A two-sex demographic model with single-dependent divorce rate

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Abstract

Divorce appears to be one of the least studied demographic processes, both empirically and in two-sex demographic models. In this paper, we study mathematical as well as biological implications of the assumption that the divorce rate is positively affected by the amount of single (i.e., unmarried/unpaired) individuals in the population. We do that by modifying the classical exponential two-sex model accounting for pair formation and separation. We model the divorce rate as an increasing function of the single population size and show that the single population pressure on the established couples alters the exponential behavior of the classical model in which the divorce rate is assumed constant. In particular, the total population size becomes bounded and a unique positive equilibrium exists. In addition, a Hopf bifurcation analysis around the positive equilibrium shows that the modified model may exhibit sustained oscillations.

Keywords: population dynamics, bifurcation, demography, divorce rate, two-sex model

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1. Introduction

Mathematical modeling addressing subtle demographic issues in both humans and animals has been the subject of intensive research [Kendall, 1949, Pollard, 1997, Caswell and Weeks, 1986, Ianelli et al., 2005, and references therein]. In spite of this effort, many important questions remain to be resolved, including an identification of appropriate marriage or pairing functions [Ianelli et al., 2005], an accounting for births outside established couples (single mothers) [Milner and Yang, 2009], or an adequate modeling of aspects that drive the frequency of divorces. It is this latter issue which we would like to contribute to in this paper.

Divorce is a complex issue, influenced by a variety of factors that are difficult to comprehend. For example, the risk of marital dissolution in humans is affected by such individual- or couple-level characteristics as the level of education, home ownership, the presence of children, or husband's income and weeks worked [South and Lloyd, 1995, Wolcott and Hughes, 1999, and references therein]. In animals, most of the research on species that form pair bonds and hence are prone to divorces has been carried out on socially monogamous birds [Choudhury, 1995, Jeschke and Kokko, 2008, and references therein]. The analysis conducted by [Jeschke and Kokko, 2008], considering 128 species and 20 potential correlates of the divorce rate, suggested that species with a high divorce rate tend to be ornamented and sexually dichromatic, live colonially, form part-time rather than continuous partnerships, and have a high mortality rate.

Difficulty to comprehend divorce as a demographic process is one of the reasons why most two-sex demographic models that account for pairs assume the divorce rate to be constant [Hadeler et al., 1988, Berec and Boukal, 2004, Maxin and Milner, 2009]. With the constant divorce rate (all other model parameters being constant), populations undergo an exponential growth [Hadeler et al., 1988]. An alternative has been to assume that the divorce rate is a non-decreasing function of the total population density [Castillo-Chavez and Huang, 1995]. There is a 'social density' argument for the divorce rate to depend on the total population density. Simply put, the divorce rate is assumed to be positively affected by the degree of urbanization (humans) or coloniality (animals). Thus, larger populations mean more divorces, but the argument does not seem to incorporate a competitive aspect. With the divorce rate a non-decreasing function of the total population density (all other model parameters being constant), populations always attain a globally stable positive equilibrium [Castillo-Chavez and Huang, 1995].

However, the marriage or pairing process might have a competitive component not only among singles but also between singles and couples. Simply put, with an increasing amount of singles in the population, coupled individuals might feel relatively safe should they contemplate a separation decision, since the chances of finding a new (and potentially better) partner (relatively quickly) are higher. Indeed, [South and Lloyd, 1995] concluded that the risk of marital dissolution in humans is highest where "either wives or husbands encounter an abundance of spouse alternatives", presumably due to a higher opportunity to meet and unite with a more attractive mate (whatever the word 'attractive' may mean – see, e.g., the above list of preferred, individual-level characteristics). An analogous marriage market characteristic has been proposed for socially monogamous birds, although the available evidence is so far only indirect. The 'better option hypothesis' states that divorce should occur "when one member of a pair is able to improve its reproductive success by obtaining a better-quality mate" [Choudhury, 1995]; an evidence for this hypothesis has been set forth, e.g., for the great skua *Catharacta skua* [Catry et al., 1997]. Assuming that the better option hypothesis is correct, we should expect the divorce rate to increase with greater availability of unpaired individuals in the population, in part because of a higher probability that better-quality mates are present and in part because of the chances that such mates will be relatively quickly located.

In this paper, we explore mathematical as well as biological implications of the assumption that the divorce rate is positively affected by the amount of single (i.e. unmarried/unpaired) individuals present in a human community or an animal population, as a novel alternative to the previous studies assuming that the divorce rate is either constant or a non-decreasing function of the total population density. In other words, we assume that married/paired individuals keep searching for potentially better unmarried/unpaired mates, and hence that intra-sexual competition occurs between a married/paired individual and an unmarried/unpaired individual. Descriptive evidence suggests that many married persons indeed continue to search for a partner even while married [South and Lloyd, 1995].

The paper is structured as follows. In Section 2, we develop a modification of the two-sex demographic model introduced by [Hadeler et al., 1988] that will include the divorce rate as an increasing function of the amount of singles in the population. In Section 3, we show that this modification alters the exponential behavior of the original model. In particular, the solutions now become bounded and a unique positive equilibrium exists. Section 4 introduces a specific example of the divorce rate as an increasing function of the amount of singles in the population and proves that, in the case of equal sex-related vital parameters, our model exhibits a supercritical Hopf bifurcation and sustained oscillations. In addition, a numerical example is given to show that this result extends also to the case of sex-dependent vital rates. In the last section, we discuss our results and suggest possible future avenues for the research related to the present topic.

2. Model formulation

Our main aim here is to explore how the positive effect of the amount of singles in the population (referred to as the single-population effect here) on the divorce rate may affect population dynamics. The simplest two-sex model, without age structure but accounting for pairs, was analyzed by [Hadeler et al., 1988]. This model, described below, is an extension of the model introduced by [Kendall, 1949] and [Keyfitz, 1949].

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

The meaning of the state variables and parameters is as follows:

- F, M and C are the densities of single females, single males and couples, respectively,
- β is the *per-couple* birth rate,
- γ_f and γ_m are the probabilities that a newborn is a female or a male, respectively ($\gamma_f + \gamma_m = 1$),
- μ_f and μ_m are the natural mortality rates for females and males, respectively,
- δ is the divorce rate,
- $\mathcal{M}(F, M)$ is the pair formation rate.

Mathematical demographers have not singled out so far any functional form for the pair formation rate that would best resemble reality. However, there are several commonly accepted features this function should satisfy (see [Hadeler et al., 1988] and references therein):

- Non-negativity: $\mathcal{M}(F, M) \geq 0$ for every positive F and M,
- Heterosexuality: $\mathcal{M}(0, M) = \mathcal{M}(F, 0) = 0$ for every positive F and M,
- Monotonicity: $\mathcal{M}(F + F', M + M') \geq \mathcal{M}(F, M)$ for every positive F, M, F' and M',
- Degree-one homogeneity: $\mathcal{M}(\lambda F, \lambda M) = \lambda \mathcal{M}(F, M)$ for every positive F, M and λ,
- Consistency: there is an $\alpha > 0$ such that $\mathcal{M}(F, M) \leq \alpha F$ and $\mathcal{M}(F, M) \leq \alpha M$ for every positive F and M.

The 'heterosexuality' condition says there should be no pairs formed in the absence of a sex. The 'monotonicity' one indicates that there should not be less couples formed if density of both single males and females increases. The 'degree-one homogeneity' condition prescribes that if density of both female and male singles increases at the same rate we should expect a respective increase in the pair formation rate. Finally, the 'consistency'condition prescribes that if one sex becomes numerous, the rate of pair formation is driven solely by the density of the less abundant sex.

