

ON THE EVOLUTION OF AN OPTIMAL RATE
OF SEXUAL REPRODUCTION

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In a previous work (Weinshall 1986), a model for competition between sexually reproducing and asexually reproducing (e.g., vegetative or parthenogenetic) individuals of the same diploid population was investigated. It was assumed that the population periodically undergoes n modes of selection (e.g., it is periodically infested by n sorts of parasite; see Haldane 1949; Maynard Smith 1978; Hamilton 1980; Hamilton et al. 1980). It was also assumed that, at a given locus, n alternative alleles, $A_1, \dots, A_n$, each makes its carrier immune to a specific type of parasite. Likewise, there are both sexual and asexual representatives of each genotype $A_i A_j$ ($i, j = 1, \dots, n$) making up the population (e.g., sexuality is determined by another locus). The sexual and the asexual individuals of the same genotype were assumed equal in all aspects, except for their way of reproduction: an asexual individual was assumed to produce, on the average, μ times as many offspring as a sexual individual of the same genotype. (Especially interesting is the case of a parthenogenetic mutant producing twice as many offspring as a sexual individual in a population whose males do not help to raise offspring.) Sexual individuals were assumed to mate at random.

Under these assumptions, it has been shown that if $n = 2$, then for all $\mu > 1$ and for any effect of the two parasites on the three genotypes, the population is bound to become fully asexual. If $n \geq 3$ and if the mortality among individuals that are not immune is sufficiently high, then the sexually reproducing individuals become fixed in the population, independently of the cost of sex μ . This is the case, more generally, for any k -ploid population, provided that the number of alternative parasites is larger than k (the ploidy number of the population). A similar result was obtained for a haploid population with recombination among sexually reproducing individuals.

Quite important for the applicability of the model to low-fertility populations is the relatively low toll of mortality by parasitism that is required in order to maintain the stability of sexual reproduction. In some variants of the model, the required toll is less than 50% of all newborn offspring when the advantage of parthenogenesis is $\mu = 2$. (For a special consideration of this phenomenon, see also Eshel and Weinshall 1987.)

A crucial question for the evolution and maintenance of sex, however, concerns the stability of sexual reproduction against a partially sexual mutant rather than against an absolutely nonsexual one. Moreover, since partially sexual reproduction is quite common in nature, especially among plants, one is interested in the existence and, indeed, the specification of some stable positive rate of sexuality in the population, that is, a strategy of partial sexuality which, when established in the population, is stable in the face of any mutant. Even more desirable is the possibility of some global analysis investigating the evolution of such a so-called "optimal rate of sexuality." A question of special interest is under what conditions full sexuality is the optimal rate, in the sense that a fully sexual population is stable in the face of any mutant that decreases the rate of sexuality and, moreover, that a partially sexual population is unstable in the face of any mutant that tends to increase the rate of sexuality (cf. Eshel and Feldman 1982, 1984).

In this work we investigate a two-locus diploid population in which individuals can reproduce both asexually and sexually, with random mating among sexually reproducing individuals. Selection operates directly on one locus in exactly the same way as assumed earlier (Weinshall 1986). The proportion $0 \leq \tau \leq 1$ of sexually produced offspring is determined, however, by another modifier locus without pleiotropic effects. Since, except for a singular case, all genotypes in this model are at least partially sexual, one should consider the effect of recombination between the two loci.

Analysis is first carried out for the case of three alleles and three environments (parasites) with certain death of the "unfit." The existence of a certain rate of sexuality, which is stable in the face of all other possible strategies of partial sexuality, is proved; its behavior as a function of μ and r (the rate of recombination) is investigated in the next section. Of particular interest is the range of parameters for which $\tau = 1$ (full sexuality) is the only stable strategy of reproduction.

We use computer simulations in order to generalize these results and to investigate further the situation of more than three seasons (parasites), with the possibility of few intermediate periods of relaxation with heterozygote effect and a substantially lower intensity of selection against the less fit homozygote. We demonstrate the existence of an "optimal" sexuality rate in the sense specified above, and we investigate its dependence upon the parameters of the model. We are specifically interested in the effect of n (the total number of parasites) on the range of parameters for which full sexuality is the only stable strategy of reproduction.

THE GENERAL MODEL AND ANALYSIS OF THE CASE $n = 3$

Consider a large diploid population in which each individual can invest in both sexual and asexual reproduction and sexually reproducing individuals mate at random. An individual is said to have a rate $0 \leq \tau \leq 1$ of sexuality (to be called τ -sexual) if it invests a proportion $0 \leq \tau \leq 1$ of its resources in sexual reproduction. The amount of resources needed to produce one sexual offspring is assumed to be larger (by a factor $\mu \geq 1$) than the amount of resources needed to produce

one asexual offspring (see Weinshall 1986 and references therein). Thus, the proportion of sexually produced offspring born to parents with the rate of sexuality τ is

$$\beta = \frac{\tau R/\mu}{\tau R/\mu + (1 - \tau)R} = \frac{\tau}{\tau + (1 - \tau)\mu}, \quad (1)$$

where R denotes the total resources allocated by an individual to reproduction.

Assume now that the population consists of the genotypes $A_i B_\tau / A_j B_\alpha$, where the combination $A_i A_j$ in one locus determines the viability of the individual at any given season, and the combination $B_\tau B_\alpha$ in a modifier locus determines its rate of sexuality. We assume n alleles, $A_1, \dots, A_n$, represented in the first locus, corresponding to n successive environments (seasons), say $S_1, \dots, S_n$, with the following viability coefficients:

$$\omega(S_i) = \begin{cases} \delta & A_j A_k \quad j, k \neq i \\ 1 & A_i A_j \quad j \neq i \\ 1 + h & A_i A_i \end{cases},$$

where $1 \gg \delta$ and h can assume any value larger than -1 . These seasons follow each other repeatedly, with possibly some intermediate stage of relaxation, in which all genotypes are equally successful and heterozygotes have a possible advantage. We also assume a recombination rate of $0 \leq r \leq 0.5$ between the main locus A and the modifier locus B .

Consider first the case for $n = 3$ (three different seasons of selection), $\delta = 0$ (certain death of individuals that are not immune), no heterozygote advantage, and no intermediate periods of relaxation. Assume that the population is fixed on allele B_τ in the second locus, determining a rate of sexuality τ , with some proportion of a rare mutant allele B_α determining some sexuality rate $\alpha \neq \tau$ as heterozygote $B_\tau B_\alpha$.

At the end of season S_1 , the only individuals to survive in the population are those carrying the combination $A_1 A_1$, $A_1 A_2$, or $A_1 A_3$ at the main locus. Thus, ignoring the negligible fraction of homozygous mutants $B_\alpha B_\alpha$, the only genotypes carrying the mutant allele B_α at the modifier locus are, at that time, $A_1 B_\alpha / A_1 B_\tau$, $A_1 B_\alpha / A_2 B_\tau$, $A_1 B_\alpha / A_3 B_\tau$, $A_2 B_\alpha / A_1 B_\tau$, and $A_3 B_\alpha / A_1 B_\tau$. Their frequencies are denoted by $2\epsilon_{11}$, $2\epsilon_{12}$, $2\epsilon_{13}$, $2\epsilon_{21}$, $2\epsilon_{31}$, respectively. Let $\epsilon_i = \sum_{j=1}^3 \epsilon_{ij}$, such that for all $i = 1, 2, 3$, ϵ_i is the frequency of the mutant chromosome $A_i B_\alpha$ at the end of season S_1 .

