

# Reduced fertility and asymptotics of the logistic model

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*This paper is dedicated to Mimmo Iannelli on the occasion of his 65th birthday.*

**Abstract:** This logistic model includes three age groups. Juveniles do not reproduce; and old individuals reproduce at a reduced rate. Pairings between individuals of different fertility rates may lead to multiple equilibria and bi-stability: the total population converges to different limits depending on its initial size. The behavior is correlated with transition rates from high to low fertility groups and with the frequency of pairing among the various groups of reproduction level. The proportions of adults at equilibrium are roots of a quartic polynomial, alternating sinks and saddles. Necessary and sufficient conditions for the existence of bi-stability are provided for a simplified model.

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## 1 Introduction

The logistic model (Verhulst, 1838) includes the effect of limiting factors on population growth. Its solutions converge to a constant called *carrying capacity of the environment*, which is independent of initial conditions.

In logistic two-sex models without age-structure, the population approaches a unique limit independent of the initial conditions, as in Verhulst's one-sex model. We show that asymptotic uniqueness is not the only possibility for two-sex models including groups with different fertility rates. Interactions between these groups may create a bi-stable regime with

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two locally stable steady states. The long-term behavior of solutions depends on the initial population size.

Maxin and Milner (2000) studied the effect of groups with null fertility on population growth. Berec and Maxin (2013) highlighted bi-stability in two-sex models for sexually transmitted diseases sterilizing infected hosts. Hilker (2010) and Berec and Maxin (2013) observed bi-stability in two-sex models with Allee effect in the birth function. The Allee effect is characterized by a positive correlation between fertility rate and population size for small population sizes. Bi-stability appears here because the population is driven to extinction if its initial value is low enough. We show that bi-stability may characterize the population if low reproduction is due to internal factors, such as of old age or personal choice regarding birth control, rather than because of external factors such as sterilizing pathogens or dispersal, as in the Allee effect. The transition from a high to a low fertility level and the frequency of pairing between groups are the likely causes of bi-stability.

## 2 Two-sex model with three fertility groups

We build a logistic model based on three groups with different fertility rates: juveniles, who do not reproduce, adults, and old individuals with reduced fertility. They are represented by  $J(t)$ ,  $A(t)$ , and  $O(t)$ .

$$\begin{cases} J'(t) &= \beta \frac{(A(t) + \sigma O(t))^2}{A(t) + O(t)} - \bar{\mu}J(t) - \alpha J(t), \\ A'(t) &= \alpha J(t) - (\bar{\epsilon} + \nu)A(t), \\ O'(t) &= \nu A(t) - \bar{\eta}O(t), \end{cases} \quad (1)$$

where  $\beta$  is the fertility rate,  $\bar{\mu} := \mu + bP(t)$ ,  $\bar{\epsilon} := \epsilon + bP(t)$ , and  $\bar{\eta} := \eta + bP(t)$  are the mortality rates, where  $P(t) := J(t) + A(t) + O(t)$  is the total population size.  $\mu$ ,  $\epsilon$ , and  $\eta$  are the exponential mortality rates, and  $b$  models the population effect on mortality. The fertility of older individuals is reduced by a factor  $0 < \sigma < 1$ ;  $\alpha$  is the transition rate from juvenile to adult, and  $\nu$  is the transition rate from adult to old age;  $\frac{(A(t)+\sigma O(t))^2}{A(t)+O(t)}$  represents the total number of matings per time unit multiplied by the probability that those matings occur between reproductive individuals.

By changing variables  $x(t) := \frac{A(t)}{A(t)+O(t)}$  and  $y(t) := \frac{J(t)}{A(t)+O(t)}$ ,

$$\begin{cases} x'(t) = \alpha y(t)(1 - x(t)) + (\eta - \epsilon)x(t)(1 - x(t)) - \nu x(t), \\ y'(t) = \beta(x(t) + \sigma(1 - x(t)))^2 - \alpha y(t) - \alpha y(t)^2 + (\eta - \mu)y(t) + (\epsilon - \eta)x(t)y(t), \\ \frac{P'(t)}{P(t)} = \frac{\beta(x(t) + \sigma(1 - x(t)))^2 - \bar{\mu}y(t) - \bar{\epsilon}x(t) - \bar{\eta}(1 - x(t))}{1 + y(t)}. \end{cases} \quad (2)$$

Eq. (2) contains a planar sub-system in  $x$  and  $y$ . Equilibria are roots of a fourth degree polynomial, of which it is difficult to establish the total number of real non-negative roots.