Examples of pair formation functions are (see e.g. [Hadeler et al., 1988]):

$$\rho \min(F, M), \ \rho F^a M^{1-a} \text{ with } a \in (0, 1), \ 2\rho \frac{FM}{F + M}.$$

Note that the last function, to be used later on in this paper, satisfies all the conditions listed above. In particular, the 'consistency' condition can be inferred from

$$\lim_{F \to \infty} 2\rho \frac{FM}{F + M} = 2\rho M \quad \text{and} \quad \lim_{M \to \infty} 2\rho \frac{FM}{F + M} = 2\rho F.$$

[Hadeler et al., 1988] proved that every solution of model (1) is exponential, with growth rate λ given by the following eigenvalue problem:

$$\mathcal{M}\left(\frac{\beta\gamma_f}{\mu_f + \lambda} - 1, \frac{\beta\gamma_m}{\mu_m + \lambda} - 1\right) = \mu_f + \mu_m + \delta + \lambda. \tag{2}$$

We use model (1) as a starting point for modeling the divorce rate with the single-population effect. As this effect is likely quite difficult to measure empirically, we will attempt to analyze the modified model without choosing any specific form for the divorce rate as an increasing function of the amount of singles in the population. Nevertheless, to push the model analysis a bit further, we will provide an example of such a divorce rate, with the disclaimer that, apart from several general biological restrictions, the chosen function is not based on any real demographic data.

We now establish a set of conditions that our divorce function $\delta(F, M)$ should satisfy. These conditions are due mostly to biological reasons while some are technical, to facilitate a later analysis of the Hopf bifurcation. We assume that the single-population effect on the divorce rate has two basic characteristics:

- An increase in the overall density of singles in the population should imply an increase in the divorce rate,
- For a constant density of singles, a higher divorce rate should occur when there is a greater imbalance between the densities of unpaired females and males.

It is important to point out that we assume the divorce function $\delta(F, M)$ should always satisfy the first condition first. The second condition is imposed when F and M change so that $F + M$ stays constant. This is due to the fact that, for the same number of singles, $F + M$, a greater pressure on divorce should occur if $F \neq M$. We need to rank these two conditions since they can be conflicting in the sense that a higher difference in the single males and females may occur for a smaller density of singles, i.e.

$$|F_1 - M_1| > |F_2 - M_2| \quad \text{and} \quad F_1 + M_1 < F_2 + M_2.$$

With these considerations, the divorce function δ is assumed to satisfy the following properties:

(i) $\delta(F, M) > 0$ for every $F > 0$ and $M > 0$,

(ii) $\delta(0, 0) = \delta_0 > 0$ and this will be the baseline divorce rate in the absence of singles,

(iii) $\frac{\partial \delta}{\partial F} > 0$, $\frac{\partial \delta}{\partial M} > 0$ for every $F \geq 0$ and $M \geq 0$,

(iv) $\delta(F,M) \geq \delta\left(\frac{F+M}{2}, \frac{F+M}{2}\right)$ for every $F>0$ and $M>0$,

(v) δ is continuously differentiable on $[0,\infty)\times[0,\infty)$.

Later in this paper, we will assume a specific form for $\delta(F,M)$. Note that if we consider a polynomial approximation for $\delta(F,M)$, the linear case will not satisfy condition (iv). Indeed, suppose $\delta(F,M) = \delta_0 + b_1F + b_2M$. Condition (iv) then becomes

$$b_1F + b_2M > (b_1+b_2)\frac{F+M}{2} \Leftrightarrow (b_1-b_2)(F-M) > 0$$

which is clearly not true for every $F>0$ and $M>0$. The next logical step is to consider a second degree polynomial and, in this case, there are examples which satisfy all the conditions stated above. In the general case,

$$\delta(F,M) = \delta_0 + b_1F + b_2M + c_0F^2 + c_1FM + c_2M^2$$

with b_1, b_2, c_0, c_1 and c_2 positive. This is the form to be used later on, with some additional technical assumptions on the coefficients designed to simplify the calculations.

The two-sex demographic model we are going to analyze thus becomes:

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

3. General model analysis

Just as in the case with constant divorce rate [Hadeler et al., 1988], the female and male net reproductive numbers are

$$\mathcal{R}_f \equiv \frac{\beta\gamma_f}{\mu_f} \quad \text{and} \quad \mathcal{R}_m \equiv \frac{\beta\gamma_m}{\mu_m},$$

respectively. However, contrary to model (1), our model (3) admits bounded solutions and a unique interior equilibrium, for suitable choices of δ and $\mathcal{M}$. We state these results in the following propositions:

PROPOSITION 3.1. *(Extinction equilibrium)*
If

$$\mathcal{R}_f < 1, \quad \text{or} \quad \mathcal{R}_m < 1, \quad \text{or} \quad \mathcal{M}(\mathcal{R}_f - 1, \mathcal{R}_m - 1) < \delta_0 + \mu_f + \mu_m$$

then the extinction equilibrium is globally asymptotically stable.

PROOF. The proof of this proposition follows the technique elaborated in [Maxin and Milner, 2009] and we only give a brief outline here. The original system (3) can be transformed into an equivalent one that follows the dynamics of total females, total males and couples, i.e. $x = F + C$, $y = M + C$ and C:

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

Note that system (4) is bounded from above by an equivalent exponential two-sex model developed by [Hadeler et al., 1988] where $\delta(x - C, y - C)$ is replaced by δ_0. The eigenvalue problem in that case is

$$\mathcal{M}\left(\frac{\beta\gamma_f}{\mu_f + \lambda} - 1, \frac{\beta\gamma_m}{\mu_m + \lambda} - 1\right) = \delta_0 + \mu_f + \mu_m + \lambda.$$

This equation, under the conditions stated in the proposition, necessarily has a negative root $\lambda < 0$ which shows that the solutions of the bounding system converge to zero [Hadeler et al., 1988]. In turn, this leads to the global stability of the extinction equilibrium.

□

Note that any of the three conditions stated in the previous proposition, if satisfied, is sufficient to cause population extinction, irrespectively of validity of the other two. In biological terms, the extinction equilibrium is globally stable if at least one of the following conditions is satisfied: (i) the female net reproductive number falls below 1, (ii) the male net reproductive numbers falls below 1, (iii) the new pairs are formed at a rate lower than the rate at which the established couples disappear. Figures 1, 2 and 3 provide three examples to illustrate these three possibilities of population extinction. In all these examples we used the following simplified divorce rate with the single-population effect

$$\delta(F, M) = [b(F+M) + \sqrt{\delta_0}]^2$$

and the harmonic mean version of the pair formation function

$$\mathcal{M}(F, M) = 2\rho \frac{FM}{F+M}.$$

Proposition 3.2. *(Interior equilibrium)*
If

$$\mathcal{R}_f > 1, \quad \mathcal{R}_m > 1 \quad \textit{and} \quad \mathcal{M}(\mathcal{R}_f - 1, \mathcal{R}_m - 1) > \delta_0 + \mu_f + \mu_m$$

then the extinction equilibrium is unstable. In addition, system (4) has a unique interior equilibrium (x^*, y^*, C^*) and its solutions are bounded for all time t provided that, along with the above conditions,

$$\lim_{t\to\infty} \frac{\mathcal{M}(F, M)}{\delta(F, M)} < \infty \quad \textit{and}$$

$$\lim_{C\to\infty} \delta[C(\mathcal{R}_f - 1), C(\mathcal{R}_m - 1)] > \mathcal{M}(\mathcal{R}_f - 1, \mathcal{R}_m - 1) - (\mu_f + \mu_m).$$

Proof. To prove that the extinction equilibrium is unstable we use the approach adopted in [Castillo-Chavez and Huang, 1995]. We consider the following function

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

and prove that it is bounded away from zero.

