RESEARCH ARTICLE

A generalized two-sex logistic model

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We provide a generalization of the logistic two-sex model with ephemeral pair-bonds and with stable couples without assuming any specific mathematical form for fertility, mortality and the mating function. In particular, we establish a necessary and sufficient condition on the fertility/mortality density dependent ratio that ensures the existence of the logistic behavior. Several differences and similarities between the two models are also provided.

Keywords: logistic model, two-sex, generalization

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1. Introduction

Two-sex models are clearly necessary in many models where the sex of individuals is important: demography, epidemics of sexually transmitted diseases, etc. The analysis of these models still faces numerous mathematical and conceptual difficulties. Most of these center around how one models the pair-formation function. This is an issue of interest for both demographers and ecologists, namely those who are interested in two-sex dynamics from human motivated problems as well as questions arising from the animal world. The mathematical form that one chooses for the mating/pair-formation function is the core of controversy.
Below we summarize several hypotheses imposed on the pair-formation function by modelers with the observation that not all functions currently used satisfy all of these hypotheses. For a comprehensive review of gender-structured population modeling see [1] and references therein.

Let F, M denote the number of females and males available for pairing. The mating/pair-formation function is denoted by $\mathcal{M}$. The conditions usually imposed on $\mathcal{M}$ are:

- **positivity**: $\mathcal{M}(F, M) \geq 0$ whenever $F \geq 0$, $M \geq 0$.
- **heterosexuality**: $\mathcal{M}(0, M) = \mathcal{M}(F, 0) = 0$. This indicates that the pair-formation function vanishes if individuals of one gender are absent.

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- **homogeneity**: $\mathcal{M}(\alpha F, \alpha M) = \alpha \mathcal{M}(F, M)$ for every $\alpha \geq 0$. This ensures the preservation of sex ratio if the number of singles in each gender changes by the same factor α.
- **monotonicity**: $\mathcal{M}(F_1 + F_2, M_1 + M_2) \geq \mathcal{M}(F_1, M_1)$ for every $F_2 \geq 0$ and $M_2 \geq 0$.
- **consistency**: $\mathcal{M}(F, M) \leq F$ and $\mathcal{M}(F, M) \leq M$ for every $F \geq 0$ and $M \geq 0$. This condition ensures that the number of pairs is smaller than the number of available singles in each sex category.

Typical examples of functional forms for $\mathcal{M}$ are:

- **harmonic mean:** $2\rho\frac{FM}{F+M}$,
- **geometric mean:** $\rho\sqrt{FM}$,
- **female/male dominance:** ρF or ρM,
- **generalized weighted mean:** $\rho[aF^b + (1-a)M^b]^{1/b}$,

where ρ denotes the pair-formation rate. The last example above was proposed by Hadeler in [2] and, for appropriate values of a and b, it corresponds to the other three examples mentioned above.

We point out that the heterosexuality condition is not satisfied by the female/male dominated form of $\mathcal{M}$. Furthermore, the consistency condition may fail in the case of the geometric mean while it is guaranteed to hold in the case of harmonic mean. This is because $\frac{M}{F+M} \leq 1$ and, consequently,

$$\lim_{M \to \infty} 2\rho\frac{FM}{F+M} \leq 2\rho F \leq F \text{ if } \rho < 0.5,$$

while

$$\lim_{M \to \infty} \rho\sqrt{FM} = \infty.$$

Neither of these forms is universally acceptable by modelers. Furthermore, there is also the issue on how one interprets what the pair-formation actually means in the model. Demographers often use this function to model marriages while the actual birth is given as a rate per-couple which is modeled separately from un-paired (single) individuals. In the ecological models, where the focus of interest is the mating process, this function typically represent actual matings where pairings are made only for copulation. This eliminates the requirement to model couples separately. Of course this will not be suitable for animals that form stable pairs.

We mention that we do not intend to argue in this paper in favor or against any of these proposed functional forms and their properties. Rather, we acknowledge that, in some cases, a modeler will adopt or reject a certain form and hypothesis. For example, if $\mathcal{M}$ represents the number of sexual acts (i.e. purely a mating function) then, perhaps, the consistency condition is not mandatory. Conversely, if $\mathcal{M}$ is strictly designed to model the formation of stable pairs then consistency conditions become more important and female/male dominated forms inappropriate. Indeed, as we will show later on, a female/male dominated function will cause the two-sex model with couples to become biologically unfeasible (solutions starting with positive values become negative).

From these considerations, we believe it is important to establish a general

logistic two-sex model (with and without couples) using a generic birth, death and mating function to allow greater flexibility in tackling problems related to gender structured populations. Another motivation is given by epidemiology. When modeling an infectious disease it is important to have a well-understood base-line demographic model of the population under study in the absence of the disease upon which to expand and incorporate the disease specific state variables: susceptibles, infected, recovered, etc.

Ideally we want a basic demographic model whose dynamics is completely determined by certain net reproductive numbers. However, most of the existing results are not as straightforward as the well known Verhulst model [3] for the one-sex case:

$$P' = rP\left(1 - \frac{P}{K}\right),$$

where $K > 0$ is the carrying capacity. Here, the sign of the intrinsic growth parameter, r, is the threshold that separates the extinction from persistence of the total population P.

Corresponding two-sex logistic models typically assume specific forms and properties for the pair formation function or for the fertility and mortality rates. Castillo-Chavez et. al. was the first to introduce a logistic version of the two-sex model with couples by introducing density dependent birth and divorce rates [6] but assuming constant mortality. They also assumed that the density dependent birth rate is not only decreasing with the total population but also converging to zero which is a strong and somewhat less realistic assumption. Maxin and Milner [7] analyzed a logistic two-sex model with couples assuming a constant birth rate and density dependent linear mortality forms. Here too we note the assumption of a specific form of the mortality rate and the proofs of the theorems actually depend on this assumption. These models still have open questions that are yet to be solved. Greater generality is achieved by Milner and Yang in [4] who analyzed a two-sex logistic model with age-structure. However, the mathematical difficulties presented by PDE models required additional technical hypotheses and the threshold between extinction and persistence is still an open problem.

If the couples are not modeled separately, results are, as expected, much stronger due to the fact that these models are planar (i.e. only females and males). In particular, global stability results can be established instead of local ones. Maxin et al. [5] analyzed the two-sex model with ephemeral pair bonds using the harmonic mean mating function and linear density dependent mortality rates with the same logistic term, i.e. the term b below,

$$\mu_f(P) = \mu_f + bP, \quad \mu_m(P) = \mu_m + bP,$$

where μ_f and μ_m are the background sex-specific mortality rates and P is the total population size. Again, some of the arguments in the proofs provided in [5] depended on that particular choice of mortality rates, i.e. having the same logistic term b, and also made use of some properties of the mating function that are not present in others such as the consistency assumption.

