Asymmetric Two-Sex Models with a Mate-Finding Allee Effect

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Abstract

In a two-sex demographic model, the most challenging mathematical components are the couple-formation functions. These functions link the number of pairs with the number of available singles. They are usually not detailed enough to include important aspects of social behavior such as: motivation for pairing which may be gender specific, scarcity or abundance of the opposite gender or social/economic factors.

In this research we analyze several two-sex models to better describe asymmetric demographic situations. In particular we focus on a mate-finding Allee effect which models the difficulty of pairing at low population densities and investigate whether this effect is sensitive to changes in sex ratios and/or overall female/male densities. We also compute the Allee threshold which separates population extinction from persistence and test these results against real demographic data from world populations.

1   Introduction

Two-sex models are demographic models where individuals are separated by sex. At the core of these models is a pair-formation function $\mathcal{P}$. The pair-formation function is the most important aspect of a two-sex model as it calculates the number of mating pairs in a given population. The pair-formation function can be varied to fit a specific situation.

1.1   Generic Two-Sex Model

A generic two-sex model can be written as follows where $F(t)$ is the population of females at time t and $M(t)$ the population of males at time t:

$$F' = \beta\gamma_f\mathcal{P}(F, M) - \bar{\mu}_f F$$

$$M' = \beta\gamma_m\mathcal{P}(F, M) - \bar{\mu}_m M$$

This is a coupled system of equations that includes the pair-formation function $\mathcal{P}(F, M)$ which is dependent on both sexes. In addition, the model contains several parameters:

β	Birth rate per pair
γ_f, γ_m, with $\gamma_f + \gamma_m = 1$	Probability a newborn is female/male
μ_f, μ_m	Intrinsic death rate of females/males
$\bar{\mu}_f = \mu_f + bP$	Logistic death rate of females
$\bar{\mu}_m = \mu_m + bP$	Logistic death rate of males

Where $P(t) = F(t) + M(t)$.

A logistic death rate is included for both sexes as it is most realistic to consider populations with a carrying capacity.

1.2   Pair Formation Function: Imposed Conditions

Since the pair-formation function is used to describe biological situations it is often useful and necessary to impose conditions. Not all pair-formation functions used in two-sex models strictly adhere to each constraint, however the following is a list of constraints commonly considered:

- **Positivity**: $\mathcal{P}(F, M) \geq 0$ when $M, F \geq 0$

  This assumes a positive number of couples when there is a positive number of singles.

- **Heterosexuality**: $\mathcal{P}(0, M) = \mathcal{P}(F, 0) = 0$

  In order for mating couples to be formed there must be a nonzero population of females and males.

- **Monotonicity**: $\frac{\partial \mathcal{P}}{\partial F} \geq 0$ and $\frac{\partial \mathcal{P}}{\partial M} \geq 0$
  As the density of single males and females in a population increases, the number of pairs is also expected to increase.

- **Consistency**: $\mathcal{P}(F, M) \leq kF$ and $\mathcal{P}(F, M) \leq kM$ for some constant $k > 0$
  The number of couples formed is limited by the number of individuals available of either sex.

- **Degree-one Homogeneity**: $\mathcal{P}(\alpha F, \alpha M) = \alpha \mathcal{P}(F, M)$ for any $\alpha > 0$
  If the number of females and males increase by the same rate, the number of couples will increase by that rate as well.

We focus our attention to the condition of Degree-one Homogeneity which can actually limit a pair-formation function from best describing a population. Take for example the pair-formation function which utilizes the harmonic mean:

$$\mathcal{P}(F, M) = K \frac{FM}{F + M}$$

A disadvantage of such a model is that supposing $F = M$, due to Degree-one Homogeneity the pair formation function becomes a scalar factor of one gender:

$$\mathcal{P}(F, M) = \frac{K}{2} F$$

In such a case we see that couples form at the same rate $\frac{K}{2}$, despite whether there are four or four million individuals in the population. While a useful mathematical simplification, logically, the constraint of Degree-One Homogeneity is in this case a biological over-simplification.

1.3 Pair Formation Considering an Allee Effect

As a means to improve upon a pair-formation function, for some populations an Allee Effect can be incorporated. The Allee Effect is a biological term describing positive correlation between population density and individual fitness. For the sake of our research we consider a Mate-Finding Allee-Effect represented by an Allee Function $\mathcal{A}$.

Consider the Allee Function:

$$\mathcal{A}(M) = \frac{M}{M + \theta}$$

The Allee Function represents the probability of finding a mate. The function is considered from the perspective of one gender. In this case, the female perspective is chosen and therefore the Allee function is in terms of the male population. The parameter θ represents the strength of the Allee Effect, or in other words, the difficulty of finding a mate at a given population model.
Furthermore note:

- $\mathcal{A}(M)$ is a non-decreasing function of M

- $\lim_{M \to \infty} \mathcal{A}(M) = 1$
  (As the male population grows infinitely large, it is expected that finding a male mate is certain.) enditemize Therefore a pair-formation function is constructed by multiplying the female population by the probability of a female finding a mate. In doing so a general Pair-Formation function including an Allee Effect is as follows:

$$\mathcal{P}(F, M) = F \cdot \mathcal{A}(M)$$

In the course of our research we utilize an Allee function dependent on male ratio to the total population as well an Allee function dependent on male density.

2   Allee Effect Dependent on Male Proportion

We first look at an Allee Effect that is dependent on the ratio of the males to the total population of the system. It may be true that in some populations, the difficulty of finding a mate does not rely on the *number* of males available, rather, what percentage of the population is male. We choose an Allee Function:

$$\mathcal{A}\left(\frac{M}{P}\right) = \frac{\frac{M}{P}}{\frac{M}{P} + \theta}$$

We see that this Allee Function still possesses the desired properties, since:

$$\lim_{M \to \infty} \mathcal{A}\left(\frac{M}{P}\right) = \lim_{\frac{M}{P} \to 1} \mathcal{A}\left(\frac{M}{P}\right) = 1$$

and $\mathcal{A}(\frac{M}{P})$ is an increasing function. We now incorporate this into the generic model.

2.1   Model

$$\begin{cases} F' &= \beta\gamma_f F(1+\theta)\frac{(M/P)}{(M/P)+\theta} - \bar{\mu}_f F, \\[2mm] M' &= \beta\gamma_m F(1+\theta)\frac{(M/P)}{(M/P)+\theta} - \bar{\mu}_m M. \end{cases} \tag{1}$$

We see that we still maintain the desired behavior of our Allee Function.

2.1.1   Simplification of Model

Using a change of variables, we have simplified the model to this system, where one of the equations is an autonomous ODE.

$$x' = x(1-x)\left(\beta(1+\theta)\frac{1}{1-x+\theta}(\gamma_f - x) - \mu_f + \mu_m\right)$$

$$P' = \left(\frac{\beta(1+\theta)x(1-x) + (\mu_f x - \mu_m(1-x))(x - (1+\theta))}{1-x+\theta} - bP\right)P$$

With $P = F + M$, $x = \frac{F}{P}$

With an autonomous ODE, it becomes easier to compute our limiting behavior.

