Vol. 138, No. 4 The American Naturalist October 1991

PARENT-OFFSPRING CONFLICT OVER THE SEX RATIO IN A DIPLOID POPULATION WITH DIFFERENT INVESTMENT IN MALE AND IN FEMALE OFFSPRING

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Submitted August 18, 1989; Revised September 4, 1990; Accepted September 21, 1990

Abstract.—A two-locus diploid model is developed in order to analyze stable mother's and offsprings' strategies concerning the offsprings' sex determination and progeny's sex ratio when the cost of rearing a male offspring is different from the cost of rearing a female offspring. It is shown that if the ratio in cost is $\lambda:1$, then the resulting stable sex ratio in the population lies between the value $1:\lambda$, obtained with full mother's control, and $1:\lambda^{1/2}$, obtained with no maternal interference. The effects of biologically relevant parameters on the sex ratio and sex determination are investigated.

Under the assumption that natural selection operates to increase the fraction of one's descendants in future generations, it has been argued by Fisher (1958, pp. 158–159) that natural selection in diploid, fully sexual populations should operate to adjust the sex ratio so that the total expenditure incurred for offspring of each sex shall be equal. This is so, as the argument goes, because in such populations each individual has exactly one male and one female parent; hence, the total number of offspring born to all males and to all females in the population must be the same. Thus, if the total expenditures incurred in producing males and females were not the same—say, if higher expenditure were incurred in producing females—"then, since the total reproductive value of males is equal to that of females, it would follow that those parents, the innate tendencies of which caused them to produce males in excess, would, for the same expenditure, produce a greater amount of reproductive value and in consequence would be the progenitors of a larger fraction of future generations. . . . Selection would thus raise the sex ratio until the expenditure upon males became equal to that upon females."

Assuming equal cost of a male and a female offspring, the assumption that natural selection operates to increase the fraction of one's descendants in future generations is readily reduced to the assumption that it operates to increase the number of one's grandoffspring (see, e.g., Eshel 1975); and, at least under the assumption of a panmictic population, Fisher's argument leads to the prediction that natural selection should then operate to establish an even sex ratio of 1:1.

Am. Nat. 1991. Vol. 138, pp. 954–972.

This prediction has been extensively studied under the exact dynamics of various genetic models. It proved false when sex was determined by a sex-linked locus (Hamilton 1967; see also Thomson and Feldman 1975; Bengtsson 1977; Charlesworth 1977; Uyenoyama and Bengtsson 1981, 1982; Eshel and Feldman 1982*b*), in which case Fisher's argument for the maximization of grandoffspring number can be replaced by the likewise intuitive argument of the maximization of the number of one's genes carried by grandoffspring (Eshel 1984*a*, 1984*b*). The prediction that, under the assumption of equal costs of a male and a female offspring, in a panmictic population the sex ratio tends to 1 : 1 has been proved when sex is determined by autosomal loci, carried either by the mother (Nur 1974; Uyenoyama and Bengtsson 1981, 1982; Eshel and Feldman 1982*a*) or by the individual (Eshel 1975; Uyenoyama and Bengtsson 1979, 1981, 1982; Eshel and Feldman 1982*a;* Karlin and Lessard 1983, 1984). Indeed, in this case the number of one's grandoffspring is easily shown to be proportional to the number of one's genes carried by grandoffspring.

These results have been recently extended to systems determined by two loci and more (Liberman et al. 1990). More specifically, it has been shown that if either one's own sex or the sex ratio among one's progeny is determined by any number of autosomal loci with any number of alleles in each and if the system is already at an internally stable equilibrium, then a new, nonepistatic mutation at any of the loci will be successfully established in the population if and only if it initially renders the population sex ratio closer to 1 : 1.

Unlike in the case of one-locus systems, however, it is not true that the short-term dynamics of changes in genotype frequencies in a closed, multilocus system lead to a sex ratio closest to 1 : 1 (Karlin and Lessard 1986).

More important to our subject, however, is the general finding that in the case of an equal cost of rearing a male and a female offspring, the same sex ratio, 1 : 1, is established in the population regardless of whether the sex ratio among the progeny is determined by the genotype of the mother or (because of individual sex determination) by the different genotypes of the offspring. In fact, if the costs of a male and a female offspring are the same, then Fisher's argument about the equality of the reproductive value of (all) males and (all) females leads to the establishment of the same sex ratio, 1 : 1, in both cases.

The situation is essentially different if rearing an offspring of one sex costs more than rearing an offspring of the other sex—say, if the cost of rearing a male is λ times the cost of rearing a female ($\lambda > 1$). We shall see that in this case, not surprisingly, natural selection, when operating on autosomal genes that affect the mother's behavior, leads to the establishment of a sex ratio of 1 : λ, which means a ratio of expenditures of 1 : 1, as predicted by Fisher. Yet, in this case, since the number of males in the population is lower than the number of females, each male has more offspring, on the average, than each female. Thus, an argument similar to Fisher's may lead to the conclusion that natural selection, when operating on genes that determine the sex of their carrier, favors those mutations that increase the chance of their carriers' becoming males. In fact, an analysis of the exact genetic model verifies this conjecture, as we see, although the situation then proves more complicated, and natural selection will not operate to establish an offspring-determined sex ratio of 1 : 1. Yet it will be different from the sex ratio 1 : λ resulting from selection pressure on the mother's locus. Hence, as long as the cost of rearing a male offspring is different from the cost of rearing a female offspring, we are likely to envisage a parent-offspring conflict over the sex of the offspring. Yet the exact formulation of this conflict in terms of population game theory is complicated since, as we see, the very payment function of the offspring is not that clear, although it seems qualitatively clear that it involves some factor of kin selection.

The main objective of this work is to analyze the dynamics of a two-locus model in which the sex of an individual is determined primarily by the pair of alleles it carries at one locus while the mother's investment in offspring of the two sexes is affected by the pair of alleles she carries in another locus. We assume that maternal interference in the progeny's sex ratio can be executed either by aborting some offspring of the more expensive sex (say, males) or, if possible, by forcing them to convert their sex.