In this paper our aim is to generalize the current results from the two-sex logistic models without age structure to a model with arbitrary mating/marriage

function and density dependent fertility and mortality rates. The only assumptions on the mating function will be : heterosexuality, non-negativity, monotonicity and degree-one homogeneity. The consistency assumption will not be needed and neither the heterosexuality in the case of the model without pairs. We will also assume a decreasing birth rate and increasing mortality rate. With this generalization we aim to make precise the threshold for existence of a logistic behavior in terms of the relative dependence of fertility and mortality rates. This should provide greater flexibility in choosing these rates according to the biological properties of the population under study. In particular, it will be possible to include different logistic effects on the population if the environment affects the two genders in a different way. For example, Edwards et. al. discuss population limiting factors in [8] and provide an example of a species (red deer) where population density effects are stronger in the males leading to skewed sex ratios. Another advantage is that one can use a density dependent mortality that does not necessarily increases without bound or a density dependent birth rate that decreases to zero as in the model proposed by Castillo-Chavez and Huang [6].

The paper is structured as follows: in the first section we introduce and analyze a logistic two-sex model without pair-formation and provide the thresholds described above. In section 3 we analyze in a similar manner the two-sex model with pair-formation. We conclude with a discussion about the similarities and differences between the two models, directions for further study, as well as some illustrative examples which are provided in the Appendix.

2.   The two-sex logistic model with ephemeral pair bonds

Consider the following model of a population where the reproductive individuals form pairs for mating purposes only (no stable couples).

$$
\begin{cases}
F' = \beta(P)\gamma_f \mathcal{M}(F, M) - \mu_f(P)F, \\
M' = \beta(P)\gamma_m \mathcal{M}(F, M) - \mu_m(P)M.
\end{cases}
\tag{1}
$$

where $P = F + M$. We assume that $\mathcal{M}$, μ_f, μ_m and β are continuously differentiable on their domains. The mating function $\mathcal{M}$ satisfies the positivity, monotonicity and homogeneity assumptions listed in the Introduction. In addition we assume:

- **non-increasing and positive birth rate:**

$$\beta'(P) \leq 0 \text{ and } \beta(P) > 0 \text{ for every } P \geq 0.$$

- **non-decreasing and positive mortality rates:**

$$\mu_f'(P) \geq 0, \ \mu_m'(P) \geq 0 \text{ and } \mu_f(P) > 0, \ \mu_m(P) > 0 \text{ for every } P \geq 0.$$

β is the *per-mating* birth rate and γ_f, γ_m with $\gamma_f + \gamma_m = 1$ are the probabilities that a newborn is female or male, respectively.

We now define several important quantities that will be used throughout this section:

$$\mathcal{R}_f := \frac{\beta(0)\gamma_f}{\mu_f(0)}, \ \mathcal{R}_m := \frac{\beta(0)\gamma_m}{\mu_m(0)} \ \text{and} \ \mathcal{R} := \mathcal{M}(\mathcal{R}_f, \mathcal{R}_m),$$

$$\mathcal{R}_f^\infty := \lim_{P\to\infty} \frac{\beta(P)\gamma_f}{\mu_f(P)}, \ \mathcal{R}_m^\infty := \lim_{P\to\infty} \frac{\beta(P)\gamma_m}{\mu_m(P)} \ \text{and} \ \mathcal{R}^\infty := \mathcal{M}\left(\mathcal{R}_f^\infty, \mathcal{R}_m^\infty\right).$$

The logistic behavior of solutions depends on the relative density dependence of mortality and fertility. Loosely speaking, the mortality should "gain traction" relative to the birth rate as the population increases. It is not sufficient to simply have a decreasing birth rate and increasing mortality (see also Fig. A1). The necessary and sufficient condition that ensures boundedness of solutions is made precise in the following theorem:

Theorem 2.1: *If $\mathcal{R}^\infty > 1$ the solution of (1) is unbounded in the positive quadrant (i.e. no logistic behavior). If $\mathcal{R}^\infty < 1$ the solution of (1) is bounded in the positive quadrant.*

In proving our main results we will use an approach similar to the one used in [6], [7].

Specifically, the proofs of all theorems (except the last one) make repeated use of bounding arguments for either the minimum or the maximum of two or three suitable functions. In general, given two differentiable functions, f and g, neither $\min\{f,g\}$ nor $\max\{f,g\}$ are differentiable but only continuous on their domains. This prevents the use of Riemann integrals in several necessary estimates. Nevertheless, the functions used in the proofs are increasing and measurable with respect to the usual Lebesgue measure on the real line. So they are differentiable almost everywhere and one can use the Lebesgue integral instead. In particular we will use the following weak version of the Fundamental Theorem of Calculus:

Theorem 2.2: *Let f be an increasing real-valued function on the interval $[a,b]$. Then f is differentiable almost everywhere. The derivative f' is measurable and*

$$\int_a^b f'(x)dx \le f(b) - f(a).$$

We will also use, several times, the following identity:

$$a\frac{\partial \mathcal{M}}{\partial x}(a,b) + b\frac{\partial \mathcal{M}}{\partial y}(a,b) = \mathcal{M}(a,b).$$

This follows from differentiating the following identity with respect to α and replacing α with 1 afterwards

$$\mathcal{M}(\alpha a, \alpha b) = \alpha \mathcal{M}(a,b).$$

Finally, since the bounding arguments are very similar we will provide full details for the first two proofs and concentrate only on the specific differences for the later ones in hope that this will avoid tedious redundancies when reading the paper.

Before proving the first theorem note that the existence, uniqueness and positivity of solutions of (1) can be derived by standard means.

Proof: [Theorem 2.1] Suppose $\mathcal{R}^\infty > 1$. This implies $\mathcal{R}_f^\infty > 0$ and $\mathcal{R}_m^\infty > 0$. Consider the following function

$$h(t) := \min\{\mathcal{R}_m^\infty F(t), \mathcal{R}_f^\infty M(t)\}.$$

For every $t > 0$ we distinguish two cases:

- $h(t) = \mathcal{R}_m^\infty F(t)$. This case implies the following lower bound on the males/females ratio:

$$\frac{M}{F} \geq \frac{\mathcal{R}_m^\infty}{\mathcal{R}_f^\infty}.$$

We use this inequality in the following estimate:

$$\frac{F'}{F} = \mu_f(P) \left[\mathcal{M}\left(\frac{\beta(P)\gamma_f}{\mu_f(P)}, \frac{\beta(P)\gamma_f M}{\mu_f(P)F} \right) - 1 \right] \geq \mu_f(0) \left[\mathcal{M}\left(\frac{\beta(P)\gamma_f}{\mu_f(P)}, \frac{\beta(P)\gamma_f \mathcal{R}_m^\infty}{\mu_f(P)\mathcal{R}_f^\infty} \right) - 1 \right].$$