Given the conditions in the proposition and the smoothness assumptions we have that there exists a positive value (x_0, y_0, C_0), with $x_0 > C_0$ and $y_0 > C_0$, such that

$$\mathcal{M}(\mathcal{R}_f - 1, \mathcal{R}_m - 1) > \delta(x_0 - C_0, y_0 - C_0) + \mu_f + \mu_m.$$

We now assume that there exists a fixed time t_0 such that

$$x(t_0) - C(t_0) < x_0 - C_0 \quad \text{and} \quad y(t_0) - C(t_0) < y_0 - C_0.$$

It follows that if $\xi(t_0)$ is either of the first two terms then either $x'(t_0)$ or $y'(t_0)$ is positive. Consider now the case

$$\xi(t_0) = C(t_0)$$

which translates into

$$\frac{x(t_0)}{C(t_0)} > \mathcal{R}_f \quad \text{and} \quad \frac{y(t_0)}{C(t_0)} > \mathcal{R}_m.$$

Then,

$$C'(t_0) > [\mathcal{M}(\mathcal{R}_f - 1, \mathcal{R}_m - 1) - \delta(x(t_0) - C(t_0), y(t_0) - C(t_0)) -$$

$$-\mu_f - \mu_m]\, C(t_0) >$$

$$> [\mathcal{M}(\mathcal{R}_f - 1, \mathcal{R}_m - 1) - \delta(x_0 - C_0, y_0 - C_0) - \mu_f - \mu_m]\, C(t_0) > 0.$$

This means that if $(x(t), y(t), C(t))$ is sufficiently close to $(0, 0, 0)$ then

$$\liminf_{\epsilon \longrightarrow 0} \frac{\xi(t+\epsilon) - \xi(t)}{\epsilon} > 0. \tag{5}$$

This shows that the extinction equilibrium is unstable.

To show the existence of an interior equilibrium (x^*, y^*, C^*), note that

$$x^* = \mathcal{R}_f C^*, \quad y^* = \mathcal{R}_m C^*.$$

From the third equation in system (4) we obtain

$$\mathcal{M}(\mathcal{R}_f - 1, \mathcal{R}_m - 1) = \delta\, [C^*(\mathcal{R}_f - 1), C^*(\mathcal{R}_m - 1)] + \mu_f + \mu_m.$$

Since the right-hand side is increasing in C^* it follows that, under the conditions of this proposition, there exists a unique positive C^* that satisfies this equality.

We now show that solutions of system (4) are bounded from above for all time t, under the conditions stated in the proposition. Note, from (5), that $x(t)$, $y(t)$ and $C(t)$ are bounded from below. Suppose

$$x(t) > \underline{x}, \quad y(t) > \underline{y}, \quad \text{and} \quad C(t) > \underline{C}.$$

It follows, from (3), that

$$F' > -\mu_f F + (\beta\gamma_f + \delta_0 + \mu_m)\underline{C} - \alpha F.$$

Integrating this inequality we obtain

$$F(t) > \frac{(\beta\gamma_f + \delta_0 + \mu_m)\underline{C}}{\alpha + \mu_f} + \left[F_0 - \frac{(\beta\gamma_f + \delta_0 + \mu_m)\underline{C}}{\alpha + \mu_f}\right] e^{-(\alpha+\mu_f)t}.$$

This shows that $F(t)$ is bounded from below, i.e.

$$F(t) > \underline{F} \quad \text{where} \quad \underline{F} = \min\left\{F_0, \frac{(\beta\gamma_f + \delta_0 + \mu_m)\underline{C}}{\alpha + \mu_f}\right\}.$$

Using a similar argument we have that $M(t)$ is bounded from below as well:

$$M(t) > \underline{M} \quad \text{where} \quad \underline{M} = \min\left\{M_0, \frac{(\beta\gamma_m + \delta_0 + \mu_f)\underline{C}}{\alpha + \mu_m}\right\}.$$

Finally, integrating the last equation in system (3) we obtain:

$$C(t) = C_0 e^{-\int_0^t [\delta(F,M)+\mu_f+\mu_m]d\tau} + \frac{\int_0^t \mathcal{M}(F,M) e^{\int_0^\tau [\delta(F,M)+\mu_f+\mu_m]d\sigma} d\tau}{e^{\int_0^t [\delta(F,M)+\mu_f+\mu_m]d\tau}} \tag{6}$$

Since

$$\mathcal{M}(F,M) > \mathcal{M}(\underline{F},\underline{M}) \quad \text{and} \quad \delta(F,M) > \delta(\underline{F},\underline{M})$$

we have that

$$\int_0^t [\delta(F,M) + \mu_f + \mu_m]d\tau > \int_0^t [\delta(\underline{F},\underline{M}) + \mu_f + \mu_m]d\tau =$$

$$= [\delta(\underline{F},\underline{M}) + \mu_f + \mu_m]t \to \infty \quad \text{as} \quad t \to \infty.$$

Similarly,

$$\int_0^t \mathcal{M}(F,M) e^{\int_0^\tau [\delta(F,M)+\mu_f+\mu_m]d\sigma} d\tau > \int_0^t \mathcal{M}(\underline{F},\underline{M}) e^{\int_0^\tau [\delta(\underline{F},\underline{M})+\mu_f+\mu_m]d\sigma} d\tau =$$

$$= \frac{\mathcal{M}(\underline{F},\underline{M})}{\delta(\underline{F},\underline{M}) + \mu_f + \mu_m} \left[e^{[\delta(\underline{F},\underline{M})+\mu_f+\mu_m]t} - 1\right] \to \infty \quad \text{as} \quad t \to \infty.$$

We can now prove that $C(t)$ is bounded from above as follows:

$$\lim_{t\to\infty} C_0 e^{-\int_0^t [\delta(F,M)+\mu_f+\mu_m]dt} = 0$$

and for the other term we can use the l'Hôpital's rule as follows:

$$\lim_{t\to\infty} \frac{\int_0^t \mathcal{M}(F,M) e^{\int_0^\tau [\delta(F,M)+\mu_f+\mu_m]d\sigma} d\tau}{e^{\int_0^t [\delta(F,M)+\mu_f+\mu_m]d\tau}} =$$

$$= \lim_{t\to\infty} \frac{\mathcal{M}(F,M) e^{\int_0^t [\delta(F,M)+\mu_f+\mu_m]d\tau}}{e^{\int_0^t [\delta(F,M)+\mu_f+\mu_m]d\tau} [\delta(F,M)+\mu_f+\mu_m]} =$$

$$= \lim_{t\to\infty} \frac{\mathcal{M}(F,M)}{\delta(F,M)+\mu_f+\mu_m} < \lim_{t\to\infty} \frac{\mathcal{M}(F,M)}{\delta(F,M)} < \infty.$$

Denoting by $\bar{C}$ the upper bound of $C(t)$, we return to (4) and, using a similar argument, we have that $x(t)$ and $y(t)$ are also bounded from above, i.e.

$$x(t) \le \max\left\{x_0, \frac{\beta\gamma_f}{\mu_f}\bar{C}\right\}, \quad \text{and} \quad y(t) \le \max\left\{y_0, \frac{\beta\gamma_m}{\mu_m}\bar{C}\right\}.$$

□

In Fig. 4, we provide a numerical example to illustrate this proposition:

The last two conditions stated in Proposition 3.2. can be interpreted biologically in the following way. As in the condition

$$\lim_{t\to\infty} \frac{\mathcal{M}(F,M)}{\delta(F,M)} < \infty$$

time figures implicitly through $F(t)$ and $M(t)$, and limiting values of F and M depend on parameter values, this condition essentially means that the pair formation rate should not be infinitely large and/or the divorce rate infinitely small, conditions that are reasonable both in humans and animals. The other condition,

$$\lim_{C\to\infty} \delta[C(\mathcal{R}_f-1), C(\mathcal{R}_m-1)] > \mathcal{M}(\mathcal{R}_f-1, \mathcal{R}_m-1) - (\mu_f+\mu_m)$$

actually introduces a form of negative density dependence into model (3). Simply put, for high enough densities of singles the rates of processes that cause pair disappearance (divorces plus deaths within couples) exceed the rate at which new couples are being formed. This is akin to the effect of large population densities in the logistic equation, where large population densities cause the mortality rate to eventually exceed the birth rate.

