

# A mathematical model for the phase of sexual reproduction in monogonont rotifers

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## Abstract

Recently, the optimal sex allocation in monogonont rotifers is studied in [1], and, as a closely related question, the relative frequencies of the relevant types of mictic females. The authors focus on the evolution of the age at which young mictic females lose their fertilization susceptibility and they address the threshold age of fertilization that maximizes resting egg production. Assuming that a stationary population is achieved, with stable age distribution, they obtain their results, without knowing the stationary population. Our aim is to study this problem in the framework of the theory of nonlinear age-dependent population dynamics developed by G. F. Webb in [13], which is more appropriate from the mathematical point of view and permits to us to obtain analytically the stationary population and consequently it is analytically shown that a threshold age of fertilization equal to the age of maturation is not an ESS, despite the fact

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that then the production of resting eggs is maximum, which has been obtained by simulation in [1].

## 1 Introduction

The theory of sex ratio evolution is one of the main topics of the modern evolutionary biology whose foundations were established by R. A. Fisher ([5]), who predicted that an equal allocation of resources of the parents in the production of both sexes should evolve (Charnov, [4]). This implies that they would produce on average an equal number of females and male if the cost of producing a male equals the cost of producing a female. Most of the work developed on sex allocation theory after this principle was stated, addressed its application to special cases, e.g., special life cycles. However, only recently the theory has been extended to monogonont rotifers ([1]). These animals are haplodiploid cyclical parthenogens who often inhabit temporal waters. Their life-history traits are critical in order to apply sex ratio theory, as important difficulties arise.

Cyclic parthenogenesis includes life cycles in which reproduction is accomplished by both sexual and asexual means. In rotifer life cycle (see, e.g., [2]), amictic (asexual) reproduction is the usual way in which the population grows by means of a repeated number of parthenogenetic generations of new amictic females producing subitaneous diploid eggs that develop into new amictic females. Beside this mode of reproduction, there are also periods of sexual reproduction or mixis of varying duration. After mixis is induced by factors such as population density ([7], [3]), the amictic females parthenogenetically produce both amictic and mictic (sexual) daughters. If the parthenogenetic population growth is constrained by intraspecific competition and the growth season is long, optimality arguments predict that mictic daughters would be produced at a constant rate for most of the growth season ([10]).

At the beginning of the mictic phase, no males are yet present in the population, newborn sexual females are not fertilized, and they produce only haploid males. But, when males occur, the sexual females can be fertilized, and they produce resting eggs, a kind of cyst that stays dormant for some time before hatching. These eggs are responsible for the reinitiation of rotifer population after periods of adverse conditions, as well as a means of dispersal. As a result, the contribution of the resting eggs produced a year to the current recruitment of females is considered to be negligible (e.g. [10]). Note also that an effect of the number of resting eggs produced during a growth season on the recruitment of mictic females in the next growth season is unlikely under

conditions of intraspecific competition and long growth season, since most of the mictic daughters will be produced when population size is at an equilibrium controlled by the competition, but not by the number of hatched resting eggs. Only if the number of resting eggs produced a year is very low, the number of females recruited from the resting egg would be very low in the next year, and so the density of mictic females might be affected.

According to the finding reported for a genus (*Brachionus*), rotifer mictic female fertilization is only possible for a few hours after birth, and a single copulation is enough to fertilize all the eggs a mictic female will produce ([9]). As a result, there is a threshold age of fertilization for the young mictic females. If a female is not fertilized while young, she will only produce males once maturity is reached. Note that there is a negative feedback loop on male density, since, if males are rare, fertilization will also be rare and male-producing mictic females will become more frequent. This complex life cycle includes three different kinds of mature females (amictic females, male-producing mictic females, and resting-egg producing mictic females) and males, which makes the extension of the sex allocation theory to monogonont rotifers elusive as it is not really clear what can be considered masculine and feminine function in these organisms (e.g., [12], [11]).

In [1], Aparici et al. focused their attention on the study of the sexual phase of the cycle and on the evolution of the threshold age of fertilization of mictic female, since the latter is an intrinsic trait affecting sex allocation that can undergo selection if we presume, as expected, that there is genetic variation for this trait. These authors found that the evolutionarily stable strategy (ESS) for the threshold age of fertilization determines that half of the mictic females should be fertilized, and half not. In other words, half of them will produce only male, and the other half only resting eggs, which hatch in the future producing only females. Given that both types of sexual females are assumed to have the same cost, this means that half of the sexual resources are going to be invested in masculine function through male-producing mictic females, accounting indirectly for male allocation, and the other half in feminine function through resting-egg producing mictic females, accounting by themselves for female allocation.

Unfortunately, the theoretical work by Aparici et al. [1] is based on simulation, and so it lacks of the generality required to draw clear conclusions. This shortcoming might be important as the authors assumed in their simulations parameter values for a single rotifer species, given the scare of empirical data in the literature, and no sensitivity analysis was performed in order to asses the robustness of their conclusions. However, they provided a echeme model that can be used in developing a more formal model in order to study it analitically.

Aparici et al. [1] used the concept of Evolutionary Stable Strategy (ESS) to predict

the evolutionary output. Using the concept of ESS as a fitness criterion is critical if we are dealing with frequency-dependent selection, since under such a kind of selection, standard fitness measurements (e.g., intrinsic rate of natural increase) might not work. It has long been known that selection on sex allocation is frequency-dependent, and that its evolution does not necessarily, if ever, maximize population growth rate. Thus, rotifer sex allocation provides an excellent opportunity to apply the ESS concept to a frequency-dependent selection problem, with the additional complication of non-linear effects on male density through a demographic feedback. Again, a more general and rigorous approach than that used in [1] is needed.

In Section 2 we are going to model the dynamics of the mictic phase using the general theory of nonlinear age-dependent population dynamics developed by G. F. Webb in [13], to address the evolution of the age for the loss of fertilization susceptibility ( $T$ ), and its effect on the proportion of the two types of mictic females (i.e., male-producing and resting egg-producing). We show in Section 3 that  $T$  maximizing the production of resting eggs is the age at maturity ( $M$ ), but this value of  $T$  does not correspond in general to an evolutionarily stable strategy. Section 4 is devoted to the computation of the evolutionarily stable threshold age of fertilization. As this trait has no competition effects, the frequency of mutants in each mictic females recruitment period is equal to that of the precedent lay of resting eggs. So the criterion of invasibility reduces to computing the frequency of mutants in the new resting eggs production after a sexual period and comparing it to the former. Section 5 contains a concrete example and some plots of equilibrium distributions for different values of the parameters  $T$  and  $M$ .