Notice that the expression in the first square braket above is always positive since the right side of the inequality is decreasing and bounded below by a positive constant and, letting $P \to \infty$, we have

$$\frac{F'}{F} \geq \mu_f(0)(\mathcal{R}^\infty - 1) > 0.$$

- $h(t) = \mathcal{R}_f^\infty M(t)$. Similar to the previous case,

$$\frac{M'}{M} = \mu_m(P) \left[\mathcal{M}\left(\frac{\beta(P)\gamma_m F}{\mu_m(P)M}, \frac{\beta(P)\gamma_m}{\mu_m(P)} \right) - 1 \right] \geq \mu_m(0) \left[\mathcal{M}\left(\frac{\beta(P)\gamma_m \mathcal{R}_f^\infty}{\mu_m(P)\mathcal{R}_m^\infty}, \frac{\beta(P)\gamma_m}{\mu_f(P)} \right) - 1 \right]$$

which implies

$$\frac{M'}{M} \geq \mu_m(0)(\mathcal{R}^\infty - 1) > 0.$$

This shows $\frac{h'}{h} > k > 0$ with

$$k = \min\{\mu_f(0)(\mathcal{R}^\infty - 1), \mu_m(0)(\mathcal{R}^\infty - 1)\}.$$

Since $\ln h(t)$ is increasing and using Theorem 2.2 we have, for a fixed $T > 0$,

$$\ln h(T) - \ln h(0) > \int_0^T \frac{h'}{h} dt > \int_0^T k dt = kT.$$

Letting $T \to \infty$ in the inequality above shows that $h(T) \to \infty$ and this, in turns, implies that the solutions of (1) are unbounded.

We now assume $\mathcal{R}^\infty < 1$. This implies, due to continuity assumptions, that there exists a P_0 sufficiently large such that

$$\mathcal{M}\left(\frac{\beta(P_0)\gamma_f}{\mu_f(P_0)}, \frac{\beta(P_0)\gamma_m}{\mu_m(P_0)} \right) - 1 < 0.$$

Consider now the function

$$g(t) = \max\{\gamma_f \mu_m(P_0) M(t), \gamma_m \mu_f(P_0) F(t)\}.$$

Assuming $P(t) > P_0$ we have the following two cases:

- $g(t) = \gamma_m \mu_f(P_0) F(t)$. Then

$$\frac{F'}{F} = \mu_f(P) \left[\mathcal{M}\left(\frac{\beta(P)\gamma_f}{\mu_f(P)}, \frac{\beta(P)\gamma_f M}{\mu_f(P) F} \right) - 1 \right] < \mu_f(P) \left[\mathcal{M}\left(\frac{\beta(P_0)\gamma_f}{\mu_f(P_0)}, \frac{\beta(P_0)\gamma_m}{\mu_m(P_0)} \right) - 1 \right] < 0.$$

- $g(t) = \gamma_f \mu_m(P_0) M(t)$. In a similar fashion this case implies

$$\frac{M'}{M} < \mu_m(P) \left[\mathcal{M}\left(\frac{\beta(P_0)\gamma_f}{\mu_f(P_0)}, \frac{\beta(P_0)\gamma_m}{\mu_m(P_0)} \right) - 1 \right] < 0.$$

Altogether, these estimates imply that as soon as $P(t) > P_0$ then $g'(t) < 0$ which means $g(t)$ and, therefore, both $F(t)$ and $M(t)$ are bounded above. This completes the proof of the first theorem.

$\square$

The system (1) always admits the extinction equilibrium $(0,0)$. In order to compute the interior (positive) steady state we see that, when solving for the equilibria,

$$\gamma_m \mu_f(P) F = \gamma_f \mu_m(P) M.$$

We use this to substitute M/F in the first equation as follows

$$F\left[\beta(P)\gamma_f \mathcal{M}\left(1, \frac{M}{F}\right) - \mu_f(P) \right] = F\left[\beta(P)\gamma_f \mathcal{M}\left(1, \frac{\gamma_m \mu_f(P)}{\gamma_f \mu_m(P)}\right) - \mu_f(P) \right]$$

$$= F\mu_f(P) \left[\mathcal{M}\left(\frac{\beta(P)\gamma_f}{\mu_f(P)}, \frac{\beta(P)\gamma_m}{\mu_m(P)} \right) - 1 \right] = 0.$$

Therefore, an interior equilibrium (F^*, M^*) exists whenever the following function has a positive root P^*:

$$f(P) = \mathcal{M}\left(\frac{\beta(P)\gamma_f}{\mu_f(P)}, \frac{\beta(P)\gamma_m}{\mu_m(P)} \right) - 1,$$

with

$$F^* = \left[\frac{\gamma_f \mu_m(P^*)}{\gamma_f \mu_m(P^*) + \gamma_m \mu_f(P^*)} \right] P^* \text{ and } M^* = \left[\frac{\gamma_m \mu_f(P^*)}{\gamma_f \mu_m(P^*) + \gamma_m \mu_f(P^*)} \right] P^*.$$

Since $f(P)$ is decreasing and $f(0) = \mathcal{R} - 1$ and $f(\infty) = \mathcal{R}^\infty - 1$, it is clear that the interior equilibrium exists if and only if the solutions are bounded, i.e. $\mathcal{R}^\infty < 1$ and $\mathcal{R} > 1$. The following theorem establishes the limiting behavior of the solutions of (1) when they are bounded.

Theorem 2.3: *Suppose $\mathcal{R}^\infty < 1$. If $\mathcal{R} < 1$ the extinction equilibrium is globally stable. If $\mathcal{R} > 1$ there exists a unique positive equilibrium (F^*, M^*) that is globally stable.*

Proof :

Using the monotonicity of $\mathcal{M}$ we see that $f(P)$ is decreasing and

$$f(0) = \mathcal{R} - 1 \text{ and } f(\infty) = \mathcal{R}^{\infty} - 1 < 0.$$

This means that, if $\mathcal{R} < 1$ then f has no roots and $(0,0)$ is the only steady state. Otherwise, if $\mathcal{R} > 1$ there exists a unique positive equilibrium P^*.

First we show that $\mathcal{R} = 1$ is the threshold between population extinction and persistence. We assume first $\mathcal{R} < 1$ and consider the following function

$$h(t) = \max\{\mathcal{R}_f M(t), \mathcal{R}_m F(t)\}.$$

For each $t > 0$ one of the following holds:

- $h(t) = \mathcal{R}_m F(t)$ implies

$$\frac{F'}{F} = \beta(P)\gamma_f \mathcal{M}\left(1, \frac{M}{F}\right) - \mu_f(P) < \beta(0)\gamma_f \mathcal{M}\left(1, \frac{M}{F}\right) - \mu_f(0)$$

$$= \mu_f(0)\left[\mathcal{R}_f \mathcal{M}\left(1, \frac{M}{F}\right) - 1\right] = \mu_f(0)\left[\mathcal{M}\left(\mathcal{R}_f, \frac{\mathcal{R}_f M}{F}\right) - 1\right]$$

$$< \mu_f(0)[\mathcal{M}(\mathcal{R}_f, \mathcal{R}_m) - 1] = -\mu_f(0)(1 - \mathcal{R}) < 0.$$

