

THE IMPACT OF NON-REPRODUCTIVE GROUPS IN TWO-SEX DEMOGRAPHIC AND EPIDEMIC LOGISTIC MODELS WITHOUT PAIR-FORMATION

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ABSTRACT. Mathematical models in demography need to incorporate population effects in the mortality rates whenever they are used for long term predictions. Logistic two-sex models that include single females, single males and couples have been already analyzed in several recent papers. Those models were extended to an STD epidemic model that included non-reproductive groups. The couple formation/dissolution mechanism together with the influence of non-reproductive groups was proved to be essential in the spread and/or containment of the disease. In this paper we establish a logistic two-sex model without pairs and investigate whether similar or different results hold true in the new framework compared to those obtained in populations with stable couples. This approach is particularly relevant in the context of gender structured animal populations that do not form stable pairs except for reproduction.

1. INTRODUCTION

The vast majority of mathematical models used to predict the long-term evolution of a population must include some form of population effect in the vital parameters. Whenever constant rates are used to denote fertility or mortality terms, the solutions of the models tend to either increase or decay exponentially neither of which represents a realistic prediction. Since almost all resources needed for survival are finite, in the long run, logistic effects should be present that will limit the growth if the total population size goes beyond a certain threshold.

The first logistic equation proposed by Verhulst is still used today:

$$\frac{dP}{dt} = r \left(1 - \frac{P}{K} \right) P.$$

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Assuming a positive net growth rate $r > 0$, the total population $P(t)$ always approaches the carrying capacity K . It is, therefore, of great interest to demography to build logistic models that are more suitable to the biological problems they study. One such area that has been the subject of intensive research concerns two-sex models.

The importance of separating the individuals by gender cannot be underestimated, in particular, in the context of Sexually Transmitted Diseases (STD). One-sex epidemiological models for STD's do not take into account important aspects such as various degrees of immunity or recovery rates for females and males or the fact that, for some diseases such as HPV, only the female will suffer disease induced mortality.

The gender structured models proposed in the beginning used constant rates for the vital parameters (birth, death, pair-formation, pair-dissolution, etc...) and, invariably, the overall dynamics was proved to be essentially exponential. The first logistic two-sex model was introduced by Chavez and Huang [3] using population effects for the birth and the divorce rate. However, in reality, the population effects are more prevalent in the mortality rates. For example, if an animal population increases too much, the lack of adequate food resources should increase the death rate.

Maxin and Milner [7] introduced a logistic two-sex model with logistic death rates. That model was extended to study the influence of sexually abstained groups on the evolution of a mild sexually transmitted disease. The STD was assumed to be transmitted only through heterosexual stable couples. In other words, they excluded the *unfaithful* sexual contacts outside established couples and also possible births from single mothers. Their model is an approximation of a conservative community. From an epidemiological perspective this environment benefits from *de-facto* quarantine since as long as two people stay in a relationship they do not acquire the disease if they are healthy nor do they transmit it if they are sick. So the most important parameter in the disease transmission is, in fact, the couple dissolution rate. They proved that, under some conditions, the abstained groups can eliminate the disease from the population.

In the present work, we propose a model that is suitable for a promiscuous population that does not form stable couples at all. This approach is evidently more suitable for animal populations that do not form stable pairs. The same questions will be addressed regarding the evolution of an STD in the presence/absence of non-reproductive groups. The presence of STD's in the animal population is of great interest for theoretical ecologists. Important questions are still open concerning the evolutionary traits such as: what is the optimal strategy for an individual facing an STD? A promiscuous individual that mates freely is more exposed to the disease but this can be compensated by a greater reproductive fitness.

In the case of humans, non-reproductive groups are represented by those who due to social/medical reasons or by choice remain childless for life after a certain moment in their lives. In the animal populations we cannot speak so much about *individual choice* regarding being non-reproductive. However, in the mating competition it is clear, in many cases, that some will benefit at the expense of others, and, presumably, some individuals will not

be able to mate after a certain time. In the presence of STD's there could be instinctual behavior patterns designed to avoid contact with an infected individual which may render such individual to be non-reproductive. The fact that non-reproduction can eliminate the disease could give additional insights when evaluating the optimal evolutionary strategy.

The paper is structured as follows: in the next section we introduce the two-sex model without pairs and in section 3 we extend this model by including the non-reproductive groups. We establish the logistic behavior of these models and compute the thresholds that separate population extinction from a globally stable positive equilibrium. Section 4 is devoted to the epidemic model with abstained groups where we establish the epidemic reproductive number. In section 5 we give the affirmative answer to the question of whether the abstained groups can eliminate an established disease from the population and compare our result to the similar one found in the case of two-sex models with pair-formation and point out some important differences between the two. We conclude with a summary of our results and some thoughts on possible avenues of further research.

2. THE LOGISTIC TWO-SEX MODEL WITHOUT PAIRS

The basic two-sex model without pair formation includes two classes of individuals: females and males. The total birth is taken to be the harmonic mean although there are other various choices in the literature such as the geometric mean or the maximum between F and M . The harmonic mean tends to be the most accepted form for the birth function in the two-sex models. It is the same function that models the pair-formation in the two-sex models with couples.

$$(1) \quad \begin{cases} F' &= \beta\gamma_f \frac{FM}{F+M} - \bar{\mu}_f F, \\ M' &= \beta\gamma_m \frac{FM}{F+M} - \bar{\mu}_m M. \end{cases}$$

Where

$$P = F + M, \quad \bar{\mu}_f = \mu_f + bP \quad \text{and} \quad \bar{\mu}_m = \mu_m + bP.$$

