MATHEMATICAL MODELLING OF
POPULATION DYNAMICS
BANACH CENTER PUBLICATIONS, VOLUME 63
INSTITUTE OF MATHEMATICS
POLISH ACADEMY OF SCIENCES
WARSZAWA 2004

TIME DISCRETE 2-SEX POPULATION MODEL WITH GESTATION PERIOD

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Abstract. A time-discrete 2-sex model with gestation period is analysed. It is significant that the conditions for local stability of a nontrivial steady state do not require that the expected number of female offspring per female equal unity. This is in contrast to results obtained by Curtin and MacCamy [4] and the author [10].

1. Introduction. Age, physiological factors, density dependence, gestation period and the mating pattern are some of the key factors that one would want to include in a realistic, mathematical model of the dynamics of a 2-sex population. However the need for mathematical tractability imposes constraints on the number of factors that a single model can accommodate. Mating pattern, physiological factors and the gestation period appear to have been the least favoured. A brief comment on some related works provides the context for the present paper.

Gurtin and MacCamy [4] introduced a 1-sex (all female), age-structured, continuous time model in which the birth and death moduli are dependent on the total population. Their result on the existence and stability of a steady state, apart from its importance to demography, indicates the importance of density dependence.

Allied with age and physiological factors is maturation. Castillo-Chavez [1] introduced a 1-sex model in which an abstract physiological factor is allowed for, whilst age and maturation are discretized. There are just two age grades: egg and adult. Gestation and density dependence are taken account of. There is a partial differential equation with a non-local boundary condition, similar to Gurtin and MacCamy's, except for a time lag owing to the period of gestation.

Dash and Cressman [3] developed a 2-sex discrete time model in which polygamy is allowed for. The age-structure consists of a number of pre-reproductive age-grades and a

2000 *Mathematics Subject Classification*: Primary 92D25; Secondary 39A11.

The paper is in final form and no version of it will be published elsewhere.

single adult age-grade. In order to study the effect of polygamy a specific function was chosen to represent the polygamous mating pattern. No account is taken of gestation.

Caswell [2] discussed 2-sex models with discrete time and age-grades. No account is taken of physiological factors and gestation period. However, within the specific mating functions chosen, he investigated the effects of competition for mates. This is a form of selective density dependence. The author had recourse to numerical simulation to understand the part played by some parameters in the emergence of certain bifurcations.

Skakauskas [7, 8] tried to accommodate quite a number of factors, gestation included, in his models. They are 2-sex with continuous time and age variables. In addition pair formation is non-permanent and mortality of infants is subject to parental care. His main focus is the existence of separable solutions although existence of steady states is also investigated.

Sowunmi's [9, 11] models of 2-sex populations have continuous time and age variables. While [9] is female-dominant, [11] is unconstrained, allows for polygamy, maturation, gestation and density dependent effects, but ignores physiological factors. In contrast to other authors polygamy is allowed for in a way that does not require the specification of a particular mating function. However in the study of the stability of steady states [13], detail of the contributions of the different factors is sacrificed to mathematical tractability.

Discretizing a model has the obvious advantage of getting round some of the mathematical complexities at little or no cost to reality of the model. It is in order to understand better the conditions for stability of equilibrium states in Sowunmi's [13] model that the author decided to study discrete time models of 2-sex populations with gestation period.

2. A special time discrete model. Suppose there is a population of males and females. Let each species be divided into three classes: pre-reproductive, reproductive and post-reproductive. Assume that membership of each class depends only on age. For the females there is only one age-grade within the pre-reproductive class, two in the reproductive and one in the post-reproductive class. Correspondingly for the males let the number of age-grades be 2,2, 0 respectively. Females either belong to the gestating subclass, or do not. That is they are either pregnant or not. Let these subclasses be denoted by the letters, (fg) and (fng) respectively. There is a finite age limit, the species life span, which no member of the population ever exceeds.