We employ a natural two-locus model to analyze the dynamics of the conflict. We find a (unique) mutually stable pair of mother's and offspring's strategies, with a resulting sex ratio that, under appropriate conditions, may be a compromise between the sex ratios "desired" by the two parties or may be fully dominated by one party as the other gives up any interference. Finally, we use the findings of the model to explain why sex conversion is less common than selective abortions and to speculatively suggest a hypothesis for the evolution of nonsymmetrical chromosomal systems.

THE MODEL

Assume a diploid, randomly mating population in which the cost of rearing a male offspring is different from (say, higher than) the cost of rearing a female offspring. Let the ratio in cost be $\lambda : 1$ ($\lambda > 1$). Assume that the sex of an offspring is determined primarily by its own genotype, but the mother can interfere and change the sex ratio among her progeny either by aborting a surplus of male offspring or, if possible, by forcing sex conversion of a certain quota of male offspring. Assume, though, that a forced conversion is of some cost in family resources (otherwise, the problem readily becomes equivalent to that of sex determination by the mother). The cost of conversion may result from the fact that a converted male is less viable, less fertile, less attractive, or still more expensive than an original female offspring. For the sake of simplicity, we assume that the cost of conversion is all manifested in viability reduction by a factor of $1 - \theta$ ($0 \leq \theta \leq 1$) on the part of the converted offspring. We refer to θ as the risk of sex conversion. Note that if $\theta = 1$ (i.e., if all the so-called "converted" males die), we end with the case in which the mother aborts a surplus of males rather than attempting to convert them. It is convenient, though, to deal with the two cases (sex conversion with a risk $0 \leq \theta < 1$ and abortion, where $\theta = 1$) by using the same parametric model. In the course of our analysis of the model, however, we pay special consideration to the case in which $\theta = 1$, which is, in fact, more common in nature (including human populations).

Finally, assume that the cost of a dead offspring is c times that of rearing a female offspring ($0 \leq c \leq \lambda$). Assume that each mother has, independent of the part of her genome that is responsible for sex conversion, a fixed amount of resources, which is the only factor limiting her progeny number. Thus, if a proportion, m, of her offspring determine themselves primarily as males and if she chooses to convert a proportion x of them, then a proportion $(1 - x)m$ of all her potential offspring will be surviving males, a proportion θxm will be lost, and a proportion $(1 - \theta)xm + 1 - m$ will become proper females. The average cost per offspring (either lost or alive, male or female) is, therefore,

$$W = (1 - x)m\lambda + \theta xmc + (1 - \theta)xm + 1 - m . \tag{1}$$

The total number of male offspring reared by the mother will therefore be proportional to

$$M = (1 - x)m/W = (1 - x)m/(1 + am - bmx) , \tag{2}$$

where

$$a = \lambda - 1 > 0 \tag{3}$$

and

$$b = \lambda - 1 + (1 - c)\theta = a + (1 - c)\theta > 0 . \tag{4}$$

(More precisely, M is the number of reared males divided by the total number of female offspring that the mother's resources are sufficient to produce.)

The total number of female offspring reared by the same mother will be proportional to

$$F = \frac{1 - m + (1 - \theta)xm}{W} = \frac{1 - m + (1 - \theta)mx}{1 + am - bmx} . \tag{5}$$

Assume now that primary sex determination depends, at least in a probabilistic sense, on the alleles carried by the offspring at one locus while the behavior of the mother depends on the alleles she carries in another locus.

Given the parameters θ, c, and λ, we are interested in an evolutionarily stable pair of strategies (x^*, m^*) such that if the primary chance of being a male, m^*, is determined by a homozygous pair of alleles AA at the offspring's locus and the chance of converting the sex of a male offspring, x^*, is determined by a homozygous pair of alleles BB at the mother's locus, then fixation of the population on the genotype AB/AB will be stable against any nonepistatic mutations at either or both of the loci.

In the course of analysis we prove, further, that once the primary sex ratio $m^* : 1 - m^*$ is fixed in the offspring's locus, the mother's strategy x^* (to be explicitly calculated) has the property of evolutionary genetic stability (EGS; Eshel and Feldman 1982*a*, 1984), namely, that (1) fixation of x^* in the mother's locus is stable against any nonepistatic mutation affecting it, and (2) if a value x, close enough to x^*, is fixed in the mother's locus, then a new, nonepistatic mutation will successfully be established in the population if and only if it initially renders the average mother's strategy in the population closer to x^*.

Assuming a mutation of small effect relative to the rate of recombination, r (>0), between the two loci, it can be shown (C. Matessi and I. Eshel, unpublished manuscript; see Motro 1991 for a somewhat similar approach) that the frequency of the double mutant tends to the order of magnitude of the product of the frequencies of mutation at the two loci. In this case, local analysis can be carried out at each of the two loci separately.

In the next section we find, thus, a (unique) mother's strategy, $x^* = x^*(m)$ (say, a proportion of interferences with the sex of a male offspring), such that, given a fixed primary proportion of males, m (and given the parameters λ, θ, and c), x^* is evolutionarily stable against any mutation at the B locus.

Following that, we find a (unique) offspring's strategy, $m^* = m^*(x)$ (say, a primary proportion of males in the progeny), such that, given a fixed proportion, x, of mothers' interferences, m^* is evolutionarily stable against any mutation at the A locus.

Finally, we use these results to find and investigate the (unique) pair of strategies (m^*, x^*) that, once fixed in the population, is stable against mutation at either locus.

Note that by using the dynamics of an exact two-locus model, we end here with a definition of two-strategy stability slightly weaker than the one suggested by Maynard Smith and Parker (1976) and formally analyzed by Selten (1980). (See Summary, Discussion, and Some Speculation for details.)

MOTHER'S EVOLUTIONARILY STABLE STRATEGY

Assume that the population is fixed on the genotype AB/AB, determining a strategy $0 < m < 1$ on the part of the offspring and $0 \leq x < 1$ on the part of the mother. Assume that a rare mutation b is introduced at the mother's locus.

Let the proportion of males being converted by a heterozygote Bb mother be x', and let the proportion of the heterozygous mutant be $\epsilon_1 > 0$ and $\epsilon_2 > 0$ among adult males and females, respectively, where ϵ_1 and ϵ_2 are small.

Assuming random mating, we know that the proportion of the homozygous mutant bb will be on the order $o(\epsilon_1, \epsilon_2)$ in both sexes.

