Evolutionary Ecology Research, 2017, **18**: 459–475

Sibling diversity gives sexual reproduction the advantage in a changing environment

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ABSTRACT

Background: Intense competition among siblings may favour sexual reproduction because phenotypic diversity is higher among sexual siblings than asexual siblings. However, previous theoretical studies concluded that competition among sibs is ineffective at promoting sexual reproduction.

Question: What are the conditions required for sib-competition to favour sexual reproduction?

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

Key assumptions: Sexual reproduction generates phenotypic diversity among siblings, whereas asexual reproduction doubles the reproductive rate. The virtual habitat consists of many patches, each with different environmental conditions. Only one individual – the most adapted – survives in each patch.

Conclusions: A greater number of environmental factors and variation of the fitness achieved by adapted phenotypes favour sexual reproduction. Intense sibling competition is likely to be an important process for maintaining sex.

Keywords: heterogeneous environment, sib-competition, two-fold cost of sex.

INTRODUCTION

Nearly 40 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 (see Mittledorf, 2016) or else confer significant short-term advantages that outweigh its two-fold cost.

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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 the many plausible models suggesting the advantages of reproducing sexually, the Red Queen hypothesis emphasizes the impact of temporal fluctuations on the selective process. In particular, Hamilton (1980) proposed that the host–parasite relationship would favour sexual reproduction due to short-term epistatic fluctuations. Recent reviews also concluded that the Red Queen Hypothesis is a potentially important process favouring sex (Otto, 2009; Hartfield and Keightley, 2012).

Another model emphasizes 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 will likely 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 (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 major advantage of sexual reproduction because it 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) analysed the sib-competition model mathematically. Bulmer (1980) was able to extend this analysis by incorporating quantitative genetics. However, Barton and Post (1986) criticized these developments for not taking environmental correlations into account. In the last 30 years, there has been no serious attempt to evaluate sib-competition as a factor potentially favouring 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 favour the advantage of sexual reproduction. We also identify processes that reduce the advantage of sexual reproduction. We conclude that, as long as suitable conditions are met, intense sib-competition is an important process for maintaining sex.

SIB-COMPETITION MODEL

We start with the sib-competition model proposed by Maynard Smith (1976, 1978). However, we consider a species with separate sexes (males and females) rather than one with

hermaphrodites. The model investigates the dynamics of sexual and asexual organisms competing within a single Mendelian population that uses a number of patches. The environment varies greatly between patches and between generations.

Population structure and reproduction of sexual and asexual organisms

To illustrate the population structure, we show an example population in Fig. 1A that consists only of sexual organisms. We consider a dioecious species (i.e. one 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. The survivors from the different patches 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 among 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 per patch. 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. Because each of the five factors has two possible values, there are 32 possible overall environmental states. The environmental state of each patch is determined independently and chosen at random 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