Let U_0, U_1, U_2, U_3 be the male age-grades in order of seniority. Let V_0, V_1, V_2, V_3 be the age-grades of the (fng) in order of seniority whilst W_1, W_2 are the (fg) age-grades in the same order. Figs. 1 and 2, below, represent the life cycle graphs of the male and female populations respectively.

$$U_0 \longrightarrow U_1 \longrightarrow U_2 \longrightarrow U_3$$

Fig. 1

$$\begin{array}{ccccccc} V_0 & \longrightarrow & V_1 & \longrightarrow & V_2 & \longrightarrow & V_3 \\ & & \downarrow & & \uparrow & & \\ & & W_1 & \longrightarrow & W_2 & & \end{array}$$

Fig. 2

W_1 and W_2 are the gestation stages. It is not possible to get pregnant and deliver at the same age. It is the case that pregnancy begins at V_1, and then the member moves immediately to W_1; delivers at W_2 and then moves immediately to V_2. No pregnancy can begin at V_2 since delivery would then have to be post-reproductive.

2.1. *Notations and governing equations.* Following from the assumptions in the Introduction, we now introduce the following notation and definitions. Let $u_0(r)$ be the population of U_0 at time $r \geq 0$. The functions $u_1, u_2, u_3, v_0, v_1, v_2, v_3, w_1, w_2$ are similarly defined.

Let $\pi_1^s(r)$ be the probability at time r that a male in age-grade U_s will survive till time $r+1$, thus attaining age-grade U_{s+1}. $\pi_2^s(r)$ and π_3^s for appropriate numerical values of s can be defined in like manner for the (fng) and (fg) respectively. In the general autonomous case the π's depend on time r implicitly through the functions u_i, v_j, w_k. Mortality is then said to be density dependent.

The age-specific birth rate of males/females is the average number of male/female offspring per individual mother at a given age. Since only females in age-grade W_2 can deliver, we denote by $\beta_1^3(r)$ and $\beta_2^3(r)$ the age specific birth rates at time r of male and female offspring respectively. Like the π's the β's could also depend on the component populations.

The population is renewed through interaction between the males in U_2 and U_3 on one hand and the females in V_1 on the other. We assume the existence of an interaction function, F_{21}, such that the total number of pregnancies, which occur at time r through U_2 and V_1 is given by $F_{21}(u_2(r), v_1(r))$. F_{31} is likewise defined. Each function is assumed to be as smooth as may be required later. More especially the functions satisfy the following:

(F1) $F_{21}(0, v) = F_{21}(u, 0) = F_{31}(0, v) = F_{31}(u, 0) = 0$.
(F2) Each is a monotone increasing function of either of its variables.
(F3) There exist positive constants $k_1(2,1), k_2(2,1), k_1(3,1), k_2(3,1)$ such that

$$\sum_{s=2}^{3} F_{s1}(u_s(r), v_1(r)) \leq \min\left[\sum_{s=2}^{3} k_1(s,1)u_s(r), \sum_{s=2}^{3} k_2(s,1)v_1(r)\right].$$

The above inequality is the Generalised Law of the Minimum (Sowunmi [11]) adapted to this particular model. The law follows from the notion of saturability. It is satisfied by two of the marriage functions listed in Caswell [2].

We are now ready to formulate the governing equations of the model. Let the duration of the gestation period be chosen as the projection interval. At time zero there is an initial population of pregnant females (fg) who will deliver within the interval $[0, 1)$. Thereafter delivery will come from those that became pregnant from time zero onwards.

From Fig.1 and the preceding definitions we have the following equations for the male species when $r \in \mathbb{N}$.

$$u_0(r+1) = \beta_1^3(r+1)\pi_3^1(r)\{F_{21}(u_2(r), v_1(r)) + F_{31}(u_3(r), v_1(r))\}, \tag{1}$$

$$u_1(r+1) = \pi_1^0(r)u_0(r), \tag{2}$$

$$u_2(r+1) = \pi_1^1(r)u_1(r), \tag{3}$$

$$u_3(r+1) = \pi_1^2(r)u_2(r). \tag{4}$$

For $r = 0$ we proceed as follows. Let $w_2(0)$ be the initial population of W_2. Since these must have got pregnant in the preceding interval, it follows that

$$u_0(0) = \beta_1^3(0)w_2(0). \tag{5}$$

Furthermore, $u_1(0) = u_{10}$, $u_2(0) = u_{20}$ and $u_3(0) = u_{30}$, where u_{s0} is specified for $s = 1, 2, 3$.

