

SEXUAL REPRODUCTION AND VIABILITY OF FUTURE OFFSPRING

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Modern Darwinian theory concerning the evolution of sexual reproduction faces a number of difficulties. The first is to establish quantitatively a sufficiently substantial selective advantage of sexual reproduction to compensate for the immediate advantage in fertility of at least some asexual alternatives, as, for example, parthenogenesis. A bulk of recent studies concerning the evolution of sex concentrate on this theoretical difficulty (e.g., Crow and Kimura 1965; Maynard Smith 1968, 1978; Williams 1975; Hamilton 1980; Hamilton et al. 1981; Huston and Law 1983; and references therein). Common to all these is the assumption that environmental variations make combinations of genes that are selected for at one generation highly unsuccessful at another one. Hence, selection for new, sexually produced combinations may be so drastic as to nullify (in a partially sexual population) or even overcome (in a fully sexual population) the "cost of meiosis" (see Williams 1975). Note that this cost is customarily approximated by two ("twofold disadvantage of sex"; Maynard Smith 1978), although it may be any number μ greater than one, depending on the specific population.

Less noticed but not less problematic is the lack of empirical indication of a substantial advantage in either viability or fertility of sexually produced over asexually produced individuals in partially sexual populations. In fact, little if any empirical work has been done on the subject. Yet, it seems hard to believe that an average advantage of about 1:2 each generation (or, maybe, 1:2ⁿ each *n*th generation) would pass unnoticed in so many different populations. Moreover, no substantial increase in the proportion of asexual reproduction is usually documented in partially sexual populations (e.g., plant populations) during periods in which sexually and asexually produced individuals appear to be about equally viable. These observations seem, however, to contradict the notion that any answer to the problem raised above will imply either some advantage in fitness for sexually produced offspring or some reduction (temporary, maybe) in their relative frequency.

Another difficulty concerns an apparent contradiction between features that seem necessary for the evolution of sex and the observed phenomenon of sexual preference. It appears that sexual reproduction can evolve only when environmental conditions change drastically so as to render genotypes that are successful

at one generation less successful, on the average, in the future. Yet, observations of sexual preference in many populations indicate an apparent tendency of females to combine their genes with those of the most successful males (e.g., Fisher 1930; Zahavi 1975).

Taylor and Williams (1982) raised the question of how natural selection can maintain both variation in fitness and parent-offspring correlation in fitness that allows for the evolution of sexual preference of the fit. As they have shown, at least one of these values must tend to zero under selection pressure in a fixed environment. A host-parasite dynamic model in which both values remain substantially positive has been developed elsewhere (Eshel and Hamilton 1984). The model is essentially the same as the one suggested by Hamilton (1980) in order to explain the evolution of sex. Unfortunately, the range of parameters required for the evolution of sex and the one required for the evolution of sexual preference of the fit have appeared to be mutually exclusive. Although drastic changes in negative parent-offspring correlation are required for the evolution of sex, slow, unsynchronized multi-loci cycles with positive parent-offspring correlation are required for the evolution of sexual preference of the fit. The problem, moreover, seems more general: although sexual reproduction appears to indicate a tendency to escape from (currently) successful phenotypic features, sexual preference of fit mates appears to indicate, on the contrary, a tendency to preserve the successful phenotypic features.

The present work is based on an earlier model (suggested in Weinshall 1986), which was further developed (in Weinshall and Eshel 1987) in order to solve some theoretical problems mentioned above, namely, the evolution of sexual reproduction in the face of asexual advantage in fertility. It was shown that if a population composed of fully sexual and fully asexual individuals is exposed to a succession of three or more parasites (or seasons), if, for any parasite, there is a specific allele responsible for the immunity of its carrier against it, and if the death toll of the individuals that are not immune is sufficiently high, then a sexually reproducing subpopulation will always increase in frequency, independent of the cost of sex. Moreover, allowing partially sexual reproduction and assuming that the rate of sexuality, τ , is determined by a second modifier locus, we have shown that for any cost of sex, μ , and for any rate of recombination, r , between the two loci, there is a positive unbeatable rate of sexuality, $\tau = \tau(r, \mu)$, which is a (unique) evolutionarily stable strategy (cf. Hamilton 1967). Likewise, if the rate of sexuality in the population is $\alpha \neq \tau$, then any mutant that determines (as a heterozygote) a rate closer to τ will be established in the population. Depending on μ and r , τ may be 1 (full sexuality).