## 2 Formulation of the model

The model parameters are assumed to be time-independent and the recruitment rate of mictic female ( $B$ ) is a parameter in our model (see the Introduction). The parameters are the following:

- $\mu$  the per capita mortality rate for females,
- $\mu_h$  the per capita mortality rate for males,
- $e$  the male-female encounter rate,
- $m$  the fecundity of male-producing mictic females,
- $M$  the age at maturity for females,
- $T$  the threshold age of fertilization ( $T \leq M$ ).

For the densities of the population, which is divided in three population subclasses, we use the following notations:

$F_v(x, t)$  virgin mictic females,  $x$ -aged, at time  $t$ ,  
 $F_m(x, t)$  mated mictic females,  $x$ -aged, at time  $t$ ,  
 $H(x, t)$  males,  $x$ -aged, at time  $t$ .

Let  $l(x, t)$  be the density with respect to age  $x$  of the population at time  $t$ , i.e.,

$$l(x, t) = (F_v(x, t), F_m(x, t), H(x, t)).$$

Then, the total population at time  $t$  of members of the population between ages  $a_1$  and  $a_2$  is

$$\int_{a_1}^{a_2} l(x, t) dx = \int_{a_1}^{a_2} F_v(x, t) dx + \int_{a_1}^{a_2} F_m(x, t) dx + \int_{a_1}^{a_2} H(x, t) dx$$

and the total population at time  $t$  is

$$P(t) = \int_0^\infty l(x, t) dx.$$

In order to formulate the model we now introduce some notation. Let  $L^1 := L^1(0, \infty; \mathbb{R}^3)$  be the Banach space of equivalence classes of Lebesgue integrable functions from  $]0, \infty[$  to  $\mathbb{R}^3$  which agree almost everywhere on  $]0, \infty[$ , with norm

$$\|\phi\|_1 := \int_0^\infty |\phi(x)| dx.$$

Let  $\mathbb{R}_+^3$  denote the positive cone in  $\mathbb{R}^3$ , i.e.,

$$\mathbb{R}_+^3 = \{(x_1, x_2, x_3) \in \mathbb{R}^3 : x_i \geq 0 \text{ for } i = 1, 2, 3\}.$$

Let  $L_+^1$  denote the positive cone in  $L^1$ , i.e.,

$$L_+^1 = \{\phi \in L^1 : \phi(x) \in \mathbb{R}_+^3 \text{ for almost all } x > 0\}.$$

Let  $S > 0$  and let  $L_S := C([0, S]; L^1)$  be the Banach space of continuous  $L^1$ -valued functions on  $[0, S]$  with the supremum norm

$$\|l\|_\infty := \sup_{0 \leq t \leq S} \|l(t)\|_1.$$

In a natural way we identify each element of  $L_S$  with an element of the space  $L^1(]0, \infty[ \times ]0, S]; \mathbb{R}^3)$ . We will use the symbol  $l$  to denote both of these elements in that

$$l(t)(x) = l(x, t) \quad 0 \leq t \leq S, \quad \text{a.e. } x > 0.$$

The formulation of age-dependent population dynamics is motivated in the following way. The average rate of change in the total population size in the time interval  $]t, t+h[$  is

$$\frac{P(t+h) - P(t)}{h} = \frac{1}{h} \int_0^h l(x, t+h) dx + \int_0^\infty \frac{1}{h} [l(x+h, t+h) - l(x, t)] dx. \quad (2.1)$$

As  $h \rightarrow 0$  in (2.1), the term on the left-hand side converges to the instantaneous rate of change of the total population size at time  $t$ , the first term on the right-hand side converges to the instantaneous birth rate at time  $t$ , and the second term on the right-hand side converges to the instantaneous rate of change of total population at time  $t$  due to causes other than births.

We are thus led to the following formulation of age-dependent population dynamics: Let  $S > 0$ , let  $l \in L_S$ , let  $F$  be a mapping from  $L^1$  to  $\mathbb{R}^3$ , let  $G$  be a mapping from  $L^1$  into  $L^1$ , and let  $\phi \in L^1$ . The *balance law* of the population is given by

$$\lim_{h \rightarrow 0^+} \int_0^\infty \left| \frac{1}{h} [l(x+h, t+h) - l(x, t)] - G(l(\cdot, t))(x) \right| dx = 0 \quad 0 \leq t \leq S. \quad (2.2)$$

The *birth law* of the population is given by

$$\lim_{h \rightarrow 0^+} \frac{1}{h} \int_0^h |l(x, t+h) - F(l(\cdot, t))| dx = 0 \quad 0 \leq t \leq S. \quad (2.3)$$

The *initial age distribution* of the population is given by

$$l(\cdot, 0) = \phi. \quad (2.4)$$

From (2.1), (2.2), (2.3) we see that the instantaneous rate of change of the total population satisfies

$$\frac{d}{dt} P(t) = F(l(\cdot, t)) + \int_0^\infty G(l(\cdot, t)) dx,$$

where  $F(l(\cdot, t))$  represents the birth rate at time  $t$  and  $\int_0^\infty G(l(\cdot, t))(x) dx$  represents the rate of change of total population at time  $t$  due to causes other than births. The function  $F$  is called the *birth function* and  $G$  the *aging function*. We will refer to the equations (2.2), (2.3) and (2.4) as the *problem (ADP)*. In [13] the following definition is given.

**Definition 2.1** Let  $S > 0$  and let  $l \in L_S$ . We say that  $l$  is a solution of (ADP) on  $[0, S]$  provided that  $l$  satisfies (2.2), (2.3) and (2.4).

In the case of a population of monogonont rotifers and assuming that the parameters are time-independent, if we define

$$H(t) = \int_0^\infty H(x, t) dx,$$

we have

$$F_v(x+h, t+h) - F_v(x, t) \approx \begin{cases} -\mu F_v(x, t)h - eF_v(x, t)H(t)h & \text{if } x < T \\ -\mu F_v(x, t)h & \text{if } x \geq T \end{cases}$$

$$F_m(x+h, t+h) - F_m(x, t) \approx \begin{cases} -\mu F_m(x, t)h + eF_v(x, t)H(t)h & \text{if } x < T \\ -\mu F_m(x, t)h & \text{if } x \geq T \end{cases}$$

$$H(x+h, t+h) - H(x, t) \approx -\mu_h H(x, t)h.$$

Consequently, in this case the aging function is the function  $G : L^1 \rightarrow L^1$  defined on  $\phi = (\phi_1, \phi_2, \phi_3)$  as

$$G(\phi)_1(x) := \begin{cases} -\mu\phi_1(x) - e\phi_1(x) \int_0^\infty \phi_3(y) dy & \text{if } x < T \\ -\mu\phi_1(x) & \text{if } x \geq T \end{cases}$$

$$G(\phi)_2(x) := \begin{cases} -\mu\phi_2(x) + e\phi_1(x) \int_0^\infty \phi_3(y) dy & \text{if } x < T \\ -\mu\phi_2(x) & \text{if } x \geq T \end{cases}$$

$$G(\phi)_3(x) := -\mu_h\phi_3(x).$$

On the other hand, we have:

$$\begin{aligned} F_v(0, t) &= B, & F_m(0, t) &= 0 \quad \forall t > 0 \\ H(0, t) &= m \int_M^\infty F_v(x, t) dx \quad \forall t \geq M. \end{aligned}$$

Therefore, in this case the birth function is the function  $F : L^1 \rightarrow \mathbb{R}^3$  defined by

$$F(\phi_1, \phi_2, \phi_3) := \left( B, 0, m \int_M^\infty \phi_1(x) dx \right).$$

We have the following existence and uniqueness result.

