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Mathematical Models of Two-Sex Population Dynamics*

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Abstract: We propose a predator-prey model with the assumption that birth and death rates for male and female preys are different. Conditions for the global stability of the boundary equilibrium and for the permanence of the prey and predators are obtained. By means of a Liapunov function we show that the predation will not alter the sex ratio of the prey eventually when it is not sex-biased. However, computer simulations indicate that the sex-biased predation will alter the ratio.

Key words: two-sex; predator-prey; sex-biased predation; sex ratio

1 Introduction

The models in mathematical biology have played a very useful role in in theoretical biology [1]. However, because most of them are restricted to modeling the dynamics of homogeneously mixing populations, these models and their generalizations incorporating age structures, such as Leslie's model [2], do not take into account gender-related factors, such as mating, that are central to the study of the life history of real populations. Furthermore, the number of marriages is an important quantitative feature of the social structure. The detailed description of the occurrence of marriages or of the formation of pairs within a bisexual population is a necessary prerequisite for the modelling of the spread of sexually transmitted diseases (Dietz and Hadelar (1988)). Therefore, it is of much importance to appropriately describe the changes in the female and in the male population separately (Impagliazzo (1985)). The problem of appropriate modelling the pair formation process has been called the "two-sex problem" (A. H. Pollard (1948), quoted in J. H. Pollard (1973)). According to whether or not considering age structure the two-sex models can be separated into two cases: populations with vital processes independent of age and populations with age structure.

Vital processes independent of age in a population mean that the rates of all vital processes are independent of age. In such a population, the force of mortality is independent of age, the birth rate is independent of age, and so on. The assumption of age-independent vital processes is, of course, highly unrealistic, and models based on the assumption will hardly be useful for purposes of population projection unless they are adjusted by adding such features as time lag.

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Nevertheless, some of the qualitative features of population growth can be illustrated by such model; in addition, some of the theoretical problems involved in describing the interactions between the sexes (marriage and childbirth) can be introduced very nicely by the models.

The focus of this paper is to formulate and analyze a predator-prey model where the prey population is separated into female and male populations. In this model, random mating, i.e., without the formation of permanent male-female couples, is the prevailing and only arrangement for propagation of the prey population. We will consider how the predator population influences the sex ratio of the prey population, i.e., the proportion of the female prey to the male prey. A description of our results requires a brief but complete summary of the results associated with populations with vital processes independent of age, which is given in this section. Section 2 formulates the predator-prey model with sex difference in the prey population and analyzes the predator's influence on the prey ratio.

In next two subsections, we consider the case where the random mating, without the formation of permanent male-female couples, is the prevailing and only arrangement for propagation of the population, and the case where permanent monogamous marriage is the prevailing and only arrangement for propagation of the population.

1.1 Random Mating Model

let $f(t)$ and $m(t)$ be the numbers of females and males, respectively, in the population at time t . Assume that the forces of mortality (independent of age) for males and females are the same, and denoted by θ which is independent of time t . Then the ordinary differential equations describing the population are those of Kendall and Goodman:

$$\begin{cases} \frac{df}{dt} = -\theta f + R, \\ \frac{dm}{dt} = -\theta m + R, \end{cases} \quad (1.1)$$

where $2R$ is the total birth rate at epoch t .

The most important problem of this model is how the birth rate R depends on the male and female populations. Kendall[3] and Goodman[4] explored a number of specific hypotheses; these were

$$mf, (mf)^{\frac{1}{2}}, \frac{1}{2}(m+f), \min\{m, f\}.$$

There are merits and shortcomings for all of these various forms. Therefore a fifth form is introduced by Fredrickson[5] which may avoid many of the shortcomings of the previous forms. It is

$$R = \frac{\gamma_f \gamma_m f m}{\gamma_f f + \gamma_m m}$$

where γ_f and γ_m are positive constants. In addition, Fredrickson got two general conditions that a birth rate must satisfy:

$$\begin{aligned} R(0, m) &= R(f, 0) = 0, \\ R(kf, km) &= kR(f, m). \end{aligned} \quad (1.2)$$

Obviously, it must also satisfy

$$\begin{aligned} R(m, f) &\geq 0, \\ R(m+u, f+v) &> \phi(m, f), \quad \text{for } u, v > 0. \end{aligned} \quad (1.3)$$

Fredrickson[5] studied model (1.1) and the result shows that the population tends to follow the Malthusian law of exponential growth and that the eventual sex ratio is 1 : 1.