The model (1) has two steady states:

$$(\bar{F}, \bar{M}) = (0, 0), \quad \text{and}$$

$$(F^*, M^*) = \left(\frac{\mu_f \mu_m [\mu_f (\mathcal{R}_f - 1) + \mu_m]}{b\beta^2} (\mathcal{R} - 1), \frac{\mu_f \mu_m [\mu_m (\mathcal{R}_m - 1) + \mu_f]}{b\beta^2} (\mathcal{R} - 1) \right)$$

The following theorem describing the long term dynamics of (1) depends on the net reproductive numbers

$$\mathcal{R}_f = \frac{\beta\gamma_f}{\mu_f}, \quad \mathcal{R}_m = \frac{\beta\gamma_m}{\mu_m} \quad \text{and} \quad \mathcal{R} = (\mathcal{R}_f - 1)(\mathcal{R}_m - 1).$$

\mathcal{R}_f and \mathcal{R}_m represent the expected female/male offspring from a female/male during her/his life-time.

\mathcal{R} represents the maximum *possible* net-growth of heterosexual pairs produced by a single pair as follows: a typical female and male are expected to

give birth to \mathcal{R}_f females and \mathcal{R}_m males during their life-time. The resulting offspring is then able to form a maximum of \mathcal{R} pairs *excluding* one pair that accounts for the original couple.

Notice also that $\mathcal{R} > 1$ implies the necessary conditions for a positive steady state, i.e. $\mathcal{R}_f > 1$ and $\mathcal{R}_m > 1$.

THEOREM 2.1. *If $\mathcal{R} > 1$ then (F^*, M^*) is globally stable. Otherwise, the extinction equilibrium (\bar{F}, \bar{M}) is globally stable.*

Proof. First notice that each of the first two conditions are sufficient to cause population extinction: If $\mathcal{R}_f < 1$ and taking into account that $\frac{M}{F+M} < 1$ then we can use the following differential inequality

$$F' < (\beta\gamma_f - \mu_f)F$$

Integrating both sides we obtain

$$F(t) < F_0 e^{(\beta\gamma_f - \mu_f)t}, \quad \text{which means } F(t) \rightarrow 0.$$

Since $F(t) \rightarrow 0$ it follows immediately that $M(t) \rightarrow 0$ from the second equation of (1). A similar argument can be used if $\mathcal{R}_m < 1$.

Suppose now that $\mathcal{R}_f > 1$ and $\mathcal{R}_m > 1$.

We follow first the dynamics of the proportion of females in the total population since this leads to a single ODE that can be integrated. Denoting $x = \frac{F}{F+M}$ we obtain the following ODE in x :

$$(2) \quad x' = \beta x(1-x)(\mathcal{K}_f - x),$$

where

$$\mathcal{K}_f = \frac{\mu_f(\mathcal{R}_f - 1) + \mu_m}{\beta}.$$

Notice also that

$$\mathcal{R}_f > 1 \quad \text{and} \quad \mathcal{R}_m > 1, \quad \text{imply} \quad 0 < \mathcal{K}_f < 1.$$

Due to symmetry and, to make our notations more consistent, we also denote

$$\mathcal{K}_m = 1 - \mathcal{K}_f = \frac{\beta\gamma_m - \mu_m + \mu_f}{\beta}.$$

(2) is a separable ODE whose implicit solution is

$$\frac{x^{\frac{1}{\mathcal{K}_f}} (1-x)^{\frac{1}{\mathcal{K}_m}}}{|\mathcal{K}_f - x|^{\frac{1}{\mathcal{K}_f \mathcal{K}_m}}} = C e^{\beta t}$$

Notice first that $0 < x < 1$ since x represents a fraction of the total population. From the sign of the derivative x' we see that, if $x_0 > \mathcal{K}_f$ then $x(t)$ is decreasing in forward time and, if $x_0 < \mathcal{K}_m$ then $x(t)$ is increasing in forward time. Both cases lead to the conclusion that $x(t)$ converges to a finite limit as $t \rightarrow \infty$. From the implicit solution above we see that the right hand side tends to infinity. The only limit of $x(t)$ that satisfies this is \mathcal{K}_f . Hence

$$\lim_{t \rightarrow \infty} x(t) = \mathcal{K}_f.$$

Therefore

$$\frac{F}{P} \rightarrow \mathcal{K}_f \quad \text{and} \quad \frac{M}{P} \rightarrow \mathcal{K}_m$$

Using these limits we obtain a double differential inequality for P' as follows:

For every $\epsilon > 0$ there exist a time t_0 such that

$$(\mathcal{K}_f - \epsilon)P(t) < F(t) < (\mathcal{K}_f + \epsilon)P(t) \quad \text{and} \quad (\mathcal{K}_m - \epsilon)P(t) < M(t) < (\mathcal{K}_m + \epsilon)P(t)$$

for every $t > t_0$.

Since

$$P' = \beta \frac{FM}{F+M} - (\mu_f + bP)F - (\mu_m + bP)M$$

we obtain

$$\beta(\mathcal{K}_f - \epsilon)(\mathcal{K}_m - \epsilon)P - (\mathcal{K}_f + \epsilon)(\mu_f + bP)P - (\mathcal{K}_m + \epsilon)(\mu_m + bP)P < P' <$$

$$< \beta(\mathcal{K}_f + \epsilon)(\mathcal{K}_m + \epsilon)P - (\mathcal{K}_f - \epsilon)(\mu_f + bP)P - (\mathcal{K}_m - \epsilon)(\mu_m + bP)P$$

which is equivalent to

$$[\beta(\mathcal{K}_f - \epsilon)(\mathcal{K}_m - \epsilon) - \mu_f(\mathcal{K}_f + \epsilon) - \mu_m(\mathcal{K}_m + \epsilon) - b(1 + 2\epsilon)]P < P' <$$

$$< [\beta(\mathcal{K}_f + \epsilon)(\mathcal{K}_m + \epsilon) - \mu_f(\mathcal{K}_f - \epsilon) - \mu_m(\mathcal{K}_m - \epsilon) - b(1 - 2\epsilon)]P$$

