

DETERMINISTIC POPULATION GROWTH

BU-174-M

Keewhan Choi

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ABSTRACT

In this paper several deterministic models for population growth are reviewed. The models discussed here were proposed by Lotka, Volterra. The models considered here are:

1. Simple growth model
2. A model in which population size deters growth
3. An age-dependent growth model
4. A model distinguishing between the sexes.

The material in pages 8 - 10 and 15 - 16 ^{is} ~~are~~ ^{ed} excerpts from the 1962 lecture notes (unpublished) of S. Karlin.

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In this paper, several deterministic models for population growth will be studied. Some of the models are overly simplified to describe the real phenomena adequately. However, even the simplest model gives us insight into the problem.

1. Simple Growth Model

We will first consider the growth of a single species. Let us first define the notation:

$N(t)$ = population size at time t

$v(t)dt$ = expected number of offspring produced by each individual in the "short" time interval $(t, t + dt)$. More precisely, the expected number of offspring produced by an individual in the interval $(t, t + h)$ is

$$v(t)h + o(h)$$

where $o(h)$ is a symbol for the term of smaller order than h , i.e. by definition

$$\lim_{h \rightarrow 0} \frac{o(h)}{h} = 0 .$$

Then we get the following equation:

$$N(t + h) = N(t) + N(t)v(t)h + o(h) .$$

$$\frac{N(t + h) - N(t)}{h} = v(t)N(t) + \frac{o(h)}{h}$$

Taking the limit of both sides as $h \rightarrow 0$, we get

$$(1) \quad \frac{dN(t)}{dt} = v(t)N(t) .$$

We solve this differential equation to obtain the formula expressing $N(t)$ in terms of the function $v(t)$ and the initial population size $N(0)$. Rewrite (1) as

$$\frac{dN(t)}{N(t)} = v(t)dt$$

Integrating both sides,

$$\log N(t) - \log N(o) = \int_0^t v(\tau)d\tau .$$

Write the left-hand side as $\log \frac{N(t)}{N(o)}$, take the exponential of both sides, and multiply the result through by $N(o)$ to obtain

$$(2) \quad N(t) = N(o) \exp \left(\int_0^t v(\tau)d\tau \right) .$$

If the integral $\int_0^t v(\tau)d\tau$ diverges as $t \rightarrow \infty$, then the population grows to infinity. If $v(\tau)$ is constant, then $N(t) = N(o)e^{vt}$, and the population grows to infinity exponentially at the rate v .

We can take death into account by introducing a death rate $\mu(t)$. But now the function $v(\tau) - \mu(\tau)$ plays the same role as the function $v(\tau)$ did in the above model, the analysis is the same, and hence

$$(3) \quad N(t) = N(o) \exp \left\{ \int_0^t [v(\tau) - \mu(\tau)]d\tau \right\} .$$

If both $v(\tau)$ and $\mu(\tau)$ are constant, then the population grows to infinity if $v > \mu$, the population dies out if $v < \mu$, and the population size remains fixed if $v = \mu$.

2. A Model in Which Population Size Deters Growth

In the first model an increase in size of the population does not deter growth. We now take population size into account by letting $v(t)$ depend upon $N(t)$. Specifically, suppose

$$v(t) = \beta \left(1 - \frac{N(t)}{\alpha} \right) \quad \text{for} \quad N(t) \leq \alpha ,$$

where α and β are positive numbers. Note that the population size cannot grow beyond α . In this case (1) becomes

$$(4) \quad \frac{dN(t)}{dt} = N(t)\beta\left(1 - \frac{N(t)}{\alpha}\right) = \beta N(t) - \frac{\beta}{\alpha} N^2(t) .$$

A differential equation of this form is called a Bernoulli differential equation. To solve it, let

$$(5) \quad z(t) = \frac{1}{N(t)} .$$

Then

$$\begin{aligned} \frac{dz(t)}{dt} &= \frac{-1}{N^2(t)} \frac{dN(t)}{dt} \\ &= -\frac{\beta}{N(t)} + \frac{\beta}{\alpha}, \text{ by (4)} \\ &= -\beta z(t) + \frac{\beta}{\alpha}, \text{ by (5)} . \end{aligned}$$