In this paper we employ the above model to show that, for some natural range of parameters, the viability of sexually produced individuals at equilibrium is, quite surprisingly, never higher on the average than that of asexually produced individuals. In all cases, the average viabilities of the two subgroups (sexually and asexually produced individuals) are not much different from each other, in accordance with empirical observations as urged above. That is true even if the cost of sex is quite high (e.g., $\mu = 2:1$).

The maintenance of sex is then explained, however, on the grounds of a crucial

advantage in average fertility of grandoffspring born (either sexually or asexually) to a sexually produced offspring over that of grandoffspring born to an asexually produced offspring, a factor that is less apparent to empirical observations.

Finally, we show that in the present model even if the unbeatable strategy of reproduction is full sexuality, father-offspring and grandfather-grandoffspring correlations remain positive. Hence, both sexual reproduction and sexual preference of the fit can evolve and be maintained simultaneously.

THE MODEL

In order to demonstrate the second- and third-generation effect of sexual reproduction on the average offspring's viability, we concentrate on the most simple version of the model, which still allows for the evolution of sex despite a ratio of $1:\mu$ between the productivity of sexual and asexual reproduction. (Traditionally, the fertility of sexual reproduction is estimated as half the expected number of offspring born to a couple; hence, under certain plausible assumptions, $\mu \approx 2$.) For the most general version of the model, the reader is referred to Weinshall and Eshel (1987). With some technical elaboration, the arguments put forth in the next two sections can be carried on for the general model.

Assume a two-locus diploid infinite population being exposed to a three-generation cycle of selection, say, "seasons" (or, more generally, n -generation cycle where $n \geq 3$). The alternative alleles at one locus are A_1 , A_2 , and A_3 , where the allele A_i ($i = 1, 2, 3$) is responsible for the immunity of its carrier against the i th parasite ($i = 1, 2, 3$). Thus, the viabilities of the six genotypes, determined by the main locus, are given in table 1.

Assume, further, that individuals in the population can produce either sexually, asexually, or partially sexually. The level of sexuality, τ , is determined by a second locus (say, a modifier locus) such that an individual of genotype $B_k B_l$ in the modifier locus has probability τ_{kl} of reproducing sexually. By reproducing asexually, an individual can produce μ times more than half the progeny it could have obtained by sexual reproduction (or, equivalently, any two individuals reproducing asexually can have μ times as many offspring as they could produce together sexually). Sexually reproducing individuals mate at random. In addition, the rate of recombination between the two loci is r .

As established in a previous paper (Weinshall and Eshel 1987), there is an unbeatable rate of sexuality τ , which, if established in the population, is immune to any mutation in the modifier locus (i.e., τ is an evolutionarily stable strategy). Moreover, if the population is fixed on another rate of sexuality, then any mutation in the modifier locus that determines (as a heterozygote) a rate of sexuality closer to τ will become established (i.e., τ is an evolutionarily genetic strategy; cf. Eshel and Feldman 1982, 1984, and references therein). The unbeatable rate of sexuality τ indeed depends on the parameters r , μ , h , and δ . However, for δ sufficiently small (i.e., for low enough viability of those that are not immune), the unbeatable rate of sexuality τ is always positive. Moreover, for μ not too high (e.g., $\mu \leq 1.38$ for $\delta = h = 0$, $r = 1/2$), τ is 1 and full sexuality is the only stable situation. In addition, the unbeatable rate of sexuality $\tau = \tau(\delta, h, r, \mu)$ does not tend

TABLE 1
THE VIABILITIES OF THE SIX MAIN-LOCUS GENOTYPES IN THREE
SUCCESSIVE HOST GENERATIONS (SEASONS)

GENOTYPE	SEASON		
	S_1	S_2	S_3
A_1A_1	$1 + h$	δ	δ
A_1A_2	1	1	δ
A_1A_3	1	δ	1
A_2A_2	δ	$1 + h$	δ
A_2A_3	δ	1	1
A_3A_3	δ	δ	$1 + h$

NOTE.— $\delta \geq 0$ is assumed to be a small number (the viability of an individual that is not immune), and h is the homozygote advantage (in order to maintain polymorphism in this model, h may be any number greater than negative one).

to zero as μ tends to infinity. For example, in the analyzed case of $\delta = h = 0$, $\tau = \tau(r, \mu) \geq \lim_{\mu \rightarrow \infty} \tau(r, \mu) \geq 2/3$.