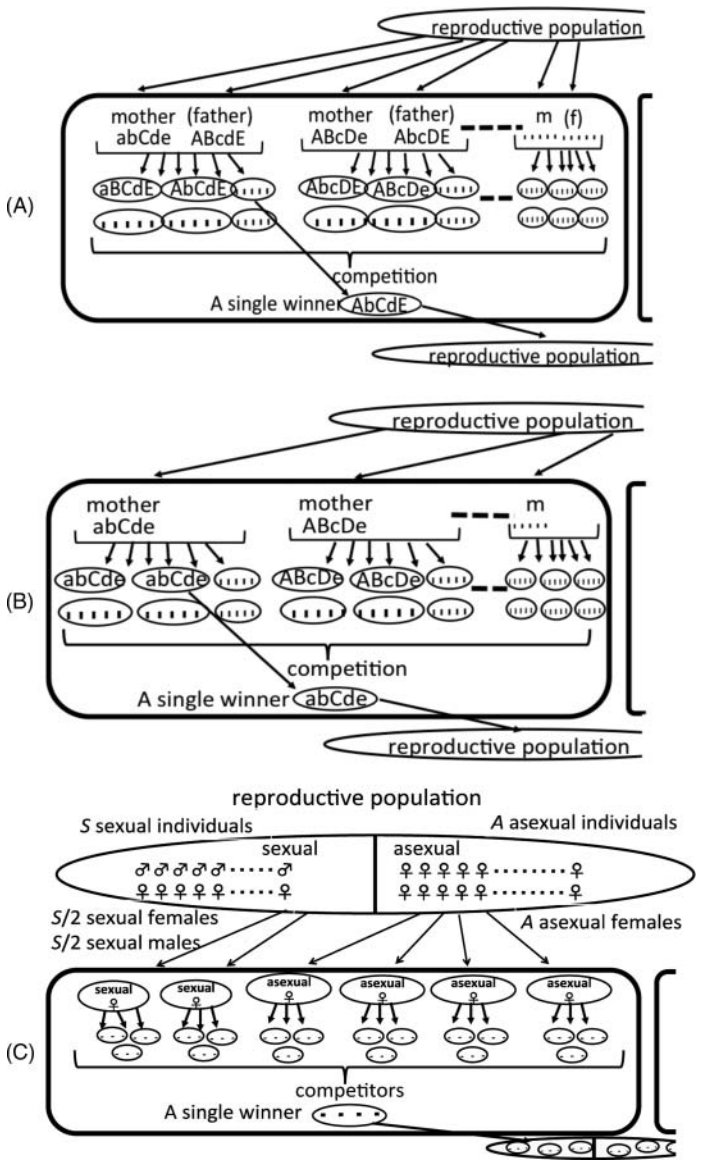

Fig. 1. Population models: (A) a population consisting of sexual organisms only; (B) a population consisting of asexual organisms only, where siblings have the same genotype; (C) a population consisting of both sexual and asexual organisms.

is AbCDe, then the score is 5, 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 3 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 0 to 5. 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 at random 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 might 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 Fig. 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-hand panel of Fig. 3A.

However, sexual reproduction lost its advantage if some environmental factors were correlated or if multiple genes controlled the same trait. The broken line in Fig. 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:

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

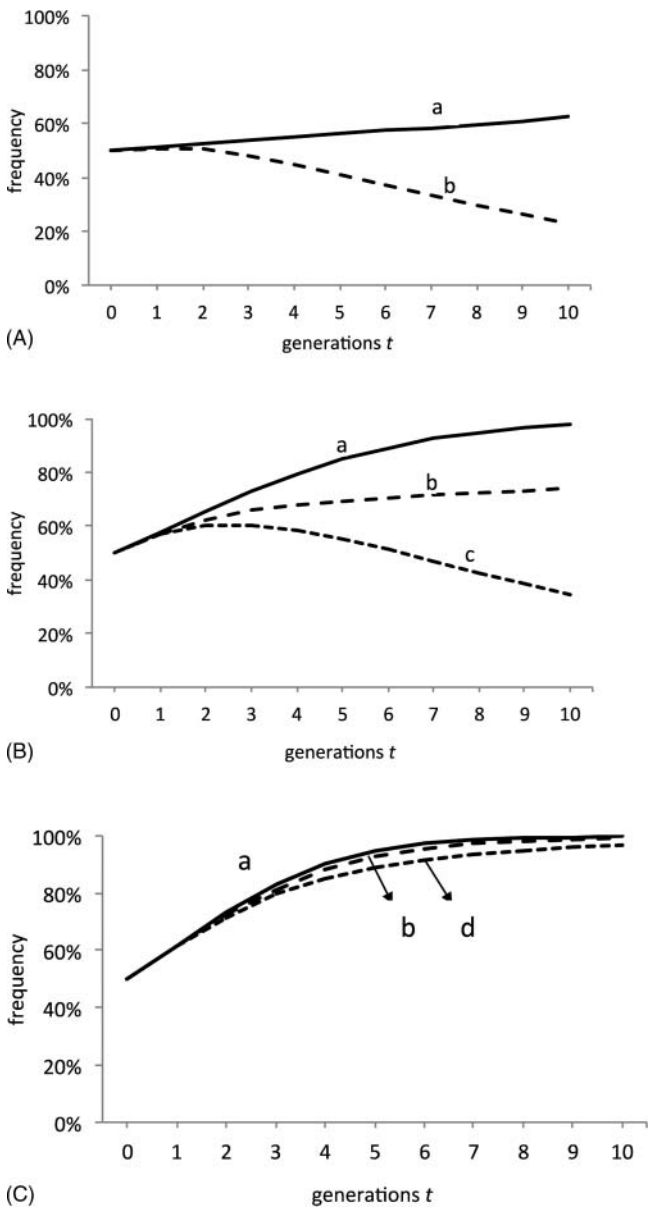

Fig. 2. The frequency of sexual organisms: (A) five environmental factors, original version; (B) five environmental factors, flexible scoring; (C) ten environmental factors, flexible scoring. Parameters are: $R = 6$ and $N = 8$. Horizontal axis is for time (number of generations). Labels for lines are: (a) when environmental factors are independent of each other; (b) when one pair of environmental factors (among two factors) correlate strongly, but all other factors are independent; (c) when two pairs of environmental factors (among four factors) correlate strongly, but all other factors are independent; and (d) when three pairs of environmental factors (among six factors) correlate strongly, but other factors are independent.