Hence

$$\frac{dz(t)}{z(t) - \frac{1}{\alpha}} = -\beta dt .$$

Integrate both sides to obtain

$$\log \left[z(t) - \frac{1}{\alpha} \right] - \log \left[z(0) - \frac{1}{\alpha} \right] = -\beta t .$$

Making the substitution (5), and solving for $N(t)$,

$$(6) \quad N(t) = \frac{\alpha N(0)e^{\beta t}}{\alpha + N(0)[e^{\beta t} - 1]}$$

or equivalently,

$$(7) \quad N(t) = \frac{\alpha N(0)}{\alpha e^{-\beta t} + N(0) - N(0)e^{-\beta t}}$$

From (7) it is clear that $N(t) \rightarrow \alpha$ as $t \rightarrow \infty$.

3. Effects of Age-Structure

We shall now consider the effect of age-structure on a growing population. We need the following notation:

(8) $\rho(u, t)$ is the density function of the distribution of age u in the population at time t . $\rho(u, t)$ has the property that

$$\int_{u_1}^{u_2} \rho(u, t) du = \text{proportion of individuals in the population at time } t$$

who are in the age-range (u_1, u_2) . The number of such individuals is, of course, $N(t)$ times the proportion.

(9) $b(t)$ is the rate at which new individuals are being created in the population at time t . More explicitly,

$$\int_{t_1}^{t_2} b(t) dt = \text{number of new individuals created in the time interval } (t_1, t_2).$$

(10) $\lambda(u) dt =$ expected number of offspring of a single individuals of age u in the next dt units of time.

(11) $l(u) =$ proportion of individuals who will survive, from birth, at least u units of time.

(12) $c(u)$ the infinitesimal death rate. $c(u) du$ is the proportion of individuals of age u who will die in the next du units of time, for "small" du . More precisely, the proportion of individuals of age u who will die in the next h units of time is $c(u)h + o(h)$.

The connection between $l(u)$ and $c(u)$ may be derived as follows: For given u , $h \geq 0$, an individual will survive, from birth, at least $u + h$ units of time if and only if he survives, from birth, at least u units of time, and then does not die in the following h units of time. Thus

$$l(u + h) = l(u)[1 - c(u)h] + o(h)$$

and

$$\frac{l(u + h) - l(u)}{h} = - \frac{l(u)c(u)h + o(h)}{h}$$

Taking limits as $h \rightarrow 0$, we obtain

$$\frac{dl(u)}{du} = - l(u)c(u) .$$

Solving [in the same manner as we solved (1)], we obtain

$$(13) \quad l(u) = l(0)e^{-\int_0^u c(\xi)d\xi} = e^{-\int_0^u c(\xi)d\xi}$$

since $l(0) = 1$.

In considering the effect of age-structure on a growing population, our interest will center on $b(t)$. The rate at which new individuals are being created in the population at time t has two components. One component, $b_0(t)$ say, is the rate of creation due to those individuals in the population at time t who already existed at time zero. The density of age u in the population at time zero is $\rho(u, 0)$. The proportion of individuals of age u at time zero will survive to time t (at which time he will be $t + u$ old) is $l(t + u)/l(u)$. The offspring rate for individuals at age $t + u$ is $\lambda(t + u)$. Hence

$$(14) \quad b_0(t) = N(t) \int_0^{\infty} \lambda(t + u) \frac{l(t + u)}{l(u)} \rho(u, 0) du .$$

The other component of $b(t)$ is the rate of creation of new individuals due to those individuals in the population at time t who were born since time zero. The rate at which new individuals are being created in the population at time τ will survive to time t (at which time he will be $t - \tau$ old) is $l(t - \tau)$. The offspring rate for individuals of age $t - \tau$ is $\lambda(t - \tau)$. It follows that

$$(15) \quad b(t) = b_0(t) + \int_0^t \lambda(t - \tau) l(t - \tau) b(\tau) d\tau ,$$

where $b_0(t)$ is given by (14).

