

Speciation by sexual selection in hybridizing populations without viability selection

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ABSTRACT

We propose a new speciation mechanism for hybridizing populations based on frequency-dependent sexual selection theory. In contrast to previous reinforcement and symmetric speciation models, this model does not require viability selection for male sexual traits, selection against unfit hybrids or disruptive selection for ecological traits. The model assumes that females exhibit mating preferences based on male secondary sexual characters. Both female mating preferences and male secondary sexual traits are independent quantitative genetic traits. Females choose using one of five tactics. All individuals, including the hybrids, have the same ability to survive and reproduce. Two populations that differ only in their average values of female preference and male sexual traits are assumed to come into contact and hybridize. Most cases of the model frequently result in complete prezygotic isolation. The likelihood of speciation decreases with the degree of phenotypic overlap between the two merging populations. However, the probability of speciation is not zero even when the two merging populations are identical.

Keywords: reinforcement, sexual selection, speciation.

INTRODUCTION

The most widely accepted theory of speciation is allopatric speciation. Dobzhansky (1951) proposed that prezygotic barriers can evolve as a response to selection against hybrids, a development known as the reinforcement process. There are some theoretical difficulties in validating the reinforcement process (Butlin, 1989; Futuyma, 1998). Theories of sympatric speciation face the same problem as the reinforcement process. The main problem is recombination. This destroys the association between alleles for adaptation and alleles for assortative mating (Rice and Hostert, 1993; Futuyma, 1998). Recently, however, empirical studies have suggested that reinforcement might be common (Coyne and Orr, 1989; Gerhardt, 1994; Guldmond and Dixon, 1994; Noor, 1995; Sætre *et al.*, 1997). Several

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models have shown how reinforcement and sympatric speciation occur in certain conditions (Maynard Smith, 1966; Lande, 1982; Liou and Price, 1994; Turner and Burrows, 1995; Kelly and Noor, 1996; Doebeli, 1996; Payne and Krakauer, 1997; Dieckmann and Doebeli, 1999; Kondrashov and Kondrashov, 1999).

Previous reinforcement and sympatric speciation models assumed that some form of hybrid disadvantage and disruptive selection might be necessary for speciation (Pimm, 1979; Lande, 1982; Liou and Price, 1994; Turner and Burrows, 1995; Kelly and Noor, 1996; Payne and Krakauer, 1997). For instance, Liou and Price (1994) showed that premating isolation can occur when hybrids between two secondary contact populations have substantially lower fitness. For sympatric speciation, phenotypes intermediate for such traits as resource use or male sexual characteristics were assumed to have lower fitness (Doebeli, 1996; Dieckmann and Doebeli, 1999; Kondrashov and Kondrashov, 1999).

However, perhaps speciation can occur without any viability selection. To address this problem, we developed a new model. In contrast to previous reinforcement and sympatric speciation models, it does not require viability selection for male sexual traits, selection against unfit hybrids, or disruptive selection for ecological traits. With this model, we examine the possibility of speciation without viability selection using individual-based simulations assuming frequency-dependent sexual selection or sexual competition (Kuno, 1992; Yoshimura, 1992; Yoshimura and Clark, 1994).

Our model is inspired by some real cases. For instance, in Lake Victoria cichlids, hybrids between different species do not have reduced fitness, and male coloration (a male sexual trait) is not determined by viability selection (Seehausen *et al.*, 1997; Seehausen and Van Alphen, 1998). Closely related sympatric species of Lake Malawi cichlids overlap considerably in terms of resource use (Reinthal, 1990; Genner *et al.*, 1999). Thus, it is difficult to imagine strong disruptive selection for ecological traits promoting resource partitioning.

METHODS

Simple model of frequency-dependent sexual selection

Suppose females search for mates until they encounter males whose quality exceeds a critical acceptance or threshold (Gibson and Langen, 1996). Then they tend to mate with males that have more common male sexual traits within an acceptable range of male traits. Starting with this assumption, we calculate the expected fitness of the male and female phenotypes under frequency-dependent sexual selection. Then, we examine whether the intermediate phenotypes are likely to have lower fitness under sexual selection when the frequency distribution of phenotypes is bimodal.

In this model, the approximate fitness can only be estimated, and the response of the phenotypes to selection cannot be predicted, because this model does not include the change in genetic variation and genetic correlation among phenotypes responding to the sexual selection.

