Advantage of sexual reproduction caused by enhanced sibling diversity

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Ph.D. Thesis

Advantage of sexual reproduction caused by enhanced sibling diversity

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Preface

In many species, including human, offspring has the genome that is a mixture of genomes of two different individuals. This is called "sexual reproduction". In the last several decades, the reason why the sexual reproduction is maintained in evolution has been a big puzzle in evolutionary biology. It still remains an unsolved problem, although a large number of different processes explaining the advantage of sexual reproduction have been proposed and studied.

Some sexual species, such as humans, have separate sexes, namely males and females, which are specialized in producing sperms (pollen) and eggs, respectively. Other organisms, such as many plants and other sedentary species, are hermaphrodite, in which a single individual produces sperms (or pollen) and eggs in its life. Hermaphrodites may engage in selfing, forming an offspring from an egg sired by a sperm, both being produced by the same individual. However, in all of these cases, the genome of an offspring differs from that of any of their parents, resulting in genetic mixis.

In contrast, there are species who lost sexual reproduction. Their offspring has the same genome as their mother. The most famous examples are water fleas and aphids. Their offspring are genetic clones of their mother. Since asexual reproduction can avoid producing males who do not contribute to the production of offspring, the asexual reproduction is more efficient than sexual reproduction. An asexual strain should increase in number at the rate twice as faster than a sexual strain, if their survivorship and fertility are the same. This is called "two-fold cost of sex" (Maynard Smith, 1976, 1978). This indicates that asexual mutants appeared in a sexual population should take over the whole population, giving a very large immediate evolutionary advantage. Nonetheless sexual reproduction is dominant in many organisms. This suggests that there must be processes that give a very strong advantage to the sexual reproduction.

In the 1930s, Fisher (1930) and Muller (1932) proposed that the advantageous mutations are accumulated in an individual in a short time by genetic recombination of sexual reproduction. Thereafter many fascinating ideas have been proposed. One emphasizing temporal fluctuation of the environment, especially biological environment caused by pathogens, is called the Red Queen Hypothesis promoted by Hamilton (1980). Another is to emphasize the role of accumulation of deleterious mutations in the population, such as Muller's Ratchet by Muller (1964) and genetic load (Kondrashov, 1988). Still another is to emphasize the spatial distribution (Peck, 1999).

One hypothesis for the advantage of sexual reproduction focuses on the diversity of offspring born from a single mother. G.C.Williams presented an idea called Lottery hypothesis (Williams and Mitton, 1973; Williams, 1975). The sexual siblings have different genotypes. In contrast, the asexual siblings have the same genotypes. Provided the environment of the next generation is unpredictable, the sexual parents having diverse offspring will be advantageous. The provability that one of their offspring has the best match with the environment may be higher than that of an asexual mother. Maynard Smith (1976, 1978) formalized this idea as "sib-competition model" and studied it by computer simulations. He concluded that the diversity of offspring cannot generate a sufficiently large advantage outweighing the two-fold cost of sex. After that the idea has not been examined intensively, except for Taylor (1979) and Bulmer (1980). Recent review articles by Nick Barton and Sarah Otto concluded that sib-competition does not provide sufficiently strong advantage to the sexual reproduction (Barton et al., 2002; Otto, 2009).

However, the assumptions of strong sib-competition and the diversity of local environment for offspring are both quite plausible. The genetic diversity among offspring of the same mother should have significant effects. I conjecture that there must be some ways to make the hypothesis work strongly.

In this thesis, I examine the sib-competition model with modified conditions, and discuss when the diversity of sexual siblings can be effective in generating a sufficiently strong advantage of sex. In the first chapter, I revise the sib-competition model of Maynard Smith in the direction to which the sexual type has more diversity than in the original version. We report that, by revising the model in two major ways, the diversity of sexual siblings has an advantage outweighing the two-fold cost. This result suggests that the diversity of sexual siblings can play an important role for the maintenance of sexual reproduction. I further examine various processes promoting and limiting the advantage to sex in detail.

In the second chapter, we examine three additional modifications that make the model more realistic. Three factors added to the model are: milder selection pressure, environmental variance, and reduced genetic diversity. They may encourage or discourage the evolution of sex.

In short, these theoretical studies show that there are situations in which the sexual type has the advantage overtaking the two-fold cost. In other words, the effect of the diversity of sexual siblings cannot be neglected in thinking of the evolution of sexual reproduction.

I summarize the contents of two chapters as follows:

Chapter 1: Sibling diversity gives sexual reproduction the advantage in a changing environment.

Background: A process potentially favoring sexual reproduction is intense competition among siblings, because the phenotypic diversity is higher among sexual siblings than asexual siblings. Previous theoretical studies concluded this process ineffective.

Question: What is the condition in which sib-competition may favor sexual reproduction?

Search method: Mathematical and numerical analyses of the model. We identify the mechanisms that reduce the advantage of sex.

Key Assumptions: Habitat consists of many patches, each with different environmental condition. Only the most adapted individual survives in each patch. Sexual reproduction generates phenotypic diversity among siblings, whereas asexual reproduction doubles the reproductive rate.

Conclusions: A greater number of environmental factors and a variation of the fitness achieved by adapted phenotypes favor sexual reproduction. Intense sib-competition is an important process for maintaining sex.

Chapter 2: Advantages of sexual reproduction resulting from sibling diversity: effects of selection intensity, environmental variance, and reduced genetic diversity.

Background: A twin paper showed that more sibling diversity among sexual offspring may help to maintain sexual reproduction in environments that are spatially heterogeneous and temporally fluctuating and in which sib-competition is very intense.

Question: Can sexual reproduction be maintained in the face of the two-fold cost of sex under milder selection pressure, environmental variance, and reduced genetic diversity?

Methodology: Mathematical and numerical analyses of the sib-competition model with several modifications.

Conclusions: The advantages of sexual reproduction are attenuated by milder selection pressure and environmental variance but enhanced by reduced genetic diversity. Sib-competition plays an important role in maintaining sex when appropriate conditions are present.

References for the preface:

Barton, N.H., Briggs, D.E.G., Eisen, J.A., Goldstein, D.B., Patel, N.H., 2002. Evolution, New York, Cold Springer Laboratory House.

Bulmer, M.G. 1980. The sib competition model for the maintenance of sex and recombination. J Theor. Biol., 82: 335-345

Fisher, R.A., 1930. The Genetical Theory of Natural Selection. Oxford, Oxford University Press.

Hamilton, W.D., 1980. Sex versus Non-sex versus Parasite. Oikos, 35, 282-290.

Kondrashov, A.S. 1988. Deleterious mutations and the evolution of sexual reproduction. Nature 336:435-440.

Maynard Smith, J. 1976. A short-term advantage for sex and recombination through sib-competition. J. Theor. Biol., 63: 245-258

Maynard Smith, J. 1978. The Evolution of Sex. Cambridge: Cambridge University Press.

Muller, H.J., 1932. Some Genetic Aspect of Sex. American Naturalist, 66, 118-138.

Muller, H.J., 1964. "The relation of recombination to mutational advance". Mutation Research, 106: 2–9

Otto, S.P., 2009. The Evolutionary Enigma of Sex. The American Naturalist, 174, S1-S14.

Taylor, P.D. 1979. An analytical model for a short-term advantage for sex. J. theor. Biol., 81: 407-421

Williams, G.C. and Mitton, J.B. 1973. Why reproduce sexually? J. Theor. Biol., 39: 545-554

Williams, G.C. 1975. Sex and Evolution. Princeton, NJ: Princeton University Press.

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Chapter 1

Sibling diversity gives sexual reproduction the advantage in a changing environment

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Introduction

Nearly forty years ago, John Maynard Smith presented the concept of the two-fold cost of sex (Maynard Smith, 1978). His hypothesis was that sexual reproduction is less effective than asexual reproduction because the number of offspring produced sexually per generation is half the number that can be produced asexually. Nonetheless, sexual reproduction predominates among multicellular organisms. This suggests that sexual reproduction must confer either a group selective advantage (e.g. Mettledorf 2016) or else confer significant short-term advantages that outweigh its two-fold cost. Since then, various possible evolutionary benefits of sexual reproduction have been suggested. However, as Agrawal (2006) observed in his review article: "We do not even know how sex typically affects the mean and variance in fitness in nature. We know even less about the forces generating variation in sexual processes within species."

Among many plausible models sugges~~ting~~ the advantages of reproducing sexually, the "Red Queen Hypothesis" emphasized the impact of temporal fluctuations on the selective process. In particular, Hamilton (1980) proposed that the host-parasite relationship would favor sexual reproduction due to short-term epistatic fluctuations. Recent reviews also concluded Red Queen hypothesis as a potentially important process favoring sex (Otto, 2009; Hartfield and Keightley, 2012).

Another model emphasized the role sexual reproduction plays in disrupting linkage disequilibrium created by random genetic drift. Natural selection can generate associations between different loci where one allele has a positive effect, and another a negative effect on fitness. In sexually reproducing species, genetic recombination reduces these negative associations allowing natural selection to work more effectively (Fisher, 1930; Muller, 1932; Barton and Otto, 2005; Barton et al., 2007; Otto, 2009).

A third model notes that sexual reproduction produces diversity, providing an advantage in environments where the direction and intensity of selection change. G. C. Williams demonstrated that in a changing environment, sexual reproduction is likely to produce the most adapted individual (the Lottery hypothesis) (Williams and Mitton, 1973; Williams, 1975). In addition, Bell (1982) proposed that a greater range of environments is accessible to sexually reproducing individuals allowing each to exploit a slightly different ecological niche (the Tangled Bank hypothesis). Williams and Mitton (Williams and Mitton, 1973; Williams, 1975) explained the advantage of sexual reproduction in terms of enhanced variations in fitness, which increased the number of very fit offspring. Maynard Smith (1976, 1978) identified competition between siblings as a key to a major advantage of sexual reproduction because this can generate variation within families. He formalized a sib-competition model and demonstrated that sexual reproduction has a strong advantage over parthenogenesis and is able to overcome the two-fold cost of sex. However Maynard Smith concluded that the model was ineffective, because the advantages of sexual reproduction were lost if the different selective features of a patch are correlated, or if several genetic loci are involved in adapting to a single selective feature.

Taylor (1979) analyzed the sib-competition model mathematically. Bulmer (1980) was able to extend the analysis by incorporating quantitative genetics. However, Barton and Post (1986) criticized these developments for not taking environmental correlations into account. In the last thirty years, there was no serious attempt to evaluate the sib-competition as a factor potentially favoring sexual reproduction.

In the present paper, we investigate a sib-competition model with modified assumptions and with a broader parameter range. A large number of environmental factors and the variance of fitness among the most adaptive phenotypes greatly favor the advantage of sexual reproduction. We also identify processes that reduce the advantage of sexual reproduction. We conclude that intense sib-competition is an important process for maintaining sex, given suitable conditions are met.

Sib-competition model

We start with the sib-competition model proposed by Maynard Smith (1976, 1978). However we here consider species with separate sexes (males and females) rather than the one with hermaphrodites. The model considers the dynamics of sexual and asexual organisms competing within a single Mendelian population, which consists of a number of patches. The environment in each patch varies greatly between patches and between generations.

Population structure and reproduction of sexual and asexual organisms

To illustrate the population structure, in Fig. 1A we show a population consisting only of sexual organisms as an example. We are considering a dioecious species (i.e., with separate sexes) where the sex ratio is 1:1. For simplicity we assume that the genome is haploid. The environment consists of many patches. Multiple individuals live in the same patch, grow, and compete with each other (such as feeding larvae of insects). Finally, only a single individual per patch survives. All the survivors from each patch are then combined into a single breeding population and random mating takes place. We assume that each female mates with only one male. As a result, offspring that have the same mother also have the same father. Females lay eggs in a patch and the number of females that can enter a patch (*R*) is restricted. Each female produces *N* offspring. This means that *RN* offspring compete within each patch. As time passes, the number of offspring in a patch decreases until only one remains. This survivor (or 'winner') is determined randomly from the individuals that are best adapted to the environment.

Next, we consider a population consisting only of parthenogenetic (i.e., asexual) organisms (Fig. 1B). Survivors from each patch are combined in a single breeding population and randomly enter patches to lay eggs. The number of females that can enter a patch is *R*, and each female produces *N* offspring.

Finally, we consider a mixed population consisting of both sexual and asexual organisms (Fig. 1C). In each patch, both sexual females and asexual individuals lay eggs. The eggs hatch, larvae grow, and after intense competition only one individual survives. All the survivors are combined into a single breeding population and sexual females mate randomly with sexual males. Next, sexual females and parthenogenetic individuals randomly enter patches to lay eggs. The number of egg-laying individuals in a patch is *R*, and each produces *N* offspring before dying. Taking into account the ratio of sexual to asexual organisms in the breeding population (including the number of males), a sexual individual is only half as likely to become an egg-laying individual as an asexual individual, representing the two-fold cost of sex.

Competition within a patch and adaptation to the local environment

Within each patch, *NR* individuals (both sexual and asexual) compete and only the individual that is the most adapted to the local environment survives. To determine the fitness of each individual, we define its "score" as follows: There are five environmental factors, each with two states. For example, if the first factor is temperature, the environment may be either hot or cold. If the second factor is humidity, the environment is either wet or dry. Therefore, each of five factors has two possible values and there are $2^5 = 32$ possible overall environmental states. The environmental state of each patch is determined independently and chosen randomly from the 32 possible overall states.

For each combination of five environmental factors (i.e., the 32 environmental states) there are 32 possible phenotypes, and each of these matches one overall environmental state. For example, if the phenotype of an individual is AbCDe and the environmental state is AbCDe, then the score is five, because all five aspects of the phenotype match the overall environmental state. However, if the environmental state is ABCDE, the score of phenotype AbCDe is three because there are three matches and two mismatches between the five phenotypic aspects and the overall environmental state. In this way, matching the local environment determines the scores of 32 phenotypes. The score may be one of six possible values: from zero to five. If only one individual from the *NR* offspring has the highest score, it will be the survivor. If more than one individual has the same highest score, one of these is selected randomly to be the winner.