(A)

without correlation

R \ N	1	2	3	4	5	6	7	8	9	10
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

R \ N	1	2	3	4	5	6	7	8	9	10
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

R \ N	1	2	3	4	5	6	7	8	9	10
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

R \ N	1	2	3	4	5	6	7	8	9	10
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

R \ N	1	2	3	4	5	6	7	8	9	10
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

R \ N	1	2	3	4	5	6	7	8	9	10
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

Fig. 3. Frequency of sexual organisms for different combinations of *R* and *N*. The section surrounded by the bold line is where sexual organisms are present at a frequency of >50% in the tenth generation. The panels on the left-hand side do not include environmental correlations, while those on the right do. The numbers in each grid are the frequencies of sexual organisms at the tenth generation. (A) The original version of the model. (B) The revised version of the model with flexible scoring and five environments. (C) The revised version of the model with flexible scoring and ten environments.

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 hatched bars are described in the following section, 'Revised sib-competition model . . .').

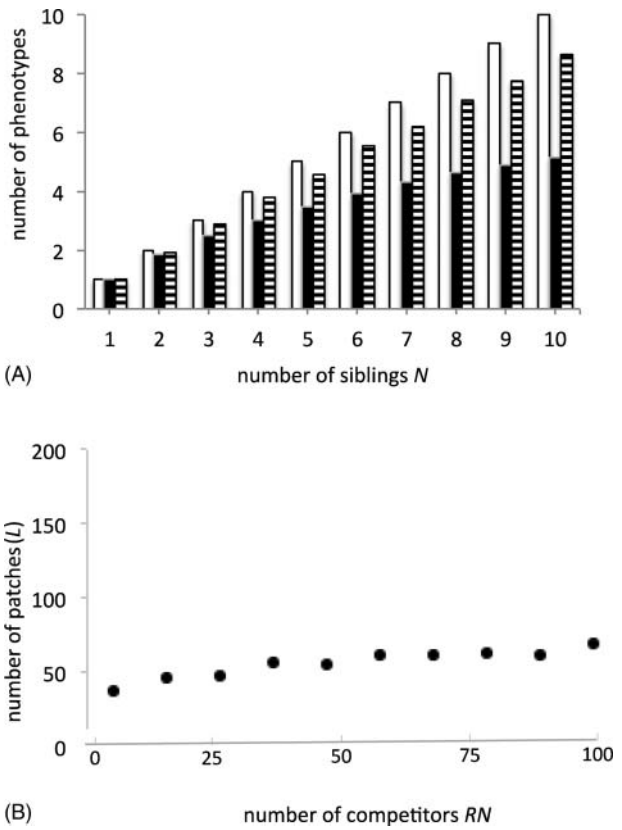

Fig. 4. Two factors that strongly jeopardize the relative advantage of sexual reproduction in the original model. (A) The number of phenotypes and sexual siblings in the simulation. Each open bar (a) represents the maximum number of phenotypes, which is the same as the number of siblings. Each solid bar (b) represents the number of phenotypes of sexual siblings in the original simulation. The hatched 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 higher in the revised version. The greater the number of siblings, the lower the ratio in both the original and revised versions. (B) Solid 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.

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 at random 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 the 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. We therefore revised the model by adjusting the following two assumptions to increase the advantage of sexual organisms over asexual ones:

The score for matching the local environment was allowed to vary between factors

In the original version of the model, the score of a phenotype matching each environmental factor was 1. 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 that different phenotypes would have the same high score.

