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On Evolutionary Genetic Stability of the Sex Ratio*

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INTRODUCTION

Under the assumption that the costs involved in producing male and female offspring were equal, Fisher (1930) argued that a sex ratio of one to one would maximize the number of grand-offspring and would, therefore, be expected to be achieved under evolution (see also Bodmer and Edwards, 1960). Simple one-locus two-allele "exact" population genetic models of sex determination by autosomal genes carried either by the individual (Eshel, 1975; Scudo, 1944) or its parents (Nur, 1974; Uyenoyama and Bengtsson, 1979) produce the result that the stable equilibria either determine a sex ratio which is one to one, or, under certain well-defined restrictions, a sex ratio which can be interpreted as being as close as possible to one to one, depending on the domains of attraction and parameters of the model. These findings may be interpreted as supporting Fisher's prediction. It is well known that the prediction may fail for sex-linked factors affecting sex determination (Hamilton, 1967; Thomson and Feldman, 1975; Charlesworth, 1977; Uyenoyama and Bengtsson, 1981; Eshel and Feldman, 1982).

The present study considers three situations of sex determination by a single gene locus with multiple alleles, in all of which diploid genotypes determine the probabilities that an individual is male or female. The results of our analysis strongly suggest that no matter how many sex determining alleles are present in these models at equilibrium, new mutations which affect the sex ratio will succeed if they bring it closer to one to one and fail if they cause increasing departure from equality. To support this conclusion only formal population genetic modeling is used; there is no recourse made to any

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criterion other than the local stability of an equilibrium involving alleles A_1, $A_2,...,A_n$, which affect the sex ratio, with respect to the initial increase of a new allele A_{n+1}.

Model I: Diploid Individual Sex Determination

Consider a single locus with n alleles $A_1, A_2,..., A_n$. Generations are nonoverlapping. The only function of the gene is to affect the probability that an individual is male. Thus m_{ij} is the probability that genotype A_iA_j is male. Let the proportion of A_iA_j in males and females be $2X_{ij}$ and $2Y_{ij}$ $(i \neq j)$ with X_{ii} and Y_{ii} the corresponding proportions for the homozygotes A_iA_i. The proportions of A_iA_j and A_iA_i in the whole population are $2Z_{ij}$ and Z_{ii}, respectively. Random mating between males and females is assumed. Set $X_i = \sum_{j=1}^{n} X_{ij}$, $Y_i = \sum_{j=1}^{n} Y_{ij}$ for the proportions of allele A_i in males and females, respectively.

Among the newborn offspring of the next generation we have

$$Z'_{ij} = (X_iY_j + X_jY_i)/2 \tag{1}$$

of genotype A_iA_j. Of these, m_{ij} are males. The male frequency among the offspring is therefore

$$M = \sum_i \sum_j Z'_{ij} m_{ij} = \sum_i \sum_j X_i Y_j m_{ij}. \tag{2}$$

The proportion of male A_iA_j in the offspring is therefore

$$X'_{ij} = m_{ij} Z'_{ij}/M. \tag{3}$$

Hence

$$X'_i = \sum_{j=1}^{n} X'_{ij} = \left\{X_i \sum_j m_{ij} Y_j + Y_i \sum_j m_{ij} X_j\right\} \Big/ 2M, \tag{4}$$

and

$$Y'_i = \left\{X_i \sum_j (1 - m_{ij})\, Y_j + Y_i \sum_j (1 - m_{ij})\, X_j\right\} \Big/ 2(1 - M) \tag{5}$$

$$= (X_i + Y_i - 2MX'_i)/2(1 - M). \tag{6}$$

At equilibrium, $X'_i = X_i$, $Y'_i = Y_i$ and therefore

$$(1 - 2M)\, X_i = (1 - 2M)\, Y_i \qquad (i = 1, 2,..., n), \tag{7}$$

so that

$$M = \tfrac{1}{2} \qquad \text{or} \qquad \hat{X}_i = \hat{Y}_i \qquad \text{for all } i = 1, 2,..., n.$$

We therefore have

RESULT 1. *There are two possible classes of equilibria,* (i) *symmetric equilibria at which* $\hat{X}_i = \hat{Y}_i$ $(i = 1, 2,..., n)$ *and* (ii) *equilibria at which the proportion of males is* $M = \frac{1}{2}$. *Note that fixation on any single allele is a symmetric equilibrium.*