We assume a situation in which $0 < \tau < 1$. We assume, further, that, concerning the modifier locus, the population is already fixed on the unbeatable rate of sexuality τ , such that the model has one locus. We assume, for simplicity, that $\delta = 0$. Also, the frequencies of the six genotypes determined by the main locus are in a three-generation-cycle equilibrium. (There is always one such equilibrium; see Weinshall and Eshel 1987.) If q_1 , q_2 , and q_3 denote the relative frequencies of the alleles A_1 , A_2 , and A_3 , respectively, among newborn offspring at the beginning of season S_2 , then by symmetry, the frequencies of these alleles will be q_3 , q_1 , and q_2 , respectively, at the beginning of season S_3 and q_2 , q_3 , and q_1 , respectively, at the beginning of season S_1 . (For an implicit representation of the vector (q_1, q_2, q_3) as a solution to a third-degree set of equations, see Weinshall and Eshel 1987.) In this work we use the relations

$$q_2 \leq q_3 \leq q_1, \quad (1a)$$

$$q_2 \leq 1/4, \quad q_3 \leq 1/2, \quad q_1 \geq 1/2, \quad (1b)$$

$$q_2^2 + q_3 = 2[\tau + (1 - \tau)\mu]q_2/\tau, \quad (1c)$$

$$2\tau^2q_2 + 2q_2(\lambda - \tau q_2)(\lambda + \tau - \tau q_2) = \tau\lambda \quad \lambda = 2[\tau + (1 - \tau)\mu], \quad (1d)$$

as obtained for the simplest case, $\delta = h = 0$.

As a special case, we have for $\tau = 1$ (Weinshall 1986),

$$q_2 \approx 0.16, \quad q_3 \approx 0.296, \quad q_1 = 1 - q_2 - q_3, \quad (2)$$

and

$$\mu \leq 1.38 \quad (3)$$

(see Weinshall and Eshel 1987).

AVERAGE VIABILITIES OF SEXUALLY AND ASEXUALLY PRODUCED OFFSPRING

Let p_{11} , p_{12} , and p_{13} be the frequencies of the genotypes A_1A_1 , A_1A_2 , and A_1A_3 among adults at the end of season S_1 in a population at an equilibrium of partial sexuality (note that at the end of season S_1 all the other genotypes have become extinct). Since the level of sexuality (in this case of fixation at the modifier locus) is independent of the genotype, the frequency of allele A_2 among newborn offspring (either sexually or asexually produced) at season S_2 is

$$q_2 = p_{12}/2. \quad (4)$$

Similarly,

$$q_3 = p_{13}/2 \quad (5)$$

and

$$q_1 = p_{11} + (p_{12} + p_{13})/2 = (1 + p_{11})/2. \quad (6)$$

Asexually produced offspring at the beginning of season S_2 will all be of the genotypes A_1A_1 , A_1A_2 , and A_1A_3 , among which only individuals of the genotype A_1A_2 will survive with a probability proportional to the heterozygote viability. The frequency of A_1A_2 among asexually produced offspring is, using equation (4), $p_{12} = 2q_2$ (as it has been among adults at the end of S_1). Hence, the average relative viability of an asexually produced offspring is

$$V_a = 2q_2. \quad (7)$$

To calculate the average viability of a sexually produced offspring, note that a proportion q_2^2 of these offspring are of the genotype A_2A_2 (with survival probability proportional to the homozygote viability), whereas a proportion $2q_1q_2 + 2q_2q_3 = 2q_2(1 - q_2)$ are of the genotypes A_1A_2 or A_2A_3 (with survival probability proportional to the heterozygote viability). The rest have zero probability of surviving. Hence, the average relative viability of a sexually produced offspring is

$$V_s = (1 + h)q_2^2 + 2q_2(1 - q_2) = 2q_2 - (1 - h)q_2^2 = V_a - (1 - h)q_2^2. \quad (8)$$

Corollary: Unless $h > 1$ (i.e., unless the viability of the immune heterozygote is less than half that of the immune homozygote), the viability of an asexually produced offspring is higher, on the average, than that of a sexually produced offspring.