The number of male and female offspring produced by a heterozygous mutant mother will be

$$M' = \frac{(1 - x')m}{1 + am - bmx'} \tag{6}$$

and

$$F' = \frac{1 - m + (1 - \theta)mx'}{1 + am - bmx'}, \tag{7}$$

respectively. If terms of order $o(\epsilon_1, \epsilon_2)$ are ignored, the number of male and female offspring of either a mutant or a resident father will be $(1 - \epsilon_2)M + \epsilon_2 M'$ and $(1 - \epsilon_2)F + \epsilon_2 F'$, like that of any father in the population, since these values are determined by his random mate. Since half the offspring of either a mother or a father of genotype Bb will be of that genotype, regardless of their sex, one gets

$$\epsilon_1' = \frac{\epsilon_1 M}{2M} + \frac{\epsilon_2 M'}{2M} = \frac{\epsilon_1}{2} + \frac{\epsilon_2}{2}\,\frac{1-x'}{1-x}\,\frac{1+am-bmx}{1+am-bmx'} \tag{8}$$

and

$$\epsilon_2' = \frac{\epsilon_1}{2}\,\frac{F}{F} + \frac{\epsilon_2}{2}\,\frac{F'}{F} = \frac{\epsilon_1}{2} + \frac{\epsilon_2}{2}\,\frac{1-m+(1-\theta)mx'}{1-m+(1-\theta)mx}\,\frac{1+am-bmx}{1+am-bmx'}. \tag{9}$$

The matrix of linear approximations of the transformation $\epsilon \rightarrow \epsilon'$ will, therefore, be

$$\left\|\frac{\partial \epsilon_i'}{\partial \epsilon_j}\right\| = \left\|\begin{matrix} \frac{1}{2} & \frac{1}{2}\,\frac{1-x'}{1-x}\,\frac{1+am-bmx}{1+am-bmx'} \\ \frac{1}{2} & \frac{1}{2}\,\frac{1-m+(1-\theta)mx'}{1-m+(1-\theta)mx}\,\frac{1+am-bmx}{1+am-bmx'} \end{matrix}\right\| . \tag{10}$$

This is a positive matrix, and, with the assumption of a small-effect mutation already made above, we know that the sum of the two expressions on its main diagonal is less than 2 (in fact, it is close to 1). By a straightforward calculation, one can thus show that a necessary condition for local stability against the specific mutation in question (i.e., for the leading eigenvalue of eq. [5] to be less than 1) is that

$$H(x, m; x') \leq 1\,, \tag{11}$$

where

$$H = \frac{1}{2}\,\frac{1+am-bmx}{1+am-bmx'}\left(\frac{1-x'}{1-x} + \frac{1-m+(1-\theta)mx'}{1-m+(1-\theta)mx}\right) \tag{12}$$

(a sufficient condition for stability is that expression [11] holds as a strict inequality).

Hence, a necessary condition for a mother's strategy x^*, if determined by BB, to be stable against all possible nonepistatic $B \rightarrow b$ mutation is that the inequality

$$H(x^*, m; x') \leq 1 \tag{13}$$

holds for all x'. But from equation (12) it follows that

$$H(x^*, m; x^*) = 1\,. \tag{14}$$

From expressions (13) and (14) it follows that (given m), if the mother's strategy x^* is stable against all mutation that changes it, then

$$H(x^*, m; x^*) \geq H(x^*, m; x') \tag{15}$$

for all $0 \leq x' \leq 1$.

If, on the other hand, expression (15) holds as a strict inequality for all $x' \neq x^*$, then we know that x^* is stable against all mutation.

Expression (15) implies that either

$$\frac{\partial H}{\partial x'}(0, m; x')\big|_{x'=0} \leq 0\,, \tag{16}$$

in which case $x^* = 0$, or, for $0 < x^* < 1$,

$$\frac{\partial H}{\partial x'}(x^*, m; x')|_{x'=x^*} = 0\,. \tag{17}$$

Note, however, that H is a linear fractional function of x' and that its denominator is always positive for $0 \leq x' \leq 1$. Hence (for given m and x), $\partial H/\partial x'$ does not change its sign as x' changes over the interval [0, 1]. Thus, if expression (16) holds as a strict inequality, then $x^* = 0$ and is, indeed, an evolutionarily stable strategy (ESS), because any mutant affecting the mother's strategy will be directly selected against.

Suppose now that

$$\frac{\partial H}{\partial x'}(x^*, m; x')|_{x'=x^*} = 0\,. \tag{18}$$

In this case, we know further that $H(x^*, m; x')$, as a function of x', is a constant (since its derivative, being zero at $x' = x^*$, must be zero for all $0 \leq x' \leq 1$). We prove, however, that the value x^*, satisfying equation (18), has the property of EGS (Eshel and Feldman 1982*a*, 1984; Eshel 1985), or, employing a terminology recently used by Taylor (1989), x^* is m-stable. That is to say, if the population is fixed on (x, m), where x is close to x^*, then natural selection will favor small-effect mutations determining maternal strategies in the direction of x^*. If expression (13) is used, this is equivalent to saying that $H(x, m; x')$ is larger than 1 when x' lies between x and x^* and smaller than 1 when x' lies on the other side of x; namely,

$$(x^* - x)\left.\frac{\partial H(x, m; x')}{\partial x'}\right|_{x'=x} > 0\,. \tag{19}$$

In order to prove this, we calculate

$$\begin{aligned}\left.\frac{\partial^2 H(x, m; x')}{\partial x \partial x'}\right|_{x=x'=x^*} &= -\frac{b^2m^2}{(1 + am - bmx^*)^2} \\ &\quad + \frac{bm}{1 + am - bmx^*}\left(\frac{1}{1 - x^*} - \frac{(1 - \theta)m}{1 - m + (1 - \theta)mx^*}\right) \\ &\quad - \frac{1}{2}\left(\frac{1}{(1 - x^*)^2} + \frac{(1 - \theta)^2m^2}{[1 - m + (1 - \theta)mx^*]^2}\right) \\ &< -\frac{b^2m^2}{(1 + am - bmx^*)^2} + \frac{bm}{1 + am - bmx^*}\,\frac{1}{1 - x^*} \\ &\quad - \frac{1}{4}\,\frac{1}{(1 - x^*)^2} \\ &= -\left(\frac{bm}{1 + am - bmx^*} - \frac{1}{2(1 - x^*)}\right)^2 < 0\,.\end{aligned} \tag{20}$$

From expressions (18) and (20), it follows that $\partial H(x,m;\, x')/\partial x'|_{x'=x^*}$ is equal in sign to $x^* - x$. However, since we already know that the sign of $\partial H(x,m;\, x')/\partial x$ is independent of x', we get

$$(x^* - x)\,\partial H(x,m;x')/\partial x' > 0 \tag{21}$$

for all x'. This implies, as a special case, expression (19), which is the condition for the evolutionary genetic stability of x^*.

