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

Makoto Douge and Yoh Iwasa

Department of Biology, Faculty of Science, Kyushu University, Fukuoka, Japan

ABSTRACT

Background: In a previous paper, we showed that greater sibling diversity among sexual offspring might 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 the appropriate conditions are present.

Keywords: evolution of sex, sib-competition, milder selection, environmental variance, reduced genetic diversity.

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 favouring 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

Correspondence: M. Douge, Department of Biology, Faculty of Science, Kyushu University, 744 Motooka, Nishi-ku, Fukuoka 819-0395, Japan. email: makotodouge@gmail.com

asexual reproduction (Kondrashov, 1988), and disrupts linkage disequilibrium created by random genetic drift (Fisher, 1930; 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 environment (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 previous 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 aspects was increased and if the fitness of different phenotypes differed between patches, sexual reproduction would have 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 best match is achieved by a single phenotype, sexual mothers have a marked 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 having the best 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 best 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 by us previously (Douge and Iwasa, 2017), the matching scores differed among patches, and there were a larger number of environmental aspects. As a result, the likelihood of different phenotypes achieving the best 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 look at 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 that individual with the best match 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 next highest score were to be 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, and the scores of different phenotypes to be different. Under this assumption, when the best match between the phenotype and the environment is achieved by two different phenotypes (one sexual and one asexual), the larger number of individuals 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 favour asexual mothers who have many offspring with the same phenotype. If this variance were sufficiently large, the large number of individuals of the asexual type might contribute to its success, 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 to the environment, each of which had two states, there would be 1024 possible combinations of environmental states. In our previous paper, these 1024 different environments would exist in some patches every generation. A more realistic assumption is that, for example, only 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 next section, 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 arguments developed by Williams and Mitton (1973) and Williams (1975). In a previous paper, we made a few additional modifications to the model that strengthen the evolutionary advantage of sexual reproduction (Douge and Iwasa, 2017). Here, we explain the model briefly (for more details, see Douge and Iwasa, 2017).

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 at random. Then each patch receives R adults (sexual females and asexual individuals), each of which oviposits N offspring. The competition between them is fierce, and only a single individual can survive 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, favouring 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 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 five 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 more. However, if we assume a strong correlation among pairs of environmental aspects, the advantage of sexual reproduction would reduce significantly. We found that the main reason for this limited advantage of sex was that the highest score was often achieved simultaneously by 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 and 1.0 with a uniform probability distribution. This latter modification introduces a stochasticity of scores 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 best 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 would allow the sexual type to 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, we noted that the observed advantage of sex is considerably less than $N/2$ (Douge and Iwasa, 2017). This was improved by the two modifications discussed above. We 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, we 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 achieve similar scores, and (3) that if the value of R – the total number of reproductive adults that arrive in the patch – is low, the selection process is less effective (Douge and Iwasa, 2017).

The sib-competition model in Douge and Iwasa (2017) 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) 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 less intense, 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 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 $R = 6000$. The proportion of sexual and asexual types in the adult pool is equal (1 : 1), but the ratio of sexual females to asexual individuals should be close to 1 : 2, because half the sexual individuals are males. Hence, roughly speaking, about 2000 sexual females and 4000 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 remains 4000.

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 highest 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, $m = 1$.

Figure 1(A) illustrates how the proportion of the sexual type changes over generations. Initially, the sexual type comprised 50% of the population. Different curves correspond to the results of different numbers of survivors per patch (m). We can see that the sexual type has an advantage 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 for the sexual type to have an advantage over the asexual type, there needs to be strong selection pressure. (The other panels in Fig. 1 will be explained later.)

Figure 2 shows the results of the simulation. The horizontal axis represents 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. Arrows pointing to the right indicate that the fraction of the sexual type increased in the simulation, whereas arrows pointing to the left indicate that the sexual type decreased in abundance in the simulation. To better distinguish between the two types of arrow, the arrows pointing to the left are shaded grey.