Note that the result is independent of the cost of sex (though the level of sexuality at equilibrium and, therefore, the vector (q_1, q_2, q_3) indeed depend on that cost; see eqs. 1, above). This theoretical finding, even though obtained for a rather special case, may account for the seeming paradox that even if sex is maintained in the face of a cost of 1:2 (i.e., $\mu = 2$), one is not confronted with an apparent selective advantage of sexually produced over asexually produced offspring (indeed, not an advantage of 2:1 in either viability or fertility).

The previous papers (Weinshall 1986; Weinshall and Eshel 1987) have established analytically that under these assumptions, sexual reproduction is always maintained in the population. The question remains, however, as to the advantage of sexual reproduction, which produces fewer offspring (as assumed) and less

viable offspring (as shown). This paradox is resolved if the fate of one's descendants in future generations is considered (cf. Fisher 1930; Eshel 1973a,b).

SECOND-GENERATION VIABILITIES

We compare the viabilities of grandoffspring born to sexually and asexually produced offspring, respectively. The relative viabilities of the corresponding asexually and sexually produced grandoffspring born to an asexually produced offspring are denoted by V_{aa} and V_{sa} . The corresponding relative viabilities of asexually and sexually produced grandoffspring born to a sexually produced offspring are denoted by V_{as} and V_{ss} .

Note, first, that the viability of an asexually produced offspring born to an asexually produced parent is always zero (no genotype can be adapted to more than two successive generations). Hence,

$$V_{aa} = 0. \quad (9)$$

An asexually produced offspring born in season S_3 to a sexually produced parent of season S_2 survives (and then has viability 1) if and only if this parent is of the genotype A_2A_3 (this is the only genotype that can possibly survive both seasons S_2 and S_3). The proportion of the genotype A_2A_3 among newborn offspring at the beginning of season S_2 is $2q_2q_3$ and its viability at S_2 is 1. Hence, its proportion after selection, at the end of season S_2 , relative to the sexually produced subpopulation, is $P_{II}^{(3)}(A_2A_3) = 2q_2q_3/V_s$, where V_s is given by equation (8). We thus obtain

$$V_{as} = P_{II}^{(3)}(A_2A_3) = 2q_2q_3/V_s = 2q_3/[2 - (1 - h)q_2]. \quad (10)$$

Consider now a sexually produced offspring, born in season S_3 to an asexually produced parent of season S_2 . Since the only asexually produced adults in season S_2 are of the genotype A_1A_2 , a sexually produced offspring of such a parent will be viable (with viability 1) if and only if it inherits the allele A_3 from the other parent. Recall, though, that the frequencies of alleles A_1 , A_2 , and A_3 at the end of season S_2 are q_3 , q_1 , and q_2 , respectively. Hence,

$$V_{sa} = q_2. \quad (11)$$

Finally, a sexually produced offspring, born in season S_3 to a sexually produced parent of season S_2 , will get the required allele A_3 from this specific parent only if this parent is of the genotype A_2A_3 (because this is the only viable genotype in S_2 that carries the allele A_3). But in the evaluation of V_{as} , we have already seen that the proportion of A_2A_3 among sexually produced adults at the end of season S_2 is $P_{II}^{(3)}(A_2A_3) = 2q_2q_3/V_s = 2q_3/[2 - (1 - h)q_2]$. Hence, the frequency of the allele A_3 among sexually produced parents is

$$\hat{q}_3 = \frac{1}{2}P_{II}^{(3)}(A_2A_3) = q_3/[2 - (1 - h)q_2]. \quad (12)$$