We conclude this section by noting that the harmonic mean function for the pair formation rate and the quadratic function for the divorce rate satisfy these two conditions . Indeed, with

$$\mathcal{M}(F, M) = 2\rho \frac{FM}{F+M}$$

and

$$\delta(F, M) = \delta_0 + b_1 F + b_2 M + c_0 F^2 + c_1 FM + c_2 M^2$$

we have

$$\frac{\mathcal{M}(F, M)}{\delta(F, M)} < \frac{2\rho}{b_1 + b_2} \quad \text{and} \quad \lim_{C \to \infty} \delta[C(\mathcal{R}_f - 1), C(\mathcal{R}_m - 1)] = \infty.$$

4. Hopf Bifurcation and sustained oscillations

In this section, we show that model (3) admits a Hopf bifurcation around the interior equilibrium. In bifurcation theory, a Hopf bifurcation is a local bifurcation around an equilibrium. As a selected bifurcation parameter varies, the equilibrium loses stability when the linearized system exhibits a pair of conjugate eigenvalues crossing the imaginary axis. Under certain general assumptions, a limit cycle emerges from the equilibrium. Textbook examples are given by predator-prey dynamics described by the Rosenzweig-MacArthur model [Rosenzweig and MacArthur, 1969], three or more species competing for the same resource [Gilpin, 1975] and the discrete-time logistic equation [May, 1974, 1976].

We choose the divorce rate without the single-population effect, δ_0, as our bifurcation parameter. In what follows, we are going to perform a bifurcation analysis in the case of equal sex-related vital parameters, i.e. $F(t) = M(t)$ for all time t. This allows us to reduce model (3) to a two-dimensional system. We will also provide a numerical example for the general case $F(t) \neq M(t)$ to illustrate that sustained oscillations are possible in the more realistic situation of sex-dependent vital rates.

Assuming $\mu_f = \mu_m = \mu$, $\gamma_f = \gamma_m = \frac{1}{2}$ and $F(0) = M(0)$, it follows that $F(t) = M(t)$ for all time t and model (3) thus reduces to the following planar system:

$$\begin{cases} F' &= -\mu F + (\frac{\beta}{2} + d(F) + \mu)C - \rho F, \\ \\ C' &= \rho F - [d(F) + 2\mu]C. \end{cases} \tag{7}$$

where $\rho = \mathcal{M}(1,1)$ and we used the fact that $\mathcal{M}(F,F) = F\mathcal{M}(1,1)$. We also denoted $d(F) = \delta(F,F)$.

The Jacobian of (7) is

$$J = \begin{bmatrix} -\mu - \rho + d'(F)C & \frac{\beta}{2} + d(F) + \mu \\ \rho - d'(F)C & -d(F) - 2\mu \end{bmatrix},$$

with

$$Tr(J) = d'(F)C - d(F) - 3\mu - \rho,$$

$$\det J = \mu[d(F) + 2\mu + \rho] - \rho\frac{\beta}{2} + d'(F)C\left(\frac{\beta}{2} - \mu\right).$$

Proposition 4.1. *The extinction equilibrium is stable if*

$$\mathcal{R} = \frac{\rho\left(\frac{\beta}{2\mu} - 1\right)}{\delta_0 + 2\mu} < 1.$$

Proof. Since there is no singularity at the origin, the conclusion follows immediately from evaluating the trace and the determinant of the Jacobian matrix at $(0,0)$:

$$Tr(J) = -\delta_0 - 3\mu - \rho < 0,$$

$$\det J = \mu(\delta_0 + 2\mu + \rho) - \rho\frac{\beta}{2} > 0.$$

where positivity of $\det J$ follows from the condition stated in the proposition. Since the trace and the determinant are the sum and the product of the corresponding eigenvalues, respectively, the eigenvalues must both have negative real part. Consequently, the extinction equilibrium must be locally asymptotically stable.

□

Proposition 4.2. *If* $\mathcal{R} > 1$ *the extinction equilibrium is unstable. In addition, if*

$$\lim_{F\to\infty} d(F) > \rho\left(\frac{\beta}{2\mu} - 1\right) - 2\mu$$

there exists a unique interior equilibrium (F^*, C^*) *which is locally asymptotically stable if*

$$F^* d'(F^*) < \left(\frac{\beta}{2\mu} - 1\right)\left(\frac{\rho\beta}{2\mu} + \mu\right)$$

and unstable otherwise.

Proof. First note that $\mathcal{R} > 1$ implies $\frac{\beta}{2\mu} > 1$ ($\mathcal{R}$ is defined in Proposition 4.1.) as well. Note also that from the second equation of model (7) we have

$$C = \frac{\rho F}{d(F) + 2\mu},$$

while F is the solution of

$$\rho\left(\frac{\beta}{2\mu} - 1\right) = d(F) + 2\mu.$$

Since $\mathcal{R} > 1$ we have that

$$\rho\left(\frac{\beta}{2\mu} - 1\right) > \delta_0 + 2\mu.$$

Combining the fact that $d(F)$ is increasing with the first condition stated in the proposition, the equation for F has a unique positive solution

$$F^* = d^{-1}\left[\rho\left(\frac{\beta}{2\mu} - 1\right) - 2\mu\right],$$

whereby

$$C^* = \frac{F^*}{\frac{\beta}{2\mu} - 1}.$$

Evaluating the Jacobian J at F^* and C^* we obtain the following trace and determinant:

$$Tr(J) = d'(F^*)C^* - \frac{\rho\beta}{2\mu} - \mu,$$

$$\det J = d'(F^*)C^* \left(\frac{\beta}{2} - \mu\right) > 0.$$

Therefore, the interior equilibrium is locally asymptotically stable if $Tr(J) < 0$, that is, if

$$d'(F^*)C^* < \frac{\rho\beta}{2\mu} + \mu,$$

which is equivalent to

$$F^* d'(F^*) < \left(\frac{\beta}{2\mu} - 1\right)\left(\frac{\rho\beta}{2\mu} + \mu\right).$$

□

Since $Tr(J)$ can be zero we have the possibility of a Hopf bifurcation. We choose the divorce rate δ_0 without the single-population effect as a bifurcation parameter. In order to study existence and nature of this bifurcation it is necessary to compute the bifurcation value of δ_0, i.e. the value that satisfies the equation $Tr(J) = 0$ when the pair of conjugate complex eigenvalues cross the imaginary axis. In order to simplify the calculations, we adopt several technical assumptions on the parameters of $d(F)$. Using the general quadratic form for the divorce function,

$$\delta(F, M) = \delta_0 + b_1 F + b_2 M + c_0 F^2 + c_1 F M + c_2 M^2,$$

we have that

$$d(F) = \delta(F, F) = \delta_0 + (b_1 + b_2)F + (c_0 + c_1 + c_2)F^2.$$

Since solving for the bifurcation value of δ_0 requires solving a quadratic equation, it is much easier to use a function $d(F)$ that is a square of a linear function. To this end, denoting $a = c_0 + c_1 + c_2$, we impose the condition

$$b_1 + b_2 = 2\sqrt{a\delta_0}.$$

This makes $d(F)$ the square of a linear function,

$$d(F) = \left(\sqrt{a}F + \sqrt{\delta_0}\right)^2.$$

While this additional constraint is somewhat artificial, it should not affect our conclusions since the single-population effect on the divorce rate is presumably very small and all the coefficients of $d(F)$ (except δ_0) are hence presumably very small as well. Actually, it is quite reasonable to assume small values for these coefficients since, otherwise, the effect of singles on the divorce rate could be overestimated, especially for small densities of singles.

The following proposition shows that under certain conditions, a supercritical Hopf bifurcation occurs. This means that, as the bifurcation parameter δ_0 increases past its bifurcation value, the interior equilibrium loses its stability and a unique stable limit cycle emerges.