Notice that both inequalities are logistic equations in P and, for ϵ sufficiently small and

$$\beta\mathcal{K}_f\mathcal{K}_m - \mu_f\mathcal{K}_f - \mu_m\mathcal{K}_m > 0, \quad \text{which is equivalent to} \quad \mathcal{R} > 1,$$

we obtain

$$\begin{aligned} \frac{[\beta(\mathcal{K}_f - \epsilon)(\mathcal{K}_m - \epsilon) - \mu_f(\mathcal{K}_f + \epsilon) - \mu_m(\mathcal{K}_m + \epsilon)]}{b(1 + 2\epsilon)} &< \lim_{t \rightarrow \infty} P(t) < \\ &< \frac{[\beta(\mathcal{K}_f + \epsilon)(\mathcal{K}_m + \epsilon) - \mu_f(\mathcal{K}_f - \epsilon) - \mu_m(\mathcal{K}_m - \epsilon)]}{b(1 - 2\epsilon)} \end{aligned}$$

Since ϵ is arbitrarily small, we conclude that

$$\lim_{t \rightarrow \infty} P(t) = \frac{\beta\mathcal{K}_f\mathcal{K}_m - \mu_f\mathcal{K}_f - \mu_m\mathcal{K}_m}{b}$$

or, equivalently,

$$\lim_{t \rightarrow \infty} P(t) = \frac{\mu_f\mu_m}{b\beta}(\mathcal{R} - 1)$$

From this, we obtain the global stability of (F^*, M^*) i.e.

$$\lim_{t \rightarrow \infty} F(t) = \frac{\mu_f\mu_m [\mu_f(\mathcal{R}_f - 1) + \mu_m]}{b\beta^2}(\mathcal{R} - 1)$$

$$\lim_{t \rightarrow \infty} M(t) = \frac{\mu_f\mu_m [\mu_m(\mathcal{R}_m - 1) + \mu_f]}{b\beta^2}(\mathcal{R} - 1)$$

□

3. THE LOGISTIC TWO-SEX MODEL WITHOUT PAIRS AND NON-REPRODUCTIVE GROUPS

In this section we extend the previous model to include the non-reproductive groups A_f and A_m . The transition rates into the non-reproductive classes are denoted by ν_f and ν_m .

$$(3) \quad \begin{cases} F' &= \beta\gamma_f \frac{FM}{F+M} - (\mu_f + bP)F - \nu_f F, \\ M' &= \beta\gamma_m \frac{FM}{F+M} - (\mu_m + bP)M - \nu_m M, \\ A'_f &= \nu_f F - (\mu_f + bP)A_f, \\ A'_m &= \nu_m M - (\mu_m + bP)A_m. \end{cases}$$

Where $P = F + M + A_f + A_m$.

The model (3) has two steady states:

$(\bar{F}, \bar{M}, \bar{A}_f, \bar{A}_m) = (0, 0, 0, 0)$ and a strictly positive one $(\tilde{F}, \tilde{M}, \tilde{A}_f, \tilde{A}_m)$ where

$$\begin{aligned} \tilde{F} &= \frac{\tilde{P}}{\left[1 + (\nu_f/(\mu_f + b\tilde{P}))\right] + \left[1 + \nu_m/(\mu_m + b\tilde{P})\right] \frac{(\mu_m + \nu_m)(\mathcal{R}_m^n - 1) + \mu_f + \nu_f}{(\mu_f + \nu_f)(\mathcal{R}_f^n - 1) + \mu_m + \nu_m}} \\ \tilde{M} &= \frac{\tilde{P}}{\left[1 + \nu_m/(\mu_m + b\tilde{P})\right] + \left[1 + \nu_f/(\mu_f + b\tilde{P})\right] \frac{(\mu_f + \nu_f)(\mathcal{R}_f^n - 1) + \mu_m + \nu_m}{(\mu_m + \nu_m)(\mathcal{R}_m^n - 1) + \mu_f + \nu_f}} \\ \tilde{A}_f &= \frac{\nu_f}{\mu_f + b\tilde{P}} \frac{\tilde{P}}{\left[1 + \nu_f/(\mu_f + b\tilde{P})\right] + \left[1 + \nu_m/(\mu_m + b\tilde{P})\right] \frac{(\mu_m + \nu_m)(\mathcal{R}_m^n - 1) + \mu_f + \nu_f}{(\mu_f + \nu_f)(\mathcal{R}_f^n - 1) + \mu_m + \nu_m}} \\ \tilde{A}_m &= \frac{\nu_m}{\mu_m + b\tilde{P}} \frac{\tilde{P}}{\left[1 + \nu_m/(\mu_m + b\tilde{P})\right] + \left[1 + \nu_f/(\mu_f + b\tilde{P})\right] \frac{(\mu_f + \nu_f)(\mathcal{R}_f^n - 1) + \mu_m + \nu_m}{(\mu_m + \nu_m)(\mathcal{R}_m^n - 1) + \mu_f + \nu_f}} \end{aligned}$$

where

$$\tilde{P} = \frac{(\mu_f + \nu_f)(\mu_m + \nu_m)}{b\beta} (\mathcal{R}^n - 1)$$

and the net reproductive numbers

$$\mathcal{R}_f^n = \frac{\beta\gamma_f}{\mu_f + \nu_f}, \quad \mathcal{R}_m^n = \frac{\beta\gamma_m}{\mu_m + \nu_m} \quad \text{and} \quad \mathcal{R}^n = (\mathcal{R}_f^n - 1)(\mathcal{R}_m^n - 1).$$

\mathcal{R}_f^n and \mathcal{R}_m^n represent the expected female/male offspring from a female/male during her/his expected reproductive life-time. \mathcal{R}^n represents the maximum *possible* net-growth of heterosexual pairs produced by a single pair as follows: a typical female and male are expected to give birth to \mathcal{R}_f^n females and \mathcal{R}_m^n males during their reproductive life-time. The resulting offspring is then able to form a maximum of \mathcal{R}^n pairs *excluding* one pair that accounts for the original couple.