The phenotypes of siblings produced by the same sexual mother are often different, but all siblings from the same asexual (parthenogenetic) mother have exactly the same phenotype. Hence, a sexual mother has a greater chance of producing offspring that achieve the highest score (i.e., are the most adapted to the local environment). Therefore sexually reproducing organisms have an advantage, despite the two-fold cost of sex.

Environmental correlations

Maynard Smith (1976, 1978) also used the model to investigate what would happen if different environmental factors were correlated. He explained this situation by saying "if hot places are always dry and cold places wet, this is formally equivalent to there being only one feature with two states, 'hot and dry' or 'cold and wet'". These correlations effectively reduce environmental heterogeneity, decreasing the advantage sexual organisms have. Maynard Smith (1978) pointed out that multiple loci controlling the same trait may also reduce the advantage that sexual organisms have: "Alleles $A1$ and $A2$, at different loci, adapt the individual to high temperatures, and $a1$ and $a2$ to low temperatures. Then genotypes of high fitness will be either $A1A2$ or $a1a2$".

The relative advantage of sexual reproduction

The solid line in Figure 2A illustrates how the frequency of sexual organisms in the population changed over the generations. The number of sexual organisms was originally 50% (i.e., there was an equal proportion of sexual and asexual organisms), but increased as time passed and was 64% by the tenth generation, implying that sexual reproduction conferred a small advantage. The parameters included were: the number of patches (*L*; which is also the number of individuals in the reproductive population) was 200, the number of mothers laying eggs in a single patch (*R*) was six, and the number of offspring (siblings) per mother (*N*) was eight. Therefore, the total number of competitors in a patch (*RN*) was 48. Numerical analyses using Maynard Smith's (1976) sib-competition model demonstrated that as the total number of competing individuals within a patch (*RN*) increased, the advantage of reproducing sexually also increased. Sexual organisms have an advantage over asexual ones, when the number of competitors in a patch (*RN*) is greater than 40, as illustrated in the left panel of Figure 3A.

However sexual reproduction lost its advantage if some environmental factors were correlated or if multiple genes control the same trait. The broken line in Figure 2A shows that the proportion of sexual organisms decreased as time passed if two environmental factors were correlated. The parameters were the same as for the solid line ($R = 6$ and $N = 8$). Based on this observation, Maynard Smith (1976, 1978) concluded that the mechanism was unlikely to be effective.

By examining simulations of the model, we observed that the following two aspects strongly jeopardize the relative advantage of sexual reproduction:

(1) *Some sexual siblings may have the same phenotype*

Some sexual siblings had the same phenotypes. For example, six siblings had not six phenotypes but an average of 3.9 (65%) phenotypes and eight siblings had not eight phenotypes but an average of 4.6 (58%) phenotypes (Fig. 4A). The number of sexual sibling phenotypes (solid bars) was significantly smaller than the number of siblings (open bars), suggesting that a fraction of sexual siblings from the same mother had the same phenotypes (note: the striped bars are described in section 3).

(2) *Both sexual and asexual organisms may have the highest score in a patch*

Asexual (parthenogenetic) reproduction generated many organisms with the same phenotype and the same score. In contrast, the number of sexual offspring with the same score was small. Since the winner in a patch is chosen randomly among those achieving the highest score, when both sexual and asexual organisms had the highest score an asexual organism was likely to be the winner. Figure 4B illustrates the proportion of patches in which both sexual and asexual organisms had the highest score; it was 23% when $RN = 20$, and 28% when $RN = 40$.

Revised sib-competition model with enhanced advantage of sex

The simplest argument for the superiority of sexual reproduction suggests there is an N-fold advantage. This occurs if the advantage of sexual organisms over asexual ones is equal to the number of phenotypes among offspring of a sexual mother and all the phenotypes are different. However, simulations of the model suggest that the sexual sibling advantage is less than N. Therefore, we revised the model by adjusting the following two assumptions to increase the advantage of sexual organisms over asexual ones:

(1) The score for matching the local environment can vary between factors.

In the original version of the model, the score of a phenotype matching each environmental factor was one. To reduce the chance of different phenotypes having the same total score, we adjusted the score for matching the local environment by varying it stochastically among factors. Therefore, in the revised version of the model, the score assigned for matching a phenotype with a local environmental factor followed a uniform distribution between 0.5 and 1.0, sampled independently among factors, patches, and generations. This modification greatly reduced the probability for different phenotypes to have the same high score.

(2) The number of environmental factors was increased.

We increased the number of environmental factors to more than five. For many organisms, especially during a period of development and growth, fitness is affected by many different environmental factors including abiotic factors (e.g., temperature, humidity, nutrients, and substrate availability) and biotic factors (e.g., the presence or absence of predators, parasites, prey, competitors, and symbionts). Each of these factors has many values. We think that ten environmental factors, each with two states, is worthwhile testing.

The evolutionary advantage of sex enhanced

The revised version of the sib-competition model, including the two changes described above, demonstrated that sexual reproduction has an increased advantage.

Figures 2B and 2C illustrate this when $R = 6$ and $N = 8$, as in the original study by Maynard Smith (1976).

Figure 2B demonstrates the effect of changing the fixed scoring system to the flexible one. Figure 2C demonstrates the effect of additionally increasing the number of environmental factors from 5 to 10. The advantage of reproducing sexually increased significantly. When both adjustments were made to the model, sexual organisms were at an advantage over asexual ones even if three pairs of environmental factors were correlated.

Figure 3 illustrates the effect of increasing *R* and *N*. In the original version of the model, sexual reproduction had an advantage over asexual reproduction when *RN* was greater than 40 (left panel of Figure 3A), but lost this advantage for all combinations of *R* (number of mothers) and *N* (number of siblings) if environmental factors were correlated (right panel of Figure 3A). In contrast, in the revised version of the model that included flexible scoring and ten environmental factors, sexual reproduction has an advantage if the number of competitors is greater than 20 (left panel of Figure 3C), even in correlated environments (right panel of Figure 3C).

The striped bars in Figure 4A demonstrate that the phenotypic diversity of sexual siblings in the revised version of the model is greater than in the original version. For example, when $N = 6$, the average number of sexual sibling phenotypes in the original version was 65% of the number of siblings ($N = 6$), but in the revised version it was 92%. Similarly, when $N = 8$, the average number of siblings increased from 58% of the number of siblings ($N = 8$) in the original version to 89% in the revised version.

Here we sought the condition in which almost all sexual individuals have different phenotypes. In the revised version of the model, different phenotypes have different scores. In most cases, sexual siblings differed from one another in their phenotypes and fitness. Therefore, the likelihood of the highest scores appearing in both sexual and asexual offspring became small.

Realized advantage of sexual versus asexual reproduction

The competition between sexual and asexual organisms is represented by changes in their relative frequency. We can measure the realized advantage for the two types of organism by the change in their proportions. Let x_t and $1 - x_t$ be the proportions of sexual and asexual organisms, respectively. The next generation would alter the relative fitness of the two types of organism, as follows:

$$\frac{x_{t+1}}{1-x_{t+1}} = \frac{x_t}{1-x_t}\left(\frac{W_s}{W_a}\right)_t, \tag{1}$$

where $(W_s/W_a)_t$ is the relative fitness of sexual organisms over asexual ones. Using the computer simulation, we can calculate the relative fitness by applying the formula shown in Equation (1). Figures 5A and 5B illustrate some of the results. We notice that the value of E_t did not change significantly over time, suggesting that this value may be used as an index for the realized advantage of sexual reproduction produced by the simulation.

We also noticed that the advantage sexual organisms have is clearly less than $N/2$, the expected value based on the simple argument above. Therefore, we define the ratio of realized fitness to the expected value using $N / 2$, as follows:

$$E_t = \left(\frac{W_s}{W_a}\right)_t / \left(\frac{N}{2}\right), \tag{2}$$

$N / 2$ is the value expected according to the following argument: suppose that all the offspring produced by a sexual mother (N) differ, and that different sexual mothers produce offspring with different phenotypes. In contrast, asexual individuals produce offspring with the same phenotype. Therefore, the phenotypic diversity of sexual organisms is N per mother, while each asexual individual produces only a single phenotype. However, sexual organisms incur the two-fold cost of sex, producing a factor of $N / 2$.

Figures 5C and 5D illustrate these results. E_t is clearly smaller than 1. Figure 5C demonstrates that E_t becomes smaller as N increases, but becomes larger as R increases.

Why is sex not as advantageous as expected?

Here we consider several reasons why the advantage of sexual offspring deviated from the prediction of the simple model, i.e., $N / 2$.

The number of phenotypes among siblings is smaller than N

Sexually produced offspring from the same mother are more likely to have the same phenotypes than random individuals drawn from the entire population because they have the same mother and father. We counted the number of phenotypes among N individuals produced by the same sexual mother. Figure 4A demonstrates that the average number of phenotypes was smaller than the number of siblings.

Sexual siblings with the same mother are similar

Siblings with different phenotypes may be more similar than non-siblings with different phenotypes. Figure 6 demonstrates that the standard deviation of scores among sexual siblings with different phenotypes is smaller than that of sexual non-siblings randomly selected from the entire population. We examined only those sexual siblings with differing phenotypes. Therefore, the sexual siblings shown in Figure 6 had the same number of phenotypes as the sexual non-siblings. This implies that even if siblings differ in phenotype (i.e., the combination of the five or ten factors), their overall scores may be more similar than is the case for non-siblings. Since only the individual with the highest score wins, a smaller standard deviation from the same mean score is a disadvantage. In Figure 6, the standard deviation in sexual siblings is about 90% of the value in non-siblings for five environmental factors and approximately 75 to 80% of the value for ten environmental factors.

Natural selection within each patch is ineffective

Natural selection operates within each patch because of the competition between sexual and asexual organisms. However the number of individuals in the same patch is finite and often rather small. If this number is very small, the advantage sexual organisms have over asexual ones is weak. For an extreme example, consider the case where $R = 1$ and each patch receives either a sexual or an asexual individual only. Since there is no competition within patches, sexual organisms have no advantage. In contrast, asexual organisms contribute double the number of egg-laying individuals from the reproductive pool providing them with an advantage over sexual organisms.

For R in general we present the following argument: Let x_t be the fraction of sexual organisms in the reproductive pool. Due to the two-fold advantage asexual organisms have, the fraction of egg-laying individuals in all patches is $x_t/(x_t + 2(1 - x_t))$. Because the number of sexual mothers within a patch follows a binomial distribution we have

$$x_{t+1} = \sum_{k=0}^{R} \binom{R}{k} \left(\frac{x_t}{x_t + 2(1 - x_t)}\right)^k \left(\frac{2(1 - x_t)}{x_t + 2(1 - x_t)}\right)^{R-k} \frac{kW}{kW + (R - k)} \ . \quad (3)$$

The right hand side of Eq. (3) is a sum of the product of two factors. The first is the probability of each case of the number of sexual mother (*R*) that follows binomial distribution, and the second is the proportion of the number of sexual phenotype with each case of R. W is the relative fitness of sexual organisms within each patch.

When *R* is very large, *k* following binomial distribution would concentrates near $k \sim x_t/(x_t + 2(1 - x_t))$. Then Eq. (3) becomes $x_{t+1} = x_t W/(x_t \mathrm{W} + 2(1 - x_t))$, which implies that advantage of sex is *W*/2. However, especially for small *R*, Equation (3) shows that the advantage of sexual type is clearly smaller than this case, as shown in Table 1.

Hence we can summarize that the advantage sexual organisms have can be reduced by three mechanisms: [1] reduced number of phenotypes among siblings, [2] similarity of siblings with different phenotypes, and [3] smallness of local populations. To quantify each of these effects, we ran several simulations incorporating some of these conditions and compared the results with the original model. Figure 7A shows how the proportion of sexual organisms changes over the generations when *R* = 6 and *N* = 8. The line at the bottom is the original model simulation. In contrast, the line at the top is generated by the following simple equation:

$$x_{t+1} = \frac{N x_t}{N x_t + 2(1 - x_t)} \tag{4}$$

which indicates that the relative fitness of sexual organisms equals *N* / 2. This overestimated the proportion of sexual organisms, but in both cases the outcome was the same and sexual organisms won.

The second line from the top is produced by the formula shown in Equation (4) where the number of phenotypes was replaced by the average value from the computer simulation. This is the average from different mothers in each generation. It differed between generations and was approximately 7 (i.e., less than *N* = 8). These curves demonstrate the effect of [1] reduced number of phenotypes among siblings and are more similar to the results observed.

The third line from the top is produced by the formula shown in Equation (3), where *N* was replaced by the observed number of phenotypes. This figure was the average taken from different sexual mothers and it varied between generations. The analysis tests the effect of stochastic variation in egg-laying individuals following a binomial distribution. It considered both [1] the reduced number of phenotypes among siblings and [3] the smallness of local populations. The plot (third line from the top) was quite similar to the observed results (the lowest line), but overestimated them a little. This is because it did not take into account [2] the similarity of siblings with different phenotypes, as demonstrated by the lower standard deviation of the sexual sibling scores compared with that of the sexual non-siblings.

Figures 7B and 7C illustrate other examples using different parameters. In both figures the bottom line represents the observed results and the other lines are predictions based on adjusting some of the parameters. These also overestimated the proportion of sexual organisms, but as more parameters were included the predictions became more accurate.

In Figure 7B, the result of competition between sexual and asexual organisms was predicted correctly, although the speed of change was not. In Figure 7C, the top line suggested that sexual organisms would prevail if the fitness value was equal to N / 2, but the curve demonstrated that asexual organisms won. Both modifications correctly predicted the outcome, but the third line from the top proved to be the most accurate, taking both [1] and [3] into account.

