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Simplest Dynamics of Dioecious Populations

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1. Discrete Model

Consider the system

$$\begin{cases} n_1(t+1) = \lambda_1 M(n_1(t), n_2(t)) \\ n_2(t+1) = \lambda_2 M(n_1(t), n_2(t)) \end{cases} \tag{1.1}$$

where $n_1(t)$ and $n_2(t)$ are the adult numbers of females and males, respectively, in generation t(t being nonnegative integer); λ_1, λ_2 the constant products of birth number per mating times survival rate from birth to adult for the two sexes; and $M(n_1(t), n_2(t))$ is the mating function of the population, i.e. the total number of matings in the population.

We shall define the sex ratio in adults by $z = n_2/n_1$. Eqs.(1) immeadiately yield

$$z(t+1) = \lambda_2/\lambda_1. \tag{1.2}$$

Thus, even if the sex ratio of adults is deviated from λ_2/λ_1, it will always come back to λ_2/λ_1 in the next generation and will continue to be in a globally stable equilibrium. This situation is similar to the Hardy-Weinberg equilibrium in population genetics. From this result we may assume in the following discussion that the sex ratio in adults is always given by (1.2).

To obtain a strong result we shall further make another assumption that $M(n_1, n_2)$ is a homogeneous function of first degree in n_1 and n_2. Then we can easily obtain

$$\begin{cases} n_1(t+1) = M(\lambda_1, \lambda_2) n_1(t) \\ n_2(t+1) = M(\lambda_1, \lambda_2) n_2(t). \end{cases} \tag{1.3}$$

Clearly this is geometric growth. Depending on $M(\lambda_1, \lambda_2) > 1$, < 1, or $= 1$, the population will increase, decrease, or be in an equilibrium, respectively.

2. Continuous Model

This section deals with a dynamical system of the special form:

$$\begin{cases} \dot{n}_1 = c_1 n_1 n_2/(n_1+kn_2)-d_1 n_1 \\ \dot{n}_2 = c_2 n_1 n_2/(n_1+kn_2)-d_2 n_2, \end{cases} \tag{2.1}$$

where n_1 and n_2 are the individual numbers of females and males, respectively; k the polygamic coefficient; c_1,c_2 the mating-birth coefficients; and d_1,d_2 are the death coefficients. These parameters are assumed to be all positive constants. When $n_1=n_2=0$ we define $\dot{n}_1=\dot{n}_2=0$.

Dynamics of the Sex Ratio

For convenience, we shall begin by analysing the sex ratio dynamics. If we define the sex ratio in survivors by $z=n_2/n_1$, we have from (2.1)

$$\dot{z} = (B-Az)z/(kz+1), \tag{2.2}$$

where $A=c_1+k(d_2-d_1)$ and $B=c_2-(d_2-d_1)$. Table 1 summarizes the stability properties of (2.2) for all possible cases.

Table 1. Stability properties of (2.2)

Case		stability of equilibrium
Case I: $A>0$	Case I-I: $B>0$	$z=0$ unstable, $z=B/A$ g.a.s.
	Case I-II: $B=0$	$z=0$ g.a.s.
	Case I-III: $B<0$	$z=0$ g.a.s. $(B/A<0)$
Case II: $A<0$	Case II-I: $B>0$	$z=0$ unstable $(B/A<0)$
	Case II-II: $B=0$	$z=0$ unstable
Case III: $A=0$		$z=0$ unstable

g.a.s. = globally asymptotically stable

Graphical Analysis

Eqs.(2.2) may be written as

$$\begin{cases} \dot{n}_1 = [-d_1 n_1+(c_1-kd_1)n_2]n_1/(n_1+kn_2) \\ \dot{n}_2 = [(c_2-d_2)n_1-kd_2 n_2]n_2/(n_1+kn_2) \end{cases} \tag{2.3}$$

so that the behavior of the solutions to (2.1) will be governed by the determinant:

$$D = \begin{vmatrix} -d_1 & c_1-kd_1 \\ c_2-d_2 & -kd_2 \end{vmatrix} = c_1 d_2+c_2(kd_1-c_1). \tag{2.4}$$