THEOREM 3.1. *If $\mathcal{R}^n > 1$ then $(\tilde{F}, \tilde{M}, \tilde{A}_f, \tilde{A}_m)$ is globally stable. Otherwise, the extinction equilibrium $(\bar{F}, \bar{M}, \bar{A}_f, \bar{A}_m)$ is globally stable.*

Proof. Using a similar bounding argument as in the previous section, we see that $\mathcal{R}_f^n > 1$, $\mathcal{R}_m^n > 1$ are necessary conditions to avoid population extinction. Notice that the first two equations of (3) differ from those of (1) by only ν_f and ν_m as additional terms to the natural mortality rates μ_f and μ_m and the total population P in the logistic part of the mortality. However, when considering the dynamics of $\frac{F}{F+M}$ as in the previous section, the logistic component of the mortality cancels. Therefore the differential equation for $\frac{F}{F+M}$ is similar to the one obtained in the previous section, i.e.

$$(4) \quad x' = \beta x(1-x)(\mathcal{K}_f^n - x),$$

where

$$\mathcal{K}_f^n = \frac{(\mu_f + \nu_f)(\mathcal{R}_f^n - 1) + \mu_m + \nu_m}{\beta}.$$

So, using the result in the previous section, we conclude that

$$\frac{F}{F+M} \rightarrow \mathcal{K}_f^n \quad \text{and} \quad \frac{M}{F+M} \rightarrow \mathcal{K}_m^n := 1 - \mathcal{K}_f^n.$$

where

$$\mathcal{K}_m^n = 1 - \mathcal{K}_f^n = \frac{\beta\gamma_m - (\mu_m + \nu_m) + (\mu_f + \nu_f)}{\beta}.$$

Notice also that

$$\mathcal{R}_f^n > 1 \quad \text{and} \quad \mathcal{R}_m^n > 1, \quad \text{imply} \quad 0 < \mathcal{K}_f^n < 1.$$

Therefore

$$M \rightarrow \frac{\mathcal{K}_m^n}{\mathcal{K}_f^n} F.$$

Using similar techniques we can relate the limits of A_f and A_m in terms of the limit of F as $t \rightarrow \infty$. First, denote $z = \frac{F}{F+A_f}$. It follows from (3) that

$$z' = [\beta\gamma_f \mathcal{K}_m^n - \nu_f - \beta\gamma_f \mathcal{K}_m^n z]z$$

which is a logistic equation. It follows that

$$z \rightarrow \frac{\beta\gamma_f \mathcal{K}_m^n - \nu_f}{\beta\gamma_f \mathcal{K}_m^n},$$

provided that

$$(5) \quad \beta\gamma_f \mathcal{K}_m^n > \nu_f.$$

If (5) does not hold then $z \rightarrow 0$ which implies $F \rightarrow 0$ which, in turn, causes the entire population to approach the extinction equilibrium.

Denoting $\omega = \frac{M}{M+A_m}$, we obtain

$$\omega' = [\beta\gamma_m \mathcal{K}_f^n - \nu_m - \beta\gamma_m \mathcal{K}_f^n \omega]\omega$$

and

$$\omega \rightarrow \frac{\beta\gamma_m \mathcal{K}_f^n - \nu_m}{\beta\gamma_m \mathcal{K}_f^n},$$

provided

$$(6) \quad \beta\gamma_m \mathcal{K}_f^n > \nu_m.$$

Again, if this condition does not hold, the male population (and then the total population) approaches the zero equilibrium.

Thus, assuming (5) and (6),

$$A_f \rightarrow \frac{\nu_f}{\beta\gamma_f \mathcal{K}_m^n - \nu_f} F \quad \text{and} \quad A_m \rightarrow \frac{\nu_m}{\beta\gamma_m \mathcal{K}_f^n - \nu_m} M = \frac{\nu_m}{\beta\gamma_m \mathcal{K}_f^n - \nu_m} \frac{\mathcal{K}_m^n}{\mathcal{K}_f^n} F,$$

Using these limits and following a similar technique as in the previous section, we are now able to obtain a limiting differential equation for F as follows: for every $\epsilon > 0$ and arbitrarily small there exist a finite time t_0 such that, for every $t > t_0$

$$[\beta\gamma_f(\mathcal{K}_m^n - \epsilon) - (\mu_f + \nu_f) - b(C_1^n + 3\epsilon)F]F < F' < [\beta\gamma_f(\mathcal{K}_m^n + \epsilon) - (\mu_f + \nu_f) - b(C_1^n - 3\epsilon)F]F$$

where

$$C_1^n = \left(1 + \frac{\nu_m}{\mu_m + bP^*}\right) + \left(1 + \frac{\nu_f}{\mu_f + bP^*}\right) \frac{(\mu_f + \nu_f)(\mathcal{R}_f^n - 1) + \mu_m + \nu_m}{(\mu_m + \nu_m)(\mathcal{R}_m^n - 1) + \mu_f + \nu_f}.$$

Since both differential inequalities are logistic, the final limit of $F(t)$ is identical to the one in the following limiting ODE:

$$(7) \quad F' = (\beta\gamma_f \mathcal{K}_m^n - (\mu_f + \nu_f) - bC_1^n F)F$$

It follows that

$$F \rightarrow \frac{\beta\gamma_f \mathcal{K}_m^n - (\mu_f + \nu_f)}{bC_1^n}$$

provided that

$$\beta\gamma_f \mathcal{K}_m^n > \mu_f + \nu_f$$

or equivalently

$$(\mathcal{R}_f^n - 1)(\mathcal{R}_m^n - 1) = \mathcal{R}^n > 1.$$

This has a similar biological interpretation as the first positivity condition discussed in regards to (1).