2.2   Model Analysis

We are able to do a full stability analysis, and have developed conditions for the existence of stable non-trivial equilibrium solutions. We introduce a few important values for notational purposes:

$$x^* = \frac{(1+\theta)\big(\beta\gamma_f - (\mu_f - \mu_m)\big)}{\beta(1+\theta) - (\mu_f - \mu_m)}$$

$$P^* = \frac{(1+\theta)\left(\beta\gamma_f^2 - \mu_m\gamma_m - \mu_f\right)}{b(\theta + \gamma_m)}$$

$$F^* = x^* P^*$$

$$M^* = (1 - x^*)P^*$$

Lemma 2.1. *The following statements are true*

1. *If $\beta\gamma_f < \mu_f - \mu_m$ then $x \to 0$*

2. *If $\beta(\gamma_f - 1)\frac{1+\theta}{\theta} < \mu_f - \mu_m < \beta\gamma_f$ then $x \to x^*$*

3. *If $\mu_f - \mu_m < \beta(\gamma_f - 1)\frac{1+\theta}{\theta}$ then $x \to 1$*

Proof. First we will show the condition of existence for x^*. Using algebra, we rewrite x' as the following:

$$x' = \frac{x(1-x)}{1 - x + \theta}(A - Bx)$$

Where

$$A = (1 + \theta)(\beta\gamma_f - (\mu_f - \mu_m))$$

$$B = \beta(1 + \theta) - (\mu_f - \mu_m)$$

It is clear to see that

$$x^* = \frac{A}{B}$$

We have several cases. We also take into consideration that in order for x^* to be feasible, it must be positive, and less than one.

1. **A > 0 and B > 0.** This means

$$\beta\gamma_f > \mu_f - \mu_m \text{ and } \beta(1 + \theta) > \mu_f - \mu_m$$

The first condition implies the second so the two combine into

$$\mu_f - \mu_m < \beta\gamma_f$$

The equilibrium value is $x^* = A/B$ and we have two subcases If

$$\mu_f - \mu_m < \beta(\gamma_f - 1)\frac{1+\theta}{\theta}$$

then x^* is not feasible and x' is positive so $x(t) \to 1$. The other case is:

$$\beta(\gamma_f - 1)\frac{1+\theta}{\theta} < \mu_f - \mu_m < \beta\gamma_f$$

In this case $0 < x^* < 1$ and since x' is positive to the left of x^* and negative to the right, then x^* is stable and $x(t) \to x^*$.

2. **A < 0 and B < 0.** Again these two conditions combine into one

$$\beta(1 + \theta) < \mu_f - \mu_m$$

Notice also that we cannot have $x^* = \frac{A}{B} < 1$ since this would imply

$$\frac{1+\theta}{\theta}\beta(\gamma_f - 1) > \mu_f - \mu_m > \beta(1 + \theta)$$

Which is impossible since the left bound is negative and the right bound positive. So, again, $0 < 1 < x^*$ and x' is negative between 0 and 1. Hence $x(t) \to 0$, and x^* exists only in case 1.

3. **A < 0 and B > 0.** This means

$$\beta\gamma_f - (\mu_f - \mu_m) < 0$$

and

$$\beta(1 + \theta) - (\mu_f - \mu_m) > 0$$

These two combine into

$$\beta\gamma_f < \mu_f - \mu_m < \beta(1 + \theta)$$

In this case $A - Bx < 0$ so $x(t) \to 0$

4. **A > 0 and B < 0.** This case is impossible since it would imply

$$\beta\gamma_f > \mu_f - \mu_m > \beta(1 + \theta)$$

But this is not possible since $\gamma_f < 1$ so the left bound is lower than the right bound.

So, all in all, we have three cases all written in threshold conditions for $\mu_f - \mu_m$:

- If $\beta\gamma_f < \mu_f - \mu_m$ then $x \to 0$
- If $\beta(\gamma_f - 1)\frac{1+\theta}{\theta} < \mu_f - \mu_m < \beta\gamma_f$ then $x \to x^*$
- If $\mu_f - \mu_m < \beta(\gamma_f - 1)\frac{1+\theta}{\theta}$ then $x \to 1$

$\square$

Lemma 2.2. *If $x \to 0$ or 1 then $P \to 0$.*

Proof.

$$P' = (T - bP)P$$

where

$$T = \frac{\beta(1 + \theta)x(1 - x) + (\mu_f x - \mu_m(1 - x))(x - (1 + \theta))}{1 - x + \theta}$$

Which is simply a logistic growth model. If T is negative, then the population will go to 0. If it is positive, the population will go to $\frac{T}{b}$. We can analyze the stability of P' using

$$\lim_{t \to \infty} P = \lim_{\lim_{t \to \infty} x} P$$

If x goes to 0, we have

$$P' = (-\mu_m - bP)P$$

And if x goes to 1, we have

$$P' = (-\mu_f - bP)P$$

In both cases, the population will tend to 0. $\square$

Theorem 2.3. *If x goes to x^*, then F and M stabilize to a non-trivial equilibrium solution if and only if the following condition is met:*

$$(\beta\gamma_f - \mu_f)(1 + \theta)\gamma_m > \mu_m\gamma_f\theta$$

If the condition is met, then F and M stabilize to (F^*, M^*). Else, F and M will stabilize to $(0, 0)$.

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Proof. Since $F = xP$ and $M = (1 - x)P$, we by Lemma 2.2 that if the population goes to 0 or 1, then the males and females will both go extinct. So, we work under the condition where $\lim_{t \to \infty} x = x^*$, or statement 2 from Lemma 2.1.

Consider the equation for P' written in terms of x:

$$P' = \left(\frac{\beta(1 + \theta)x(1 - x) + (\mu_f x - \mu_m(1 - x))(x - (1 + \theta))}{1 - x + \theta} - bP \right) P$$

We now have P as a logistic model. Let

$$T = \frac{\beta(1 + \theta)x(1 - x) + (\mu_f x - \mu_m(1 - x))(x - (1 + \theta))}{1 - x + \theta}$$

We're most interested in when $T > 0$, as this will allow our population to persist. This case will also inform us when $T \leq 0$.

We know in the future that we will be evaluating $x \in (0, 1)$, so then the denominator of T is always positive. So we simply will look at when the numerator is greater than 0, or

$$\beta(1 + \theta)x(1 - x) + \left(\mu_f x - \mu_m(1 - x) \right)(x - (1 + \theta))) > 0$$

This expands to:

$$-\left(\beta - (\mu_f - \mu_m) \right)x^2 + (1 + \theta)\left(\beta - (\mu_f - \mu_m) \right)x + \mu_m x - \mu(1 + \theta) > 0$$

Here, we use a clever 1 that will help us in the future. We know $(\gamma_f + \gamma_m) = 1$, so we rewrite what we have above as:

$$-\left(\beta - (\mu_f - \mu_m) \right)x^2 + (1 + \theta)(\beta(\gamma_f + \gamma_m) - (\mu_f - \mu_m))x + \mu_m x - \mu(1 + \theta) > 0$$
$$\text{or}$$
$$-\left(\beta - (\mu_f - \mu_m) \right)x^2 + (1 + \theta)\left(\beta\gamma_f - (\mu_f - \mu_m) \right)x + \left(\mu_m + \beta\gamma_m(1 + \theta) \right)x - \mu(1 + \theta) > 0$$

Since

$$\lim_{t \to \infty} x = x^*$$

then

$$\lim_{t \to \infty} P = \lim_{x \to x^*} P$$

Here, we evaluate the limit as x goes to x^*, and plug it in. When we do this, and simplify, we arrive at:

$$(\beta\gamma_f - \mu_f)(1 + \theta)\gamma_m > \mu_m \gamma_f \theta$$

.