The indexes i and j for the above ϵ_{ij} 's have the following meanings: 1 stands for the most recently resistant allele, 2 for the allele needed for the next catastrophe, and 3 for the allele needed in the preceding catastrophe. Thus, the frequencies of the five surviving genotypes $A_2 B_\alpha / A_2 B_\tau$, $A_2 B_\alpha / A_3 B_\tau$, $A_2 B_\alpha / A_1 B_\tau$, $A_3 B_\alpha / A_2 B_\tau$, and $A_1 B_\alpha / A_2 B_\tau$ after season S_2 are denoted by $2\epsilon'_{11}$, $2\epsilon'_{12}$, $2\epsilon'_{13}$, $2\epsilon'_{21}$, and $2\epsilon'_{31}$, respectively. Likewise, the vector $\mathbf{q} = (q_1, q_2, q_3)$ indicates the equilibrium frequencies of the alleles A_1 , A_2 , and A_3 after season S_1 in the originally τ -sexual population. However, applying the symmetry among the three alleles, we can deduce that, at all times, q_1 is the equilibrium frequency of the most recently favored allele, q_2 is the equilibrium frequency of the allele needed for the next catastrophe, and q_3 is the equilibrium frequency of the allele needed in the preceding catastrophe (see Weinshall 1986).

By straightforward calculations (as specified in Appendix A), one can show that

$$2q_1 - 1 = \tau q_2^2 / \bar{w} \quad (2a)$$

$$2q_2 = 2\tau q_2 q_3 / \bar{w} \quad (2b)$$

$$2q_3 = [2\tau q_2 q_1 + 2(1 - \tau)\mu q_2] / \bar{w} ; \quad (2c)$$

$\bar{w}$, the average fitness in the population at equilibrium, is given by $\bar{w} = \tau q_2(2 - q_2) + 2(1 - \tau)\mu q_2$. An immediate result, used later in this work, is

$$\bar{w} = \tau q_3 . \quad (3)$$

Assume that the population is at equilibrium with respect to A_1 , A_2 , and A_3 when B_α invades the population. Thus, the vector of frequencies q_1, q_2, q_3 is the actual frequencies of A_1 , A_2 , and A_3 (not always in this order, however). Accordingly, before S_2 we have the following gametes' frequencies among the parents (after recombination and before selection):

$$\text{freq}(A_2 B_\tau) = q_2 + O(\epsilon) ,$$

$$\text{freq}(A_3 B_\tau) = q_3 + O(\epsilon) ,$$

$$\text{freq}(A_1 B_\tau) = q_1 + O(\epsilon) ,$$

$$\text{freq}(A_2 B_\alpha) = (1 - r)\epsilon_2 + r\epsilon_{12} = \epsilon_2' ,$$

$$\text{freq}(A_3 B_\alpha) = (1 - r)\epsilon_3 + r\epsilon_{13} = \epsilon_3' ,$$

$$\text{freq}(A_1 B_\alpha) = \epsilon_{11} + (1 - r)(\epsilon_{12} + \epsilon_{13}) + r(\epsilon_2 + \epsilon_3) = \epsilon_1' ,$$

for $\epsilon = \sum_{i=1}^3 \epsilon_i$.

To calculate the frequency $2\epsilon_{11}'$ of the genotype $A_2 B_\alpha / A_2 B_\tau$ after season S_2 , note that no individual of the genotype $A_2 A_2$ could possibly survive the preceding season, S_1 ; hence, all representatives of this genotype are offspring from sexual reproduction. The frequency of the combination $A_2 B_\alpha$ among all gametes, at the end of season S_1 , is ϵ_2' , and a fraction α of all the carriers of this gamete reproduce sexually. The probability that an individual at the end of season S_1 will reproduce sexually and transmit the gamete $A_2 B_\alpha$ is, therefore, $\alpha\epsilon_2' + o(\epsilon)$. Assuming random mating among sexually reproducing individuals, the probability that a gamete $A_2 B_\alpha$, transmitted through sexual reproduction, will combine with a gamete $A_2 B_\tau$ is, indeed, $q_2 + O(\epsilon)$. Hence,

$$\epsilon_{11}' = 1/2 \text{freq}(A_2 B_\alpha / A_2 B_\tau) = \alpha q_2 \epsilon_2' / \bar{w} + o(\epsilon) , \quad (4)$$

where the coefficient of normalization $\bar{w}$, say the fitness of the population, is the sum of frequencies of all surviving offspring, born to both sexual and asexual reproduction.

In the same way, we obtain

$$\epsilon_{12}' = 1/2 \text{freq}(A_2 B_\alpha / A_3 B_\tau) = \alpha q_3 \epsilon_2' / \bar{w} + o(\epsilon) \quad (5)$$

and

$$\epsilon_2' = 1/2 \text{freq}(A_3 B_\alpha / A_2 B_\tau) = \alpha q_2 \epsilon_3' / \bar{w} + o(\epsilon) . \quad (6)$$

(Note that neither $A_3 B_\alpha / A_2 B_\tau$ nor $A_2 B_\alpha / A_3 B_\tau$ could possibly survive the season S_1 .)

To calculate the frequency $2\epsilon_{13}'$ (or $2\epsilon_3'$) of the genotype $(A_2B_\alpha/A_1B_\tau) A_1B_\alpha/A_2B_\tau$, note that a proportion ϵ_2 (ϵ_{12}) of all parents at the end of season S_1 were of this genotype and that a proportion $(1 - \alpha)$ of them reproduced asexually with a rate of success μ , relative to the success of sexual reproduction. Hence,

$$\epsilon_{13}' = \frac{1}{2} \text{freq}(A_2B_\alpha/A_1B_\tau) = [\alpha q_1 \epsilon_2' + (1 - \alpha)\mu \epsilon_2]/\bar{w} + o(\epsilon) \quad (7)$$

$$\epsilon_3' = \frac{1}{2} \text{freq}(A_1B_\alpha/A_2B_\tau) = [\alpha q_2 \epsilon_1' + (1 - \alpha)\mu \epsilon_{12}]/\bar{w} + o(\epsilon), \quad (8)$$

where $\bar{w}$ is the sum of the numerators of the right-hand sides of equations (5)–(8).

Because of the symmetry of the alleles in this model, the same transformation takes the ϵ_{ij} 's through S_3 and S_2 back to the initial five genotypes. Iterating the above transformation three times like this, we get the change in the relative frequencies of the five mutant genotypes that exist after S_1 and before S_2 during one cycle of catastrophes. It is, therefore, sufficient to analyze the one-stage transformation to see whether the new mutant genotypes increase their frequency under the assumed selection or vice versa. Note, however, that at each iteration the transformation is the same but the meaning of the ϵ_{ij} 's and the q_i 's is changed.