PROPOSITION 4.3. *The 'one-sex' system (7) admits a supercritical Hopf bifurcation and sustained oscillations.*

PROOF. Denoting $\mathcal{A} = \frac{\beta}{2\mu}$, a Hopf bifurcation will occur if $Tr(J) = 0$ when the pair of complex eigenvalues cross the imaginary axis, i.e.

$$F^* d'(F^*) = (\mathcal{A} - 1)(\rho\mathcal{A} + \mu),$$

where

$$F^* = d^{-1}[\rho(\mathcal{A} - 1) - 2\mu].$$

Using our choice for $d(F)$, these two equations become

$$2\sqrt{a}F^*(\sqrt{a}F^* + \sqrt{\delta_0}) = (\mathcal{A} - 1)(\rho\mathcal{A} + \mu)$$

and

$$F^* = \sqrt{\frac{1}{a}[\rho(\mathcal{A} - 1) - 2\mu]} - \sqrt{\frac{\delta_0}{a}}.$$

Substituting F^* in the first equation we obtain the bifurcation value δ_0^H for δ_0:

$$\sqrt{\delta_0^H} = \frac{\frac{\rho}{2}(\mathcal{A} - 1)(2 - \mathcal{A}) - \frac{\mu}{2}(\mathcal{A} + 1) - \mu}{\sqrt{\rho(\mathcal{A} - 1) - 2\mu}}.$$

As $\mathcal{A} > 1$ for the interior equilibrium to exist, a straightforward calculation shows that

$$\frac{d}{d\delta_0}(Tr(J)) = -\frac{1}{\mathcal{A} - 1}\left(\frac{2aF^*}{\sqrt{a\delta_0}} + 1\right) < 0,$$

which means that δ_0^H must be positive for a Hopf bifurcation to occur. To ensure that δ_0^H is positive the following condition must be satisfied:

$$\frac{\mu}{\rho} < \frac{(\mathcal{A} - 1)(2 - \mathcal{A})}{\mathcal{A} + 3}. \tag{8}$$

This means that the net reproductive number $\mathcal{A}$ needs to satisfy

$$1 < \mathcal{A} < 2;$$

this is a necessary condition for a positive bifurcation value and hence for a possibility of sustained oscillations in population densities to occur. Furthermore, condition (8) represents a lower bound on ρ and an upper bound on μ, together with the existence condition on the interior equilibrium, i.e.

$$\mathcal{R} = \frac{\rho\,(\mathcal{A}-1)}{\delta_0 + 2\mu} > 1.$$

To see whether the Hopf bifurcation is subcritical or supercritical, we calculate the first Lyapunov coefficient corresponding to this bifurcation using a formula found in various books such as [Perko, 2001]. First, we introduce the following parameter:

$$\epsilon_0 = \delta_0^H - \delta_0$$

and replace δ_0 by $\delta_0^H - \epsilon_0$. Now, the bifurcation parameter is ϵ_0 and its bifurcation value is $\epsilon_0^H = 0$. The equilibrium values for $\epsilon_0 = 0$ are

$$F_0^* = \frac{1}{2\sqrt{a}}\left[\frac{(\mathcal{A}-1)\,(\rho\mathcal{A}+\mu)}{\sqrt{\rho\,(\mathcal{A}-1)-2\mu}}\right]$$

and

$$C_0^* = \frac{1}{2\sqrt{a}}\left[\frac{\rho\mathcal{A}+\mu}{\sqrt{\rho\,(\mathcal{A}-1)-2\mu}}\right].$$

We now perform the following coordinate change to place the equilibrium to the origin:

$$F = x + F_0^* \quad \text{and} \quad C = y + C_0^*.$$

The new system is

$$\begin{cases} x' &= -(\mu+\rho)(x+F_0^*) + \left\{\frac{\beta}{2} + [\sqrt{a}(x+F_0^*) + \sqrt{\delta_0^H}]^2 + \mu\right\}(y+C_0^*), \\ y' &= \rho(x+F_0^*) - \left\{[\sqrt{a}(x+F_0^*) + \sqrt{\delta_0^H}]^2 + 2\mu\right\}(y+C_0^*). \end{cases} \tag{9}$$

After several rearrangements of the terms we obtain the following form for (9):

$$\begin{cases} x' &= mx + ny + f(x, y), \\ \\ y' &= px + qy + g(x, y), \end{cases} \tag{10}$$

with

$$A = \begin{bmatrix} m & n \\ p & q \end{bmatrix} = \begin{bmatrix} \rho\,(\mathcal{A}-1) & (\mathcal{A}-1)\,(\mu+\rho) \\ -\rho\,(\mathcal{A}-1)-\mu & -\rho\,(\mathcal{A}-1) \end{bmatrix}$$

and

$$f(x, y) = (a_{20}x^2 + a_{11}xy + a_{02}y^2) + (a_{30}x^3 + a_{21}x^2y + a_{12}xy^2 + a_{03}y^3),$$

$$g(x, y) = (b_{20}x^2 + b_{11}xy + b_{02}y^2) + (b_{30}x^3 + b_{21}x^2y + b_{12}xy^2 + b_{03}y^3),$$

where

$$a_{20} = aC_0^*, \quad a_{11} = 2\sqrt{a}(\sqrt{a}F_0^* + \sqrt{\delta_0^H}), \quad a_{02} = 0,$$

$$a_{30} = 0, \quad a_{21} = a, \quad a_{12} = 0, \quad a_{03} = 0,$$

$$b_{20} = -aC_0^*, \quad b_{11} = -2\sqrt{a}(\sqrt{a}F_0^* + \sqrt{\delta_0^H}), \quad b_{02} = 0,$$

$$b_{30} = 0, \quad b_{21} = -a, \quad b_{12} = 0, \quad b_{03} = 0.$$

Note that, as expected, $m + q = 0$ and

$$\Delta = mq - np = \mu\,(\mathcal{A}-1)\,(\rho\mathcal{A}+\mu) > 0.$$

Following [Perko, 2001], the first Lyapunov coefficient τ is given by the following formula

$$\tau = \frac{-3\pi}{2n\Delta^{3/2}} \left\{ \left[mp\left(a_{11}^2 + a_{11}b_{02} + a_{02}b_{11}\right) + mn\left(b_{11}^2 + a_{20}b_{11} + a_{11}b_{02}\right) + \right.\right.$$

$$+ p^2\,(a_{11}a_{02} + 2a_{02}b_{02}) - 2mp\left(b_{02}^2 - a_{20}a_{02}\right) - 2mn\left(a_{20}^2 - b_{20}b_{02}\right) -$$

$$\left. - n^2\,(2a_{20}b_{20} + b_{11}b_{20}) + \left(np - 2m^2\right)(b_{11}b_{02} - a_{11}a_{20}) \right] -$$

$$\left. - \left(m^2 + np\right)\left[3\,(pb_{03} - na_{30}) + 2m\,(a_{21} + b_{12}) + (pa_{12} - nb_{21})\right] \right\}.$$

Although this expression is difficult to simplify, we are interested only in its sign. To this end, we use a suitable substitution which will not shorten the expression but will allow us to establish the sign of τ. First, we introduce the following notation:

$$k = \sqrt{\rho(\mathcal{A} - 1) - 2\mu}$$

and substitute

$$\mathcal{A} = \frac{k^2 + 2\mu}{\rho} + 1.$$

Then, the first Lyapunov coefficient is

$$\tau = \frac{-3\pi}{2n\Delta^{3/2}} \frac{a}{2k^2\rho^2}(k^2 + 2\mu)T,$$

where

$$T = (\mu^2 + 2\rho^2 + 11\rho\mu)k^6 + (8\mu^3 + 38\rho\mu^2 + 2\rho^3 + 8\rho^2\mu)k^4 +$$

$$+(49\rho\mu^3 + 7\rho^3\mu + 21\mu^4 + 35\rho^2\mu^2)k^2 + 14\rho^2\mu^3 + 2\rho^3\mu^2 + 30\rho\mu^4 + 18\mu^5$$

which is clearly positive. Hence, $\tau < 0$ and a unique stable limit cycle bifurcates from the origin of (9) as ϵ_0 increases from 0, or, equivalently, as δ_0 decreases from δ_0^H. This means the Hopf bifurcation is supercritical.

□

Figure 5 illustrates Proposition 4.3. using $d(F) = (0.02F + \sqrt{\delta_0})^2$.

However, numerical simulations show that the possibility of sustained oscillations goes beyond the assumption of sex-independent vital rates. In Fig. 6 we provide a numerical example to indicate that sustained oscillations are possible also in the general case of sex-dependent vital rates. The parameter values are selected for illustration purposes only and do not reflect real data.