COROLLARY 1. If, for a fixed value of m, the value $0 \leq x^* < 1$ satisfies either expression (16) or equation (17), then it has the property of EGS. Moreover, x^* is the only maternal strategy that, once fixed in the population, can be stable against all mutation affecting it.

Now, by interchange of parameters, expression (21) can be written as $(x^* - x')\,\partial H(x',m;\, x)/\partial x > 0$, which implies that

$$H(x',m;\, x^*) > H(x',m;\, x') \tag{22}$$

for all $x' \neq x^*$.

We therefore get

COROLLARY 2. For any fixed primary sex ratio $m\!:\!1 - m$, the conditions stated in expressions (16) and (17) for genetic stability (and, thus, in this case also EGS) of the mother's strategy x^* are equivalent to those of an ESS in a mother's population game in which $H(x,m;\, x')$ is the payment function of an individual (say, a mother) who plays x' where the population strategy is x (here, m is considered a natural force). More specifically, for $x' \neq x^*$, $H(x^*,m;\, x^*) \geq H(x^*,m;\, x')$; in the case of equality, $H(x',m;\, x^*) > H(x',m;\, x')$ (see Maynard Smith and Price 1973).

Moreover, from expression (13) it follows that natural selection pressure on the mother's behavior always operates to increase the individual's value of H. We can therefore say that the mother's payment function H is objectively deduced from the dynamics of the genetic model. Furthermore, inequality (20) guarantees that any m-dependent mother's ESS $x^* = x^*(m)$ is also continuously stable (Eshel and Motro 1981; Eshel 1983; see also Taylor 1989); that is, it is an ESS such that, if the population's strategy is close to it, each individual player can gain (in terms of the payment function H) by getting even closer to it. (For the condition stated in expression [20] for continuous stability, when $\partial^2 H(x^*,m;x')/\partial x'^2|_{x^*=0} = 0$, see Eshel 1983.) In a different terminology used by Taylor (1989), x^* is both a δ-stable and m-stable equilibrium of the mothers' population game in which H is the payment function.

For the biological interpretation of the payment function H, equations (2), (5), (6), (7), and (12) yield

$$H = \tfrac{1}{2}\,(M'/M + F'/F). \tag{23}$$

Hence, H can naturally be interpreted as the expected number of grandoffspring, where a male grandoffspring weighs λ times a female grandoffspring (cf. Fisher 1958). We can therefore conclude that, for any value of m, natural selection operates on the mother's locus to maximize an individual's (mother's) weighted number of grandoffspring.

We now check the condition stated in expression (16) for the evolutionary stability of the mother's strategy of no interference, $x^* = 0$. Employing equation (12), we get

$$H(0,m;x') = K\frac{2(1-m) - (1 - 2m + \theta m)x'}{1 + am - bmx'}, \tag{24}$$

where $K > 0$ and does not depend on x'. We know that $x^* = 0$ is stable if $H(0,m;x')$ is a nonincreasing function of x'. This holds if

$$2bm(1 - m) - (1 + am)(1 - 2m + \theta m) \leq 0. \tag{25}$$

Denote the left-hand side of expression (25) by $\varphi(m) = \varphi_{\lambda,\theta,c}(m)$, which we know to be a polynomial of order two with $\varphi(0) = -1 < 0$ and $\varphi(1) = (1 + a)(1 - \theta) = (1 - \theta)\lambda > 0$. Hence, $\varphi(m)$ changes its sign exactly once in the interval [0, 1].

COROLLARY 3. For any given values $\lambda > 1$, $0 \leq \theta \leq 1$, and $0 \leq c \leq \lambda$, there is a critical value m_0 between zero and one, with $m_0 = m_0(c,\lambda,\theta)$, such that, if the primary male frequency is less than m_0, the mother's strategy $x^* = 0$ of noninterference is externally stable (exhibits EGS). If the primary frequency of males is above this value, then the mother's strategy of noninterference is unstable against any mutation that introduces a positive level of interference.

We refer to m_0 as the maximal frequency of males tolerated by the mother. By straightforward calculations, employing expressions (3), (4), and (25), one can easily verify that $\varphi_{\lambda,\theta,c}(m)$ is a decreasing function of c. We already know that the curve of $\varphi_{\lambda,\theta,c}(m)$ intersects the m-axis from below at $m = m_0$. From the implicit-function theorem, therefore, it follows that $m_0 = m_0(\lambda,\theta,c)$ and is an increasing function of c. Moreover, one can see that, for $c = 0$, $\varphi_{\lambda,\theta,0}(1/[1 + \lambda]) = 0$; hence, $m_0(\lambda,\theta,0) = 1/(1 + \lambda)$.

COROLLARY 4. The maximal male-frequency m_0 tolerated by the mother is an increasing function of the cost c. It tends to $1/(\lambda + 1)$ as c tends to zero.

Note that as $c = 0$ and $m_0 = 1/(\lambda + 1)$, the sex ratio $1/(\lambda + 1)$: $\lambda/(\lambda + 1)$ guarantees an equal maternal investment in male and female offspring, as predicted by Fisher for the case in which the sex ratio among the progeny is fully determined by the parents. Since $c > 0$, the mother is forced to tolerate a higher frequency of males and, thus, to invest more in males than in females without interference. In the same way it can be shown that the maximal frequency of males, m_0, tolerated by the mother is an increasing function of θ (as long as $c > 0$) and a decreasing function of λ.