Environmental correlations reduce the advantage of sex

When a pair of environment factors was correlated, the advantage of sexual reproduction was considerably reduced. Strong environmental correlation reduces the effective number of environmental factors. For example, if an environment has two factors A/a and B/b that are strongly correlated resulting in the actual states AB and ab but never Ab or aB, then effectively it only has a single factor with two states. In contrast, because phenotypes are coded using two separate loci (A/a and B/b), phenotype AB only fits environment AB and phenotype ab only fits environment ab. Phenotypes aB and Ab are not as well adapted and are created by recombination from potentially fitter phenotypes (AB and ab) during sexual reproduction. Having phenotypes with lower scores is a disadvantage for sexual organisms compared with asexual ones. This disadvantage, resulting from pairing of environmental factors should be reduced as the total number of loci increases. In addition, in the environment with n aspects including a tightly correlated pair, sexual reproduction would be favored less strongly than in the environment with n-1 aspects. This is because, in the latter, 2^{n-1} combinations of aspects occur with equal probability, whilst, in the former, some combinations of aspects occur more frequently than others.

Discussion

In Maynard Smith's sib-competition model, competition within each patch is intense and only the individual that best matches the local environment survives. The phenotype that fits best is unpredictable and varies between patches and across generations. Therefore, a mother's reproductive success increases with the phenotypic diversity of her offspring, because the likelihood of one of her offspring achieving the highest score in a patch then increases with the number of her offspring. In contrast, an asexual mother has a low probability of generating the fittest individual because all her offspring have the same phenotype. This suggests that we might be able to estimate the advantage sexual organisms have from the number of offspring produced by a mother. However, this would overestimate the advantage of sexual reproduction, because some sexual siblings have the same phenotype. In addition, both sexual and asexual organisms can have the highest score in a patch. In this study, we examined a version of the model in which the score for matching the local environment varied stochastically and independently between factors, patches, and generations. This modification greatly reduced the chance of two different phenotypes having the same highest score. In addition, we increased the number of environmental factors in the model to more than five.

However, the advantage of reproducing sexually was not as large as predicted by the simplest model based on the assumption that all sexual offspring differ in phenotype. We identified the following three factors responsible for this: [1] some siblings have the same phenotype; [2] the variance of score among sexual siblings with differing phenotypes is smaller than among non-siblings; and [3] the low number of egg-laying individuals within each patch reduces the effectiveness of natural selection. We also discussed the effect that environmental correlations have on reducing the advantages of sexual reproduction.

We demonstrated that increasing the variation in scores for matching phenotypes with the local environment enhances the advantage of reproducing sexually because it reduces the likelihood of both sexual and asexual organisms achieving the highest score simultaneously. However, we assumed that individuals in the same patch and with the same phenotype had the same score. Alternatively, there could be additional variation between individuals with the same phenotype in the same patch. This would benefit asexual reproduction because asexual organisms are more likely to generate a number of individuals with the same highest score. This effect should be tested by future theoretical studies.

We believe that the assumptions adopted by the sib-competition model are plausible and ecologically sound, although their effects may be difficult to quantify. The sib-competition model suggests that sexual reproduction has a strong advantage if: sib-competition is significant; the environment is heterogeneous and varies over time; there are numerous environmental factors; and there is pressure to adapt. The effect of the intensity of the competition should also be tested in future work.

Despite its critics (e.g., Barton et al. 2007), this mechanism still remains one of the most important and promising hypotheses to explain the evolutionary maintenance of sex. However, further theoretical studies will be needed to establish which of the many hypotheses proposed provides the best answer to this question.

References

Agrawal, A.F., 2006. Evolution of sex: why do organisms shuffle their genotype? Current Biol, 16, 696-704.

Barton, N.H., Post, R.J., 1986. Sibling competition and the advantage of mixed families. J. Theor. Biol. 120, 381-387.

Barton, N.H., Otto, S.P., 2005. Evolution of recombination due to random drift. Genetics 169, 2353-2370

Barton, N.H., Briggs, D.E.G., Eisen, J.A., Goldstein, D.B., Patel, N.H., 2007. Evolution of genetic systems. Cold Springer Harbor Laboratory House, New York.

Bell, G., 1982. The Masterpiece of Nature, University of California Press, Berkeley.

Bulmer, M.G., 1980. The sib competition model for the maintenance of sex and recombination. J. Theor. Biol. 82, 335-345.

Hamilton, W.D., 1980. Sex versus non-sex versus parasite. Oikos 35, 282-290.

Hartfield, N. and R. D. Keightley. 2012. Current hypotheses for the evolution of sex and recombination. Integrative Zoology 7: 192-209.

Fisher, R.A., 1930. The Genetical Theory of Natural Selection. Clarendon Press, Oxford.

Maynard Smith, J., 1976. A short-term advantage for sex and recombination through sib-competition, J. Theor. Biol. 63, 245-258.

Maynard Smith, J., 1978. The Evolution of Sex. Cambridge University Press, Cambridge.

Mittledorf, J., 2016. Aging is a Group-selected Adaptation: Theory, Evidence, and Medical Implications. Boca Raton, FL: CRC Press.

Muller, H.J., 1932. Some genetic aspect of sex. Am. Nat. 66, 118-138.

Otto, S.P. 2009. The evolutionary enigma of Sex. Am. Nat. 174, S1-S14.

Taylor, P.D., 1979. An analytical model for a short-term advantage for sex. J. Theor. Biol. 81, 407-421.

Williams, G.C., Mitton, J.B., 1973. Why reproduce sexually? J. Theor. Biol. 39, 545-554.

Williams, G.C., 1975. Sex and Evolution. Princeton University Press, Princeton.

Captions to table and figures

Table 1

Comparisons of the solution to Equation (3) with W / (W+2) where W = 8, x_t = 0.5, and R = 2–20.

Figure 1

Population models. (A) A population consisting of sexual organisms only. (B) A population consisting of asexual organisms only, where siblings have the same genotype. (C) A population consisting of both sexual and asexual organisms.

Figure 2

The frequency of sexual organisms. (A) Five environmental factors. Original version. (B) Five environmental factors. Flexible scoring. (C) Ten environmental factors. Flexible scoring. Parameters are: R = 6 and N = 8. Horizontal axis is for time (number of generations). Labels for lines are: (a) when environmental factors are independent of each other, (b) when one pair of environmental factors (among two factors) are correlated strongly, but all other factors are independent, (c) when two pairs of environmental factors (among four factors) are correlated strongly, but all other factors are independent, and (d) when three pairs of environmental factors (among six factors) are correlated strongly, but other factors are independent.

Figure 3

The frequency of sexual organisms for different combinations of R and N. The section surrounded by a line in bold is where sexual organisms are present at a frequency of greater than 50% in the tenth generation. The figure on the left hand side does not include environmental correlations, while the figure on the right hand side does. The numbers in each grid are the frequencies of sexual organisms at the tenth generation. These notes also apply to Figures 3B and 3C. (A) The original version of the model. (B) The revised version of the model with flexible scoring and 5 environments.
(C) The revised version of the model with flexible scoring and 10 environments.

Figure 4

Two considerations that strongly jeopardize the relative advantage sexual reproduction has in the original model. (A) The number of phenotypes and sexual siblings in the simulation. Each open bar (a) represents the maximum number of phenotypes, which is the same as the number of siblings. Each closed bar (b) represents the number of phenotypes of sexual siblings in the original simulation. The striped bar (c) shows the same information for the revised simulation. The ratio of the number of phenotypes and number of siblings in the original [(b) / (a)] and revised versions [(c) / (a)] is greater in the revised version. The greater the number of siblings, the smaller the ratio in both versions. (B) Closed circles indicate the number of patches in which both sexual and asexual organisms have the highest score. The total number of patches (L) was 200. The horizontal axis is the product RN.

Figure 5

Realized fitness of sexual organisms compared with asexual ones, and E_t, the ratio of the realized fitness to $N/2$. Time (generations) is shown on the horizontal axis. (A) Different curves for different values of N, indicated by numerals. $R = 6$ for all curves. (B) Different curves for different values of R, indicated by numerals. $N = 6$ for all curves. The dotted line indicates $N / 2$. Realized fitness increases with R, but is always less than $N / 2$. (C) The value of E_t decreases with N. Parameters are the same as in (A). (D) The value of E_t increases with R. Parameters were the same as in (B).

Figure 6

Standard deviation of the scores of sexual organisms. Flexible scoring was assumed. Open squares and circles show the standard deviation of the scores of sexual non-siblings (open squares) and sexual siblings (open circles) where there were ten environmental factors. Closed squares and circles show the same information for sexual non-siblings (closed squares) and sexual siblings (closed circles) where there were five environmental factors. The horizontal axis is the number of offspring per mother (N).

Figure 7

The proportion of sexual organisms. Horizontal axis is for time (number of generations). Parameters were: (A) $R = 6$ and $N = 8$. (B) $R = 8$ and $N = 3$. (C) $R = 3$ and $N = 4$. In each graph, the line at the top (a) shows the predicted plot where $N / 2$. The second line from the top (b) shows the effect of factor [1]. The number of phenotypes is the value observed in evolutionary simulations. The third line from the top (c) shows the effects of factors [1] and [3]. The number of phenotype from the simulation is substituted for Eq. (3). The solid line at the bottom (d) shows the result of the model simulation.

Table

Table 1

R	1	2	3	4	5	6	7	8	9	10	20
$W/(W+2)$...(a)	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80
answer of Eq.(3)...(b)	0.33	0.51	0.60	0.66	0.69	0.72	0.73	0.74	0.75	0.76	0.78
ratio...(b)/(a)	42%	63%	75%	82%	87%	89%	91%	93%	94%	95%	98%