To calculate the fitness, we assume the simple conditions described in the following text. We assume 11 phenotypic values of male sexual traits and female choice. A female with the value of female choice (S) chooses a single mate randomly from the males with the values of sexual trait M ($S - R \leq M \leq S + R$). R is called the range of female choice. We assume that the numbers of females and males are the same and that each female mates with one male

that can mate also with other females. Then, the number of successful matings of males with male sexual traits i is:

$$M_{Mi} = \sum_{k=-R}^R \left(N_{Fi+k} \frac{N_{Mi}}{\sum_{j=i+k-R}^{i+k+R} N_{Mj}} \right)$$

where N_{Fi} is the number of females with the value of female choice i and N_{Mi} is the number of males with male sexual trait i . We assume that the genetic correlation is also affected by the frequency distribution of the traits. Here, we simply assumed that females with values of female choice (S) can have unexpressed male sexual traits M ranging from $S - C$ to $S + C$. For instance, if females with a mate choice value of 5 potentially have unexpressed male sexual traits ranging from three to seven (range of genetic correlation $C = 2$) and the frequency of male trait three is greater in the population than trait five, then the females are more likely to have unexpressed male sexual trait three than trait five. If the frequency distribution of male sexual traits that one female has is simply related to the frequency distribution of male sexual traits in the population, then the number of matings of females with unexpressed male sexual trait i is:

$$M_{FMi} = \sum_{k=-C}^C \left(N_{Fi+k} \frac{N_{Mi}}{\sum_{j=i+k-C}^{i+k+C} N_{Mj}} \right)$$

where N_{Mi} is the number of males with sexual trait i and C is the range of genetic correlation and is set at 2. Owing to this simplified calculation of inheritance, the number of males with male sexual trait i in the next generation ($N_{Mi}(t + 1)$) is $0.5 (M_{FMi} + M_{Mi})$. Then, the fitness of male sexual trait i is $N_{Mi}(t + 1)/N(t)$.

Individual-based model

The above calculation is based on simple assumptions. It can only examine the fitness of the phenotypes and cannot predict their response to sexual selection. Thus, this simple model does not predict the changes that can occur in a population throughout many generations. Therefore, we conducted individual-based simulations to determine whether frequency-dependent sexual selection can lead to speciation.

We assume that both a male trait (M) and a female preference trait (S) are polygenic quantitative characters. Each character is controlled by L loci. All L loci have two alleles (1 and 0) and are independent of each other. Therefore, in both traits (M and S), the phenotype value ranges from zero (all loci are homozygous at 0-alleles) to $2L$ (homozygous at 1-alleles). Thus, phenotype variance is due to additive genetic variance without environmental variation.

We assumed one of five possible tactics of female choice:

- *Threshold-based rule I.* Females cannot reproduce without an appropriate mate. Nm males are randomly chosen from the entire male population (initial $N = 800$). Among the Nm males, a female chooses a single mate randomly from the males with the value of

sexual trait M , where $M - S$ is in a given range R . R is called the range of female choice. If no appropriate male is found, the female fails to reproduce.

- *Threshold-based rule II.* Same procedure as (I) except that, if appropriate males are not found, a female chooses the value of sexual traits M , where $M - S$ is the smallest.
- *Threshold-based rule III.* Same procedure as (I) except that a female chooses a single male ($|M - S| \leq R$) among all males (i.e. $Nm =$ all males).
- *Best-of- n model.* A female chooses the best males among Nm males. Nm males are randomly chosen from the entire male population ($N = 800$). Among the Nm males, a female chooses a single mate with sexual trait M , where $M - S$ is smallest.
- *Preference with a normal function.* Females choose mates according to a preference function $P(z|y)$, which is distributed normally with mean y and standard deviation v . The mate choice procedure is the same as described in Liou and Price (1994).

Mate choice tactics according to the threshold-based rules or best-of- n rule might be a reasonable assumption for real animals (Gibson and Langen, 1996; Widemo and Sætre, 1999).

We maintained a total of 800 individuals in each generation except when we examined the effect of the number of individuals. We kept the sex ratio at 0.5. All females select a mate by a given choice mode described above. Then, one female, chosen randomly from all the mated females, produces two offspring. We repeat this female selection procedure 400 times to get 800 offspring. All offspring inherit one randomly chosen allele from each parent for all loci. At this point in the simulation, both the same male and female can be chosen for a successful mating repeatedly. Successful females were randomly chosen and, therefore, the distribution of the number of offspring of the female followed a Poisson distribution. All parents die immediately after all offspring are produced. No mutation was allowed. Each simulation started from two merging populations I and II (population sizes are 400 individuals each, sex ratio is 1/2).