We now turn to the condition stated in equation (17) for the evolutionary stability of a mother's strategy $0 < x^* < 1$. When equation (12) is used, this condition becomes

$$\frac{2bm}{1 + am - bmx^*} + \frac{(1-\theta)m}{1 - m + (1-\theta)mx^*} - \frac{1}{1 - x^*} = 0.$$

Since all denominators are positive, this is reduced to a linear equation of x^* (with all x^{*2} terms canceling) with the (unique) solution

$$x^* = \frac{2bm(1 - m) + (1 + am)[(2 - \theta)m - 1]}{m\{-b[(2 - \theta)m - 1] + 2(1 + am)(1 - \theta)\}}, \tag{26}$$

provided that the left-hand side of equation (26) is positive. Note, however, that the numerator of equation (26) is equal to the left side of expression (25). The condition for the existence of a (then unique) positive mother's ESS $x^* > 0$ is, thus, that the mother's strategy $x = 0$ of noninterference is not evolutionarily stable.

In this case one can readily verify that x^* is an increasing function of m and a decreasing function of c. It is always less than one, since, for all $0 < m < 1$,

$$x^*(m) < x^*(1) = \lambda/[\lambda + 1 - (1 - c)\theta] < 1. \tag{27}$$

COROLLARY 5. For any given values $c > 0$, $0 \leq \theta \leq 1$, $\lambda > 1$, and $0 < m < 1$ there is a unique stable strategy x^* of the mother. This strategy, $x^* = x^*_{\lambda,\theta,c}(m)$, is a continuous function of c, λ, θ, and m. It is a nondecreasing function of m and a nonincreasing function of c.

In the special case of mother's pure abortion ($\theta = 1$), one can readily calculate $\varphi_{\lambda,1,c} = [2bm - (1 + am)](1 - m) = [2(\lambda - c)m - (1 + am)](1 - m)$. Hence,

$$m_0 = 1/(\lambda + 1 - 2c). \tag{28}$$

Equation (12) can be written as $H = K_m(x)(2 - x - x')/[1 + (\lambda - 1)m - (\lambda - c)mx']$, and equation (26), which determines the evolutionarily stable strategy $x^* > 0$, thus becomes

$$x^* = \frac{m(\lambda + 1 - 2c) - 1}{m(\lambda - c)}, \tag{29}$$

which is positive if and only if $m > m_0$.

COROLLARY 6. In the case of mother's pure abortion, ($\theta = 1$), the mother's ESS is given by

$$x^* = \begin{cases} 0 & \text{if } \; m \leq 1/(\lambda + 1 - 2c) = m_0 \\ \dfrac{m(\lambda + 1 - 2c) - 1}{m(\lambda - c)} & \text{if } \; m > 1/(\lambda + 1 - 2c). \end{cases} \tag{30}$$

OFFSPRING'S EVOLUTIONARILY STABLE STRATEGY

Assume, as in the preceding section, that the population is fixed on the genotype *AB*/*AB*, determining the pair of strategies (m, x). Assume now that the rare mutation is introduced into the offspring's locus. Let the primary rate of males among heterozygous mutant offspring *Aa* be m', and let the proportion of the heterozygous mutant *Aa* be $\delta_1 > 0$ and $\delta_2 > 0$ among adult males and females, respectively, with δ_1 and δ_2 small. Assuming random mating of males and females, we ignore, as before, the lower order of the proportions $o(\delta_1, \delta_2)$ of homozygous mutants.

Half the offspring of a heterozygous mutant parent, either a mother or a father, are of the same heterozygous type; therefore, the primary proportion of males in such parent's progeny is $(m + m')/2$. Employing equation (1), we calculate the average expenditure per offspring (male, female, or lost) in such progeny as

$$W' = 1 + (a - bx)(m + m')/2\,, \tag{31}$$

where a and b are given by expressions (3) and (4).

The total number of offspring (male, female, or lost) produced by such a parent, measured in units of family resources, is the reciprocal of equation (31). Of these, proportions $(1 - x)m'/2$ and $(1 - x)m/2$ will be of nonconverted mutant males and nonconverted wild-type males, respectively. Hence, the total number of mutant male offspring produced by a mutant parent is

$$M' = \frac{1}{2}\frac{(1 - x)m'}{1 + (a - bx)(m + m')/2} = \frac{(1 - x)m'}{2 + (a - bx)(m + m')}\,. \tag{32}$$

In the same way, the total number of mutant female offspring produced by a mutant parent is

$$F' = \frac{1 - m' + (1 - \theta)xm'}{2 + (a - bx)(m + m')}\,. \tag{33}$$

We compare these with the M males and F females as given by equations (2) and (5), respectively.

The frequency of heterozygous mutants among all surviving male offspring of the next generation is, thus,

$$\delta_1' = \tfrac{1}{2}(\delta_1 + \delta_2)M'/M\,. \tag{34}$$

Among female offspring of the next generation, it is

$$\delta_2' = \tfrac{1}{2}(\delta_1 + \delta_2)F'/F\,. \tag{35}$$

From equations (32) to (35), we get

$$\begin{aligned}\frac{\delta_1' + \delta_2'}{\delta_1 + \delta_2} &= \frac{1}{2}\left(\frac{F'}{F} + \frac{M'}{M}\right)\\ &= \frac{1 + am - bmx}{2 + (a - bx)(m + m')}\left(\frac{m'}{m} + \frac{1 - m' + (1 - \theta)m'x}{1 - m + (1 - \theta)mx}\right)\\ &= G(x, m; m')\,.\end{aligned} \tag{36}$$

The new mutation will, thus, successfully enter the population if $G > 1$. It will become extinct if $G < 1$.