**Theorem 2.2** *Given  $\phi \in L_+^1$ , there exists a unique global solution  $l$  of (ADP) (i.e., a solution of (ADP) on  $[0, S]$  for all  $S > 0$ ) such that  $l(\cdot, t) \in L_+^1$  for  $t \geq 0$ .*

### 3 The stationary population

In this section we are going to calculate the stationary population of the monogonont rotifers involved in the sexual phase given by our model.

As a consequence of [13, Theorem 3.2], if we define  $S(t)\phi := l(\cdot, t)$ , being  $l$  the unique solution of problem (ADP) with initial datum  $\phi \in L_+^1$  given by Theorem 2.2, then  $(S(t))_{t \geq 0}$  is a strongly continuous nonlinear semigroup in  $L_+^1$  with infinitesimal generator  $-A$ , being  $A$  the operator from  $L_+^1$  into  $L^1$  defined by

$$A\phi := \phi' - G(\phi) \quad \text{for } \phi \in D(A),$$

where

$$D(A) := \{\phi \in L_+^1 : \phi \text{ absolutely continuous on } [0, \infty[, \phi' \in L^1 \text{ and } \phi(0) = F(\phi)\}.$$

Let  $\phi \in L_+^1$ , and let  $l$  be the solution of (ADP) with initial datum  $\phi$ , i.e.,  $l(t) = S(t)\phi$ . Then,  $l$  is an *equilibrium solution* of (ADP) if and only if  $l(\cdot, t) = \phi$  for all  $t \geq 0$ , that is, if  $\phi$  is a fixed point of the semigroup  $(S(t))_{t \geq 0}$ . Now, by [13, Proposition 4.1],  $l$  is an equilibrium solution of (ADP) if and only if  $A\phi = 0$ . Consequently, to obtain the equilibrium solution of (ADP) we have to find the absolutely continuous functions  $\phi^T \in L_+^1$ , with  $(\phi^T)' \in L^1$ , satisfying:

$$(\phi^T)' = G(\phi^T) \quad \text{and} \quad \phi^T(0) = \left( B, 0, m \int_M^\infty \phi_1^T(x) dx \right).$$

Therefore, we need to solve the following ODE initial value-problem:

$$(\phi^T)'_1(x) = \begin{cases} -\mu\phi_1^T(x) - e\phi_1^T(x) \int_0^\infty \phi_3^T(y) dy & \text{if } x < T \\ -\mu\phi_1^T(x) & \text{if } x \geq T \end{cases} \quad (3.1)$$

$$(\phi^T)'_2(x) = \begin{cases} -\mu\phi_2^T(x) + e\phi_1^T(x) \int_0^\infty \phi_3^T(y) dy & \text{if } x < T \\ -\mu\phi_2^T(x) & \text{if } x \geq T \end{cases} \quad (3.2)$$



$$(\phi^T)'_3(x) = -\mu_h \phi_3^T(x) \quad \text{if } x \geq 0 \quad (3.3)$$

$$\phi_1^T(0) = B, \quad \phi_2^T(0) = 0, \quad \phi_3^T(0) = m \int_M^\infty \phi_1^T(y) dy. \quad (3.4)$$

From (3.3) we obtain that

$$\phi_3^T(x) = m \left( \int_M^\infty \phi_1^T(y) dy \right) \exp(-\mu_h x).$$

Now, since  $\phi_1^T(x) = \phi_1^T(T) \exp(\mu(T-x))$  for all  $x \geq T$ , and  $T \leq M$ , it follows that

$$\int_M^\infty \phi_1^T(y) dy = \frac{\phi_1^T(T)}{\mu} \exp(\mu(T-M)).$$

Hence,

$$\phi_3^T(x) = \frac{m\phi_1^T(T)}{\mu} \exp(\mu(T-M)) \exp(-\mu_h x). \quad (3.5)$$

Then,

$$\int_0^\infty \phi_3^T(y) dy = \frac{m\phi_1^T(T)}{\mu\mu_h} \exp(\mu(T-M)).$$

Thus, for  $x < T$ , we have

$$(\phi^T)'_1(x) = -\mu\phi_1^T(x) - \frac{em\phi_1^T(T)}{\mu\mu_h} \exp(\mu(T-M))\phi_1^T(x).$$

From where it follows that

$$\phi_1^T(x) = \phi_1^T(0) \exp \left[ \left( -\mu - \frac{em\phi_1^T(T)}{\mu\mu_h} \exp[\mu(T-M)] \right) x \right] \quad \text{for } 0 \leq x \leq T.$$

Then, since  $\phi_1^T$  is continuous, we get

$$\phi_1^T(T) = B \exp(-\mu T) \exp \left[ -\frac{emT}{\mu\mu_h} \exp(\mu(T-M))\phi_1^T(T) \right]. \quad (3.6)$$

Since  $B \exp(-\mu T) > 0$  and  $-\frac{emT}{\mu\mu_h} \exp(\mu(T-M)) < 0$ , the equation (3.6) has a unique solution  $\phi_1^T(T)$ . Consequently, we have

$$\phi_1^T(x) = \begin{cases} B \exp \left[ \left( -\mu - \frac{em\phi_1^T(T)}{\mu\mu_h} \exp[\mu(T-M)] \right) x \right] & \text{for } 0 \leq x \leq T \\ \phi_1^T(T) \exp(\mu T) \exp(-\mu x) & \text{for } x \geq T, \end{cases} \quad (3.7)$$

with  $\phi_1^T(T)$  given by (3.6).