For the female population we use Fig. 2 to obtain (when $r \in \mathbb{N}$)

$$v_0(r+1) = \beta_2^3(r+1)\pi_3^1(r)\{F_{21}(u_2(r)v_1(r)) + F_{31}(u_3(r), v_1(r))\}, \tag{6}$$

$$v_1(r+1) = \pi_2^0(r)v_0(r) - \{F_{21}(u_2(r+1), v_1(r+1)) + F_{31}(u_3(r+1), v_1(r+1))\}, \tag{7}$$

$$v_2(r+1) = v_1(r)\pi_2^1(r) + \pi_3^1(r)\{F_{21}(u_2(r-1), v_1(r-1)) + +F_{31}(u_3(r-1), v_1(r-1))\}, \tag{8}$$

$$v_3(r+1) = v_2(r)\pi_2^2(r). \tag{9}$$

For $v_0(0)$ we have, as for the males,

$$v_0(0) = \beta_2^3(0)w_2(0), \tag{10}$$

$$v_s(0) = v_{s0},\ s = 1, 2, 3, \tag{11}$$

where v_{s0} is arbitrary, but non-negative.

Finally for the (fg), using Fig. 2, we have

$$w_1(r+1) = F_{21}(u_2(r+1), v_1(r+1)) + F_{31}(u_3(r+1), v_1(r+1)), \tag{12}$$

$$w_2(r+1) = \pi_3^1(r)w_1(r) - \{F_{21}(u_2(r-1), v_1(r-1)) + +F_{31}(u_3(r-1), v_1(r-1))\}\pi_3^1(r), \tag{13}$$

$$w_1(0) = w_{10}, \tag{14}$$

$$w_2(0) = w_{20}. \tag{15}$$

Both prescribed values should likewise be non-negative.

We shall consider only the situation of density independence. Thus the birth and death rates will be assumed not to depend on any of the population components. In this case we can solve eqns. (1) - (9) for the u's and v's, then substitute these values in the right hand side of the eqns. (12) - (13) to obtain w's.

For the sake of continuity we shall however not alter the notations in any way. We shall investigate the local stability of nontrivial equilibria, assuming they exist.

2.2. *Density independence.* As in [5] we shall try to express all other variables in terms of u_0, v_0. From eqns. (2) - (4) we have

$$u_2(r+1) = \pi_1^1(r)\pi_1^0(r-1)u_0(r-1), \tag{16}$$

$$u_3(r+1) = \pi_1^2(r)\pi_1^1(r-1)\pi_1^0(r-2)u_0(r-2). \tag{17}$$

Substitution for u_2, u_3 from eqns (16) - (17) in eqn (7) yields an equation, which expresses $v_1(r+1)$ as an implicit function of $v_0(r)$, $u_0(r-2)$, $u_0(r-1)$. The equation is obviously satisfied when all the variables vanish. Let the interaction functions F_{21}, F_{31}, be C^1 throughout their domain. At any equilibrium of the system of equations (1) - (15) the relations will be independent of r. Thus all the ten variables of the model will assume values, which are independent of r. Suppose there is a nontrivial equilibrium. Then u_0, v_0 are both non-zero, equal to U, V, say. Hence the said equation holds when U is substituted for $u_0(r-1)$ and $u_0(r-2)$, and V for $v_0(r)$. Recall that the parameters are independent of r. Then by the Implicit Function Theorem the equation is at least locally solvable, provided

$$\frac{\partial F_{21}(U,V)}{\partial v_1} + \frac{\partial F_{31}(U,V)}{\partial v_1} + 1 \neq 0. \tag{18}$$