Example: Assume both the offspring rate and the infinitesimal death rate are constants, i.e., $\lambda(u) = \lambda$, $c(u) = c$. Then, by (13), the proportion of individuals, surviving from birth, at least u units of time is

$$(16) \quad l(u) = e^{-cu} .$$

Suppose that the population started with the creation of a single individual at time zero. Then, by (14) and (16), we have

$$(17) \quad b_0(t) = \lambda e^{-ct},$$

and so, by (15), (16), and (17), we get

$$(18) \quad b(t) = \lambda e^{-ct} + \lambda \int_0^t e^{-c(t-\tau)} b(\tau) d\tau$$

We wish to solve (18) for the function $b(t)$. Multiply both sides of the equation by e^{ct} to obtain

$$e^{ct} b(t) = \lambda + \int_0^t e^{c\tau} b(\tau) d\tau$$

and let

$$(19) \quad f(\tau) = e^{c\tau} b(\tau).$$

Then the equation, to be solved for $f(t)$ now, becomes

$$f(t) = \lambda + \lambda \int_0^t f(\tau) d\tau.$$

Clearly $f(0) = \lambda$, and upon differentiating both sides with respect to t we obtain

$$f'(t) = \lambda f(t),$$

so

$$f(t) = \lambda e^{\lambda t},$$

and hence, by (19),

$$(20) \quad b(t) = \lambda e^{(\lambda-c)t}.$$

Having found $b(t)$ in this example, we next use this result to determine the age-structure as given by $N(t)\rho(u, t)$. Since we have assumed, in deriving (20), that the population started with the creation of a single individual at time zero, we need only consider the case $u \leq t$. An individual is of age u at time t if and only if it was created at time $t - u$. The rate at which new individuals are being created in the population at time $t - u$ is $b(t - u)$. The proportion of individuals who will live to at least age u is, by (16), e^{-cu} . It follows that

$$(21) \quad N(t)\rho(u, t) = e^{-cu}b(t - u), \quad u \leq t .$$

Substituting (20) into (21), we get

$$(22) \quad N(t)\rho(u, t) = e^{-cu}\lambda e^{(\lambda-c)(t-u)} = \lambda e^{-\lambda u} e^{(\lambda-c)t}$$

4. Effect of Age-Structure on Population Growth (continued)

In Section 3, we derived an integral equation [equation (15)] for $b(t)$, the rate at which new individuals are being created in the population at time t . We then considered a special case in which both the offspring rate, $\lambda(u)$, and the infinitesimal death rate, $c(u)$, were constants. Under the further assumption that the population started with the creation of a single individual at time zero, we solved the integral equation for $b(t)$ [equation (20)], and determined the age-structure as given by $N(t)\rho(u, t)$ [equation (22)].

We now consider a more general case. The analysis for continuous time will be heuristic. A rigorous analysis is possible, but we will content ourselves here with the heuristic analysis which will then be justified to a certain extent by a precise treatment of the simpler discrete-time model.

To begin the continuous-time analysis, which is due to Lotka and Volterra, note that

$$(1) \quad N(t)\rho(u, t) = b(t - u)l(u) , \quad u \leq t .$$

For the special case considered in the previous section, this relation appears as equation (21), and the simple derivation given there applies here. We also derived there, as equation (15), the integral equation satisfied by the function $b(t)$ in the general case. This equation is

$$(2) \quad b(t) = b_0(t) + \int_0^t \lambda(t - \tau)l(t - \tau)b(\tau)d\tau$$

where $b_0(t)$ is the contribution to the rate of creation of new individuals at time t made by those individuals in the population at time t who already existed at time zero.