On the other hand, by (3.2), for  $x \geq T$ ,  $\phi_2^T(x) = \phi_2^T(T) \exp(\mu T) \exp(-\mu x)$ , and for  $x < T$ , we have

$$(\phi_2^T)'(x) = -\mu\phi_2^T(x) + \frac{em\phi_1^T(T)}{\mu\mu_h} \exp[\mu(T-M)]\phi_1^T(x).$$

From here, using (3.7), it follows that for  $x < T$ ,

$$\phi_2^T(x) = B \exp(-\mu x) \left[ 1 - \exp \left( -\frac{em\phi_1^T(T)}{\mu\mu_h} \exp[\mu(T-M)]x \right) \right].$$

Then, by the continuity of  $\phi_2^T$  we obtain

$$\phi_2^T(T) = B \exp(-\mu T) \left[ 1 - \exp \left( -\frac{em\phi_1^T(T)}{\mu\mu_h} \exp[\mu(T-M)]T \right) \right]. \quad (3.8)$$

Therefore,

$$\phi_2^T(x) = \begin{cases} B \exp(-\mu x) \left[ 1 - \exp \left( -\frac{em\phi_1^T(T)}{\mu\mu_h} \exp[\mu(T-M)]x \right) \right] & \text{for } 0 \leq x \leq T \\ B \exp(-\mu x) \left[ 1 - \exp \left( -\frac{em\phi_1^T(T)}{\mu\mu_h} \exp[\mu(T-M)]T \right) \right] & \text{for } x \geq T. \end{cases} \quad (3.9)$$

Consequently, at the demographic equilibrium, the number of males ( $H(T)^*$ ), of virgin mictic females ( $F(T)_v^*$ ) and of mated mictic females ( $F(T)_m^*$ ), is given by:

$$H(T)^* = \int_0^\infty \phi_3^T(x) dx = \frac{m\phi_1^T(T)}{\mu\mu_h} \exp(\mu(T-M)). \quad (3.10)$$

$$F(T)_v^* = \int_0^\infty \phi_1^T(x) dx = \frac{\phi_1^T(T)}{\mu} + \frac{B}{\mu + eH^*(T)} \left[ 1 - \exp \left( (-\mu - eH(T)^*)T \right) \right]. \quad (3.11)$$

$$F(T)_m^* = \int_0^\infty \phi_2^T(x) dx = B \left( \frac{1}{\mu + eH(T)^*} - \frac{1}{\mu} \right) \left( \exp \left[ (-\mu - eH(T)^*)T \right] - 1 \right). \quad (3.12)$$

At the equilibrium, we have that the number of resting egg-producing mictic females ( $F(T)_r^* := \int_M^\infty \phi_2^T(x) dx$ ) is given by

$$F(T)_r^* = \frac{B}{\mu} \exp(-\mu M) \left[ 1 - \exp \left( -\frac{em\phi_1^T(T)}{\mu\mu_h} \exp(\mu(T - M))T \right) \right]. \quad (3.13)$$

Now, by (3.8) and (3.10), we also have

$$F(T)_r^* = \frac{\phi_2^T(T)}{\mu} \exp(\mu(T - M)) \quad (3.14)$$

and

$$F(T)_r^* = \frac{B}{\mu} \exp(-\mu M) \left[ 1 - \exp(-eH(T)^*T) \right]. \quad (3.15)$$

On the other hand, the number at the equilibrium of male-producing mictic females ( $F(T)_h^* := \int_M^\infty \phi_1^T(x) dx$ ) is given by

$$F(T)_h^* = \frac{\phi_1^T(T)}{\mu} \exp(\mu(T - M)). \quad (3.16)$$

Then, by (3.10) we have

$$F(T)_h^* = \frac{\mu_h}{m} H(T)^*. \quad (3.17)$$

Now, by (3.6) and (3.10), it follows that

$$\phi_1^T(T) = B \exp(-\mu T) \exp(-eH(T)^*T). \quad (3.18)$$

By combining equations (3.16) and (3.18), we obtain

$$F(T)_h^* = \frac{B}{\mu} \exp(-eH(T)^*T) \exp(-\mu M). \quad (3.19)$$

Hence, by (3.17) and (3.19), we can write the equation

$$H(T)^* = \frac{mB}{\mu\mu_h} \exp(-eH(T)^*T) \exp(-\mu M). \quad (3.20)$$

Finally, combining equations (3.15) and (3.20), we get

$$F(T)_r^* = \frac{B}{\mu} \exp(-\mu M) - \frac{\mu_h}{m} H(T)^*. \quad (3.21)$$

From this equation, where  $T$  is absent, we conclude that maximizing resting eggs production involves the choice of a value of  $T$  that minimizes the number of males at equilibrium. Now (3.20) yields

$$T = \frac{K - \log(H(T)^*)}{eH(T)^*}, \quad (3.22)$$

where

$$K = \log\left(\frac{mB}{\mu\mu_h}\right) - \mu M$$

is constant. On the other hand, since  $T > 0$ , we have that  $H(T)^* < \exp(K)$ . Hence, since the function  $f(x) = \frac{K - \log(x)}{ex}$  is decreasing if  $x \leq \exp(K + 1)$ , from (3.22) it follows that the value of  $T$  maximizing the production of resting eggs is the maximum possible, that is,  $M$ . In conclusion, we have proved that:

*In order to maximize the production of resting eggs in a population of monogonont rotifers the threshold age of fertilization should be the age at maturity.*

The same conclusion has been obtained in [1].

## 4 Evolutionarily Stable Strategy

Laboratory populations studies, of different rotifer species, show that susceptibility to fertilization disappears a significant time before mictic females reach maturity (see [1] and the references therein). So, in [1], it is studied if  $T = M$  is an *Evolutionarily Stable Strategy* (ESS) in the sense of Maynard Smith and Price ([8]), that is, a strategy that, if all the members of a population adopt it, no mutant strategy could invade the population under the influence of natural selection, and the authors show by simulation that  $T = M$  is not an ESS. In this section we obtain this result analytically.

The invasibility of a value  $T$  of the threshold age of fertilization can be tested by assuming a small rate of recruitment  $B_i$  of sexual females with a dominant mutant allele determining a different value  $T' \leq M$  of the threshold age of fertilization. As usual, one assumes that the (small) invading population does not change the environmental conditions determined by the resident one. In this case these reduce to the population density  $\phi_1^T$  of the resident virgin mictic females and to the total population  $H(T)^*$  of the resident males, both at the demographic equilibrium.

For the invading population we write a system of four linear equations where the state variables are the density  $\psi_1(x, t)$  of virgins mictic females (heterozygotic), the density  $\psi_2(x, t)$  of mictic mated females (heterozygotic too), the density  $\psi_3(x, t)$  of males (haploid, carrying the mutant allele  $T'$ ) and the density  $\psi_4(x, t)$  of resident resting-egg producing mictic females mated with mutant males (whose eggs will be heterozygotic). With mutant alleles being rare, homozygote mutant individuals have negligible frequency under random mating, and they will not be considered.