Denote by M^* the matrix of the linear approximation near $\epsilon = (\epsilon_{11}, \epsilon_{12}, \epsilon_{13}, \epsilon_2, \epsilon_3) = 0$ and let

$$M = \bar{w} M^* = \begin{bmatrix} 0 & \alpha r q_2 & 0 & \alpha(1-r)q_2 & 0 \\ 0 & \alpha r q_3 & 0 & \alpha(1-r)q_3 & 0 \\ 0 & \alpha r q_1 & 0 & \alpha(1-r)q_1 & 0 \\ 0 & 0 & \alpha r q_2 & 0 & \alpha(1-r)q_2 \\ \alpha q_2 & \alpha(1-r)q_2 & \alpha(1-r)q_2 & \alpha r q_2 & \alpha r q_2 \\ & + (1-\alpha)\mu & & & \end{bmatrix}. \quad (9)$$

Since M is a nonnegative matrix, we know that its leading eigenvalue is real and positive. Moreover, for $r > 0$ it can readily be verified that M^3 is strictly positive (this is equivalent to the claim that, no matter what mutant genotype started the cycle, after one cycle of selection there is a positive probability for a great-grandson of all the five possible mutant genotypes). It therefore follows from the Perron-Frobenius theorem that the leading eigenvalue of M is also simple (i.e., a simple real root to the characteristic equation of M) for $r > 0$. Denote this eigenvalue by $\rho(q, \alpha)$, where $q = q_\mu(\tau)$ is given by equations (2). (Note that ρ is also a function of μ and r which, at the moment, we keep fixed.) After some manipulations, the characteristic equation of M , divided by the independent variable x , may be written as

$$\begin{aligned} \psi(x) &= \frac{\det(xI - M)}{x} = \psi_{r\mu}[q_\mu(\tau), \alpha; x] \\ &= (x - \alpha r q_2)(x - \alpha r q_3)x^2 - x(x - \alpha r q_3)\alpha r q_2 \\ &\quad \times [\alpha(1-r)q_2 + (1-\alpha)\mu] - (x - \alpha r q_3)\alpha^2(1-\alpha)\mu q_2^2(1-2r) \quad (10) \\ &\quad - \alpha^3 q_2^2 x(1-r)[r^2 q_3 + (1-2r) + r q_2] \\ &\quad - \alpha^2 q_2 x(1-r)^2 q_3(1-\alpha)\mu - \alpha^2 x^2 q_2 q_1 r(1-r), \end{aligned}$$

and $x = \rho(q, \alpha)$ is the largest root of this fourth-degree polynomial.

Note that for $r = 0$, $\psi(x) = x[x^3 - \alpha^2(1 - \alpha)\mu q_2(q_2 + q_3) - \alpha^3 q_2^2]$; the real and positive leading eigenvalue of M is therefore simple (there are no multiple real roots to the equation $\psi(x) = 0$) when $r = 0$. Hence, $\rho(q, \alpha)$ is real, positive, and simple for all the values of r .

For the matrix of linear approximation M^* , we know that $M^* = M/\bar{w}$; its leading eigenvalue is thus

$$\rho^*(q, \alpha) = \rho(q, \alpha)/\bar{w}. \quad (11)$$

But for the neutral mutation $\alpha = \tau$, $\rho^*(q, \tau) = 1$; thus,

$$\bar{w} = \rho(q, \tau). \quad (12)$$

Inserting equation (12) into equation (11) yields

$$\rho^*(q, \alpha) = \rho(q, \alpha)/\rho(q, \tau). \quad (13)$$

This implies that the allele B_τ for sexuality rate τ , once fixed in the population, is stable against the modifier mutant B_α if

$$\rho(q, \alpha)/\rho(q, \tau) < 1. \quad (14)$$

The sexuality rate τ , once fixed in the population, is stable against any modifier allele B_α if condition (14) holds for any $\alpha \neq \tau$ or, equivalently, if the function $\rho(q, \alpha)$ achieves its maximum over all possible α 's at $\alpha = \tau$.

Definition: Such a sexuality rate τ , if it exists, will be called an *evolutionarily stable sexuality rate* for given parameters μ and r .

Recall that $\rho(q, \alpha)$ is the maximal solution of the equation $\psi_{r\mu}[q_\mu(\tau), \alpha; x] = 0$ and that it is a simple positive root. It follows that $\psi(x)$ increases in the neighborhood of $x = \rho$ and that the first derivative of $\psi(x)$ with respect to x is strictly positive for $x \geq \rho$ (because the absolute value of ρ is larger than the absolute value of any other root, real or complex). Moreover, from equations (12) and (3) we know that $\rho(q, \tau) = \bar{w} = q_3\tau$. Using the continuity of $\psi(x)$, we reach the following conclusion.

Lemma 1: τ is an evolutionarily stable sexuality rate if and only if $\psi_{r\mu}[q_\mu(\tau), \alpha; x]|_{x=q_3\tau}$, as a function of α , achieves its minimum over $0 \leq \alpha \leq 1$ at the point $\alpha = \tau$.

In other words, for

$$f(\alpha) = f_{r\mu\tau}(\alpha) = \psi_{r\mu}[q_\mu(\tau), \alpha; q_3\tau], \quad (15)$$

τ is an evolutionarily stable sexuality rate if and only if $f(\tau)$ is the minimum of $f(\alpha)$, with $0 \leq \alpha \leq 1$.

The following lemmas are needed to establish proposition 1, which proves the existence of such τ and characterizes it.

Lemma 2: (a) For any $\mu > 0$, $0 < \tau \leq 1$ and $0 < r < 1/2$, $f(\alpha)$ is a polynomial of the fourth degree with $f(0) > 0$, $f'(\alpha)|_{\alpha=0} < 0$ and $\lim_{\alpha \rightarrow \infty} f(\alpha) = -\infty$. (b) For $r = 0$, $f(\alpha)$ is a polynomial of the third degree with $f(0) > 0$, $f'(\alpha)|_{\alpha=0} = 0$, $f''(\alpha)|_{\alpha=0} < 0$ and $\lim_{\alpha \rightarrow \infty} f(\alpha) = \infty$ if $\mu > q_2/(q_2 + q_3)$. (It is easy to show that $4/11 > q_2/(q_2 + q_3)$),

and we are mainly interested in the case $\mu \geq 1$.) (c) For $r = 1/2$, $f(\alpha)$ is a polynomial of the third degree with $f(0) > 0$, $f'(\alpha)|_{\alpha=0} < 0$ and $\lim_{\alpha \rightarrow \infty} f(\alpha) = -\infty$.

Proof: Employing equations (10) and (15), one obtains by straightforward calculations

$$\begin{aligned} f(\alpha) = & x^4 - \alpha x^3 r(q_2 + q_3) - \alpha^2 x^2 q_2 r(1 - q_3 - r) \\ & - \alpha^3 q_2^2 (1 - r) x [(1 - 2r) + r q_2] \\ & - \alpha (1 - \alpha) x^2 q_2 r \mu - \alpha^2 (1 - \alpha) x q_2 (1 - 2r)(q_2 + q_3) \mu \\ & + \alpha^3 (1 - \alpha) r q_2^2 q_3 (1 - 2r) \mu, \end{aligned} \quad (16)$$

with $x = q_3 \tau$, and lemma 2 immediately follows.

Let

$$\begin{aligned} \mu^* = \mu^*(r) = & [2q_2 q_3 r(1 - r) + q_3^2 (q_3 - q_2) r + 3q_2^2 (1 - r)(1 - 2r) \\ & + 3q_2^3 r(1 - r)] / [q_2 q_3 (1 - r) + q_2^2 (1 - r)(1 - 2r)], \end{aligned} \quad (17)$$

where $q = q_\mu(\tau)|_{\tau=1}$. When $\alpha = \tau = 1$, μ^* is the root of f' as a function of μ . The importance of this expression will be clarified in proposition 1 below.

Lemma 3: μ^* increases with r from $\mu^*(0) \approx 1.05$ to $\mu^*(1/2) \approx 1.38$. (The proof of this lemma is given in Appendix B.)

From lemma 2, it follows that $f_{r\mu\tau}(\alpha)$ has one local minimum at the most when $\mu > 0$, $0 \leq r \leq 1/2$, and $0 < \tau \leq 1$. This minimum, when it exists, is denoted by $\alpha^*(\tau) = \alpha^*_{r\mu}(\tau)$.

Lemma 4: (a) Whenever it exists, $\alpha^*(\tau)$ is a continuous and differentiable function of τ . (b) $\lim_{\tau \rightarrow 0} \alpha^*(\tau) > 0$. (c) If for given μ and r there exists a value τ^* such that $\alpha^*(\tau^*) = \tau^*$, then $\tau^* \geq 2/3$. (d) If $\mu > 1$, $\alpha^*(\tau)$ exists for all $0 < \tau \leq 1$. (The proof of this lemma is given in Appendix C.)

Proposition 1: For any rate of recombination r between the main locus and the modifier locus, there is a fixed value $\mu^* = \mu^*(r) > 1$ being defined in equation (17) and characterized by lemma 3 such that (a) if $\mu \leq \mu^*$, then $\tau = 1$ (i.e., full sexuality) is an evolutionarily stable rate of sexuality; and (b) if $\mu > \mu^*$, then there exists a (positive) evolutionarily stable rate of sexuality τ with $2/3 \leq \tau < 1$.

Proof: (a) Employing equation (16), differentiating $f_{r\mu\tau}(\alpha)$ with respect to α , and inserting $\tau = 1$, $\alpha = 1$, and $x = q_3(1)$ (as given by eqs. 2), one can immediately verify that

$$\partial f_{r\mu 1}(\alpha) / \partial \alpha|_{\alpha=1} < 0$$

if $\mu < \mu^*$, where μ^* is given by equation (17). (Recall that μ^* is a function of r only.) Also, from lemma 2,

$$\partial f_{r\mu 1}(\alpha) / \partial \alpha|_{\alpha=0} < 0$$

for $0 < \mu$ (if $r > 0$; for $r = 0$, $\partial f_{r\mu 1}(\alpha) / \partial \alpha < 0$ for α sufficiently small).

It follows from equation (16) that $\partial f_{r\mu 1}(\alpha) / \partial \alpha|_{\alpha=1}$ is a linear function of μ (because $q_\mu(1)$ does not depend on μ) and therefore changes sign only once, at $\mu = \mu^*$, as μ decreases. Since $f_{r\mu 1}(\alpha)$ has (at most) one local minimum over $[0, \infty)$ and since $f_{r\mu 1}(\alpha)$ is a continuous function of μ , either the positive local minimum of $f_{r\mu 1}(\alpha)$ is larger than 1 for all $0 < \mu \leq \mu^*$ or it falls within the interval $(0, 1)$ for all $0 < \mu \leq \mu^*$ (if it exists). However, by straightforward calculations one can

readily verify that for μ sufficiently small, $f_{r\mu 1}(\alpha)$ does not achieve a local minimum over $0 < \alpha < 1$; hence, this is true for all $\mu < \mu^*$. Thus, when $\mu < \mu^*$, $f_{r\mu 1}(\alpha)$ is a decreasing function of α for all $0 \leq \alpha \leq 1$, obtaining its minimum over this interval at $\alpha = \tau = 1$. Employing lemma 1, $\tau = 1$ is an evolutionarily stable rate of sexuality.

(b) Suppose $\mu > \mu^*$. From lemma 4(b), it follows that $\alpha = 0$ cannot be an evolutionarily stable rate. From the inequality

$$\partial f_{r\mu 1}(\alpha) / \partial \alpha|_{\alpha=1} > 0$$

proved above for $\mu > \mu^*$, it follows that $\alpha = 1$ cannot be an evolutionarily stable rate of sexuality.

To prove the existence of an evolutionarily stable rate of sexuality $0 < \tau < 1$, employ the function $\alpha^*(\tau)$ as defined in lemma 4. This lemma implies that $\alpha^*(\tau)$ is defined for all $0 < \tau \leq 1$ if $\mu > \mu^* > 1$; that $\alpha^*(\tau)$, when defined, is a continuous function of τ ; and that $\lim_{\tau \rightarrow 0} \alpha^*(\tau)$ is strictly positive. Also, since

$$\partial f_{r\mu 1}(\alpha) / \partial \alpha|_{\alpha=1} > 0$$

for $\mu > \mu^*$, it follows that $\alpha^*(1)$ satisfies $\alpha^*(1) < 1$. Hence there exists at least one value $0 < \tau^* < 1$ with $\alpha^*(\tau^*) = \tau^*$.

In Appendix D it is shown that $f_{r\mu\tau^*}(\tau^*) < f_{r\mu\tau^*}(1)$ so that

$$f_{r\mu\tau^*}[\alpha^*(\tau^*)] = \min_{0 \leq \alpha \leq 1} f_{r\mu\tau^*}(\alpha). \quad (18)$$

From lemma 1 it therefore follows that τ^* is an evolutionarily stable rate of sexuality. From lemma 4 it also follows that $\tau^* \geq 2/3$.

Conclusions: (1) An evolutionarily stable rate of sexuality τ always exists where $\tau \geq 2/3$. (2) If the cost of sex factor μ is not too high, say 1.38 when $r = 1/2$ (see lemma 3), then absolute sexuality $\tau = 1$ is the evolutionarily stable strategy. (3) The stability of pure sexuality becomes more likely as the rate of recombination between the main locus and the modifier locus increases.

GLOBAL BEHAVIOR OF THE GENERAL MODEL: A COMPUTER SIMULATION MODEL

To study the global behavior of the model, a computer program that simulates the selection process on the population has been used. We are interested in the existence of a stable sexuality rate in the general model and how it is affected by some change in any of the variables such as n , the number of different catastrophes; μ , the cost of sex factor; δ , the survival probability of the unfit homozygote during a catastrophe; r , the recombination rate; s , the number of intermediate rest seasons between two successive catastrophes; and k , the heterozygote advantage in a rest season.

Each of the following graphs represents the results of the selection process for a different set of parameters; a point (x, y) would indicate the case in which an x -sexual population (of the genotype $B_x B_x$) is invaded by a new dominant mutant B_y (whose carrier is y -sexual) in small frequencies. B_y enters the population for those (x, y) points in regions marked "success" and is eliminated in regions marked "failure." Thus, figures 1-4 illustrate cases that hold for the parameters of the general model as defined above.

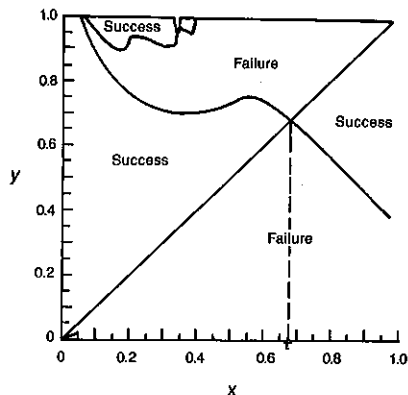
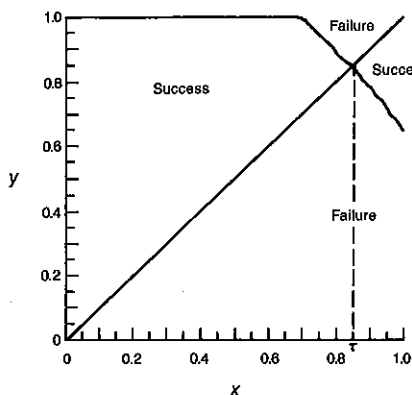


FIG. 1 (left).—Success or failure of a heterozygotic mutant with a rate of sexuality y in a population with a rate of sexuality x . When $h = \frac{1}{2}$, $k = 0$, $\delta = 0$, $n = 3$, $s = 0$, $\mu = 2$, and $r = \frac{1}{2}$, the unbeatable rate of sexuality, τ , is 0.85. Note that for all $y \neq \tau$, the straight line $x = \tau$ is in the failure domain, which means that $x = \tau$ is stable in the face of any mutation. For any $x \neq \tau$, the straight line $y = \tau$ is in the success domain, which means that a mutation $y = \tau$ is always established in the population. Moreover, for any value $x \neq \tau$, the range for a successful mutation y is shown to be some interval around τ , which increases as x becomes farther from τ .

FIG. 2 (right).—When $h = \frac{1}{2}$, $k = -0.17$, $\delta = 0$, $n = 5$, $s = 2$, $\mu = 2.5$, and $r = 0$, the unbeatable rate of sexuality, τ , is 0.67. The straight line $x = \tau$ is still in the failure domain, and $y = \tau$ is in the success domain. Note, however, that for certain values of x (say, around 0.2) the population is invisable either by mutations in an interval around τ or by those that determine a rate of sexuality close to one. These, in turn, are unstable to a mutation close to τ .

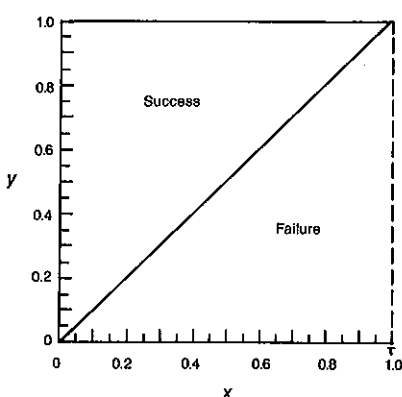
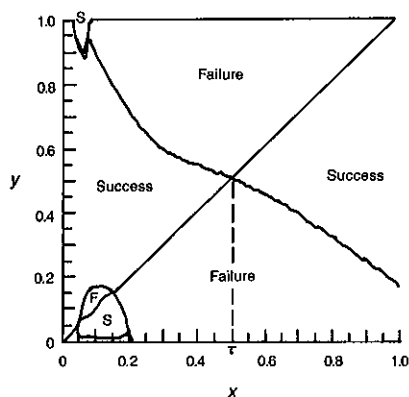


FIG. 3 (left).—When $h = \frac{1}{2}$, $k = -0.17$, $\delta = 0.0001$, $n = 4$, $s = 2$, $\mu = 3$, and $r = 0$, the unbeatable rate of sexuality, τ , is 0.5.

FIG. 4 (right).—When $h = 0$, $k = -0.17$, $\delta = 0$, $n = 6$, $s = 1$, $\mu = 1.8$, and $r = 0.3$, the unbeatable rate of sexuality is one. A mutation is successful if and only if it determines, as a heterozygote, a rate of sexuality higher than the prevailing one.

As can be seen from the above examples, a stable sexuality rate τ does exist in the general case and it is unique. Moreover, in all the examples being studied, the stable rate of sexuality τ has the property of evolutionary genetic stability (EGS, see Eshel and Feldman 1982); namely, τ is stable against any invading mutation, and any other rate of sexuality, when fixed in the population, is unstable against those mutations that determine, as heterozygotes, rates of sexuality closer to τ than to the rate of sexuality of the wild type (see also Motro 1982*a,b*, 1983).

Figures 5–8 show the behavior of this stable sexuality rate τ when one of the variables is changed and all the others are fixed as follows: $h = 0$, $k = 0$, $\delta = 0$, $n = 3$, $s = 0$, $\mu = 2$, $r = \frac{1}{2}$.

A conspicuous property of τ , as demonstrated in the figures, is that it is always positive. Absolute asexuality, $\tau = 0$, has not been found stable in any of the investigated examples. However, when δ is increased above 0, figures 9 and 10 show that what happens to a y -sexual mutant in an x -sexual population does not necessarily define a stable rate τ as has been the case so far. If δ is small enough, such τ exists. For larger δ 's, τ is locally stable only in the sense that it succeeds against all α -sexual mutants for α 's above some positive threshold, whereas α -sexual populations for some α 's under this threshold fail against highly sexual mutants with $\tau \approx 1$. For still larger δ 's, the only stable sexual rate is $\tau = 0$. For larger values of δ , with the rest of the parameters remaining the same, the situation is illustrated by figures 9 and 10.

We know from the preceding section that a stable sexuality rate τ is not necessarily the sexuality rate that brings the fitness of the population to its maximum. Let a sexuality rate $\hat{\beta}$ be called best if it brings the total fitness of the population to a maximum. Using a computer program to calculate $q_{\mu}(\tau)$ exactly from equations (2), we see that for the case in which $n = 3$, $\delta = 0$, $h = 0$, and $\mu = 2$, the total fitness of the population is maximized for $\hat{\beta} = 0.96$. However, the stable sexuality rate τ satisfies $0.74 \leq \tau \leq 0.84$ for the different possible values of the recombination rate. The highest (and closest to $\hat{\beta}$) value of τ is obtained for $r = \frac{1}{2}$.

SUMMARY

A model of seasonal selection acting on a prime locus with a modifier locus that determines the sexuality rate of the individual has been proposed. A fluctuating environment was assumed, such that in each generation some catastrophe may occur, in which case the only individuals that survive carry an allele resistant to the current catastrophe on the prime locus and the other individuals are most likely exterminated. Under such selection pressure, the proportion of the whole population that is exterminated depends on the number of possible catastrophes. For three catastrophes, possibly half to two-thirds but no more of the population may die (see Weinshall 1986). We have investigated how this process affects the modifier locus that determines the sexuality rate where, for some τ , a τ -sexual individual is one that produces a proportion τ of its descendants sexually and the rest asexually.

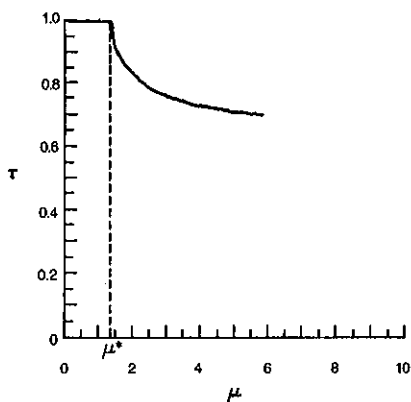


FIG. 5 (left).—The dependence of τ on the cost of the sex factor μ . For $\mu < \mu^* \approx 1.38$, $\tau = 1$.

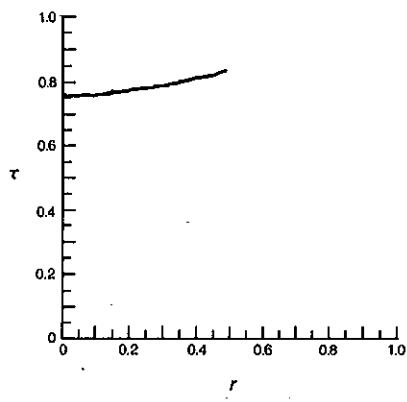


FIG. 6 (right).—The dependence of τ on the recombination rate, r .

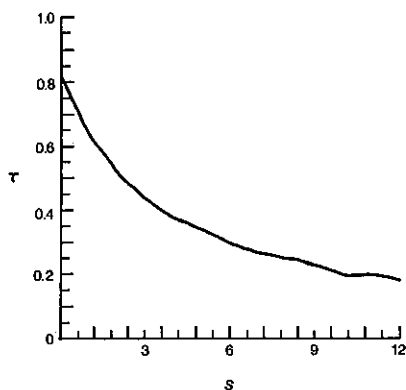


FIG. 7 (left).—The dependence of τ on the length of an intermediate rest period, s .

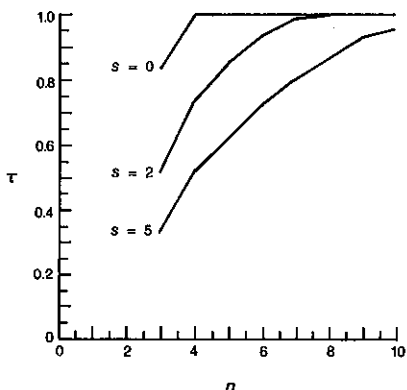


FIG. 8 (right).—The dependence of τ on the number of possible catastrophes, n , for different values of the length of the rest period: no rest period, and rest periods of two and five generations.

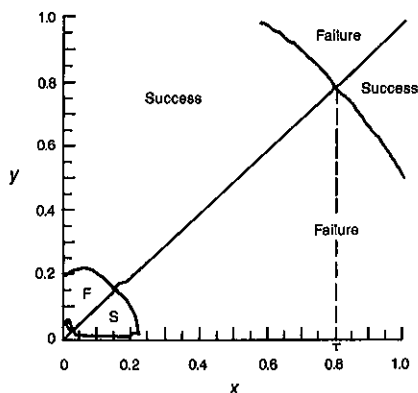


FIG. 9.—Success or failure of a y -mutant in a population with a fixed rate of sexuality x , where $k = 0$, $\delta = 0.0015$, $n = 3$, $s = 0$, $\mu = 2$, and $r = 1/2$. An unbeatable rate of sexuality at $\tau \approx 0.8$ still exists.

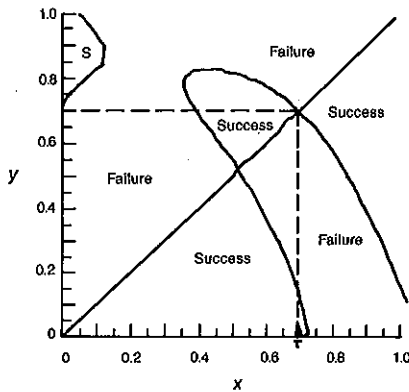


FIG. 10.—Success or failure of a y -mutant in a population with a fixed rate of sexuality x , where $k = 0$, $\delta = 0.003$, $n = 3$, $s = 0$, $\mu = 2$, and $r = \frac{1}{2}$. Two rates of sexuality, $\tau_1 = 0$ and $\tau_2 \approx 0.7$, are stable only against mutations of small effect, but none is stable against all mutations.

We have shown that, in general, as long as the catastrophes are intensive enough, there is one and only one evolutionarily stable sexuality rate τ , in the sense that a τ -sexual population is stable in the face of any mutant in the modifier locus. Likewise, in any other type of population, a τ -sexual mutant is likely to become fixed even if it appears at first in small frequencies. This stable sexuality rate decreases with the cost of sex and with the duration of the rest period between two consecutive catastrophes. It increases with the number of possible catastrophes. At any rate, if the intensity of a catastrophe is high enough, some positive sexuality rate is always favored over complete asexuality. Moreover, if the cost of sex is not too high (e.g., a sexual descendant demands up to 1.4 times the resources needed for an asexual descendant), the fixed sexuality rate is one; in other words, there is complete sexuality.

ACKNOWLEDGMENTS

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APPENDIX A

FREQUENCIES OF ALLELES IN A PARTIAL-SEXUALITY EQUILIBRIUM

In a τ -sexual population, we have defined the vector $\mathbf{q} = (q_1, q_2, q_3)$ to indicate the equilibrium frequencies of A_1 , A_2 , and A_3 as follows: q_1 , the equilibrium frequency of the most recently favored allele; q_2 , the equilibrium frequency of the allele needed for the next catastrophe; and q_3 , the equilibrium frequency of the allele needed in the preceding catastrophe (see Weinshall 1986). Thus, after S_1 , q_1 , q_2 , and q_3 indicate the frequencies of A_1 , A_2 , and A_3 , respectively.

After random mating and selection of an S_2 -type generation, we obtain

$$\begin{aligned}\text{freq}(A_2A_2) &= \tau q_2^2/\bar{w}, \\ \text{freq}(A_2A_3) &= 2\tau q_2q_3/\bar{w}, \\ \text{freq}(A_2A_1) &= [2\tau q_2q_1 + 2(1 - \tau)\mu q_2]/\bar{w} \\ \text{freq}(A_1A_1) &= \text{freq}(A_1A_3) = \text{freq}(A_3A_3) = 0,\end{aligned}$$

for $\bar{w}$, the mean fitness of the population.

However, from the definition of (q_1, q_2, q_3) , we know that q_1, q_2 , and q_3 indicate the frequencies of A_2, A_3 , and A_1 , respectively, after S_2 . That is,

$$\begin{aligned}\text{freq}(A_2A_2) &= 2q_1 - 1, \\ \text{freq}(A_2A_3) &= 2q_2, \\ \text{freq}(A_2A_1) &= 2q_3.\end{aligned}$$

This led us to the equations defining the equilibrium frequencies vector $\mathbf{q}$ (eqs. 2).

Result 1:

$$q_2^2 + q_3 = 2q_2[\tau + (1 - \tau)\mu]/\tau. \quad (\text{A1})$$

Proof: From equation (3) and the definition of $\bar{w}$, $\tau q_3 = 2q_2[\tau + (1 - \tau)\mu] - \tau q_2^2$; therefore, $q_2^2 + q_3 = 2q_2[\tau + (1 - \tau)\mu]/\tau$.

Conclusion:

$$\mu \geq 1 \rightarrow q_3\tau \leq 2\mu q_2. \quad (\text{A2})$$

Result 2:

$$q_2 \leq q_3 \leq q_1. \quad (\text{A3})$$

Proof: (a) From equation (A1), $q_2 + q_3 \geq q_2^2 + q_3 = 2q_2[\tau + (1 - \tau)\mu]/\tau \geq 2q_2$; therefore, $q_3 \geq q_2$. (b) From equation (A1) we get $q_1 \geq 1/2$, such that $q_2, q_3 \leq q_1$.

As a marginal result of the proof of result 2, we obtain result 3.

Result 3:

$$q_2 \leq 1/4, \quad q_3 \leq 1/2, \quad q_1 \geq 1/2. \quad (\text{A4})$$

Inserting equation (A4) into equation (A1) obtains result 4.

Result 4:

$$\mu \geq 1 \rightarrow q_3\tau \geq 1/4 q_2. \quad (\text{A5})$$

Result 5: q_2 is a root of the third-degree polynomial

$$2\tau^2 q_2^2 + 2q_2(\lambda - \tau q_2)(\lambda + \tau - \tau q_2) = \tau\lambda \quad \lambda = 2[\tau + (1 - \tau)\mu]. \quad (\text{A6})$$

APPENDIX B

THE PROOF OF LEMMA 3

Note, first, that $\mu^*(r)$ is well defined, since we know that $q_\mu(\tau)|_{\tau=1}$ does not depend on μ from equations (2). Thus, $\mu^*(r)$ is a function of r only. For

$$\mu^*(r) = \frac{2q_3r + 3q_2(1 - 2r) + 3q_2^2r}{q_3 + q_2(1 - 2r)} + \frac{r}{(1 - r)} \frac{q_3^2(q_3 - q_2)}{q_2q_3 + q_2^2(1 - 2r)},$$

derivation with respect to r gives

$$\begin{aligned}\frac{d\mu^*(r)}{dr} &= \frac{(2q_3 + 3q_2^2)(q_2 + q_3) - 6q_2q_3}{[q_3 + q_2(1 - 2r)]^2} + \frac{(1 - 2r)}{(1 - r)} \frac{q_3^2(q_3 - q_2)}{q_2q_3 + q_2^2(1 - 2r)} \\ &\quad + \frac{r}{(1 - r)} \frac{q_3^2(q_3 - q_2)2q_2^2}{[q_2q_3 + q_2^2(1 - 2r)]^2}.\end{aligned}$$

From equations (A1) and (A3) it follows that $q_2^2 + q_3 \geq 2q_2$ and $q_3 \geq q_2$. In addition, for $\tau = 1$, $q_2 \approx 0.16$, $q_3 \approx 0.296$, and $q_1 \approx 0.544$ (see Weinshall 1986), such that $q_3 < 2q_2$. Thus,

$$\frac{d\mu^*(r)}{dr} > \frac{6q_2^2 - q_3(q_2 + q_3)}{[q_3 + q_2(1 - 2r)]^2} > \frac{6q_2^2 - 2q_2(q_2 + 2q_2)}{[q_3 + q_2(1 - 2r)]^2} = 0.$$

APPENDIX C

THE PROOF OF LEMMA 4

(a) If $\alpha^*(\tau)$ is defined for a given value $\tau = \tau_0$ (given μ and r), then $\alpha^*(\tau_0)$ is the only point in which $\partial f_{r\mu\tau_0}(\alpha)/\partial\alpha$ intersects the x -axis from below. From the fact that $f(\alpha)$ is at most a fourth-degree polynomial with $\lim_{\alpha \rightarrow \infty} f(\alpha) = \lim_{\alpha \rightarrow -\infty} f(\alpha) = -\infty$ (lemma 2), it follows that $\partial^2 f(\alpha)/\partial^2\alpha$ is strictly positive. Hence, from the theorem of implicit functions, it follows that $\alpha^*(\tau)$ is defined in the vicinity of τ_0 , that it is continuous there, and that

$$\left. \frac{d\alpha^*(\tau)}{d\tau} \right|_{\tau=\tau_0} = \frac{-\partial^2 f_{r\mu\tau}(\alpha)}{\partial\alpha\partial\tau} \bigg|_{\tau=\tau_0, \alpha=\alpha^*(\tau_0)} / \frac{\partial^2 f_{r\mu\tau_0}(\alpha)}{\partial^2\alpha} \bigg|_{\alpha=\alpha^*(\tau_0)}.$$

(b) It follows from Appendix A that, for a τ small enough,

$$\begin{aligned} q_1 &= \frac{1}{2} + o(1), \\ q_2 &= \pi/4\mu + o(\tau), \\ q_3 &= \frac{1}{2} + o(1), \\ x &= q_3\tau = \frac{1}{2}\tau + o(\tau), \end{aligned} \tag{C1}$$

which implies that

$$\begin{aligned} f(\alpha) &= \{ -[(1 - 2r)\frac{1}{2}\mu\alpha^2(1 - \alpha)]/8\mu + r[\frac{1}{2}(1 - 2r)\mu\alpha^3(1 - \alpha)]/16\mu^2 \} \tau^2 + o(\tau^2) \\ &= (1 - 2r)\alpha^2(1 - \alpha)(r\alpha/2\mu - 1)/16 + o(\tau^2). \end{aligned} \tag{C2}$$

Hence, for $r \neq \frac{1}{2}$, the minimum point $\alpha^*(\tau)$ of $f(\alpha)$ tends, as $\tau \rightarrow 0$, to the minimum point of $\alpha^2(1 - \alpha)(r\alpha/2\mu - 1)$, which is readily shown to be of positive value. A similar argument holds for $r = \frac{1}{2}$.

(c) For τ such that $\alpha^*(\tau) = \tau$, it follows that

$$\begin{aligned} 0 &= \frac{\partial f(\alpha)}{\partial\alpha} \bigg|_{\alpha=\tau} = -\mu [(1 - 2\tau)\tau^2 q_2 q_3^2 r + (2 - 3\tau)\tau^2 q_2 q_3(1 - 2r)(q_2 + q_3) \\ &\quad - (3 - 4\tau)\tau^2 q_2^2 q_3 r(1 - 2r)] - \tau^3 q_3^3 (q_2 + q_3)r \\ &\quad - 2\tau^3 q_3^2 q_2 r(1 - q_3 - r) - 3\tau^3 q_2^2 q_3(1 - r)[(1 - 2r) + r q_2]. \end{aligned}$$

Thus, since $\tau > 0$,

$$\begin{aligned} \tau &= [q_3 r + 2(q_2 + q_3)(1 - 2r) - 3q_2 r(1 - 2r)] / \{ 2q_3 r + 3(q_2 + q_3)(1 - 2r) - 4q_2 r(1 - 2r) \\ &\quad - [q_3^3(q_2 + q_3)r + 2q_3^2 q_2 r(1 - q_3 - r) + 3q_2^2 q_3(1 - r)(1 - 2r + r q_2)] / \mu q_2 q_3 \}. \end{aligned}$$

Using the results in Appendix A, one can show that

$$\begin{aligned} \tau &= [2q_3(1 - r) + 2q_2(1 - 2r) + q_2 r(1 - r) + 3q_2 r^2] / \{ 3q_3(1 - r) + 3q_2(1 - 2r) + 4q_2 r^2 \\ &\quad - [(q_1 - q_3)q_3 r + 4q_2 r(1 - r) + 3q_2(1 - r)(1 - 2r) + q_2^2 r(1 - r)] / \mu \}. \end{aligned}$$

Since the numerator is always positive, the denominator must be positive as well for $\tau > 0$, and therefore

$$\tau \geq [2q_3(1 - r) + 2q_2(1 - 2r) + 3q_2 r^2] / [3q_3(1 - r) + 3q_2(1 - 2r) + 4q_2 r^2] \geq \frac{1}{3}.$$

From Appendix A and the expression above, it follows that τ is approximately $\frac{1}{3}$ for a large cost of sex, μ , independent of r (note that q depends on μ).

(d) We show first that $\partial f(\alpha)/\partial \alpha|_{\alpha=2} > 0$ if $\mu > 1$, where

$$\begin{aligned} \partial f(\alpha)/\partial \alpha|_{\alpha=2} = & -rq_2q_3^3\tau^3 - rq_3^4\tau^3 - 4r(1-r)q_2q_3^2\tau^2 + 4rq_2q_3^3\tau^2 \\ & - 12(1-r)q_2^2q_3\tau(1-2r) - 12r(1-r)q_2^3q_3\tau \\ & + \mu [3rq_2q_3^2\tau^2 + 8(1-2r)q_2^2q_3\tau + 8(1-2r)q_2q_3^2\tau - 20r(1-2r)q_2^2q_3]. \end{aligned} \quad (C3)$$

(i) Take $r \leq 1 - 2r$, such that $r \leq 1/3$.

Since $r \leq 1/3$ and $q_3\tau \geq 1/4 q_2$ for $\mu > 1$ (see eq. A5), it follows, for a part of the coefficient of μ in equation (C3), that

$$\begin{aligned} \frac{80}{21} (1-2r)q_2q_3^2\tau - 20r(1-2r)q_2^2q_3 &= (1-2r)q_2q_3 \left(\frac{80}{21} q_3\tau - 20rq_2 \right) \\ &\geq (1-2r)q_2q_3 \left(\frac{80}{21} \frac{7}{4} q_2 - \frac{20}{3} q_2 \right) = 0. \end{aligned} \quad (C4)$$

Since $q_3 \leq 1/2$ and $q_3\tau \leq 2\mu q_2$ for $\mu > 1$ (see eqs. A4, A2), it follows, for one of the other elements in equation (C3), that

$$-rq_3^4\tau^3 \geq -rq_3^3\tau^2 2\mu q_2 \geq -rq_2q_3^2\tau^2 \mu. \quad (C5)$$

From inserting relations (C4) and (C5) into equation (C3), it is sufficient to show that

$$\mu > \hat{\mu} \quad (C6)$$

for

$$\begin{aligned} \hat{\mu} = & [rq_2q_3^2\tau^2 + 4r(1-r)q_2q_3\tau - 4rq_2q_3^2\tau + 12(1-r)q_2^2(1-2r) \\ & + 12r(1-r)q_2^3]/[2rq_2q_3\tau + 8(1-2r)q_2^2 + 88(1-2r)q_2q_3/21]. \end{aligned} \quad (C7)$$

Note that, since $q_3 \geq 1/4 q_2$,

$$\begin{aligned} \hat{\mu} \leq & [2rq_2q_3\tau/(1-2r) + 2rq_2q_3\tau + 12q_2^2 + 12rq_2^3 + 12r^2q_2^3/(1-2r) - 12rq_2^2 \\ & - rq_2q_3^2\tau(4-\tau)/(1-2r)]/[2rq_2q_3\tau/(1-2r) + q_2^2 + 40q_2q_3/21]. \end{aligned}$$

From the assumption of $r \leq 1/3$ and relation (A5), which implies that $q_2 \leq 1/7 q_3\tau \leq 1/7 q_3$ when $\mu > 1$, it further follows that

$$\begin{aligned} \hat{\mu} \leq & [2rq_2q_3\tau/(1-2r) + 12q_2^2 + 1/3 q_2q_3\tau - 12rq_2^2(1-q_2) \\ & - rq_2q_3^2\tau(4-\tau-64/49)/(1-2r)]/[2rq_2q_3\tau/(1-2r) + 12q_2^2 + 40q_2q_3/21]; \end{aligned}$$

thus, $\hat{\mu} \leq 1$.

(b) Take $r > 1 - 2r$, such that $1/2 \geq r > 1/3$. Since in this case $r \leq 1/2$, replace equation (C4) by

$$\begin{aligned} (40/7)(1-2r)q_2q_3^2\tau - 20r(1-2r)q_2^2q_3 &= (1-2r)q_2q_3[(40/7)q_3\tau - 20rq_2] \\ &\geq (1-2r)q_2q_3[(40/7)(7/4)q_2 - (20/2)q_2] = 0. \end{aligned} \quad (C8)$$

Consequently, $\hat{\mu}$ will be

$$\begin{aligned} \hat{\mu} = & [rq_2q_3^2\tau^2 + 4r(1-r)q_2q_3\tau - 4rq_2q_3^2\tau + 12(1-r)q_2^2(1-2r) \\ & + 12r(1-r)q_2^3]/[2rq_2q_3\tau + 8(1-2r)q_2^2 + 16(1-2r)q_2q_3/7]. \end{aligned} \quad (C9)$$

Using the same arguments, one obtains

$$\begin{aligned} \hat{\mu} \leq & [2rq_2q_3\tau/(1-2r) + 2rq_2q_3\tau + 12q_2^2(1-r) + 12rq_2^3 + 12r^2q_2^3/(1-2r) \\ & - rq_2q_3^2\tau(4-\tau)/(1-2r)]/[2rq_2q_3\tau/(1-2r) + 8q_2^2 + 16q_2q_3/7]. \end{aligned}$$

Since $1 - r \leq 2/3$, $r \leq 1/2$, $q_2 \leq 1/4$, and also $q_2 \leq 1/4 q_3 \tau$ for $\mu > 1$ (see eq. A5), it can be shown that

$$\hat{\mu} \leq \{2rq_2q_3\tau/(1-2r) + 8q_2^2 + q_2q_3\tau(1 + 12 \cdot 1/2 \cdot 1/4 \cdot 1/4) - rq_2q_3^2\tau[4 - \tau - 12 \cdot 1/2(1/4)^2\tau]/(1-2r)\}/[2rq_2q_3\tau/(1-2r) + 8q_2^2 + 16q_2q_3/7];$$

thus, $\hat{\mu} \leq 1$.

Hence, $\hat{\mu} \leq 1$ always, which proves that condition (C6) holds for all r and τ as long as $\mu > 1$.

Since $f'(0) < 0$ for $r > 0$ and $f'(2) > 0$ for $\mu > 1$, as has been shown for r and τ given, $f(\alpha)$ has a minimum for any given $0 < \tau \leq 1$, $0 \leq r \leq 1/2$, and $\mu > 1$ because of continuity.

APPENDIX D

THE PROOF OF EQUATION (18)

To complete the proof of proposition 1, it remains to be shown that $f_{r\mu\tau^*}(\tau^*) < f_{r\mu\tau^*}(1)$. For this, denote

$$\Delta = f_{r\mu\tau^*}(1) - f_{r\mu\tau^*}(\tau^*). \quad (D1)$$

For $x = q_3\tau$, we employ equation (15) to obtain

$$\begin{aligned} \Delta &= (1 - \tau^*)[-x^3r(q_2 + q_3) - x^2rq_2(1 - r - q_3)(1 + \tau^*) \\ &\quad - q_2^2x(1 - r)(1 - 2r + rq_2)(1 + \tau^* + \tau^{*2})] \\ &\quad - \mu(1 - \tau^*)[-x^2rq_2\tau^* - xq_2(q_2 + q_3)(1 - 2r)\tau^{*2} + rq_2^2q_3(1 - 2r)\tau^{*3}]. \end{aligned}$$

However, since $\partial f_{\tau^*}(\alpha)/\partial \alpha|_{\alpha=\tau^*} = 0$,

$$\begin{aligned} \Delta &= \Delta - (1 - \tau^*) \partial f_{\tau^*}(\alpha)/\partial \alpha|_{\alpha=\tau^*} \\ &= (1 - \tau^*)^2 q_2 q_3 \tau^{*2} \left(-\{q_3 r(1 - r - q_3) + (2 + 1/\tau^*) q_2(1 - r)(1 - 2r + rq_2)\} \right. \\ &\quad \left. + \mu[rq_3 + 2(q_2 + q_3)(1 - 2r) - 3rq_2(1 - 2r)] \right). \end{aligned}$$

That is,

$$\begin{aligned} \Delta^{\text{sign}} \Delta^* &= rq_3(\mu - 1) + rq_3(q_3 + r) + q_2(1 - 2r)(1 - r)(4\mu - 2 - 1/\tau^*) \\ &\quad + (1 - 2r)\mu 2(q_3 - q_2) - r(1 - r)q_2^2(2 + 1/\tau^*) + \mu r(1 - 2r)q_2. \end{aligned} \quad (D2)$$

Since $\tau^* \geq 1/2$ by lemma 4(c),

$$\begin{aligned} \Delta^* &\geq \Delta^{**} = (\mu - 1)[rq_3 + 4q_2(1 - r)(1 - 2r)] + rq_3(q_3 + r) \\ &\quad + (1 - 2r)\mu[2(q_3 - q_2) + rq_2] - 4r(1 - r)q_2^2. \end{aligned}$$

With some calculations one can show, using Appendix A, that if Δ^{**} achieves its minimum over $-\infty < r < \infty$, this minimum is achieved for $r \geq 1/2$ if $\mu > 1$. Hence, at least when $\mu > 1$, $\Delta^{**}(r)$ obtains its minimum over the interval $[0, 1/2]$ on either $r = 1/2$ or $r = 0$. In either case, since $q_2 \leq q_3 \leq 1/2$ from equations (A3) and (A4),

$$\begin{aligned} \Delta^{**}(r, \mu, \tau)|_{r=1/2} &= 1/2 q_3(\mu - 1) + 1/2 q_3(1/2 + q_3) - q_2^2 \\ &\geq 1/2 q_3[\mu - 1 + (1/2 - q_2) + (q_3 - q_2)] \geq 0, \\ \Delta^{**}(r, \mu, \tau)|_{r=0} &= 4q_2(\mu - 1) + 2\mu(q_3 - q_2) \geq 0. \end{aligned}$$

Thus, $\Delta^* \geq \Delta^{**} \geq 0$, and, therefore, $\Delta \geq 0$, which completes the proof.

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