Model (1.1) supports an exponential solution; hence it is not real in a ecology system. Hanwu Liu[20] proposed a two-sex model which was density-dependent(or compensatory). The model is as follows

$$\begin{cases} \dot{x} = b_1 y - d_1 x - \frac{x+y}{k} x, \\ \dot{y} = (b_2 - d_2) y - \frac{x+y}{k} y, \end{cases} \quad (1.4)$$

where $x(t)$ and $y(t)$ denote the numbers of males and females, respectively, in the population at time t ; d_1 and d_2 are per-capita death rates for males and females, b_1 and b_2 per-capita birth rates for males and females, and k carrying capacity of the population. The result shows that the unique positive equilibrium is globally asymptotically stable as long as it exists.

1.2 Monogamous Marriage Model

We let $m_s(t)$ denote the population of single males at time t , $f_s(t)$ the population of single females time t , and $p(t)$ the population of paired individuals (heterosexual pairing) time t . Furthermore, we let μ_m and μ_f denote the per-capita death rates for males and females, and β_m, β_f the per-capita birth rates for males and females while σ denotes the separation rate. Using these definitions we arrive at the following demographic pair-formation model:

$$\begin{cases} \dot{m}_s = -\mu_m m_s + (\beta_m + \mu_f + \sigma)p - \phi(m_s, f_s), \\ \dot{f}_s = -\mu_f f_s + (\beta_f + \mu_m + \sigma)p - \phi(m_s, f_s), \\ \dot{p} = -(\mu_m + \mu_f + \sigma)p + \phi(m_s, f_s), \end{cases} \quad (1.5)$$

where ϕ denotes the pair-formation rate.

The work of Fredrickson, MacFarland, Keyfitz, Pollard, Kendall and Hadeier(refer to [5], [6], [7], [8], [3], [9]) proposes various functional forms of ϕ . This ϕ is a function of the population sizes of single males m and single females f . An important class of functions ϕ is derived from the means

$$\phi(x, y) = \rho(\beta x^\alpha + (1 - \beta)y^\alpha)^{1/\alpha} \quad (1.6)$$

where $0 < \beta < 1$, $\alpha \in [-\infty]$, $\rho > 0$. For $\alpha = -1$ we obtain the harmonic mean

$$\phi(x, y) = \rho \frac{xy}{\beta x + (1 - \beta)y},$$

in particular, for $\beta = \frac{1}{2}$,

$$\phi(x, y) = \rho \frac{xy}{x + y}.$$

We obtain the geometric mean

$$\phi(x, y) = \rho x^\beta y^{1-\beta}$$

by taking $\alpha \rightarrow 0$ in (1.6) and the minimum function

$$\phi(x, y) = \rho \min(x, y)$$

for $\alpha \rightarrow -\infty$. It is clear that the function ϕ satisfies 1.2 and 1.3.

System (1.5) is a homogeneous system of degree one. Hadelar and collaborators have developed an extensive theory for homogeneous system of this type (see [10]) and made a complete analysis of system (1.5). They shown that if there exists a positive exponential solution it is globally asymptotically stable; therefore, the sex ratio will tend to a constant. Detailed descriptions can be referred to [9] or [11].

Most of the work on demographic pairing models has focussed on homogeneous systems. It is obviously important to study models that also incorporate nonlinear birth and separation processes. Let $T = m_s + f_s + 2p$ (the total population), and assume that the birth rate $\beta = \beta(T)$ and the separation rate $\sigma = \sigma(T)$ depend on the total population. Furthermore, if we let $0 < \gamma_m < 1$ and $\gamma_f = 1 - \gamma_m$ represent the proportion of the male and female birth rates respectively, then model (1.5) becomes

$$\begin{cases} \dot{m}_s = -\mu_m m_s + [\gamma_m \beta(T) + \mu_f + \sigma(T)]p - \phi(m_s, f_s), \\ \dot{f}_s = -\mu_f f_s + [\gamma_f \beta(T) + \mu_m + \sigma(T)]p - \phi(m_s, f_s), \\ \dot{p} = -[\mu_m + \mu_f + \sigma(T)]p + \phi(m_s, f_s), \end{cases} \quad (1.7)$$

where it is assumed that β and γ satisfy the following properties:

$$\frac{d\beta(T)}{dT} < 0, \quad \lim_{T \rightarrow +\infty} \beta(T) = 0, \quad \frac{d\sigma(T)}{dT} < 0.$$

Carlos Castillo-Chavez and Wenzhang Huang [12] studied the model and obtained that the positive equilibrium is locally asymptotically stable as long as it exists. Again we can conclude that the sex ratio is a constant.

Remark From above summaries it can always be concluded that the sex ratio is a constant in despite that the population development is Random Mating or Monogamous.

2 Predator-prey System

Most populations can be separated into female and male populations. Due to some reasons, male (female) populations are predated more easily than female (male) populations (see [23]). So it is important to consider how predation influence the dynamics of prey population, especially how to influence the sex ratio of prey population. From section 1 we see that the ratios in the models with vital processes independent of age always tend to a constant. Therefore, for a simplicity in mathematics, we will establish our predator-prey model with the prey population based on the two-sex model (1.4).