In this system, the rate of transition from virgin to mated is proportional to the density of virgin mictic females and to the population number of resident males for ages below the threshold  $T'$  and it is zero above it. The rate of production of resident females mated to a mutant male is proportional to the density of virgin resident females and to the population number of mutant males for ages below the threshold  $T$  and it is zero above it. Finally, the birth rate of mutant males is equal to the fecundity rate of virgin (heterozygotic) females times half the number of them older than the maturity age  $M$ . Notice that this is in agreement with the hypothesis that terms of second (or higher order) as, for instance, the number of heterozygotic females mating with mutant males, can be ignored because the proportion of the mutant allele is small.

Assuming that the demographic equilibrium is also prevalent for the invading population (cf. [1]), we compute the production rate of heterozygotic resting eggs and define a measure  $s(T, T')$  of the *fitness* of a dominant allele  $T'$  invading a resident homozygotic population  $T$ .  $s(T, T')$  is defined as the frequency of the rare allele  $T'$  in the resting egg production divided by the frequency of  $T'$  in the production of mictic females (this latter is  $B_i/B$ ). This definition is motivated by the following reasoning. Notice that, as the phenotypic differences between alleles  $T$  and  $T'$  only affect the length of the fertilizable period of the sexual mictic females, i.e., they do not have any competition effect, the frequency of allele  $T'$  in the recruitment of sexual females in the next sexual reproduction period (following a parthenogenetic reproduction period ended at a demographic equilibrium), i.e., the “new”  $B_i/B$ , will be the same as the frequency of  $T'$  in the resting egg production was, i.e.,  $s(T, T')B_i/B$ . Therefore,  $s(T, T') < 1$  will imply an exponential extinction of the mutant allele and  $s(T, T') > 1$  will imply a spread of the mutant allele, at least while its frequency is so

small that the number of heterozygotic females mating with mutant males and hence, the nonlinear or global dynamics effects, can be ignored.

To obtain the function  $s(T, T')$ , observe that the system for the invading population can be written as a non-homogeneous linear (ADP)-problem with birth function ( $\tilde{F}$ ) and aging function ( $\tilde{G}$ ) given by:

$$\tilde{F}(\psi_1, \psi_2, \psi_3, \psi_4) := \left( B_i, 0, \frac{m}{2} \int_M \psi_1(y) dy, 0 \right),$$

and  $\tilde{G} : L^1 \rightarrow L^1$  defined on  $\psi = (\psi_1, \psi_2, \psi_3, \psi_4)$  as

$$\tilde{G}(\psi)_1(x) := \begin{cases} -\mu\psi_1(x) - eH(T)^*\psi_1(x) & \text{if } x < T' \\ -\mu\psi_1(x) & \text{if } x \geq T' \end{cases}$$

$$\tilde{G}(\psi)_2(x) := \begin{cases} -\mu\psi_2(x) + eH(T)^*\psi_1(x) & \text{if } x < T' \\ -\mu\psi_2(x) & \text{if } x \geq T' \end{cases}$$

$$\tilde{G}(\psi)_3(x) := -\mu_h\psi_3(x)$$

$$\tilde{G}(\psi)_4(x) := \begin{cases} -\mu\psi_4(x) + e\phi_1^T(x) \int_0^\infty \psi_3(y) dy & \text{if } x < T \\ -\mu\psi_4(x) & \text{if } x \geq T \end{cases}$$

Working as in the previous sections, we can associate with this (ADP)-problem the operator  $B$ , with domain

$$D(B) := \{ \psi \in L^1_+ : \psi \text{ absolutely continuous on } [0, \infty[, \psi' \in L^1 \text{ and } \psi(0) = \tilde{F}(\psi) \}$$

and defined by

$$B\psi := \psi' - \tilde{G}(\psi) \quad \text{for } \psi \in D(B).$$

Consequently, to obtain the equilibrium solution of (ADP) we have to find the absolutely continuous functions  $\psi \in L^1_+$ , with  $\psi' \in L^1$ , satisfying:

$$\psi' = \tilde{G}(\psi) \quad \text{and} \quad \psi(0) = \left( B_i, 0, \frac{m}{2} \int_M \psi_1(x) dx, 0 \right).$$

Therefore, we need to solve the following ODE initial value-problem:

$$\psi'_1(x) = \begin{cases} -\mu\psi_1(x) - eH(T)^*\psi_1(x) & \text{if } x < T' \\ -\mu\psi_1(x) & \text{if } x \geq T' \end{cases} \quad (4.1)$$

$$\psi_2'(x) = \begin{cases} -\mu\psi_2(x) + eH(T)^*\psi_1(x) & \text{if } x < T' \\ -\mu\psi_2(x) & \text{if } x \geq T' \end{cases} \quad (4.2)$$

$$\psi_3'(x) = -\mu_h\psi_3(x) \quad \text{if } x \geq 0 \quad (4.3)$$

$$\psi_4'(x) = \begin{cases} -\mu\psi_4(x) + e\phi_1^T(x) \int_0^\infty \psi_3(y) dy & \text{if } x < T \\ -\mu\psi_4(x) & \text{if } x \geq T \end{cases} \quad (4.4)$$

$$\psi_1(0) = B_i, \quad \psi_2(0) = 0, \quad \psi_3(0) = \frac{m}{2} \int_M^\infty \psi_1(y) dy, \quad \psi_4(0) = 0. \quad (4.5)$$

Solving this ODE initial value-problem, we obtain:

$$\psi_1(x) = \begin{cases} B_i \exp \left[ - \left( \mu + eH(T)^* \right) x \right] & \text{for } 0 \leq x \leq T' \\ B_i \exp(-eT'H(T)^*) \exp(-\mu x) & \text{for } x \geq T' \end{cases} \quad (4.6)$$

$$\psi_2(x) = \begin{cases} B_i \exp(-\mu x) \left[ 1 - \exp \left( - exH(T)^* \right) \right] & \text{for } 0 \leq x \leq T' \\ B_i \exp(-\mu x) \left[ 1 - \exp \left( - eT'H(T)^* \right) \right] & \text{for } x \geq T' \end{cases} \quad (4.7)$$

$$\psi_3(x) = \frac{mB_i}{2\mu} \exp \left( - eT'H(T)^* \right) \exp(-\mu M) \exp(-\mu_h x) \quad (4.8)$$

$$\psi_4(x) = \begin{cases} e \left( \int_0^\infty \psi_3(y) dy \right) \exp(-\mu x) \int_0^x \exp(\mu y) \phi_1^T(y) dy & \text{for } 0 \leq x \leq T \\ e \left( \int_0^\infty \psi_3(y) dy \right) \left( \int_0^T \exp(\mu y) \phi_1^T(y) dy \right) \exp(-\mu x) & \text{for } x \geq T \end{cases} \quad (4.9)$$