Figures

Figure 1

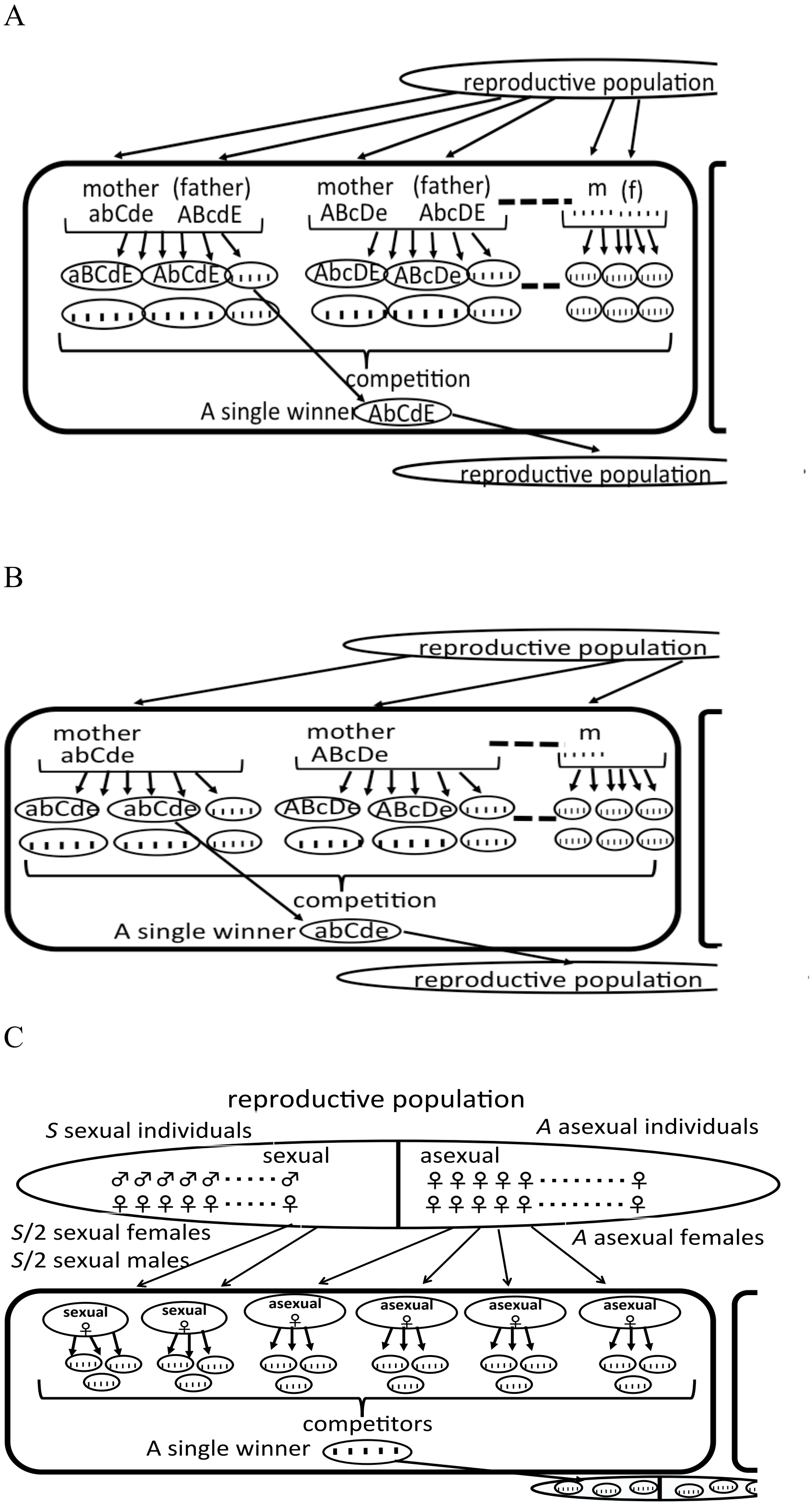


Figure 2

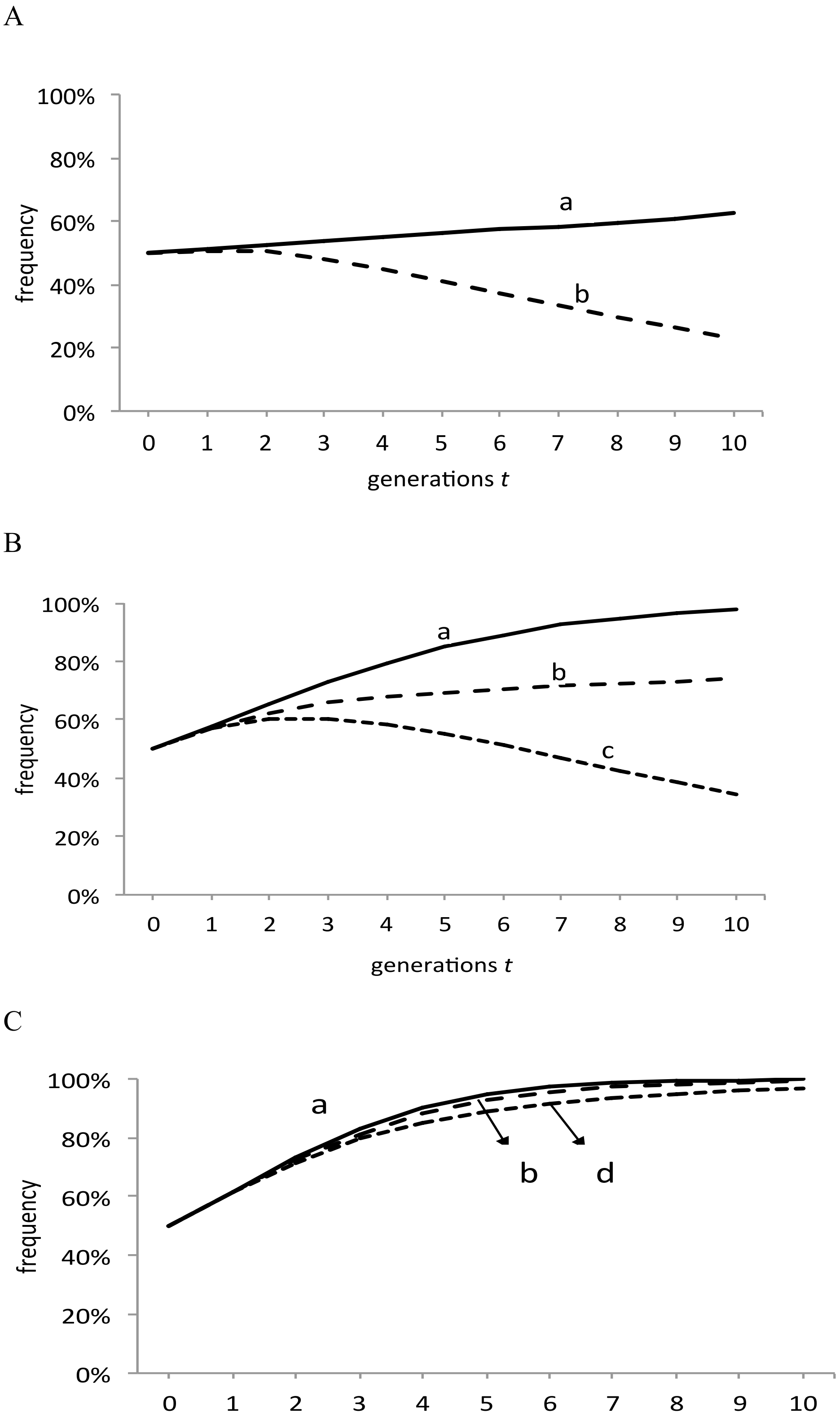

A
100%
80%
60%
40%
20%
0%
frequency
a
b
0 1 2 3 4 5 6 7 8 9 10
generations *t*
B
100%
80%
60%
40%
20%
0%
frequency
a
b
c
0 1 2 3 4 5 6 7 8 9 10
generations *t*
C
100%
80%
60%
40%
20%
0%
frequency
a
b
d
0 1 2 3 4 5 6 7 8 9 10
generations *t*

Figure3

A

without correlation

		N									
		1	2	3	4	5	6	7	8	9	10
R	1	0	0	0	0	0	0	0	0	0	0
	2	0	0	1	1	2	2	2	3	4	3
	3	0	1	2	4	7	9	12	15	17	20
	4	0	1	4	8	14	21	28	36	41	48
	5	0	1	6	12	22	33	44	52	61	68
	6	0	2	7	18	29	41	53	64	72	77
	7	0	2	8	22	36	50	60	72	78	83
	8	0	2	10	24	40	57	65	76	82	86
	9	0	2	11	25	44	58	70	79	83	89
	10	0	3	13	28	47	62	74	83	87	90

with 1 correlation

		N									
		1	2	3	4	5	6	7	8	9	10
R	1	0	0	0	0	0	0	0	0	0	0
	2	0	0	1	1	2	2	2	2	3	3
	3	0	1	2	3	5	8	9	12	14	15
	4	0	1	2	4	8	12	15	20	23	27
	5	0	1	2	5	10	14	19	23	29	34
	6	0	1	2	5	10	14	21	27	34	38
	7	0	1	2	5	10	15	23	29	35	42
	8	0	1	3	6	10	17	24	30	37	42
	9	0	1	3	6	11	17	24	32	37	46
	10	0	1	2	6	11	18	25	33	40	45

B

without correlation

		N									
		1	2	3	4	5	6	7	8	9	10
R	1	0	0	0	0	0	0	0	0	0	0
	2	0	1	2	3	4	5	6	7	8	9
	3	0	2	7	16	25	38	44	53	64	67
	4	0	3	15	37	59	71	83	88	94	95
	5	0	4	23	54	76	89	94	96	97	98
	6	0	5	32	67	85	94	96	98	99	99
	7	0	7	37	72	90	95	97	98	99	99
	8	0	8	46	80	91	96	98	99	99	99
	9	0	10	50	81	92	97	98	99	99	99
	10	0	11	52	82	92	97	98	99	99	99

with 1 correlation

		N									
		1	2	3	4	5	6	7	8	9	10
R	1	0	0	0	0	0	0	0	0	0	0
	2	0	1	2	2	4	5	6	6	7	7
	3	0	2	6	11	17	26	32	40	47	52
	4	0	2	9	18	31	49	58	67	72	75
	5	0	2	11	22	39	55	67	74	79	85
	6	0	2	11	27	45	59	71	77	82	86
	7	0	2	12	26	47	60	71	79	83	86
	8	0	2	11	30	50	61	72	79	83	86
	9	0	2	12	28	47	60	71	77	82	84
	10	0	2	12	30	45	59	69	76	78	82

C

without correlation

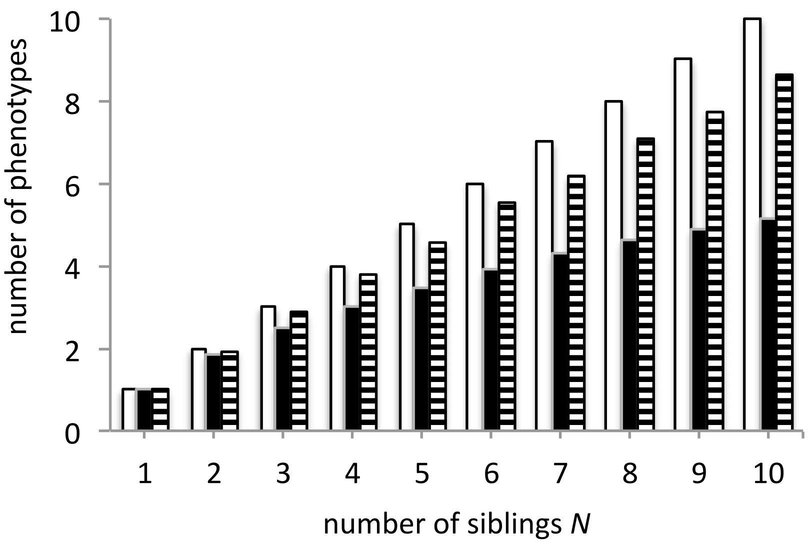
		N									
		1	2	3	4	5	6	7	8	9	10
R	1	0	0	0	0	0	0	0	0	0	0
	2	0	1	2	4	5	7	11	11	13	15
	3	0	2	9	23	42	59	69	81	88	92
	4	0	2	23	55	79	92	96	98	99	99
	5	0	2	39	75	91	98	99	99	100	100
	6	0	10	53	86	96	99	100	100	100	100
	7	0	12	61	90	98	99	100	100	100	100
	8	0	14	70	94	98	100	100	100	100	100
	9	1	18	77	96	99	100	100	100	100	100
	10	1	21	80	96	99	100	100	100	100	100

with 3 correlations

		N									
		1	2	3	4	5	6	7	8	9	10
R	1	0	0	0	0	0	0	0	0	0	0
	2	0	1	2	3	5	9	9	12	12	15
	3	0	2	9	20	38	66	66	77	85	89
	4	0	4	19	49	70	93	93	97	98	99
	5	0	5	31	64	86	97	97	99	99	100
	6	0	6	42	76	92	99	99	99	100	100
	7	0	8	46	81	93	99	99	100	100	100
	8	0	10	52	84	96	99	99	100	100	100
	9	0	12	57	87	96	99	99	100	100	100
	10	0	13	57	89	97	100	100	100	100	100

Figure 4

A


number of phenotypes
0
2
4
6
8
10
1
2
3
4
5
6
7
8
9
10
number of siblings N

B

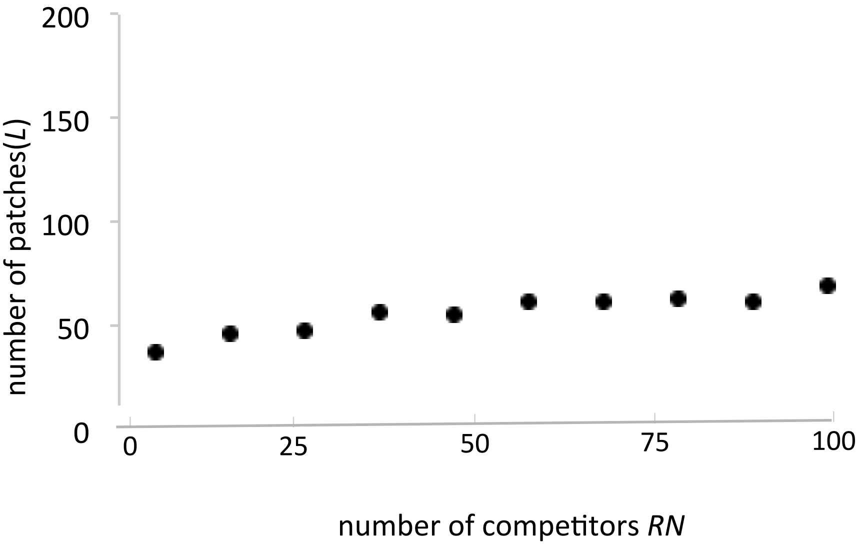
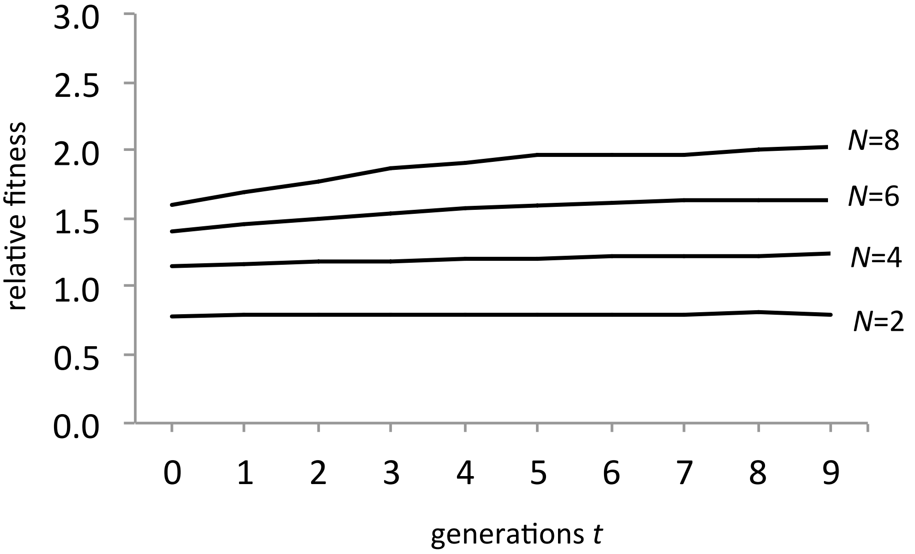

number of patches(L)
0
50
100
150
200
0
25
50
75
100
number of competitors RN

Figure 5

A


3.0
2.5
2.0
1.5
1.0
0.5
0.0
relative fitness
0
1
2
3
4
5
6
7
8
9
generations *t*
N=8
N=6
N=4
N=2

B

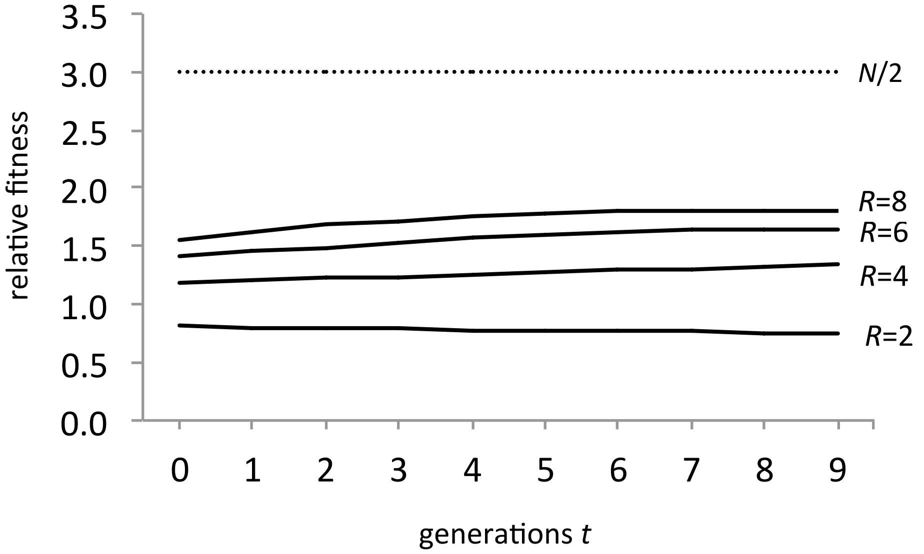
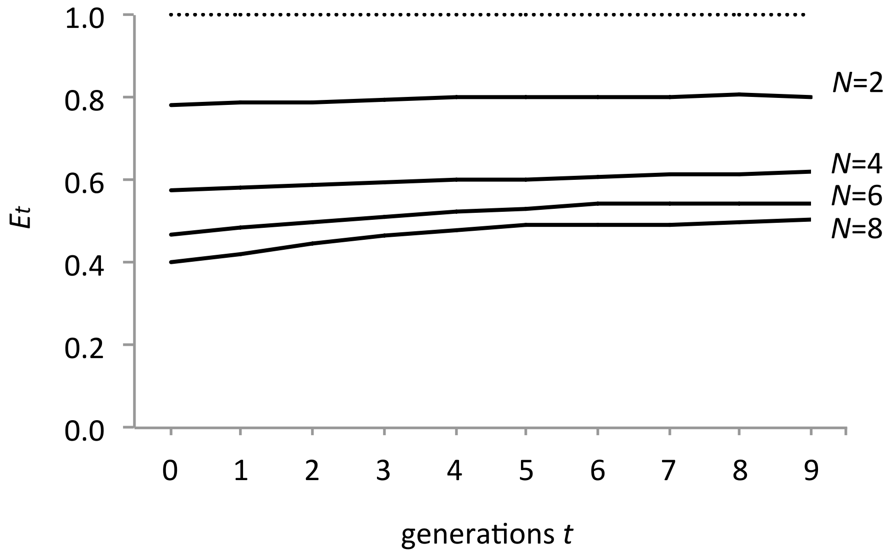

