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Effects of Selection on the Evolution of the Sex Ratio

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Abstract

Hypotheses as to the biological bases of observed sex ratios must explain the departures found in natural populations from the ratio which might be expected from the mechanism of sex determination in the species. Models based on the concept of parental investment (Fisher 1930) have been used to explain such departures but do not predict equilibrium sex ratios when viability selection discriminates between the sexes in the period between the end of parental investment and the maturity of the offspring. In the present paper, a model is presented which allows examination of the effect of selection on the allelic frequencies at an autosomal locus which has an effect on the sex ratio of offspring. Conditions are given for the maintenance of a (stable) polymorphism and for an allelic substitution in cases of uni- or biparental control of the ratio.

Introduction

The ratio of the numbers of individuals of the two sexes in a species is often near that which might be expected from the mechanism of sex determination of that species. The ratios need not, however, be solely controlled by these mechanisms. There are numerous instances of genetic and other factors causing distortions of the sex ratios in a species (Crow and Kimura 1970; Eshel 1975). Mechanisms of large effect have been found in meiotic drive in *Drosophila melanogaster* (Peacock and Miklos 1973) and the 'sex-ratio' condition in *Drosophila* spp. (Poulson and Sakaguchi 1961) and other organisms (Lanier and Oliver 1966). Smaller distortions have been discovered in plants (Mulcahy 1967; Lloyd 1973) and in humans (Lerner 1968) and other animals (Parkes 1935; Howe 1977; Maynard Smith and Stenseth 1978; Mori *et al.* 1979).

Fisher (1930) proposed that the sex ratio is controlled by the relative cost of rearing males and females. An individual would be expected to maximize its potential reproductive success by making an optimal allocation of investment to the rearing of sons and daughters. Fisher hypothesized that the maximization would lead to an equal total investment in males and females by the end of the period of such parental investment. Then, if the ratio of the costs of rearing males and females is $1 : c$, the sex ratio at the cessation of investment is $c : 1$.

The average cost of rearing an individual must take account of the cost of rearing individuals which die before the end of the period of parental investment. That is, the cost of rearing confounds the effects of viability selection between the sexes and of parental investment. Now, selection will not usually terminate with investment.

In those cases where selection does not so terminate, the sex ratio at other stages of the life cycle, such as reproductive maturity, is related to that at the end of parental investment by parameters describing the relative viabilities of males and females (Fisher 1930; Crow and Kimura 1970; Spieth 1974). Selection after the period of investment may alter the genotypic composition of the population when frequencies differ between the sexes. There will then be a consequential change in the genotypic frequencies and sex ratio of the zygotic population of the next generation. Hence the actual sex ratios and the identities of the alleles which persist at a locus determining the ratio in offspring are dependent on the dynamics of the selection process. The aim of the present paper is to develop a model of these dynamics which allows prediction of equilibrium sex ratios and allelic frequencies at an autosomal locus.

The Model

Description of the Model

The model assumes two alleles (A_1 and A_2) at an autosomal locus which controls the sex ratio among offspring. The zygotic proportion of males from the parental mating $A_1A_1 \times A_1A_1$ is m and is m' in all other matings so that if an individual has an A_2 allele then there will be a fraction m' of males in its offspring regardless of the genotype of its mating partner. The model assumes that the sexes have a similar effect on the sex ratio of progeny. In general, however, the magnitude of the effects would differ between the sexes. In particular, alleles may have an effect in one sex only. This situation has been widely modelled (Spieth 1974; Uyenoyama and

Table 1. Mating types of the parental generation and sex and genotype frequency of the F_1 generation
The upper value(s) in each cell refer to male genotypic frequencies

Female	Male: A_1A_1	A_1A_2	A_2A_2
A_1A_1	f_1g_1m; A_1A_1 f_1g_1f; A_1A_1	$\frac{1}{2}f_2g_1m'$; A_1A_1 and A_1A_2 $\frac{1}{2}f_2g_1f'$; A_1A_1 and A_1A_2	f_3g_1m'; A_1A_2 f_3g_1f'; A_1A_2
A_1A_2	$\frac{1}{2}f_1g_2m'$; A_1A_1 and A_1A_2 $\frac{1}{2}f_1g_2f'$; A_1A_1 and A_1A_2	$\frac{1}{4}f_2g_2m'$; A_1A_1 and A_2A_2 $\frac{1}{2}f_2g_2m'$; A_1A_2 $\frac{1}{4}f_2g_2f'$; A_1A_1 and A_2A_2 $\frac{1}{2}f_2g_2f'$; A_1A_2	$\frac{1}{2}f_3g_2m'$; A_1A_2 and A_2A_2 $\frac{1}{2}f_3g_2f'$; A_1A_2 and A_2A_2
A_2A_2	f_1g_3m'; A_1A_2 f_1g_3f'; A_1A_2	$\frac{1}{2}f_2g_3m'$; A_1A_2 and A_2A_2 $\frac{1}{2}f_2g_3f'$; A_1A_2 and A_2A_2	f_3g_3m'; A_2A_2 f_3g_3f'; A_2A_2