As in the case of an evolutionarily stable mother's strategy, we are interested in an offspring's strategy $m^* = m^*(x)$ $(0 < m^* < 1)$, such that for all m and m' that are close to it,

$$\begin{cases} G(x, m; m') > 1 & \text{if } (m - m')(m - m^*) > 0 \\ G(x, m; m') < 1 & \text{if } (m - m')(m - m^*) < 0\,. \end{cases} \tag{37}$$

In other words, we are interested in a strategy m^* with the property of evolutionary genetic stability. We find a (unique) value m^* that satisfies expression (37) at least for a mutation of small effect. Since $G(x, m; m) = 1$ for all $0 < m < 1$, this is equivalent to

$$\begin{cases} \partial G(x, m; m')/\partial m' \,|_{m'=m} > 0 & \text{if } \; m < m^* \\ \partial G(x, m; m')/\partial m' \,|_{m'=m} < 0 & \text{if } \; m > m^* . \end{cases} \tag{38}$$

But G, as defined in equation (36), is a linear fraction of m'. It can be written as

$$G = T(m,x)\frac{m + [1 - 2m + 2x(1 - \theta)m]m'}{2 + (a - bx)m + (a - bx)m'},$$

where $T(m,x) > 0$ is independent of m'. Hence,

$$\partial G/\partial m' = \tau\{1 - 2[1 - (1 - \theta)x]m - [1 - (1 - \theta)x](a - bx)m^2\}, \tag{39}$$

where $\tau > 0$. One can easily verify that the right-hand side of equation (39) is positive for $0 < m < m^*$ and negative for $m^* < m < 1$, where

$$m^* = \frac{1}{1 - (1 - \theta)x + \{[1 - (1 - \theta)x][(1 - x)\lambda + \theta cx]\}^{1/2}}. \tag{40}$$

Corollary 7. Given the mother's strategy x (and, indeed, the parameters c, λ, and θ), the primary frequency of males, m^*, determined by equation (40), is the only one with the property of evolutionary genetic stability.

Employing the same technique as in the preceding section, one can readily show that, given the mother's strategy x, the offspring's strategy with EGS, $m^* = m^*(x)$, is an ESS of the offspring's population game in which each individual tends to choose an individual strategy m' that maximizes his own payment function, $G(x, m; m')$. Moreover, such an ESS is always continuously stable C (m-stable, in the terminology of Taylor 1989).

While the biological interpretation of the mother's payment function, H, is easy to interpret, it appears that the offspring's payment function, G, deduced from genetic dynamics, is less easy to obtain intuitively. However, a recent result by Taylor (1989) indicates that, under the assumption of weak selection, m-stability of the exact, one-locus genetic model (in this case, the offspring's locus) is equivalent to m-stability of the population game in which the payment function is the inclusive fitness, calculated with the appropriate regression coefficients. Hence, G should be recognized as equivalent to (i.e., monotonously increasing with) the offspring's inclusive fitness.

One can easily verify that the stable primary proportion of males, m^*, is a decreasing function of c, θ, and λ. It is an increasing function of the level of maternal interference, x.

Corollary 8. If the mother can interfere only by aborting a surplus of males (i.e., if $\theta = 1$), then the stable primary proportion of males in the population is

$$m^* = \frac{1}{1 + [\lambda(1 - x) + cx]^{1/2}}. \tag{41}$$

Finally, in the special case of $x = 0$, when the mother does not interfere at all, equation (40) becomes $m^*(0) = 1/(1 + \lambda^{1/2})$.

COROLLARY 9. The "desired" offspring sex ratio, selected for in the case of absence of maternal interference, is

$$m^*(0):[1 - m^*(0)] = 1:\lambda^{1/2}. \tag{42}$$

This sex ratio guarantees the reverse ratio, $\lambda^{1/2}:1$, between parents' investments in male and parents' investments in female offspring.

Note that when the sex ratio stated in equation (42) is maintained in the population, there is an advantage of $\lambda^{1/2}:1$ to an investment in a female over an investment in a male offspring in terms of one's direct expected contribution to future generations. However, there is the same advantage of $\lambda^{1/2}:1$ to a female over a male offspring in terms of the family's contribution to future generations (indeed, the cost of each male offspring is λ times that of a female offspring, whereas his expected contribution to future generations is only $\lambda^{1/2}$ times that of a female offspring).

MOTHER-OFFSPRING STABLE PAIR OF STRATEGIES

We are now interested in a pair $(\hat{x}, \hat{m})$ of mother's and offspring's strategies that is stable against mutation at any of the two loci. For this, we have to solve the equations

$$\hat{x} = x^*(\hat{m}) \tag{43}$$

and

$$\hat{m} = m^*(\hat{x}), \tag{44}$$

in which the functions $x^*(m)$ and $m^*(x)$ are defined in equations (26) and (40), respectively. We are looking for solutions in the biologically relevant range of $0 < \hat{m} < 1$ and $0 \le \hat{x} < 1$.

We start by investigating a possible solution of the form $0, \hat{m}$, in which the sex ratio $\hat{m}:(1 - \hat{m})$ is fully determined by the offspring and in which the mother's strategy of noninterference is evolutionarily stable. Following equations (42) and (44), we know that in this case $\hat{m} = m^*(0) = 1/(1 + \lambda^{1/2})$, regardless of θ and c. Hence, the condition stated in expression (25) for the stability of $\hat{x} = 0$ becomes $2b\lambda^{1/2} - (1 + \lambda^{1/2} + a)(\lambda^{1/2} - 1 + \theta) \le 0$. When expressions (3) and (4) are used, this becomes

$$\lambda - 1 \le \theta(\lambda^{1/2} - 1 + 2c). \tag{45}$$

COROLLARY 10. (i) A necessary and sufficient condition for the evolutionary stability of the mother's strategy of noninterference, $\hat{x} = 0$, is

$$c \ge (\lambda^{1/2} - 1)(\lambda^{1/2} + 1 - \theta)1/2\theta = c^*. \tag{46}$$

(ii) In the case of mother's pure abortion, $\theta = 1$, the condition stated in expression (46) becomes

$$c \ge (\lambda - \lambda^{1/2})/2. \tag{47}$$

(iii) For any value of $\theta \le 1$, the condition stated in expression (47) is necessary for the stability of $\hat{x} = 0$. Once it is satisfied, then a necessary and a sufficient condition for the stability of $\hat{x} = 0$ is

$$\theta \geq \frac{\lambda - 1}{\lambda^{1/2} - 1 + 2c} = \theta^* . \tag{48}$$

(iv) Whenever $\hat{x} = 0$ is the mother's stable strategy, the offspring's stable strategy is $\hat{m} = 1/(1 + \lambda^{1/2})$, and the sex ratio maintained in the population is the offsprings' determined sex ratio $1:\lambda^{1/2}$. The proof is immediate from expressions (45) and (42).