By the property (F2), the derivatives in (18) are non-negative, hence (18) is satisfied everywhere in $\mathbb{R}^2_+$. Hence there exists a function Ψ_1, defined in an open neighbourhood of (V, U, U) in $\mathbb{R}^3_+$, such that

$$v_1(r+1) = \Psi_1(v_0(r), u_0(r-1), u_0(r-2)). \tag{19}$$

Similarly from eqns. (8) - (9) we have

$$v_2(r+1) = \Psi_2(u_0(r-2), u_0(r-3), u_0(r-4), v_0(r-1), v_0(r-2)), \tag{20}$$

$$v_3(r+1) = \pi_2^2(r)\Psi_2(u_0(r-3), u_0(r-4), u_0(r-5), v_0(r-2), v_0(r-3)). \tag{21}$$

Substituting for $u_2(r)$, $u_3(r)$, $v_1(r)$ in equations (1) and (6) from eqns (16, 17, 19) yields a simultaneous pair of difference equations with delay in the two unknowns u_0, v_0. Since

$$\frac{u_0(r+1)}{v_0(r+1)} = \frac{\beta_1^3}{\beta_2^3} = m,$$

say, we can write eqn. (6) as

$$\begin{aligned} v_0(r+1) &= \beta_2^2(r+1)\pi_3^1(r)\times \\ &(F_{21}(\pi_1^1(r-1)\pi_1^0(r-2), mv_0(r-2), \Psi_1(v_0(r-1), mv_0(r-2), mv_0(r-3))) \\ &+F_{31}(\pi_1^2(r-1)\pi_1^1(r-2)\pi_1^0(r-3)mv_0(r-3), \Psi_1(v_0(r-1), mv_0(r-2), mv_0(r-3)))). \end{aligned} \tag{22}$$

Eqn. (22) can be written more briefly as

$$v_0(r+1) = \gamma(v_0(r-1), v_0(r-2), v_0(r-3)). \tag{23}$$

Higher order difference equations are analogous to higher order ordinary differential equations. The latter can be transformed to first order systems by a well-known device, the analogue of which we now employ to reduce eqn. (23) to a system of difference equations without delay.

We define functions x, y, z as follows:

$$\begin{aligned} x(r) &= v_0(r-1), \\ y(r) &= x(r-1) = v_0(r-2), \\ z(r) &= y(r-1) = x(r-2) = v_0(r-3). \end{aligned}$$

Hence the equivalent first order system of difference equations is given by

$$\begin{aligned} v_0(r+1) &= \gamma(x(r), y(r), z(r)), \\ x(r+1) &= v_0(r), \\ y(r+1) &= x(r), \\ z(r+1) &= y(r). \end{aligned} \tag{24}$$

Corresponding to the steady state solution (U, V) of eqn. (23) there is the solution $v_0(r) = x(r) = y(r) = z(r) = V$ of (24). Consideration of the local stability of the steady state solution (V, V, V, V) of eqn. (24) yields the following characteristic equation in λ : $\lambda^4 - \gamma_x\lambda^2 - \gamma_y\lambda - \gamma_z = 0$, where the derivatives of γ are evaluated at (V, V, V). The sufficient condition for local stability of the steady state solution of eqn. (24) is therefore that all the roots of this characteristic equation have moduli less than unity. The following are the necessary and sufficient Jury conditions (cf. [6], Appendix 2) appropriate to the quartic:

$$\gamma_z < 1, \tag{25}$$

$$\pm\gamma_y < 1 - \gamma_x - \gamma_z, \tag{26}$$

$$\gamma_y + \gamma_x\gamma_z < |1 - \gamma_z^2|, \tag{27}$$

$$(\gamma_x + \gamma_y\gamma_z)(\gamma_y + \gamma_x\gamma_z) < |(1 - \gamma_z)^2 - (\gamma_y + \gamma_x\gamma_z)^2|. \tag{28}$$