For plotting Fig. 6, we chose the following divorce rate (similar to the one used in the bifurcation analysis earlier in this section):

$$\delta(F, M) = [b(F + M) + \sqrt{\delta_0}]^2,$$

with $b = 0.01$. Note that the coefficient b that indicates the single-population effect in the divorce rate does not affect the bifurcation value δ_0^H. Its only effect is on the actual values of the interior equilibrium. This means that the possibility of sustained oscillations is independent on the magnitude of the single-population effect. Furthermore, we exaggerated the difference between

γ_f and γ_m and also between μ_f and μ_m for the sole purpose of showing a clearer picture (in humans as well as many animal populations the sex ratio at birth is close to 0.5 and $\mu_f < \mu_m$ but with a smaller difference than the one chosen above). The mortality rates and the birth rate we used to create Figs 5 and 6 are close to the values obtained from U.S. 2000 Census data. In that year, $\beta = 0.07338$, $\mu_f = 0.01258$, and $\mu_m = 0.01350$.

REMARK 4.1. *One of the original motivations in assuming that the divorce rate depends increasingly on the population of singles was to capture the competitive aspect in the pair formation process. It is interesting to note that system (7) considered in this section resembles predator-prey dynamics where the single population F acts as a predator and the couples C as a prey, with the important distinction that the "predator" has a direct positive contribution to the "prey" through the pair formation process. This, of course, does not happen in the classical Lotka-Volterra model. On the other hand, if the divorce rate is a function of the total population density then in the "prey" equation (equation for C) the expression in the square brackets increases with C for any fixed female density F. In the predator-prey parallel we propose here this can be viewed as an analogy with the logistic growth of prey, the mechanism which is known to have a strong stabilizing effect on predator-prey dynamics. Indeed, for the divorce rate dependent on the total population density, a unique positive equilibrium of a model equivalent to ours (such as that of [Castillo-Chavez and Huang, 1995] in which the birth rate would be kept constant) would always be locally asymptotically stable; see also Conclusions.*

REMARK 4.2. *With the divorce function used in Proposition* 4.3., *the stability condition of the interior equilibrium established in Proposition* 3.2., *i.e.*

$$F^* d'(F^*) < \left(\frac{\beta}{2\mu} - 1\right)\left(\frac{\rho\beta}{2\mu} + \mu\right),$$

can be written as

$$\sqrt{\delta_0} > \frac{\frac{\rho}{2}(\mathcal{A}-1)(2-\mathcal{A}) - \frac{\mu}{2}(\mathcal{A}+1) - \mu}{\sqrt{\rho(\mathcal{A}-1) - 2\mu}}.$$

Recall that in order to have a positive bifurcation value for δ_0 it was necessary that $1 < \mathcal{A} < 2$. On the other hand, if

$$\mathcal{A} > 2$$

we see from stability condition (8) that the interior equilibrium is always stable for any positive value of δ_0 *since the right-hand side in this condition is negative. This means that to maintain dynamics in the model with sustained oscillations the net reproductive number should not be too large. One possible explanation, related to the previous remark, is given by the singles' dual role of both "predators" through their influence on the divorce rate and of "prey" through pair formation. If the net reproductive number is relatively large there will always be enough pairs formed whose positive contribution to the couples overcomes the single-population effect on the divorces that will otherwise cause the oscillations.*

Remark 4.3. *One explanation for the 'better option hypothesis', described in Introduction and [Choudhury, 1995], is given by the possibility that a low reproductive fitness may compel the bird to look more actively for better options, i.e. single birds. This suggests that* $\mathtt{a}$, *the parameter in* $d(F)$ *which captures the single-population effect, may be negatively correlated with the net reproductive number* $\mathcal{A}$. *If this is the case then the equilibrium value*

$$F^* = \frac{1}{\sqrt{a}}\left[\sqrt{\rho(\mathcal{A}-1)-2\mu} - \sqrt{\delta_0}\right]$$

is positively correlated with $\mathcal{A}$. *This means that a negative correlation between the single-population effect and the reproductive fitness is in agreement with the expected outcome that larger populations should occur for larger values of* $\mathcal{A}$.

5. Conclusions

In this paper, we modified the classical exponential two-sex model [Kendall, 1949, Keyfitz, 1949, Hadeler et al., 1988] by assuming that the larger the amount of singles in the population the higher is the divorce rate of established couples. Although conceptual arguments supporting this assumption are convincing – coupled individuals are prone to separation the more often the higher are the chances of meeting and uniting with a more attractive mate (the better option hypothesis) [Choudhury, 1995, South and Lloyd, 1995], which in turn is more likely to occur the larger is the amount of singles in the population, empirical data remain rare (though they already span both humans and animals) [South and Lloyd, 1995, Catry et al., 1997]. That is also why we avoid as much as possible to claim any specific formulation for the divorce function. A specific form of this function was only used in the final section in order to push the model analysis forward a bit more.

With the single-population effect on the divorce rate, and under several conditions on the vital parameters, we showed in this paper that the exponential behavior of the classical two-sex model is altered as follows: the total population density is bounded and a unique positive equilibrium exists. In addition, using the divorce rate in the absence of singles as a bifurcation parameter, we proved that in the case of equal sex-related vital parameters the model exhibited a supercritical Hopf bifurcation and hence sustained oscillations are possible. More generally, we showed via numerical simulations that even when the vital parameters differ with sex, the model solutions may still attain a limit cycle.

Divorce appears to be one of the least studied demographic processes, both empirically and in two-sex demographic models. In models, the divorce rate is either assumed constant [Hadeler et al., 1988, Berec and Boukal, 2004, Maxin and Milner, 2009] or a non-decreasing function of the total population density [Castillo-Chavez and Huang, 1995]. In the latter case, all the other model parameters assumed constant, the divorce rate itself is a source of negative density dependence and makes the respective two-sex model a two-sex version of the logistic equation provided that $\delta(0) < \delta^*$ and $\lim_{T\to\infty} \delta(T) > \delta^*$, where $T = M + F + 2C$ is the total population density and δ^* is the threshold divorce rate from the exponential two-sex model of [Hadeler et al., 1988] below which a positive solution exists and above which population extinction is the globally stable solution. A parallel argument applies also here, as precisely formulated in Proposition 3.2. This implies that although the divorce rate is in both cases a source of negative density dependence, its effect on population dynamics may differ. Specifically, whereas the divorce rate as a function of the total population density causes the population to always attain a globally stable positive equilibrium [Castillo-Chavez and Huang, 1995], the divorce rate as a function of the amount of singles also allows the population to oscillate around an unstable positive equilibrium (this work).

Given that determinants of divorce in humans and birds, not to speak of other taxa, are still relatively poorly known, the distinction in model outcomes could serve as a working hypothesis on what marriage market characteristic eventually drives the divorce rate – is it the total population density or the amount of singles in the population? A way to discern between these two hypotheses could be to analyze population dynamics of monogamous birds in an environment free of predators and with an abundance of food, i.e. an environment where effects of negative density dependence in births and deaths are negligible and where density-independent divorce rate would imply exponential population growth [Hadeler et al., 1988]. If the population is bounded we could argue that divorces may have a role in this boundedness. In addition, if the population is found to oscillate in density then the amount of singles in the population rather than the total population density might be a competent driver of divorces. In this way, results of our model are relevant in pattern-oriented modeling – they could supply a bulk of testable hypotheses on what induces the divorce rate in humans and animals if oscillatory patterns of population trajectories were observed. We note that a logistic two-sex model can also be obtained by considering non-linear birth rate [Castillo-Chavez and Huang, 1995, Berec and Boukal, 2004] or non-linear mortality rates [Maxin and Milner, 2009].

The two 'competing hypotheses' of the divorce rate can also be looked at from a different perspective. As a matter of fact, [Castillo-Chavez and Huang, 1995] did not provide any explanation – behavioral, social, economical, psychological, evolutionary or whatever – for the total population density dependence of the divorce rate. They just employed a statistical observation that in large urban areas the divorce rate is higher. From this perspective, the total population density dependence hypothesis can be considered a proximate causation of divorce rate. On the contrary, the better option hypothesis can be thought of as an ultimate causation of divorce rate, causing higher divorce rates in densely populated areas and thus responsible for statistical observations employed by [Castillo-Chavez and Huang, 1995].

