

THE EFFECT OF ASSORTATIVE MATING AND ENVIRONMENTAL VARIATION ON SELECTION FOR SEXUAL REPRODUCTION

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Received 11 July 1994, 28 March 1995

ABSTRACT The reasons given for the ubiquitous presence of sexual reproduction are many. Most involved the genetic variation possible with meiosis. This variation is proposed as necessary for adaptation to various forms of environmental changes. Other theories propose an immediate benefit to the organism. The opportunity available for mate selection has an immediate fitness value for the adult because the offspring will receive good genes from the chosen parent. A computer model is presented here for the evaluation of mate selection and environmental variability as the cause of sexual reproduction. Competition between asexual and sexual sister species is modeled under different conditions. Results show that assortative mating between individuals of similar phenotypes, as opposed to random pairing, greatly favors the sexual species. The effect of changing the direction of selection has a negative effect on the success of the sexual form.

INTRODUCTION

Theories for the existence of sexual reproduction can be divided into two groups. One is based on the genetic variation produced by meiosis. The other is concerned with the immediate benefits for the individual (For reviews see: Bellig and Stevens 1987, Michod and Levine 1988 and Kondrashov 1993).

Various computer simulations of competition between sexual and asexual sister species have been developed. Low mutation rate has been found important for the success of the sexual species (Findlay and Row 1990). Mate selection against rare alleles was shown to benefit sexual reproduction if the mutation rate was high (Koeslag and Koeslag 1993). The computer model reported here assumes that sex is an adult activity that usually involves two individuals who have survived Darwinian selection. This natural separation in time between selection and mating is incorporated into this model. Simulating mating and selection/replication separately allows the evaluation of different mating strategies. In particular mating of random pairs can be compared to mating between individuals of similar phenotypes. The latter has proved very beneficial for the sexual species.

THE MODEL

A genetic algorithm (Goldberg 1989, Holland 1975) is used to simulate a population of 50 hermaphroditic haploid individuals with five loci. The first locus determines the mode of reproduction, (sexual or asexual). The sum of the other four loci represents the phenotype. The population is subject to the following steps: initialization, randomization, mutation, mate selection, recombination, and replication. An experiment is started with an equal number of sexual and asexual forms. The four phenotype loci of each individual are initialized at a value of 500. Since the original population does not contain genetic variations the effect of mutation produced variation can be measured. The population is randomized. A mutation subroutine is run that adds a random number between -100 and +100 to 5% of the loci. This scheme of net neutral rather than the usual detrimental new mutations has been used to allow the direction of selection to be reversed mimicking the effect of environmental variability. In the case of assortative mating the phenotypes are used to order the sexual forms from high to low. In either reproductive mode (random or sorted), adjacent sexual pairs are then allowed to recombine. As the progeny are formed they replace their parents. No genetic linkage is evoked. There is a 50% chance of exchange of alleles between parents at each loci. After recalculating the sum of the phenotype loci, a truncated soft selection is evoked (Crow and Kimura 1979, Kondrashov 1988). Copies of the genomes of the 16% most fit replace those of the 16% least fit. The cost of sex is introduced at this point by skipping a sexual form in favor of the next most fit 50% of the time. Environmental variation is mimicked by changing the definition of fitness. The most fit can be either the largest sum or the smallest sum. The direction of selection is reversed stochastically at the rate set for that particular experiment. The program is then repeated starting with randomization until the population is all sexual or all asexual. The complete program is rerun 100 times starting

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Evolutionary Theory 11: 51-53 (August, 1995)

The editors thank S. Findlay and J.H. Kreslag for help in evaluating this paper.

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with all phenotype alleles set at 500 and with equal numbers of sexual and asexual individuals. The proportion of runs in which the sexual variation.

Table I. The Effect of Environmental Variation and Assortative mating.

Probability of Selection Reversal	Percent Fixation for Sexual Forms	
	Random Mating	Assortative Mating
0	44%	65%
.01	38%	48%
.02	36%	48%
.05	34%	50%

RESULTS AND DISCUSSION

Table I shows that assortative mating allows the sexual form to replace the asexual species 65% of the time. This occurs in the presence of a twofold penalty for being sexual. If mating occurs between randomly associated pairs, the sexual form is much less successful. Environmental variation does not sustain the long standing expectation of enhancement of sexuality but in fact is inhibitory to the sexual form in its competition with the asexual. The assortative mating evoked in this study is identical with mate selection for the most fit. In nature there is evidence for mate selection for the most fit (Korzeniak and Jasienski 1989, Mitchell 1990, Partridge 1980, Pruett-Jones, Pruett-Jones 1980, Taylor *et al* 1987, Trivers 1976). If the most fit mate with the most fit, the less fit have no choice but to mate among themselves. Also mating between adults who have survived significant juvenile mortality can be thought of as mate selection for the most fit.

The introduction of environmental variation in the form of selection reversal is detrimental to the survival of the sexual forms. With both the random and assortative mating, the sexual species survives less often if the direction of selection is changed (Table I). This effect can be explained if one observes the values of alleles during a run. It is obvious that selection for the most fit reduces the genetic variation as beneficial alleles accumulate. In the absence of mate selection, meiotic produced variation is the only remaining 'benefit' of sexual reproduction. Adaptation in the opposite direction requires time for the production of new mutations. During this interval the twofold sexual penalty continues.

It can be argued that this model does not represent nature. Matings and reproduction have been separated. A limited number of additive loci have been used to determine the phenotype in a one dimensional world. The population size is small and does not change. The mutation paradigm holds mutation constant at an arbitrary rate. These deviations from nature have been used for parsimony and the reduction of computation time. Each deserves to be studied by itself. This paper attempts to look at only two issues, assortatives mating and environmental variability. These computer experiments show that mate selection for the most similar is a much stronger influence for the spread of sexual reproduction than the adaptation to a changing environment. The Koeslags have come to a similar conclusions using the absence of rare alleles to determine mate choice (Koeslag and Koeslag 1993).

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