We simplify further by assuming  $\mu = \epsilon = \eta$  and  $\alpha = \nu$ . Then,

$$\begin{cases} x'(t) = \alpha y(t)(1 - x(t)) - \alpha x(t), \\ y'(t) = \beta(x(t) + \sigma(1 - x(t)))^2 - \alpha y(t) - \alpha y(t)^2. \end{cases} \quad (3)$$

Once the behaviors of  $x(t)$  and  $y(t)$  are known,  $P(t)$  is governed by

$$P'(t) = \left( \frac{\beta(x(t) + \sigma(1 - x(t)))^2}{1 + y(t)} - \bar{\mu} \right) P(t). \quad (4)$$

The equilibrium points  $(x^*, y^*)$  of Eq. (3) satisfy  $y^* = \frac{x^*}{1-x^*}$ , where  $x^*$  is a root of

$$\begin{aligned} f(x) = & \beta(1 - \sigma)^2 x^4 + 2\beta(1 - \sigma)(2\sigma - 1)x^3 + \beta\sigma^2 \\ & + \beta(1 - 6\sigma + 6\sigma^2)x^2 + (2\beta\sigma(1 - 2\sigma) - \alpha)x. \end{aligned} \quad (5)$$

Biologically,  $x^*$  and  $y^*$  must be in the interval  $[0, 1]$ . We show that equilibrium points are either sinks or saddles, and these two types alternate.

**THEOREM 2.1.** *Equilibrium points of Eq. (3) alternate between sinks and saddle points. Hence, there are no periodic solutions.*

*Proof.* The Jacobian associated with Eq. (3) is

$$J(x, y) = \begin{pmatrix} -\alpha(1 + y) & \alpha(1 - x) \\ 2\beta(1 - \sigma)(x + \sigma(1 - x)) & -\alpha(1 + 2y) \end{pmatrix}. \quad (6)$$

Because its trace is negative, every equilibrium point is either a saddle or a sink. Also, because solutions of the system are bounded, periodic solutions are ruled out by Bendixson's criterion: denoting  $F_1(x, y)$  and  $F_2(x, y)$  the right-hand sides of Eq. (3),

$$\frac{\partial F_1}{\partial x} + \frac{\partial F_2}{\partial y} = -3\alpha y - 2\alpha < 0. \quad (7)$$

To show that equilibria alternate between sinks and saddles, we analyze the determinant of  $J(x, y)$  using the identities  $y^* = \frac{x^*}{1 - x^*}$ ,  $\beta = \frac{\alpha x^*}{(1 - x^*)^2(x^* + \sigma(1 - x^*))^2}$ . It is

$$\det J(x^*, y^*) = \frac{\alpha^2(3(1 - \sigma)(x^*)^2 + (2\sigma - 1)x^* + \sigma)}{(1 - x^*)^2(x^* + \sigma(1 - x^*))}. \quad (8)$$

Because the trace is negative, the determinant is positive if and only if  $(x^*, y^*)$  is a sink, that is whenever

$$3(1 - \sigma)(x^*)^2 + (2\sigma - 1)x^* + \sigma > 0. \quad (9)$$

Eq. (5) implies that

$$f'(x^*) = \frac{-\alpha(3(1 - \sigma)(x^*)^2 + (2\sigma - 1)x^* + \sigma)}{(1 - x^*)(x^* + \sigma(1 - x^*))}. \quad (10)$$

From Eq. (9) and (10),  $(x^*, y^*)$  is a sink if and only if  $f'(x^*) < 0$  and a saddle if and only if  $f'(x^*) > 0$ . Also,  $f(0) = \beta\sigma^2 > 0$  shows that the first equilibrium is a sink, followed by a saddle, and so on.  $\square$

In this proof, we assumed  $f(x^*) \neq f'(x^*)$ . The non-hyperbolic equilibrium points at which  $f(x^*) = f'(x^*)$  require extra conditions on the parameters, but these conditions are unlikely to occur in reality, so that we ignore them.

We shall determine a necessary and sufficient condition on the parameters for existence of multiple equilibria. We use Sturm's theorem to analyze the number of real roots of  $f$  in  $(0, 1)$  (Dörrie 2013).

**Definition 2.1.** A Sturm chain  $\{p_n(x)\}_{n=0}^\infty$  for  $f$  in Eq. (5) is:

$$\begin{cases} p_0(x) = f(x), & p_1(x) = f'(x), \\ p_{i+1}(x) = -\text{rem}(p_{i-1}(x), p_i(x)), \end{cases} \quad (11)$$

where  $\text{rem}$  returns the remainder from the long-division of the polynomial arguments.