There are several potential avenues for future research. First, related to the above discussion of the total-population vs. single-population effects on the divorce rate, the challenging issue is to try and quantify the effect on the divorce rate of divorce drivers in general and of the amount of singles in the population in particular. This is by no means an easy task and is akin to the long-standing efforts to quantify the marriage or pair formation rate as a function of the amount of single males and single females in the population. For the latter, at least some qualitative features have been formulated and perhaps an analogous and broadly accepted list could be composed for the divorce rate as well (see the Model Formulation section of this paper). Second, the model we analyzed in this paper can be modified in a number of ways, to investigate impacts of a variety of other mechanisms known to affect population demography. For example, one might be interested in the effects of negative density dependence in birth and/or death rates [Castillo-Chavez and Huang, 1995, Maxin and Milner, 2009], Allee effects [Berec and Boukal, 2004, Courchamp et al., 2008], or a strong positive correlation between the divorce rate and the mortality rate observed in monogamous birds [Jeschke and Kokko, 2008]. In every case, modeling as well as empirical investigation of divorce rates will certainly remain one of the key topics in population demography.

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Berec, L., Boukal, D.S., 2004. Implications of mate search, mate choice and divorce rate for population dynamics of sexually reproducing species. Oikos 104, 122–132.

Castillo-Chavez, C., Huang, W., 1995. The logistic equation revisited: the two-sex case. Math. Biosc. 128, 299–316.

Caswell, H., Weeks, D.E., 1986. Two-sex models: chaos, extinction, and other dynamic consequences of sex. Amer. Natur. 128, 707–735.

Catry, P., Ratcliffe, N., Furness, R.W., 1997. Partnerships and mechanisms of divorce in the great skua. Anim. Behav. 54, 1475–1482.

Choudhury, S., 1995. Divorce in birds: a review of the hypotheses. Anim. Behav. 50, 413–429.

Courchamp, F., Berec, L., Gascoigne, J., 2008. Allee effects in ecology and conservation. Oxford University Press.

Gilpin, M.E., 1975. Limit cycles in competition communities. Amer. Natur. 109, 51–60.

Hadeler, K.P., Waldstätter, R., Wörz-Busekros, A., 1988. Models for pair formation in bisexual populations. J. Math. Biol. 26, 635–649.

Ianelli, M., Martcheva, M., Milner, F.A., 2005. Gender-structured population modeling: mathematical methods, numerics, and simulations. SIAM.

Jeschke, J.M., Kokko, H., 2008. Mortality and other determinants of bird divorce rate. Behav. Ecol. Sociobiol. 63, 1–9.

Kendall, D.G., 1949. Stochastic processes and population growth. J. Roy. Stat. Soc. Ser. B 11, 230–264.

Keyfitz, N., 1949. The mathematics of sex and marriage. Proceedings of the Sixth Berkeley Symposium on Mathematical Statistics and Probability, Vol. IV: Biology and Health, 89–108.

Maxin, D., Milner, F.A., 2009. The role of sexually abstained groups in two-sex demographic and epidemic logistic models with non-linear mortality. J. Theor. Biol. 258, 389–402.

May, R.M., 1974. Biological populations with nonoverlapping generations: stable points, stable cycles, and chaos. Science 186, 645–647.

May, R.M., 1976. Simple mathematical models with very complicated dynamics. Nature 261, 459–467.

Milner, F.A., Yang, K., 2009. The logistic, two-sex, age-structured population model. J. Biol. Dynamics 3, 252–270.

Perko, L., 2001. Differential Equations and Dynamical Systems. Springer-Verlag, New York.

Pollard, J., 1997. Modeling the interaction between the sexes. Math. Comput. Modeling 26, 11–24.

Rosenzweig, M.P., MacArthur, R.H., 1969. Graphic representation and stability conditions of predator-prey interaction. Amer. Natur. 97, 209–223.

South, S.J., Lloyd, K.M., 1995. Spousal alternatives and marital dissolution. Am. Sociol. Rev. 60, 21–35.

Wolcott, I., Hughes, J., 1999. Towards understanding the reasons for divorce. Australian Institute of Family Studies, Working Paper 20. Available online at `http://www.aifs.gov.au/institute/pubs/WP20.html`.

Figure legends:

Figure 1: Trajectories of model (3) showing the global stability of the extinction equilibrium in the case $\mathcal{R}_f < 1$. Parameter values: $\beta = 0.05$, $\mu_f = 0.022$, $\mu_m = 0.02$, $\gamma_f = 0.35$, $\gamma_m = 0.65$, $\rho = 0.36$, $\delta_0 = 0.0004$, $b = 0.01$, hence $\mathcal{R}_f = 0.8$ and $\mathcal{R}_m = 1.63$.

Figure 2: Trajectories of model (3) showing the global stability of the extinction equilibrium in the case $\mathcal{R}_m < 1$. Parameter values: $\beta = 0.05$, $\mu_f = 0.012$, $\mu_m = 0.04$, $\gamma_f = 0.35$, $\gamma_m = 0.65$, $\rho = 0.36$, $\delta_0 = 0.0004$, $b = 0.01$, hence $\mathcal{R}_f = 1.46$ and $\mathcal{R}_m = 0.81$.

Figure 3: Trajectories of model (3) showing the global stability of the extinction equilibrium in the case $\mathcal{M}(\mathcal{R}_f - 1, \mathcal{R}_m - 1) < \delta_0 + \mu_f + \mu_m$. Parameter values: $\beta = 0.05$, $\mu_f = 0.012$, $\mu_m = 0.02$, $\gamma_f = 0.35$, $\gamma_m = 0.65$, $\rho = 0.12$, $\delta_0 = 0.08$, $b = 0.01$, hence $\mathcal{R}_f = 1.46$, $\mathcal{R}_m = 1.62$, and $\mathcal{M}(\mathcal{R}_f - 1, \mathcal{R}_m - 1) - (\delta_0 + \mu_f + \mu_m) = -0.049$.

Figure 4: Trajectories of model (3) showing the existence of a unique (and this time also stable) interior equilibrium in the case $\mathcal{R}_f > 1$, $\mathcal{R}_m > 1$ and $\mathcal{M}(\mathcal{R}_f - 1, \mathcal{R}_m - 1) > \delta_0 + \mu_f + \mu_m$. Parameter values: $\beta = 0.05$, $\mu_f = 0.012$, $\mu_m = 0.02$, $\gamma_f = 0.35$, $\gamma_m = 0.65$, $\rho = 0.36$, $\delta_0 = 0.004$, $b = 0.004$.

Figure 5: Trajectories of model (7) showing the stable limit cycle in the $F - C$ plane in the case of sex-independent vital rates. Parameter values: $\beta = 0.05$, $\mu = 0.017$, $\rho = 0.36$, $\delta_0 = 0.0002$, hence $\mathcal{A} = 1.47$.

Figure 6: Trajectories of model (3) showing densities of single females, single males and couples in a case of sex-dependent vital rates. These trajectories approach a limit cycle and thus demonstrate sustained oscillations. Parameter values: $\beta = 0.05$, $\mu_f = 0.012$, $\mu_m = 0.02$, $\gamma_f = 0.35$, $\gamma_m = 0.65$, $\rho = 0.46$, $\delta_0 = 0.0004$, $b = 0.01$.