The nullclines in the (n_1, n_2) plane are composed of $n_1=0$, $n_2=0$,

$$n_2 = (c_2-d_2)n_1/kd_2, \tag{2.5}$$

and

$$n_2 = d_1n_1/(c_1-kd_1). \tag{2.6}$$

We find also that a ray exists and that it is given by

$$n_2 = [c_2-(d_2-d_1)]n_1/[c_1+k(d_2-d_1)]. \tag{2.7}$$

When D=0 the straight lines (2.5), (2.6), and (2.7) coincide with one another and there exist on them an infinite number of neutrally stable equilibrium points. When D<0, on the other hand, slope of (2.5)>slope of (2.7)>slope of (2.6) and the population will ultimately increase. When D>0 the population will ultimately decrease.

Asymptotic Behavior

From (2.1) we can have the asymptotic equations:

$$\begin{cases} \dot{n}_1 = [c_1z(\infty)/(kz(\infty)+1)-d_1]n_1 \\ \dot{n}_2 = [c_2/(kz(\infty)+1)-d_2]n_2, \end{cases} \tag{2.8}$$

where $z(\infty)=\lim_{t\to\infty}z(t)=0$, B/A, or $+\infty$.

In the case of $z(\infty)=B/A$, Eqs.(2.8) become

$$\dot{n}_i = rn_i \quad (i=1,2), \tag{2.9}$$

where $r=-D/(c_1+kc_2)$. Evidently this is exponential growth.

Sex Ratio Distortion and the Fold Catastrophe

When A>0 and B>0, i.e. when Case I-I holds, consider the perturbed dynamics of the sex ratio:

$$\dot{z} = (B-Az)z/(kz+1)-g, \tag{2.10}$$

where g designates some external force and is assumed to be a nonnegative constant. The behavior manifold is given by $M_z=\{\bar{z}\,|\,A\bar{z}^2+(kg-B)\bar{z}+g=0\}$, where $\bar{z}$ is an equilibrium point of z. It is then clear that the fold catastrophe will arise at the point of $(g,z)=(g_f,z_f)$, where

$$\begin{cases} g_f = [2A+kB-2\sqrt{A(A+kB)}]/k^2 \\ z_f = [\sqrt{1+kB/A}-1]/k. \end{cases} \tag{2.11}$$

Eq.(2.10) corresponds, for instance, to the system:

$$\begin{cases} \dot{n}_1 = c_1 n_1 n_2/(n_1+kn_2)-d_1 n_1 \\ \dot{n}_2 = c_2 n_1 n_2/(n_1+kn_2)-d_2 n_2-gn_1. \end{cases} \tag{2.12}$$

This type of fold catastrophe may be applied to pest management and other technologies.

Effect of the Sex Ratio at Birth on Population Growth

As shown in (2.9), the ultimate exponential growth rate is $r=[c_2(c_1-kd_1)-c_1d_2]/(c_1+kc_2)$. The sex ratio at birth maximizing the r value subject to $c_1+c_2=C$(const.) is then given by

$$c_2/c_1=[1+(d_2-d_1)/C]/[1-(d_2-d_1)/C] \tag{2.13}$$

if k=1, and by

$$c_2/c_1=(-1+\sqrt{E})/(k-\sqrt{E}), \tag{2.14}$$

where $E=k[1+(k-1)(d_2-d_1)/C]$, if $k\neq 1$.

In most human populations, k=1 and $d_2>d_1$ so that the "optimum" sex ratio at birth in the sense of maximizing r is to be somewhat greater than unity. At least qualitatively and apparently this is in good agreement with actual data, although our present discussion has no genetic basis.

Finally, in relation to the problem of sex control of babies, we have to point out that such control should bring about great deviations of the normal sex ratio and hence is very dangerous.