

RESEARCH ARTICLE

A note on “A generalized two-sex logistic model”

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We re-visit the recently published paper on a generalization of the two-sex logistic model by Maxin and Segal [1]. We show that the logistic assumption of a non-increasing birth rate can be replaced by a more general assumption of a non-increasing ratio between the female/male birth and mortality rate. In this note we indicate the changes necessary in the proofs of the theorems in [1] and discuss several situations where this new assumption is useful.

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1. Introduction

In [1] we provided a generalization of the two-sex logistic model with and without pairs without assuming a specific birth and death rate for the individuals. We only imposed the standard logistic assumptions made on these rates: non-increasing birth rate and non-decreasing mortality rates for both females and males as functions of the total population size. These are typical assumptions that capture the competition for limited resources (whatever those may be) which, in turn, cause the population to remain bounded. Often modelers assume a constant birth rate and assume only an increasing mortality rate with the total population. Similarly (albeit less often) mortality rates are assumed constant but, in that case, the birth rate needs to be a decreasing function to ensure that the population remains bounded. This was the approach in the first two-sex logistic model introduced by Chavez and Huang [2].

After the publication of our paper it was pointed to us that it may be useful to have a logistic model in which the assumptions made on the birth rate could be relaxed. Logistic assumptions are typically made on the mortality rate (for example with larger populations the limited food resources may cause an increase in the death rate), however, the birth rate may not be subjected to the same effect. In fact, one can argue that the birth rate could be an *increasing* function of the total population by assuming, for example, that, with higher population densities,

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the mating opportunities and, consequently, the birth rate should increase. For example, pollen limitation in low densities of trees negatively impacts fruit set and maturation [3]. The Allee effect is another typical example when this assumption is made. Of course, it is still necessary to assume that, in the long run, the mortality “takes over” the birth rate in order to still have a logistic model with a bounded population but, instead of making an assumption on the monotonicity of the birth rate, we will make such an assumption on the ratio between the birth and mortality rates and show that all results from [1] still hold. This slightly more general condition allows more freedom in modeling the birth rate in these models.

In the following sections of this note we provide a brief overview of the models and the statements of the theorems. These theorems hold under the new assumptions with only minor adjustments. We will only point out the steps that are different from the original paper.

The main ingredient of the two-sex models analyzed in [1] is the pair formation function \mathcal{M} described below:

Let F , M denote the number of females and males available for pairing. The conditions usually imposed on \mathcal{M} are:

- **positivity:** $\mathcal{M}(F, M) \geq 0$ whenever $F \geq 0$, $M \geq 0$.
- **heterosexuality:** $\mathcal{M}(0, M) = \mathcal{M}(F, 0) = 0$.
- **homogeneity:** $\mathcal{M}(\alpha F, \alpha M) = \alpha \mathcal{M}(F, M)$ for every $\alpha \geq 0$.
- **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 $M \geq 0$.

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

The first model analyzed in [1] considers a population where the reproductive individuals form pairs for mating purposes only (no stable couples).

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

where $P = F + M$. We assume that \mathcal{M} , μ_f , μ_m and β are continuously differentiable on their domains and positive for $P > 0$. The mating function \mathcal{M} satisfies the positivity, monotonicity and homogeneity assumptions listed in the Introduction. In addition we assume:

- **non-increasing birth to death female and male ratios:**

$$\frac{d}{dP} \left(\frac{\beta(P)}{\mu_f(P)} \right) \leq 0 \text{ and } \frac{d}{dP} \left(\frac{\beta(P)}{\mu_m(P)} \right) \leq 0 \text{ for every } P \geq 0. \quad (2)$$

Remark 1: This is the new assumption that replaces $\beta'(P) \leq 0$ from [1].

- **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.

All other notations from [1] are maintained and reproduced here for convenience:

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

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

Recall also the following identity used several times:

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

We now state the theorems from [1] and indicate the steps in the proofs that are different from the original paper:

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.*

The proof of this theorem is identical to the corresponding one in [1] without any modification.

Theorem 2.2: *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.*

This theorem requires some minor adjustments on the lower and upper estimates used in the original proof and a different Dulac function in the argument that shows the model does not admit periodic solutions. In the main argument (here and in other similar theorems) we used minimum or maximum functions such as the one below with the goal of estimating the ratio h'/h :

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

Below we provide an example on how we should modify the estimate under the new assumption (2):

If $h(t) = \mathcal{R}_m F(t)$ then

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

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

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

Similar re-arrangements can be used in all other arguments of this type.