The number of environmental factors was increased

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

The evolutionary advantage of sex enhanced

The revised version of the sib-competition model, including the two changes described above, demonstrated an increased advantage for sexual reproduction. 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 five to ten. The advantage of reproducing sexually increased significantly. When both adjustments were made to the model, sexual organisms had 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-hand panel of Fig. 3A), but lost this advantage for all combinations of R (number of mothers) and N (number of siblings) if environmental factors were correlated (right-hand panel of Fig. 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-hand panel of Fig. 3C), even in correlated environments (right-hand panel of Fig. 3C).

The hatched bars in Fig. 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 sexual siblings increased from 58% of the total 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 as 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. Note 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:

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

where $N/2$ 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 SEX IS NOT AS ADVANTAGEOUS AS EXPECTED

In the following four subsections, we consider four reasons why the advantage of sexual offspring deviated from the prediction of the simple model, i.e. $N/2$.

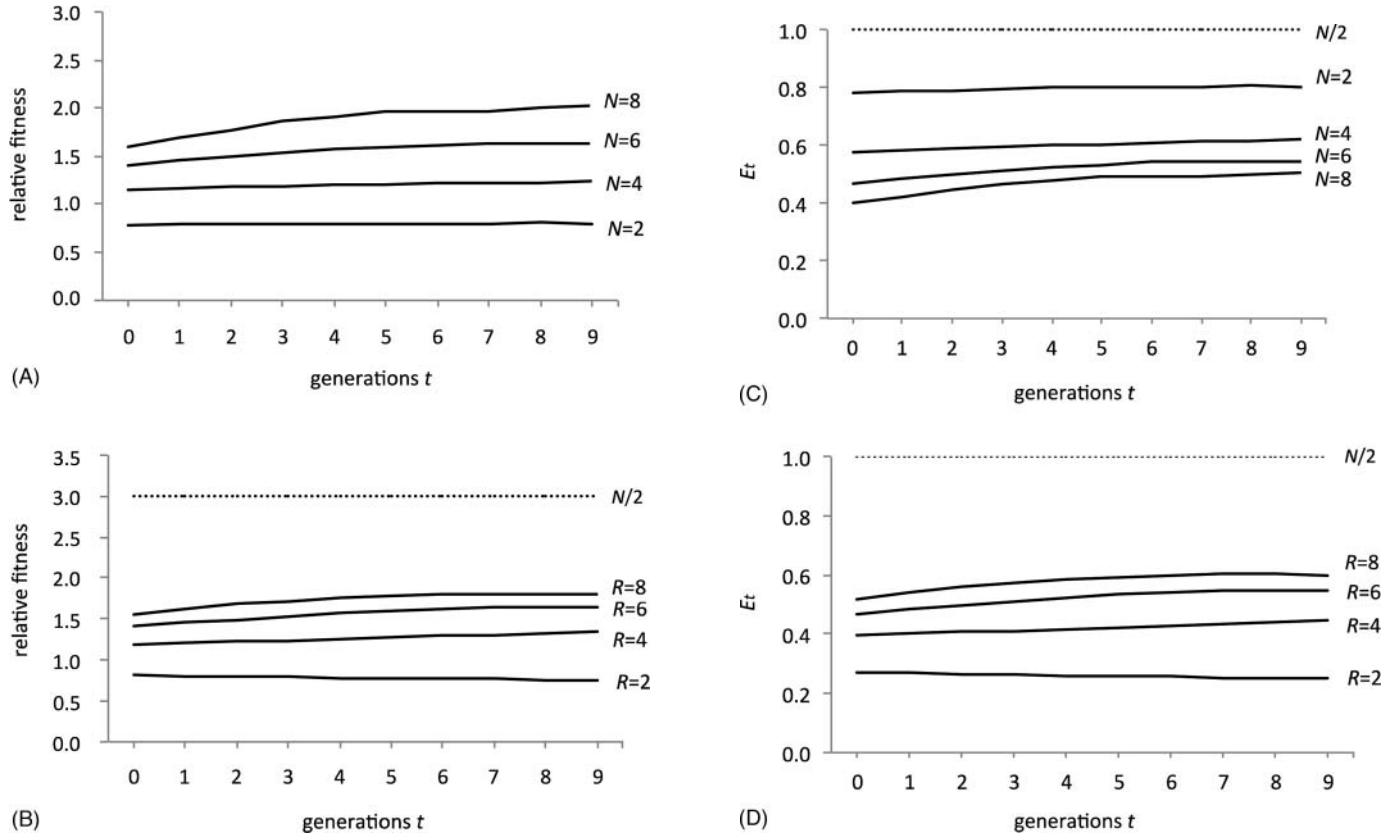

Fig. 5. Realized fitness of sexual organisms compared with asexual ones, and E_t, the ratio of the realized fitness to $N/2$. Time (generations) is shown on the horizontal axis. (A) Different curves for different values of N, indicated by numerals. $R = 6$ for all curves. (B) Different curves for different 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 are the same as in (B).