We assigned L loci of all individuals randomly as follows. In population I, the frequency of allele-1 is 0.5 for eight independent loci. Thus, the probability that the phenotypic value of an individual is z for L loci can be calculated as ${}_L C_z p^z q^{L-z}$, where ${}_L C_z$ is the number of combinations that the number of allele-1 is z , p is the frequency of allele-1 and q is the frequency of allele-0. Thus, the probability that the phenotypic value of an individual is 8 for eight loci can be 0.1963 ($= {}_{16} C_8 0.5^8 0.5^8$). When the overlap value of two populations (OV) is set at 1, population II is set at the same condition as population I (Fig. 1A). When the frequency of allele-1 is 0.5 for eight loci and zero for three loci for population I and the frequency of allele-1 is 1 for three loci and 0.5 for eight loci for population II (the total number of loci = 11), the degree of overlap becomes 0.143 (Fig. 1C). Similarly, when the frequency of allele-1 is 0.5 for eight loci and zero for five loci for population I and the frequency of allele-1 is 1 for five loci and 0.5 for eight loci for population II (the total number of loci = 13), the degree of overlap is 0.013 (Fig. 1D). In addition to the above case (in which the number of polymorphic loci in one population is eight), we also set the number of polymorphic loci to three or five to examine the effects of the number of loci on speciation.

Each simulation ran 30 times for about 200 generations to determine whether the population would diverge into two populations for each initial condition and parameter setting. We considered the speciation to be complete when the initially hybridizing population was split into two populations with gene flow impossible between them.

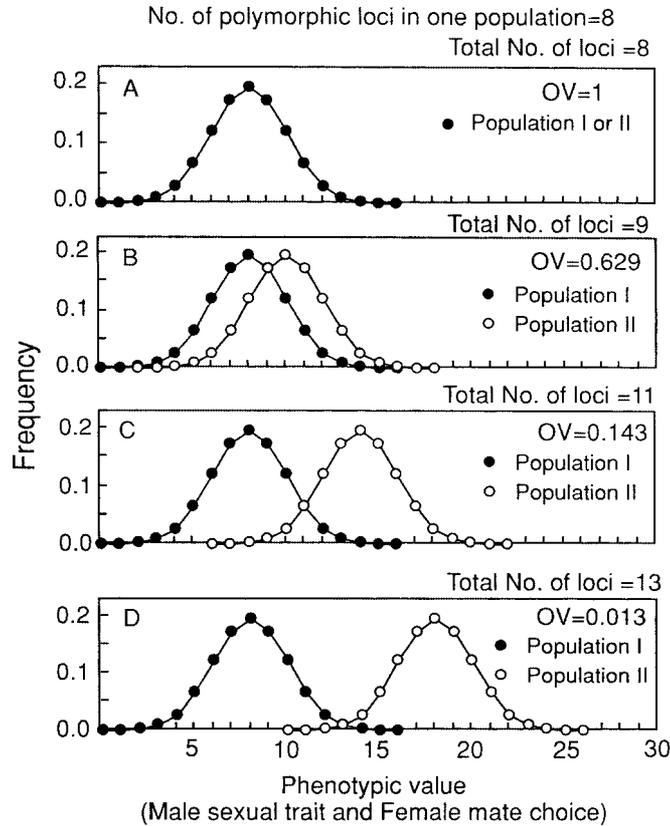


Fig. 1. Four examples of the initial distribution of phenotype values of male sexual traits and female choice values in two populations. OV = the degree of overlap of two populations I and II. R = the range of female choice. Modes of female choice are described in the Methods section.

RESULTS

Expected fitness of simple model

Figure 2 shows a simple calculation of fitness of sexual traits under frequency-dependent sexual selection, assuming three different frequency distributions of phenotypes. This shows that intermediate phenotypes are not likely to be chosen by females when the frequency distribution of phenotype values is bimodal (Fig. 2A). The fitness of intermediate phenotypes is also low for uniform (Fig. 2B) or long-tailed skewed distributions (Fig. 2C). The lower fitness of intermediate phenotypes under uniform distribution comes from an edge effect. The edge phenotype has low fitness because these phenotypes have a restricted phenotype range over which to choose or be chosen. This gives the near-edge phenotypes (phenotype values 2 and 8 in Fig. 2B, right) an advantage. This, in turn, appears as slightly lower fitness in the intermediate phenotypes. Thus, we predict that the fitness of male sexual traits is likely to be affected by the trait frequency distribution under frequency-dependent sexual selection.