Denoting by  $s(a)$  the total number of sign changes in the Sturm chain Eq. (11) for  $x = a$ , Sturm's theorem states that:

**THEOREM 2.2.** For real numbers  $a$  and  $b$  not roots of a given polynomial  $P$ , the total number of distinct real roots of  $P$  in  $(a, b)$  is equal to  $s(a) - s(b)$ .

The total number of roots of  $f$  in  $(0, 1)$  is  $s(0) - s(1)$ , if neither 0 nor 1 is a multiple root of  $f$ .  $f$  being of fourth degree, this method requires the polynomials  $p_2$ ,  $p_3$ , and  $p_4$ . We used Maple to generate them and to evaluate them at  $x = 0$  and  $x = 1$ . We only show the terms affecting the sign of the relevant quantity, or simply the sign “+” or “-” when that quantity has a fixed sign for all parameter values.

For the Sturm chains at  $x = 0$  and  $x = 1$ ,

$$p_0(0), p_1(0), p_2(0), p_3(0), p_4(0) \quad (12)$$

are equivalent to

$$+, 2\beta\sigma(1 - 2\sigma) - \alpha, \alpha - 2\sigma(\alpha + \beta), \frac{3\alpha}{8}(2\sigma - 1) + \beta\sigma, T, \quad (13)$$

and

$$p_0(1), p_1(1), p_2(1), p_3(1), p_4(1) \quad (14)$$

are equivalent to

$$-, -, 7 - 8\sigma, \frac{3\alpha}{4}(8\sigma - 7) + \beta, T, \quad (15)$$

where the sign of  $T$  depends on  $\alpha$  through the quadratic function

$$g(\alpha) = -27(1 - \sigma)\alpha^2 + 256\beta\left(\sigma^2 - \sigma - \frac{1}{32}\right)\left(\sigma - \frac{1}{2}\right)\alpha - 16\beta^2\sigma. \quad (16)$$

We seek conditions for the existence of more than one equilibrium. From Theorem 2.1, Eq. (3) cannot have exactly two positive equilibria because this would imply either a homoclinic orbit or two heteroclinic orbits forming a cycle.

The Sturm chains in Eq. (13) and (15) have at most four sign changes. Eq. (15) has at least one sign change since  $7 - 8\sigma < 0$  implies  $\frac{3\alpha}{4}(8\sigma - 7) + \beta > 0$ . Eq. (13) has at least one sign change, because  $2\beta\sigma(1 - 2\sigma) - \alpha > 0$  implies  $\alpha - 2\sigma(\alpha + \beta) < 0$ . The total number of sign changes in Eq. (13) is 1, 2, 3, or 4 and in Eq. (15) 1, 2, or 3. Because it is impossible to have exactly two equilibrium points in the interval  $(0, 1)$ , we look for exactly three equilibrium points. This requires that  $s(0) = 4$  and  $s(1) = 1$ .

In order to have  $s(0) = 4$ , the Sturm chain in Eq. (13) must be:  $+, -, +, -, +$ . Therefore,

$$\alpha > 2\beta\sigma(1 - 2\sigma), \alpha > \frac{2\beta\sigma}{1 - 2\sigma}, \alpha > \frac{8\beta\sigma}{3(1 - 2\sigma)}, \sigma < \frac{1}{2}, T > 0, \quad (17)$$

and

$$\alpha > \frac{8\beta\sigma}{3(1-2\sigma)}, \quad \sigma < \frac{1}{2}, \quad T > 0. \quad (18)$$

Because  $\sigma < 1/2$  implies  $\sigma < 7/8$ , the only Sturm chain in Eq. (15) at  $x = 1$  with  $s(1) = 1$  is  $-, -, +, +, +$ , which requires

$$\alpha < \frac{4\beta}{3(7-8\sigma)}, \quad T > 0. \quad (19)$$

Combining Eq. (18) and (19), we obtain the necessary conditions

$$\frac{8\beta\sigma}{3(1-2\sigma)} < \alpha < \frac{4\beta}{3(7-8\sigma)}, \quad \sigma < \frac{1}{2}, \quad T > 0. \quad (20)$$

The bounds on  $\alpha$  in Eq. (20) imply that

$$\sigma^2 - \sigma + \frac{1}{16} > 0. \quad (21)$$

We analyze the sign of  $T$  through the quadratic function  $g$  in Eq. (16). Its discriminant is positive because, by Eq. (21),

$$\Delta_\alpha = 65536\beta^2 \left( \sigma^2 - \sigma + \frac{1}{16} \right)^3 > 0. \quad (22)$$

The roots  $\alpha_1$  and  $\alpha_2$  of  $g$  in Eq. (16) are

$$\frac{128\beta}{27(1-\sigma)} \left( \left( \frac{1}{2} - \sigma \right) \left( \frac{1}{32} + \sigma - \sigma^2 \right) \pm \left( \sigma^2 - \sigma + \frac{1}{16} \right)^{3/2} \right). \quad (23)$$

They are both positive. So, in order to have  $g(\alpha) > 0$ , we need  $\alpha \in (\alpha_1, \alpha_2)$ .