Evolutionary Genetic Stability in Model I

The stability of these two classes of equilibria can, in principle, be analyzed in the usual way, that is, with respect to the n alleles already present in the population. An equally interesting evolutionary question, however, concerns the stability of these equilibria to invasion by an arbitrary new allele; this is the question of evolutionary genetic stability. First consider a symmetric equilibrium with alleles $A_1, A_2,..., A_n$ and frequencies $\hat{X}_1 = \hat{Y}_1$, $\hat{X}_2 = \hat{Y}_2,...,$ $\hat{X}_n = \hat{Y}_n$, and introduce a new mutant A_{n+1}, with frequencies X_{n+1} and Y_{n+1} in males and females small enough that quadratic terms may be neglected. Then from (4) and (5) we have

$$X'_{n+1} = (X_{n+1} + Y_{n+1}) \sum_{j=1}^{n} m_{n+1j}\hat{X}_j/2M + o(X_{n+1}, Y_{n+1}), \tag{8}$$

$$Y'_{n+1} = (X_{n+1} + Y_{n+1}) \left(1 - \sum_{j=1}^{n} m_{n+1j}\hat{X}_j\right)\Big/2(1-M) + o(X_{n+1}, Y_{n+1}). \tag{9}$$

Write $M_{n+1} = \sum_{j=1}^{n} m_{n+1j}\hat{X}_j$, the fraction of males with the mutant allele. Then, to the same order,

$$\frac{(X'_{n+1} + Y'_{n+1})}{X_{n+1} + Y_{n+1}} = \frac{M_{n+1}}{2M} + \frac{1 - M_{n+1}}{2(1-M)}$$

$$= 1 + \frac{(1-2M)(M_{n+1} - M)}{2M(1-M)}. \tag{10}$$

The right-hand side of (10) is larger than unity if either $M < \frac{1}{2}$ and $M_{n+1} > M$ or $M > \frac{1}{2}$ and $M_{n+1} < M$. These are therefore the conditions for local instability of a symmetric equilibrium to invasion by A_{n+1}. Numerical iteration of (4) and (6) suggests that under these conditions the population will eventually achieve an equilibrium sex ratio involving $A_1, A_2,..., A_{n+1}$ which is closer to 1:1 than at the original n-allele equilibrium.

The other equilibrium, characterized by $M = \frac{1}{2}$, may be investigated in the same way. X_{n+1} and Y_{n+1} have the same interpretation as before, but since the equilibrium value of M is $\frac{1}{2}$ the linearized versions of (4) and (5) are now

$$X'_{n+1} = X_{n+1} \sum_{j=1}^{n} m_{n+1j}\hat{Y}_j + Y_{n+1} \sum_{j=1}^{n} m_{n+1j}\hat{X}_j \tag{11}$$

$$Y'_{n+1} = X_{n+1}\left(1 - \sum_{j=1}^{n} m_{n+1,j}\hat{Y}_j\right) + Y_{n+1}\left(1 - \sum_{j=1}^{n} m_{n+1,j}\hat{X}_j\right). \quad (12)$$

One eigenvalue of the matrix on the right of (11), (12) is unity and the other is $\sum_{j=1}^{n} m_{n+1,j}(\hat{Y}_j - \hat{X}_j)$ which is less than or equal to unity in absolute value, with equality only in degenerate cases. Numerical iteration of (4) and (6) from the neighborhood of an equilibrium with $M = \frac{1}{2}$ suggests that there is very fast return to an $(n+1)$-allele surface characterized by $M = \frac{1}{2}$ so that the even sex-ratio is preserved from such a starting condition.

Model II: Diploid Offspring Sex Determined by Mother's Autosomal Genes

As for model I, X_{ii} and $2X_{ij}$ are the proportions of A_iA_i and A_iA_j in males with Y_{ii} and $2Y_{ij}$ the corresponding fractions in females. Also, as before,

$$X_i = \sum_j X_{ij}, \qquad Y_i = \sum_j Y_{ij}.$$

Now let m_{ij} be the fraction of males in the progeny of an A_iA_j mother, and set

$$Z_i = \sum_j m_{ij} Y_{ij}. \quad (13)$$

The fraction of males among the offspring produced by this generation is

$$M = \sum_{i=1}^{n}\sum_{j=1}^{n} m_{ij} Y_{ij} = \sum_{i=1}^{n} Z_i. \quad (14)$$

Under the assumption of random mating, exactly $X_k/2$ of the offspring of a mother of genotype A_iA_j will be of genotype A_iA_k $(k = 1, 2, \ldots, n)$. Hence

$$\begin{aligned} X'_{ik} &= \left(X_k \sum_{j=1}^{n} m_{ij} Y_{ij} + X_i \sum_{j=1}^{n} m_{kj} Y_{kj}\right)\Big/ 2M \\ &= (X_k Z_i + X_i Z_k)/2M. \end{aligned} \quad (15)$$