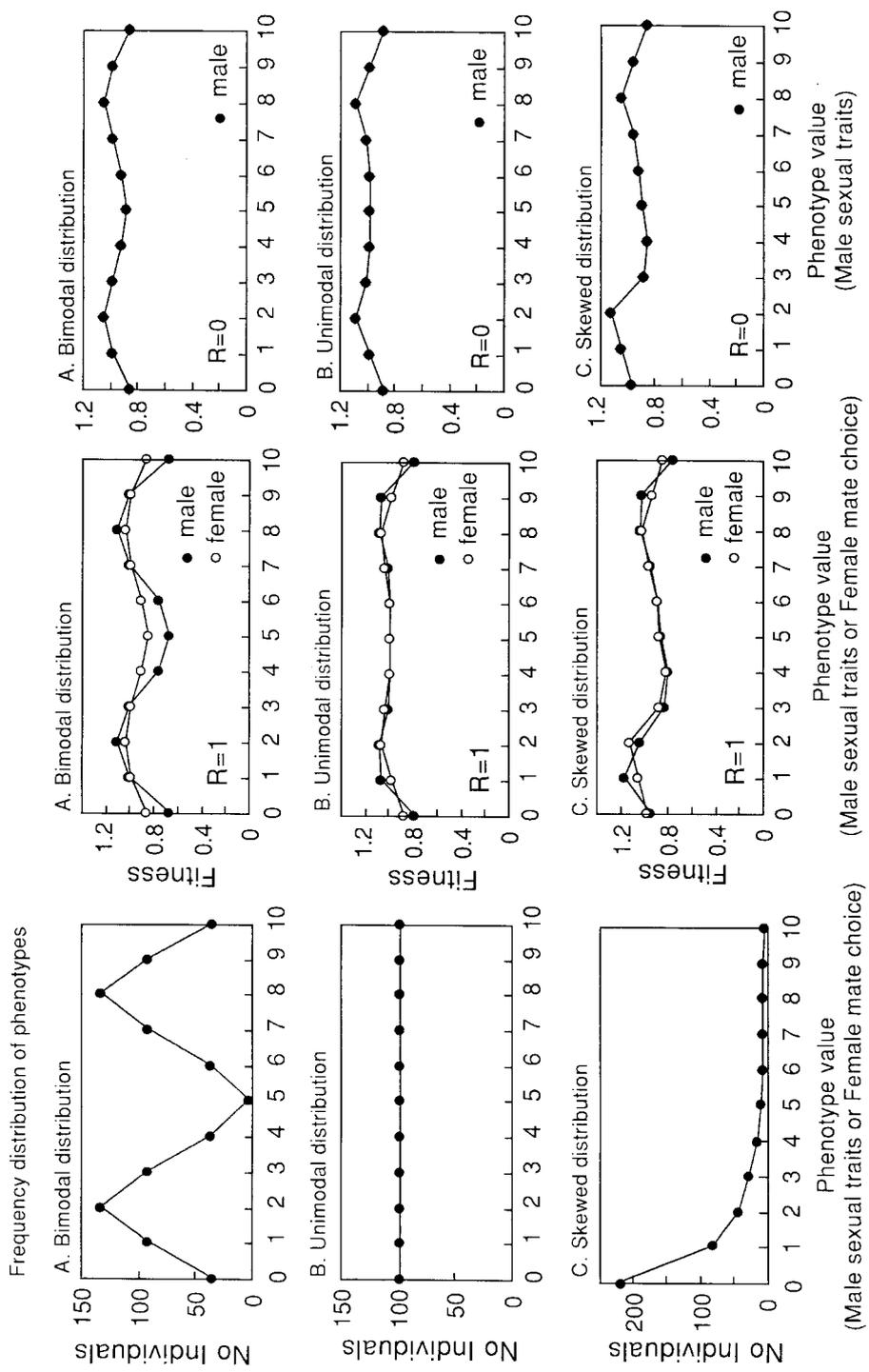


Fig. 2. Expected fitness of male sexual traits by female choice. Eleven phenotypic values of male sexual traits and female choice are assumed. Right and central figures show the fitness of phenotype values calculated from the frequency distributions of phenotypes shown in left figures. R is the range of female choice.

Individual-based model

Figure 3 shows the probability of speciation during 200 generations for four mating tactics. Most cases of the current models show that, when two divergent populations that differ in the average values of male sexual character and female preference come into contact, complete prezygotic isolation frequently occurs (Fig. 3). The likelihood of speciation decreases with increasing overlap (*OV*) of the two merging populations (Fig. 3). The probability of speciation is not zero even when the two merging populations are identical (a single initial population) and when the range of choice (*R*) is small (three of four models). The average time for speciation when it occurs is very short, below 150 generations (Fig. 4). It tends to be slightly shorter when the overlap is small.