Theorem 2.3 shows that the thresholds on  $\alpha$  in Eq. (20) are outside the interval  $(\alpha_1, \alpha_2)$ .

**THEOREM 2.3.**  $\alpha_1$  and  $\alpha_2$  are given by Eq. (23). Eq. (3) admits three equilibrium points, two locally stable and one unstable, if and only if  $\alpha \in (\alpha_1, \alpha_2)$  and  $\sigma < \frac{2 - \sqrt{3}}{4} \approx 0.07$ .



*Proof.* Compute

$$\begin{cases} g\left(\frac{8\beta\sigma}{3(1-2\sigma)}\right) = -\frac{16}{3}\frac{\beta^2\sigma}{(1-2\sigma)^2}(16\sigma^2 - 16\sigma + 1)^2 < 0, \\ g'\left(\frac{8\beta\sigma}{3(1-2\sigma)}\right) = \frac{64\beta(\sigma^2 - \sigma + 1/16)(1 + 8\sigma(1 - \sigma))}{1 - 2\sigma} > 0, \end{cases} \quad (24)$$

$$\begin{cases} g\left(\frac{4\beta}{3(7-8\sigma)}\right) = -\frac{32\beta^2}{3}\frac{(16\sigma^2 - 16\sigma + 1)^2}{(7 - 8\sigma)^2} < 0, \\ g'\left(\frac{4\beta}{3(7-8\sigma)}\right) = -\frac{4\beta(32\sigma^2 - 44\sigma + 11)(16\sigma^2 - 16\sigma + 1)}{7 - 8\sigma} < 0. \end{cases} \quad (25)$$

Eq. (24) implies  $\frac{8\beta\sigma}{3(1-2\sigma)} < \alpha_1$  and Eq. (25) implies  $\alpha_2 < \frac{4\beta}{3(7-8\sigma)}$ . Eq. (21) gives  $\sigma < \frac{2 - \sqrt{3}}{4} \approx 0.07$ .  $\square$

Eq. (4) for  $P(t)$  implies that each interior equilibrium of Eq. (3) may lead to extinction of the total population if the mortality rate  $\mu$  is large enough. For an equilibrium  $(x^*, y^*)$ ,

$$\begin{aligned} P(t) &\longrightarrow 0 \quad \text{if} \quad \beta(1-x^*)(x^* + \sigma(1-x^*))^2 \leq \mu, \\ P(t) &\longrightarrow \frac{\beta(1-x^*)(x^* + \sigma(1-x^*))^2 - \mu}{b} \quad \text{otherwise.} \end{aligned} \quad (26)$$

Eq. (1) can exhibit bi-stability between the trivial equilibrium and a positive one. This phenomenon is called strong Allee effect. Here, it is caused by the transitions from higher to lower fertility groups rather than by low population densities.

We use two numerical simulations to show this phenomenon. Figure 1 shows bi-stability between two positive equilibria, and Figure 2 shows bi-stability between extinction and a positive equilibrium, which is obtained just by increasing the mortality rate from the first case.