From (3.7), (3.10), (4.8) and (4.9), it follows that, at the demographic equilibrium, the number of resting egg-producing mictic females mated with mutant males is given by

$$\begin{aligned}
n^* &:= \int_M^\infty \psi_4(x) dx = e \left( \int_0^\infty \psi_3(y) dy \right) \left( \int_0^T \exp(\mu y) \phi_1^T(y) dy \right) \int_M^\infty \exp(-\mu x) dx = \\
&= \frac{emB_i}{2\mu\mu_h} \exp \left( -\mu M - eT'H(T)^* \right) \frac{1}{\mu} \exp(-\mu M) \times \\
&\quad \times \int_0^T \exp(\mu y) B \exp \left( -(\mu + eH(T)^*)y \right) dy = \\
&= \frac{mBB_i}{2\mu^2\mu_h H(T)^*} \exp \left( -2\mu M - eT'H(T)^* \right) \left[ 1 - \exp \left( -eTH(T)^* \right) \right].
\end{aligned}$$

From (4.7) we have that, at the demographic equilibrium, the number of resting egg-producing heterozygotic females is given by

$$m^* := \int_M^\infty \psi_2(x) dx = \frac{B_i}{\mu} \exp(-\mu M) \left[ 1 - \exp \left( -eT'H(T)^* \right) \right].$$

Consequently, the production of resting eggs of genotype  $(TT')$  is given by

$$\begin{aligned}
&\tilde{m} \left( \frac{1}{2} m^* + n^* \right) = \frac{\tilde{m}B_i}{2\mu} \exp(-\mu M) \times \\
&\times \left[ 1 - \exp \left( -eT'H(T)^* \right) \left( 1 - \frac{mB}{\mu\mu_h H(T)^*} \exp(-\mu M) [1 - \exp \left( -eTH(T)^* \right)] \right) \right],
\end{aligned}$$

where  $\tilde{m}$  stands for the fecundity of resting eggs-producing females.

Then by (3.20), we get

$$\tilde{m} \left( \frac{1}{2} m^* + n^* \right) = \frac{\tilde{m}B_i}{2\mu} \exp(-\mu M) \left[ 1 - \exp \left( -eT'H(T)^* \right) \left( 2 - \exp \left( eTH(T)^* \right) \right) \right].$$

From here and (3.15), we have the following expression for the fitness:

$$s(T, T') = \frac{\frac{1}{2} + \left( \frac{1}{2} \exp(eTH(T)^*) - 1 \right) \exp \left( -eT'H(T)^* \right)}{1 - \exp \left( -eTH(T)^* \right)}. \quad (4.10)$$

From (4.10) it follows that the function  $s(T, T')$  takes the value 1 when  $T = T'$  (as expected) and also when  $\exp(eTH(T)^*) = 2$  (for any  $T'$ ). Then, if we denote this value of  $T$  by  $T_{\text{ess}}$ , by (3.20) we obtain



$$T_{\text{ess}} = \frac{\mu\mu_h \log(4) \exp(\mu M)}{emB}. \quad (4.11)$$

We have that the function  $s(T, T')$  is monotonous as a function of  $T'$  for any other value of  $T \neq T_{\text{ess}}$ , strictly increasing when  $T < T_{\text{ess}}$ , and strictly decreasing when  $T > T_{\text{ess}}$ . Finally,  $s(T, T_{\text{ess}}) > 1$  if  $T \neq T_{\text{ess}}$ . This means that  $T_{\text{ess}}$  (provided that it is less than  $M$ ) is an Evolutionarily Stable Strategy in the sense that it can not be invaded by a small population of mutants carrying any different allele (the frequency of them would not increase) and, on the other hand, it can invade (as a mutant) any resident allele. Moreover, it is *globally convergence* in the sense of [6] because any value of  $T$  different from  $T_{\text{ess}}$  can be invaded by mutants carrying alleles determining values of  $T$  closer to  $T_{\text{ess}}$ .

The ESS value deduced analytically here for the threshold age of fertilization coincides with the one obtained in [1] by numerical evidence of the fact that an invading/noninvadable strategy  $T$  is such that the frequency of male-producing females equals the frequency of resting egg-producing females at equilibrium. Observe that we obtain also this result since from (4.11), (3.15) and (3.19), it follows that

$$F(T_{\text{ess}})_r^* = F(T_{\text{ess}})_h^*. \quad (4.12)$$

As it is remarked in [1], (4.12), which is the prediction that evolution proceeds toward the state at which the stable numbers of male-producing mictic females versus resting eggs-producing mictic females are equal, can be interpreted in the context of the sex allocation theory of Fisher ([5]). Moreover, from (3.14), (3.16) and (4.12), it follows that

$$\phi_1^{T_{\text{ess}}}(T_{\text{ess}}) = \phi_2^{T_{\text{ess}}}(T_{\text{ess}}). \quad (4.13)$$

Finally, when  $T_{\text{ess}}$  given by (4.11) is large than  $M$  and hence unattainable, an analysis of  $s(T, T')$  easily gives that any resident strategy  $T < M$  can be invaded by any mutant with allele  $T' > T$  since then  $s(T, T') > 1$ . As  $s(M, T') < 1$  for any  $T' < M < T_{\text{ess}}$ ,  $T = M$  turns out to be an ESS which is globally convergence stable also in this case.

## 5 Concrete Example

In this section we are going to calculate, using *Mathematica*, the stationary population for concrete values of the constant parameters.

In some rotifer species, belonging to the genera *Brachionus*, the constant parameters of the model are well known (see [1]), and they are the following:

The per capita mortality rate for females  $\mu = \frac{1}{60} h^{-1}$ ,

The per capita mortality rate for males  $\mu_h = \frac{0.7}{24} h^{-1}$ ,

The male-female encounter rate  $e = \frac{0.04}{24} lh^{-1}\text{male}^{-1}$ ,

The fecundity of male-producing mictic females  $m = \frac{1.5}{24} \text{male female}^{-1}h^{-1}$ .

First of all, we get that with this values of the parameters and assuming that  $B = 1$  and  $M = 24h$ , we obtain from (4.11) that  $T_{ess} \approx 9.651$ . Consequently, in this example, the optimal threshold age of fertilization to have ESS is strictly less than the age at maturity.