- $h(t) = \mathcal{R}_f M(t)$ implies

$$\frac{M'}{M} = \beta(P)\gamma_m \mathcal{M}\left(\frac{F}{M}, 1\right) - \mu_m(P) < \beta(0)\gamma_m \mathcal{M}\left(\frac{F}{M}, 1\right) - \mu_m(0)$$

$$= \mu_m(0)\left[\mathcal{R}_m \mathcal{M}\left(\frac{F}{M}, 1\right) - 1\right] = \mu_m(0)\left[\mathcal{M}\left(\frac{\mathcal{R}_m F}{M}, \mathcal{R}_m\right) - 1\right]$$

$$< \mu_m(0)[\mathcal{M}(\mathcal{R}_f, \mathcal{R}_m) - 1] = -\mu_m(0)(1 - \mathcal{R}) < 0.$$

From these inequalities we see that, for any $t > 0$,

$$\frac{h'(t)}{h(t)} < -k < 0 \text{ where } k = \min\{\mu_f(0)(1 - \mathcal{R}), \mu_m(0)(1 - \mathcal{R})\}.$$

Consider now a fixed time $T > 0$. Since $-\ln h(t)$ is increasing and using Theorem 2.2,

$$kT = \int_0^T k\,dt \leq \int_0^T -\frac{h'(t)}{h(t)}dt = \int_0^T [-\ln h(t)]'dt \leq -\ln h(T) + \ln h(0).$$

Finally, letting $T \to \infty$ in

$$kT \leq -\ln h(T) + \ln h(0)$$

implies

$$\lim_{T \to \infty} h(T) = 0 \text{ which, in turns, means } F(T) \to 0 \text{ and } M(T) \to 0.$$

We now assume $\mathcal{R} > 1$. Notice that, due to continuity assumptions, there exists $P_0 > 0$ such that

$$\mathcal{M}\left[\frac{\beta(P_0)\gamma_f}{\mu_f(P_0)}, \frac{\beta(P_0)\gamma_m}{\mu_m(P_0)}\right] > 1.$$

We use a similar approach to show that the population persists: Consider the function

$$g(t) = \min\{\gamma_f \mu_m(P_0)M(t), \gamma_m \mu_f(P_0)F(t)\}.$$

Suppose now that $P(t) < P_0$. Then for every $t > 0$ we have the following cases:

- $g(t) = \gamma_m \mu_f(P_0)F(t)$. Then

$$\frac{F'}{F} > \beta(P_0)\gamma_f \mathcal{M}\left(1, \frac{M}{F}\right) - \mu_f(P_0) = \mu_f(P_0)\left[\mathcal{M}\left(\frac{\beta(P_0)\gamma_f}{\mu_f(P_0)}, \frac{\beta(P_0)\gamma_f M}{\mu_f(P_0)F}\right) - 1\right]$$

$$> \mu_f(P_0)\left[\mathcal{M}\left(\frac{\beta(P_0)\gamma_f}{\mu_f(P_0)}, \frac{\beta(P_0)\gamma_m}{\mu_m(P_0)}\right) - 1\right] > 0.$$

- $g(t) = \gamma_f \mu_m(P_0)M(t)$. Then

$$\frac{M'}{M} > \beta(P_0)\gamma_m \mathcal{M}\left(\frac{F}{M}, 1\right) - \mu_m(P_0) = \mu_m(P_0)\left[\mathcal{M}\left(\frac{\beta(P_0)\gamma_m F}{\mu_m(P_0)M}, \frac{\beta(P_0)\gamma_m}{\mu_m(P_0)}\right) - 1\right]$$

$$> \mu_m(P_0)\left[\mathcal{M}\left(\frac{\beta(P_0)\gamma_f}{\mu_f(P_0)}, \frac{\beta(P_0)\gamma_m}{\mu_m(P_0)}\right) - 1\right] > 0.$$

This shows that $g'(t) > 0$ as soon as $P(t) < P_0$ which shows that, if $\mathcal{R} > 1$ then $(0,0)$ is a repeller and the full solution of (1), together with its limit points, belongs to a compact subset of the positive quadrant.
Furthermore, using Dulac's criterion with the Dulac function $\frac{1}{FM}$ we obtain:

$$FM\left[\frac{\partial}{\partial F}\left(\frac{1}{FM}F'\right) + \frac{\partial}{\partial M}\left(\frac{1}{FM}M'\right)\right]$$

$$= \beta(P)\gamma_f \frac{\partial \mathcal{M}}{\partial F}(F,M) + \beta(P)\gamma_m \frac{\partial \mathcal{M}}{\partial M}(F,M) + \beta'(P)\gamma_f \mathcal{M}(F,M) + \beta'(P)\gamma_m \mathcal{M}(F,M)$$

$$-\mu'_m(P)M - \mu'_f(P)F - \beta(P)\gamma_f \mathcal{M}\left(1,\frac{M}{F}\right) - \beta(P)\gamma_m \mathcal{M}\left(\frac{F}{M},1\right).$$

Now from $F\frac{\partial \mathcal{M}}{\partial F}(F,M) + M\frac{\partial \mathcal{M}}{\partial M}(F,M) = \mathcal{M}(F,M)$ we use the following substitutions in the expression above:

$$\frac{\partial \mathcal{M}}{\partial F}(F,M) = -\frac{M}{F}\frac{\partial \mathcal{M}}{\partial M}(F,M) + \mathcal{M}\left(1,\frac{M}{F}\right) \text{ and}$$

$$\frac{\partial \mathcal{M}}{\partial M}(F,M) = -\frac{F}{M}\frac{\partial \mathcal{M}}{\partial F}(F,M) + \mathcal{M}\left(\frac{F}{M},1\right).$$

With these, we now have

$$FM\left[\frac{\partial}{\partial F}\left(\frac{1}{FM}F'\right) + \frac{\partial}{\partial M}\left(\frac{1}{FM}M'\right)\right] = -\beta(P)\gamma_f \frac{M}{F}\frac{\partial \mathcal{M}}{\partial M}(F,M) - \beta(P)\gamma_m \frac{F}{M}\frac{\partial \mathcal{M}}{\partial F}(F,M)$$

$$+\beta'(P)\mathcal{M}(F,M) - \mu'_m(P)M - \mu'_f(P)F < 0.$$

This follows from $\beta'(P) < 0$, $\mu'_f(P) > 0$, $\mu'_m(P) > 0$.

Thus periodic solutions or homoclinic orbits are excluded and from Poincare-Bendixson trichotomy it follows that $P(t) \to P^*$. This completes the proof.

$\square$

Note that these results hold without the heterosexuality assumption, $\mathcal{M}(0,M) = \mathcal{M}(F,0) = 0$, which makes the model suitable for female/male dominated birth rates, i.e. $\mathcal{M}(F,M) = \rho F$ or ρM. This will not be the case for the model with pair-formation as seen in Fig. A2.