Using a symmetric argument we obtain the following limiting ODE for the male population

$$(8) \quad M' = (\beta\gamma_m \mathcal{K}_f^n - (\mu_m + \nu_m) - bC_2^n M)M$$

where

$$C_2^n = \frac{\mathcal{K}_m^n}{\mathcal{K}_f^n} \left(1 + \frac{\nu_m}{\mu_m + bP^*}\right) + \left(1 + \frac{\nu_f}{\mu_f + bP^*}\right) \frac{(\mu_f + \nu_f)(\mathcal{R}_f^n - 1) + \mu_m + \nu_m}{(\mu_m + \nu_m)(\mathcal{R}_m^n - 1) + \mu_f + \nu_f}.$$

It follows that

$$M \rightarrow \frac{\beta\gamma_m \mathcal{K}_f^n - (\mu_m + \nu_m)}{bC_2^n}$$

provided that

$$\beta\gamma_m \mathcal{K}_f^n > \mu_m + \nu_m$$

which is also equivalent to

$$(\mathcal{R}_f^n - 1)(\mathcal{R}_m^n - 1) = \mathcal{R}^n > 1.$$

Notice that this is the same positivity condition required for the limit of F . This condition also implies the positivity conditions (5) and (6) for the limits of A_m and A_f .

Thus $(\bar{F}, \bar{M}, \bar{A}_f, \bar{A}_m)$ is globally stable if and only if

$$\mathcal{R}^n > 1.$$

Otherwise, the global stability of $(\bar{F}, \bar{M}, \bar{A}_f, \bar{A}_m)$ follows. \square

4. THE EPIDEMIC LOGISTIC TWO-SEX MODEL WITHOUT PAIRS AND SEXUALLY ABSTAINED GROUPS

From an STD perspective we need to separate the non-reproductive groups into two different classes: the sexually abstained groups who not only do not reproduce but also abstain (by choice or not) from sexual activity and those who remain sexually active but non-reproductive. In animal populations both types of individuals are likely to be present. Sexually abstinence can be a consequence of mating competition coupled with an instinctive avoidance of infected individuals which would justify a higher abstinence rate among the infected. A non-reproductive but sexually active individual is more prevalent in the human populations but also in the animal populations since some STD's cause sterility.

It is difficult to incorporate both types of non-reproduction and we chose to treat the two cases separately. First we build the following model assumint that the non-reproductive groups are abstained from sexual activity.

$$(9) \quad \begin{cases} F' &= \beta\gamma_f \frac{(F+\varphi)(M+\chi)}{F+\varphi+M+\chi} - \lambda_1 F \frac{\chi}{M+\chi} - \bar{\mu}_f F - \nu_f F \\ M' &= \beta\gamma_m \frac{(F+\varphi)(M+\chi)}{F+\varphi+M+\chi} - \lambda_2 M \frac{\varphi}{F+\varphi} - \bar{\mu}_m M - \nu_m M \\ \varphi' &= \lambda_1 F \frac{\chi}{M+\chi} - \bar{\mu}_f \varphi - \alpha_f \varphi \\ \chi' &= \lambda_2 M \frac{\varphi}{F+\varphi} - \bar{\mu}_m \chi - \alpha_m \chi \\ A'_f &= \nu_f F - \bar{\mu}_f A_f \\ A'_m &= \nu_m M - \bar{\mu}_m A_m \\ A'_\varphi &= \alpha_f \varphi - \bar{\mu}_f A_\varphi \\ A'_\chi &= \alpha_m \chi - \bar{\mu}_m A_\chi \end{cases}$$

where

$$P = F + M + \varphi + \chi + A_f + A_m + A_\varphi + A_\chi.$$

For simplicity and for the sake of a stronger mathematical result, we treat first the case when the transition rates into the abstained classes are independent of the disease, i.e.

$$\nu_f = \alpha_f \quad \text{and} \quad \nu_m = \alpha_m,$$

and the two infection rates are equal,

$$\lambda_1 = \lambda_2 := \lambda.$$

First notice that the dynamics of the total females and males is identical to the one of (3), i.e. summing up the first with the third equation, the second with the fourth, the fifth with the seventh and the sixth with the eighth we obtain

$$(10) \quad \begin{cases} (F + \varphi)' &= \beta\gamma_f \frac{(F+\varphi)(M+\chi)}{F+\varphi+M+\chi} - \tilde{\mu}_f(F + \varphi) \\ (M + \chi)' &= \beta\gamma_m \frac{(F+\varphi)(M+\chi)}{F+\varphi+M+\chi} - \tilde{\mu}_m(M + \chi) \\ (A_f + A_\varphi)' &= \nu_f(F + \varphi) - \tilde{\mu}_f(A_f + A_\varphi) \\ (A_m + A_\chi)' &= \nu_m(M + \chi) - \tilde{\mu}_m(A_m + A_\chi) \end{cases}$$

which is precisely (3).