Suppose now that the condition stated in expression (46) for the stability of the pair $0, 1/(1 + \lambda^{1/2})$ does not hold. For any $0 \leq x \leq 1$, we define a function

$$\psi(x) = x^*[m^*(x)] . \tag{49}$$

Employing equation (42), we know that, since expression (46) does not hold,

$$\psi(0) = x^*\left(\frac{1}{1 + \sqrt{\lambda}}\right) > 0 . \tag{50}$$

From expressions (41) and (27), we get

$$\begin{aligned} \psi(1) &= x^*\left(\frac{1}{1 + \sqrt{c}}\right) < x^*(1) \\ &= \frac{\lambda}{\lambda + 1 - (1 - c)\theta} < 1 . \end{aligned} \tag{51}$$

Hence, there is (at least one) solution to the equation $\psi(\hat{x}) = \hat{x}$. Define $m^*(\hat{x}) = \hat{m}$, equations (43) and (44) are automatically satisfied by the pair $\hat{x}, \hat{m}$.

COROLLARY 11. If the condition stated in expression (47) for the mutual stability of the pair 0, $1/(1 + \lambda^{1/2})$ is not satisfied, then there is at least one stable pair of strategies, $\hat{x}, \hat{m}$ for which $\hat{x} > 0$ and $\hat{m} > 1/(1 + \lambda^{1/2})$.

We now concentrate on the case of surplus male abortion ($\theta = 1$), and we assume that the condition stated in expression (47) for the evolutionary stability of the pair $0, 1(1 + \lambda^{1/2})$ is not satisfied. In this case, equations (43) and (44), together with equations (29) and (41), yield

$$\hat{x} = \frac{\hat{m}(\lambda + 1 - 2c) - 1}{\hat{m}(\lambda - c)} \tag{52}$$

and

$$\hat{m} = \frac{1}{1 + \sqrt{\lambda(1 - \hat{x}) + c\hat{x}}} . \tag{53}$$

Let us define

$$y = (1 - x)\lambda + cx \tag{54}$$

(this is the expected investment in a potential male offspring of a mother with a strategy x). The system of equations (52) and (53) becomes

$$\hat{y} = 2c - 1 + 1/\hat{m} \tag{55}$$

and

$$\hat{m} = 1/(1 + \hat{y}^{1/2}). \tag{56}$$

Thus,

$$\hat{y} - \sqrt{\hat{y}} - 2c = 0,$$
$$\hat{y} = [1 + (1 + 8c)^{1/2}]/2,$$

and, therefore,

$$\hat{y} = [1 + (1 + 8c)^{1/2}]^2/4 = [1 + 4c + (1 + 8c)^{1/2}]/2. \tag{57}$$

From equation (57), together with equations (54) and (56), we get

$$\hat{x} = \frac{\lambda - \hat{y}}{\lambda - c} = \frac{2\lambda - [4c + 1 + (8c + 1)^{1/2}]}{2(\lambda - c)} \tag{58}$$

and

$$\hat{m} = 2/[3 + (1 + 8c)^{1/2}]. \tag{59}$$

It is worth mentioning that once the condition $c < (\lambda - \lambda^{1/2})/2$ for positive maternal interference ($\hat{x} > 0$) is satisfied, neither the primary proportion of male offspring, $\hat{m}$, nor the average mother's investment in males, $\hat{y}$ (including the cost of male abortion), depends on λ. Both values depend on c alone (the probability of abortion, $\hat{x}$, does, in fact, depend on both c and λ). We see, further, that the mother's expected investment in males, $\hat{y}$, is a monotonic function of c, increasing from 1 when $c = 0$ to λ when $c = (\lambda - \lambda^{1/2})/2$ (relative to the unit of fixed investment in a female). The primary proportion of males, $\hat{m}$, is a monotonic function of c, decreasing from ½ when $c = 0$ to $1/(1 + \lambda^{1/2})$ when $c \geq (\lambda - \lambda^{1/2})$.

Finally, we are interested in the real (secondary) stable proportion of males in the population,

$$\hat{\mu} = (1 - \hat{x})\hat{m}/(1 - \hat{x}\hat{m}), \tag{60}$$

namely, the proportion of males among surviving adults.

We know that for $c \geq (\lambda - \lambda^{1/2})/2$, $\hat{\mu} = \hat{m} = 1/(1 + \lambda^{1/2})$. As for $c < (\lambda - \lambda^{1/2})/2$, equations (57) through (60) yield

$$\hat{\mu} = \frac{\hat{y} - c}{\hat{y} + (\lambda - c)\sqrt{\hat{y}} - c} = \frac{1 + 2c + \sqrt{1 + 8c}}{1 + \lambda + c + (1 + \lambda - c)\sqrt{1 + 8c}}. \tag{61}$$

By straightforward differentiation, it can be shown that $\hat{\mu}$ is a decreasing function of λ and an increasing function of c. It increases from $1/(1 + \lambda)$ when $c = 0$ to $1/(1 + \lambda^{1/2})$ when $c \geq (\lambda - \lambda^{1/2})/2$.

COROLLARY 12. (i) In the case of surplus male abortion ($\theta = 1$), there is always a unique pair of strategies ($\hat{x}, \hat{m}$) that is stable against mutation in both loci. (ii) If the cost of abortion, c, is higher than $(\lambda - \lambda^{1/2})/2$, then nonabortion ($\hat{x} = 0$) is the only stable strategy of the mother, in which case both the primary and the secondary stable proportions of males in the population are $1/(1 + \lambda^{1/2})$. (iii) As the cost of abortion decreases from the critical value $(\lambda - \lambda^{1/2})/2$ to zero, the primary proportion of males increases from $1/(1 + \lambda^{1/2})$ to $\frac{1}{2}$ and the rate of male abortion increases from zero to $(\lambda - 1)/\lambda$; the secondary proportion of males among surviving adults decreases from the offsprings' determined value, $1/(1 + \lambda^{1/2})$, to the mother's determined value, $1/(1 + \lambda)$. The proportion of mother's investment in males will, then, decrease from $\lambda^{1/2}/(1 + \lambda^{1/2})$ to $\frac{1}{2}$.

SUMMARY, DISCUSSION, AND SOME SPECULATION ABOUT THE EVOLUTION OF CHROMOSOMAL DIFFERENCES

We have analyzed a two-locus model for sex determination and resource allocation in a two-sex, diploid, randomly mating population in which the cost of rearing a male offspring is different from—say, λ times higher than—the cost of rearing a female offspring.