If the condition is false, then T is negative, and the population goes to zero. $\square$

3 Allee Effect Dependent on Total Male Population

Next we utilize an Allee effect that is dependent on the density of males. We choose the Allee Function:

$$\mathcal{A}(M) = \frac{M}{M + \theta}$$

3.1 Model

$$F' = \beta\gamma_f \frac{FM}{M + \theta} - \bar{\mu}_f F$$

$$M' = \beta\gamma_m \frac{FM}{M + \theta} - \bar{\mu}_m M$$

3.1.1 Jacobian Matrix of Model

Taking the partial derivatives with respect to F and M, we find the Jacobian matrix for this system of differential equations:

$$J(F, M) = \begin{bmatrix} \frac{\beta\gamma_f M}{M+\theta} - \mu_f - 2bF - bM & \beta\gamma_f \frac{F\theta}{(M+\theta)^2} - bF \\ \\ \beta\gamma_m \frac{M}{M+\theta} - bM & \beta\gamma_m F \frac{\theta}{(M+\theta)^2} - \mu_m - bF - 2bM \end{bmatrix}$$

The only feasible equilibrium points for our model are $(0, 0)$, P_1, and P_2.

3.1.2 Reduction of Jacobian

We are interested in the stability of non-zero equilibria, so we assume $M^*, F^* \neq 0$ and can rewrite the Jacobian as:

$$J = \begin{bmatrix} -bF^* & \beta\gamma_f \frac{F^*\theta}{(M^*+\theta)^2} - bF^* \\ \beta\gamma_m \frac{M^*}{M^*+\theta} - bM^* & \frac{\beta\gamma_m F^*}{M^*+\theta}\left(\frac{\theta}{M^*+\theta} - 1\right) - bM^* \end{bmatrix}$$

It is trivial that the trace is always negative.

3.2 Model Analysis

We are able to do a full stability analysis, and have developed conditions for the existence of stable non-trivial equilibrium solutions. We introduce $P^* = F^* + M^*$ for notational purposes.

Lemma 3.1. *The determinant of the Jacobian evaluated at non-zero equilibrium solutions is positive when the following condition holds:*

$$P^* > \frac{\beta\gamma_f\gamma_m - \mu_f\gamma_m - b\theta}{2b\gamma_m}$$

Proof. Begin with the reduced Jacobian. Then the determinant is

$$\det(J) = -bF\left(\beta\gamma_m\theta F\frac{1}{((M+\theta)^2} - \beta\gamma_m F\frac{1}{M+\theta}\right) + b^2FM - FM\left(\beta\gamma_m\frac{1}{M+\theta} - b\right)\left(\beta\gamma_f\theta\frac{1}{(M+\theta)^2} - b\right)$$

Which can be rewritten as:

$$\beta FM\left(b\theta^2 + \left(b(P\gamma_m + M) - \beta * \gamma_m\gamma_f\theta + \gamma_m bM\right)\right)$$

And then using

$$M = \theta\frac{\mu_f + bP}{\beta\gamma_f - \mu_f - bP}$$

$$F = (M + \theta)\frac{\mu_m + bP}{\beta\gamma_m}$$

We have

$$\det(J) = \frac{1}{\beta\gamma_f\gamma_m}(\mu_m + bP)(\mu_f + bP)\left(-\beta\gamma_f\gamma_m + \mu_f\gamma_m + b\theta + 2b\gamma_m P\right)$$

We are interested in when $\det(J) > 0$, or

$$-\beta\gamma_f\gamma_m + \mu_f\gamma_m + b\theta + 2b\gamma_m P > 0$$

$\square$

Theorem 3.2. $(0,0)$ *is always locally asymptotically stable.*

Proof. It is clear that $(0, 0)$ is an equilibrium point. Using $J\big((0,0)\big)$ we have

$$\det\left(J\big((0,0)\big)\right) = \mu_f\mu_m$$

$$\mathrm{tr}\left(J\big((0,0)\big)\right) = -\mu_f - \mu_m$$

We need $\det(J) > 0$ and $\mathrm{tr}(J) < 0$ for the equilibrium solution to be stable. Since μ_f and μ_m are always positive values, their product will be positive and therefore $\det(J) > 0$. Furthermore, subtraction of a positive number from a negative number yields a negative result, and therefore we see $\mathrm{tr}(J) < 0$. Thus E_1 is always stable. $\square$

Theorem 3.3 (Existence and Stability of Non-Trivial Equilibrium). *The population has two non-trivial equilibrium points when the following conditions are met:*

$$P^* < \frac{\beta\gamma_f - \mu_f}{b}$$

$$0 < \theta < \theta_1$$

Where

$$\theta_1 = \frac{\gamma_m}{b}\left[\beta\gamma_f - \mu_f + 2(\mu_m\gamma_f + \mu_f\gamma_m) - 2\sqrt{\gamma_f(\beta - \mu_f + \mu_m)(\mu_f\gamma_m + \mu_m\gamma_f)}\right]$$

Furthermore, when these equilibrium points exist, it implies P_1 unstable, and P_2 stable with:

$$P_1, P_2 = -\frac{1}{2}\frac{-b\theta + \gamma_m(\beta\gamma_f - \mu_f) \pm \sqrt{(b\theta - \beta\gamma_m)^2\gamma_f^2 + 2\gamma_m(b^2\theta^2 - b(\beta\gamma_m - \mu_f + 2\mu_m)\theta - \beta\mu_f\gamma_m)\gamma_f + \gamma_m^2(b\theta - \mu_f}}{b\gamma_m}$$

With $P_1 < P_2$

Proof. In order to obtain our nontrivial equilibrium points for F and M, we first set our differential equations for F and M equal to zero, with $F, M \neq 0$:

$$0 = \beta\gamma_f \frac{FM}{M+\theta} - \bar{\mu}_f F$$

$$0 = \beta\gamma_m \frac{FM}{M+\theta} - \bar{\mu}_m M$$

Solving for F and M in terms of $P = F + M$, we get:

$$F^* = \frac{\theta\gamma_f(P^*b + \mu_m)}{\beta\gamma_f\gamma_m - P^*b\gamma_m - \mu_f\gamma_m}$$

$$M^* = \frac{\theta(P^*b + \mu_f)}{\beta\gamma_f\gamma_m - P^*b\gamma_m - \mu_f\gamma_m}$$