We are principally interested in the asymptotic behavior of the population. Assume that $b_0(t) \rightarrow 0$ as $t \rightarrow \infty$, and set $b_0(t) = 0$ in (2). Thus

$$\begin{aligned} (3) \quad b(t) &= \int_0^t \lambda(t - \tau) \ell(t - \tau) b(\tau) d\tau \\ &= \int_0^t b(t - u) \lambda(u) \ell(u) du \\ &= \int_0^t b(t - u) \phi(u) du \end{aligned}$$

where

$$(4) \quad \phi(u) = \lambda(u) \ell(u) .$$

As a tentative solution of (3), try

$$(5) \quad b(t) = e^{\gamma t} ,$$

where γ is to be determined. Note that if a solution of the form (5) exists, then any constant multiple of this solution also satisfies (3). Substituting (5) into (3)

$$e^{\gamma t} = \int_0^t e^{\gamma(t - u)} \phi(u) du = e^{\gamma t} \int_0^t e^{-\gamma u} \phi(u) du ,$$

and hence

$$(6) \quad 1 = \int_0^t e^{-\gamma u} \phi(u) du .$$

Let

$$(7) \quad R(\gamma) = \int_0^{\infty} e^{-\gamma u} \phi(u) du .$$

Set $t = \infty$ in (6), and then, by (7), we have

$$(8) \quad R(\gamma) = 1 .$$

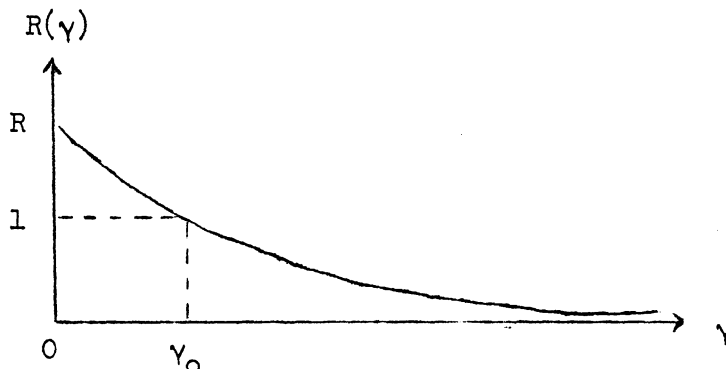
The γ required in (5) is the solution of (8). From (7) it is clear that $R(\gamma)$ is a strictly decreasing function of γ , and hence (8) has at most one solution.

Let

$$(7) \quad R = \int_0^{\infty} \lambda(u)l(u)du = \int_0^{\infty} \phi(u)du$$

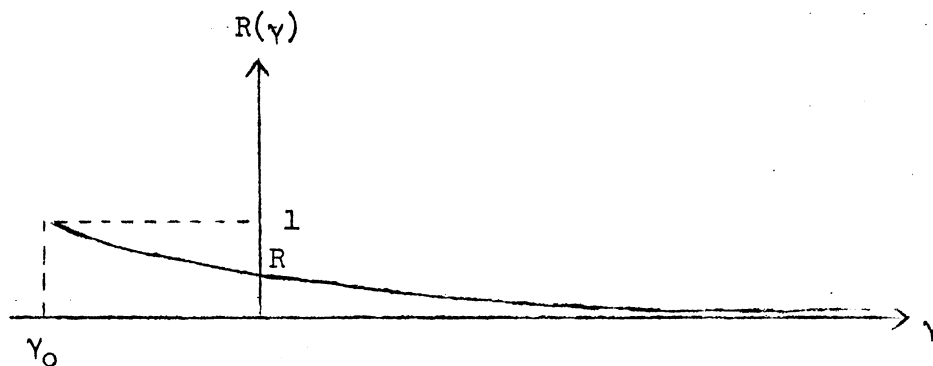
R is the reproductive value of an individual; it is the expected number of his offspring during his lifetime. R is sometimes called the Malthusian rate.

If $R > 1$, then $R(\gamma)$ has the form



and a solution $\gamma_0 > 0$ of (8) exists.