3.   The logistic two-sex model with pair-formation

The purpose of this section is to provide a similar generalization for the two-sex model where single individuals form stable pairs and the fertility is modeled as a per-couple birth rate. The meaning of the variables is similar with the difference that F and M represent single females and males, C are the couples and δ is the couple-separation (i.e. divorce) rate. The model is as follows

$$\begin{cases} F' = -\mu_f(P)F + [\beta(P)\gamma_f + \delta + \mu_m(P)]C - \mathcal{M}(F,M), \\ M' = -\mu_m(P)M + [\beta(P)\gamma_m + \delta + \mu_f(P)]C - \mathcal{M}(F,M), \\ C' = \mathcal{M}(F,M) - [\delta + \mu_f(P) + \mu_m(P)]C. \end{cases} \quad (2)$$

where $P = F + M + 2C$. The couple-formation function $\mathcal{M}$ satisfies the same conditions as the one for (1) with the additional heterosexuality condition

$$\mathcal{M}(0, M) = \mathcal{M}(F, 0) = 0, \text{ for every } F \geq 0, \ M \geq 0.$$

It is worth mentioning that this condition is essential for a biological feasible solution. Indeed, as seen in Fig. A2, if one chooses a female dominated pair-formation function, i.e. $\mathcal{M}(F, M) = \rho F$ it is possible for $M(t)$ to be negative even if the initial condition is positive. However this is not an issue since, in the case of (1), one can assume that females control the mating process and, in the absence of males they may find partners outside the community modeled. On the other hand, in the case of (2), the function $\mathcal{M}$ does not represent the number of matings but the number of pairs formed per unit of time. So it will not make sense to use a function independent of either males or females.

The model (2) can be better analyzed through an equivalent one that follows the dynamics of total females, males and couples (see also [6], [7], [9]):

$$\begin{cases} x' = -\mu_f(P)x + \beta(P)\gamma_f C, \\[2mm] y' = -\mu_m(P)y + \beta(P)\gamma_m C, \\[2mm] C' = \mathcal{M}(x - C, y - C) - [\delta + \mu_f(P) + \mu_m(P)]C, \end{cases} \tag{3}$$

where $x = F + C$, $y = M + C$ and $P = x + y$.

The relevant threshold quantities for this model are as follows (note that we preferred to use similar notations as for (1) to maintain the tradition of using $\mathcal{R}$ when referring to reproductive numbers):

$$\mathcal{R}_f := \frac{\beta(0)\gamma_f}{\mu_f(0)}, \ \ \mathcal{R}_m := \frac{\beta(0)\gamma_m}{\mu_m(0)}, \ \ \mathcal{R} := \frac{\mathcal{M}(\mathcal{R}_f - 1, \mathcal{R}_m - 1)}{\delta + \mu_f(0) + \mu_m(0)},$$

$$\mathcal{R}_f^\infty := \lim_{P \to \infty} \frac{\beta(P)\gamma_f}{\mu_f(P)}, \ \ \mathcal{R}_m^\infty := \lim_{P \to \infty} \frac{\beta(P)\gamma_m}{\mu_m(P)},$$

$$\text{and } \mathcal{R}^\infty := \lim_{P \to \infty} \frac{1}{\delta + \mu_f(P) + \mu_m(P)} \mathcal{M}\left(\frac{\beta(P)\gamma_f}{\mu_f(P)} - 1, \frac{\beta(P)\gamma_m}{\mu_m(P)} - 1\right).$$

The main results are formulated in the following theorems:

Theorem 3.1: *If $\mathcal{R}_f^\infty > 1$, $\mathcal{R}_m^\infty > 1$ and $\mathcal{R}^\infty > 1$ then the solution of (3) is unbounded. If either $\mathcal{R}_f^\infty < 1$, $\mathcal{R}_m^\infty < 1$ or $\mathcal{R}^\infty < 1$ the solution of (3) is bounded for all time t.*

Proof: Due to the similarity of the approach we will skip some details that are similar to the ones used in the previous sections while still pointing out some key differences. Suppose first $\mathcal{R}_f^\infty > 1$, $\mathcal{R}_m^\infty > 1$ and $\mathcal{R}^\infty > 1$. We shall prove that the solution of (3) is unbounded. This case requires a stronger estimate on the threshold parameters (and a similar situation will occur when proving the extinction case below). Specifically, we first note that, since the mortality rates are increasing, they either approach a positive limit or infinity. However, since the

overall limits above are greater than 1, we must have all mortality rates bounded above and converging to a positive value.

From continuity assumptions, we can choose a strictly positive number $k > 0$, small enough, such that:

$$\lim_{P\to\infty} \frac{\beta(P)\gamma_f}{\mu_f(P) + k} := \mathcal{L}_f^\infty > 1, \;\; \lim_{P\to\infty} \frac{\beta(P)\gamma_m}{\mu_m(P) + k} := \mathcal{L}_m^\infty > 1 \text{ and}$$

$$\lim_{P\to\infty} \frac{\mathcal{M}(\mathcal{L}_f^\infty - 1, \mathcal{L}_m^\infty - 1)}{\delta + \mu_f(P) + \mu_m(P)} := \mathcal{L}^\infty > 1.$$

With this choice for k we now consider the following function

$$h(t) = \min\left\{ \frac{x(t)}{\mathcal{L}_f^\infty}, \frac{y(t)}{\mathcal{L}_m^\infty}, C(t) \right\}.$$

For every $t > 0$ we have the following cases:

- $h(t) = \frac{x(t)}{\mathcal{L}_f^\infty}$. Then

$$\frac{x'}{x} = -\mu_f(P) + \beta(P)\gamma_f \frac{C}{x} \geq -\mu_f(P) + \beta(P)\gamma_f \frac{1}{\mathcal{L}_f^\infty} = k + [\mu_f(P) + k]\left[\frac{\beta(P)\gamma_f}{[\mu_f(P) + k]\mathcal{L}_f^\infty} - 1 \right]$$

$$\geq k + [\mu_f(0) + k]\left[\frac{\beta(P)\gamma_f}{[\mu_f(P) + k]\mathcal{L}_f^\infty} - 1 \right] \geq k > 0 \text{ as } P \to \infty.$$

In a similar way we can show that $\frac{y'}{y} > k$ if $f(t) = \frac{y(t)}{\mathcal{L}_m^\infty}$.

- $h(t) = C(t)$. Then

$$\frac{C'}{C} = \mathcal{M}\left(\frac{x}{C} - 1, \frac{y}{C} - 1 \right) - [\delta + \mu_f(P) + \mu_m(P)] \geq \mathcal{M}\left(\mathcal{L}_f^\infty - 1, \mathcal{L}_m^\infty - 1 \right) - [\delta + \mu_f(P) + \mu_m(P)]$$

$$\geq [\delta + \mu_f(0) + \mu_m(0)]\left[\frac{\mathcal{M}(\mathcal{L}_f^\infty - 1, \mathcal{L}_m^\infty - 1)}{\delta + \mu_f(P) + \mu_m(P)} - 1 \right] \geq [\delta + \mu_f(0) + \mu_m(0)](\mathcal{L}^\infty - 1) > 0.$$

Choosing $k_1 := \min\{k, [\delta + \mu_f(0) + \mu_m(0)](\mathcal{L}^\infty - 1)\}$ and using Theorem 2.2 we now obtain

$$\ln h(T) - \ln h(0) \geq \int_0^T \frac{h'}{h} dt \geq \int_0^T k_1 dt = k_1 T,$$

which shows that $h(T) \to \infty$ as claimed.