Bengtsson 1979). Examples of paternally controlled distortions of progeny sex ratio are known in mosquitoes (Hickey and Craig 1966), *Drosophila melanogaster* (Novitski and Hanks 1961) and cattle (Bar-Anan and Robertson 1975). Grant (1975) described a mechanism in dioecious angiosperms which may result in maternally caused sex ratio distortion. It is shown in the discussion of this paper that the present model is readily reducible to cover cases where such uniparental control of progeny sex ratio is associated with an autosomal locus. The model is, also, sometimes applicable to biparental control of the sex ratio. It covers cases where the probability of fertilization by the two types of sperm is the same for all matings except that of A_1A_1 males and females. Differences in the probability of fertilization would arise if there was

an association between sperm type and the A_1A_1 genotype affecting the relative viability of sperm or the compatibility of gametes. In the most general case there may be distinct progeny sex ratios for all matings. The extension of the present model to the general case is not attempted in this paper, owing to its algebraic intractibility.

The parental population in any given generation has fractions of $f_1A_1A_1$, $f_2A_1A_2$ and $f_3A_2A_2$ males and $g_1A_1A_1$, $g_2A_1A_2$ and $g_3A_2A_2$ females, where $\Sigma f_i = \Sigma g_i = 1$. It is assumed that mating is random and that all mating types have equal average fertility. The sex and genotype of the zygotes of the F_1 is indicated in Table 1. It is further assumed that there is a uniform selection against males whatever their genotype. The relative viabilities are written as $1-s$ for males and 1 for females. The frequencies in Table 1 are weighted by these viabilities to give the following equations for calculation of the genotypic frequencies after one generation of selection:

$$h(A_1A_1) = \{(f_1g_1+\tfrac{1}{2}f_2g_1+\tfrac{1}{2}f_1g_2+\tfrac{1}{4}f_2g_2)[m'(1-s)+f'] + f_1g_1[(m-m')(1-s)+(f-f')]\}/\overline{W}, \quad (1)$$

$$h(A_1A_2) = (f_2g_1+f_2g_3+f_1g_2+f_3g_2+f_2g_2+2f_1g_3+2f_3g_1)[m'(1-s)+f']/2\overline{W}, \quad (2)$$

$$h(A_2A_2) = (\tfrac{1}{4}f_2g_2+\tfrac{1}{2}f_3g_2+\tfrac{1}{2}f_2g_3+f_3g_3)[m'(1-s)+f']/\overline{W}, \quad (3)$$

where $f(=1-m)$ and $f'(=1-m')$ are the proportions of female offspring from a mating and $\overline{W}$, the mean fitness of the population, equals

$$m'(1-s)+f'+f_1g_1[(m-m')(1-s)+(f-f')]$$

and can be written as

$$1-sm'-sf_1g_1(m-m').$$

The definitions are adopted that k is the proportion of males in the parental population, that F_n and G_n are the frequencies of allele A_2 in males and females of the nth generation and that symbols with a $\wedge$ (e.g. $\hat{F}$) are the equilibrium values of these parameters.