Observe that the numerator of both the equation for F and the equation of M are always positive. Therefore for F and M to be positive values, their denominators must be positive. Thus we establish:

$$0 < \beta\gamma_f\gamma_m - P^*b\gamma_m - \mu_f\gamma_m$$

Which can be simplified to the condition:

$$P^* < \frac{\beta\gamma_f - \mu_f}{b}$$

Returning to the equations of F and M, we then add these values such that:

$$F^* + M^* = P^*$$

and therefore

$$F^* + M^* - P^* = 0$$

Substituting our values for F^* and M^* in terms of P^*, the left-hand side of this equation becomes:

$$\frac{b\gamma_m P^2 + (b\theta - \beta\gamma_f\gamma_m + \gamma_m\mu_f)P - (\gamma_f\mu_m + \gamma_m\mu_f)\theta}{\beta\gamma_f\gamma_m - Pb\gamma_m - \mu_f\gamma_m}$$

We observe that as long as the condition $\mu_f + bP < \beta\gamma_f$ is met, the denominator of this fraction will be positive. Therefore we focus on the numerator as a quadratic $f(P)$:

$$b\gamma_m P^2 + (b\theta - \beta\gamma_f\gamma_m + \gamma_m\mu_f)P + (\gamma_f\mu_m + \gamma_m\mu_f)\theta$$

When $f(P)$ has two real roots, F and M will have two nontrivial equilibrium solutions, one which is stable. If $f(P)$ does not have two real roots, then we have at most one nontrivial equilibrium solution. However, because the trivial solution $F = M = 0$ is a stable equilibrium point, if there only exists one nontrivial equilibrium point, then this solution will be unstable. For this reason, we analyze the discriminant of $f(P)$ to determine the threshold for when P has two real roots.

We investigate the discriminant of $f(P)$ to assess what root behavior it has. We want $f(P)$ to have real roots so we solve for the conditions under which the discriminant of $f(P)$ is positive. Taking the discriminant we find:

$$0 < (b\theta - \beta\gamma_f\gamma_m + \gamma_m\mu_f)^2 - 4(b\gamma_m)(\gamma_f\mu_m + \gamma_m\mu_f)$$

It is not clear when this quantity is greater than 0 strictly through computation. Therefore we continue the analysis of the discriminant in another way. Note that the discriminant of $f(P)$ can be written as a quadratic $g(\theta)$:

$$g(\theta) = b^2\theta^2 + (2b\gamma_m((-\beta\gamma_f + \mu_f) - 2(\mu_f\gamma_m + \mu_m\gamma_f))\theta - \gamma_m^2(\beta\gamma_f - \mu_f)^2$$

Furthermore, we find the discriminant of $g(\theta)$:

$$16b^2\gamma_f\gamma_m^2(\mu_f\gamma_m + \mu_m\gamma_f)(\beta - \mu_f + \mu_m))$$

Since $\beta > \mu_f$ by previous assumption, we see the discriminant of $g(\theta)$ is always positive. Consequently, the quadratic $g(\theta)$ has two distinct real-valued solutions and so we determine the sign of these roots.

Vieta's formula states that for a quadratic in the form $ax^2 + bx + c$, $x_1 x_2 = \frac{c}{a}$ and the sum of the roots $x_1 + x_2 = -\frac{b}{a}$. It is clear that both a and c are positive, so both roots are of the same parity. Since we know the sign of a is always positive, the sign of the b term in the $g(\theta)$ equation will determine whether both real roots are to the left or right of the origin.

In the equation $g(\theta)$, the b term is:

$$(2b\gamma_m((-\beta\gamma_f + \mu_f) - 2(\mu_f\gamma_m + \mu_m\gamma_f))$$

Using the assumption $\mu_f + bP < \beta\gamma_f$ we know $\mu_f < \beta\gamma_f$ and therefore that the above expression of the b term is negative. So both zeros are to the right of the origin.

We now know the discriminant of $f(P)$ is positive to the left of the first root ($\theta < \theta_1$) and to the right if the second root ($\theta_2 < \theta$), thus for θ values in those ranges, we see $f(P)$ has real roots. However, we will show that $\theta < \theta_1$ is the only possible case.

Considering the case where the assumptions needed for $f(P)$ to have real roots are satisfied, we then determine the conditions for these roots to be positive. Since $b\gamma_m$ and $(\gamma_f\mu_m + \gamma_m\mu_f)\theta$ are both positive quantities, by Vieta's formula we then have the condition

$$(b\theta - \beta\gamma_f\gamma_m + \gamma_m\mu_f) < 0$$

for $f(P)$ to have positive roots. Isolating θ, we then have the inequality:

$$\theta < \frac{\gamma_m(\beta\gamma_f - \mu_f)}{b}$$

Next, we evaluate:

$$g(\theta) = b^2\theta^2 + (2b\gamma_m((-\beta\gamma_f + \mu_f) - 2(\mu_f\gamma_m + \mu_m\gamma_f))\theta - \gamma_m^2(\beta\gamma_f - \mu_f)^2$$

when

$$\theta = \frac{\gamma_m(\beta\gamma_f - \mu_f)}{b}$$

We see that the first and last terms of the quadratic cancel, and it only remains to assess the value of the middle term:

$$(2b\gamma_m((-\beta\gamma_f + \mu_f) - 2(\mu_f\gamma_m + \mu_m\gamma_f))\theta$$

This evaluates to:

$$(-2\beta^2\gamma_f^2 + 2\mu_f^2)\gamma_m^3 + (-2\gamma_f(\beta\gamma_f - \mu_f)(\beta\gamma_f - \mu_f + 2\mu_m))\gamma_m^2$$

Where given our previous condition that $\mu_f < \beta\gamma_f$, this is value is always negative. Therefore, we see

$$g\left(\frac{\gamma_m(\beta\gamma_f - \mu_f)}{b}\right)$$

is a negative value.

Thus, this indicates that this point lies between the two positive roots of $g(\theta)$, and the right root is not feasible. So, we have existence of non-trivial equilibria when:

$$0 < \theta < \theta_1$$

where

$$\theta_1 = \frac{\gamma_m}{b}\left[\beta\gamma_f - \mu_f + 2(\mu_m\gamma_f + \mu_f\gamma_m) - 2\sqrt{\gamma_f(\beta - \mu_f + \mu_m)(\mu_f\gamma_m + \mu_m\gamma_f)}\right]$$

Lastly, to check that any real positive roots determined for P satisfy our conditions for P^*. We evaluate $f(P)$ and $f'(P)$ at:

$$P^* = \frac{\beta\gamma_f - \mu_f}{b}$$

in order to see where the constraint lies with respect to the roots of $f(P)$, the equilibria.

$$f(\frac{\beta\gamma_f - \mu_f}{b}) = \theta\gamma_f(\beta - \mu_f + \mu_m)$$

$$f'(\frac{\beta\gamma_f - \mu_f}{b}) = (\beta\gamma_f - \mu_f)\gamma_m + b\theta$$

Using the condition $\mu_f + bP < \beta\gamma_f$, we see that both of these values are positive. Thus, this constraint is to the right of both roots, and P_1 and P_2 are both feasible.

Now we will show the stability of P_1 and P_2.