For brevity in writing we shall adopt the tensor notation for covariant differentiation of the derivatives of the interaction functions F_{ij}. For example $F_{21,1}(u_2, v_1)$ abbreviated to $F_{21,1}$ denotes $\frac{\partial F_{21}}{\partial v_1}(u_2, v_1)$. Hence in terms of the parameters of the model, the coefficients of the quartic are:

$$\gamma_x = \beta_2^3\pi_3^1\pi_2^0 \left\{ \frac{F_{21,1} + F_{31,1}}{1 + F_{21,1} + F_{31,1}} \right\}, \tag{29}$$

$$\gamma_y = \beta_1^3\pi_3^1\pi_1^1\pi_1^0 \left\{ \frac{F_{21,2}}{1 + F_{21,1} + F_{31,1}} \right\}, \tag{30}$$

$$\gamma_z = \beta_1^3\pi_3^1\pi_1^2\pi_1^1\pi_1^0 \left\{ \frac{F_{31,3}}{1 + F_{21,1} + F_{31,1}} \right\}. \tag{31}$$

Note that all the derivatives are evaluated at (U, V).

We therefore have the following result:

THEOREM 1. *Given a 2-sex time discrete population model in which the male sex has 2 pre-reproductive, 2 reproductive and 0 post-reproductive age-grades and the female sex has 1 pre-reproductive, 2 reproductive and 1 post-reproductive age-grades; the gestation period equals the projection interval; the birth and death rates are density independent. Given also that the interaction functions F_{21}, F_{31} are continuously differentiable. Suppose a non-trivial equilibrium exists, then necessary and sufficient conditions that it is locally asymptotically stable are given by the inequalities (25) - (28) subject to (29) - (31).*

3. Comments. Conditions (25) and (26) are easy to interpret.

$$(F_{21,1} + F_{31,1})(\beta_2^3\pi_3^1\pi_2^0 - 1) < 1 + \beta_1^3\pi_3^1\pi_1^1\pi_1^0(\pm F_{21,2} - \pi_1^2 F_{31,3}). \tag{32}$$

In particular

$$(F_{21,1} + F_{31,1})(\beta_2^3\pi_3^1\pi_2^0 - 1) < 1 - \beta_1^3\pi_3^1\pi_1^1\pi_1^0(F_{21,2} + \pi_1^2 F_{31,3}). \tag{33}$$

The term $\beta_2^3\pi_3^1\pi_2^0$ is the productive rate of female offspring for the female population. In the Gurtin and MacCamy model [4] as well as my female-dominant model [9], this factor has to be equal to unity at a steady state. In the case being studied, this is not required. The reproductive rate could be less than or greater than unity if the remaining factors in the inequalities (32) or (33) are suitably chosen. If the left hand side of (33) is positive, implying that the females are more than reproducing themselves then its right hand side must be positive. This imposes a constraint on the production of male offspring. On the contrary if the females less than reproduce themselves then the constraint on the production of male offspring is relaxed.

The closest 2-sex, time-continuous models to mine are by Skakauskas [7, 8]. The difference consists in a further differentiation of the pre-reproductive and reproductive age-grades and the choice of a particular, saturable interaction function, namely the harmonic mean. I am not aware of a study of the steady states of any Skakauskas' 2-sex, age-structured models with gestation period, whether time continuous or discrete.

It is possible to study the special case in Section 2 differently, by taking the system of delayed difference eqns. (1) - (11), and transforming it to an equivalent system without delay. Although there would be eleven equations in eleven unknowns the characteristic equation for the stability of equilibrium would be of degree six in contrast to the quartic obtained in this paper. This brings to mind a similar behaviour observed in my paper [10]. Perturbing the system of partial differential equations for the 2-sex dominant models introduced in [9] led to a sixth degree characteristic equations, whilst perturbing the system of four integral equations derived from the partial differential equations led to a quartic characteristic equation. Either way, in the case of Gurtin and MacCamy 1-sex model, the characteristic equation remains quadratic.

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