The proportion of A_3 in the entire population at the end of season S_2 is q_2 ; hence, the probability that a sexually produced offspring born to a sexually produced

parent at season S_3 will be of the genotype A_3A_3 (and then of viability $1 + h$) is $q_2\hat{q}_3$. The probability that it will be of the genotype A_1A_3 or A_2A_3 (and then of viability 1) is $q_2(1 - \hat{q}_3) + \hat{q}_3(1 - q_2) = q_2 + \hat{q}_3 - 2q_2\hat{q}_3$. In all other cases, the viability of the newborn offspring will be 0. We therefore conclude that the average viability of a sexually produced offspring born to a sexually produced parent is

$$\begin{aligned} V_{ss} &= (1 + h)q_2\hat{q}_3 + (q_2 + \hat{q}_3 - 2q_2\hat{q}_3) = q_2 + [1 - (1 - h)q_2]\hat{q}_3 \\ &= q_2 + [1 - (1 - h)q_2]q_3/[2 - (1 - h)q_2]. \end{aligned} \quad (13)$$

Corollary: A sexually produced parent always has more viable offspring than an asexually produced parent, propagating in the same way (either sexually or asexually).

Proof: From equations (9) and (10) we see that $V_{as} > V_{aa}$. From equations (11) and (13) we see that $V_{ss} > V_{sa}$ since $q_2 < 1/2$ (i.e., because $2q_1 - 1$ is the frequency of the adult favorable homozygote; thus, $q_1 \geq 1/2$) and $h > -1$.

Since the rate of sexuality at equilibrium is the same for all genotypes, the sexually produced parents have more viable offspring, on the average, than asexually produced parents (even though asexually produced parents may be slightly more viable, on the average, than sexually produced ones).

The expected numbers of viable offspring born to sexually and asexually produced adult parents are denoted by w_s and w_a , respectively. Then,

$$w_a = \tau V_{sa} + (1 - \tau)\mu V_{aa} = \tau q_2 \quad (14)$$

and

$$\begin{aligned} w_s &= \tau V_{ss} + (1 - \tau)\mu V_{as} = \tau\{q_2 + [1 - (1 - h)q_2]\hat{q}_3\} + (1 - \tau)\mu 2\hat{q}_3 \\ &= w_a + \{[1 - (1 - h)q_2]\tau + 2\mu(1 - \tau)\}\hat{q}_3; \end{aligned} \quad (15)$$

thus, $w_s > w_a$. (This last result follows immediately, though, from the corollary.)

The expected number of adult grandoffspring descending from a random asexually produced offspring is denoted by $w_a^{(2)}$. The expected number of adult grandoffspring descending from a random sexually produced offspring is denoted by $w_s^{(2)}$. Since the number of newborn offspring is assumed to be the same, $\tau + (1 - \tau)\mu$, for all surviving adults in the population, we obtain

$$w_a^{(2)} = V_a w_a = 2\tau q_2^2 \quad (16)$$

and

$$w_s^{(2)} = V_s w_s, \quad (17)$$

where V_s and w_s are given by equations (8) and (15). It follows that

$$w_s^{(2)} = q_2\{2\tau q_2 - (1 - h)\tau q_2^2 + [1 - (1 - h)q_2]\tau q_3 + 2\mu(1 - \tau)q_3\}. \quad (18)$$

Recall that by investing a unit of effort in asexual reproduction, one can produce μ times as many offspring as by sexual reproduction. Hence, the ratio of the expected number of viable grandoffspring obtained by sexual reproduction to

the expected number obtained by asexual reproduction is

$$w_s^{(2)}/\mu w_a^{(2)} = \{[2 - (1 - h)q_2]\tau q_2 + [1 - (1 - h)q_2]\tau q_3\}/2\tau q_2\mu + (1 - \tau)q_3/\tau q_2. \quad (19)$$

After some manipulations we obtain

$$w_s^{(2)}/\mu w_a^{(2)} = [q_1/2 + (q_2 + q_3)/2q_2 + h(q_2 + q_3)/2]/\mu + (1 - \tau)q_3/\tau q_2,$$

where the values of (q_1, q_2, q_3) depend on h, μ , and τ , which, in turn, depends also on the rate of recombination, r , between the main locus and the modifier locus.