Figure 5 shows examples of the average relative fitness of males with the values of male sexual traits (A) and the consequences of genetic correlation between male sexual traits and female choice (B) during simulation runs. Two examples of the average fitness among 10 generations before the completed speciation (Fig. 5A) and the average genetic correlation among five generations (100th to 105th generation) (Fig. 5B) are shown. The number of loci for one population was set at 5 to make the results comparable to Fig. 2. The fitness distributions are very similar to those calculated in Fig. 2. Furthermore, the data shown here roughly support the two assumptions made in the simple model: first, that females with a value of female choice (*S*) have a limited range of unexpressed male sexual traits (e.g. females with female choice value 5 have unexpressed male sexual traits ranging from 2 to 7; Fig. 2B) and, second, that the frequency distribution of unexpressed male sexual

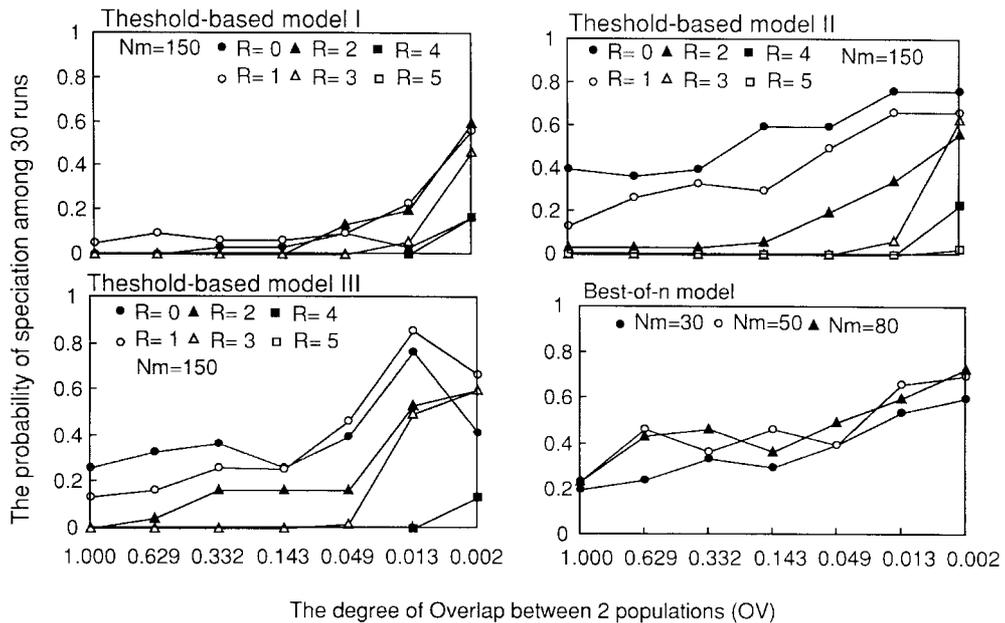


Fig. 3. The probability of speciation in 30 simulation runs during 200 generations for four different mate choice tactics. *OV* = the degree of overlap of two populations I and II. *R* = the range of female choice. *Nm* = the number of males sampled for female choice. Modes of female choice are described in the Methods section.

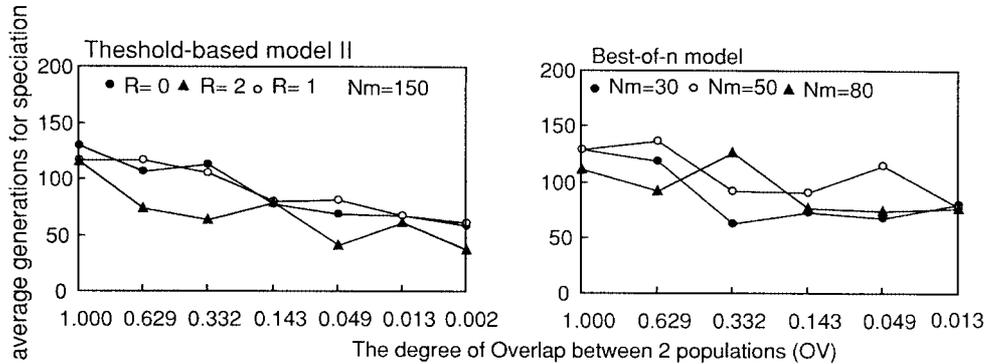


Fig. 4. The average generation time for speciation. OV = the degree of overlap of two populations I and II. R = the range of female choice. Nm = the number of males sampled for female choice.

traits of females is related to the frequency distribution of male sexual traits in the population.

