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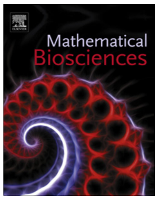

A nonsmooth two-sex population model

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ABSTRACT

This paper considers a two-dimensional logistic model to study populations with two genders. The growth behavior of a population is guided by two coupled ordinary differential equations given by a non-differentiable vector field whose parameters are the secondary sex ratio (the ratio of males to females at time of birth), inter-, intra- and outer-gender competitions, fertility and mortality rates and a mating function. For the case where there is no inter-gender competition and the mortality rates are negligible with respect to the density-dependent mortality, using geometrical techniques, we analyze the singularities and the basin of attraction of the system, determining the relationships between the parameters for which the system presents an equilibrium point. In particular, we describe conditions on the secondary sex ratio and discuss the role of the average number of female sexual partners of each male for the conservation of a two-sex species.

1. Introduction

When studying biological populations in nature, it is usual to recognize an unvarying proportion of the genders in a stable environment. Such a prevalent observation has been a remarkable motivation for fundamental contributions in the theory of sex-structured populations. Fisher's comprehension [3] of the commonness of nearly 1:1 sex ratios, Hamilton's explanation [10] for the existence of biased sex ratios, Trivers–Willard hypothesis [18] on the parental capability to adjust the sex ratio of offsprings as a response to environmental changes and Charnov mathematical proposal [1] for sex allocations are some relevant examples of this kind of legacy.

In a previous work [6], we have developed a dynamic-programming model in order to discuss whether the identification of a stable sex ratio in nature might mirror a population maintenance cost under finite resources. Here we propose another dynamical approach to study sex-structured populations which consists in modeling the time evolution of two-sex populations with differential equations. Under this point of view, the interactions of the individuals are represented as a mean tendency of the whole population. Furthermore, instead of looking for a sex ratio that would maximize the efficiency of individuals in the use of available resources, in the population-dynamics formulation, secondary sex ratio is actually one of the parameters of the system. In such a case, the aim is thus, for suitable mating functions, to describe and classify the behavior of the population for distinct progeny sex ratios and distinct mortality sex ratios [4,7,12,16,17,19,20]. For instance, it has been argued in [16,20] that the marriage rate plays an important role in the stability of the population, since polygamy would amplify the sensitivity of the system to the variation of the other parameters. In another direction, a model with stable solutions for monogamous and polygamous populations was presented in [17].

In this paper, we propose a nonsmooth two-sex logistic model (which may be seen as an extension of previous formulations) and we use the qualitative-geometric theory of ordinary differential equations to study it. Considering sex-ratio dependent competition terms, we obtain sufficient and necessary conditions for the persistence of the population. In particular, we show that the dynamical behavior of the population is governed by a highly nonlinear relationship between the secondary sex ratio and the competition parameters, and that the average number of male's reproductive partners is an important parameter that may allow a two-sex species to find a stable equilibrium.

The paper is organized as follows. In Section 2, we recall some classical models for two-sex populations and we define the model that will be studied. In Section 3, we detail its singularities by analyzing two vector fields defined on the plane and naturally associated with the original one. In Section 4, we study the relationships between secondary and tertiary sex ratios and the competition parameters of the model. In Section 5, we describe the local and global behavior of the two associated vector fields. In particular, we point out conditions on the secondary sex ratio that assure

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the existence of asymptotically stable singularities and the nonexistence of cycles. Hence, we discuss the local and global dynamics for the original vector field. In Section 6, we outline open questions about the dynamics of the model and some possible extensions.

2. The model

We consider here a two-sex logistic model which follows the basic lines of the classical logistic model: the population growth is given by the balance between the birth rate (which depends on the quantity of individuals in the population) and the death rate (which depends on square of the quantity of individuals, representing the interactions between them).

Non-logistic models for two-sex populations have been proposed at least since the 1940's (for a review see [9]). For instance, Kendall [13, p. 247], proposed two non-logistic models. The first one consists in a model for the behavior of male and female populations described by the following coupled ODE's:

$$\begin{aligned} \dot{x} &= b_x F(x,y) - m_x x, \\ \dot{y} &= b_y F(x,y) - m_y y, \end{aligned} \tag{1}$$

where x and y denote the quantity of females and males at time t, respectively, m_x and m_y denote the mortality rates of females and males, b_x and b_y are independent parameters for the birth rate of each gender, and F is the mating function (which was supposed to be nonnegative and symmetric in x and y) and represents the contribution of males and females to the birth rate. In his work, Kendall studied the case where $m_x = m_y,\ b_x = b_y = 1/2$ and F has one of the following forms:

$$xy,\ (xy)^{1/2},\ x+y \quad \text{or} \quad \min\{x,y\}.$$

The second model proposed by Kendall addresses the problem of pair formation in two-sex populations. In such a model, three coupled ODE's take into account the numbers of unmarried males, unmarried females and married couples. Once again, a central role is played by the mating function.