In the same way

$$\begin{aligned} Y'_{ik} &= (X_k Y_i + X_i Y_k - X_k Z_i - X_i Z_k)/2(1-M) \\ &= (X_k Y_i + X_i Y_k - 2MX'_{ik})/2(1-M). \end{aligned} \quad (16)$$

Sum (15) and (16) over k to obtain

$$X_l' = X_l/2 + Z_l/2M \tag{17}$$

and

$$Y_l' = (Y_l + X_l - 2MX_l')/2(1-M). \tag{18}$$

Hence at equilibrium

$$(1-2M)\,Y_l = (1-2M)\,X_l$$

and as before either $M = \frac{1}{2}$ at equilibrium or $X_l = Y_l$. In addition, from (17) at equilibrium

$$Z_l = MX_l,$$

and inserting this into (15) at equilibrium we have

$$X_{lk} = X_l X_k. \tag{19}$$

If $M \neq \frac{1}{2}$ at equilibrium, so that $X_l = Y_l$ then (16) becomes

$$Y_{lk} = X_l X_k = Y_l Y_k \tag{20}$$

at equilibrium, with $M = \sum_{l=1}^{n} \sum_{j=1}^{n} m_{lj} X_l X_j$.

Evolutionary Genetic Stability for Model II

Consider first any equilibrium at which $M \neq \frac{1}{2}$ and assume that a new allele A_{n+1} appears at low frequency. Set $\varepsilon_l = X_{ln+1}$ and $\delta_l = Y_{ln+1}$, half the frequency of heterozygotes $A_l A_{n+1}$ in males and females, respectively. Also set $\varepsilon = \sum_{l=1}^{n} \varepsilon_l$, and denote equilibrium values for the alleles and genotypes involving $A_1, A_2, \ldots, A_n$ by $\hat{X}_{lj}$, $\hat{Y}_{lj}$, etc. Then from (15) and (16) we have

$$\varepsilon' = \varepsilon/2 + \sum_{l=1}^{n} \delta_l m_{ln+1}/2M \tag{21}$$

and

$$\delta_i' = \varepsilon(\hat{Y}_i - \hat{Z}_l)/2(1-M) + \hat{X}_i \sum_{j=1}^{n} (1 - m_{j,n+1})\,\delta_j/2(1-M) \tag{22}$$

for $i = 1, 2, \ldots, n$ with quadratic terms form A_{n+1} neglected.

At a symmetric equilibrium from (17) to (20) the linear approximation in (21), (22) may be written

$$\begin{pmatrix} \varepsilon \\ \boldsymbol{\delta} \end{pmatrix}' = \mathbf{A} \begin{pmatrix} \varepsilon \\ \boldsymbol{\delta} \end{pmatrix}, \tag{23}$$

where $\boldsymbol{\delta} = (\delta_{1,n+1},\ldots,\delta_{n,n+1})$ written as a column, and

$$\mathbf{A} = \begin{bmatrix} 1/2 & m_{1n+1}/2M & \cdots & m_{nn+1}/2M \\ \hat{X}_1/2 & \dfrac{\hat{X}_1(1-m_{1n+1})}{2(1-M)} & \cdots & \dfrac{\hat{X}_1(1-m_{nn+1})}{2(1-M)} \\ \vdots & \vdots & & \vdots \\ \hat{X}_n/2 & \dfrac{\hat{X}_n(1-m_{1n+1})}{2(1-M)} & \cdots & \dfrac{\hat{X}_n(1-m_{nn+1})}{2(1-M)} \end{bmatrix}. \tag{24}$$

Now $\mathbf{A}$ is a strictly positive matrix and therefore has a unique strictly positive eigenvector associated with its largest eigenvalue. For such a right eigenvector to take the form $(\eta, \xi\hat{X}_1, \xi\hat{X}_2,\ldots,\xi\hat{X}_n)$ the associated eigenvalue must solve the 2×2 system

$$\begin{aligned} \eta/2 + \xi M_{n+1}/2M &= \lambda\eta \\ \eta/2 + \xi(1-M_{n+1})/2(1-M) &= \lambda\xi. \end{aligned} \tag{25}$$

The leading eigenvalue of this 2×2 system will therefore also be the leading eigenvalue of $\mathbf{A}$. A necessary and sufficient condition that this leading eigenvalue be greater than unity is that either $M < \frac{1}{2}$ and $M_{n+1} > M$ or $M > \frac{1}{2}$ and $M_{n+1} < M$, where $M_{n+1} = \sum_i \hat{X}_i m_{in+1}$. These are therefore the conditions for local instability of a symmetric equilibrium to invasion by A_{n+1}. Numerical iteration of (15) and (16) suggests that under these local instability conditions the population will eventually achieve an $(n+1)$-allele equilibrium at which the sex ratio is closer to 1:1 than at the original n-allele equilibrium.