From Fig. 2, we can ascertain 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, eventually, the sexual type completely outcompetes the asexual type. In contrast, when the number of survivors is large (e.g. $m \geq 26$), 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, denying invasion by the other type. There is a threshold fraction of the sexual type near the boundary between the shaded and unshaded regions. If the sexual type were more abundant than this threshold, it would win out; but if the sexual type were less abundant 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 favour 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. The sexual and asexual types are unlikely to co-exist in the same population. Rather, the initially more abundant type enjoys 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 $x_t : 2(1 - x_t)$. Here, we consider the fact that half the sexual individuals in the adult pool are male, which 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

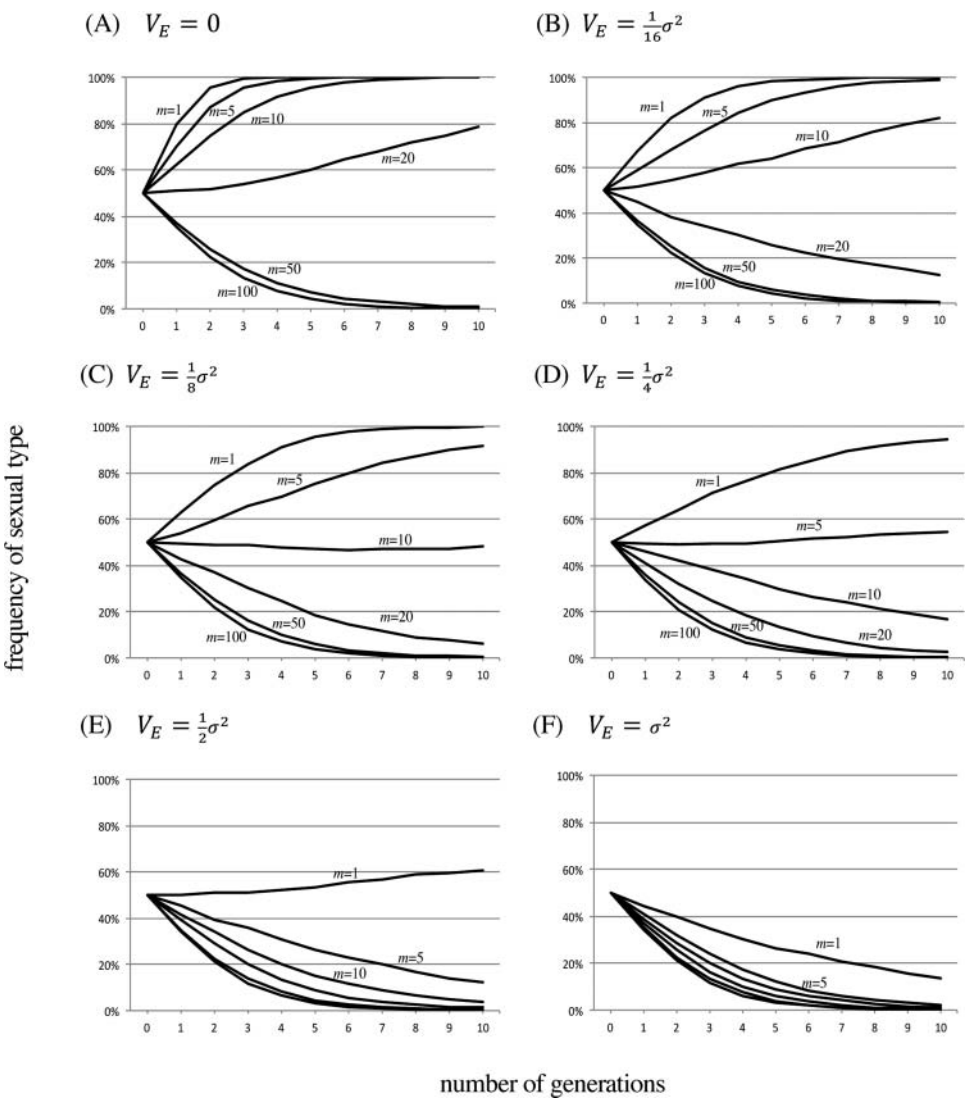

Fig. 1. Frequency of sexual individuals in the system. The horizontal axis shows the number of generations from the start of the simulation. The vertical axis shows the frequency of the sexual type. Each panel represents the frequency of the sexual type for different values of environmental variance, V_E. In each graph, different curves indicate the results obtained with different values of m, the number of survivors per patch. Larger m indicates milder selection within each patch. The advantage for the sexual type decreases as environmental variance increases and as selection becomes milder. Parameters were: $R = 10$, $N = 40$. Genetic variance was $\sigma^2 = 1.21$. See text for further explanation.