Following Kendall's work, Goodman [7] studied the cases where $m_x \neq m_y$ and $b_x \neq b_y$ for several mating functions, including the above ones as well as $F(x,y) = x$ and $F(x,y) = y$. In [4], Fredrickson assumed two hypotheses on the mating function F: *heterosexuality* (that is, $F(0,y) = F(x,0) = 0$) and *homogeneity* (in the sense that $F(kx,ky) = kF(x,y)$). Using these hypotheses, he found a general form for differentiable mating functions and deduced that they are *consistent*: if there is a preponderance of some gender in the population, then the birth rate will be limited by the number of individuals of the other gender. Another natural hypothesis on F is *monotonicity* [19], namely, if $\bar{x} \geqslant x$ and $\bar{y} \geqslant y$, then $F(\bar{x},\bar{y}) \geqslant F(x,y)$.

Logistic models for two-sex populations have been considered by the academic community [2,17,19]. The model in [2] incorporates nonlinear birth and separation processes in Kendall's pair-formation model, while the model studied in [19] is an age-dependent two-sex model with density dependence in the birth and death rates. On the other hand, Rosen [17, Section 4], studied a model which admits in (1) terms for competition:

$$\begin{aligned} \dot{x} &= b_x F(x,y) - (m_x x + X_x x^2 + X_{xy} xy), \\ \dot{y} &= b_y F(x,y) - (m_y y + Y_y y^2 + Y_{xy} xy), \end{aligned} \tag{2}$$

where X_x and Y_y describe the effects of intrasexual competition of females and males, respectively, and X_{xy} and Y_{xy} characterize the intersexual competition of males on females and females on males, respectively. Furthermore, [17] considered the mating function given by

$$F(x,y) = \min\{x, ry\}, \tag{3}$$

where r is the average number of female sexual partners that each male has along each reproductive cycle ($r < 1$ may be interpreted as polyandrous population, $r = 1$ is understood as a monogamous population, and $r > 1$ may be seen as a polygynous population).

We recall that models like (1) and (2) do not inspect in an explicit way certain internal mechanisms of the populations, like pair formation or age structure. In fact, such mechanisms are captured by the parameters of the models. Consider, for example, a population of a total of m males and f females of which $\tilde{m}$ males are sexually active and $\tilde{f}$ females are receptive and each one of them has fertility rate $\tilde{s}$. Suppose further that each sexually active male successfully breeds with $\tilde{r}$ females. In such a case, these models will interpret that all the males successfully breeds with $r = (\tilde{m}\tilde{r})/m$ females and all the females are receptive (each one of them with fertility rate s), so the net number of individuals being born and the magnitude of competitions will be virtually the same and the models will reveal the behavior of the population growth. Notice that competition for mating is not focused by these models, since it is part of the pair formation mechanism and in general it does not affect the mortality rate. Besides, since the parameters $r$and $s$absorb the age structure and pair formation, the sex-ratio type considered in the models is the tertiary sex ratio (the number of adult males divided by the number of adult females – also named adult sex ratio), which, when adopting such a point of view, is indistinguishable from the operational sex ratio (the number of sexually active males divided by the number of receptive females).

Note that competition terms of the form xy in the above equations may not capture some aspects of the relationship between the genders. In fact, although for predator–prey models it is reasonable to suppose that a great number of predators or prey will increase the probability of interactions between the species and then the population growth of both species will be affected by the quantity xy, this interpretation does not necessarily hold for two-sex populations, in which one of the genders is not a vital resource but in general both genders coexist and have common resources. The causes and consequences of adult sex ratio and operational sex ratio have been extensively investigated by biologists. There are pieces of evidence that the sex ratio has an impact on fitness prospects of males and females and on optimal sex allocation decisions [15]. It was noticed that a male-biased sex ratio could amplify male–male competition with negative impact on female survival and fecundity (see, for instance, [5,8]). The excess of males against females has also been pointed out as a likely negative factor for females in the human case [11]. In other words, when y is much greater than x, even if xy is small, one may detect a negative impact on the $x$population.

These facts lead us to incorporate in Eq. (2) a mortality term for each gender which takes into account the ratio between the genders on the intersexual competitions. More precisely, we remark that the mortality rates are usually expressed *per capita*, which means that they are of the form $M(x,y)x$ for the female population and $N(x,y)y$ for the male population, where $M$and N are given functions. For example, in (1) we realize that $M$and N are identically constant functions, while in (2) we have $M(x,y) = m_x + X_x x + X_{xy} y$ and $N(x,y) = m_y + Y_y y + Y_{xy} x$. The phenomena reported in the previous paragraph suggest that this modeling should be reevaluated in situations far from gender equilibrium, namely, when $x$and $y$are not near each other. Actually, those biological observations propose for consideration an extension of (2) with additional terms that reflect the stress on a population of a certain gender due to a population bias for the other gender. This particular kind of impact on the morality rates may be integrated into the model by supposing that intersexual competitions have components that dependent on the sex ratio. Formally, the function M is supposed to