It has been assumed that one locus is responsible for the individual's primary sex determination, while the other locus affects the mother's behavior toward potential offspring of the two sexes. It has been shown that if the mother can manipulate the sex ratio within her progeny without any cost, then natural selection operates to establish the genes that determine, through the mother's manipulation, a sex ratio of $1:\lambda$ and, thus, a ratio of 1 : 1 in total expenditure incurred for offspring of each sex. In this case, natural selection operating on the mother's genes tends to maximize the total number of the mother's grandoffspring (cf. Fisher 1958, pp. 158–159). If, on the other hand, the cost of the mother's manipulation is higher than some critical value c^* (depending on the cost, λ, of rearing a male offspring), then it has been shown that natural selection operates to establish the genes that through their effect on the offspring determine a sex ratio of $1:\lambda^{1/2}$ (cf. Trivers 1974). It is quite interesting that this is the geometric mean between the sex ratio 1 : 1 that would be expected if each individual sought to increase its own contribution to future generations and the sex ratio $1:\lambda$ expected if each individual sought to increase the total contribution of its family to the future generations.

In the more general case, assuming an exact genetic model of two loci, one being responsible for the individual's (say, offspring's) sex determination and the other for the mother's interference, we have found a unique pair of values (strategies) $\hat{x}, \hat{m}$, with $\hat{m}$ being the primary proportion of males in the progeny and $\hat{x}$ the mother's level of interference, that, once fixed in the population, has the property of evolutionary genetic stability against all nonepistatic mutation. This pair of strategies can be equivalently determined by the rules of an asymmetrical population game in which the mother's and offspring's payment functions are objectively determined by (well-known) population dynamics. The (unique) externally stable pair of strategies, determined by the two-locus dynamics, is shown, more specifically, to be identical to the (unique) ESS of the asymmetric population game if and only if an asymmetric ESS is defined as a pair of strategies $(\hat{x}, \hat{m})$ in which $\hat{x}$ is a usual (symmetrical) ESS in a mother's population game as long as $\hat{m}$, being fixed among offspring, is regarded as "natural force" and $\hat{m}$ is an ESS of an offspring's population game, given $\hat{x}$ as a "natural force." Note that this definition is somewhat weaker than the one suggested by Maynard Smith and Parker (1976) and further analyzed by Selten (1980) since, according to the terminology of the latter, the condition obtained from the two-locus dynamic system requires only stability against mutant strategies of either the form $\hat{x}, m'$ or the form $x', \hat{m}$ and (unlike the latter) not of the general form x', m'.

In a separate work, we deal with biological conditions under which dynamic stability of the genetic population leads to the stronger ESS requirement of Maynard Smith, Parker, and Selten.

As we show, if the cost of the mother's manipulation is larger than zero but smaller than the critical value c^*, then the secondary sex ratio, established in the adult population, lies between the mother's determined sex ratio of $1:\lambda$ and the offspring-determined sex ratio of $1:\lambda^{1/2}$. Moreover, as the cost, c, of losing an offspring increases from 0 to c^*, the evolutionarily stable (secondary) sex ratio in the adult population monotonically increases from $1:\lambda$ to $1:\lambda^{1/2}$. Quite interestingly, it is shown that as the cost c increases, the offspring's primary sex ratio (contrary to the secondary sex ratio) decreases from $1:1$ to the value $1:\lambda^{1/2}$ at c^*, from which point and above the mother does not interfere and the two sex ratios coincide. Not surprisingly, the mother's rate of interference decreases from $(\lambda - 1)/\lambda$ when the cost c is zero, to zero when the cost c approaches c^*.

If a mother's manipulations can be executed only through abortion of a surplus of males, then the critical value c^*, above which she will not interfere, is $(\lambda - \lambda^{1/2})/2$. If (for fixed costs of $\lambda > 1$ for rearing a male offspring and $c > 0$ for losing it) the mother can interfere by converting the sex of a male, instead of aborting him, (say, if $\theta < 1$) then the critical value c^* will be higher, and it will increase as the risk θ involved in a forced sex conversion decreases.

It seems quite obvious that the possibility of sex conversion is always preferable, both for the mother and for the offspring, to the possibility of abortion. And in the case of sex conversion, a low value of risk is preferable to a high value of risk. It thus seems obvious that any biological factor under natural selection that is responsible for the success of sex conversion will be so selected as to decrease the risk, θ, involved in it.

That differential abortion of male and female offspring is more common, by far, than the more "economic" sex conversion (including in human populations; see, e.g., Crew 1954; Bacci 1965) can possibly be explained by technical restrictions. Yet, in order for natural selection to operate on factors that affect the risk of conversion, θ, one has to assume some inherited variance with respect to this parameter among offspring primarily determined as males. Since in this work we are not concerned with the question of how the mother should choose the candidates for an attempt at sex conversion, we have adopted the simplifying working assumption of an average chance, $1 - \theta$, of successful conversion. Yet, if the individual chance of surviving a sex conversion is positively correlated with some detectable factor, τ, of the offspring, there appears to be an obvious selective advantage to a more subtle mother's strategy: choosing the candidates for sex conversion from among those male offspring whose detectable factor τ (and thus, the chance of surviving a sex conversion) is relatively high. This, in turn, endows low values of τ (and thus, high values of θ) with an apparent selective advantage in offspring affecting loci because, in any stable situation, males have higher reproductive values than females (notwithstanding the risk, even if small at the beginning, involved in sex conversion). Hence, quite paradoxically, natural selection operating both on factors involving the risk of sex conversion and on a mother's reaction to these factors appears to favor those factors that increase rather than decrease the risk of sex conversion. As a result, it is possible that, under plausible conditions, the only evolutionarily stable situation will concern the case of pure abortion of a surplus of males ($\theta = 1$). Moreover, since the critical cost, c^*, is a decreasing function of θ, this in turn may increase the range of parameters for which mother's noninterference is the only stable strategy. In a different work, we intend to study this possibility.

ACKNOWLEDGMENTS

We thank F. Weissing for his helpful remark on Fisher's argument and M. W. Feldman, U. Motro, P. Taylor, and M. Uyenoyama for their helpful remarks on this manuscript. I.E. wishes to thank the Department of Mathematics and Its Applications at the University of Naples and the Italian Council for Scientific Research for their support and hospitality. He wishes also to thank the United States–Israel Binational Science Foundation (grant 8500023).

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