Recall from earlier that

$$f(P) = b\gamma_m P^2 + (b\theta - \beta\gamma_f\gamma_m + \gamma_m\mu_f)P - (\gamma_f\mu_m + \gamma_m\mu_f)\theta$$

Is the function that determines the location of the non-trivial equilibria. Recall the condition on the determinant be denoted

$$P^* > C$$

where

$$C = \frac{\beta\gamma_f\gamma_m - \mu_f\gamma_m - b\theta}{2b\gamma_m}$$

The two equilibrium solutions are the roots of $f(P)$. We want to show that the threshold of stability lies between these roots, making one stable and the other unstable. Note $f(P)$ is an upward facing parabola, so we need that $f(C) < 0$. We will show that this is true.

Recall from earlier the discriminant of $f(P)$, written as:

$$g(\theta) = b^2\theta^2 + (2b\gamma_m((-\beta\gamma_f + \mu_f) - 2(\mu_f\gamma_m + \mu_m\gamma_f))\theta - \gamma_m^2(\beta\gamma_f - \mu_f)^2$$

Well, when evaluate f at our condition, we have.

$$f(C) = -\frac{1}{\beta\gamma_m\left((\beta\gamma_f - \mu_f) + b\theta\right)}g(\theta)$$

Meaning $f(C) < 0 \iff g(\theta) > 0$. We know $g(\theta) > 0$ is a condition for the existence of non-negative equilibria, therefore P_1 is unstable and P_2 is stable. $\qquad\square$

Corollary 3.3.1. (F_1, M_1) *is an unstable equilibrium point, and* (F_2, M_2) *is a stable equilibrium point with:*

$$F_1 = \frac{\theta\gamma_f(P_1 b + \mu_m)}{\beta\gamma_f\gamma_m - P_1 b\gamma_m - \mu_f\gamma_m}$$

$$M_1 = \frac{\theta(P_1 b + \mu_f)}{\beta\gamma_f\gamma_m - P_1 b\gamma_m - \mu_f\gamma_m}$$

$$F_2 = \frac{\theta\gamma_f(P_2 b + \mu_m)}{\beta\gamma_f\gamma_m - P_2 b\gamma_m - \mu_f\gamma_m}$$

$$M_2 = \frac{\theta(P_2 b + \mu_f)}{\beta\gamma_f\gamma_m - P_2 b\gamma_m - \mu_f\gamma_m}$$

Proof. We know that

$$F^* = \frac{\theta\gamma_f(P^* b + \mu_m)}{\beta\gamma_f\gamma_m - P^* b\gamma_m - \mu_f\gamma_m}$$

$$M^* = \frac{\theta(P^* b + \mu_f)}{\beta\gamma_f\gamma_m - P^* b\gamma_m - \mu_f\gamma_m}$$

Therefore equilibrium values are dependent on the values of P^* they contain. As P_1 is proven unstable and P_2 is proven stable, likewise (F_1, M_1) is an unstable equilibrium point, and (F_2, M_2) is a stable equilibrium point. $\qquad\square$

3.2.1 Values for P^*, F^* and M^*

Assuming the existence and stability conditions are satisfied for P, we have these final expressions for P, F and M:

As the roots of our function $f(P)$ we have

$$P_1 = -\frac{1}{2}\frac{-b\theta + \gamma_m(\beta\gamma_f - \mu_f) - \sqrt{(b\theta - \beta\gamma_m)^2\gamma_f^2 + 2\gamma_m(b^2\theta^2 - b(\beta\gamma_m - \mu_f + 2\mu_m)\theta - \beta\mu_f\gamma_m)\gamma_f + \gamma_m^2(b\theta - \mu_f)^2}}{b\gamma_m}$$

$$P_2 = -\frac{1}{2}\frac{-b\theta + \gamma_m(\beta\gamma_f - \mu_f) + \sqrt{(b\theta - \beta\gamma_m)^2\gamma_f^2 + 2\gamma_m(b^2\theta^2 - b(\beta\gamma_m - \mu_f + 2\mu_m)\theta - \beta\mu_f\gamma_m)\gamma_f + \gamma_m^2(b\theta - \mu_f)^2}}{b\gamma_m}$$

Where $P_1 < P_2$, P_1 is unstable and P_2 is stable.

The corresponding equilibrium values for F and M are

$$F_1 = \frac{\theta\gamma_f(P_1 b + \mu_m)}{\beta\gamma_f\gamma_m - P_1 b\gamma_m - \mu_f\gamma_m}$$

$$M_1 = \frac{\theta(P_1 b + \mu_f)}{\beta\gamma_f\gamma_m - P_1 b\gamma_m - \mu_f\gamma_m}$$

$$F_2 = \frac{\theta\gamma_f(P_2 b + \mu_m)}{\beta\gamma_f\gamma_m - P_2 b\gamma_m - \mu_f\gamma_m}$$

$$M_2 = \frac{\theta(P_2 b + \mu_f)}{\beta\gamma_f\gamma_m - P_2 b\gamma_m - \mu_f\gamma_m}$$

3.3 Final Result

When the female and male populations surpass the sizes of F_1 and M_1, we have a system where the populations will stabilize at sizes F_2 and M_2. If the populations are below F_1 and M_1, then both populations will go extinct.

3.4 Data Analysis

Considering the population of Japan in the census years 1995, 2000, 2005, 2010, and 2015 we fit our model to the data to assess its application. For our analysis we consider the total population, number of males, females and total births in these years.

For a given β we determined what value of θ corresponds. From this we determined an approximate threshold for when an Allee effect would appear in this population. The birth rates that gave us theta values closest to zero were:

$$\beta = 0.017, \ \theta = 0$$

$$\beta = 0.017246, \ \theta = 0$$

$$\beta = 0.0172461, \ \theta = 0.1177$$

$$\beta = 0.01726, \ \theta = 50.139$$

We note that when the birth rate increases just slightly, an Allee effect would be present in the population. Further, when the birth rate increases to just $\beta = 0.01726$ a significant Allee effect is already present.

A greater interest/trend in mating therefore corresponds to a higher Allee effect. As the population increases its mating, it is necessary for mating pairs to have already formed to produce those offspring. Thus, it is expected it would be more challenging for singles to find a mate among that population.

4 Allee Effect with Coupling

We acknowledge that a two-equation system may not be the best environment to model all populations. Indeed, there are populations, human and ecological, where there exist stable couples. These couples will remain after a mating act has taken place.

4.1 The Model

$$\begin{cases} F' = -\rho\frac{FM}{M+\theta} + (\beta\gamma_f + \delta + \bar{\mu}_m)C - \bar{\mu}_f F \\ M' = -\rho\frac{FM}{M+\theta} + (\beta\gamma_m + \delta + \bar{\mu}_f)C - \bar{\mu}_m M \\ C' = \rho\frac{FM}{M+\theta} - (\delta + \bar{\mu}_f + \bar{\mu}_m)C \end{cases}$$

With C being the number of couples, ρ being the willingness to marry, and δ being the divorce rate. It is important to notice that the total population, P, is now $(F + M + 2C)$.

4.1.1 Assumptions

There are few additional assumptions we encounter when modeling the system with stable couples.