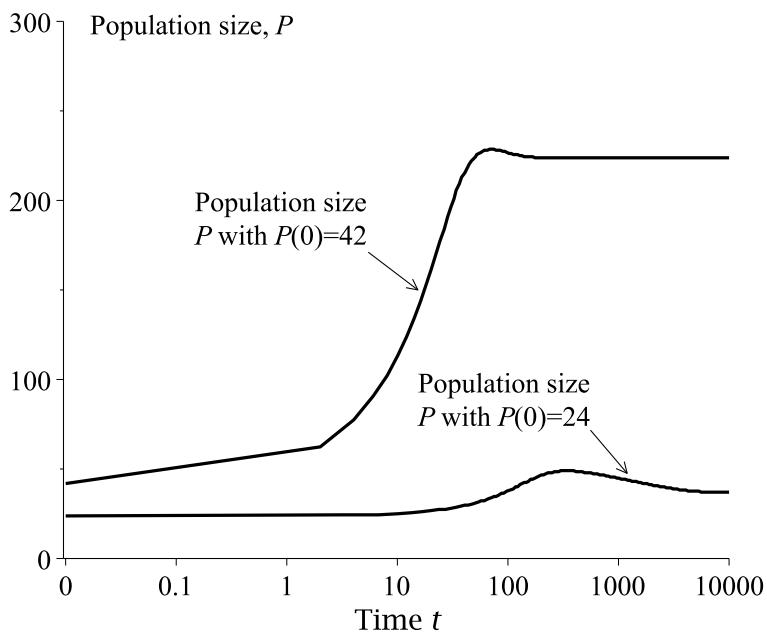


Figure 1: Bi-stability between two positive equilibria.  $\beta = 0.55$ ,  $\mu = 0.001$ ,  $\sigma = 0.0353$ ,  $\alpha = 0.08$ ,  $\alpha_1 = 0.00691$ ,  $\alpha_2 = 0.095$ .

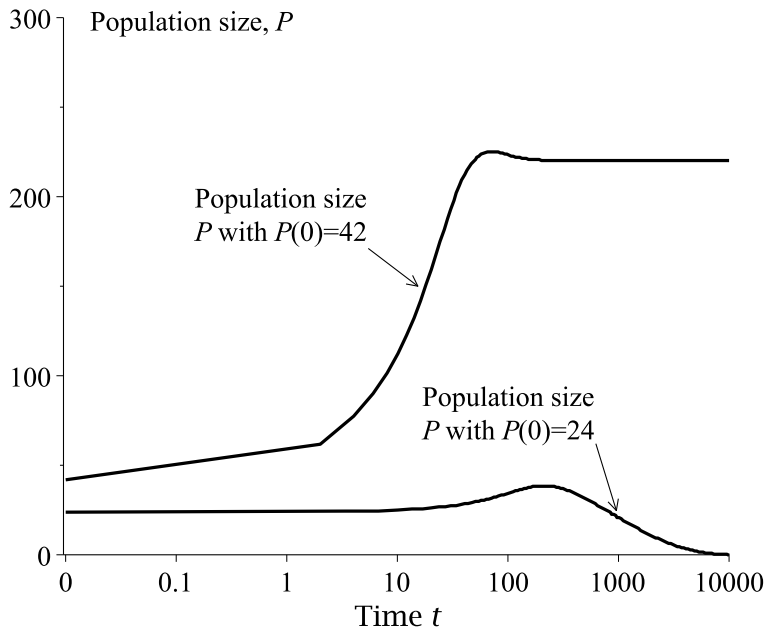


Figure 2: Bi-stability between extinction and a positive equilibrium.  $\beta = 0.55$ ,  $\mu = 0.002$ ,  $\sigma = 0.0353$ ,  $\alpha = 0.08$ ,  $\alpha_1 = 0.00691$ ,  $\alpha_2 = 0.095$ .

### 3 Necessary conditions for bi-stability

We analyze several scenarios identifying parameters or assumptions responsible for bi-stability.

In each scenario, we only address the existence of more than one equilibrium for the simplified version of the corresponding model.

#### 3.1 Inter-age group mating necessary for bi-stability

We add the assumption of no mating between adult and old individuals to Eq. (1):

$$\begin{cases} J'(t) = \beta A(t) + \beta \sigma^2 O(t) - \bar{\mu} J(t) - \alpha J(t), \\ A'(t) = \alpha J(t) - \bar{\epsilon} A(t) - \nu A(t), \\ O'(t) = \nu A(t) - \bar{\eta} O(t). \end{cases} \quad (27)$$

The sub-system in  $x(t)$  and  $y(t)$  is:

$$\begin{cases} x'(t) = \alpha y(t)(1 - x(t)) - \alpha x(t), \\ y'(t) = \beta x(t) + \beta \sigma^2(1 - x(t)) - \alpha y(t) - \alpha y(t)^2. \end{cases} \quad (28)$$

For any equilibrium,  $y^*$  is a root of

$$f(y) = \alpha y^3 + 2\alpha y^2 + (\alpha - \beta)y - \beta \sigma^2. \quad (29)$$

Denoting by  $y_1$ ,  $y_2$ , and  $y_3$  the roots of  $f$ ,

$$y_1 + y_2 + y_3 = -2 < 0 \quad \text{and} \quad y_1 y_2 y_3 = \beta \sigma^2 > 0. \quad (30)$$

If the three roots are real, at least two of them are negative. Hence, there cannot exist three equilibrium points in the interval  $(0, 1)$ , which is a necessary condition for bi-stability.