Now consider the equilibrium $M = \frac{1}{2}$, and refer again to (21) and (22). Clearly, to this order of approximation,

$$\varepsilon' + \sum_{i=1}^{n} \delta_i = \varepsilon + \sum_{i=1}^{n} \delta_i,$$

so that there is an eigenvalue of unity for the linear approximation. Further manipulation of the local stability matrix in this case produces $n-2$ zero eigenvalues while the remaining two are the roots of the quadratic

$$\lambda^2 - \lambda(\tfrac{1}{2} - M_{n+1}) + \sum_{i=1}^{n} (M_{n+1} - m_{in+1})(\hat{Y}_i - \hat{Z}_i).$$

These last two are less than unity in absolute value. As with model I, although we cannot answer the local stability question here, numerical iteration of (15) and (16) suggests that there is fast return to an $(n+1)$-allele surface characterized by $M = \frac{1}{2}$ from such a starting condition.

Model III: *XY* System with Mother Controlling Sex Determination

Here females are XX, males XY, and m_{ij} is the proportion of males (i.e., haploids) in the progeny of an A_iA_j female. Again let $2Y_{ij}$ and Y_{ii} be the frequency of A_iA_j and A_iA_i females (diploids), respectively, and X_i the frequency of A_i males. Set $Y_i = \sum_j Y_{ij}$ and $M = \sum_i \sum_j Y_{ij} m_{ij}$. Then

$$X_i' = \sum_j Y_{ij} m_{ij}/M, \tag{26}$$

and

$$Y_{ij}' = \frac{1}{2(1-M)} \sum_k [(1-m_{ik})\, Y_{ik} X_j + (1-m_{jk})\, Y_{jk} X_i] \tag{27}$$

$$= \frac{1}{2(1-M)} [X_j Y_i + X_i Y_j - M X_i' X_j - M X_i X_j'], \tag{28}$$

using (26). Then clearly

$$Y_i' = \frac{1}{2(1-M)} [Y_i + X_i - M(X_i + X_i')]. \tag{29}$$

At equilibrium $X_i' = X_i$, $Y_i' = Y_i$ and (29) produces

$$(1-2M)\, X_i = (1-2M)\, Y_i.$$

Thus as in the previous models, at equilibrium either $M = \frac{1}{2}$ or $X_i = Y_i$.

Evolutionary Genetic Stability for Model III

Consider first the symmetric equilibrium with $X_i = Y_i = X_i' = Y_i'$. Assume that a new mutant allele A_{n+1} arises near this equilibrium with frequency ε in males. Replace the small variables Y_{in+1} by δ_i for $i = 1, 2, \ldots, n$. From (26) and (27) $\delta\varepsilon'/\partial\varepsilon = 0$, $\partial\varepsilon'/\partial\delta_i = m_{in+1}/\hat{M}$. $\partial\delta_i'/\partial\varepsilon = \hat{X}_i/2$, $\partial\delta_i'/\partial\delta_j = (1-m_{jn+1})\, \hat{X}_i/2(1-M)$. Hence the local stability matrix for the symmetric equilibrium $\mathbf{C}$ is

$$\mathbf{C} = \begin{bmatrix} 0 & m_{i,n+1}/\hat{M} & \cdots & m_{n,n+1}/\hat{M} \\ \hat{X}_1/2 & (1-m_{1n+1})\, \hat{X}_1/2(1-\hat{M}) & \cdots & (1-m_{nn+1})\, \hat{X}_1/2(1-\hat{M}) \\ \hat{X}_2/2 & (1-m_{1n+1})\, \hat{X}_2/2(1-\hat{M}) & \cdots & (1-m_{nn+1})\, \hat{X}_2/2(1-\hat{M}) \\ \vdots & \vdots & & \vdots \\ \hat{X}_n/2 & (1-m_{1n+1})\, \hat{X}_n/2(1-\hat{M}) & \cdots & (1-m_{nn+1})\, \hat{X}_n/2(1-\hat{M}) \end{bmatrix}.$$