In the argument where we showed the non-existence of periodic solutions we can use (instead of $\frac{1}{FM}$) the Dulac function $\frac{1}{\beta(P)FM}$ which leads to:

$$\begin{aligned} & \beta(P)FM \left[\frac{\partial}{\partial F} \left(\frac{1}{\beta(P)FM} F' \right) + \frac{\partial}{\partial M} \left(\frac{1}{\beta(P)FM} M' \right) \right] \\ &= \frac{\beta'(P)}{\beta(P)} \mu_f(P) F + \frac{\beta'(P)}{\beta(P)} \mu_m(P) M + \beta(P) \gamma_f \frac{\partial \mathcal{M}}{\partial F}(F, M) + \beta(P) \gamma_m \frac{\partial \mathcal{M}}{\partial M}(F, M) \\ & \quad - \beta(P) \gamma_f \mathcal{M} \left(1, \frac{M}{F} \right) - \beta(P) \gamma_m \mathcal{M} \left(\frac{F}{M}, 1 \right) - \mu'_f(P) F - \mu'_m(P) M. \end{aligned}$$

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

$$\begin{aligned} & \beta(P)FM \left[\frac{\partial}{\partial F} \left(\frac{1}{\beta(P)FM} F' \right) + \frac{\partial}{\partial M} \left(\frac{1}{\beta(P)FM} M' \right) \right] \\ &= F \left[\frac{\beta'(P) \mu_f(P)}{\beta(P)} - \mu'_f(P) \right] + M \left[\frac{\beta'(P) \mu_m(P)}{\beta(P)} - \mu'_m(P) \right] \\ & \quad - \beta(P) \gamma_f \frac{M}{F} \frac{\partial \mathcal{M}}{\partial M}(F, M) - \beta(P) \gamma_m \frac{F}{M} \frac{\partial \mathcal{M}}{\partial F}(F, M) \\ &= \beta(P) F \left[\frac{\beta(P)}{\mu_f(P)} \right]' + \beta(P) M \left[\frac{\beta(P)}{\mu_m(P)} \right]' \\ & \quad - \beta(P) \gamma_f \frac{M}{F} \frac{\partial \mathcal{M}}{\partial M}(F, M) - \beta(P) \gamma_m \frac{F}{M} \frac{\partial \mathcal{M}}{\partial F}(F, M) < 0. \end{aligned}$$

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

In this section we present the proofs of the theorems from [1] related to the two-sex logistic model with pair-formation shown below:

$$\begin{cases} F' = -\mu_f(P)F + [\beta(P)\gamma_f + \delta + \mu_m(P)]C - \mathcal{M}(F, M), \\ M' = -\mu_m(P)M + [\beta(P)\gamma_m + \delta + \mu_f(P)]C - \mathcal{M}(F, M), \\ C' = \mathcal{M}(F, M) - [\delta + \mu_f(P) + \mu_m(P)]C. \end{cases} \quad (3)$$

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

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

The model (3) is equivalent to one that follows the dynamics of total females, males and couples:

$$\begin{cases} x' = -\mu_f(P)x + \beta(P)\gamma_f C, \\ y' = -\mu_m(P)y + \beta(P)\gamma_m C, \\ C' = \mathcal{M}(x - C, y - C) - [\delta + \mu_f(P) + \mu_m(P)]C, \end{cases} \quad (4)$$

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

The relevant threshold quantities are:

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

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

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

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 (4) is unbounded. If either $\mathcal{R}_f^\infty < 1$, $\mathcal{R}_m^\infty < 1$ or $\mathcal{R}^\infty < 1$ the solution of (4) is bounded for all time t .*

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 (4) is bounded away from zero.*

The proofs of these two theorems have identical steps as those from [1] or require small adjustments in the estimates similar to those presented in the previous section of this note.

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 (4) that is locally asymptotically stable.*

The only relevant modification in the proof of this theorem concerns the Routh-Hurwitz criteria in proving the local stability of the interior equilibrium. Recall also the notations used here:

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

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

The Jacobian of (4) 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 $\beta' \mu_f^* - \beta^* \mu'_f \leq 0$, $\beta' \mu_m^* - \beta^* \mu'_m \leq 0$, $\mu'_f \geq 0$ 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:

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

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

Denoting the characteristic polynomial as

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

then the Routh-Hurwitz conditions become:

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

$$p_2 = \frac{1}{\beta^* C^*} \{ (\beta^* \mu'_f - \beta' \mu_f^*) [x^* (x^* \mathcal{M}_x + y^* \mathcal{M}_y) + y^* \mu_m^* C^*] \\ + (\beta^* \mu'_m - \beta' \mu_m^*) [y^* (x^* \mathcal{M}_x + y^* \mathcal{M}_y) + x^* \mu_f^* C^*] + \beta^* C^* (x^* \mu'_f + y^* \mu'_m) (\mu_f^* + \mu_m^*) \\ + \beta^* (x^* \mu_m^* \mathcal{M}_x + y^* \mu_f^* \mathcal{M}_y) + \beta^* C^* \mu_f^* \mu_m^* \} > 0.$$

$$p_3 = \left(\frac{x^* + y^*}{\beta^* C^*} \right) [\beta^* \mu_f^* \mu_m^* C^* (\mu'_f + \mu'_m) + x^* \mu_m^* \mathcal{M}_x (\beta^* \mu'_f - \beta' \mu_f^*) \\ + y^* \mu_f^* \mathcal{M}_y (\beta^* \mu'_m - \beta' \mu_m^*)] > 0.$$

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

4. Conclusions

In this note we showed that the assumption that the birth rate $\beta(P)$ is a decreasing function of the total population size can be relaxed to a similar assumption on the ratio between the birth and mortality rates $\frac{\beta(P)}{\mu_f(P)}$ and $\frac{\beta(P)}{\mu_m(P)}$. All theorems from [1] remain valid while their proofs needed only small adjustments. This modification allows a greater variety in choosing a specific form for the birth rate. In particular, it allows the use of fertility rates that increase with the total population size which is an underlying assumption in some cases.

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