Let $x(t)$ be the number of the male prey, $y(t)$ the number of the female prey and $z(t)$ the number of predators at time t . At first, we give some assumptions:

- There is the sex difference in the prey population but not in the predator population;
- the prey is limited only by predators, and in its absence would grow according to the logistic law.
- In the absence of the prey, predators die off and it is dependantary.
- The functional response of predators is of Holling type II and the predation is not sex-biased. Let $\phi_1(x, y), \phi_2(x, y)$ be the functional responses of predator to male and female prey separately, then $\phi_1(x, y) = \frac{ax}{1+b(x+y)}, \phi_2(x, y) = \frac{ay}{1+b(x+y)}$.

Then a predator-prey system is given by the following equations

$$\begin{cases} \dot{x} = b_1y - d_1x - \frac{x+y}{k}x - \phi_1(x, y)z, \\ \dot{y} = ry - \frac{x+y}{k}y - \phi_2(x, y)z, \\ \dot{z} = z[-d - cz + e(\phi_1(x, y) + \phi_2(x, y))], \end{cases} \quad (2.1)$$

where the meanings of parameters b_1, d_1 and k are as those of model (1.4), e is the conversion factor of prey to predator, d the death rate of predator and c the density-restricting factor. All above parameters are positive.

If $\frac{ae-bd}{d} \leq \frac{1}{rk}$, then system (2.1) has only two boundary equilibria $E_0(0, 0, 0)$ and $E_1(\frac{b_1rk}{A}, \frac{d_1kr+kr^2}{A}, 0)$, where $A = b_1 + d_1 + r$. If $\frac{ae-bd}{d} > \frac{1}{rk}$, then system (2.1) may have one, two or three positive equilibria besides boundary equilibria E_0 and E_1 .

Theorem 2.1 For any positive solution of system (2.1) $(x(t), y(t), z(t))$ we have

$$\lim_{t \rightarrow +\infty} \frac{x}{y} = \frac{b_1y}{d_1 + r},$$

that is, the ω limit sets of all positive solutions belong to plane

$$\Pi: \frac{x}{b_1} = \frac{y}{d_1 + r}.$$

Proof Let

$$V(x, y, z) = \frac{1}{2}[(d_1 + r)x - b_1y]^2.$$

Calculating the derivative of V along the solutions of system (2.1), we obtain

$$\begin{aligned} \frac{dV}{dt} &= [(d_1 + r)x - b_1y][(d_1 + r)\dot{x} - b_1\dot{y}] \\ &= - \left[d_1 + \frac{x+y}{k} + \frac{az}{1+b(x+y)} \right] [(d_1 + r)x - b_1y]^2 \\ &\leq 0. \end{aligned}$$

It is obvious to show that

$$\frac{dV}{dt} = 0 \iff (x(t), y(t), z(t)) \text{ is in plane II.}$$

Therefore, $\lim_{t \rightarrow +\infty} \frac{x}{y} = \frac{b_1}{d_1 + r}$ and the proof is completed. \square

Substituting $x = \frac{b_1 y}{d_1 + r}$ into the second and third equations of system 2.1 yields

$$\begin{cases} \dot{y} = y \left[r - \frac{A}{k(d_1 + r)} y - \frac{a(d_1 + r)z}{d_1 + r + bAy} \right], \\ \dot{z} = z \left[-d - cz + \frac{eaAy}{d_1 + r + bAy} \right]. \end{cases} \quad (2.2)$$

In view of Theorem 2.1, studying system (2.1) comes down to studying system (2.2). In this paper, we only present some preliminary analysis for (2.2).

Since the prey and predators are density-dependent, it is easy to obtain the following lemma.

Lemma 2.1 *There exists a positive constant M such that for any positive solution $(y(t), z(t))$ of system (2.2) we have*

$$\limsup_{t \rightarrow +\infty} y(t) < M, \quad \limsup_{t \rightarrow +\infty} z(t) < M.$$

Consequently, system (2.2) is point dissipative.

