A DETERMINISTIC GENETIC MODEL FOR SYMPATRIC SPECIATION BY SEXUAL SELECTION

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Abstract.—A deterministic haploid genetic model confirms and explores in more detail the results of our previous individual-based simulation model for sympatric speciation by sexual selection. With the deterministic model, we are able to elucidate parameter dependence by phase plane analysis. We clarify how and why sympatric speciation by sexual selection can happen in a number of ways: (1) Female preferences for or against particular types of males have different effects. Whereas the former affects how readily speciation is invoked, the latter changes the stability of speciation equilibrium. (2) When there is no cost on male ornamentations, speciation is triggered regardless of initial haplotype frequencies if sufficient female preference is provided. (3) There exists a threshold for female initial frequencies for speciation to be invoked, but male initial frequencies have little effect. (4) A small cost on female mate choice does not cancel speciation, but when large, it greatly reduces the possibility of speciation.

Key words.—Cichlids, disruptive sexual selection, interbreeding, mate recognition system, separatrix, sexual selection, speciation.

Sexual selection was first suggested by Darwin (1871) to explain exaggerated male secondary sexual characters and female preference for them. Fisher (1930) argued that the co-adaptation between male secondary sexual characters and female preference occurs through a runaway process, and this argument was confirmed by theoretical models (O'Donald 1967; Lande 1981; Kirkpatrick 1982). Paterson (1985) coined the term, mate recognition system (MRS) for such a co-adapted mating system and reasoned that it assures species' identities by providing a concrete species recognition mechanism and preventing mating with other close species. Because the direction of runaway process, which is thought to be initiated by a random increase of female preference, is also random (Lande 1981), the resulting MRSs will differ among geographically isolated populations. Sexual selection has therefore been considered to be a strong force that causes allopatric speciation (Andersson 1994). A question that arises here is whether two different MRSs are established in one population sympatrically, if some initial variabilities of male secondary sexual characters and female preference are provided.

This idea has been examined by computer simulation models (Wu 1985; Turner and Burrows 1995; Higashi et al. 1999). We and Turner and Burrows attained stable sympatric speciation. Turner and Burrows, starting from a population with an already established MRS, demonstrated the evolution of an alternative MRS while the first MRS remains in the population. Their analysis, however, is limited. They did not examine the dependence of their key parameter: the cost of the male secondary sexual character (Higashi et al. 1999). Simulations of our individual-based model started from evolutionary established (stationary) trait distributions, where the divergence of mating traits of a population was hindered by environmental factors. We showed environmental changes of these factors may result in rapid evolution of two sexually isolated subpopulations. Our analysis, however, was not fully

detailed due to computational complexity; it especially lacked the examination of various initial trait distributions. In this paper, we provide a deterministic analogue to our individual-based model and remedy this shortcoming.

Using this deterministic model with eight independent variables (nine haplotypes that sum to one), we focus on a population with symmetric trait distributions and reduce the number of variables to draw two-dimensional (male secondary sexual character and female preference) phase planes that give us an intuitive understanding of overall model behavior. Next, we study the effects of asymmetry of initial trait distributions and asymmetric parameter sets. Finally, the effects of the cost for female choice are checked.

THE MODEL

The model we employed is a three-locus haploid model. Two of the three loci determine male secondary sexual character: either T_0 or T_1 allele occupies the loci and three haplotypes, T_0T_0, T_0T_1, and T_1T_1, designate different male secondary sexual characters. Female preference is coded at the remaining one locus. Three alleles for the locus, P_0, P_1, and P_2, determine the female preference. Types of males and females are represented by integer i ($i = 0, 1,$ or 2), where male types are defined as the sum of their allele numbers and female types their allele number. The frequencies of respective types are denoted as t_i for male and p_i for female ($i = 0, 1,$ or 2). The combinations of the alleles on the three loci produce nine haplotypes, the frequencies of which are represented by z_i ($i = 0, \ldots, 8$) (Table 1). Our basic model consists of recursive equations of these variables, which will be rewritten into another equivalent model through variable reductions and transformations. We choose this genetic system because this is the simplest formalization that enables variable reduction and phase plane analysis. We previously constructed an equivalent two-locus-two-allele model and ascertained that the same conclusions follow. Our basic model

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[2] Masahiko Higashi passed away on March 27, 2000.

TABLE 1. Haplotype frequencies.