3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
relative fitness
0
1
2
3
4
5
6
7
8
9
generations *t*
N/2
R=8
R=6
R=4
R=2

Figure 5

C


1.0
0.8
0.6
0.4
0.2
0.0
E_t
0
1
2
3
4
5
6
7
8
9
generations t
N=2
N=4
N=6
N=8

D

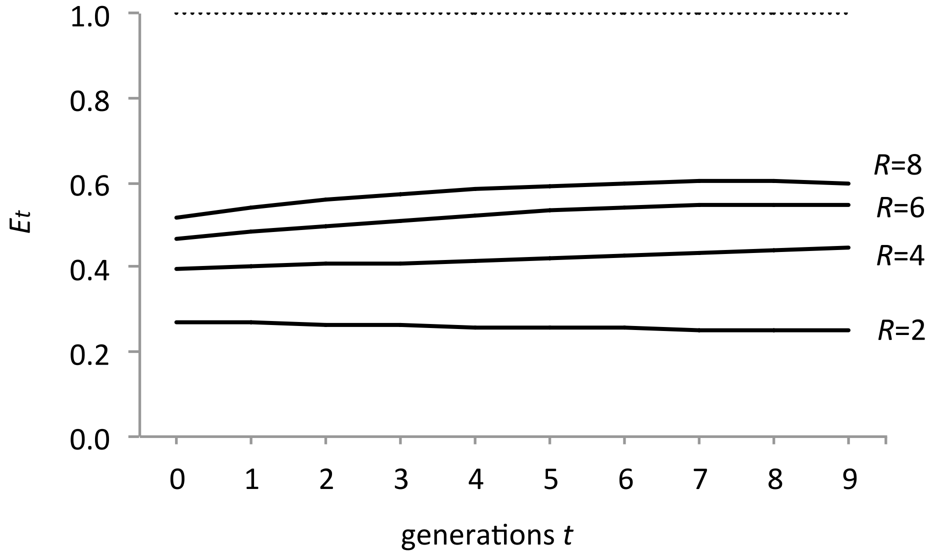

1.0
0.8
0.6
0.4
0.2
0.0
E_t
0
1
2
3
4
5
6
7
8
9
generations t
R=8
R=6
R=4
R=2

Figure 6

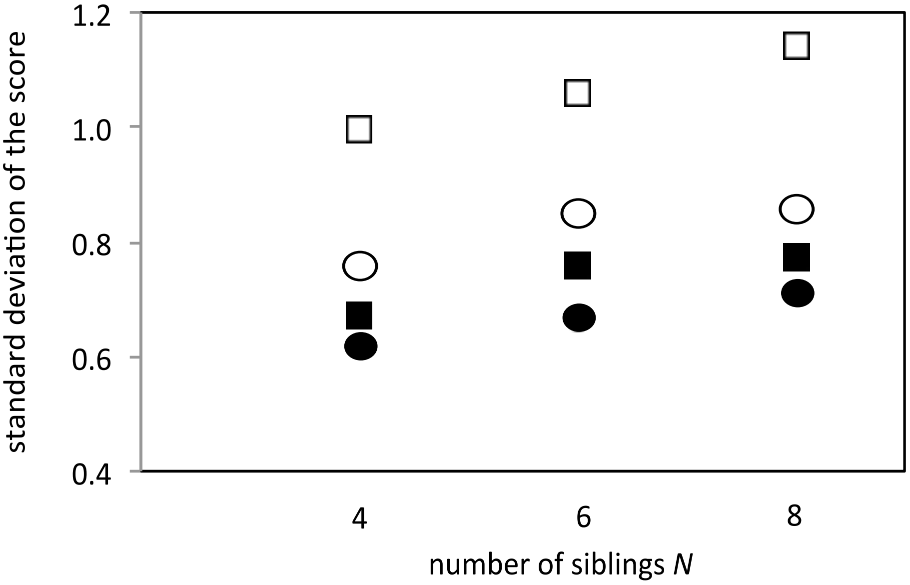
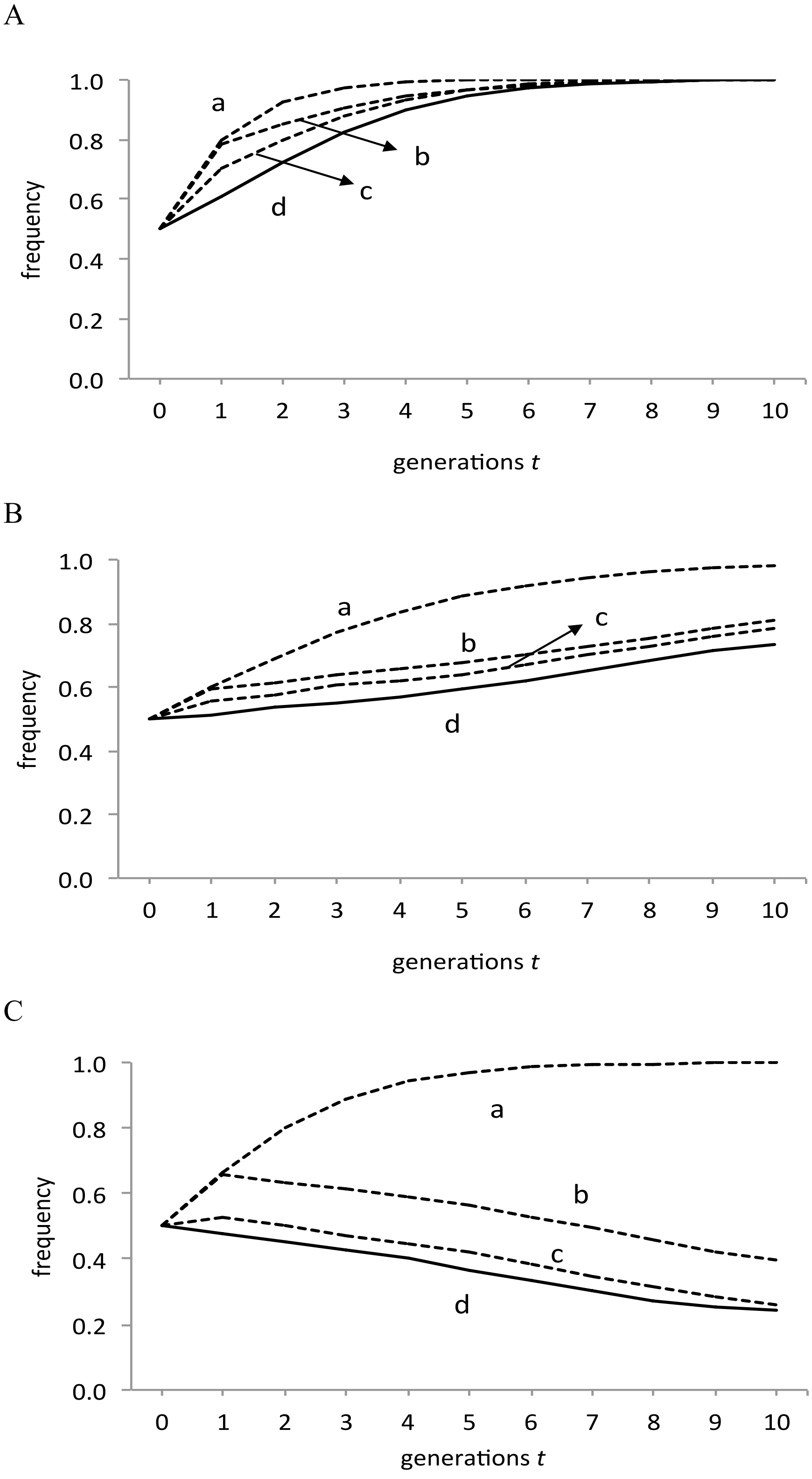

1.2
1.0
0.8
0.6
0.4
standard deviation of the score
4
6
8
number of siblings *N*

Figure 7


A
1.0
0.8
0.6
0.4
0.2
0.0
frequency
a
b
c
d
0
1
2
3
4
5
6
7
8
9
10
generations *t*
B
1.0
0.8
0.6
0.4
0.2
0.0
frequency
a
b
c
d
0
1
2
3
4
5
6
7
8
9
10
generations *t*
C
1.0
0.8
0.6
0.4
0.2
0.0
frequency
a
b
c
d
0
1
2
3
4
5
6
7
8
9
10
generations *t*

Chapter 2

Advantages of sexual reproduction resulting from sibling diversity:

effects of selection intensity, environmental variance, and reduced genetic diversity

The study of this chapter, done in collaboration with Dr. Yoh Iwasa, was accepted for the publication in Evolutionary Ecology Research

Introduction

About 40 years ago, John Maynard Smith pointed out the two-fold cost of sex and noted that the selective advantage of sexual reproduction is an important and difficult theoretical problem in evolutionary biology (Maynard Smith, 1978). Since then, many hypotheses purporting to explain the advantages of sex have been proposed. For instance, Hamilton (1980) proposed that the presence of pathogens or parasites would encourage sexual reproduction because they would tend to generate strong selection favoring currently rare host genotypes, with the intensity and direction of selection changing over generations (the "Red Queen" hypothesis). Sexual reproduction slows the irreversible accumulation of deleterious mutations (Muller, 1964), reduces the genetic load of deleterious mutations compared with asexual reproduction (Kondrashov, 1988), and disrupts linkage disequilibrium created by random genetic drift (Fisher, 1939; Muller, 1932; Barton and Otto, 2005; Barton et al., 2007; Otto, 2009).

G.C. Williams proposed that the diversity of offspring might be the main reason for the maintenance of sexual reproduction (Lottery Hypothesis: Williams and Mitton, 1973; Williams, 1975). Maynard Smith (1976; 1978) formalized this idea as the "sib-competition model". However, Maynard Smith concluded that the sib-competition model was unable to maintain sex in the face of the two-fold cost of sex when different aspects of the environments (e.g., temperature and humidity) are strongly correlated.

Since then, only a few theoretical studies have further investigated the sib-competition model (Taylor, 1979; Bulmer, 1980; Barton and Post, 1986). The general consensus within the theoretical biology community is that sibling diversity is unlikely to play an important role in the maintenance of sex. In a twin paper (Douge and Iwasa, 2017), we explored the conditions under which sib-competition works more effectively than observed in previous studies. We found that if the number of environmental aspect were larger and if the fitness of different phenotypes differed between patches, sexual reproduction would enjoy a significant advantage over asexual reproduction and could be maintained even in correlated environments.

In the sib-competition model (Maynard Smith, 1976; 1978), an organism's habitat is composed of a large number of small patches in which sexual and asexual mothers oviposit a number of offspring. Larvae compete with one another, and only a single individual can survive. The fitness of an individual is strongly determined by the match between its phenotype and the local environment in a patch. As the closest match is achieved by a single phenotype, sexual mothers have a strong advantage over asexual mothers: the offspring of sexual mothers are more likely to be diverse, whereas asexual mothers have many offspring of the same phenotype. Hence, the likelihood of a sexual mother bearing an offspring achieving the closest match between the phenotype and the local environment is much higher than the likelihood of an average asexual mother doing so. However, this advantage would be suppressed if the closest match were achieved by different phenotypes, as many individuals would have an equal chance of survival under such conditions; this provides an advantage to asexual mothers bearing many offspring of the same phenotype. This outcome often occurs in Maynard Smith's simulations (Douge and Iwasa, 2017). In the modified version studied in a twin paper (Douge and Iwasa 2017), the matching score differed among patches, and there was a larger number of environmental aspects. As a result, the likelihood of different phenotypes achieving the closest match with the environment was greatly reduced, and sexual reproduction could be maintained in the face of the two-fold cost of sex.

In the current paper, following Douge and Iwasa (2017), we further study several different ways of modifying the sib-competition model such that the evolution of sex may be encouraged or discouraged.

First, in our previous sib-competition models, only the single individual with the best matching score could survive per patch. However, the advantage of the sexual type could be reduced if selection were to become milder (e.g., if multiple individuals per patch could survive). Consider the case in which the 10 individuals with the highest matching scores can survive. The sexual type would have the advantage of generating the individual with the best score. Perhaps it could also achieve the second-best score. However, if the third-highest score were achieved by an asexual type, then the fourth, fifth, and other remaining survivors (seven in total) would also be asexual, because all offspring of the asexual type would have equal fitness. Hence, increasing the number of survivors per patch would reduce the advantage of sex.

Second, in Douge and Iwasa (2017), the scores of individuals with the same phenotype in the same patch were assumed to be the same, but the scores of different phenotypes were different. Under this assumption, when the closest match between the phenotype and the environment is achieved by two different phenotypes (one sexual and one asexual), the larger number of the asexual type does not contribute to its success. However, individuals growing in the same patch may differ in fitness owing to developmental differences. This environmental source of variance should favor asexual mothers who have many offspring with the same phenotype. If this variance were sufficiently large, the larger number of individuals of the asexual type might contribute to the success of the latter, reducing the advantage of the sexual type. Based on the quantitative genetics argument, Bulmer (1980) concluded that the advantage of sex should disappear if the environmental variance were as large as the additive genetic variance. However, we must know how much smaller the environmental variance needs to be for the advantage of sex through sib-competition to persist.