By arguments similar to those of the previous sections the nonzero eigenvalues of **C** are those of the 2×2 matrix **D**:

$$\mathbf{D} = \begin{bmatrix} 0 & M_{n+1}/M \\ \frac{1}{2} & (1 - M_{n+1})/2(1 - M) \end{bmatrix}, \tag{30}$$

where $M_{n+1} = \sum_{l=1}^{n} m_{ln+1}\hat{X}_l$. Now $\mathbf{D}^2$ is a strictly positive matrix and hence, by the Frobenius theorem, the largest eigenvalue of the matrix is positive. This largest eigenvalue is greater than unity if and only if

$$(1 - 2M)(M - M_n) < 0. \tag{31}$$

Thus, as with models I and II we infer in the standard way that a symmetric n-allele equilibrium is unstable to invasion by A_{n+1} if either $M < \frac{1}{2}$ and $M_{n+1} < M$. Numerical iteration of (26) and (28) suggests that under these conditions the $(n+1)$-allele equilibrium achieved has a more even sex ratio than $M: 1 - M$.

At the $M = \frac{1}{2}$ equilibrium the local stability to invasion by A_{n+1} is governed by an eigenvalue of unity with the other nonzero eigenvalues given by the roots of a quadratic which are less than unity in absolute value. As with the other models we expect that there is fast return to an $(n+1)$-allele surface $M = \frac{1}{2}$ in this case.

Discussion

There are three components to the equilibrium structure common to models I–III, and these are independent of the number of alleles, n, involved:

(i) There are two classes of equilibria; a symmetric class with allele frequencies equal in the sexes and unequal sex ratio, and another class at which the sex ratio is one to one.

(ii) Any n-allele symmetric equilibrium is unstable to allele A_{n+1} if the marginal sex ratio M_{n+1} induced by A_{n+1} satisfies the property that $M_{n+1} > M$ if $M < \frac{1}{2}$ or $M_{n+1} < M$ if $M > \frac{1}{2}$. This condition is satisfied if the marginal sex ratio is more even than $M: 1 - M$, but it may also be satisfied if, for example, $M_{n+1} > \frac{1}{2}$ with $M_{n+1} - \frac{1}{2} > \frac{1}{2} - M$. Even so, numerical iteration of the various recursions suggests that in all three models, when a symmetric n-allele equilibrium is unstable the $(n+1)$-allele equilibrium ultimately reached has a more even sex ratio than $M: 1 - M$. It remains a conjecture that this is generally true in all three models. The proof promises to be difficult in view of the lack of monotonicity of the population sex ratio over time.

(iii) At any n-allele equilibrium with one to one sex ratio the leading eigenvalue controlling the local stability of the equilibrium to invasion by a new allele is unity. Thus, local linear analysis is not informative for stability. There appears, however, from numerical work, to be an $(n+1)$-allele surface of even sex ratio which is rapidly reached from a starting condition near an n-allele even sex ratio equilibrium.

These results produce the conjecture that there is a long-term evolutionary tendency to favor those alleles producing a more even sex ratio.

Suppose, more generally, that in a population with alleles $A_1, A_2, \ldots, A_n$ affecting only the sex ratio there is a sex ratio $M^*: 1-M^*$ with the following two properties:

I. Any equilibrium of the population with alleles $A_1, A_2, \ldots, A_n$ and a sex ratio $M: 1-M$ other than $M^*: 1-M^*$ is unstable to allele A_{n+1} if $M < M^*$ and $M_{n+1} > M$ or if $M > M^*$ and $M_{n=1} > M$, where M_{n+1} is the marginal sex ratio for A_{n+1} at the n-allele equilibrium.

II. At any n-allele equilibrium with sex ratio $M^*: 1-M^*$ the leading eigenvalue controlling the local stability of the equilibrium to invasion by a new allele is unity.

A sex ratio $M^*: 1-M^*$ satisfying properties I and II is said to exhibit *evolutionary genetic stability*, EGS. In the models considered above the even sex ratio appears to have EGS. Properties I and II are not sufficient to guarantee that the population sex ratio should approach $M^*: 1-M^*$; the latter would require global dynamic analysis of the genotype frequency recursions. Numerical work on the three models treated above suggests that there is long-term global evolution toward the even sex ratio.

It should be stressed that EGS invokes only the kinetics (and therefore only the parameters) of the genetic model. Fisher's original argument and many subsequent studies of the sex ratio (and other evolutionary problems) were made in terms of optimal population strategies. Many have used the concept of evolutionary stable strategy introduced by Maynard Smith and Price (1973). We suggest that since properties I and II involve only the underlying population genetic recursions, and require the introduction of no "payment" functions extraneous to the kinetic genotype frequency model, EGS arguments constitute a more direct population genetic approach, one which may prove to be useful for population genetic models of the evolution of other parameters.

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