma$ as in (14).

To compare both dynamics (adaptive versus adaptation), we simulate a sudden decrease in the growth rate of the prey: r which is divided by two after time $t = 4500$. In Fig. 12, we see that adaptation involves less oscillations (in amplitude and more rapidly converging) than for the adaptive behavior.

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