Third, in the evolutionary simulations in Douge and Iwasa (2017), as well as in many previous theoretical papers focusing on sib-competition models, the simulations started from an initial population in which all phenotypes were available. This may be acceptable when the number of patches is infinitely large and when each phenotype finds some patches in which it achieves the best match with the local environment. However, the diversity of environments realized in a particular generation might be limited. For example, if there were 10 aspects of the environment, each having two states, there would be 1024 possible combinations of environmental states. In a twin paper, these 1024 different environments would exist in some patches every generation. A more realistic assumption is that only, say, 20 of 1024 different environmental combinations exist in a particular generation. Under such conditions, the loss of genetic diversity would occur very quickly, especially for the asexual type. In contrast, the sexual type can recover a phenotype that does not exist in one generation by the genetic recombination of two types that exist in that generation. Hence, the loss of genetic diversity should be much slower for the sexual type than for the asexual type.

In the following sections, we consider the effects of these modifications and examine their impacts on the importance of sib-competition in the maintenance of sex.

Sib-competition model

The sib-competition model explaining the evolution of sex was first formalized by Maynard Smith (1976; 1978) based on the arguments developed by Williams and Mitton (1973) and Williams (1975). In a twin paper, we developed the model with a few additional modifications that strengthen the evolutionary advantage of sexual reproduction (Douge and Iwasa, 2017). Here, we explain the model briefly (see Douge and Iwasa, 2017 for more details).

We consider insect-like organisms. The population includes two types of individuals, sexual and asexual. The entire habitat consists of a large number of patches for larvae. In the adult stage, the organisms join a single pool in which females and males of sexual species mate randomly. Then each patch receives R adults (sexual females and asexual individuals), each of which oviposits N offspring. They compete with each other fiercely, and only a single winner survives per patch. These winners from different patches join a single adult pool. Half of all sexual adults are males who do not lay eggs, whereas all asexual individuals lay eggs. This represents the two-fold cost of sex, favoring the asexual type over the sexual type.

The competition among the larvae within a patch depends on the local environment. The environment within a patch is characterized by the alternative states of the five aspects discussed in Maynard Smith (1976; 1978). There are $2^5 = 32$ different combinations of states that exist at equal frequency in the entire population. Let A and a be alternative environmental states of the first aspect, B and b be alternative states of the second aspect, and so on. Thus, there are five environmental aspects (A/a. B/b, C/c, D/d, and E/e), and their combinations are ABcdE, aBCde, and so on.

Individuals are diploid with 5 loci, each segregating two alleles (A/a, B/b, C/c, D/d, and E/e), which correspond to the five environmental aspects. Because complete dominance is assumed, there are $2^5 = 32$ phenotypes. The fitness of a particular phenotype depends on the score, defined as the number of aspects that match its phenotype (say A and A, a and a, B and B, etc.). For example, genotype AABbccDdee has phenotype ABcDe, which has three matches with environment aBcde. The winner of larval competition is the one that achieves the highest score among all larvae in the patch. If there were multiple individuals achieving the best score, each of them would be chosen to be the winner with equal probability. Each sexual mother produces genetically diverse offspring, whereas asexual mothers produce N offspring with the same phenotype. Hence, sexual mothers have an advantage concerning the likelihood of one of her N offspring achieving the best score.

The initial population contains both alleles at all five loci. For each locus, the gene frequency of the dominant allele (say A) is chosen to be $1 - \sqrt{2}/2 \approx 0.2929$ (the recessive allele has frequency $\sqrt{2}/2 \approx 0.7071$), which leads two phenotypes to appear with equal frequency because of complete dominance.

Results of the sib-competition model

According to the original version of the sib-competition model formulated by Maynard Smith (1976; 1978), the sexual type outcompeted the asexual type when the total number of competing larvae was 30–40 or greater. However, if we assume a strong correlation among pairs of environmental aspects, the advantage of sexual reproduction would drop significantly. We found that the main reason for this limited advantage of sex was that the highest score was often simultaneously achieved by both a sexual phenotype and an asexual phenotype. When this occurs, the asexual type has an advantage owing to their several offspring with the same phenotype. To reduce the likelihood of such events, we made two modifications. First, we increased the number of environmental aspects from 5 to 10. Second, the score achieved by matching one environmental aspect and the corresponding phenotype was not an integer (say, 1) but rather a decimal number between 0.5 to 1.0 with a uniform probability distribution. This latter modification introduces a stochasticity of score that differs between patches (but remains the same among individuals with the same phenotype in the same patch). As a result, the sexual type is much more likely to achieve the highest score, providing a strong benefit to the sexual type over the asexual type (Douge and Iwasa, 2017). If *RN* were greater than 20 or 30, the sexual type would outcompete the asexual type, even when aspects of the environment were strongly correlated.

In short, sib-competition makes the sexual type outcompete the asexual type if the environment were to vary temporally and spatially, if the number of environmental aspects were large, and if selection were very intense.

The advantage of the sexual type over the asexual type can be estimated based on the following simple argument: if all *N* offspring of a sexual mother differed in phenotype, there would be a higher probability that one of her offspring —versus an offspring of an asexual reproductive individual who produces *N* offspring of the same phenotype—would achieve the best score. Considering the two-fold cost of sex (caused by half of sexual adults in the reproductive pool being male), the advantage of sexual versus asexual reproduction should be *N*/2. However, based on simulations, Douge and Iwasa (2017) noted that the observed advantage of sex is considerably smaller than *N*/2. This was improved by the two modifications discussed above. They found that the advantage of the sexual type over the asexual type was enhanced. However, there remained a discrepancy between the simplistic sexual advantage of *N*/2 and the observed advantage in model simulations. By further examining the model, Douge and Iwasa (2017) were able to identify three processes responsible for this difference: [1] that siblings have some probability of having the same phenotype, [2] that siblings with different phenotypes have similar scores, and [3] that the value of R, the total number of reproductive adults that arrive at the patch, is low makes the selection process less effective.

The sib-competition model studied in Douge and Iwasa has a number of simplifying assumptions. It is important to evaluate how the effectiveness of the model changes when we consider additional modifications. In the present paper, we consider three different modifications: [1] the selection within each patch might be milder than assumed, [2] the success of larvae might be affected by developmental variation (i.e., environmental variance), and [3] the diversity of the environment in each generation might be limited, reducing phenotypic diversity. In the following sections, we summarize the results of our analyses.

Multiple survivors per patch

In the classic sib-competition model, only the single individual with the highest score can survive per patch. This is a scenario in which selection among larvae is very intense. If selection within each patch were milder, multiple individuals with high scores might survive. Under this more moderate mode of selection, the advantage of sex should be reduced.

This can be illustrated by the case in which $m = 10$ individuals with the highest scores among larvae can survive. For simplicity, we consider the case in which the total number of sexual females and asexual individuals is very large, say, $R = 6{,}000$. The proportion of sexual and asexual types in the adult pool is equal (1:1), but the ratio of sexual females and asexual individuals should be about 1:2, because half the sexual individuals are males. Hence, roughly speaking, about 2,000 sexual females and 4,000 asexual individuals oviposit in a patch. As each of these produces 10 offspring, there are about 20,000 sexual offspring and 40,000 asexual offspring in a patch. However, because the sexual offspring of a single mother differ from one another, the total number of phenotypes for the sexual species should be about 20,000, whereas the total number of phenotypes of the asexual species is still 4,000.

However, if 10 individuals with the highest scores within a patch could survive, the probability of an asexual mother having more surviving offspring would increase. The top score and the second-highest score might be achieved by sexual species. However, if the third-highest score were achieved by an asexual type, then the fourth, fifth, and all other survivors would also be asexual if N were greater than or equal to seven. This is because N asexual individuals exist for each phenotype. Let m be the number of survivors. In the standard model of sib-competition, $m = 1$.

The left top panel of Fig. 1(A) illustrates how the fraction of the sexual type changes over generations. The initial fraction was 50%. Different curves correspond to the results of different numbers of survivors per patch (m). We can see that the sexual type is advantageous over the asexual type when the number of survivors is $m = 1$, $m = 5$, $m = 10$, or $m = 20$; however, the sexual type is outcompeted by the asexual type when the number of survivors is $m = 50$ or $m = 100$. This indicates that the advantage of the sexual type over the asexual type requires strong selection pressure. (The other panels in Fig. 1 will be explained later).

Fig. 2 shows the results of the simulation. The horizontal axis is the frequency of the sexual type in the population, x, and the vertical axis displays different values for the number of survivors per patch, m. Right-pointing arrows indicate that the fraction of the sexual type increased in the simulation, whereas left-pointing arrows indicate that the sexual type decreased in abundance in the simulation. To more clearly distinguish between the two types of arrow, the left-pointing arrows are shaded. From this figure, we can see the following.

First, when the number of survivors per patch is small (e.g. $m = 18$), the frequency of the sexual type increases for all x, suggesting that the sexual type eventually completely outcompetes the asexual type. In contrast, when the number of survivors is large (e.g. $m = 26$ or greater), the proportion of the sexual type decreases for all x, suggesting that it eventually disappears from the population. Between these two situations ($m = 19$–25), there are alternative stable outcomes. Both the population dominated by the sexual type ($x = 1$) and the population dominated by the asexual type ($x = 0$) are stable, refusing invasion by the other type. There is a threshold fraction of the sexual type near the boundary between shaded and unshaded regions. If the sexual type were more abundant than this threshold, it would win out; but if the sexual type were lower in abundance than this threshold, it would disappear from the population. We also note that as m increased, the threshold fraction increased. We can summarize these results as follows:

[1] A larger number of survivors per patch should favor the evolution of the asexual type, and fewer survivors should encourage the maintenance of sex. This implies that sufficiently strong selection is required for sex to be advantageous. However, even if multiple individuals could survive per patch, the sib-competition model can make sexual reproduction advantageous.

[2] There is a clear tendency for evolutionary bistability. Sexual and asexual types are unlikely to coexist in the same population. Rather, the initially more abundant type enjoys a greater competitive ability, and which of the two types eventually wins may depend on initial frequencies.

Mathematical arguments

When multiple individuals survive per patch, we can estimate the advantage of the sexual type over the asexual type as follows: for simplicity, let us suppose that the number of adults that arrive at a single patch is very large (*R* is infinitely large) and that they consist of sexual females and asexual reproductives. Let x_t be the fraction of the sexual type in the adult pool. The ratio of sexual females to asexual individuals is then $x_t\colon 2(1 - x_t)$. Here, we consider the fact that half the sexual individuals in the adult pool are male, who do not oviposit. Each sexual female produces *N* offspring, which may differ in phenotype. In contrast, each asexual female produces *N* offspring of the same phenotype. Hence, the total number of phenotypes in the sexual species should be multiplied by factor *N*. The fraction of phenotypes for offspring of sexual mothers among all phenotypes in a patch becomes

$$\mathrm{q_t} = \frac{\mathrm{Nx_t}}{\mathrm{Nx_t+2(1\text{-}x_t)}}$$

$$q_t = \frac{Nx_t}{Nx_t+2(1-x_t)} \quad .$$

(1)

The phenotype achieving the highest score may belong to a sexual individual with a probability of q_t. However, the second-highest score may be achieved by a sexual individual with a probability of ${q_t}^2$. This is smaller than q_t, because the second-highest score could be achieved by a sexual individual only if the highest score were also achieved by a sexual individual. If the asexual type were to have the highest score, it would occupy second place as well, because it would have *N* siblings with the same phenotype. Similarly, the probability of the *k*th-highest position being occupied by a sexual individual would be ${q_t}^k$; hence, the top k highest scores would be achieved by sexual individuals, whereas the rest would be achieved by asexual individuals with probability ${q_t}^k(1 - q_t)$. The expected fraction of survivors of the sexual type would therefore be as follows:

$$x_{t+1} = \sum_{k=0}^{m-1} \frac{k}{m} {q_t}^k (1 - q_t) + 1 * {q_t}^m \quad . \tag{2}$$

This is rewritten as

$$x_{t+1} = \frac{q_t(1-{q_t}^m)}{m(1-q_t)} \quad . \tag{3}$$

Eq. (3), together with Eq. (1), provides a formula for predicting the dynamics of sexual individuals within the population. Note that this argument overestimates the success of sexuals, because there are many processes that reduce the success of sexual reproduction (see Douge and Iwasa 2017). However, we can use Eqs. (3) and (1) as the case favoring the success of sexual type to the maximum degree.

Fig. 2 shows the prediction of the model given by Eqs. (2) and (3). The horizontal axis represents the fraction of the sexual type, and the vertical axis shows the number of survivors in each patch. A smaller m implies more intense selection within each patch. The conditions are $R = 10$, $N = 40$. Because $RN = 400$, $m = 10$ indicates that 2.5% of larvae can survive to adulthood, whereas $m = 1$ indicates that only 0.25% of the larvae can survive. The fraction of the sexual type decreases when m is greater than 26, and it increases when m is smaller than 18. For m between 19 and 25, the results depend on the initial fraction of the sexual type. The dynamics are bistable, and the sexual type increases and becomes fixed when the initial fraction is greater than a threshold value ($x > x_c$). Conversely, the sexual type is outcompeted by the asexual type and disappears from the system when the initial fraction is smaller than the threshold ($x < x_c$). The threshold value x_c can be calculated as an unstable equilibrium of Eqs. (1) and (3), which is represented by solid circles in Fig. 2. There is no possibility of coexistence between the two types.

Note that Eqs. (1) and (3) represent a scenario in which the advantage of the sexual type is overestimated. There are many processes that reduce the effective advantage of the sexual type. For example, some offspring might share the same phenotype. Additionally, if sexual siblings of the different phenotype were similar to one another in their scores, fewer mothers in a patch would decrease the relative advantage of the sexual type, as shown in Douge and Iwasa (2017). As shown in Fig. 2, the range of scenarios in which the equations predict the sexual type to have an advantage is considerably larger than the corresponding range observed through direct simulations, indicated by the unshaded region. However, the qualitative behavior of the model is quite similar. Larger values for m reduce the advantage for the sexual type and create bistable dynamics.