Taking into account that the disease does not have additional mortality and using the main result for (3) we conclude that if $\mathcal{R}^n > 1$

$$\begin{aligned} \lim_{t \rightarrow \infty} [F(t) + \varphi(t)] &= \tilde{F}, & \lim_{t \rightarrow \infty} [M(t) + \chi(t)] &= \tilde{M} \\ \lim_{t \rightarrow \infty} [A_f(t) + A_\varphi(t)] &= \tilde{A}_f, & \lim_{t \rightarrow \infty} [A_m(t) + A_\chi(t)] &= \tilde{A}_m \end{aligned}$$

The following theorem will establish the threshold between a stable DFE (disease free equilibrium) and an endemic situation when both susceptible and infected individuals co-exist.

The model (9) has three steady states. Two boundary equilibria

$$(\bar{F}, \bar{M}, \bar{\varphi}, \bar{\chi}, \bar{A}_f, \bar{A}_m, \bar{A}_\varphi, \bar{A}_\chi) = (0, 0, 0, 0, 0, 0, 0, 0) \quad \text{and} \quad (\tilde{F}, \tilde{M}, \tilde{A}_f, \tilde{A}_m, 0, 0, 0, 0)$$

and an interior steady state $(F^o, M^o, \varphi^o, \chi^o, A_f^o, A_m^o, A_\varphi^o, A_\chi^o)$ where

$$\begin{aligned} F^o &= \tilde{F} \left(1 - \frac{\lambda^2 - (\tilde{\mu}_f + \nu_f)(\tilde{\mu}_m + \nu_m)}{\lambda(\lambda + (\tilde{\mu}_f + \nu_f))} \right) & \varphi^o &= \frac{\tilde{F}(\lambda^2 - (\tilde{\mu}_f + \nu_f)(\tilde{\mu}_m + \nu_m))}{\lambda(\lambda + (\tilde{\mu}_f + \nu_f))} \\ M^o &= \tilde{M} \left(1 - \frac{\lambda^2 - (\tilde{\mu}_f + \nu_f)(\tilde{\mu}_m + \nu_m)}{\lambda(\lambda + (\tilde{\mu}_m + \nu_m))} \right) & \chi^o &= \frac{\tilde{M}(\lambda^2 - (\tilde{\mu}_f + \nu_f)(\tilde{\mu}_m + \nu_m))}{\lambda(\lambda + (\tilde{\mu}_m + \nu_m))} \\ A_f^o &= \tilde{A}_f - \frac{\nu_f \tilde{F}(\lambda^2 - (\tilde{\mu}_f + \nu_f)(\tilde{\mu}_m + \nu_m))}{\tilde{\mu}_f \lambda(\lambda + (\tilde{\mu}_f + \nu_f))} & A_\varphi^o &= \frac{\nu_f \tilde{F}(\lambda^2 - (\tilde{\mu}_f + \nu_f)(\tilde{\mu}_m + \nu_m))}{\tilde{\mu}_f \lambda(\lambda + (\tilde{\mu}_f + \nu_f))} \\ A_m^o &= \tilde{A}_m - \frac{\nu_m \tilde{M}(\lambda^2 - (\tilde{\mu}_f + \nu_f)(\tilde{\mu}_m + \nu_m))}{\tilde{\mu}_m \lambda(\lambda + (\tilde{\mu}_m + \nu_m))} & A_\chi^o &= \frac{\nu_m \tilde{M}(\lambda^2 - (\tilde{\mu}_f + \nu_f)(\tilde{\mu}_m + \nu_m))}{\tilde{\mu}_m \lambda(\lambda + (\tilde{\mu}_m + \nu_m))} \end{aligned}$$

and where $\tilde{\mu}_f = \mu_f + b\tilde{P}$, $\tilde{\mu}_m = \mu_m + b\tilde{P}$ and $\tilde{P} = \tilde{F} + \tilde{M} + \tilde{A}_f + \tilde{A}_m$.

Assuming $\mathcal{R}^n > 1$, the following theorem describes the long term dynamics of (9) which depends on the epidemic reproductive number

$$\mathcal{R}_0^n = \frac{\lambda^2}{(\tilde{\mu}_f + \nu_f)(\tilde{\mu}_m + \nu_m)}$$

$\frac{\lambda}{\tilde{\mu}_f + \nu_f}$ and $\frac{\lambda}{\tilde{\mu}_m + \nu_m}$ represent the expected number of secondary cases of new female/male individuals throughout her/his reproductive lifetime. \mathcal{R}_0^n is the possible number of pairs made of secondary infection cases produced by a typical female and male during their *reproductive* lifetimes.

THEOREM 4.1. *If $\mathcal{R}_0^n < 1$, then $(\tilde{F}, \tilde{M}, \tilde{A}_f, \tilde{A}_m, 0, 0, 0, 0)$ is globally stable. Otherwise, if $\mathcal{R}_0^n > 1$, then the endemic equilibrium $(F^o, M^o, \varphi^o, \chi^o, A_f^o, A_m^o, A_\varphi^o, A_\chi^o)$ is globally stable.*