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 Fig. 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 Fig. 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

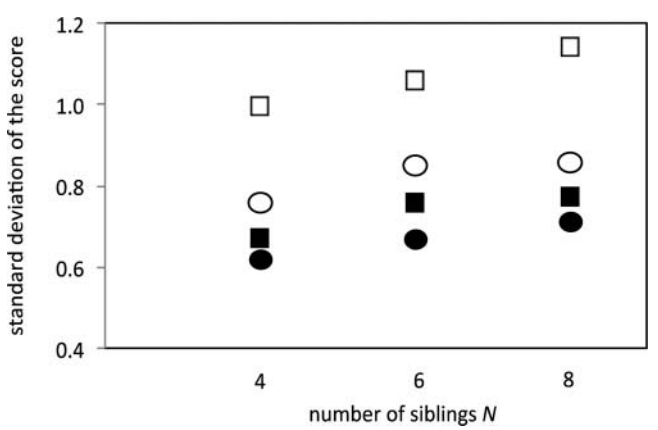

Fig. 6. Standard deviation of the scores of sexual organisms. Flexible scoring was assumed. Open squares and circles show the standard deviation of the scores of sexual non-siblings (□) and sexual siblings (○) where there were ten environmental factors. Solid squares and circles show the same information for sexual non-siblings (■) and sexual siblings (●) where there were five environmental factors. The horizontal axis is the number of offspring per mother (N).

receives either a sexual or an asexual individual only. Since there is no competition within patches, sexual organisms have no advantage. In fact, asexual organisms contribute double the number of egg-laying individuals from the reproductive pool, providing them with a considerable 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 that 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 equation (3) is the product of two factors. The first is the probability of each possible number of sexual mothers (R), which follows a binomial distribution, and the second is the proportion of the number of sexual phenotypes with each possible R. W is the relative fitness of sexual organisms within each patch.

When R is very large, any k that follows a binomial distribution would concentrate near $k \sim x_t/(x_t + 2(1 - x_t))$. Equation (3) then becomes $x_{(t+1)} = x_t W/(x_t W + 2(1 - x_t))$, which implies that the advantage of sex is $W/2$. However, especially for small R, equation (3) shows that the advantage of the sexual type is smaller than $W/2$, as shown in Table 1.

Hence we can summarize that the advantage possessed by sexual organisms may be reduced by three conditions: (1) a reduced number of phenotypes among siblings; (2) similarity of siblings with different phenotypes; and (3) small 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 solid line at the bottom (d) is the original model simulation. In contrast, the line at the top (a) is generated by the following simple equation,

$$x_{t+1} = \frac{Nx_t}{Nx_t + 2(1 - x_t)}, \quad (4)$$

which indicates that the relative fitness of sexual organisms equals $N/2$. This overestimates the proportion of sexual organisms but, no matter, the outcome was the same in both cases: sexual organisms won.

The second line from the top in Fig. 7A (b) 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 seven (i.e. less than $N = 8$). These curves

Table 1. Comparisons of the solution to equation (3) with $W/(W + 2)$, where $W = 8$, $x_t = 0.5$, and $R = 1$–20

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 to equation (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%