Environmental variance

In the sib-competition model studied by Douge and Iwasa (2017), the fitness of individuals of the same phenotype is equal, although it can differ between patches. However, it is quite plausible that individuals experience different conditions during their growth and development, and their fitness may therefore differ even if their genotypes were to be identical. This environmental variance should favor the asexual type, as they have many offspring with the same phenotype.

Bulmer (1980) studied the effects of environmental variance in the sib-competition model. Based on an analysis of quantitative genetics, Bulmer concluded that the advantage of sex disappears when environmental variance is of the same magnitude as the additive genetic variance ($V_E = V_A$). In other words, the advantage of sex requires the environmental variance to be smaller than the genetic variance. In the current paper, we examined how low levels of environmental variance destroy the advantage of sex and investigated whether sexually reproducing species can still enjoy the benefits of generating genetically diverse offspring when environmental variance is low.

We adopted the model studied by Douge and Iwasa (2017), which did not account for any environmental variance. The variance of the score was $\sigma^2 = 1.21$ (standard deviation: σ = 1.1). We then studied the case in which the score of an individual was augmented by an independent stochastic variable with a mean of zero and a variance of $\sigma^2/16$, $\sigma^2/8$, $\sigma^2/4$, $\sigma^2/2$, and σ^2.

The results are shown in Fig. 1(B–F), in which the starting number of adults in a patch was R = 10, and each adult produced N = 40 offspring. In the absence of environmental variance, as in the standard sib-competition model, the sexual type was maintained when m = 20 or less; however, the asexual type won out when m was 50 or greater. If environmental noise were added, the advantage of the sexual type would decrease. As the magnitude of the environmental noise increases, the sexual type becomes less competitive at smaller m values. For example, when environmental variance V_E is small ($V_E = \sigma^2/16$), the sexual type persisted when m = 10 or less and was outcompeted when m = 20, 50 or 100. When $V_E = \sigma^2/8$, the sexual type increased when m = 5 or less, but it decreased when m = 10 or greater. When $V_E = \sigma^2/4$, the sexual type increased clearly when m = 1, and it decreased when m = 10 or more. For m = 5, the trend was unclear. When $V_E = \sigma^2/2$, the sexual type was maintained only when m = 1, and it was extinguished when m = 5 or greater. Finally, when $V_E = \sigma^2$, the sexual type was outcompeted for all values of m, including m = 1. The last result corresponds to the case studied by Bulmer (1980), who stated that when the environmental variance is equal to the genetic variance, the sexual type does not have an advantage over the asexual type.

Environmental noise provides an advantage to asexual mothers: because it creates variation in the fitness scores of offspring, the probability that at least one offspring will achieve the highest fitness score within a patch increases.

Reduced number of phenotypes by selection

In the evolutionary simulation of the sib-competition model, the initial populations of sexual and asexual types include all phenotypes at equal frequencies. For example, in Douge and Iwasa (2017), the adult pool of the asexual type consisted of 1024 combinations of phenotypes, from which reproductive individuals arriving at patches were chosen at random. How can this high phenotypic diversity be maintained?

This question can be answered by considering frequency-dependent selection favoring rare genotypes. For instance, regarding the genetic diversity for the sexual species, let us consider each locus separately for the sake of simplicity (free recombination). Consider the maintenance of two alleles, A and a, at the first locus. The environment is $\underline{\mathrm{A}}$ in half the patches, and it is $\underline{\mathrm{a}}$ in the other half. Suppose allele A were very abundant and a were rare. In the patches with environment $\underline{\mathrm{A}}$, the fittest individual would likely be A. However, in patches with environment $\underline{\mathrm{a}}$, allele a would enjoy a selective advantage over A, and individuals carrying the a allele would be more likely to survive. If selection were sufficiently strong, the frequency of allele a should be higher among survivors than among arriving reproductive individuals. Allele a would therefore tend to increase in frequency. In a similar manner, allele A enjoys an advantage when it is rare. This type of frequency-dependent selection encourages the maintenance of genetic diversity. In simulation models, the number of patches is finite; hence, there exists random genetic drift resulting in the stochastic loss of alleles. However, in the presence of frequency-dependent selection favoring rare alleles, genetic diversity is likely to be maintained at a high level. For asexual populations, this principle would also hold if the total number of patches were much larger than the total number of phenotypes (1024). If the number of patches were infinitely large, the environmental states in these patches would be chosen from 1024 possibilities with equal probability.

On the other hand, we might reason that the likelihood of all 1024 possible combinations appearing in every generation is low. It would be much more difficult to maintain genetic diversity if there were fewer environmental types chosen randomly from the total number of possibilities. For example, in each generation, 20 combinations of environmental aspects are randomly chosen from all 1024 possibilities. In a given generation, each patch has one of these combinations with equal probability. For the sexual type, this may have a rather small effect on the maintenance of genetic diversity. The frequency of environment A may fluctuate between generations following a binomial distribution B (20, 1/2), but allele A would still be favored in about half the patches, and allele a would be favored in the other half. There is therefore still frequency-dependent selection that serves to maintain genetic diversity. Conversely, owing to the lack of recombination in the asexual type, phenotypes that disappear in a generation can never be recovered. We should therefore regard all 1024 combinations of binary alleles at 10 loci as 1024 alleles at a single locus. A particular combination of environmental aspects may not occur among the existing 20 for a number of generations. During this period, the abundance of the corresponding phenotype should decrease. When the number of patches is finite, this should result in the loss of a phenotype from the population. We may thus conjecture that this modification of the model should reduce the genetic diversity of the asexual type to a greater extent than it does the sexual type. This may favor the sexual type in the sib-competition model.

To study the effects of the loss of genetic diversity owing to competition between the sexual and asexual types, we considered simulations in which the sexual and asexual species propagate separately for a certain number of generations (which we call the pre-selection period), after which they are mixed and begin competing with each other. The number of patches during this pre-selection period was 100, which is half the number of patches present during the competition between the sexual and asexual types. Fig. 3 illustrates how the number of phenotypes declines over time when the sexual and asexual species do not mix with one another. The figure shows the trajectories of five independent runs for the sexual and asexual types. Here, the total number of patches was 100; 20 combinations of environmental aspects were randomly chosen from 1024 possibilities, and each combination was adopted in 5 (100/20) patches.

The number of phenotypes decreased in the first generation. For the sexual species, the number of phenotypes persisted at around the same level for many generations after the initial drop. In contrast, for the asexual type, the number of phenotypes decreased by an even greater amount in the first generation, then continued declining to a minimum value of 1. It should be noted that, in asexual species, phenotypes that are lost can never be recovered. This is quite different from the case in sexual species, in which phenotypes that are absent in one generation can subsequently appear as a result of genetic recombination.

The disadvantage of asexual species compared with sexual species increases as the pre-selection period becomes longer. We adopted a pre-selection period of 50 generations for subsequent competition between the sexual and the asexual species.

The results of competition between the sexual and asexual types with a pre-selection period of 50 generations are shown in Table 1. We show the results obtained when the patches' environments were randomly chosen from 1024 possibilities (original model), when only 20 environments were randomly chosen from 1024 each generation, and when only 5 environments were chosen and realized equally in patches. The magnitude of environmental variance was assessed at six levels: V_E = $0, \sigma^2/16$, $\sigma^2/8$, $\sigma^2/4$, $\sigma^2/2$, and σ^2. The number of survivors per patch was m = 1, 5, 10, 20, 50, and 100, respectively. Other parameters were: R = 10 and N = 40.

The table shows the number of phenotypes, sampled after a pre-selection period of 50 generations followed by 10 generations of competition between the sexual and asexual types. The table also shows the relative frequencies of the sexual and asexual types. The cases in which sexual individuals accounted for more than 50% of the population are marked by open circles; the other cases are marked by closed circles.

In both the sexual type and the asexual type, the number of phenotypes decreased more sharply when the number of environments was smaller, the number of survivors per patch was smaller, and the environmental variance was smaller. The decrease was especially dramatic for the asexual type, which had between 2 and 20 phenotypes. For the sexual type, the number of phenotypes ranged from 41 to 1020. The sexual type had many more phenotypes than the asexual type, which enhanced the advantage of sex. It can be seen that, as the number of environments decreases (from 1024 to 20, and then to 5), the number of cases in which the sexual type predominates increases. As discussed in previous sections, a larger m (i.e., number of survivors) provides an advantage to the asexual type. In the original model (the left column) without environmental variance ($V_E = 0$), sexual reproduction provided an advantage over asexual reproduction when $m = 20$ or less, whereas the asexual type won out when $m = 50$ or more. However, if only five environments were realized in each generation, sex would be advantageous even when $m = 50$. This trend was also observed in scenarios with greater environmental variance (positive V_E).

In summary, the reduction of phenotypic diversity in the pre-selection period favored the evolution of the sexual type over the asexual type. This factor is comparable to other processes, such as a milder selection per patch (larger m) and environmental variance (larger V_E), that disfavor the sexual type.

Discussion

In a twin paper (Douge and Iwasa 2017), we showed that, owing to the greater phenotypic diversity of sexual offspring compared with asexual offspring, sexual species can outcompete asexual species in the face of the two-fold cost of sex provided that the number of environmental aspects is sufficiently large and the competition among siblings is sufficiently intense. To make the sib-competition mechanism more effective than in the original model developed by Maynard Smith (1976; 1978), we increased the number of environmental aspects from 5 to 10. We also made the score generated by matching each locus to the corresponding environmental aspects a stochastic variable to avoid scenarios in which the sexual and asexual types were equally ranked. We examined the reasons that sexual reproduction is not as advantageous as a simple argument would predict. We found that sexual offspring from the same mother may have the same phenotype, that two sexual offspring of the same mother may be similar in score even if they differ in phenotype, and that the low number of reproducing individuals within each patch may reduce the strength of selection compared with the simple model.

In the present paper, we further examined several aspects of the sib-competition model. First, if the strength of selection were lower than that assumed in the standard model, the advantage of the sexual type would be lower as well. This was demonstrated clearly by the scenario in which more than one individual per patch could survive. Second, the fitness score of individuals may be affected by factors experienced during growth, and this environmental variance would further reduce the advantage of the sexual type. In fact, Bulmer (1980) previously showed that if the magnitude of environmental variance were as large as the genetic variance, there would be no advantage of sexual reproduction over asexual reproduction.

The third factor we examined is that phenotypic diversity may not be maintained equally by the sexual and asexual types. To demonstrate this, we first modeled a pre-selection period, in which sexual type and asexual type are maintained separately before competing with each other in a shared system. The number of phenotypes declined very rapidly in the asexual population. In contrast, the number of phenotypes in the sexual population did not follow a clear declining trend. This is because the sexual type can recover a phenotype by genetic recombination even when it is lost in one generation. In contrast, in an asexual species, lost phenotypes never appear again. This loss of diversity in the asexual type favors the sexual type.

Whether the sexual or asexual type predominates when they are mixed depends on all these processes. The results are shown in Table 1. Here, in the leftmost column, $m = 1$ (only one individual survives per patch), $V_E = 0$ (no environmental variance), and there are 1024 environments; this is the case we studied in our last paper (Douge and Iwasa, 2017). Table 1 shows that all three factors have some effect on the outcome of competition between sexual and asexual types. A larger m or V_E would favor the asexual type, whereas fewer environments that reduce the phenotypic diversity of asexual individuals would favor the sexual type. Hence, we must conclude that whether sib-competition can maintain sexual reproduction depends on the quantitative measurement of different processes. These results, together with our findings in the twin paper (Douge and Iwasa 2017), provide new insight into the situations in which sib-competition is most effective in the maintenance of sex. Further investigations, particularly field measurements of the magnitude of specific processes, are required to provide a more complete picture of the maintenance of sexual reproduction.

References

Barton, N.H. and Post, R.J. 1986. Sibling competition and the advantage of mixed families. *J. Theor. Biol.,* 120: 381-387.

Barton, N.H., Otto, S.P., 2005. Evolution of Recombination Due to Random Drift, Genetics, 169, 2353-2370

Barton, N.H., Briggs, D.E.G., Eisen, J.A., Goldstein, D.B., Patel, N.H., 2002. Evolution, New York, Cold Springer Laboratory House.

Bulmer, M.G. 1980. The sib competition model for the maintenance of sex and recombination. J Theor. Biol., 82: 335-345

Douge, M. and Iwasa, Y. 2017. Sibling deversity gives sexual reproduction the advantage in a changing environment. EER., 18: 459-475

Fisher, R.A., 1930. The Genetical Theory of Natural Selection. Oxford, Oxford University Press.

Hamilton, W.D., 1980. Sex versus Non-sex versus Parasite. Oikos, 35, 282-290.

Kondrashow, A.S. 1988. Deleterious mutations and the evolution of sexual reproduction. Nature 336:435-440.

Maynard Smith, J. 1976. A short-term advantage for sex and recombination through sib-competition. J. Theor. Biol., 63: 245-258

Maynard Smith, J. 1978. The Evolution of Sex. Cambridge: Cambridge University Press.

Muller, H.J., 1932. Some Genetic Aspect of Sex. American Naturalist, 66, 118-138.

Muller, H.J., 1964. "The relation of recombination to mutational advance". Mutation Research, 106: 2–9

Otto, S.P., 2009. The Evolutionary Enigma of Sex. The American Naturalist, 174, S1-S14.

Taylor, P.D. 1979. An analytical model for a short-term advantage for sex. J. theor. Biol., 81: 407-421

Williams, G.C. 1975. Sex and Evolution. Princeton, NJ: Princeton University Press.