### 3.2 Transition from lower to higher fertility may not be necessary for bi-stability

We determine whether bi-stability is possible when we remove the juveniles. This case leaves only transitions from higher to lower fertility groups. Eq. (1) becomes

$$\begin{cases} A'(t) = \beta \frac{(A(t) + \sigma O(t))^2}{A(t) + O(t)} - \bar{\mu}A(t) - \alpha A(t), \\ O'(t) = \alpha A(t) - \bar{\mu}O(t), \end{cases} \quad (31)$$

and the ordinary differential equation for the fraction  $x(t) = \frac{A(t)}{A(t)+O(t)}$  is

$$x'(t) = \beta(1 - x(t))(x(t) + \sigma(1 - x(t)))^2 - \alpha x(t). \quad (32)$$

For the Sturm chains at  $x = 0$  and at  $x = 1$ ,

$$p_0(0), p_1(0), p_2(0), p_3(0) \quad (33)$$

are equivalent to

$$+, \beta\sigma(2 - 3\sigma) - \alpha, \alpha - \sigma(3\alpha + 2\beta), T, \quad (34)$$

and

$$p_0(1), p_1(1), p_2(1), p_3(1) \quad (35)$$

are equivalent to

$$-, -, (7 - 9\sigma)\alpha - 2\beta, T, \quad (36)$$

where the function

$$T = g(\alpha) = 4\alpha^2 + \beta(27\sigma^2 - 18\sigma - 1)\alpha + 4\beta^2\sigma. \quad (37)$$

The existence of three roots in the interval  $(0, 1)$  requires that the chain of Eq. (33) have three sign changes and the chain of Eq. (35) have no sign changes:

$$\beta\sigma(2 - 3\sigma) - \alpha < 0, \quad \alpha - \sigma(3\alpha + 2\beta) > 0, \quad (7 - 9\sigma)\alpha - 2\beta < 0, \quad T < 0. \quad (38)$$

In summary,

$$\frac{2\beta\sigma}{1 - 3\sigma} < \alpha < \frac{2\beta}{7 - 9\sigma}, \quad \sigma < \frac{1}{9} \quad \text{and} \quad \alpha_1 < \alpha < \alpha_2, \quad (39)$$

where

$$\alpha_{1,2} = \beta \left( -\frac{27\sigma^2}{8} + \frac{9\sigma}{4} + \frac{1}{8} \pm \frac{1}{8}(1 - \sigma)^{1/2}(1 - 9\sigma)^{3/2} \right). \quad (40)$$

These conditions are similar to those found for Eq. (3), which shows that transition from higher to lower fertility groups may be more important in creating bi-stability than the opposite (such as from juvenile to adult).

### 3.3 Partial sterility at birth does not cause bi-stability

We assume that a fraction  $\delta \in [0, 1]$  of newborn individuals are sterile, in order to assess the importance of transitions from high to low fertility rates for bi-stability to occur, in contrast with a reduction of fertility at birth. The model is

$$\begin{cases} A'(t) = \beta(1 - \delta) \frac{(A(t) + \sigma O(t))^2}{A(t) + O(t)} - \bar{\mu}A(t), \\ O'(t) = \beta\delta \frac{(A(t) + \sigma O(t))^2}{A(t) + O(t)} - \bar{\mu}O(t), \end{cases} \quad (41)$$

and the equation for the adult fraction  $x(t) = \frac{A(t)}{A(t) + O(t)}$  is

$$x'(t) = \beta(x(t) + \sigma(1 - x(t)))^2(1 - \delta - x(t)). \quad (42)$$

There is just one positive steady state,  $x^* = 1 - \delta$ , which is globally stable. Bi-stability is then impossible.

## 4 Inter-group matings and their role in bi-stability

Bi-stability requires the existence of a low fertility group, a transition from high to low fertility groups, and pairings between these groups. We derive parameter thresholds for bi-stability.

We begin with a two-sex model with two age-classes (Milner and Yang, 2009). We assume that each of the four age-sex groups mates only within their age-classes, except for a fraction  $p \in [0, 1]$  of the old male population mating with the adult female population.

$$\left\{ \begin{array}{l} F'_a(t) = \beta\gamma_f \left( \mathcal{M}(F_a(t), M_a(t) + pM_o(t)) \frac{M_a(t) + \sigma_m p M_o(t)}{M_a(t) + pM_o(t)} \right. \\ \qquad \qquad \qquad \left. + \sigma_f \sigma_m \mathcal{M}(F_o(t), (1-p)M_o(t)) \right) - \bar{\mu}_f F_a(t) - \alpha_f F_a(t), \\ M'_a(t) = \beta\gamma_m \left( \mathcal{M}(F_a(t), M_a(t) + pM_o(t)) \frac{M_a(t) + \sigma_m p M_o(t)}{M_a(t) + pM_o(t)} \right. \\ \qquad \qquad \qquad \left. + \sigma_f \sigma_m \mathcal{M}(F_o(t), (1-p)M_o(t)) \right) - \bar{\mu}_m M_a(t) - \alpha_m M_a(t), \\ F'_o(t) = \alpha_f F_a(t) - \bar{\mu}_f F_o(t), \quad M'_o(t) = \alpha_m M_a(t) - \bar{\mu}_m M_o(t). \end{array} \right. \quad (43)$$