In this case $b(t)$ is asymptotically proportional to $e^{\gamma_0 t}$, and the population grows exponentially. If $R < 1$, then $R(\gamma)$ has the form



and a solution $\gamma_0 < 0$ of (8) exists. $b(t)$ is asymptotically proportional to $e^{\gamma_0 t}$, but in this case the population dies out.

If $R = 1$, then an adequate treatment requires that the problem be studied stochastically.

For the case $R > 1$, we shall determine the asymptotic age-structure as given by the density function $\rho(u, t)$. By (1),

$$\rho(u, t) = \frac{b(t-u)\ell(u)}{N(t)}, \quad u \leq t.$$

Now $b(t-u)$ is asymptotically proportional to $e^{\gamma_0(t-u)}$, and hence $N(t)$ is asymptotically proportional to $e^{\gamma_0 t}$. Therefore $\rho(u, t)$ is asymptotically proportional to

$$\frac{e^{\gamma_0(t-u)} \ell(u)}{e^{\gamma_0 t}} = e^{-\gamma_0 u} \ell(u).$$

The factor of proportionality is determined from the fact that $\rho(u, t)$ is the density function of a distribution. Therefore, the age-structure of the population for large t is given by the asymptotic density function

$$(10) \quad \rho(u, t) \sim \frac{e^{-\gamma_0 u} \ell(u)}{\int_0^{\infty} e^{-\gamma_0 x} \ell(x) dx}.$$

5. Discrete-time Model

We now give a precise treatment of the problem for a discrete-time model. This model was studied by Leslie. Let $t = 0, 1, 2, \dots$, and let

$N_{x,t}$ = number of individuals of age x at time t .

P_x = proportion of individuals of age x surviving to age $x + 1$.

$$\begin{aligned} \underline{1/} \quad \text{Asymptotically } N(t) &= \int_0^t b(t-u) du = \int_0^t e^{\gamma_0(t-u)} du \\ &= \frac{e^{\gamma_0 t}}{\gamma_0} [1 - e^{-\gamma_0 t}] \end{aligned}$$

$$\text{Hence } N(t) \sim \frac{e^{\gamma_0 t}}{\gamma_0} \text{ as } t \rightarrow \infty.$$

F_x = number born, in next unit of time, to each parent of age x .

Assume that no one lives beyond age m , i.e., set $P_m = 0$. Then the transition relationship for age-structure between $t = 0$ and $t = 1$ is given by

$$N_{0,1} = \sum_{x=0}^m N_{x,0} F_x$$

$$N_{1,1} = P_0 N_{0,0}$$

$$N_{2,1} = P_1 N_{1,0}$$

$$\vdots$$

$$N_{m,1} = P_{m-1} N_{m-1,0}$$

Since P_x and F_x do not depend on time, the same transition relationship holds between any two consecutive times. We write this transition relationship in matrix form as

$$\begin{bmatrix} N_0^1 \\ N_1^1 \\ \vdots \\ N_m^1 \end{bmatrix} = M \begin{bmatrix} N_0 \\ N_1 \\ \vdots \\ N_m \end{bmatrix},$$

where $N_i^1 \equiv N_{i,1}$ and $N_i \equiv N_{i,0}$ for $i = 1, 2, \dots, m$ and the matrix M is

$$(11) \quad M = \begin{bmatrix} F_0 & F_1 & F_2 & \dots & F_m \\ P_0 & 0 & \dots & \dots & 0 \\ 0 & P_1 & 0 & \dots & 0 \\ \vdots & & & & \vdots \\ 0 & \dots & 0 & P_{m-1} & 0 \end{bmatrix}.$$