Haplotype frequency	Haplotype
z_0	$T_0T_0P_0$
z_1	$T_0T_0P_1$
z_2	$T_0T_0P_2$
z_3	$T_0T_1P_0$ $(T_1T_0P_0)$
z_4	$T_0T_1P_1$ $(T_1T_0P_1)$
z_5	$T_0T_1P_2$ $(T_1T_0P_2)$
z_6	$T_1T_1P_0$
z_7	$T_1T_1P_1$
z_8	$T_1T_1P_2$

is available on request from the authors as a computer program written in C language.

To model sexual selection, we basically follow the orthodox assumptions of Fisherian sexual selection (Kirkpatrick 1982; Seger 1985; Pomiankowski 1987; Andersson 1994). Generations are nonoverlapping. Viability selection reduces the survival of ornamented males (T_0T_0 and T_1T_1) to $1 - s_0$ and $1 - s_2$, respectively, compared to one in the intermediate T_0T_1 males. Mating is polygynous and male contributions to the next generation are only through their sperm (no parental care). We use the fixed-relative-preference for mating (Kirkpatrick 1982). Its application for our current speciation model is illustrated in Figure 1. P_0 females favor the ornamented T_0T_0 males and disfavor the T_1T_1 males that are ornamented in an alternative fashion. The T_0T_1 males have no ornamentation and the P_0 females neither favor nor disfavor them. P_2 females have the opposite preference and P_1 females have

no preference. Preference parameters are defined as a_i, 1, and c_i ($i = 0$ or 2) for type i females' preference toward their favored, normal, and disfavored males, respectively. For type 1 females, the preference parameters are fixed as one for all males. Actual mating probability for a female to choose a mate is determined by both her preference parameters and male frequencies. For example, a P_0 female chooses a T_0T_0 male as her mate with a probability, $a_0t_0'/(a_0t_0' + t_1' + c_0t_2')$, where t_i' is the frequency of type i males after viability selection. The cost of female mate choice is not incorporated here, but will be considered in a later section.

As for the two loci for the male trait, we assume equiprobability of genotypes T_0T_1 and T_1T_0. This allows us to treat the T_0T_1 and T_1T_0 males in a lump when calculating the frequencies. This is a form of ''hypergeometric model'' approach developed by Shpak and Kondrashov (1999), which is useful for studying diverging traits such as speciation. Recombination rate is incorporated in the model as the parameter r.

ANALYSIS AND RESULTS

Variable Reduction and Transformation

We first focus on a population with symmetric trait distributions and the split of it into two sexually isolated subpopulations. This suffices to illustrate the overall parameter dependence of sympatric speciation by sexual selection, and is useful because it enables variable reduction and the two-dimensional (male secondary sexual character and female preference) phase plane representation that gives us an in-
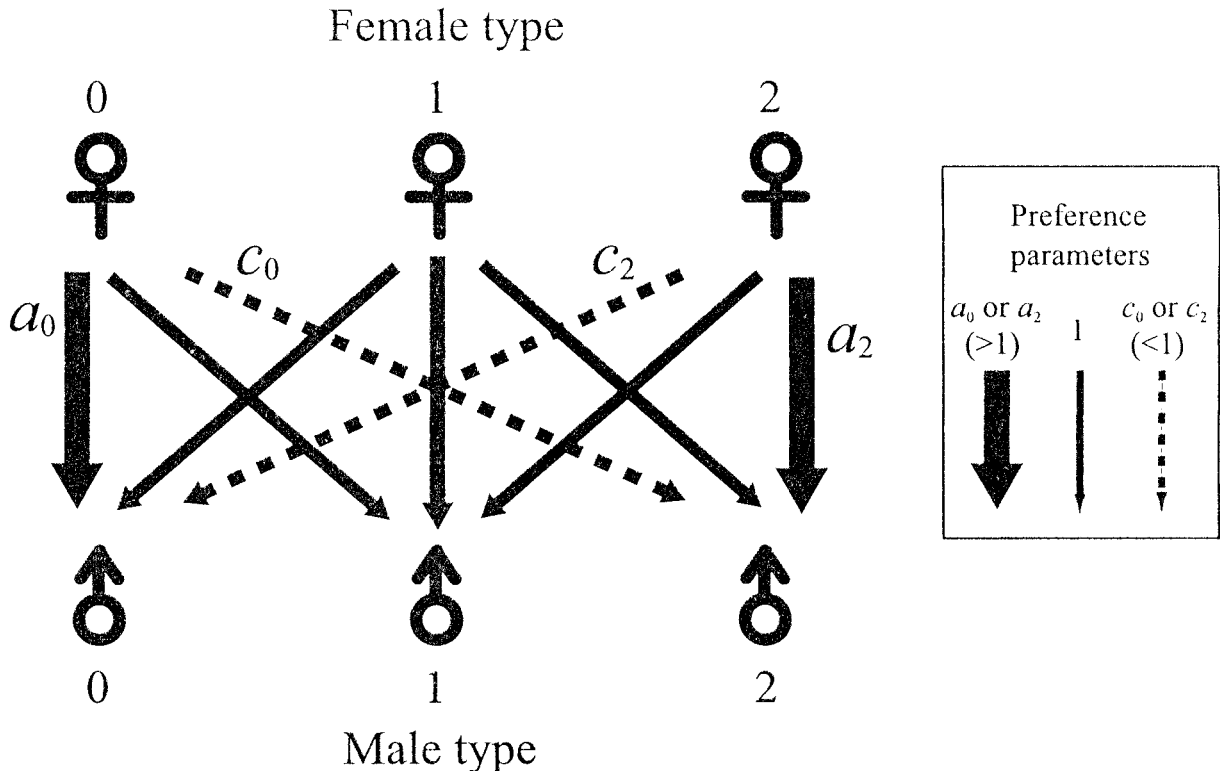