Take $h = 0$ for simplicity. In this case we know that $\tau \geq 2/3$. If $\tau = 1$ (i.e., $\mu < 1.38$ from eqs. 2), the values of the alleles' frequencies as given in equations (2) are used to show that

$$w_s^{(2)}/\mu w_a^{(2)} > 1. \quad (20)$$

For all cases in which condition (20) holds, the disadvantage of sexual reproduction (in parent fertility and offspring viability) is fully compensated by grand-offspring advantage, particularly for all cases in which full sexuality is the unbeatable rate of sexuality and $h = 0$.

FATHER-OFFSPRING AND GRANDFATHER-GRANDOFFSPRING CORRELATIONS IN FITNESS

We discuss here the possible advantage of sexual preference of fit mates (say, males) under conditions favorable for the evolution (or maintenance) of sex. We adopt the common assumption that a choosing female cannot directly assess the genotypes of potential mates. Rather, she is attracted by an apparent marker that indicates the current fitness of its carrier (see Zahavi 1975). When males do not participate in rearing the young, the only advantage gained by the choosing female is the good genes inherited by her offspring (Fisher 1930). Assuming repeated environmental changes drastic enough to allow for the evolution of sex, we ask what the conditions are under which sexual preference of the fit guarantees higher fitness of the offspring.

In order to answer this question, let us concentrate on a random, adult female at the end of season S_1 who must choose between adult males. These males may be of the genotypes A_1A_1 , A_1A_2 , or A_1A_3 . Aware of only the mate's fitness, she can choose between males of either fitness $1 + h$ (say, A_1A_1) or 1 (say, A_1A_2 or A_1A_3). The alternatives are shown in table 2.

If a female chooses a mate of fitness $1 + h$ (namely, A_1A_1), the expected offspring's fitness is $w_{1+h} = q_2$. If her mate has a fitness of 1 (which is A_1A_2 or A_1A_3 in probabilities $q_2/(q_2 + q_3)$ or $q_3/(q_2 + q_3)$, respectively), the offspring's viability is

$$w_1 = \frac{q_2q_3}{q_2 + q_3} + \frac{q_2(1 + q_2 + q_2h)}{2(q_2 + q_3)} = w_{1+h} + \frac{q_2(1 - q_2 + q_2h)}{2(q_2 + q_3)} > w_{1+h}.$$

Therefore, $w_1 > w_{1+h}$ for all h (note that $q_2 < 1/2$ and $h > -1$; thus, $(1 - q_2 + q_2h)/2 > 0$).

Hence, if $h < 0$ (i.e., in a case of immediate heterozygote advantage), it is

TABLE 2
OFFSPRING DISTRIBUTION OF FITNESS (IN SEASON S_2) AS A FUNCTION
OF THE FATHER'S GENOTYPE AND FITNESS (IN SEASON S_1)

FATHER'S GENOTYPE	FATHER'S FITNESS	FREQUENCY	PROBABILITY OF OFFSPRING'S FITNESS		
			0	$1 + h$	1
A_1A_1	$1 + h$	$2q_1 - 1$	$1 - q_2$	0	q_2
A_1A_2	1	$2q_2$	$(1 - q_2)/2$	$q_2/2$	$1/2$
A_1A_3	1	$2q_3$	$1 - q_2$	0	q_2

NOTE.—Offspring's genotype A_2A_2 is indicated by the fitness $1 + h$, whereas A_1A_2 and A_2A_3 are indicated by the fitness 1; the rest have zero fitness.

always advantageous to prefer mates of higher fitness (namely, 1). The opposite is true if $h > 0$ (i.e., in the case of heterozygote disadvantage), in which case the preferable mates are of the lower fitness (again 1). We show, however, that sexual preference of fit mates can evolve (at least with a rather plausible assumption of heterozygote advantage) under conditions that are also favorable for the evolution of sex. Moreover, since the model suggested here is the first to explain the evolution of both phenomena under the same parametric assumptions, we tentatively suggest that the very ubiquity of sexual preference of fit mates may stand as indirect evidence for average heterozygote advantage, at least in these cases.