Figure 6 shows the effect of the number of loci, the number of sampled males (Nm) and the total population size on speciation. When $R=0$, the number of loci does not affect speciation in threshold model II, but it decreases speciation in threshold model I (Fig. 6A). For $R=2$ in both models, an increase in the number of loci increased the probability of speciation. The probability of speciation tends to increase with the number of males sampled for female choice (Nm) (Fig. 6B). The total population size does not appear to have any systematic effects on the probability of speciation as long as it is above 400 individuals (Fig. 6C). In all cases, speciation was more probable with threshold model II than model I.

DISCUSSION

The results of the individual-based simulations indicate that speciation can occur when the initial distribution is bimodal. Reinforcement can complete speciation under sexual selection. For the case of complete sympatry (i.e. $OV=1$), speciation can occur, but the conditions required for speciation are restricted (e.g. $R=0$ or $R=1$) and might not be realistic. However, when overlap is small (e.g. $OV=0.002$ or 0.013), even a large R can easily cause speciation. When $R=3$, females potentially accepted 25% of all males of the combined populations as their mates, and 41% of males of one of the initial two populations. This might be realistic. In a best-of- n model, the probabilities of speciation were higher than those of the threshold models, especially when the overlap was small. In this model, females can choose the best males (i.e. male trait values equal to the choice value) when the frequency of the best males is high. For $Nm=30$, most of the females can choose the best or second males (i.e. $R \leq 1$) for $OV=1$. Thus, the likelihood of speciation in best-of- n models is similar to those of threshold models II and III with $R=1$.

The mechanism underlying the speciation could be frequency-dependent sexual selection. If females choose mates according to threshold-based rules, females tend to mate with males having more common male sexual traits within the acceptable range of male traits. The predictions from the simple model (Fig. 2) and the resulting fitness of the individual-based model (Fig. 5) support the prediction that, when the frequency