To prove the boundedness threshold, we first assume that $\mathcal{R}_f^\infty < 1$. Then we see that, using $C \leq x$,

$$\frac{x'}{x} \leq -\mu_f(P)\left[\frac{\beta(P)\gamma_f}{\mu_f(P)} - 1 \right] < 0 \text{ for } P > P_0, \text{ where } P_0 \text{ is sufficiently large .}$$

This shows that $x(t)$ is bounded above which, in turns, implies $C(t)$ bounded above and, finally, from the equation of y' we see that $y(t)$ bounded above as well.

A similar argument shows that the solutions are bounded if $\mathcal{R}_m^\infty < 1$. We now assume $\mathcal{R}_f^\infty > 1$, $\mathcal{R}_m^\infty > 1$ and $\mathcal{R}^\infty < 1$.

Consider P_0 sufficiently large such that

$$\frac{\mathcal{M}\left(\frac{\beta(P_0)\gamma_f}{\mu_f(P_0)} - 1, \frac{\beta(P_0)\gamma_m}{\mu_m(P_0)} - 1\right)}{\delta + \mu_f(P_0) + \mu_m(P_0)} < 1$$

and the following function

$$g(t) = \max\left\{\frac{\mu_f(P_0)x(t)}{\beta(P_0)\gamma_f}, \frac{\mu_m(P_0)y(t)}{\beta(P_0)\gamma_m}, C(t)\right\}.$$

Analyzing again all three possible cases for $g(t)$, one can show, in a similar manner as above, that $\frac{g'}{g} < 0$ whenever $P(t) > P_0$ which means the solution of (3) is bounded.

$\square$

The following theorem establishes the threshold that separates extinction from persistence:

Theorem 3.2: *Suppose either $\mathcal{R}_f^\infty < 1$, $\mathcal{R}_m^\infty < 1$ or $\mathcal{R}^\infty < 1$. If either $\mathcal{R}_f < 1$, $\mathcal{R}_m < 1$ or $\mathcal{R} < 1$ then the extinction steady state is globally stable. Otherwise, the solution of (3) is bounded away from zero.*

Proof:

First assume $\mathcal{R}_f < 1$. Then

$$\frac{x'}{x} \leq -\mu_f(0) + \beta(0)\gamma_f < 0.$$

This implies $x(t) \to 0$ and then $C(t) \to 0$ since $C(t) \leq x(t)$. Finally from the equation of y' we also conclude that $y(t) \to 0$.

Similarly, if $\mathcal{R}_m < 1$ one can show the entire population goes extinct.

We now assume $\mathcal{R}_f > 1$, $\mathcal{R}_m > 1$ and $\mathcal{R} < 1$. Due to similar continuity assumptions as the ones used in the previous theorems, one can choose a strictly positive number $k > 0$ small enough such that

$$\mu_f(0) - k > 0, \ \mu_m(0) - k > 0 \text{ and } \frac{\mathcal{M}\left(\frac{\beta(0)\gamma_f}{\mu_f(0) - k} - 1, \frac{\beta(0)\gamma_m}{\mu_m(0) - k} - 1\right)}{\delta + \mu_f(0) + \mu_m(0)} < 1.$$

Now consider the function

$$g(t) = \max\left\{\frac{(\mu_f(0) - k)x(t)}{\beta(0)\gamma_f}, \frac{(\mu_m(0) - k)x(t)}{\beta(0)\gamma_m}, C(t)\right\}.$$

Analyzing all three possibilities for every $t > 0$ we see that, if $g(t) = \frac{(\mu_f(0) - k)x(t)}{\beta(0)\gamma_f}$ then

$$\frac{x'}{x} \leq -\mu_f(P) + \beta(P)\gamma_f\frac{(\mu_f(0) - k)}{\beta(0)\gamma_f} \leq -k < 0.$$

Analogously $g(t) = \frac{(\mu_m(0)-k)x(t)}{\beta(0)\gamma_m}$ implies $\frac{y'}{y} \leq -k < 0$.

Finally if $g(t) = C(t)$ we can see that

$$\frac{C'}{C} \leq \mathcal{M}\left(\frac{\beta(0)\gamma_f}{\mu_f(0) - k} - 1, \frac{\beta(0)\gamma_m}{\mu_m(0) - k} - 1\right) - [\delta + \mu_f(0) + \mu_m(0)] := -k_1 < 0.$$

Choosing $k_2 := \min\{k, k_1\}$, the estimates above show that $\frac{g'}{g} \leq -k_2 < 0$. From this and Theorem 2.2 we have that

$$k_2 T = \int_0^T k_2 dt \leq \int_0^T -\frac{g'(t)}{g(t)} dt = \int_0^T [-\ln g(t)]' dt \leq -\ln g(T) + \ln g(0)$$

which implies that $g(T) \to 0$.

We now assume $\mathcal{R}_f > 1$, $\mathcal{R}_m > 1$ and $\mathcal{R} > 1$. And we choose $P_0 > 0$ small enough such that

$$\frac{\beta(P_0)\gamma_f}{\mu_f(P_0)} > 1, \ \frac{\beta(P_0)\gamma_m}{\mu_m(P_0)} > 1 \text{ and } \frac{\mathcal{M}\left(\frac{\beta(P_0)\gamma_f}{\mu_f(P_0)} - 1, \frac{\beta(P_0)\gamma_m}{\mu_m(P_0)} - 1\right)}{\delta + \mu_f(P_0) + \mu_m(P_0)} > 1.$$

Consider now the function

$$h(t) = \min\left\{\frac{\mu_f(P_0)x(t)}{\beta(P_0)\gamma_f}, \frac{\mu_m(P_0)y(t)}{\beta(P_0)\gamma_m}, C(t)\right\}.$$

Using very similar steps as in Theorem 2.2 (which we prefer to omit at this point) one can show that as soon as $P(t) < P_0$ then $\frac{h'}{h} > 0$ which shows that the population is bounded away from zero. $\qquad\square$

The existence and uniqueness of the interior steady state is complicated by the fact that, in the model with pair-formation, the monotonicity of $\mathcal{M}$ may change if its arguments become negative. Specifically, an interior steady state is a solution P^* of the following equation

$$f(P) := \frac{\mathcal{M}\left(\frac{\beta(P)\gamma_f}{\mu_f(P)} - 1, \frac{\beta(P)\gamma_m}{\mu_m(P)} - 1\right)}{\delta + \mu_f(P) + \mu_m(P)} = 1.$$