Equilibrium of the Sex Ratio

(1) $\hat{F} = \hat{G}$

The mean fitness of the males regarded as a population is written as

$$\overline{W}_m = (1-s)m'+f_1g_1(1-s)(m-m')$$

and that of females as

$$\overline{W}_f = (1-m')-f_1g_1(m-m').$$

The difference of the frequency of A_2 in males and females can be written as

$$F_1-G_1 = [x(1-s)m'/\overline{W}_m]-(xf'/\overline{W}_f), \quad (4)$$

where the term x is derived from equations (1) to (3) by summing the male and female fractions of the genotypic frequencies and is equal to

$$F_0G_0+\tfrac{1}{2}F_0(1-G_0)+\tfrac{1}{2}G_0(1-F_0)$$

which simplifies to $\frac{1}{2}(F_0+G_0)$. Then, after expansion and simplification,

$$F_1-G_1 = (F_0+G_0)(1-s)f_1g_1(m'-m)/2\overline{W}_m\overline{W}_f. \tag{5}$$

At equilibrium $F_1 = F_0$ and $G_1 = G_0$ so that if $\hat{F} = \hat{G}$ then

$$(\hat{F}+\hat{G})(1-s)f_1g_1(m'-m) = 0.$$

This equation can be satisfied if $\hat{F} = 0, f_1 = 0$ or $m = m'$. That is to say, the only possible equilibria when the alleles do not have identical effect on the sex ratio are the trivial cases when the frequency of allele A_2 is 1 or 0. The equilibrium value of the sex ratio can be calculated as follows:

$$\hat{k} = \hat{\overline{W}}_m/\hat{\overline{W}} = [m'(1-s)+f_1g_1(m-m')(1-s)]/\hat{\overline{W}}. \tag{6}$$

Therefore

$$m'(1-f_1g_1)(1-s+\hat{k}s) = \hat{k}-f_1g_1m(1-s+\hat{k}s). \tag{7}$$

Then if A_1 is fixed in the population

$$\hat{k} = m(1-s)/(1-sm),$$

and if A_2 is fixed

$$\hat{k} = m'(1-s)/(1-sm').$$

(2) $\hat{F} \neq \hat{G}$

The change in the frequency (Δfr.) of A_2 from the parental generation to the filial generation is given by the equation

$$\Delta\text{fr.}(A_2) = [(1-sm')(F_0+G_0)/2\overline{W}_0-(F_0k_0+G_0(1-k_0)],$$

where $\overline{W}_0$ and k_0 are the parental values of these parameters. Writing $sf_1g_1(m-m')$ as a we have:

$$\begin{aligned}\Delta\text{fr.}(A_2) &= [\overline{W}_0(F_0+G_0)+a(F_0+G_0)]-2\overline{W}_0[(F_0-G_0)k_0+G_0)]/2\overline{W}_0\\ &= [\overline{W}_0(F_0-G_0)+a(F_0+G_0)-2k_0\overline{W}_0(F_0-G_0)]/2\overline{W}_0. \end{aligned}\tag{8}$$

At equilibrium, $\Delta\text{fr.}(A_2) = 0$ so that

$$\begin{aligned}\hat{k} &= [\hat{\overline{W}}(\hat{F}-\hat{G})+a(\hat{F}+\hat{G})]/2\hat{\overline{W}}(\hat{F}-\hat{G})\\ &= \tfrac{1}{2}+a(\hat{F}+\hat{G})/2\hat{\overline{W}}[(\hat{F}+\hat{G})(1-s)\hat{f}_1\hat{g}_1(m'-m)/2\hat{\overline{W}}_m\hat{\overline{W}}_f]\end{aligned}$$

when the value derived from equation (5) is substituted for $\hat{F}-\hat{G}$. Therefore

$$k = \tfrac{1}{2}-s\hat{\overline{W}}_m\hat{\overline{W}}_f/(1-s)\hat{\overline{W}} \tag{9}$$

$$\simeq \tfrac{1}{2}-0(s)/4. \tag{10}$$

When s is small the equilibrium sex ratio of the population will be near 1 : 1. When, however, s is large the ratio may be markedly different from this ratio.

(3) *Attainment of equilibria*

Substitution of one allele for another requires that the successful allele increases in frequency in both sexes when it is present in low or high frequencies. The change of the frequency of the allele A_2 in males is

$$\tfrac{1}{2}(F_0+G_0)(1-s)m'/\overline{W}_m-F_0$$

which depends in sign on

$$(G_0-F_0)m'-2F_0f_1g_1(m-m').$$

The change in frequency in females depends on

$$(F_0-G_0)(1-m')+2G_0f_1g_1(m-m').$$

If the frequency of A_2 increases in both sexes then, by addition,

$$(G_0-F_0)[2m'-1+2f_1g_1(m-m')] > 0.$$

If $m > m'$ then by application of equation (5) to the previous generation $(G_0-F_0) > 0$ so that A_2 may increase in both sexes when $[2m'-1+2f_1g_1(m-m')] > 0$. When A_2 is low in frequency $f_1g_1 \simeq 1$ so that the increase of A_2 is conditional on m being larger than $\frac{1}{2}$. When A_2 is high in frequency the expression will be positive when $m' > \frac{1}{2}$. So a necessary condition for the increase in frequency of A_2 in both sexes is that $\frac{1}{2} < m' < m$. The corresponding condition when $m < m'$ is that $m < m' < \frac{1}{2}$. Similar conditions can be derived for the decrease of allele A_2 in frequency in both sexes. The conditions are not, however, sufficient for the increase or decrease of the frequency of an allele since the term