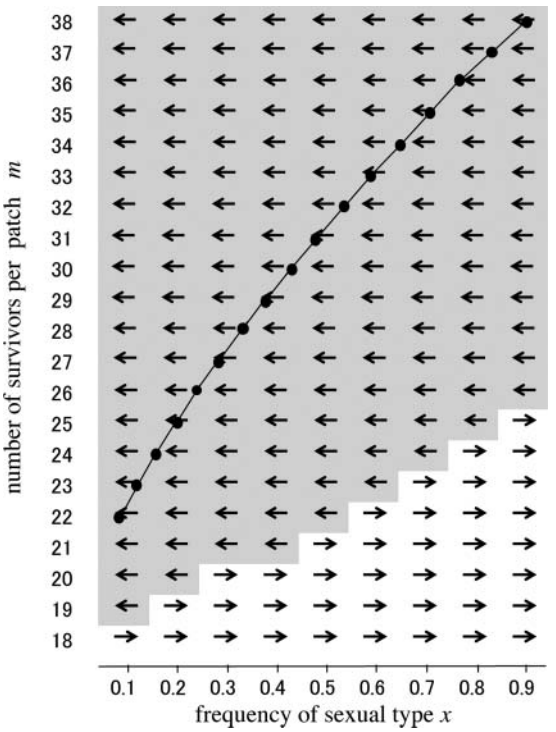

Fig. 2. Direction of change in the frequency of the sexual type. The horizontal axis shows the current frequency of the sexual type, x, and the vertical axis shows the number of survivors per patch, m. The arrows indicate the direction of change (increase or decrease of x per generation). To aid visualization, increases in x are represented on a white background and decreases in x on a grey background. The solid circles connected by a line represent the prediction by simplified mathematical analysis (equations 1 and 3). Both computer simulations and mathematical arguments state that smaller values of m tend to increase x. Larger values of m 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.

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:

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

The phenotype achieving the best score may belong to a sexual individual with probability q_t. However, a sexual individual might achieve the second highest score with probability q_t^2. This is smaller than q_t, because a sexual individual could only achieve the second highest score if a sexual individual also achieved the best score. 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 kth-highest position being occupied by a sexual individual would be q_t^k; hence, sexual individuals would achieve the k highest scores, while asexual individuals would achieve the rest with

probability $q_t^k(1-q_t)$. The expected fraction of survivors of the sexual type would therefore be as follows:

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

This can be rewritten as

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

Equation (3), together with equation (1), provides a formula for predicting the dynamics of sexual individuals within the population. Note that this argument overestimates the success of the sexual type, because there are many processes that reduce the success of sexual reproduction (see Douge and Iwasa, 2017). However, we can use equations (3) and (1) to represent the case favouring the maximal success of the sexual type.

The prediction of the model given by equations (2) and (3) is shown in Fig. 2. 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 $m > 26$, and it increases when $m < 18$. 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 higher 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 below the same threshold ($x < x_c$). The threshold value x_c can be calculated as an unstable equilibrium of equations (1) and (3), which is represented by black dots in Fig. 2. There is no possibility of co-existence between the two types.

Note that equations (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. In addition, if sexual siblings of different phenotypes were to have similar 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 the advantage is considerably wider than the corresponding range observed through direct simulations, indicated by the unshaded region. However, the qualitative behaviour of the model is quite similar. Larger values of 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 favour 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 less than the genetic variance. Here, 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: $\sigma = 1.1$). 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 variance of $\sigma^2/16$, $\sigma^2/8$, $\sigma^2/4$, $\sigma^2/2$ or σ^2.