FIG. 1. Preference scheme.

tuitive understanding. We assume that the corresponding parameters are the same for type 0 and type 2 individuals, namely, $a_0 = a_2$, $c_0 = c_2$, and $s_0 = s_2$. With this provided, starting from a set of symmetric initial frequencies (produced by setting $z_i = z_{8-i}$ [$i = 0, \ldots, 3$]) automatically results in a symmetric evolutionary trajectory, that is, the relationship, $z_i = z_{8-i}$ (for $i = 0, \ldots, 3$), holds for an entire evolutionary process. This assures that it is sufficient to focus only on the dynamics of type 0 and 1 for both sexes because the dynamics of type 2 is the same as type 0 for both sexes.

Therefore, we only must focus on five variables, z_i ($i = 0, \ldots, 4$). We can further reduce one more variable using the fact that the sum of all the frequencies is one. The remaining four variables can then be transformed into t_0 (type 0 male frequency), p_0 (type 0 female frequency), and two linkage coefficients, D_1 and D_2 (see Appendix for details). Eventually, after complicated algebra, a model similar in form to Kirkpatrick's (1982) model and others (Seger 1985; Pomiankowski 1987) results (see Appendix for ΔD_1):

$$\Delta t_0 = \frac{1}{2}(W_0 - 1)t_0 + 2r(1 - r)$$

$$\times \left[\frac{(a_0 - c_0)(1 - s_0)t_0}{\{(a_0 + c_0)(1 - s_0) - 2\}t_0 + 1}D_2 \right.$$

$$\left. - \frac{1}{2}(W_1 + 1)t_0 + \frac{1}{4}W_1 \right], \quad (1a)$$

$$\Delta p_0 = \frac{D_1}{1 - 2t_0}(W_0 - 1), \quad (1b)$$

$$\Delta D_2 = \frac{1}{2}(1 - r)(W_0 - 1)D_1$$

$$+ \frac{1}{2}r \left[\frac{2(a_0 - c_0)(1 - s_0)}{\{(a_0 + c_0)(1 - s_0) - 2\}t_0 + 1} \left(\frac{t_0 p_0}{4} + D_2^2 \right) \right.$$

$$\left. - 2D_2 \right], \quad (1c)$$

where

$$W_0 = \frac{1 - s_0}{1 - 2s_0 t_0} \left[\left(\frac{(a_0 + c_0)(1 - 2s_0 t_0)}{\{(a_0 + c_0)(1 - s_0) - 2\}t_0 + 1} - 2 \right) p_0 + 1 \right],$$

$$(2a)$$

and

$$W_1 = \frac{1}{1 - 2s_0 t_0} \left[2\left(\frac{1 - 2s_0 t_0}{\{(a_0 + c_0)(1 - s_0) - 2\}t_0 + 1} - 1 \right) p_0 + 1 \right].$$

$$(2b)$$

Null-Isoclines and Equilibria on Phase Planes

Setting the right sides of equations (1a–c) equal to zero yields multidimensional null-isoclines, which can be projected onto the t_0-p_0 plane (see Appendix for details). Note that $0 \leq t_0, p_0 \leq 0.5$ because $t_0 + t_1 + t_2 = 2t_0 + t_1 = 1$ and $p_0 + p_1 + p_2 = 2p + p_1 = 1$. A set of one-dimensional curves are obtained and two of the intersections are the stable equilibria of the model (Fig. 2a). The two equilibria on the