M is a matrix with non-negative elements. Properties of such matrices are given in Section 8.2 of Karlin: Mathematical Methods and Theory in Games, Programming and Economics. The t ration relationship for age-structure between two times differing by t is given by

$$(12) \quad \begin{bmatrix} N_0^t \\ N_1^t \\ \vdots \\ N_m^t \end{bmatrix} = M^t \begin{bmatrix} N_0 \\ N_1 \\ \vdots \\ N_m \end{bmatrix}$$

where $N_i^t = N_{i,t}$ for $i = 1, 2, \dots, m$. For sufficiently large t , all of the elements of M^t are strictly positive. Also, there exists a largest eigenvalue $\lambda_0 > 0$ which is strictly greater in absolute value than any other eigenvalue.^{1/} For any vector \bar{N} , $M^t \bar{N}$ is asymptotically equal to $\lambda_0^t \bar{z}$, where \bar{z} is a certain linear combination of the left-hand and right-hand eigenvectors corresponding to the eigenvalue λ_0 . Asymptotically, as $t \rightarrow \infty$, (12) becomes

$$\begin{bmatrix} N_0^t \\ N_1^t \\ \vdots \\ N_m^t \end{bmatrix} = M^t \begin{bmatrix} N_0 \\ N_1 \\ \vdots \\ N_m \end{bmatrix} \sim \lambda_0^t \bar{z} = e^{t \log \lambda_0} \bar{z},$$

where $\log \lambda_0$ is the γ_0 introduced in the heuristic continuous-time analysis. The population grows exponentially if $\lambda_0 > 1$, and the population dies out if $\lambda_0 < 1$. If the intervals of discrete time tend to zero, then the discrete-time model approaches the continuous-time model, and the discrete-time result tends to the Lotka-Volterra result derived heuristically.

^{1/} An eigenvalue λ is any root of the equation

$$|M - \lambda I| = 0.$$

6. Study of Growth, Distinguishing Between the Sexes

In these models we ignore age-structure of the population at a given time, and are interested only in the rates of growth of the population.

I. Two Sexes

Let: $M(t)$ - Number of males at time t

$F(t)$ - Number of females at time t

μ - rate of death in time t . The assumption is made that μ is the same for both male and female population, and that it is independent of time and of population size.

$\Delta(M, F)$ - rate of increase of the whole population. We assume that half of the progeny are males and half females.

These assumptions have an equalizing effect on the structure of the population concerning proportions of females and males. Under the above assumptions we get the following set of differential equations:

$$(1) \quad \frac{dM(t)}{dt} = -\mu M(t) + \frac{1}{2}\Delta(M, F)$$
$$\frac{dF(t)}{dt} = -\mu F(t) + \frac{1}{2}\Delta(M, F)$$

By subtraction:

$$\frac{d(M - F)}{dt} = -\mu(M - F)$$

the solution of which, is:

$$(2) \quad M(t) - F(t) = [M(o) - F(o)]e^{-\mu t}$$

So, for large t , the imbalance between the number of males and of females tends to disappear.

In the sequel, we will treat special cases of $\Delta(M, F)$.

Example 1: Random Mating:

Here $\Delta(M, F) = 2\lambda M \cdot F$, where λ can be interpreted as the number of progeny produced by a mating of a male and a female. Further, we assume $M(o) = F(o)$.

(Since eventually $M(t) \sim F(t)$ we may assume it without loss of the characteristics of the growth) By (2), $M(t) = F(t)$ for all t . Hence, (1) reduces to:

$$(3) \quad \frac{dM}{dt} = -\mu M + \lambda M^2$$

which is Ricatti's equation, and can be easily solved, by reducing it to a linear differential equation. Indeed, divide by M^2 and substitute $z = \frac{1}{M}$. Then we get

$$\frac{dz}{dt} = uz - \lambda$$

The general solution of which is

$$z = \frac{\lambda}{\mu} + \frac{c}{\mu} e^{\mu t}.$$

Hence

$$M(t) = \frac{1}{\frac{\lambda}{\mu} + \left(\frac{1}{M(0)} - \frac{\lambda}{\mu}\right)e^{\mu t}}.$$

Therefore, we distinguish among three cases:

i) if $M(0) < \frac{\mu}{\lambda}$ then $M(t) \xrightarrow[t \rightarrow \infty]{} 0$

ii) if $M(0) = \frac{\mu}{\lambda}$ then $M(t) = \frac{\mu}{\lambda}$

iii) if $M(0) > \frac{\mu}{\lambda}$ then $M(t) \rightarrow \infty$ when $t \rightarrow -\frac{1}{\mu} \log \left[1 - \frac{\mu}{\lambda M(0)}\right]$.