Proof. We will use the theory of asymptotically autonomous systems established by Thieme and Castillo-Chavez in [11] and [12] to study the behavior of (9) using a limiting planar system in $\varphi, \chi, A_\varphi, A_\chi$. Notice that the equations for φ and χ in (9) form an asymptotically autonomous system in φ, χ :

$$(11) \quad \begin{cases} \varphi' &= \lambda F \frac{\chi}{M+\chi} - \tilde{\mu}_f \varphi - \nu_f \varphi = \bar{f}(t, \varphi, \chi) \\ \chi' &= \lambda M \frac{\varphi}{F+\varphi} - \tilde{\mu}_m \chi - \nu_m \chi = \bar{g}(t, \varphi, \chi) \end{cases}$$

with the following limiting system:

$$(12) \quad \begin{cases} \varphi' &= \frac{\lambda}{\tilde{M}} (\tilde{F} - \varphi) \chi - (\tilde{\mu}_f + \nu_f) \varphi = f(\varphi, \chi) \\ \chi' &= \frac{\lambda}{\tilde{F}} (\tilde{M} - \chi) \varphi - (\tilde{\mu}_m + \nu_m) \chi = g(\varphi, \chi). \end{cases}$$

The Poincaré-Bendixson-type trichotomy established by Thieme and Chaves in [11] and [12] ensures that every bounded forward solution of (11) converges to an equilibrium of the limiting system (12). All solutions of (9) and, consequently, of (12) are obviously bounded in the positive quadrant due to the logistic mortality assumptions. It remains to establish the local stability conditions for the non-zero equilibria in the limiting system and to exclude the possibility of periodic solutions. From these the global stability of the DFE and the endemic steady state will follow.

In order to check the local stability of the equilibrium points, we will compute the Jacobian of (12):

$$J(\varphi, \chi) = \begin{bmatrix} -\frac{\lambda\chi}{\tilde{M}} - (\tilde{\mu}_f + \nu_f) & \frac{\lambda(\tilde{F}-\varphi)}{\tilde{M}} \\ \frac{\lambda(\tilde{M}-\chi)}{\tilde{F}} & -\frac{\lambda\varphi}{\tilde{F}} - (\tilde{\mu}_m + \nu_m) \end{bmatrix}$$

From this we see

$$\text{Tr} J(\varphi, \chi) = -\frac{\lambda\chi}{\tilde{M}} - (\tilde{\mu}_f + \nu_f) - \frac{\lambda\varphi}{\tilde{F}} - (\tilde{\mu}_m + \nu_m) < 0$$

for all possible real positive values for φ and χ .

$$\det J(\varphi, \chi) = \frac{\lambda(\lambda + (\tilde{\mu}_f + \alpha_f))}{\tilde{F}} \varphi + \frac{\lambda(\lambda + (\tilde{\mu}_m + \alpha_m))}{\tilde{M}} \chi + (\tilde{\mu}_f + \alpha_f)(\tilde{\mu}_m + \alpha_m) - \lambda^2 > 0.$$

Furthermore,

$$\det(J(0, 0)) > 0 \quad \text{if and only if} \quad \lambda^2 < (\tilde{\mu}_f + \alpha_f)(\tilde{\mu}_m + \alpha_m) \Leftrightarrow \mathcal{R}_0^n < 1$$

and

$$\det(J(\varphi^o, \chi^o)) > 0 \quad \text{if and only if} \quad \lambda^2 > (\tilde{\mu}_f + \alpha_f)(\tilde{\mu}_m + \alpha_m) \Leftrightarrow \mathcal{R}_0^n > 1.$$

Hence the DFE is locally asymptotically stable if $\mathcal{R}_0^n < 1$ and it is the only equilibrium in the biologically feasible region. Otherwise if $\mathcal{R}_0^n > 1$, the DFE is unstable and the endemic equilibrium is locally asymptotically stable.

The existence of periodic solutions is ruled out by the Poincaré-Bendixson Criterion:

$$\frac{\partial f}{\partial \varphi} + \frac{\partial g}{\partial \chi} = -\frac{\lambda \chi}{\tilde{M}} - (\tilde{\mu}_f + \alpha_f) - \frac{\lambda \varphi}{\tilde{F}} - (\tilde{\mu}_m + \alpha_m) < 0,$$

which proves the global stability of the equilibria analyzed above.

Having established the limits for φ and χ , the limits for A_φ and A_χ follow immediately from the last two equations of (9). We now summarize the conclusions of this theorem:

- If $\mathcal{R}^n < 1$ then $(\tilde{F}, \tilde{M}, \tilde{\varphi}, \tilde{\chi}, \tilde{A}_f, \tilde{A}_m, \tilde{A}_\varphi, \tilde{A}_\chi)$ is globally stable,
- If $\mathcal{R}^n > 1$ and $\mathcal{R}_0^n < 1$ then the DFE $(\tilde{F}, \tilde{M}, \tilde{A}_f, \tilde{A}_m, 0, 0, 0, 0)$ is globally stable and
- If $\mathcal{R}^n > 1$ and $\mathcal{R}_0^n > 1$ then the endemic equilibrium $(F^o, M^o, \varphi^o, \chi^o, A_f^o, A_m^o, A_\varphi^o, A_\chi^o)$ is globally stable.

□

We now turn to the case when the transition rates into the abstained groups are dependent on the disease, i.e.

$$\nu_f \neq \alpha_f \quad \text{and} \quad \nu_m \neq \alpha_m.$$

In this case we can only establish the local stability of each steady state. To simplify the computation we use the next-generation matrix method provided by van den Driessche in [6]. Following the equations for the infected classes only we have the following new infection and removal rates from each of the infected classes.