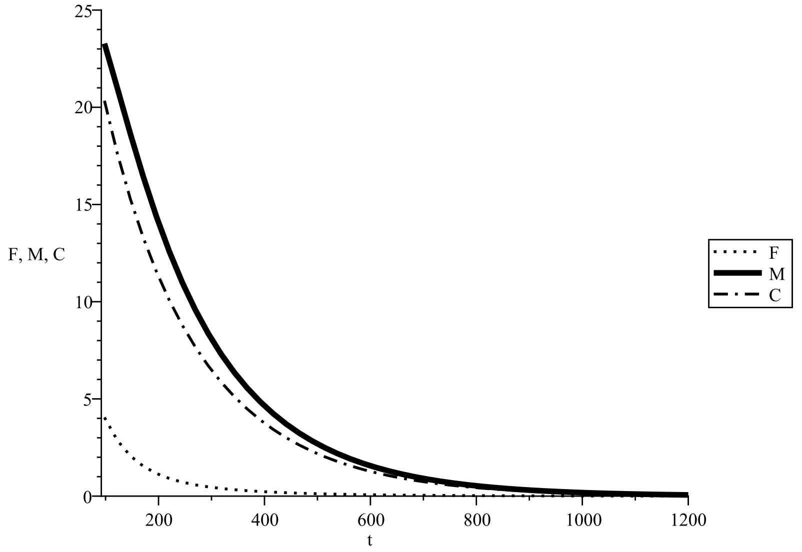

Figure 1:

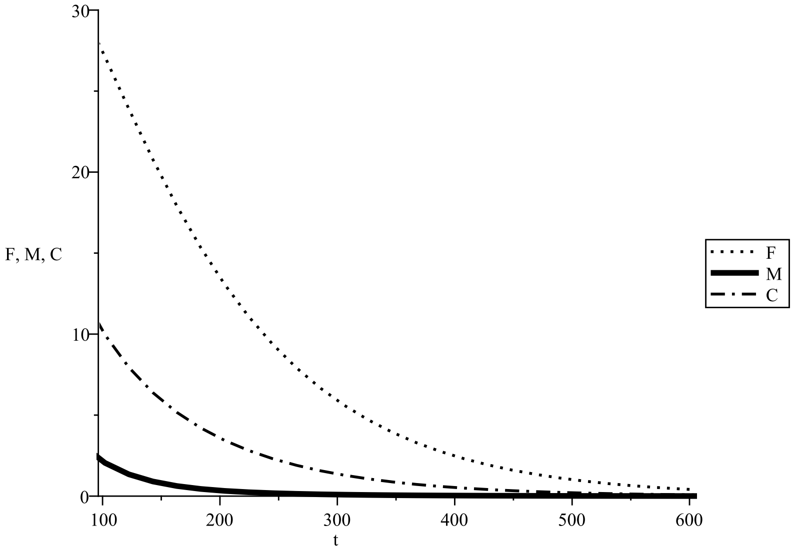

Figure 2:

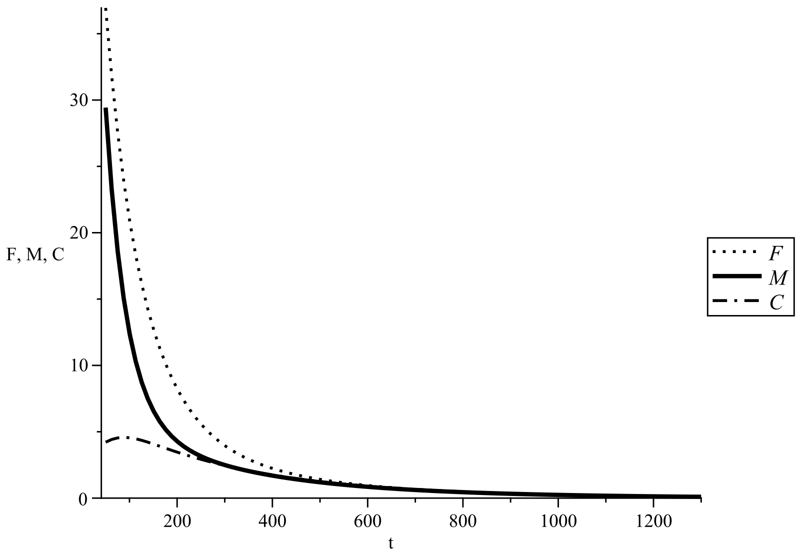

Figure 3:

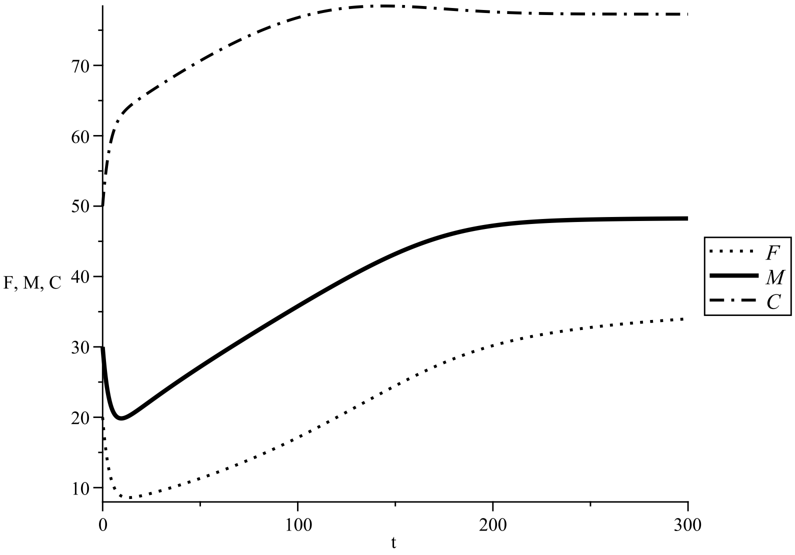

Figure 4:

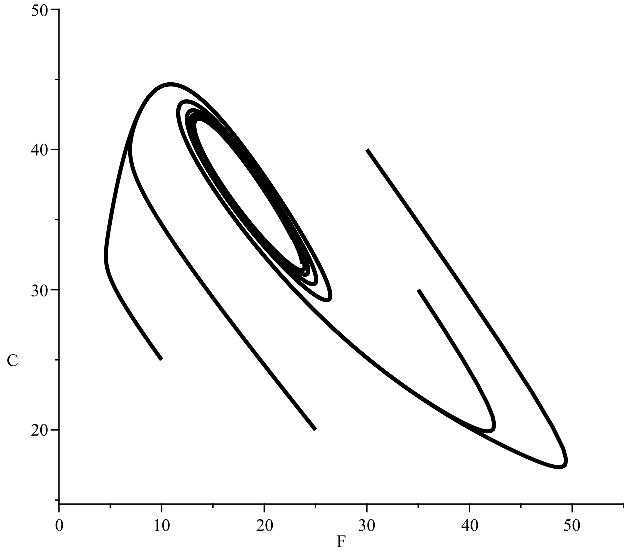

Figure 5:

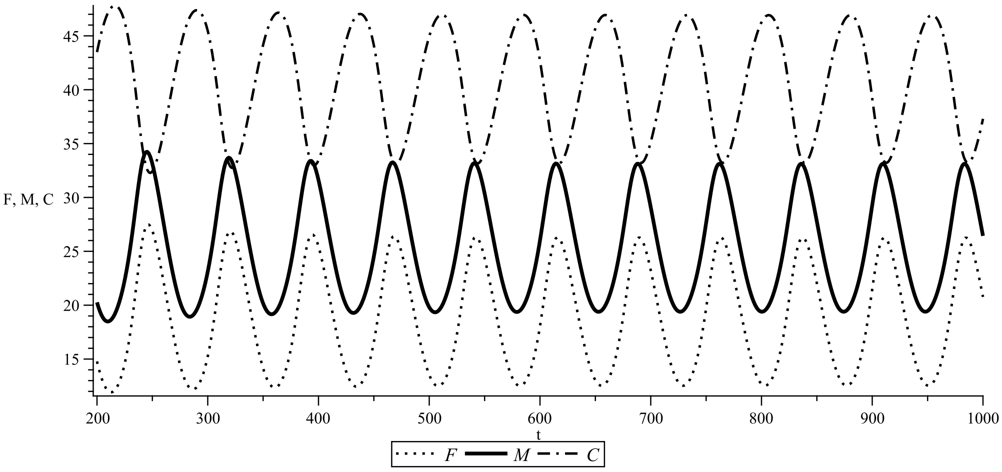

Figure 6: