

An Analytical Model for a Short-term Advantage for Sex

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An analytical treatment is given for a model of Maynard Smith in which a short-term advantage for sex and recombination is provided by the mechanism of sib-competition. Suppose the next generation is formed by the winners of a large number of contests. Suppose a number of parents each contribute M offspring to a given contest, but the offspring of an asexual parent are identical whereas those of a sexual parent are distributed with some variance. If M is large there is a high probability that a sexual offspring will have a high enough fitness to win the contest. Calculations show that values of M around 3 and 4 are generally enough for sexual behaviour to overcome its two-fold disadvantage.

1. Introduction

One of the major unsolved problems in evolutionary biology is to account for the widespread establishment of sexual behaviour in the plant and animal world. What is the nature of the selective forces which maintain sexual reproduction in nature, and under what circumstances are they effective? Can these same forces account for its origin? Many recent papers and at least two extremely interesting books (Williams, 1975; Maynard Smith, 1978) have addressed this problem. Of course, sexual reproduction can involve a high or a low level of genetic recombination, and an essential part of this problem is to decide why present levels of recombination are what they are observed to be.

There are advantages and disadvantages to sexual behaviour and recombination. The literature considers two main types of disadvantages. The first arises when there is unequal investment by the two parents in their offspring. This may be the result of greater offspring care by one parent, or, in the absence of any parental care, of anisogamy: male and female gametes of different size. Usually it is the female who has the greater investment, but sometimes, for example in some fishes, it can be the male. Assume for now that it is the female. The disadvantage then stems from the fact that the

female, who is required to put equal investment into males and females, is unable to produce as many females, as a parthenogenetic female who produces *only* females. In the extreme case where the male investment is effectively zero, the sexual female produces only half as many females as the parthenogenetic female. This is referred to as the two-fold cost of sex.

The second main disadvantage of sex is that the offspring are not faithful copies of either parent. Since both parents are probably fit and well suited to the environment (after all they have managed to reproduce) it would seem that their best bet would be to stick with a genotype of proven ability rather than to "mix things up". This is an effect which is amplified by high recombination. Genes that work well, work well together. When recombination breaks apart gene complexes in successful parents it must usually disrupt favourable gene combinations. The average fitness of sexual offspring is expected to be lower than the average fitness of the two parents.

What are the advantages of sex? Interestingly enough there is only one significant advantage mentioned in the literature and that is the same as the second disadvantage: offspring are more varied than parents. Again, this effect is amplified by recombination. This variation in offspring can be an advantage in the following sense. Although sexual behaviour usually permits fewer descendents than asexual behaviour and gives them lower average fitness, a few of these descendents may just happen to have the right combination of alleles to surpass in fitness all their ancestors.

All models that I will mention that attempt to account for the maintenance of sex, present conditions under which some form of this advantage can outweigh the two disadvantages described above. The advantage claimed for sex is then really an advantage of recombination, which of course only becomes possible with sexual behaviour. The models all use essentially the same argument to account for the success of an allele for recombination in a sexual population: the allele for recombination, although suffering inherent disadvantages, eventually attains an advantage over alternative alleles, because it produces good individuals more quickly than can the alternative alleles, and it rides to success on the high fitness of these individuals.

This basic argument appears in a wide variety of guises. These can be categorized into two main forms: long-term and short-term. In the long-term argument it takes many generations for the production of these good individuals and in the meantime sexual behaviour will certainly appear to be at a disadvantage. The short-term argument looks for conditions under which the good individuals are produced in the next generation so that one can measure the advantage of sex with relative fitness in the classical sense (numbers of surviving offspring) of sexual and asexual individuals.

In the long-term models, good individuals are those who have managed to

incorporate a large number of favourable mutations and/or a small number of unfavourable ones. The idea is that these individuals will be more quickly generated (in fewer generations) in sexual than in asexual populations because recombination hastens the attainment of linkage equilibrium. The argument was originated by Fisher (1930) and Muller (1932). More recently Crow & Kimura (1965) and Maynard Smith (1968, 1971) consider models of this type. The last paper stands on the shoulders of the first two and builds an analytical model to decide whether a large number of favourable mutations can arise and be incorporated more quickly in a sexual or asexual population. Sex has an advantage when the population size and mutation rate are large and the selective advantage of each favourable mutation small. Indeed, in these cases, mutations do not take long to appear and become established in the population, but they take a long time to attain fixation. Recombination will create, early in the game, an individual with all mutations, so that in very little more than the time taken to fix one favourable mutation, they will all be fixed.

More recently, long-term models have been built by Strobeck, Maynard Smith & Charlesworth (1976) and by Felsenstein & Yokoyama (1976). These papers do simulation studies on small populations (≤ 1000). The first paper considers three loci: at one there is a balanced polymorphism, at another a favourable mutation, and the third has an allele promoting high recombination between the first two. In this model the high recombination allele is successful because it creates a good combination of genes, and increases in frequency because it is linked to that combination of genes. Hence the term *hitch-hiking* is introduced to describe the way in which the recombination allele hitches a ride on the back of the successful gene combination. The second paper investigates the effects of recurrent favourable and deleterious mutations on the success of an allele for high recombination. These models are long-term, in that the recombination allele does not increase in frequency in every generation, but does so when summed over many generations.

The short-term models attempt to find conditions under which this ultimate benefit of variation in offspring might actually confer greater personal fitness on sexual individuals. The process by which the long-term models find an advantage can be enhanced by making the environment of ones offspring uncertain, so that variation in offspring has some merit. These environmental variations can be temporal in nature (change from generation to generation) as in Charlesworth (1976) and Maynard Smith (1971) or spatial (change from patch to patch) as in Maynard Smith (1971), Slatkin (1975), Ghiselin (1974), Williams & Mitton (1973), Williams (1975) and Maynard Smith (1976). The last three papers discuss the effects of sib-

competition, an important new feature that greatly amplifies any sexual advantage through variation of offspring. In fact to obtain any short-term advantage without sib-competition, circumstances seem to have to be unreasonably special.

The essential idea behind sib-competition is that offspring of sexual individuals will differ somewhat from one another and will therefore compete less fiercely than asexual offspring. One way to look at this is to suppose you have to send several offspring to try to colonize an uncertain environment which can house only one mature individual. You want to maximize the fitness (for that environment) of your fittest offspring, so you may be better off to make your offspring all different than all the same. This is just what a sexual individual (with high recombination) does.

Maynard Smith (1976) built a simulation model to study these effects of sib-competition. He studied variation in five different environmental features, with five corresponding genetic loci. Our purpose is to build an analytical model to describe this type of situation.

Let us look more closely at the factors contributing to this short-term advantage. Suppose we have a patch of ground and a number of seeds are competing to grow on that patch. Suppose there are M seeds from an asexual parent and M seeds from a sexual parent. The M asexual seeds are all identical (to the parent) and presumably have high fitness since the parent already has high fitness by virtue of having survived. Of course, if the demands of the patch they are trying to dominate are different from those the parent experienced, this will tend to lower their fitness. The M sexual seeds are all different (especially if there is a significant amount of genetic recombination) and if M is large (which means a high level of sibling competition) one of them may have higher fitness than that of the asexual seeds. Thus to give sex as much advantage as possible, we want large uncertainty in predicting offspring environment from parental environment, a high level of sib-competition (large M) and probably significant genetic recombination (although genetic recombination will also break up favourable combinations which the parents may (*a posteriori* probably will) have had, and thus lower the mean offspring fitness).

2. Description of the Model

We have a large number of environmental patches. The patches are described by the values of N binary variables. A large number of individuals are trying to colonize the patches. Each individual sends M seeds to each of a number (the same number for every individual) of patches. Suppose this results in each patch having contributions from $K + 1$ individuals.

Suppose individuals are haploid with one of two alternative alleles at each of N loci; each allele matches one of the two values of the corresponding binary patch variable. Let the *fitness* of any individual, with respect to a certain patch, be the number of loci at which her allele matches the patch value. Suppose exactly one seed will grow on each patch, and this will be the one with maximum fitness.

We suppose there are two types of individuals: asexual and sexual. An asexual individual produces seeds which are identical to herself, a sexual individual finds another individual at random and chooses the genetic composition of each seed by taking at each of the N loci, with probability 50–50, the allele from herself and her partner. So we have perfect genetic recombination.

Our objective is to find conditions on K and M which will (1) allow a rare sexual mutant to invade an asexual population, and (2) allow a sexual population to resist invasion by a rare sexual mutant.

Now, under the assumption that one or other of the behaviours is rare, there will be two types of patches: those in which all $K + 1$ parents are of the common type, and those with K common and 1 rare parent. To decide whether the rare behaviour is at a relative advantage, we need only look at the outcome of the struggle to colonize the second type of patch. We will argue carefully in Appendix A that in case sexual behaviour is rare, it will be at an advantage provided the winning offspring in a mixed patch, has a sexual mother with probability at least $2/K + 1$. (Roughly speaking we need the 2 because only half of these sexual winners will actually have the gene for sex.) In case asexual behaviour is rare, it will be at an advantage provided the winning offspring has an asexual mother with probability at least $(K - 1)/(K + 1)(2K - 1)$. (This is approximately $1/2(K + 1)$ and is all we need because in those cases in which the winning offspring has a sexual mother, there is probability $\sim 1/K$ that he had an asexual father and hence probability $\sim 1/2K$ that he is asexual himself.) The factor of 2 which we see coming in here is what we have referred to as the two-fold cost of sex.

Finally, we need in our model a variable to describe the relationship between parental characteristics, and the characteristics of the patch into which she contributes seeds. Let us take a typical parent and a typical patch she is attempting to colonize. Suppose her fitness *relative to that patch* is drawn from some probability distribution on the integers from 0 to N . Let us assume that this distribution is binomial $B(p, N)$ with mean pN and variance $pN(1 - p)$. This would be the case if the colonizing parent has, independently at each locus, probability p of matching the patch characteristic.

If the parent is asexual, her offspring have fitness the same as her own. If the parent is sexual she chooses a partner who we will suppose bears the

same binomial relation to the patch as herself (with the same p), but independently of herself, and the distribution of the fitness of their offspring can be worked out. Indeed, one of our tasks in the next section will be to find approximately, the mean and variance of this distribution.

3. Mathematical Analysis

Let us focus attention on a fixed patch. Fitnesses will be measured relative to this patch. Define the following random variables. Let A be the fitness of a typical asexual offspring on that patch. (Then A is distributed as $B(p, N)$.) Let A_K be the maximum fitness of K randomly chosen asexual offspring on that patch. Let $S(z)$ be the fitness of a typical sexual offspring from a pair of parents with average fitness z . Let $S_M(z)$ be the maximum fitness of M randomly chosen offspring from a pair of parents with average fitness z . Let S_M be the average of $S_M(z)$ over z . It is the fitness of the best of M offspring from a typical pair of parents. Finally, let $S_{M,K}$ be the best of K samples of S_M . It is the fitness of the best of all the MK offspring produced by K sets of parents, each producing M offspring. We will now provide reasonable descriptions of the distributions of these random variables.

In general, suppose we sample n times from a standard normal distribution. The largest of these n numbers (the so-called first order statistic) is a variate with a certain distribution. Let us denote by μ_n and σ_n^2 the mean and variance of this distribution. If n is not too large ($n < 50$) this distribution is nearly normal. It is slightly skewed to the right, the skew becoming more pronounced the larger we take n . If we start with a general normal distribution with mean μ and variance σ^2 , the maximum of n samples will be distributed with mean $\mu + \sigma_n$ and variance $\sigma^2 \sigma_n^2$.

Now we can easily find the distribution of A_K . Recall that A is binomially distributed with mean Np and variance $Np(1-p)$. If N is large and p not too close to 0 or 1, this distribution is close to normal, hence A_K is approximately normally distributed with mean and variance

$$\begin{aligned}\mu(A_K) &= Np + \sqrt{Np(1-p)}\mu_K \\ \sigma^2(A_K) &= Np(1-p)\sigma_K^2.\end{aligned}\tag{1}$$

Now let us look at the S -distributions. First we will look at $S(z)$. Suppose a pair of parents have fitness v and w . Let r be the number of loci at which they both match the patch characteristic. Then the fitness of a typical offspring is distributed as $r+x$ where $x \sim B(1/2, w+v-2r)$. Setting $w+v = 2z$ where z is the average fitness of the parents, the offspring are approximately normally distributed with mean

$$r + \mu(x) = r + (1/2)(2z - 2r) = z$$

and variance

$$\sigma^2(x) = (2z - 2r)/4 = (z - r)/2.$$

In order to get an expression which we can work with later on, we will replace r by its average value in terms of z , that is, by its expectation conditional on z . Now r is hypergeometrically distributed with parameters N, v, w and so has mean vw/N . The average of this, given z , is expected to be approximately z^2/N . Actually, a precise calculation shows that the conditional expectation of r is

$$E(r|z) = \frac{z^2}{N} - \frac{z(N-z)}{2N-1}$$

but we will ignore the last term which is small, when N is large, compared to z^2/N . Hence, conditional on z , $S(z)$ is approximately normally distributed with mean and variance

$$\begin{aligned} \mu(S(z)) &= z \\ \sigma^2(S(z)) &= z(1 - z/N)/2. \end{aligned}$$

Hence $S_M(z)$ is approximately normally distributed with mean and variance

$$\begin{aligned} \mu(S_M(z)) &= z + \sqrt{z(1 - z/N)/2} \mu_M \\ \sigma^2(S_M(z)) &= z(1 - z/N)\sigma_M^2/2. \end{aligned}$$

To find the distribution of S_M we must average this over z , which has mean Np and variance $Np(1-p)/2$. [It is the sum of $v/2$ and $w/2$, two independent variates with mean $Np/2$ and variance $Np(1-p)/4$.] We will show in Appendix B that S_M then is approximately normally distributed with mean and variance

$$\begin{aligned} \mu(S_M) &= Np + \sqrt{Np(1-p)/2} \mu_M \\ \sigma^2(S_M) &= (\sigma_M^2 + \alpha^2)Np(1-p)/2 \end{aligned} \tag{2}$$

where

$$\alpha = 1 + \mu_M(1 - 2p)/2\sqrt{2Np(1-p)}. \tag{3}$$

If p is close to $1/2$ or if N is large then α is very close to 1.

Finally, $S_{M,K}$ is approximately normally distributed with mean and variance

$$\begin{aligned} \mu(S_{M,K}) &= Np + \sqrt{Np(1-p)/2} [\mu_M + \sqrt{\sigma_M^2 + \alpha^2} \mu_K] \\ \sigma^2(S_{M,K}) &= \sigma_K^2(\sigma_M^2 + \alpha^2)Np(1-p)/2. \end{aligned} \tag{4}$$

(A) CASE 1

Sex rare

In this case a mixed patch has contributions from K asexual parents and 1 sexual parent. The best asexual seed is distributed as A_K and the best sexual seed as S_M . From the results of Appendix A, sex will invade if the distribution of $S_M - A_K$ has mass at least $2/(K+1)$ above 0. Using independence,

$$\mu(S_M) - \mu(A_K) + \sqrt{\sigma^2(S_M) + \sigma^2(A_K)} m(2/(K+1)) \geq 0$$

where for any ε , $m(\varepsilon)$ is that value of x for which the standard normal distribution has mass ε to the right of x . Substituting from (1) and (2), this condition becomes

$$\mu_M \geq \sqrt{2}\mu_K - \sqrt{2\sigma_K^2 + \sigma_M^2 + \alpha^2} m(2/(K+1)). \quad (5)$$

Observe that p and N have dropped out of the condition except for their occurrence in α . But if p is close to $1/2$, or N is large, then α is close to 1.

(B) CASE 2

Sex common

In this case a mixed patch has contributions from K sexual pairs and 1 asexual parent. The best asexual seed is distributed as A and the best sexual seed as $S_{M,K}$. From Appendix A, sex will withstand invasion if the distribution of $S_{M,K} - A$ has mass at least $(K-1)/(K+1)(2K-1)$ above 0. Using independence,

$$\mu(S_{M,K}) - \mu(A) + \sqrt{\sigma^2(S_{M,K}) + \sigma^2(A)} m((K-1)/(K+1)(2K-1)) \geq 0.$$

Substituting from (4) and the paragraph above (1), this condition becomes

$$\mu_M \geq -\sqrt{\sigma^2 + \alpha^2} \mu_K + \sqrt{2 + (\sigma_M^2 + \alpha^2)\sigma_K^2} m((K-1)/(K+1)(2K-1)). \quad (6)$$

To summarize, given values of p , N and K , condition (5) describes those values of M for which sex will invade an asexual population, and (6) describes those values of M for which a sexual population, once established, can prevent asexual invasion. We have always found that if either condition holds for a particular value of M , it will hold for all larger values.

4. Numerical Calculations

The figures needed to calculate (5) and (6) are found in Table 1. Values of μ_n and σ_n can be found in the *CRC Handbook of Tables for Probability and Statistics* and in a paper of Tippett (1925).

TABLE 1

n	μ_n	σ_n^2	$m(2/(n+1))$	$m((n-1)/(n+1)(2n-1))$
2	0.564	0.682		
3	0.846	0.560		
4	1.029	0.492		
5	1.163	0.448	0.431	1.446
10	1.539	0.344	0.908	1.715
20	1.867	0.276	1.309	1.992
40	2.161	0.230	1.657	2.256
100	2.508	0.184	2.058	2.580

We first make a sample calculation for $N = 50$, $p = 1/2$ (so that α will be 0). For $K = 5, 10, 20, 40$ and 100 it is found that there is some threshold value of M for which conditions (5) and (6) hold for M greater than or equal to this threshold and fail for M less than the threshold. For $K = 5$ this threshold is $M = 4$ for both conditions while for $K = 10, 20, 40$ and 100, the threshold is $M = 3$, again for both conditions.

If p is not approximately $1/2$ it is likely to be somewhat greater than $1/2$. This describes the case when an individual has a greater than even chance of matching a typical characteristic of a patch she attempts to colonize. As p departs from $1/2$, the parameter α (which is the only place p and N occur in (5) and (6)) decreases slowly from 1. For $p = 0.8$, $N = 50$, α is 0.92 for $M = 2$ and 0.85 for $M = 4$.

Sample calculations for $N = 50$, $p = 0.8$, yield the results in Table 2. The value of M tabulated is the smallest value for which the indicated conditions (5) and (6), hold.

We see that for $p = 0.8$, $K = 20, 40$ and $M = 3$, sex is strong enough to invade an asexual population, but not strong enough to establish itself and withstand reinvasion by asexual behaviour.

TABLE 2

Under (5) we have the smallest value of M for which sex will invade an asexual population. Under (6) we have the smallest value of M for which a sexual population can prevent asexual invasion

K	$N = 50$ $p = 0.5$		$N = 50$ $p = 0.8$	
	(5)	(6)	(5)	(6)
5	4	4	4	4
10	3	3	4	4
20	3	3	3	4
40	3	3	3	4

Although we have tabulated results only for $N = 50$, other values of N could be handled from a complete $N = 50$ table, because p and N only appear in (5) and (6) via the parameter α . For example, $N = 160$, $p = 0.9$ gives the same value of α as $N = 50$, $p = 0.8$, so can be read from the second column of our table. And for all values of N , $p = 0.5$ gives $\alpha = 0$, and the results can be read from the first column.

It will be noticed that the results are fairly insensitive to changes in K or p , within reasonable limits.

5. Simulation

In order to check the reasonableness of our approximations, we did a simulation with $N = 50$ and $p = 0.5$. First, we generated some sexual offspring in the following manner. We generated 1000 pairs of parents—a parent is a 0, 1 vector of length 50 where each slot contains a 0 or 1 independently with probability 0.5. We then crossed each pair of parents to produce 4 offspring—an offspring is a 0, 1 vector of length 50 which, in each slot, contains a 0 (or 1) if both parents have a 0 (or 1) and a 0 or 1 each with probability 1/2 if the parent entries differ in that slot. We calculated the fitness of each of these 4000 offspring and for each pair of parents obtained values of S_M , the best of the first M offspring, $M = 1, 2, 3, 4$. Thus we obtained 1000 samples of each S_M for $M = 1, 2, 3, 4$. Table 3 compares the mean and standard deviation of these numbers with the values of $\mu(S_M)$ and $\sigma(S_M)$ calculated from (2) (with $\alpha = 1$).

Then we took these 1000 sets of offspring and formed them into 100 groups of 10. For each M , we took the best value of S_M in each group. We thus generated 100 samples of $S_{M,10}$ for each $M = 1, 2, 3, 4$. Table 4 compares the mean and standard deviation of these numbers with the values of $\mu(S_{M,K})$ and $\sigma(S_{M,K})$ obtained from (4) (with $\alpha = 1$ and $K = 10$).

To run simulations we also need some asexual offspring. We sampled 1000 times from a binomial distribution with parameters 0.5 and 50. We thus

TABLE 3

Comparison of theoretical estimates of mean and standard deviation of S_M with values calculated from 1000 samples

$M =$	2	3	4
sample mean	26.47	27.18	27.66
$\mu(S_M)$ from (2)	26.41	27.12	27.57
sample standard deviation	3.33	3.14	3.05
$\sigma(S_M)$ from (2)	3.24	3.12	3.05

TABLE 4

Comparison of theoretical estimates of mean and standard deviation of $S_{M,K}$ for $K = 10$ with values calculated from 100 samples

$M =$	2	3	4
sample mean	31.54	32.00	32.37
$\mu(S_{M,10})$ from (4)	31.40	31.92	32.27
sample standard deviation	1.81	1.87	1.81
$\sigma(S_{M,10})$ from (4)	1.90	1.83	1.79

TABLE 5

Number of sexual wins in 100 contests with $p = 1/2$, $N = 50$ and $K = 10$

$M =$	1	2	3	4
<i>Sex rare</i>				
No. sexual wins (100 contests)	8.5	16	19	24.5
<i>Sex common</i>				
No. asexual wins (100 contests)	10	5.5	5	2.5

obtained 1000 samples of A . We formed these into 100 groups of 10 and took the best in each group to obtain 100 samples of A_{10} .

(A) CASE 1

Sex rare

We matched the 100 samples of A_{10} with the first 100 of our samples of S_M . The number of sexual wins (instances in which S_M is larger than A_{10}) is tabulated in Table 5. A tie was counted as 1/2 of a win. For sex to invade we need a sexual win at least $2/11 = 0.18$ of the time. Thus we get sexual invasion if $M \geq 3$. This agrees with the value provided by formula (5) in the first column of Table 2.

(B) CASE 2

Sex common

We matched the first 100 of our samples of A with the 100 samples of $S_{M,10}$. The number of asexual wins is tabulated in Table 5. Again a tie was

counted as $1/2$ of a win. For sex to withstand invasion we need an asexual win no more than $9/209 = 0.043$ of the time. (This is the value of $(K-1)/(K+1)(2K-1)$ for $K = 10$.) This happens if $M \geq 4$. This is one greater than the value provided in Table 2 by the formula (6).

6. Discussion

We have built a model of the following general type. A population consists of two types of individuals, sexual and asexual. To form a new generation, each individual sends forth a number of offspring. Asexual offspring are identical to the parent, and sexual offspring are formed by the crossing (with perfect genetic recombination) of the sexual parent with another member of the population. The offspring engage in local contests on a large number of patches and the winners (one per patch) form the next generation. The problem is, under what conditions will one or the other type of behaviour increase in number?

There is an advantage and a disadvantage to sexual behaviour. The disadvantage is that sexual individuals may choose asexual individuals as fathers (assume no paternal investment except for the small genetic contribution, hence no increase in the number of offspring mothered by a sexual individual) resulting in only half their offspring being sexual. The advantage is that the offspring of a sexual parent are variable whereas the offspring of an asexual parent are identical. Thus if a sexual and an asexual parent each contribute M offspring to a contest, the one of highest fitness is more likely to be sexual (if $M > 1$). This advantage will be increased with increasing M . The problem becomes, how big should M be for the advantage to outweigh the disadvantage?

By analysing the distributions involved and making a number of simplifying assumptions, we have produced formulae to give threshold values for M in the cases that sexual or asexual behaviour is rare (formulae (5) and (6)). Calculations show that values of M around 3 and 4 are generally sufficient to give sexual advantage. These results are fairly insensitive to changes in p , the probability that a parent will match any characteristic in a patch she is trying to colonize, N , the number of loci, and K the number of parents who contribute offspring to a given patch—at least for $p \sim 1/2$, N large, and K between 5 and 100. There is a slight tendency for M to increase as p increases above $1/2$, and to decrease as K increases. We have run simulations to confirm our results for the case $p = 1/2$, $N = 50$, $K = 10$.

Of course our model only describes a single generation of selection. The process will continue, generation after generation, and the real issue is whether sex wins in the long-term. This problem is more difficult to handle

with an analytical model than with a simulation model, so we have restricted attention to the situation in which sex is rare or common. It is probably safe to interpolate our results for intermediate situations. For example, we read from Table 2 that for $N = 50$, $p = 1/2$ and $K = 10$ a value of $M = 3$ will provide sexual advantage both when sex is rare and common. It is not unreasonable to suppose that sex will be at advantage at all intermediate levels. The alternative, that there is some intermediate balance between sexual and asexual behaviour at which they are both equally fit is unlikely, although it is not ruled out by our analysis.

There are a number of factors that our model does not take account of. The most important of these is probably the interdependence of different loci (epistasis). A model which took account of epistatic effects would find the mean fitness of sexual offspring lower than that of the parents because of the tendency of recombination to break up favoured combinations. The effect of this will be to increase the threshold value of M somewhat. Of course, the effect of this factor will be less if recombination is incomplete, or if dependent loci are closely linked.

A simple model to try to accommodate this factor, suggested by Maynard Smith, has r loci for each trait instead of only 1. A set of r 1's means the trait is perfectly matched, and r 0's means its opposite is matched. One then has to decide on two things: what fitness to assign to intermediate cases, and the extent to which genetic recombination will be allowed to dismantle the r -set belonging to one trait.

Other factors we have not treated are incomplete recombination and diploidy (the individuals of our model are haploid). The former should reduce the diversity of sexual offspring and the latter should increase it. Finally, we have not considered the possibility that p , M and K will vary from patch to patch.

Bulmer (1980), using the methods of quantitative genetics, has simplified and improved our model.

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APPENDIX A

Suppose we have a group of $K + 1$ individuals, S of which are sexual and $K + 1 - S$ asexual. Suppose each contributes one seed to the next generation. An asexual contributes an asexual seed, and a sexual chooses a mate from the rest of the group at random and contributes a seed with 50% chance of being like her and 50% chance of being like her mate. Suppose one seed will be "selected" from the group and let P be the probability that this seed has a sexual mother. Our job is to find that value of P for which the probability that the winning seed will be sexual is $S/(K + 1)$, the proportion of sexual genes presently in the group.

Given that a seed has a sexual mother, what, we ask, is the probability that it will be sexual? It will be sexual if the mother chooses a sexual mate (which she does with probability $(S - 1)/K$), and sexual with probability $1/2$ if she chooses an asexual mate (which she does with probability $(K + 1 - S)/K$). Hence this probability is

$$(S - 1)/K + (K + 1 - S)/2K = (K - 1 + S)/2K.$$

Hence our "break-even" equation is

$$P \cdot (K - 1 + S)/2K = S/(K + 1).$$

In case $S = 1$ this gives a value for P of $1/2(K + 1)$. In case $S = K$ this gives a value for $1 - P$ of $(K - 1)/(K + 1)(2K - 1)$.

APPENDIX B

We assume that $S_M(z)$ has distribution with mean $z + \sqrt{z(1 - z/N)}/2\mu_M$ and variance $z(1 - z/N)\sigma_M^2/2$ and that z has mean $\mu = Np$ and variance $\sigma^2 = Np(1 - p)/2$. We obtain S_M by averaging $S_M(z)$ over z . What is the mean and variance of S_M ?

First let $\varepsilon = z - \mu$ and observe that

$$\begin{aligned} \sqrt{z(1-z/N)} &= \sqrt{\mu(1-\mu/N)}\sqrt{1+\varepsilon(N-2\mu)/\mu(N-\mu)} \\ &\simeq \sqrt{\mu(1-\mu/N)}\left[1 + \frac{\varepsilon(N-2\mu)}{2\mu(N-\mu)}\right] \end{aligned} \tag{B1}$$

if ε is generally small compared to μ and $N - \mu$. Since the average value of ε is 0, the average value of $S_M(z)$ is

$$\mu + \sqrt{\mu(1-\mu/N)/2}\mu_M.$$

This then is the mean of S_M .

The variance of S_M is calculated from

$$\sum_{t,z} [t - (\mu + \sqrt{\mu(1-\mu/N)/2}\mu_M)]^2 P_z(t) Q(z)$$

where P_z is the probability function for $S_M(z)$ and Q is the probability function for z . The term in the square brackets can be written as the sum of two terms:

$$\begin{aligned} [t - (z + \sqrt{z(1-z/N)/2}\mu_M)] \\ + [z + \sqrt{z(1-z/N)/2}\mu_M - (\mu + \sqrt{\mu(1-\mu/N)/2}\mu_M)]. \end{aligned}$$

When this is squared and summed over t , the cross-terms sum to zero, the first term squared gives the variance of t , which is $z(1-z/N)\sigma_M^2/2$, and the last term squared gives

$$\begin{aligned} \left[(z - \mu) + \sqrt{\mu(1-\mu/N)/2} \left(1 + \frac{\varepsilon(N-2\mu)}{2\mu(N-\mu)} - 1 \right) \mu_M \right]^2 \\ = \left[\varepsilon + \frac{\mu_M \varepsilon}{2} \frac{(1-2\mu/N)}{\sqrt{2\mu(1-\mu/N)}} \right]^2 = \varepsilon^2 \alpha^2 \end{aligned}$$

using (B1).

When these terms are multiplied by $G(z)$ and summed over z we get, approximately

$$\frac{\mu(1-\mu/N)}{2} \sigma_M^2 + \sigma^2 \alpha^2,$$

which is the same as (2).