Notice that, under the persistence conditions established in the previous theorem, i.e. $\mathcal{R}_f > 1$, $\mathcal{R}_m > 1$ and $\mathcal{R} > 1$, we have that $f(0) > 1$, $f(P)$ is initially decreasing and the initial arguments of $\mathcal{M}$ are also positive and decreasing. If $\mathcal{R}_f^\infty > 1$ and $\mathcal{R}_m^\infty > 1$ then $f(P)$ is decreasing on its entire domain. Thus the existence and uniqueness of P^* is equivalent to $\mathcal{R}^\infty < 1$, $\mathcal{R}_f^\infty > 1$ and $\mathcal{R}_m^\infty > 1$. If either $\mathcal{R}_f^\infty < 1$ or $\mathcal{R}_m^\infty < 1$ the arguments of $\mathcal{M}$ become negative as $P \to \infty$. In this case $f(P)$ crosses the horizontal axis which ensures the existence of P^*. Depending on the pair-formation function chosen, $f(P)$ may become negative or undefined after its first crossing. It may also increase as soon as both the arguments of $\mathcal{M}$ become negative, as it happens in the case of geometric mean $\mathcal{M}(x,y) = \rho\sqrt{xy}$, which is undefined whenever $xy < 0$. In this case the existence of a second root for $f(P) = 1$ is possible. However this second root will satisfy $\frac{\beta(P)\gamma_f}{\mu_f(P)} < 1$ or $\frac{\beta(P)\gamma_m}{\mu_m(P)} < 1$ and this is always outside the invariant region of biological feasibility of the solutions of (3). Specifically, all solutions starting in the positive quadrant remain bounded away from zero. This implies that the total number of females and males are at least

as large as the number of couples for all time t. It follows that, in the biologically feasible region, an interior steady state satisfies

$$\frac{\beta(P)\gamma_f}{\mu_f(P)} = \frac{x}{C} \geq 1 \text{ and } \frac{\beta(P)\gamma_m}{\mu_m(P)} = \frac{y}{C} \geq 1.$$

Therefore, regardless of the choice of the pair-formation function, the existence and uniqueness of the interior steady state P^* that is biologically relevant is equivalent to either $\mathcal{R}^\infty < 1$, $\mathcal{R}_f^\infty < 1$ or $\mathcal{R}_m^\infty < 1$. This is precisely the boundedness condition established in Theorem 3.1. We now show that the interior steady state is locally asymptotically stable by generalizing the similar theorem in [6], [7].

Theorem 3.3: *Suppose either $\mathcal{R}_f^\infty < 1$, $\mathcal{R}_m^\infty < 1$ or $\mathcal{R}^\infty < 1$. If $\mathcal{R}_f > 1$, $\mathcal{R}_m > 1$ and $\mathcal{R} > 1$ then there exists a unique positive steady state of (3) that is locally asymptotically stable.*

Proof: The existence and uniqueness of a positive steady state (x^*, y^*, C^*) follows from the arguments presented before stating the theorem in the previous section. We denote also

$$\mu_f^* := \mu_f(x^*+y^*), \ \mu_m^* := \mu_m(x^*+y^*), \ P^* := x^*+y^*, \ \mu_f' := \mu_f'(P^*), \ \mu_m' := \mu_m'(P^*),$$

$$\beta^* := \beta(P^*), \ \beta' := \beta'(P^*), \ \mathcal{M}_x := \frac{\partial \mathcal{M}}{\partial x}(x^*-C^*, y^*-C^*) \text{ and } \mathcal{M}_y := \frac{\partial \mathcal{M}}{\partial y}(x^*-C^*, y^*-C^*).$$

The Jacobian of (3) is

$$J(x,y,C) = \begin{pmatrix} -\mu_f' x^* - \mu_f^* + \beta'\gamma_f C^* & -\mu_f' x^* + \beta'\gamma_f C^* & \beta^*\gamma_f \\ -\mu_m' y^* + \beta'\gamma_m C^* & -\mu_m' y^* - \mu_m^* + \beta'\gamma_f C^* & \beta^*\gamma_m \\ \mathcal{M}_x - [\mu_f' + \mu_m']C^* & \mathcal{M}_y - [\mu_f' + \mu_m']C^* & -\mathcal{M}_x - \mathcal{M}_y - \delta - \mu_f^* - \mu_m^* \end{pmatrix}.$$

Note that $\beta' \leq 0$, $\mu_f' \geq 0$ and $\mu_m' \geq 0$. To simplify the computation of the coefficients of the characteristic polynomial of $J(x^*, y^*, C^*)$ we will also use the following identities:

$$\gamma_f = \frac{\mu_f^* x^*}{\beta^* C^*}, \ \gamma_m = \frac{\mu_m^* y^*}{\beta^* C^*},$$

$$\mathcal{M}_x + \mathcal{M}_y + \delta + \mu_f^* + \mu_m^* = \frac{1}{C^*}(x^*\mathcal{M}_x + y^*\mathcal{M}_y).$$

If we denote the characteristic polynomial as

$$\lambda^3 + p_1\lambda^2 + p_2\lambda + p_3$$

we can now analyze the Routh-Hurwitz conditions for ensuring that all its roots have a negative real part:

$$p_1 = (\mu_f^* + \mu_m^*) + (\mu_f' x^* + \mu_m' y^*) + \frac{1}{C^*}(x^*\mathcal{M}_x + y^*\mathcal{M}_y) - \frac{\beta'}{\beta^*}(\mu_f^* x^* + \mu_m^* y^*) > 0.$$

$$p_2 = \frac{1}{\beta^* C^*}\left\{ \beta^*(\mu_f' x^* + \mu_m' y^*)(x^*\mathcal{M}_x + y^*\mathcal{M}_y) + \beta^*(x^*\mu_m^*\mathcal{M}_x + y^*\mu_f^*\mathcal{M}_y) \right.$$

$$+ \beta^* C^*(x^* + y^*)(\mu_f^*\mu_m' + \mu_m^*\mu_f') + \beta^* C^*(x^*\mu_f^*\mu_f' + y\mu_m^*\mu_m' + \mu_f^*\mu_m^*)$$

$$\left. -\beta'[(x^*\mathcal{M}_x + y^*\mathcal{M}_y)(\mu_m^* y^* + \mu_f x^*) + \mu_f^*\mu_m^* C^*(x^* + y^*)] \right\} > 0.$$

$$p_3 = \left(\frac{x^* + y^*}{\beta^* C^*}\right)[\beta^* \mu_f^* \mu_m^* C^*(\mu_f' + \mu_m') + \beta^*(\mu_f^* \mu_m' y^* \mathcal{M}_y + \mu_f' \mu_m^* x^* \mathcal{M}_x)$$

$$-\beta' \mu_f^* \mu_m^*(x^* \mathcal{M}_x + y^* \mathcal{M}_y)] > 0.$$

A tedious but straightforward computation shows that $p_1 p_2 - p_3 > 0$ as well. Thus (x^*, y^*, C^*) is locally asymptotically stable.

$$\square$$

We believe (as Castillo-Chavez and Huang conjectured in [6]) that this equilibrium is in fact globally stable under the condition of the previous theorem but we still lack a proof of this assertion.

4.   Conclusions

We revisited two logistic gender structured models that have been used in various forms in the literature and generalized them to models using milder conditions on the pair-formation function, fertility and mortality rates. In particular, we established the thresholds between logistic and exponential behavior as well as the threshold between extinction and persistence. If the population persists, the unique interior equilibrium was found to be globally stable for the model with ephemeral pair bonds. We believe the same holds for the model with stable couples although we only managed to prove local stability in this case.