For these concrete value of the parameters, to get the value of  $\phi_1^T(T)$  given by (3.6), we need to find the root of the equation

$$x - B \exp\left(-\frac{T}{60}\right) \exp\left[-\frac{1.5}{7} \exp\left(\frac{1}{60}(T-M)\right)x\right] = 0. \quad (5.1)$$

Then, by (3.10), (3.11), (3.12), (3.15) and (3.16), we have the following formulas:

$$H(T, M)^* = \frac{900}{7} \phi_1^T(T) \exp\left(\frac{1}{60}(T-M)\right).$$

$$F(T, M)_v^* = 60 \phi_1^T(T) + \frac{B}{\frac{1}{60} + \frac{1.5}{7} \phi_1^T(T) \exp\left(\frac{1}{60}(T-M)\right)} \times \\ \times \left(1 - \exp\left[\left(-\frac{1}{60} - \frac{1.5}{7} \phi_1^T(T) \exp\left(\frac{1}{60}(T-M)\right)\right)T\right]\right).$$

$$F(T, M)_m^* = B \left(\frac{1}{\frac{1}{60} + \frac{1.5}{7} \phi_1^T(T) \exp\left(\frac{1}{60}(T-M)\right)} - 60\right) \times \\ \times \left(\exp\left[\left(-\frac{1}{60} - \frac{1.5}{7} \phi_1^T(T) \exp\left(\frac{1}{60}(T-M)\right)\right)T\right] - 1\right).$$

$$F(T, M)_r^* = 60B \exp\left(-\frac{M}{60}\right) \left(1 - \exp\left[-\frac{1.5}{7} \phi_1^T(T) \exp\left(\frac{1}{60}(T-M)\right)T\right]\right).$$

$$F(T, M)_h^* = 60 \phi_1^T(T) \exp\left(\frac{1}{60}(T-M)\right).$$

Using *Mathematica* we can obtain the following plots for the total numbers of equilibrium populations for different values of  $T$  and  $M$ , assuming that  $B = 1$ :

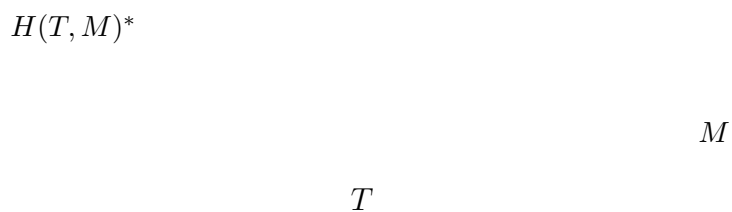


Figure 1: *Plot of the function  $H(T, M)^*$ , giving the males at equilibrium for different values of the parameters  $T$  and  $M$ .*

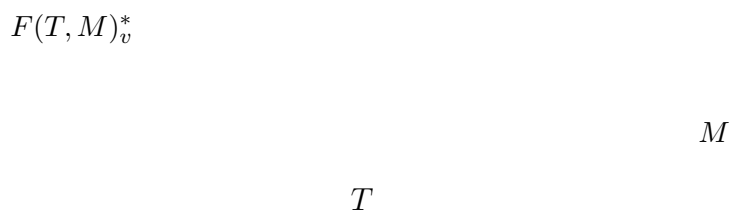


Figure 2: *Plot of the function  $F(T, M)^*_v$ , giving the virgin females at equilibrium for different values of the parameters  $T$  and  $M$ .*

$F(T, M)_m^*$

$M$

$T$

Figure 3: *Plot of the function  $F(T, M)_m^*$ , giving the mated females at equilibrium for different values of the parameters  $T$  and  $M$ .*

$F(T, M)_r^*$

$M$

$T$

Figure 4: *Plot of the function  $F(T, M)_r^*$ , giving the resting eggs-producing females at equilibrium for different values of the parameters  $T$  and  $M$ .*

$F(T, M)_h^*$  $M$  $T$ 

Figure 5: *Plot of the function  $F(T, M)_h^*$ , giving the male-producing mictic females at equilibrium for different values of the parameters  $T$  and  $M$ .*

## 6 Concluding remarks

Sex allocation theory is a robust branch of the evolutionary biology, founded long time ago. The generality of that theory should be tested by applying it to special cases, particularly to organisms with sexual reproduction associated to complex life cycles. We have shown that the theory can be developed for organisms with haplodiploid cyclical parthenogens, in which sexual reproduction is episodic and combined to asexual reproduction, and males are haploids. Rotifers are haplodiploid cyclical parthenogens with density dependent frequency of males. We have shown that the technical difficulties arisen from the non-linear effects in its life cycle can be overcome. We have proved that the main result from the sex allocation theory (i.e., the even sex allocation theorem) holds in such a complex life cycle, if the meaning of sex allocation in this context concept is adequately clarified. It refers the allocation in two types of females: male-producing mictic females and resting-egg producing mictic females. This result confirms the generality of the findings in [1] on a more rigorous basis relying in the analytical computation of the evolutionarily stable value of the threshold age of fertilization  $T$  of the mictic females. This value, less than the age at maturity in most of the biologically realistic cases, turns out to be convergence stable in the sense that a resident allele with another value of  $T$  is invadable by any mutant with a threshold age of fertilization closer to  $T_{\text{ess}}$  than  $T$ . Although a threshold age of fertilization

equal to the age at maturity is the value of  $T$  maximizing resting eggs production, it is not, typically, the value towards which evolution proceeds.

## 7 Appendix A: Proof of Theorem 2.2

By [13, Theorem 2.4], to get a unique local positive solution we only need to verify that (2.1), (2.2), (2.22) and (2.23) of [13] hold. In fact:

$$|F(\phi) - F(\psi)| = m \left| \int_M^\infty (\phi_1(x) - \psi_1(x)) dx \right| \leq m \|\phi - \psi\|_1.$$

Hence, (2.1) holds with  $c_1(r) = m$  for all  $r > 0$ .

Let  $\phi, \psi \in L^1$  with  $\|\phi\|_1 \leq r$  and  $\|\psi\|_1 \leq r$ . Then,

$$\begin{aligned} & \int_0^\infty |G(\phi)_1(x) - G(\psi)_1(x)| dx = \\ &= \int_0^T \left| -\mu\phi_1(x) - e\phi_1(x) \int_0^\infty \phi_3(y) dy + \mu\psi_1(x) + e\psi_1(x) \int_0^\infty \psi_3(y) dy \right| dx + \\ & \quad + \int_T^\infty |-\mu\phi_1(x) + \mu\psi_1(x)| dx \leq \mu \int_0^\infty |\phi_1(x) - \psi_1(x)| dx + \\ & \quad + e \int_0^T \left| \phi_1(x) \left( \int_0^\infty \phi_3(y) dy \right) - \psi_1(x) \left( \int_0^\infty \psi_3(y) dy \right) \right| dx \leq \\ & \leq \mu \|\phi_1 - \psi_1\|_1 + e \int_0^T \left| \int_0^\infty \phi_3(y) dy - \int_0^\infty \psi_3(y) dy \right| |\phi_1(x)| dx + \\ & \quad + e \int_0^T \left| \int_0^\infty \psi_3(y) dy \right| |\phi_1(x) - \psi_1(x)| dx \leq \\ & \leq \mu \|\phi_1 - \psi_1\|_1 + e \|\phi_1\|_1 \|\phi_3 - \psi_3\|_1 + e \|\psi_3\|_1 \|\phi_1 - \psi_1\|_1. \end{aligned}$$