Williams, G.C. and Mitton, J.B. 1973. Why reproduce sexually? J. Theor. Biol., 39: 545-554

Captions to table and figures

Table 1

The number of phenotypes after pre-selection and the frequency of the sexual type after 10 generations of competition with the asexual type. Parameters were: R = 10, N = 40. Each sexual and asexual type is independently selected in 100 patches over 50 generations. Thereafter, both types are integrated and compete with each other over 10 generations. The table is divided into three columns. The left column shows the scenario including 1024 kinds of environment, the middle column shows that including 20 kinds, and the right column shows that including 5 kinds. In each column, the left side (two blocks) shows the number of phenotypes for the asexual type (A) and the sexual type (S) after pre-selection. The right side (two blocks) shows the frequency of the sexual type in the tenth generation. Cases in which the sexual type is more abundant are marked by open circles; others are marked by closed circles. Each column is vertically divided into six cases of V_E with six cases of the number of survivors (m).

Figure 1

Frequency of sexual individuals in the system. The horizontal axis shows the number of generations from the start of the simulation. The vertical axis shows the frequency of the sexual type. Each graph represents the frequency of the sexual type for different values of environmental variance, V_E. In each graph, different curves indicate the results obtained with different values of m, the number of survivors per patch. A larger m indicates milder selection within each patch. The advantage for the sexual type decreases as environmental variance increases and as selection became milder. Parameters were: R = 10, N = 40. Genetic variance was σ^2=1.21. See text for further explanation.

Figure 2

Direction of change in the frequency of the sexual type. The horizontal axis shows the current frequency of the sexual type, x, and the vertical axis shows the number of survivors per patch, m. The arrows indicate the directions of change (increase or decrease of x per generation). We visualized increases in x using white background and decreases in x using a shaded background. The solid circles connected by a line represent the prediction by simplified mathematical analysis, Eqs. (1) and (3). Both computer simulations and mathematical arguments state that smaller vales for m tend to increase x. Larger values for x also tend to increase x, indicating a bistability. The sexual type tends to outcompete the asexual type when it is initially abundant. Parameters were as follows: $R = 10$, $N = 40$, $V_E = 0$. The total number of patches was 200.

Figure 3

Decrease in the number of phenotypes in the pre-selection period. The horizontal axis reflects the time since the beginning of the simulation (number of generations on a logarithmic scale). The vertical axis represents the number of phenotypes. Five independent replicates are shown in lines. The top section is for the sexual type, and the bottom part is for the asexual type. The broken vertical line indicates 50 generations from the beginning of the simulation, which were used for competition between the sexual type and the asexual type. The number of phenotypes for the sexual type decreased in the first generation, but it was subsequently maintained without a clear decline. In contrast, the number of phenotypes for the asexual type decreased greatly in the first generation and continued to decline. This clearly shows that the asexual type lost phenotypic diversity during the pre-selection period. Parameters were as follows: $R = 10$, $N = 40$, $V_E = 0$, $m = 20$. The number of patches was 100 for both for sexual and asexual types; 20 combinations of environmental aspects were randomly chosen from 1024 possibilities, and each combination was adopted in 5 (100/20) patches.

Table

Table 1

	potentially1024 environments				20 kinds of environments				5 kinds of environments			
$V_E = 0$	phenotype		result		phenotype		result		phenotype		result	
m	A	S	10g		A	S	10g		A	S	10g	
1	9	95	100 %	○	6	80	100 %	○	2	41	100 %	○
5	9	292	100 %	○	6	240	100 %	○	2	136	100 %	○
10	9	471	100 %	○	7	388	100 %	○	2	229	100 %	○
20	9	703	95 %	○	7	593	98 %	○	2	350	100 %	○
50	11	950	2 %	●	8	858	6 %	●	3	539	73 %	○
100	13	1014	0 %	●	11	972	0 %	●	4	675	8 %	●
$V_E = \sigma^2/16$												
1	9	95	100 %	○	6	83	100 %	○	2	36	97 %	○
5	10	321	99 %	○	8	273	99 %	○	3	165	100 %	○
10	10	518	91 %	○	7	443	96 %	○	2	261	98 %	○
20	10	745	34 %	●	7	644	63 %	○	3	397	89 %	○
50	11	967	1 %	●	9	893	2 %	●	3	608	45 %	●
100	14	1016	0 %	●	11	975	0 %	●	5	744	4 %	●
$V_E = \sigma^2/8$												
1	9	95	100 %	○	7	83	100 %	○	2	54	98 %	○
5	10	333	94 %	○	7	283	97 %	○	3	178	98 %	○
10	10	534	71 %	○	8	457	81 %	○	3	275	95 %	○
20	10	762	16 %	●	7	668	37 %	●	3	412	79 %	○
50	12	972	1 %	●	9	902	1 %	●	4	651	24 %	●
100	15	1016	0 %	●	12	968	0 %	●	5	722	1 %	●
$V_E = \sigma^2/4$												
1	8	95	98 %	○	6	88	97 %	○	2	55	99 %	○
5	10	345	74 %	○	7	309	83 %	○	3	194	89 %	○
10	10	548	36 %	●	8	472	47 %	●	3	304	83 %	○
20	11	775	6 %	●	8	691	13 %	●	3	467	60 %	○
50	12	980	0 %	●	10	927	1 %	●	4	660	17 %	●
100	15	1018	0 %	●	13	990	0 %	●	7	776	0 %	●
$V_E = \sigma^2/2$												
1	8	95	75 %	○	6	89	83 %	○	2	70	91 %	○
5	10	361	24 %	●	8	328	42 %	●	3	245	75 %	○
10	11	569	9 %	●	8	512	16 %	●	4	342	53 %	○
20	12	799	2 %	●	9	728	5 %	●	4	495	27 %	●
50	14	986	0 %	●	12	935	0 %	●	6	665	4 %	●
100	18	1020	0 %	●	15	983	0 %	●	9	687	0 %	●
$V_E = \sigma^2$												
1	8	94	27 %	●	6	92	38 %	●	3	75	66 %	○
5	11	369	5 %	●	8	346	9 %	●	4	266	27 %	●
10	12	583	2 %	●	10	535	4 %	●	5	394	17 %	●
20	13	812	0 %	●	11	741	1 %	●	5	531	9 %	●
50	17	989	0 %	●	13	930	0 %	●	8	690	1 %	●
100	20	1019	0 %	●	18	987	0 %	●	12	751	0 %	●

Figures

Figure 1

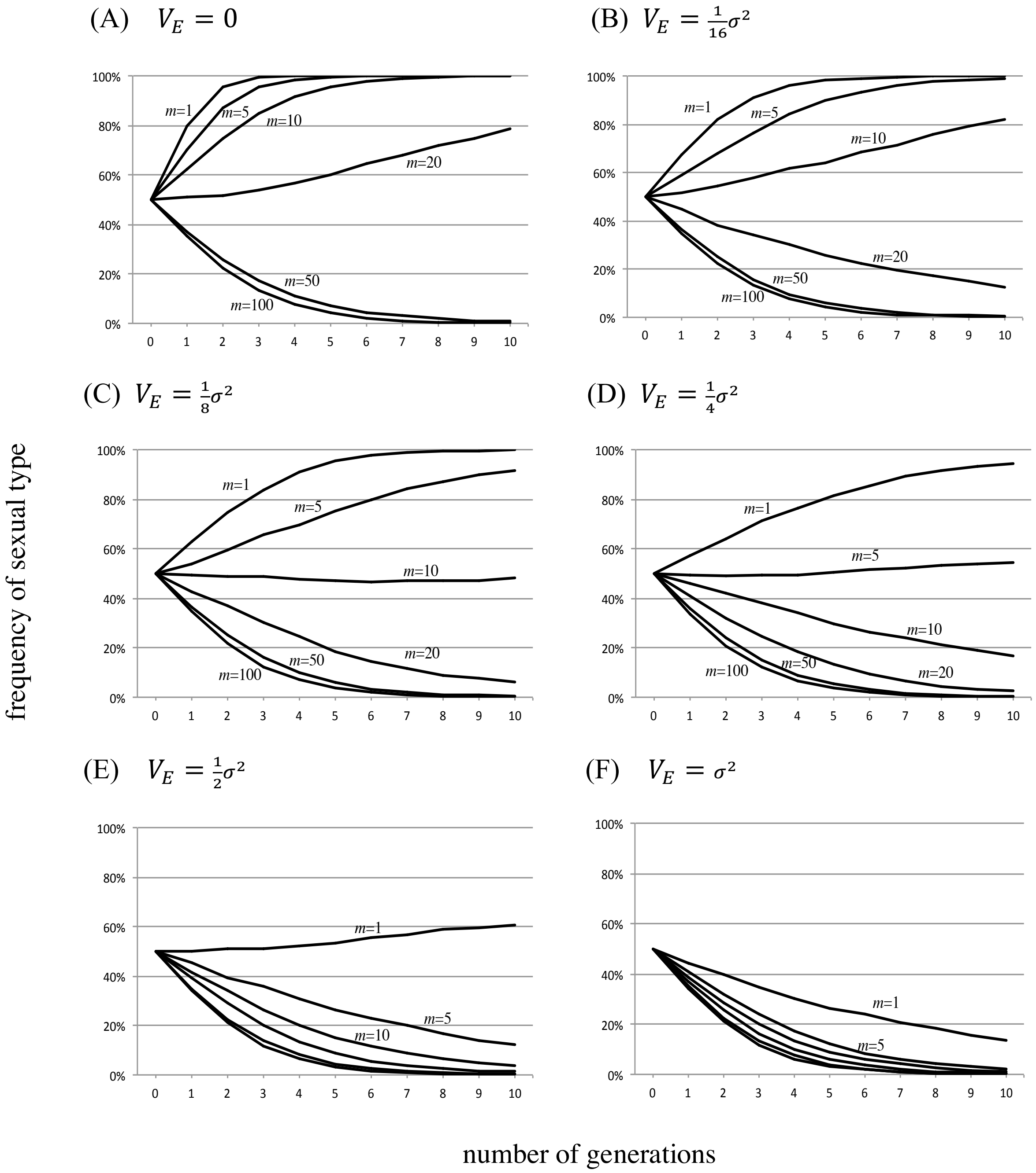


Figure 2

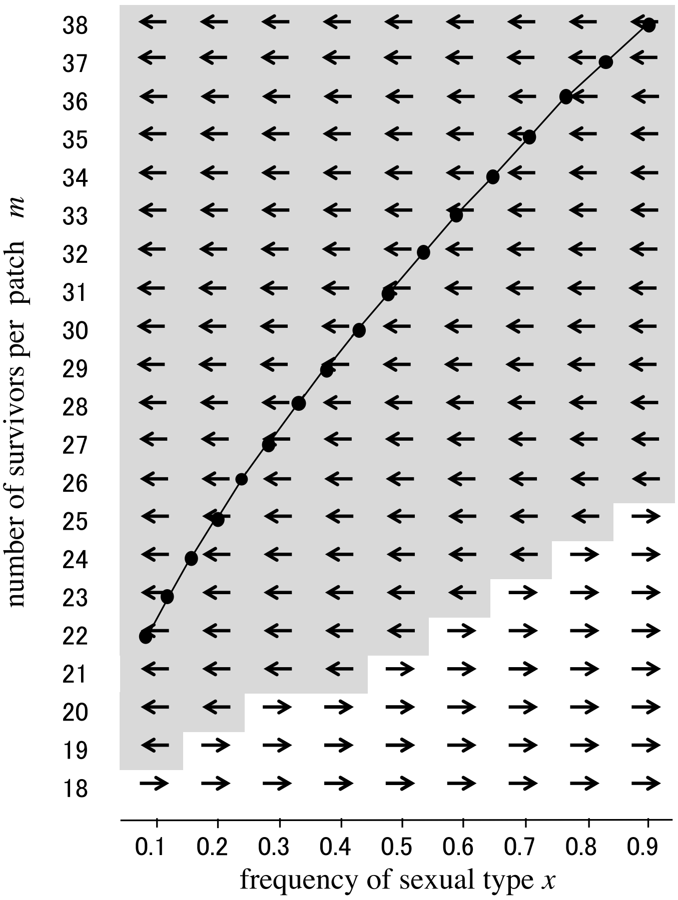
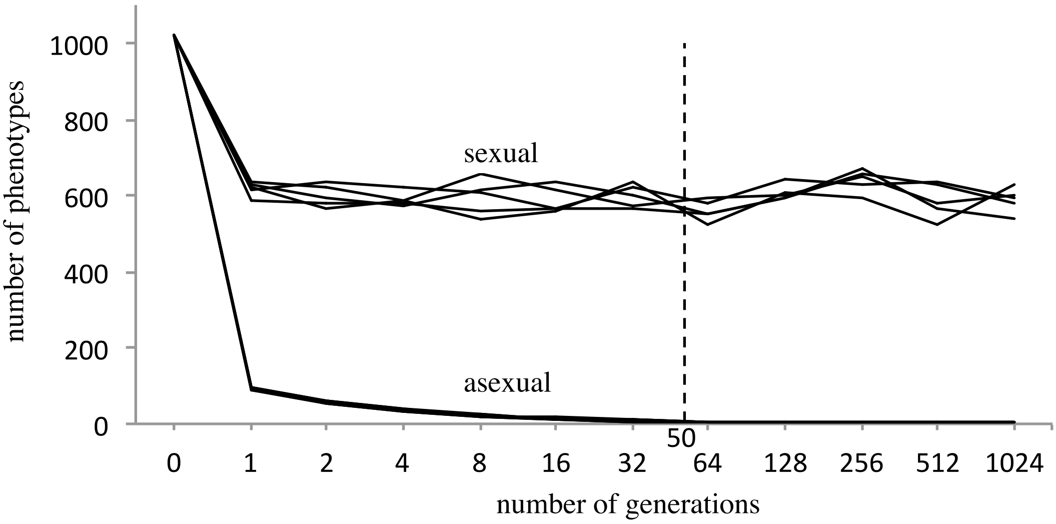

number of survivors per patch m
38
37
36
35
34
33
32
31
30
29
28
27
26
25
24
23
22
21
20
19
18
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
frequency of sexual type x

Figure 3


number of phenotypes
1000
800
600
400
200
0
sexual
asexual
50
0
1
2
4
8
16
32
64
128
256
512
1024
number of generations