The main advantage of this generalization is the possibility of more freedom in choosing the specific mathematical forms for these rates that may be more appropriate depending on the population under study and the environmental effects that impose the logistic behavior.

From [6] and [7] and the results in the present paper, we see that, in the case of a population model with stable couples, the solution approaches a positive steady state provided that

$$\mathcal{R}_f > 1, \ \mathcal{R}_m > 1 \text{ and } \mathcal{M}(\mathcal{R}_f - 1, \mathcal{R}_m - 1) > \delta + \mu_f(0) + \mu_m(0).$$

Thus, the threshold requires each sex-specific reproductive number to be greater than one, in addition to having enough marriages among the net-offspring population to compensate for the couple removal rate given here by divorce rate (δ) and spousal mortality. This is not needed in the model without pairs for some forms of the mating function. It is true that some mating functions actually imply $\mathcal{R}_f > 1$ and $\mathcal{R}_m > 1$ as we can see in the case of harmonic mean, $\mathcal{M}(x, y) = 2\rho \frac{xy}{x+y}$ with $\rho < \frac{1}{2}$. Note that

$$2\rho \frac{\mathcal{R}_f \mathcal{R}_m}{\mathcal{R}_f + \mathcal{R}_m} > 1 \text{ implies both } \mathcal{R}_f > 1 \text{ and } \mathcal{R}_m > 1.$$

However, other mating functions, such as the geometric mean $\mathcal{M}(F, M) = \rho\sqrt{FM}$, do not require this as we can see in Fig. A3.

The results obtained in this paper can be extended in several ways. First, it would be useful to construct a Lyapunov function corresponding to (3) to close the remaining gap in the proof that would guarantee global stability of the interior equilibrium. Secondly, further generality can be attempted in order to include more important types of density dependence such as: Allee effects incorporated in the birth function, density dependence in the separation rate of couples to account for

a competitive mating environment, etc. We plan to follow these directions in the near future.

Acknowledgements

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Appendix A. Examples and figures

In this section we provide the examples quoted several times in remarks done throughout the paper. We mention again that our choice for the mathematical forms of the birth and death rates are chosen for illustrating purposes only and are not related to real data. Consider the following birth and death rates:

$$\beta(P) = \beta_0 + \frac{b}{1+P}, \ \mu_f(P) = \mu_f^0 + \frac{c_f P}{1+P}, \ \mu_m(P) = \mu_m^0 + \frac{c_m P}{1+P}.$$

One reason for choosing these forms is to point out that the birth rate need not decrease to zero nor the mortality needs to increase to infinity as $P \to \infty$ in order to have the logistic behavior in the model. In Fig. A1 we show a case where the model (1) exhibits exponential behavior despite the fact that the birth rate is decreasing and the death rate increasing. The pair-formation chosen was the harmonic mean, $\mathcal{M}(F, M) = 2\rho \frac{FM}{F+M}$.

The second example illustrates that male/female dominance in the form of the pair-formation function may lead to a biologically ill-posed model. This happens when one drops the heterosexuality condition in the model (2):

$$\mathcal{M}(F, 0) = \mathcal{M}(0, M) = 0.$$

Suppose the pair formation depends only on females, i.e. $\mathcal{M}(F, M) = \rho F$. Then it is possible to obtain negative solutions of M even if $M(0) > 0$ as seen in Fig.

A2.

Finally, in the last example (Fig. A3), we illustrate that, in the case of the model with ephemeral pair-bonds (1), the population may persist even if one sex-specific reproductive number is less than one. The mating function chosen was the geometric mean, $\mathcal{M}(F, M$
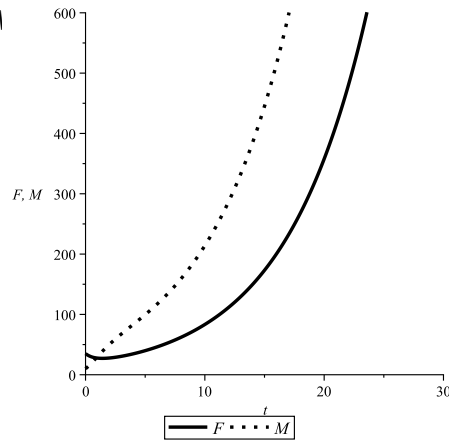
Figure A1. $\mathcal{R}^{\infty} = 1.2$. Parameter values: $\beta_0 = 0.8$, $b = 0.3$, $c_f = 0.7$, $c_m = 0.6$, $\mu_f^0 = 0.02$, $\mu_m^0 = 0.04$, $\rho = 2.5$, $\gamma_f = 0.3$, $\gamma_m = 0.7$.
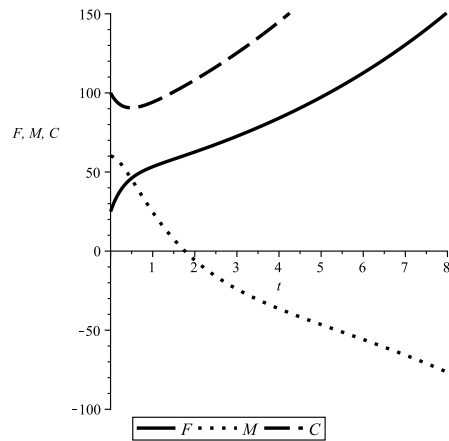
Figure A2.   The case of a biologically ill posed model (2) with female dominated pair-formation. Parameter values: $\beta_0 = 1$, $b = 0.3$, $c_f = 0.007$, $c_m = 0.006$, $\mu_f^0 = 0.1$, $\mu_m^0 = 0.7$, $\rho = 2$, $\gamma_f = 0.4$, $\gamma_m = 0.6$.
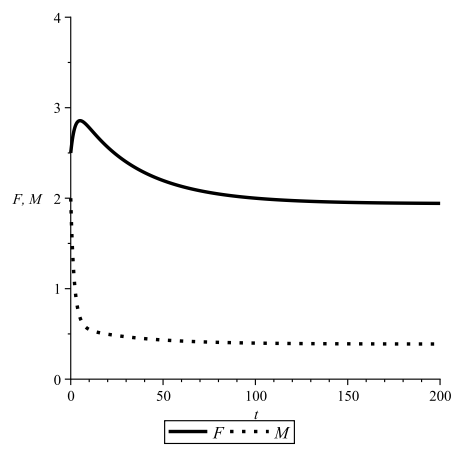
Figure A3. $\mathcal{R}_f = 8$, $\mathcal{R}_m = 0.86$, $\mathcal{R} = 1.83$. Parameter values: $\beta_0 = 0.7$, $b = 0.3$, $c_f = 0.07$, $c_m = 0.06$, $\mu_f^0 = 0.05$, $\mu_m^0 = 0.7$, $\rho = 0.7$, $\gamma_f = 0.4$, $\gamma_m = 0.6$.