- Couples are monogamous, and consist of one male, and one female.
- Only couples can create new individuals.
- An individuals preference to find a partner is independent of that individual's history of partners

4.2 System when $b = 0$

As we increase the number of variables, the amount of computation it takes to analyze the system analytically increases, and we begin to contract less and less meaningful results. As a consequence, we simplify the system and look at the case where $b = 0$ in a attempt to get insight into our expected behavior for this system.

4.2.1 Jacobian

We will use the Jacobian matrix to analytically analyze our system. Taking the partial derivatives with respect to F, M, and C, we find the Jacobian matrix for this system of differential equations:

$$J = \begin{bmatrix} -\rho\frac{M}{M+\theta} - \mu_f & -\frac{\theta}{(M+\theta)^2} & \beta\gamma_f + \delta + \mu_m \\ -\rho\frac{M}{M+\theta} & -\rho F\frac{\theta}{(M+\theta)^2} - \mu_m & \beta\gamma_m + \delta + \mu_f \\ \rho\frac{M}{M+\theta} & \rho F\frac{\theta}{(M+\theta)^2} & -(\delta + \mu_f + \mu_m) \end{bmatrix}$$

Where the trace is:

$$\frac{(-\delta - 2\mu_f - 2\mu_m)\theta^2 + ((-\rho - 2\delta - 4\mu_f - 4\mu_m)M - \rho F)\theta - M^2(\rho + \delta + 2\mu_f + 2\mu_m)}{(M+\theta)^2}$$

And the determinant is:

$$\frac{\mu_f(M+\theta)^2\mu_m^2 + (-(M+\theta)^2\mu_f^2 + (-\delta\theta^2 + ((-\rho - 2\delta)M - \rho F)\theta - M^2(\rho + \delta))\mu_f + M\rho\beta\gamma_f(M+\theta))\mu_m + F\beta\mu_f\rho\theta\gamma_m}{(M+\theta)^2}$$

It can be observed that the trace of our Jacobian is negative for any $F \geq 0$, $M \geq 0$, and $C \geq 0$. Therefore, we focus on the determinant when analyzing our equilibrium points for this system.

4.2.2   Routh-Hurwitz Stability Criterion

Let $\lambda^3 + p_1\lambda^2 + p_2\lambda + p_3 = 0$ be the characteristic polynomial equation for a 3 x 3 matrix. In order to have stable equilibria, the following conditions must be met:

$$p_1 > 0, p_2 > 0, p_3 > 0$$

$$p_1 p_2 > p_3$$

Where

$$p_1 = -Tr(J)$$

$$p_2 = a_{11}a_{22} - a_{21}a_{12} + a_{11}a_{33} - a_{31}a_{33} - a_{31}a_{13} + a_{22}a_{33} - a_{32}a_{23}$$

$$p_3 = -Det(J)$$

And a_{ij} is the term in the ith row and jth column of our Jacobian matrix.

4.3   Theorems

Theorem 4.1 $(b = 0)$. *Under the simplifying assumption $b = 0$, if the following conditions are met:*

$$\beta\gamma_f > \mu_f$$
$$\beta\rho\gamma_f - \delta\mu_f - \mu_f^2 - \mu_f\mu_m - \mu_f\rho > 0$$

Then there exists a positive equilibrium which is unstable. Depending on the initial conditions, the population either goes extinct or grows exponentially. If the above conditions are not met the extinction equilibrium is globally stable.

Proof. We will first show the conditions of existence for equilibria.

Solving the system for its equilibria values, we find two solutions, the trivial solution, $(0, 0, 0)$, and (F_2, M_2, C_2) where:

$$F_2 = \frac{(\beta\delta\gamma_f + \beta\mu_f\gamma_f + \beta\mu_m\gamma_f - \delta\mu_f - \mu_f^2 - \mu_f\mu_m)\theta\mu_m}{(-\mu_f^2 - (\rho + \delta + \mu_m)\mu_f + \beta\rho\gamma_f)(\beta\gamma_m - \mu_m)}$$

$$M_2 = \frac{(\delta + \mu_f + \mu_m)\mu_f\theta}{\beta\rho\gamma_f - \delta\mu_f - \mu_f^2 - \mu_f\mu_m - \mu_f\rho},$$

$$C_2 = \frac{\mu_f\mu_m\theta(\delta + \mu_f + \mu_m)}{(-\mu_f^2 - (\rho + \delta + \mu_m)\mu_f + \beta\rho\gamma_f)(\beta\gamma_m - \mu_m)}$$

In order for these values to be positive, we look at the numerator and denominator of each value. In the case of M_2 and C_2 it is clear that the numerators are always positive. Thus we look at the constraints necessary such that the denominators of each M_2 and C_2 would also always be positive. Further, the conditions of positivity for the denominator of C_2 will help determine the positivity of F_2. For the denominator of M_2 to be positive we obtain the inequality:

$$\rho(\beta\gamma_f - \mu_f) - \mu_f(\delta + \mu_f + \mu_m) > 0$$

Where we see it must be true that $\rho(\beta\gamma_f - \mu_f)$ is a positive value, otherwise the expression would be negative. Therefore we conclude:

$$\beta\gamma_f > \mu_f$$

Further, it must be true that:

$$\rho > \frac{\mu_f(\delta + \mu_f + \mu_m)}{(\beta\gamma_f - \mu_f)}$$

Similarly, for the denominator of C_2 to be positive both the above inequality must hold as well as:

$$\beta\gamma_m > \mu_m$$

Finally, rewriting to F_2 as:

$$F_2 = \frac{(\delta(\beta\gamma_f - \mu_f) + (\mu_f + \mu_m)(\beta\gamma - \mu_f))\theta\mu_m}{(-\mu_f^2 - (\rho + \delta + \mu_m)\mu_f + \beta\rho\gamma_f)(\beta\gamma_m - \mu_m)}$$

We see that the denominator and numerator are proven to be positive by the above constraints.

We have now shown the condition for existence of the equilibria. We will now show that $(0, 0, 0)$ is always stable, and then that (F_2, M_2, C_2), when it is an equilibrium solution, is always unstable.

Evaluating at the equilibrium point $(0, 0, 0)$, our Jacobian matrix simplifies to:

$$J(0, 0, 0) = \begin{bmatrix} -\mu_f & 0 & \beta\gamma_f + \delta + \mu_m \\ 0 & -\mu_m & \beta\gamma_m + \delta + \mu_f \\ 0 & 0 & -(\delta + \mu_f + \mu_m) \end{bmatrix}$$

Which then gives us:

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$$Det(J(0,0,0)) = -\mu_f \mu_m (\delta + \mu_f + \mu_m)$$

$$Tr(J(0,0,0)) = -2\mu_f - 2\mu_m - \delta$$

Here we see the determinant is negative, the trace is negative and further that $p_1 p_2 > p_3$. Consequently, we conclude that this is a stable equilibrium point always.

Next, we will show the non-trivial equilibrium solution is unstable.