$$(G_0-F_0)[2m'-1+2f_1g_1(m-m')]$$

may have the appropriate sign if the changes are in different directions in the two sexes.

Allele A_2 may increase in frequency in both sexes where it is rare and decrease when it is common. This will result in a polymorphism at the locus. In such cases, the values of m and m' lie either side of $\frac{1}{2}$.

In many species, the mechanism of sex determination, in the absence of gametic selection, leads to an expected zygotic sex ratio of 1 : 1. It is of interest to ascertain whether a new allele can be established in a population where the common allele produces male and female progeny in equal numbers. It has not been possible to answer this question analytically in the absence of conditions for the increase or decrease of allelic frequencies in a particular sex. But if $m' = \frac{1}{2}$, it can be shown that an A_2-type allele can not be eliminated from the population. In this case,

$$(G_0-F_0)[2m'-1+2f_1g_1(m-m')] = E(m-m')^2 > 0,$$

since E is positive, and hence alleles of the A_2 type cannot decrease in frequency in both sexes. On the other hand, computer analysis of a deterministic model incorporating equations (1) to (3) has shown that a polymorphic equilibrium may result when $m \neq \frac{1}{2}$, $m' = \frac{1}{2}$ and A_1-type alleles are initially at low frequencies. Similar

equilibria are obtained when $m = \frac{1}{2}$, $m' \neq \frac{1}{2}$ and A_1 is low in frequency but do not seem to occur when A_1 is high in frequency, since then the frequency of A_1 is found to increase in each case modelled. This implies that an A_1 allele with $m = \frac{1}{2}$ is protected against the establishment of an A_2 allele.

Discussion

Analysis of the present model permits a description of the sex ratio as a function of the genotypic frequencies in the two sexes and of the differences in their viabilities. The degree to which the equilibrium sex ratio at maturity deviates from an expected value of 1 : 1 depends on the selective differential. The present description is not dependent on knowledge of the relative cost of rearing of the two sexes and therefore it may be more useful to the prediction of the sex ratio in subsequent generations than models based on rearing costs in which it is difficult to measure cost parameters.

Uyenoyama and Bengtsson (1979) have recently investigated the evolution of the sex ratio in cases of maternal uniparental control with variable brood size and no selection. The model described in the present paper can be reduced to the case of uniparental control by substituting the value of 1 for f_1 (maternal control) or for g_1 (paternal control) in any term in the analysis of the form $sf_1g_1(m-m')$. When $s = 0$, the model is equivalent to a simplified Uyenoyama–Bengtsson model with dominance and no differences in fertility. As expected, the equilibrium sex ratio in this case is 1 : 1. When $s \neq 0$, however, the sex ratio depends on the values of s, m and m'. When selection is operative the sex ratio may differ from that predicted by the relative rearing costs of the sexes. This is in contrast to the finding of Uyenoyama and Bengtsson (1979) that the sex ratio would evolve towards the value predicted by the relative rearing costs despite variation in the maternal fertility. No analysis has yet been made of the interaction of selection and brood size in the determination of sex ratios.

There are four further factors which may complicate the determination of the sex ratio in a given population. Firstly, the ratio is dependent on the history of substitution and polymorphism at the locus. A general model would describe the progress of an allele arising at a locus which already has an arbitrary number of alleles. The second complication is the possibility that other loci with a modifying effect on the sex ratio may not be independent of the studied locus in action and/or linkage. Thirdly, it has long been recognized that sex linkage of a locus controlling the ratio alters the expected value of the ratio (Hamilton 1967; Eshel 1975). Finally, departures from random mating, particularly inbreeding, have an effect on the expected sex ratio (Maynard Smith 1978). The present model, whilst offering an explanation of the effect of selection on population sex ratios, would need to be extended to take account of the operation of one or more of these complicating factors.

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