Theorem 2.2 *If $\frac{ae-bd}{d} < \frac{1}{rk}$, then the boundary equilibrium $E_1(\frac{b_1rk}{A}, \frac{d_1kr+kr^2}{A}, 0)$ is globally asymptotically stable.*

Proof It is obvious to see that, if $\frac{ae-bd}{d} < \frac{1}{rk}$, system (2.2) has only two boundary equilibria $E'_0(0, 0)$ and $E'_1(\frac{d_1kr+kr^2}{A}, 0)$ and has no positive equilibrium. To complete the proof it is sufficient to show that E'_1 is a globally asymptotically stable equilibrium of system (2.2) by Theorem 2.1. By trivial calculations we have that the Jacobian matrixes of system (2.2) at equilibria E'_0 and E'_1 are

$$J_0 = \begin{pmatrix} r & 0 \\ 0 & -d \end{pmatrix}, \quad J_1 = \begin{pmatrix} -r & * \\ 0 & \frac{kr(ae-bd)-d}{bkr+1} \end{pmatrix}$$

separately, where $*$ denotes a constant only depending on the parameters. Therefore, E'_1 is locally asymptotically stable and E'_0 is a saddle whose unstable manifold belongs to y axis and whose stable manifold is z axis. So it is impossible that E'_0 is in the ω limit set of positive solutions of (2.2). In addition, periodic solution does not exist since there is not positive equilibrium. Since system (2.2) is point dissipative, Poincaré-Bendixson theorem yields that the ω limit set of positive solution of (2.2) must be equilibrium E'_1 . Therefore, E'_1 is globally attractive. The proof is completed. \square

Theorem 2.3 *The male population x and female population y in system (2.1) are permanent.*

Proof To complete the proof it is sufficient to prove that the female population y in system (2.2) is permanent. Let $X_0 = \{(y, z) : y \geq 0, z = 0\}$, $X^0 = \{(y, z) : y > 0, z > 0\}$. By Lemma 2.1 and the proof of Theorem 2.2, the conditions of Theorem 2.2 in paper [24] are satisfied and the proof is completed. \square

Theorem 2.4 *If $\frac{ae-bd}{d} > \frac{1}{rk}$, then system (2.1) is permanent.*

The proof for Theorem 2.4 is similar to that of Theorem 2.3 by finding that equilibrium E'_1 is a saddle if $\frac{ae-bd}{d} > \frac{1}{rk}$.

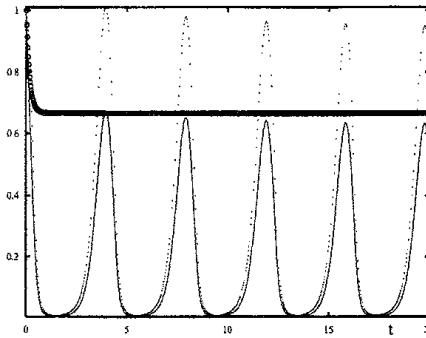


Figure 1: The dynamics of system (2.1) with parameters $b_1 = 4, d_1 = 1, b=1, d=0.5, e=0.5, k=1, r=5, a=10, c=1$. solid curve denotes $x(t)$, dashed curve $y(t)$ and circles $\frac{x(t)}{y(t)}$.

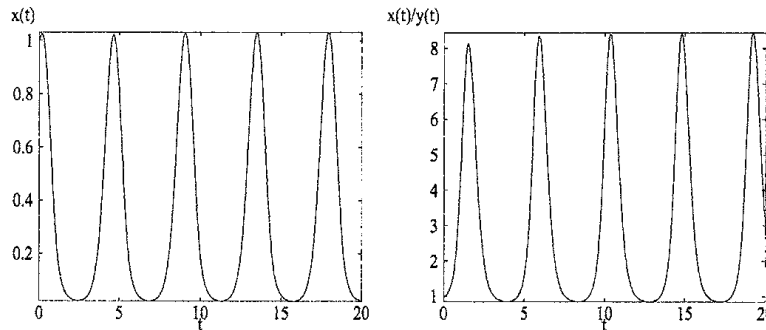


Figure 2: Effect made by sex-biased predation. $\gamma = 0.8$ and other parameters are the same as those in figure 1.

Theorem 2.1 indicates that when the predation is not sex-biased the eventual proportion of male prey to female prey is a constant $\frac{d_1+r}{b_1}$ which does not depend on the parameters of predator, that is, the predator's predation of prey will not change the sexual ratio in the end. In Figure 1 we can find that system (2.1) has a global asymptotically stable periodic solution. However, the ratio $\frac{x(t)}{y(t)}$ quickly goes to a constant.

Now we consider how sex-biased predation influences the sex ratio of prey by computer simulations. Let γ denote the degree of sex-biased predation of female prey. Consequently,

$1 - \gamma$ is the degree of sex-biased predation of male prey. It is natural that $0 < \gamma < 1$. Let $\phi_1(x, y) = \frac{(1-\gamma)ax}{1+b(x+y)}$ and $\phi_2(x, y) = \frac{\gamma ay}{1+b(x+y)}$. Then the behaviors of the sex-biased predation are described by system (2.1). In Figure 2 we can find that there still exists a global asymptotically stable periodic solution. However, unlike figure 1 the ratio $\frac{x(t)}{y(t)}$ will fast go to a periodic function.

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