Evaluating at the (F_2, M_2, C_2), our Jacobian matrix simplifies to:

$$J(F_2, M_2, C_2) = \begin{bmatrix} \frac{-\mu_f(\beta\gamma_f + \delta + \mu_m)}{\beta\gamma_f - \mu_f} & \frac{\mu_m(\mu_f^2 + (\rho + \delta + \mu_m)\mu_f - \beta\rho\gamma_f)(\delta + \mu_f\mu_m)}{(\beta\gamma_f - \mu_f)\rho(\beta\gamma_m - \mu_m)} & \beta\gamma_f + \delta + \mu_m \\ \frac{-(\delta + \mu_f + \mu_m)\mu_f}{\beta\gamma_f - \mu_f} & \frac{\mu_f^3 + (\rho + 2\delta + 2\mu_m)\mu_f^2 - (((\gamma_f - \gamma_m)\beta - \delta)\rho - (\delta + \mu_m)^2)\mu_f + \rho\beta\gamma_f(\beta\gamma_m + \delta))\mu_m}{(\beta\gamma_f - \mu_f)\rho(\beta\gamma_m - \mu_m)} & \beta\gamma_m + \delta + \mu_f \\ \frac{(\delta + \mu_f + \mu_m)\mu_f}{\beta\gamma_f - \mu_f} & \frac{\mu_m(-\mu_f^2 - (\rho + \delta + \mu_m)\mu_f + \beta\rho\gamma_f)(\delta + \mu_f\mu_m)}{(\beta\gamma_f - \mu_f)\rho(\beta\gamma_m - \mu_m)} & -\delta - \mu_f\mu_m \end{bmatrix}$$

And its corresponding determinant is:

$$Det(J(F_2, M_2, C_2)) = \frac{(\delta + \mu_f + \mu_m)\mu_m\mu_f(\beta\rho\gamma_f - \delta\mu_f - \mu_f^2 - \mu_f\mu_m - \mu_f\rho)}{\rho(\beta\gamma_f - \mu_f)}$$

Given our assumptions $\beta\gamma_f > \mu_f$ and $(\beta\rho\gamma_f - \delta\mu_f - \mu_f^2 - \mu_f\mu_m - \mu_f\rho) > 0$, we see that this nontrivial solution always has a positive determinant. Consequently, we conclude that this is an unstable equilibrium point. $\qquad\square$

4.4   Data Analysis

Considering the population of Japan in the census years 1995, 2000, 2005, 2010, and 2015 we were able to try and estimate appropriate parameter values using the data, and some data fitting software. For our analysis we consider the total population, number of males, females and total marriages in these years. For a given ρ we determined what value of θ corresponds. From this we determined an approximate threshold for when an Allee effect would appear in this population. The marriage rates that gave us theta values closest to zero were:

$$\rho = 0.0301, \ \theta = 0$$

$$\rho = 0.030171, \ \theta = 0$$

$$\rho = 0.030172, \ \theta = 0.015229$$

$$\rho = 0.0302, \ \theta = 17.8425$$

We see here that when the marriage rate increases just slightly, an Allee effect can be noted in the population and when the marriage rate increases to just $\rho = 0.030172$ an Allee effect is already present.

A greater willingness to marry therefore corresponds to a higher Allee effect. This conclusion is plausible as it suggests when the willingness to marry is lower there is a greater population of singles to choose from. However, when the desire to form couples increases, there would be greater challenge in finding remaining singles to pair with.

4.5 Numerical Results

We ran test simulations on parameter values and initial conditions appropriate for biological meaning. Our goal was to gather additional insight into the behavior of the three equation model, trying to gather evidence that when $b \neq 0$, there are conditions for persistence. Furthermore, we wanted to show that these conditions are sensitive, not only to the parameter values, but also the initial values.

4.5.1 Separated Populations

We first seperated the populations along the line of their variables, so we could analyze how *each* population behaved. We ran three tests, Tests A, B and C, with a blue text means there was a change in value from Run A. We first showed that the persistence of the system not only depends on the parameter values, but also the initial condition. Figure 1 shows that in our base case (Run A), the population persists. Figure 2 (Run B) shows that when we adjust our initial condition, the population now becomes extinct. Lastly, Figure 3 (Run C) shows that when we maintain the same parameter values of Run A, and slightly change our death rate of males, our population also goes extinct, confirming our suspicions.

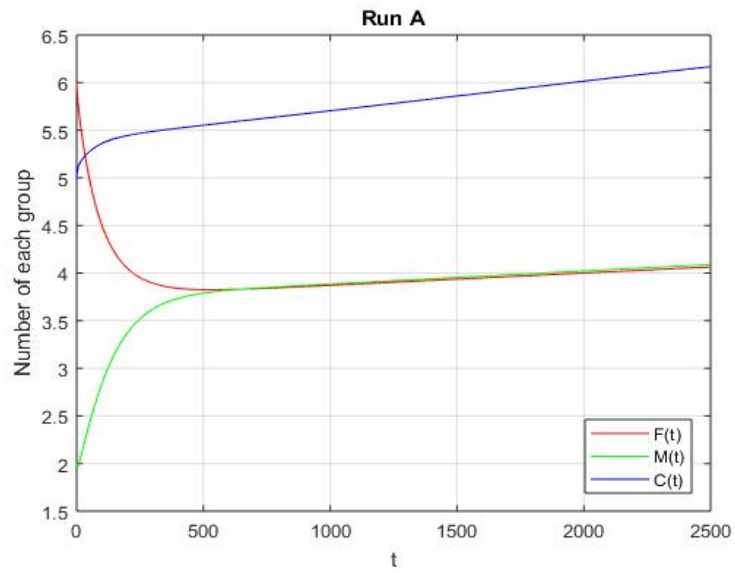| Parameter	Run A	Run B	Run C
ρ	.28	.28	.28
θ	7	7	7
β	.03	.03	.03
γ_f	.48	.48	.48
γ_m	.52	.52	.52
μ_f	.007	.007	.007
μ_m	.0077	.0077	.0092
δ	.05	.05	.05
b	.00008	.00008	.00008
F_0	6	6	6
M_0	2	1	2
C_0	5	2	5

Below are the results.

Figure 1: Simulation with standard parameters, showing the solution curves of each population.
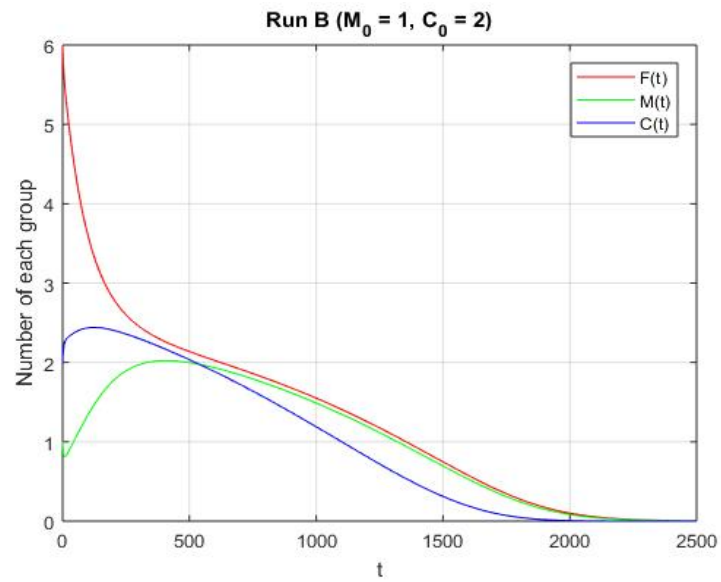