In order to study the effect of female choice quantitatively, the fitness of the adult father (either 1 or $1 + h$) is denoted by X and that of its newborn offspring (either 0, 1, or $1 + h$) by Y (cf. Eshel and Hamilton 1984). We assume heterozygote advantage, such that $h < 0$. We assume further that $|h|$ is a small number (hence, females have to choose among rather close contenders). By straightforward calculations, we obtain the average and variance of the fitness of adults:

$$EX = 1 + (2q_1 - 1)h = 1 + (1 - 2q_2 - 2q_3)h;$$

$$\text{var } X = 2(1 - q_1)(2q_1 - 1)h^2 = 2(q_2 + q_3)(1 - 2q_2 - 2q_3)h^2.$$

The average and variance of the fitness of sexually produced newborn offspring are

$$EY = q_2(2 - q_2) + q_2^2h;$$

$$\text{var } Y = q_2(2 - q_2)(1 - q_2)^2 + 2q_2^2(1 - q_2)^2h + q_2^2(1 - q_2^2)h^2.$$

In addition,

$$\begin{aligned} E(XY) &= E[XE(Y|X)] = (1 + h)E(Y|X = 1 + h)P(X = 1 + h) \\ &\quad + E(Y|X = 1)P(X = 1), \end{aligned}$$

where $E(Y|X = 1 + h) = w_{1+h}$ and $E(Y|X = 1) = w_1$. The covariance is, therefore,

$$\text{cov}(X, Y) = -q_2(1 - q_2)(2q_1 - 1)h - q_2^2(2q_1 - 1)h^2.$$

Thus, the father-offspring correlation is

$$\rho(X, Y) = \frac{-h}{|h|} \left[\frac{q_2(2q_1 - 1)}{2(1 - q_1)(2 - q_2)} \right]^{1/2} + O(h),$$

which is positive for small $|h|$ since $h < 0$ as we have assumed and $2q_1 - 1 > 0$.

If the population is fully sexual, we know, moreover, the values of the alleles' frequencies q_1 , q_2 , and q_3 (see eqs. 2, above); hence, $\rho(X, Y) \approx 0.09$. This is, indeed, a much smaller value than the upper bound $\rho = 1/2$ obtained earlier (Eshel and Hamilton 1984) for slow, non-synchronized cyclings of weak selection forces operating independently on various loci. Yet the value $\rho \approx 0.09$ is obtained under conditions favorable for the evolution of sex itself, and as far as we know, the model studied here is the only one attempting to explain the evolution of sexual reproduction and still allowing some advantage to preference for the most fit mate. Since females are likely to invest little in choosing the appropriate male (only males are required to invest in means of sexual attraction), even the slight advantage resulting from a positive father-offspring correlation of about 0.09 may be sufficient to start a "running" process of sexual preference (Fisher 1930).

In light of the results of the preceding two sections, one may expect the positive father-offspring correlation in fitness to be negated by a negative grandfather-grandoffspring correlation in fitness (after all, we have already seen that the advantageous effect of sexual reproduction does not reveal itself until the second generation). This, however, is not the case.

Assume, as before, a certain heterozygote advantage (i.e., $h < 0$). We know that the less fit adults at the end of season S_1 must be of the genotype A_1A_1 with viability $1 + h$. But the only viable offspring of A_1A_1 fathers are those inheriting the allele A_2 from their mother, and these are all A_1A_2 . None of them carries the allele A_3 , required for grandoffspring survival in season S_3 . Hence, the survival probability of a grandoffspring of the less fit A_1A_1 grandfather equals the probability q_2 that it inherits the allele A_3 from the other parent (recall that the frequency of the allele A_3 at the end of season S_2 equals the frequency of A_2 at the end of season S_1 , namely q_2). Thus, for X as defined above, $E(Z|X = 1 + h) = q_2$, where Z is the viability of a grandoffspring born to a random viable descendant.

A father of relatively high fitness 1, however, may be either A_1A_2 or A_1A_3 . One can readily show that a viable offspring (in season S_2) of a father of genotype A_1A_2 (in season S_1) has probability $q_3/[1 + q_2(1 + h)]$ of carrying the allele A_3 . A viable offspring of a father of the genotype A_1A_3 has a probability of $1/2$ of carrying the allele A_3 . Thus, when choosing a father of the higher fitness at random at the end of season S_1 , the probability that a viable offspring of the choosing female will carry the allele A_3 (in which case he must be of the genotype A_2A_3) is