So, in the last case, we have an explosion at a finite time. This suggests that the model is unsatisfactory.

Example 2: $\Delta(M, F) = 2\lambda\sqrt{M \cdot F}$

Introduce the auxilliary variables R, S by:

$$M = R^2 \quad \frac{dM}{dt} = 2R \frac{dR}{dt}$$

$$F = S^2 \quad \frac{dF}{dt} = 2S \frac{dS}{dt}$$

Then after dividing throughout by $2R$, we get:

$$(4) \quad \begin{aligned} \frac{dR}{dt} &= -\frac{\mu}{2} R + \frac{\lambda}{2} S \\ \frac{dS}{dt} &= -\frac{\mu}{2} S + \frac{\lambda}{2} R \end{aligned}$$

which can be condensed into a vectorial differential equation:

$$(5) \quad \frac{dX}{dt} = AX$$

where

$$X = \begin{bmatrix} R(t) \\ S(t) \end{bmatrix}, \quad A = \begin{bmatrix} -\frac{\mu}{2} & \frac{\lambda}{2} \\ \frac{\lambda}{2} & -\frac{\mu}{2} \end{bmatrix}.$$

As is well known in the theory of functions of matrices, the general solution is:

$$(6) \quad X(t) = e^{At} X(0)$$

where

$$X(0) = \begin{bmatrix} R(0) \\ S(0) \end{bmatrix} \quad \text{the initial conditions.}$$

Let us treat now the properties of the general equation of this type, when A has n distinct eigenvalues.

The eigenvalues of e^{At} are $e^{\gamma_i t}$ if γ_i are the eigenvalues of A and the eigenvectors (of A and e^A) are the same. That is observed easily for any polynomial $f(A)$ and can be extended to general functions of matrices.

Since the eigenvalues are different, we know that the eigenvectors u_i are linearly independent and so they span the whole space. In particular the initial conditions can be represented as $X(0) = \sum_{i=1}^n c_i u_i$. Then,

$$(7) \quad \begin{aligned} X(t) &= e^{At} \left(\sum_{i=1}^n c_i u_i \right) = \sum_{i=1}^n c_i e^{At} u_i \\ &= \sum_{i=1}^n c_i e^{\gamma_i t} u_i \end{aligned}$$

(Verify that this X(t) satisfies the equation and the initial conditions.)

Thus, in order to be able to examine the behavior of the solution with respect to time, all we have to do is to find the eigenvalues of A.

Return now to our case. A has the form $\begin{pmatrix} a & b \\ b & a \end{pmatrix}$, so that the characteristic polynomial is $(a - \gamma)^2 - b^2 = (a - \gamma + b)(a - \gamma - b)$, the roots of which are $\gamma_1 = a + b$, $\gamma_2 = a - b$. So $\gamma_1 = (\lambda - \mu)/2$, $\gamma_2 = (-\mu - \lambda)/2$. Therefore, these are three cases:

- i) $\lambda > \mu$, $\gamma_1 > 0$ and the population increases in the exponential rate $(\lambda - \mu)$ [since $M(t) = R^2(t)$, $F(t) = S^2(t)$].
- ii) $\lambda < \mu$, $\gamma_1, \gamma_2 < 0$ and the population decreases in the exponential rate $(\lambda - \mu)$.
- iii) $\lambda = \mu$, $\gamma_2 < 0$, $\gamma_1 = 0$ and the population tends to the constant $c_2 u_2$ with the rate -2μ .