line $p_0 = 0$ and $p_0 = 0.5$ correspond to two evolutionary outcomes, speciation and failed speciation, respectively. The speciation equilibrium is close or identical to a point $t_0 = p_0 = 0.5$, which means the population is dominated by two sexually isolated groups of individuals of type 0 and 2 (note that the dynamics of type 2 is the same as type 0), whereas the failed speciation equilibrium is a state where female preference has not evolved and no sexual isolation has been established in the population.

Intensive computer simulations from numerous initial values of t_0, p_0, D_1, and D_2 find that the four-dimensional t_0-p_0-D_1-D_2 space is divided into two separate basins of attraction by one separatrix. It is also found that the three-dimensional surface of this separatrix is nearly parallel to the t_0-, D_1-, and D_2-axis. Therefore, we can project the three-dimensional separatrix to obtain an almost one-dimensional line separatrix with a narrow width that is nearly parallel to the t_0-axis on the two dimensional t_0-p_0 space. In this case, it is shown that the separatrix always lies on the intersection of (A8) and (A9) (see Appendix).

The result asserts that, for sympatric speciation to be invoked, the initial frequencies of females with preference are exclusively important, whereas the initial frequencies of males is not important at all. The reason for this is because a driving force for speciation in this model is the runaway process caused by sexual selection. In many studies of sexual selection, one can see that the initial female frequencies crucially determines whether the runaway process is triggered (e.g., see the phase planes and evolutionary trajectories shown in the figures in Kirkpatrick 1982; Seger 1985; Pomiankowski 1987; Heisler and Curtsinger 1990). Similarly, the initial female frequencies must play a critical role to invoke the runaway process for speciation in our model.

Parameter Dependence

The effects of involved parameters are elucidated by looking at the phase plane dynamics with different sets of parameter values (Fig. 3). We focus on two things. One is the shift of speciation equilibrium away from the point $t_0 = p_0 = 0.5$, where subpopulations are completely sexually isolated. The other is the location of the separatrix. When it is located high in the phase plane, the attractive basin of the speciation equilibrium is small, whereas the basin is large when it is located low.

The speciation equilibrium locates at the point $t_0 = p_0 = 0.5$, when a_0 is small and c_0 and s_0 is small (Fig. 3a). The shift of the speciation equilibrium occurs when a_0 is small (Fig. 3b) or c_0 or s_0 is large (Fig. 3d, e, respectively). The larger the shift, the more often interbreeding occurs between the subpopulations (Fig. 4). These shifts, however, can be partly cancelled by setting the recombination rate, r, smaller than 0.5 (Fig. 3g). The equilibria that are already on the point $t_0 = p_0 = 0.5$ (Fig. 3a, c, f) are not moved further by a small r. Large a_0 and small s_0 push down the separatrix and speciation becomes more likely (Fig. 3c, f, respectively). Surprisingly, when $s_0 = 0$, the separatrix merges with the line $p_0 = 0$ and speciation always results, regardless of initial conditions (Fig. 3f); c_0 has little effect on the position of the separatrix (Fig. 3d).
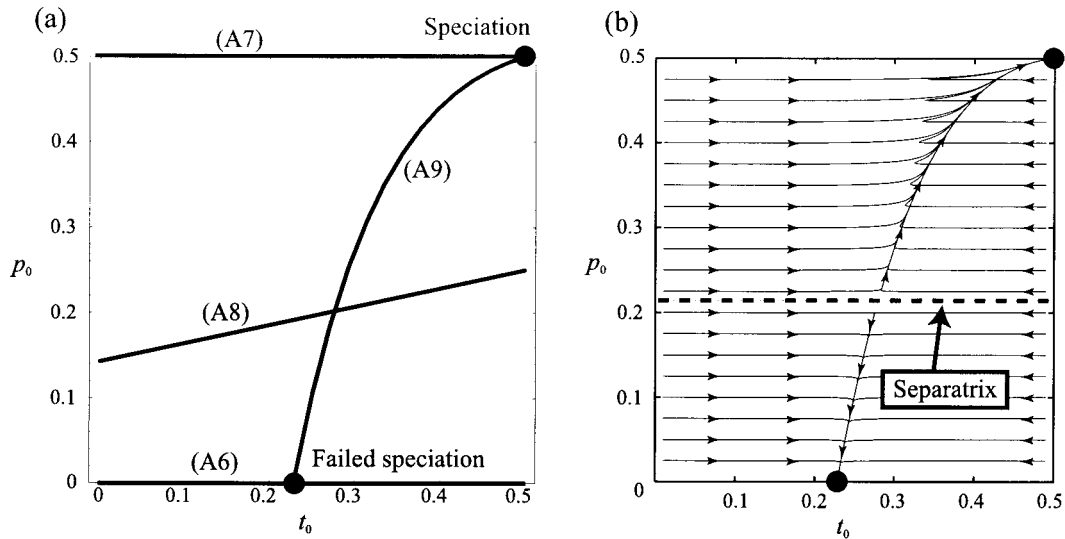
FIG. 2. Null-isoclines, equilibria, and separatrix. Parameter values: $a_0 = 5$, $c_0 = 0$, $s_0 = 0.3$, and $r = 0.5$ for (a) and (b). (A6–9) in (a) are explained in the Appendix.