$$G = \begin{bmatrix} 0 & \frac{\lambda FM}{(M+\chi)^2} & 0 & 0 \\ \frac{\lambda FM}{(F+\varphi)^2} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix}$$

$$V = \begin{bmatrix} \bar{\mu}_f + b\varphi + \alpha_f & b\varphi & b\varphi & b\varphi \\ b\chi & \bar{\mu}_m + b\chi + \alpha_m & b\chi & b\chi \\ bA_\varphi + \alpha_f & bA_\varphi & \bar{\mu}_f + bA_\varphi & bA_\varphi \\ bA_\chi & bA_\chi + \alpha_m & bA_\chi & \bar{\mu}_m + bA_\chi \end{bmatrix}$$

$$G(0, 0, 0, 0) = \begin{bmatrix} 0 & \frac{\tilde{F}}{\tilde{M}} & 0 & 0 \\ \frac{\tilde{M}}{\tilde{F}} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix}$$

$$V^{-1}(0, 0, 0, 0) = \begin{bmatrix} \frac{1}{\bar{\mu}_f + \alpha_f} & 0 & 0 & 0 \\ 0 & \frac{1}{\bar{\mu}_m + \alpha_m} & 0 & 0 \\ -\frac{\alpha_f}{\bar{\mu}_f(\bar{\mu}_f + \alpha_f)} & 0 & \frac{1}{\bar{\mu}_f} & 0 \\ 0 & -\frac{\alpha_m}{\bar{\mu}_m(\bar{\mu}_m + \alpha_m)} & 0 & \frac{1}{\bar{\mu}_m} \end{bmatrix}$$

$$GV^{-1}(0, 0, 0, 0) = \begin{bmatrix} 0 & \frac{\lambda \tilde{F}}{\tilde{M}(\tilde{\mu}_m + \alpha_m)} & 0 & 0 \\ \frac{\lambda \tilde{M}}{\tilde{F}(\tilde{\mu}_f + \alpha_f)} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix}$$

$$\mathcal{L}_0^n = \rho(GV^{-1}) = \max |\delta| = \frac{\lambda}{\sqrt{(\tilde{\mu}_f + \alpha_f)(\tilde{\mu}_m + \alpha_m)}}$$

where δ is an eigenvalue.

This means that the epidemic reproductive number can be taken as

$$\mathcal{L}_0^n = \frac{\lambda^2}{(\tilde{\mu}_f + \alpha_f)(\tilde{\mu}_m + \alpha_m)}$$

and we have the following result

- If $\mathcal{R}^n < 1$ then $(\bar{F}, \bar{M}, \bar{\varphi}, \bar{\chi}, \bar{A}_f, \bar{A}_m, \bar{A}_\varphi, \bar{A}_\chi)$ is globally stable,
- If $\mathcal{R}^n > 1$ and $\mathcal{L}_0^n < 1$ then the DFE $(\tilde{F}, \tilde{M}, \tilde{A}_f, \tilde{A}_m, 0, 0, 0, 0)$ is locally asymptotically stable and
- If $\mathcal{R}^n > 1$ and $\mathcal{L}_0^n > 1$ then the endemic equilibrium $(F^o, M^o, \varphi^o, \chi^o, A_f^o, A_m^o, A_\varphi^o, A_\chi^o)$ is locally asymptotically stable.

5. DISCUSSION

We address here the question of whether the abstained groups can eliminate the disease from an endemic situation. In other words, we would like to verify if the following inequality is possible

$$(13) \quad \mathcal{R}_0^n < 1 < \mathcal{R}_0.$$

where $\mathcal{R}_0 = \frac{\lambda^2}{\mu_f^* \mu_m^*}$ which is the epidemic reproductive number in the absence of the non-reproductive groups (obtained by replacing ν_f and ν_m in \mathcal{R}_0^n with zero). μ_f^* and μ_m^* are the mortality rates at the equilibrium obtained in section 2:

$$\mu_f^* = \mu_m + b(F^* + M^*), \quad \mu_m^* = \mu_m + b(F^* + M^*).$$

In the case of disease independent transition rates, $\nu_f = \alpha_f$ and $\nu_m = \alpha_m$, the right hand side means that in the absence of the abstained groups the situation is endemic. Similar to previous work, under certain conditions the inclusion of the abstinent groups into the system can cause the elimination of the disease.

In order for (13) to be true we need

$$\mu_f^* \mu_m^* < (\tilde{\mu}_f + \nu_f)(\tilde{\mu}_m + \nu_m) \Leftrightarrow$$

$$\Leftrightarrow (\nu_f - \nu_m) \cdot (\beta\gamma_f - (\mu_f + \nu_f) - \mu_f - \beta\gamma_m + (\mu_m + \nu_m) + \mu_f) > 0.$$

Notice that, in order for this inequality to be true, we need $\nu_f \neq \nu_m$. The similar condition found in [7] did not require gender distinct values for the

rate at which healthy females/males enter the abstinent groups.

6. CONCLUSIONS

In this paper we introduced and analyzed a two-sex logistic model without pair-formation. We further extended this model to include non-reproductive groups and a generic mild and long-lasting sexually transmitted disease. The main result concerning the demographic models (without the disease) is that the dynamics of the population depends on the ability of the females and males to form sufficient *possible* pairs. Specifically, the condition

$$(\mathcal{R}_f - 1)(\mathcal{R}_m - 1) > 1$$

means that the expected female and male offspring from a typical pair needs to be able to form at least one pair in *addition* to the one that replaces the original pair.

Another important result is that, while the abstained groups can eliminate the disease in an endemic situation, this is only possible if the transition rates into the isolated classes are gender **dependent**. This requirement is in the context of *disease-independent* transition rates. There are biological reasons for both situations. For example, if the STD is mild and asymptomatic (such as Herpes) many individuals will have the same sexual behavior whether they are infected or not. On the other hand, if an infected person is aware of the disease, he/she may refrain from sexual activity and, thus, increase the non-reproduction rate.

We plan to extend these results to groups isolated from reproduction but sexually active. Another important avenue of related research is adapting the models analyzed herein to various animal populations that do not form pairs and investigate the evolutionary role of isolation from reproduction.

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