The results are shown in Fig. 1(B–F), in which the initial 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 $m \leq 20$; however, the asexual type won out when m was ≥50. If environmental noise were added, the advantage of the sexual type decreased. As the environmental noise increased, the sexual type became less competitive at smaller values of m. For example, when environmental variance V_E was small ($V_E = \sigma^2/16$), the sexual type persisted when $m \leq 10$ and was outcompeted when $m = 20$, 50 or 100. When $V_E = \sigma^2/8$, the sexual type increased when $m \leq 5$, but it decreased when $m \geq 10$. When $V_E = \sigma^2/4$, the sexual type increased clearly when $m = 1$, and it decreased when $m \geq 10$. 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 eradicated when $m \geq 5$. 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 the 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 favouring 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 A in half the patches and it is a in the other half. Suppose allele A was very abundant and a was rare. In the patches with environment A, the fittest individual would likely be A. However, in patches with environment 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. Therefore, allele a would tend to increase in frequency. In a similar manner, allele A would enjoy an advantage when 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 favouring 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 was much larger than the total number of phenotypes (1024). If the number of patches was 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 at random 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 favoured in about half the patches, and allele a would be favoured 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 that of the sexual type. This may favour 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 to compete 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. Figure 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 to decline to a minimum value of 1. It should be noted that, in asexual species, phenotypes that are lost can never be

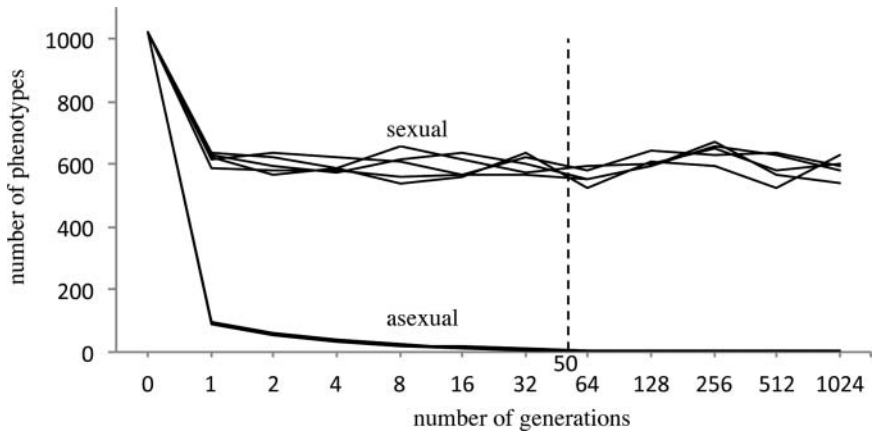

Fig. 3. Decrease in the number of phenotypes in the pre-selection period. The horizontal axis reflects the time since the beginning of the simulation (number of generations on a logarithmic scale). The vertical axis represents the number of phenotypes. Five independent replicates are shown (lines). The top part is for the sexual type, and the bottom part is for the asexual type. The dashed 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 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 = 100 for both the 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.

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.

Compared with sexual species, the disadvantage of asexual 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 $N = 40$.

Table 1 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. Open circles represent cases in which the sexual type was more abundant; solid circles represent cases in which the asexual type was more abundant.

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

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

	Potentially 1024			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 % ●

Note: 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 four columns. The second column shows the scenario with all 1024 kinds of environment, the third column shows that with 20 kinds of environment, and the fourth column that with 5 kinds of environment. In each of these three columns, the left-hand side (two blocks) shows the number of phenotypes for the asexual type (A) and the sexual type (S) after pre-selection. The right-hand side (two blocks) shows the frequency of the sexual type in the tenth generation: ○ = cases in which the sexual type is more abundant; ● = cases in which the asexual type is more abundant. Each column is divided vertically into six cases of V_E with six cases of the number of survivors (m).

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, 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 $m \leq 20$, whereas the asexual type won out when $m \geq 50$. However, if only 5 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 favoured 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), which favour the asexual type.

DISCUSSION

In a previous 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 ranked equally. We examined the reasons why 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 have a similar 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 also be lower. This was demonstrated clearly by the scenario in which more than one individual in a 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 was that the maintenance of phenotypic diversity might differ between the sexual and asexual type. To demonstrate this, we first modelled a pre-selection period, in which the 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 decline in the number of phenotypes in

the sexual population did not follow a clear 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 favours 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. In the second column from the left, we have $m = 1$ (only one individual survives per patch), $V_E = 0$ (no environmental variance), and there are 1024 environments; this is the case we studied previously (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 favour the asexual type, whereas fewer environments that reduce the phenotypic diversity of asexual individuals would favour 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 previous findings (Douge and Iwasa 2017), provide new insight into the circumstances 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.

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