$F_a(t)$  and  $M_a(t)$  denote the adult women and men population sizes and  $F_o(t)$  and  $M_o(t)$  represent the old women and men population sizes.  $\gamma_f$  is the probability that a newborn is female, and  $\gamma_m := 1 - \gamma_f$ .  $\mathcal{M}$  is the mating function with one argument for each sex (Iannelli et al., 2005). All other parameters have the same meaning as those in Eq. (1) with subscript indicating sex.

Assuming no sex effect on the parameters, Eq. (43) becomes

$$\left\{ \begin{array}{l} A'(t) = \beta \left( \mathcal{M}(A(t), A(t) + pO(t)) \frac{A(t) + \sigma p O(t)}{A(t) + pO(t)} + \sigma^2 \mathcal{M}(O(t), (1-p)O(t)) \right) \\ \qquad \qquad \qquad - \bar{\mu} A(t) - \alpha A(t), \\ O'(t) = \alpha A(t) - \bar{\mu} O(t), \end{array} \right. \quad (44)$$

and the equation for the adult fraction  $x(t) = \frac{A(t)}{A(t) + O(t)}$  is

$$x'(t) = \beta(1 - x(t)) \left( \mathcal{M}(x(t), x(t) + p(1 - x(t))) \frac{x(t) + \sigma p(1 - x(t))}{x(t) + p(1 - x(t))} + \sigma^2 \mathcal{M}(1, 1 - p)(1 - x(t)) \right) - \alpha x(t). \quad (45)$$

Using the harmonic mean mating function

$$\mathcal{M}(x(t), y(t)) = \frac{x(t)y(t)}{x(t) + y(t)}, \quad (46)$$

Eq. (45) becomes

$$x'(t) = \beta(1 - x(t)) \left( \frac{x(t)(x(t) + \sigma p(1 - x(t)))}{2x(t) + p(1 - x(t))} + \frac{\sigma^2(1 - p)}{2 - p}(1 - x(t)) \right) - \alpha x(t) \quad (47)$$

and, with the substitution

$$y(t) = \frac{x(t)}{1 - x(t)} \in [0, \infty), \quad (48)$$

any positive equilibrium  $(x^*, y^*)$  has  $y^*$  solution of

$$\frac{y(y + p\sigma)}{2y + p} + \frac{\sigma^2(1 - p)}{2 - p} - \frac{\alpha}{\beta}y(y + 1) = 0, \quad (49)$$

equivalent to the cubic

$$a_3 y^3 + a_2 y^2 + a_1 y + a_0 = 0, \quad (50)$$

where

$$\begin{aligned} a_3 &= 2\alpha(p - 2), & a_2 &= (p - 2)(\alpha p + 2\alpha - 1), \\ a_1 &= (\alpha - \sigma)p^2 + 2(\sigma - \sigma^2 - \alpha)p + 2\sigma^2, & a_0 &= \sigma^2 p(1 - p). \end{aligned} \quad (51)$$

The discriminant of Eq. (50) is

$$\Delta = a_2^2 a_1^2 - 4a_3 a_1^3 - 4a_2^3 a_0 - 27a_3^2 a_0^2 + 18a_3 a_2 a_1 a_0 \quad (52)$$

and Eq. (50) has three real roots if  $\Delta > 0$ . Because  $a_3 < 0$  and  $a_0 > 0$ , the three roots, if real, will be positive whenever  $a_2 > 0$  and  $a_1 < 0$ .  $a_2 > 0$  implies

$$\alpha < \frac{1}{p+2} \quad (53)$$

and  $a_1 < 0$  implies

$$\alpha > \frac{2\sigma^2(1-p) + p\sigma(2-p)}{p(2-p)}. \quad (54)$$

Combining Eq. (53) and (54), we obtain

$$\frac{2\sigma^2(1-p) + p\sigma(2-p)}{p(2-p)} < \alpha < \frac{1}{p+2}, \quad (55)$$

and

$$\sigma < \frac{4p - 2p^2}{4p - p^3 + (p(4 - p^2)(8 - 4p - p^3))^{1/2}}. \quad (56)$$

The condition  $\Delta > 0$  is not easy to write in terms of similar thresholds. However, the upper bound on  $\sigma$  written in Eq. (56) indicated that the reduction in fertility causing bi-stability is related to the frequency of pairings across age groups. Figure 3 shows the regions in the  $(\sigma, \alpha)$ -plane where  $f$  has three real positive roots, for various values of the fraction of the old male population mating with adult females,  $p$ . The larger the inter-age pairing, the larger the probability of having more than one equilibrium.