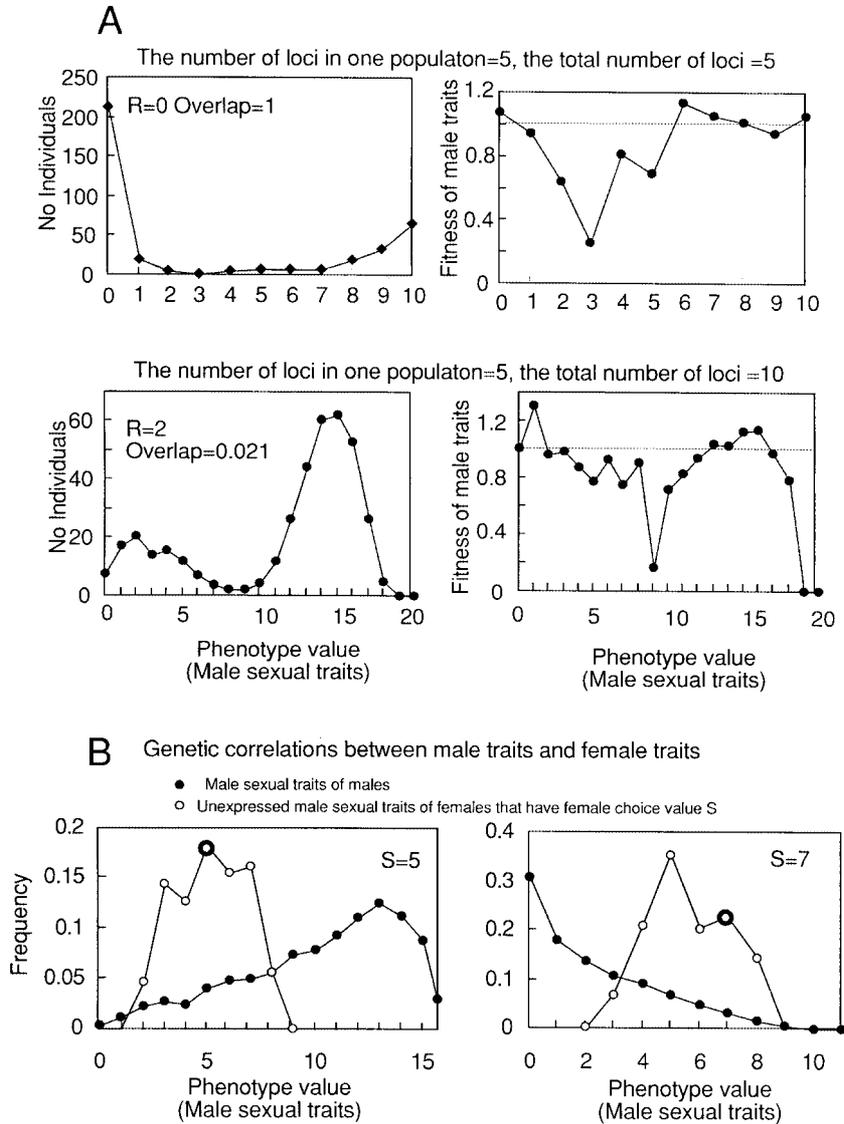


Fig. 5. The relative fitness of males with the values of male sexual traits (A) and the consequences of genetic correlation between male sexual traits and female mate choice (B) during simulation runs. (A) Two examples of the average fitness among 10 generations before the completed speciations. Left panels show the frequency distribution of male sexual traits and right panels their relative fitness. Relative fitness of male phenotypes i was calculated as (the number of successful matings of males with male sexual trait i)/(the number of males with male sexual trait i). (B) Two examples of average genetic correlation among five generations (100th to 105th generation). We arbitrarily chose the females with female choice values five and seven ($S=5$ and $S=7$). The frequency distributions of unexpressed male sexual traits of females that have female choice values five and seven (○), and the skewed frequency distribution of male sexual traits of males (●).