Analogously,

$$\begin{aligned} & \int_0^\infty |G(\phi)_2(x) - G(\psi)_2(x)| dx \leq \\ & \leq \mu \|\phi_2 - \psi_2\|_1 + e \|\phi_1\|_1 \|\phi_3 - \psi_3\|_1 + e \|\psi_3\|_1 \|\phi_1 - \psi_1\|_1 \end{aligned}$$

and

$$\int_0^\infty |G(\phi)_3(x) - G(\psi)_3(x)| dx \leq \mu_h \|\phi_3 - \psi_3\|_1.$$

Therefore,

$$\|G(\phi) - G(\psi)\|_1 \leq \mu \|\phi_1 - \psi_1\|_1 + \mu \|\phi_2 - \psi_2\|_1 + \mu_h \|\phi_3 - \psi_3\|_1 + 2e \|\phi_1\|_1 \|\phi_3 - \psi_3\|_1 +$$

$$+2e\|\psi_3\|_1\|\phi_1 - \psi_1\|_1 \leq \gamma\|\phi - \psi\|_1 + 2er\|\phi - \psi\|_1,$$

with  $\gamma = \max\{\mu, \mu_h\}$ . Hence, (2.2) of [13] holds with  $c_2(r) = \gamma + 2er$  for all  $r > 0$ .

On the other hand, it is obvious that  $F(L_+^1) \subset \mathbb{R}_+^3$ , i.e., (2.22) of [13] holds, and it is easy to see that if  $c_3(r) = \gamma + er$ , then

$$G(\phi) + c_3(r)\phi \in L_+^1 \quad \text{if } \phi \in L_+^1, \quad \|\phi\|_1 \leq r,$$

so (2.23) of [13] holds too.

Consequently, for every  $\phi \in L_+^1$  there exists a unique solution  $l$  of (ADP) on a maximal interval of existence  $[0, T_\phi[$ . Let us see that  $T_\phi = \infty$ . Suppose that  $\|\phi\|_1 \leq r_1$ . Having in mind the proof of [13, Proposition 2.2], the solution  $l$  exists on  $[0, T_1]$  if  $T_1$  satisfies

$$T_1 \frac{c_1(2r_1) + c_2(2r_1) + (|F(0)| + \|G(0)\|_1)}{2r_1} + \frac{1}{2} \leq 1.$$

Now,  $|F(0)| = B$  and  $\|G(0)\|_1 = 0$ . Hence, we can take

$$T_1 = \frac{r_1}{m + \gamma + B + 4er_1}.$$

Then, we have  $\|l(T_1)\|_1 \leq 2r_1 = r_2$ . Thus, by the fixed point argument used in the proof of [13, Proposition 2.2], if

$$T_2 = \frac{r_2}{m + \gamma + B + 4er_2},$$

there exists a solution  $\hat{l}$  on  $[0, T_2]$  of the integral equation

$$\hat{l}(x, t) = \begin{cases} F(\hat{l}(\cdot, t-x)) + \int_0^x G(\hat{l}(\cdot, s+t-x))(s) ds & x \in ]0, t[ \\ l(x-t, T_1) + \int_{x-t}^x G(\hat{l}(\cdot, s+t-x))(s) ds & x \in ]t, +\infty[. \end{cases}$$

Hence, by [13, Proposition 2.4], if we define  $l(\cdot, t) := \hat{l}(\cdot, t - T_1)$  for  $T_1 < t \leq T_1 + T_2$ , then  $l$  is a solution on  $[0, T_1 + T_2]$ . Repeating this argument, if

$$T_n = \frac{r_n}{m + \gamma + B + 4er_n}, \quad r_n = 2^{n-1}r_1,$$

then  $l$  is solution of (ADP) on  $[0, T_1 + \dots + T_n]$  for all  $n \in \mathbb{N}$ . Therefore, since  $\lim_{n \rightarrow \infty} T_n = \frac{1}{4e}$ , we get that  $T_\phi = \infty$ , and the proof concludes.

## 8 Appendix B: The Mathematica codes

In this appendix we give the Mathematica code that produce the figures of section 5.

```
Clear[functmale]
functmale[T,M][variable]:=Module[{tabla},tabla=variable/.
FindRoot[x-Exp[-T/60]*Exp[-1.5/7*T*
Exp[1/60(T-M)]x]==0,{x,0}];
solution=N[tabla];
male=900/7*solution*Exp[1/60(T-M)];male]
Plot3D[functmale[T,M][x],{T,9,24},{M,24,26}] (see figure 1)

Clear[functvirgin]
functvirgin[T,M][variable]:=Module[{tabla},tabla=variable/.
FindRoot[x-Exp[-T/60]*Exp[-1.5/7*T*
Exp[1/60(T-M)]x]==0,{x,0}];
solution=N[tabla];
virgin=solution*60+(1/(1/60+1.5/7*solution*
Exp[1/60*(T-M)]))*(1-Exp[-(1/60+1.5/7*solution*
Exp[1/60*(T-M)])T]);virgin]
Plot3D[functvirgin[T,M][x],{T,9,24},{M,24,26}] (see figure 2)

Clear[functmated]
functmated[T,M][variable]:=Module[{tabla},tabla=variable/.
FindRoot[x-Exp[-T/60]*Exp[-1.5/7*T*
Exp[1/60(T-M)]x]==0,{x,0}];
solution=N[tabla];
mated=(1/(1/60+1.5/7*solution*Exp[1/60*(T-M)])-60)
(Exp[-(1/60+1.5/7*solution*Exp[1/60*(T-M)])T]-1);mated]
Plot3D[functmated[T,M][x],{T,9,24},{M,24,26}] (see figure 3)

Clear[functresting]
functresting[T,M][variable]:=Module[tabla,tabla=variable/.
FindRoot[x-Exp[-T/60]*Exp[-1.5/7*T*
Exp[1/60(T-M)]x]==0,{x,0}];
solution=N[tabla];
resting=60*Exp[-M/60]*(1-Exp[-1.5/7*solution*
Exp[1/60*(T-M)]T]);resting]
Plot3D[functresting[T,M][x],{T,9,24},{M,24,26}] (see figure 4)
```



```

Clear[functhaplo]
functhaplo[T,M][variable]:=Module[tabla,tabla=variable/.
FindRoot[x-Exp[-T/60]*Exp[-1.5/7*T*
Exp[1/60(T-M)]x]==0,{x,0}];
solution=N[tabla];
haplo=60*solution*Exp[1/60*(T-M)];haplo]
Plot3D[functhaplo[T,M][x],{T,9,24},{M,24,26}] (see figure 5)

```

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