Figure 2: Simulation with a change in initial condition, showing the solution curves of each population.
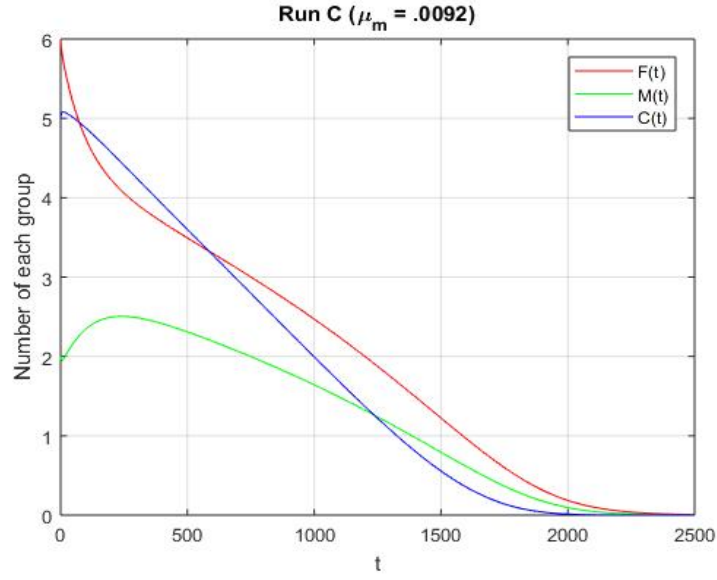
Figure 3: Simulation with 0.15% increase in male death rate, showing the solution curves of each population.

4.5.2   Total Population

We ran simulations with the parameter values from Run A, and varied the initial condition of one of the groups to see if the system persisted or not. We varied M_0, as well as C_0 to see how our solution curve behaved. The purpose of these simulations (Figure 4 and Figure 5) was to verify the location of an unstable equilibrium point.
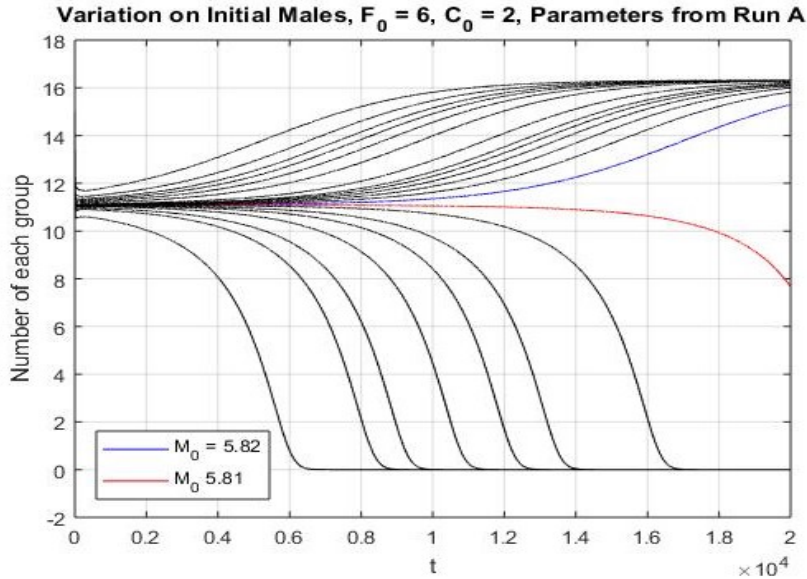

Figure 4: Simulation varying the initial single males population, showing the solution curve of the total population.
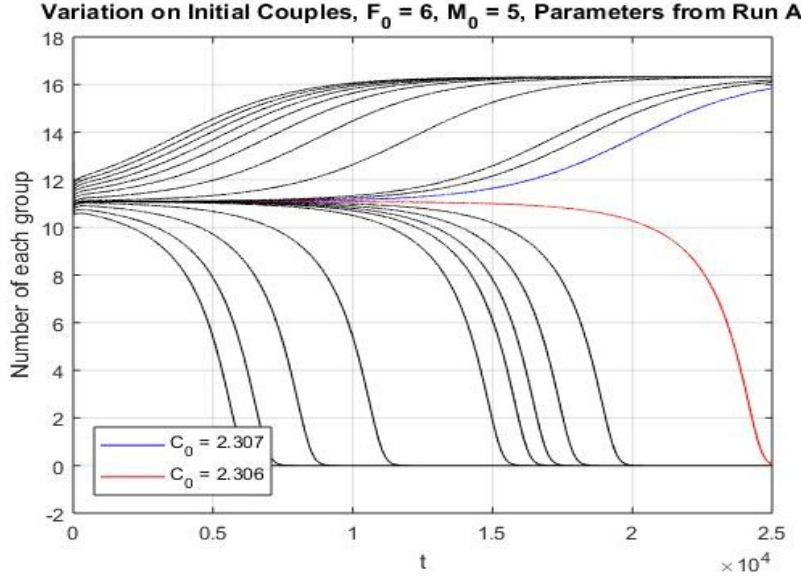
Figure 5: Simulation varying the initial amount of couples, showing the solution curve of the total population.

We saw that in the variation on M_0, the switch between population persistence and extinction occurs somewhere between 5.81 and 5.82. Likewise, the switch for initial couples varied between 2.306 and 2.307, which implies in both cases that our initial condition was around some unstable equilibrium point, confirming our suspicions.

5   Conclusion

In demographic studies the desired state is that of population persistence. In the models considered, a mate-finding Allee effect can be a determining factor in whether a population persists or goes extinct. In such cases where an Allee effect is present, a population may go extinct either because the searching gender has a low reproductive number or because the mate-finding Allee effect is too high.

In the model considering the ratio of males to the total population, our results express that population persistence is reliant on the satisfaction of a biological threshold dependent on birth of females, the mortality of males and the strength of the Allee effect. In the two-equation model considering male density, our main result quantifies precisely the Allee threshold which separates persistence from extinction. Therefore in addition to a birth rate exceeding the rate of mortality among the seeking, female, population, the strength of the Allee effect determines population persistence.

Furthermore, our analysis in a simplified, exponential model with couples suggests a similar result as the previous - there exists an Allee threshold on which population persistence is dependent. This is supported by several simulated examples in the logistic case.

Considering analytic results in application to world populations, census data from Japan shows that there can be a significant change in mate finding Allee effect for relatively small variations

of birth rate and willingness to marry. This data suggests that the models studied may prove useful in understanding trends in real-world populations.

This research can be extended in several ways. There are various forms of Mate-Finding Allee effect functions proposed in the literature and it would be useful to either provide a generalization of our result or to independently perform the analysis in this paper separately for each type of Allee effect function. Secondly, in order to to truly measure whether an Allee effect is present in human populations, one needs to perform a sociological investigation in order to estimate the true marriage willingness of the searching gender. We plan to explore these avenues in the near future.

Acknowledgments

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