$$\frac{q_2}{q_2 + q_3} \frac{q_3}{1 + q_2(1 + h)} + \frac{q_3}{q_2 + q_3} \frac{1}{2} = \frac{q_3[1 + (3 + h)q_2]}{2(q_2 + q_3)[1 + q_2(1 + h)]} = p_{23}^*,$$

say. An offspring of a parent of genotype A_2A_3 survives with probability $1/2 + 1/2q_2(1 + h)$, whereas an offspring of the other type of parent survives with

probability q_2 . Thus, the viability of a random grandoffspring of a random high-fitness father is

$$\begin{aligned} E(Z|X = 1) &= p_{23}^* [1 + q_2(1 + h)]/2 + (1 - p_{23}^*)q_2 = q_2 + p_{23}^* [1 - q_2(1 - h)]/2 \\ &= q_2 + [1 - q_2(1 - h)] \frac{q_3[1 + (3 + h)q_2]}{4(q_2 + q_3)[1 + q_2(1 + h)]} \\ &> q_2 = E(Z|X = 1 + h), \end{aligned}$$

which completes the proof of a positive grandfather-grandoffspring correlation.

SUMMARY AND DISCUSSION

We have shown earlier (Weinshall 1986; see also Weinshall and Eshel 1987) that when a population is repeatedly exposed to environmental disasters (e.g., parasite attacks; see Hamilton 1980), when there is a specific allele (or alleles) for each parasite that makes its carrier immune to it, and when, most crucially for the model, there are three or more different parasites, then natural selection may operate in favor of sexual reproduction. When the cost of sex is higher, natural selection operates to stabilize a mixture of sexual and asexual reproduction. In the latter case, one would expect that the immediate disadvantage of sexual reproduction in terms of the average fertility for one reproducing parent will be compensated, on the average, by the higher fitness (either viability or fertility) of the sexually produced offspring. In fact, this is expected to be the case for any other model attempting to explain the evolution of sexual reproduction on the grounds of environmental changes. If so, the compensating factor must be rather substantial, for example, 2:1 in a partially parthenogenetic (or vegetative) population (see, e.g., Maynard Smith 1978 and references therein). It seems that such a factor would be most unlikely to escape the eye of plant breeders in so many agricultural populations. Quite surprisingly, no phenomenon of the sort has ever been documented.

We have shown here that in contrast to intuitive expectations, sexual reproduction, even when it drastically lowers the parents' fertility (with the waste of about half the population's being male), can be stably maintained in a population without any apparent advantage in the average fitness of sexually produced offspring. Indeed, the distribution of genotypes among sexually produced offspring is different from the distribution of genotypes among asexually produced offspring. Yet, under quite plausible assumptions, the proportion of genotypes that are better adapted to the new environment is, quite surprisingly, even slightly lower among sexually produced offspring. At any rate, the average difference in fitness between sexually and asexually produced offspring is negligible. This theoretical finding, though in agreement with the lack of empirical evidence for the advantage of sexually produced offspring, raises again the inevitable question of what hidden advantage can still explain, at an intuitive level, the stable maintenance of sexual reproduction in the population.

Analysis of the three-environment three-allele model has shown that grand-offspring born (either sexually or asexually) to sexually produced offspring are

substantially more viable, on the average, than those born to asexually produced offspring. This advantage is, moreover, high enough to compensate for the disadvantage of sexual reproduction in both parental fertility and offspring viability. It is speculated that in a more realistic situation, say of more different sorts of environments (for computer simulations, see Weinshall and Eshel 1987), the advantageous effect of sexual reproduction can be delayed to even further generations. Such a phenomenon can, understandably, escape the eye of the observer who is not a student of theory. We therefore suggest more-careful observations of the fate of the descendants of sexually reproducing and asexually reproducing stocks throughout a substantial number of generations.

Another result of the model, demonstrated in this work, is the positive correlation between the adaptability (say, viability) of a random adult parent to its environment and the adaptability of its sexually produced offspring to the environment of the next generation. This result can explain the evolution of sexual preference of the fittest mate (cf. Taylor and Williams 1982; Eshel and Hamilton 1984). Unlike previous works, this result can explain the evolution of sexual preference by the same model that attempts to explain the evolution of sexual reproduction itself. It is shown, moreover, that some positive correlation in fitness is also maintained between a random sexually reproducing parent and its grand-offspring.

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