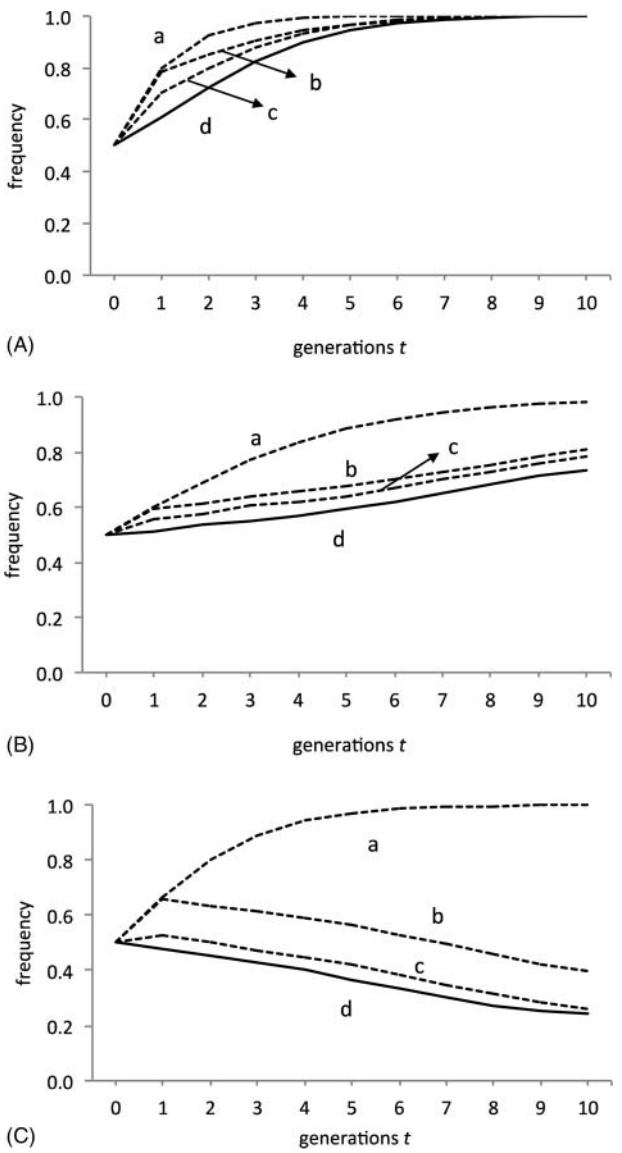

Fig. 7. The proportion of sexual organisms. Time (number of generations) is represented on the horizontal axis. Parameters are: (A) $R = 6$ and $N = 8$; (B) $R = 8$ and $N = 3$; (C) $R = 3$ and $N = 4$. In each panel, the line at the top (a) shows the predicted plot where $N/2$. The next line from the top (b) shows the effect of factor (1) a reduced number of phenotypes among siblings. 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) small local populations. The number of phenotypes from the simulation is substituted for equation (3). The solid line at the bottom (d) shows the result of the model simulation.

demonstrate the effect of (1) a reduced number of phenotypes among siblings and are more similar to the results observed.

The third line from the top (c) results from the formula shown in equation (3), in which the observed number of phenotypes replaced *N*. 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) a reduced number of phenotypes among siblings and (3) small local populations. This plot (c) was quite similar to the observed results (the lowest line, d) but did overestimate 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 panels, the bottom line (d) represents the observed results and the other lines are predictions based on the adjustment of some of the parameters. These also overestimated the proportion of sexual organisms, but as more parameters were included the predictions became more accurate.

In Fig. 7B, the result of competition between sexual and asexual organisms was predicted correctly, although the speed of change was not. In Fig. 7C, the top line (a) 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 (c) proved to be the most accurate, taking both (1) a reduced number of phenotypes among siblings and (3) small local populations into account.

Environmental correlations reduce the advantage of sex

When a pair of environmental 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 the environment has only 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 the strong correlation of environmental factors, should decline as the total number of loci increases. In addition, in the environment with n aspects including a tightly correlated pair, sexual reproduction would be favoured 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, while 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 possessed by sexual organisms by looking at the number of offspring produced by a mother. However, this procedure would overestimate the advantage of sexual reproduction because some sexual siblings share a single phenotype. In addition, both sexual and asexual organisms may 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 sharing the 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 grteat as predicted by the simplest model based on the assumption that all sexual offspring differ in phenotype. We identified three factors that are responsible for this:

- Some siblings had the same phenotype.
- The variance in scores among sexual siblings with differing phenotypes was smaller than among non-siblings
- The low number of egg-laying individuals within each patch reduced the effectiveness of natural selection.

We also found that correlations between environmental variables reduce 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 examined in 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 competition should also be examined in future work.

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

ACKNOWLEDGEMENTS

This work was supported by a Grant-in-Aid for General Scientific Research (B) 15H004423 of JSPS to Y.I. We would like to thank Professor Naruo Niko of the Open University of Japan for his encouragement and supervision of M.D. during the initial phase of this research. We also thank the following people for their helpful comments: K. Itoh, S. Iwami, M. Morishita, and Y. Nakasuji.

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