Then, bi-stability thresholds depend on the fertility reduction factor  $\sigma$ , on the fraction of the old male population mating with adult females  $p$ , and on the transition rate  $\alpha$  from young to adult. Furthermore, the lower the fertility rate due to  $\sigma$ , the larger the range of the transition rate  $\alpha$  causing bi-stability.



$\alpha$  = transition rate from young to adult,  $\sigma$  = reduction factor of fertility from adult to old,  $p$  = fraction of the old male population mating with adult females.

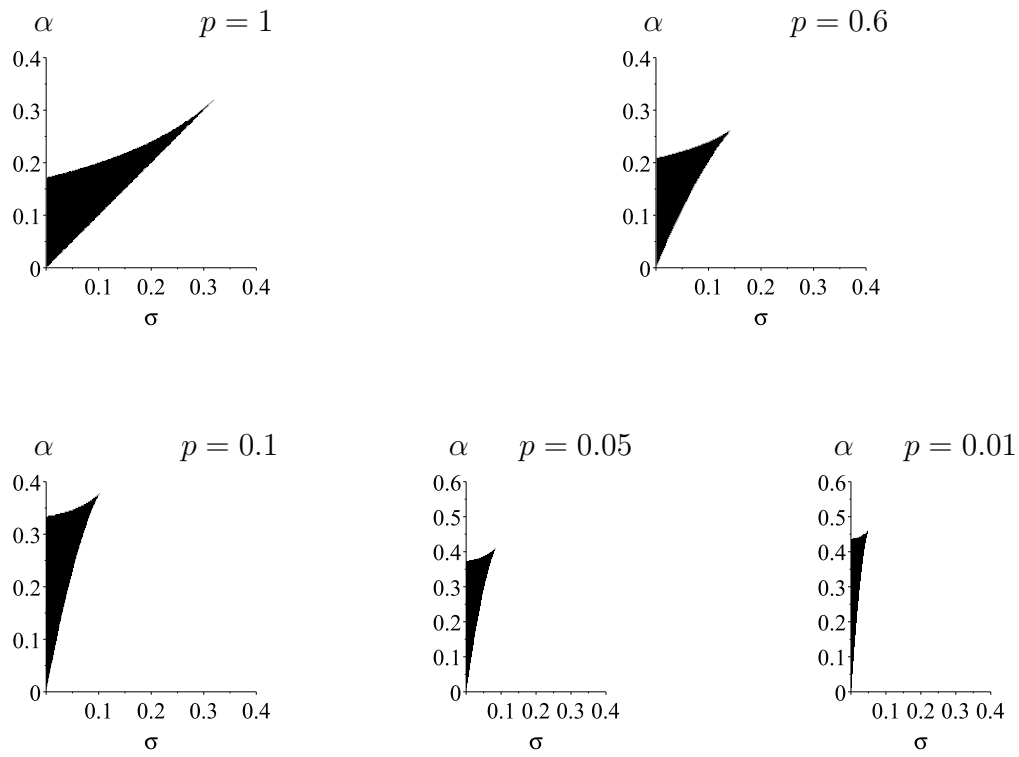


Figure 3: Regions of bi-stability

## 5 Conclusion

The age-structured logistic model has a threshold below which the population goes extinct and above which the population size converges to a unique positive limit value. When fertility decreases with age and matings occur across age groups, the total population size converges to one of two different limits, depending on its initial value. This behavior is due to the existence of two locally stable positive equilibria.

Empirical applications of the model include problems in ecology related to conservation and to pest control. In conservation, the purpose is to maintain the population size at high levels while in pest control the purpose is to drop the population. In both cases, the Allee effect for populations falling below a certain level should be taken into account. We showed that the Allee effect can not only result from lower population densities or external factors, but also from varying fertility and from mating across groups.

According to Courchamp et al. (2008), the population grows slower or declines at low densities because of individual fertility and mate choice. This is what we have developed here. Females of certain species of fish mate with big size males because of their higher sperm count, which could be linked to a better reproductive outcome. This behavior was also reported for the Blue crab (*Callinectes sapidus*), the Caribbean spiny lobster (*Panulirus argus*), and the New Zealand rock lobster (*Jasus Edwardsii*). Courchamp et al. (2008), give more examples of species with assortative mating linked to fertility.

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