Example 3: $\Delta(M, F) = \lambda(M + F)$

Then
$$\frac{dM}{dt} = (-\mu + \frac{1}{2}\lambda)M + \frac{1}{2}\lambda F$$

$$\frac{dF}{dt} = \frac{1}{2}\lambda M + (-\mu + \frac{1}{2}\lambda)F$$

Again, the same type as in (5). The eigenvalues, by the above discussion, are

$$\gamma_1 = -\mu + \lambda, \quad \gamma_2 = -\mu.$$

So, that again we distinguish three cases:

- i) $\lambda > \mu$, $\gamma_1 > 0$ and the rate of increase is $(\lambda - \mu)$.
- ii) $\lambda < \mu$, $\gamma_1, \gamma_2 < 0$ and the rate of decrease is $(\lambda - \mu)$.
- iii) $\lambda = \mu$, $\gamma_2 < 0$, $\gamma_1 = 0$ and the rate of approach to the constant $c_2 u_2$ is $-\mu$.

Example 4: $\Delta(M, F) = 2\lambda \min(M, F)$

Since, by (2), if $F(0) \geq M(0)$ then $F(t) \geq M(t)$, and the converse for the

case of $M(0) \geq F(0)$, we may assume one of these cases without loss of generality. Assume $M(0) \leq F(0)$. Then:

$$\frac{dM}{dt} = -\mu M + \lambda M = (\lambda - \mu)M$$

$$\frac{dF}{dt} = -\mu F + \lambda M$$

The eigenvalues are $\gamma_1 = \lambda - \mu$, $\gamma_2 = -\mu$, so that the analysis is exactly the same as in the previous case.

The models developed in Examples 2, 3, and 4 have the same qualitative behavior. The only thing they differ in is the rate of approach to a constant in the third case.

II. A Model with Three Types of Population

Let: $M(t)$ - number of unmarried males at time t

$F(t)$ - number of unmarried females at time t

$N(t)$ - number of married couples at time t

μ - rate of death (assumed equal for all males and females)

2λ - rate of birth (assumed that boys and girls are equally likely)

$K(M, F)$ - number of marriages (net after subtracting the number of divorces).

Then the change in the unmarried male population is: the sum of $-\mu M(t)$ (the number of deaths), $-K(M, F)$ (the number of those who get married), $+\mu N(t)$ (the number of widowers), $+\lambda N(t)$ (half the progeny). These considerations give us the system

$$\frac{dM}{dt} = -\mu M + \lambda N + \mu N - K(M, F)$$

$$\frac{dF}{dt} = -\mu F + \lambda N + \mu N - K(M, F)$$

$$\frac{dN}{dt} = -2\mu N + K(M, F)$$

Assume that $K(M, F) = 2\alpha \min(M, F)$. By subtracting the second equation from the first, we get again:

$$M(t) - F(t) = [M(o) - F(o)]e^{-\mu t}$$

so that again, no loss of generality in assuming $\min(M, F) = M(t)$, or, $K(M, F) = 2\alpha M(t)$. Note that in this case the first and third equations contain only N, M , so that they can be solved separately.

$$\frac{dN}{dt} = (-\mu - 2\alpha)M + (\lambda + \mu)N$$

$$\frac{dM}{dt} = 2\alpha M - 2\mu N.$$

The characteristic equation in this case is:

$$\gamma^2 + (3\mu + 2\alpha)\gamma + 2\mu^2 + \alpha(\mu - \lambda) = 0$$

$$\gamma_{1,2} = \frac{-(3\mu + 2\alpha) \pm \sqrt{\mu^2 + 4\mu\alpha + 4\alpha^2 + 8\alpha\lambda}}{2}$$

so that there are two real roots. The larger root is with the (+) sign. The other one is always negative, so that the larger root will be positive if the product of the roots $2\mu^2 + \alpha(\mu - \lambda) < 0$ or: $\lambda > \mu(1 + \mu/\alpha)$. In this case the population grows to infinity. If $\lambda = \mu(1 + \mu/\alpha)$. The population approaches a constant, and if $\lambda < \mu(1 + \mu/\alpha)$ the population decreases at an exponential rate.