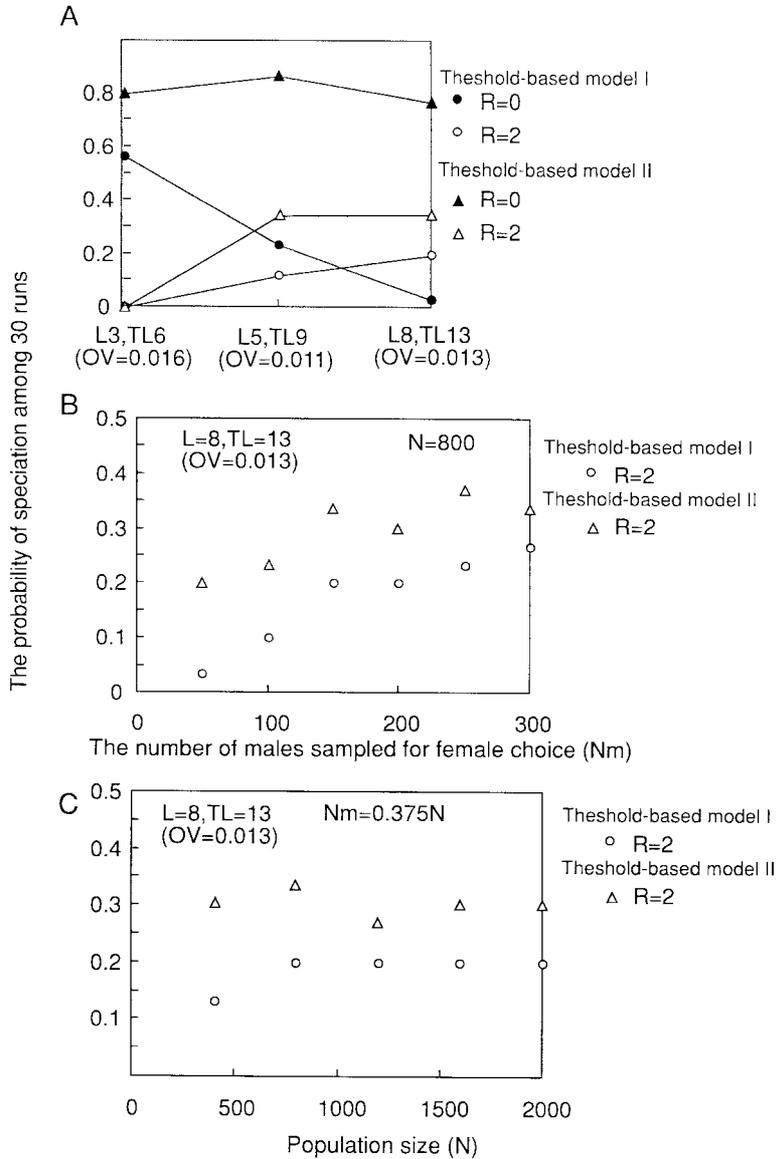


Fig. 6. The effects of the number of loci (A), the number of males sampled (B) and population size (C) on the probability of speciation. L is the number of polymorphic loci in one population and TL is the total number of loci. The initial conditions of the two populations are as follows: (1) $L = 3$, $TL = 6$ ($OV = 0.016$). The total number of loci used for male sexual traits and female mate choice is six. The number of polymorphic loci ($p = 0.5$) for one population is three, where p is the gene frequency of allele-1. In addition to the three polymorphic loci, three monomorphic loci ($p = 0$ for population I and $p = 1$ for population II) were assumed. (2) $L = 5$, $TL = 9$ ($OV = 0.011$). The total number of loci used for male sexual traits and female mate choice is nine. The number of polymorphic loci ($p = 0.5$) for one population is five. In addition to the five polymorphic loci, four monomorphic loci ($p = 0$ for population I and $p = 1$ for population II) were assumed. (3) $L = 8$, $TL = 13$ ($OV = 0.013$). The conditions are the same as in Fig. 1, bottom. R = the range of female choice values.

distribution of phenotypes is bimodal, the intermediate phenotypes of female mate choice characters and male characters have lower fitness. When the initial populations are unimodal or monomodal, random factors may sometimes lead the distribution of phenotypes to a long-tailed skewed distribution as in Fig. 2C and Fig. 5A. Then, intermediate phenotypes are unlikely to be chosen by females and speciation can occur.

When $R = 0$, the number of loci does not affect speciation in threshold model II, but it decreases speciation in threshold model I (Fig. 4A). For $R = 2$ in both threshold models I and II, an increase in the number of loci increased the probability of speciation. In threshold model I, when R is small and the number of phenotypes is large, females often cannot find mates and do not reproduce. Thus, during the course of speciation, a smaller population may become extinct because of the difficulty of mating. The probability of speciation tends to increase with decreasing R when the number of loci is constant, because decreasing R increases the genetic correlation between male sexual traits and female preference. An increase in the number of loci decreases the relative range of mate acceptance when R is constant. Thus, when $R = 2$ in both models I and II, the probability of speciation increases with an increasing number of loci.

The probability of speciation tends to increase with the number of males sampled for female choice (Nm). Perhaps a small number of samplings makes it more difficult to find appropriate mates. The total population size does not appear to have any systematic effects on the probability of speciation as long as it is above 400 individuals (Fig. 6C). This shows that the speciation does not merely result from genetic drift or demographic stochasticity.

Liou and Price (1994) used models similar to ours, but obtained results different from ours. They found that speciation requires a reduced fitness of hybrids between two populations. They assumed a normal distribution for mate preference functions. When we incorporated normal preference functions in our model (the fifth mate preference rule in the Methods), we did not observe speciation when $OV = 0.013$ and the standard deviation of normal function of preference, v , was 0.5σ (σ = standard deviation of male phenotype value in one population). Thus, without hybrid disadvantages, mating tactics such as the threshold rules or best-of- n rule are important to complete speciation. Kondrashov and Shpak (1998) also considered speciation by assortative mating using a hypergeometric model, but their model did not include sexual selection. Their model showed that speciation can occur but very slowly, requiring thousands of generations.

Our model differs strikingly from traditional reinforcement models, in which hybrid inferiority is a key assumption that leads to reinforcement (Butlin, 1989). However, our results show that speciation does not require hybrid inferiority in survivorship and reproduction. For a set of the populations in which females have evolved mating preferences, when two partially divergent populations come into contact, or stochastic or environmental factors accidentally lead one population to a bimodal frequency distribution, mating preferences alone may be enough to promote reproductive isolation.

Previous models for sympatric and reinforcement models assumed the divergence of resource use before reproductive isolation. Our model suggests that neither the divergence of resource use nor a niche shift is a necessary condition for creating prezygotic reproductive isolations. However, after attaining a complete reproductive isolation, the two reproductively isolated populations may not be able to co-exist unless they diverge rapidly in resource or habitat use.

The key initial conditions in our models are large variations in both female preference and male sexual traits. Certainly, a bimodality of phenotypes causes large variations in both male and female traits, thus leading to large fitness variations in phenotypic values. We suspect such situations are met with short-term allopatry or even parapatry. The significance of our models is a high likelihood of reinforcement. Our results suggest that the reinforcement of speciation can be much more common in communities with little or no intraspecific competition. For example, in African lakes, small changes in lake depth may lead to a partial geographic isolation or a short-term allopatry. Such changes may initiate speciation in fishes there. These speciation mechanisms may play a role in creating communities of high species diversity such as cichlid fish communities (Seehausen *et al.*, 1997; Galis and Metz, 1998). Sexual selection alone can be a force for speciation, creating and/or maintaining an extreme diversity of species in a community. Having sexual selection as a cause of speciation may be responsible for the fact that many species can hybridize and produce viable offspring under laboratory conditions.

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