The shifts of the speciation equilibrium due to parameter changes can be explained as follows. Because large a_0 and small s_0 both increases type 0 males' fitness, the frequency balance between the type 0 and 1 males at the equilibrium shifts toward the type 0 males. However, large c_0 increases interbreeding by decreasing females' discrimination against disfavored males, so that more intermediate (type 1) males are produced through interbreeding and recombination, leading to the shift of the speciation equilibrium to the left. With smaller recombination rate, fewer type 1 males are produced through interbreeding, thus shifting the equilibrium to the right.

In sexual selection theory, stronger female preference and lower male cost of being conspicuous more easily trigger the runaway process (Lande 1981; Kirkpatrick 1982). Because the same mechanism works in our current model, large a_0 and small s_0 enlarge the attractive basin for speciation.

EFFECT OF ASYMMETRY

In this section, we check whether and how the results obtained in the previous section are changed when the symmetry assumption is relaxed. We first focus on the equilibria and the stability of them under more general asymmetric setting. We then show that the critical initial female frequencies, in which speciation is invoked, do not hinge on the subtle balance of the symmetry. Other results concerning the parameter dependence are also shown to give qualitatively the same results as in the symmetric case. All of our analysis here is done numerically, with the basic recursive equation model of nine variables.

Equilibria and Their Stability

In general, there are more equilibria than those identified in the previous section. These equilibria and their stability are explained below and summarized in Table 2 together with those of the symmetric model.

The speciation equilibrium that is stable in the symmetric setting is changed, in the general asymmetric setting, to either a neutrally stable line or an unstable saddle point depending on the values of the parameters c_0 and c_2. When $c_0 = c_2 = 0$, the equilibrium is a neutrally stable line where $z_0 + z_8 = 1$ ($z_i = 0$, for $i = 1, \ldots, 7$). The points on the line are the end points of evolution, in which a population first quickly diverges and speciates into two sexually isolated subpopulations. When c_0 and/or c_2 are not zero, the equilibrium becomes an unstable saddle point and other two stable equilibria emerge. We call the latter two extinction equilibria because, in an entire evolutionary process, an initial population first speciates (toward the saddle point) into two sexually isolated subpopulations, and then one of them goes to extinction very slowly (toward one of the extinction equilibria).

The extinction occurs as follows. When c_0 or c_2 is not 0, sexual isolation between them is incomplete (see Fig. 4). The incompleteness arises from females' incomplete discrimination against the males from the other subpopulation. When there is even a slight difference in the relative abundance of the subpopulations after they become sexually isolated (i.e., the system is near the saddle point), the females from the smaller subpopulation suffer from a greater chance of interbreeding than those from the larger one because mate choice is frequency dependent. Interbreeding decreases females' fitness because hybrid sons from interbreeding tend to have intermediate phenotype (i.e., type 1) and thus have fewer chances of winning mates. Therefore, the smaller subpopulation further decreases and eventually goes to extinction. As Figures 3b and e show, sexual isolation is also incomplete even if c_0 ($= c_2$) $= 0$ when a_0 (a_2) is small or s_0 (s_2) is large. It is confirmed, however, that the incomplete isolation in this case does not destabilize the speciation equilibrium because females' mating with the other types of males can still be avoided with c_0 ($= c_2$) $= 0$. The generation time required for the extinction after speciation is very long. This long period could allow a population to experience further rein-
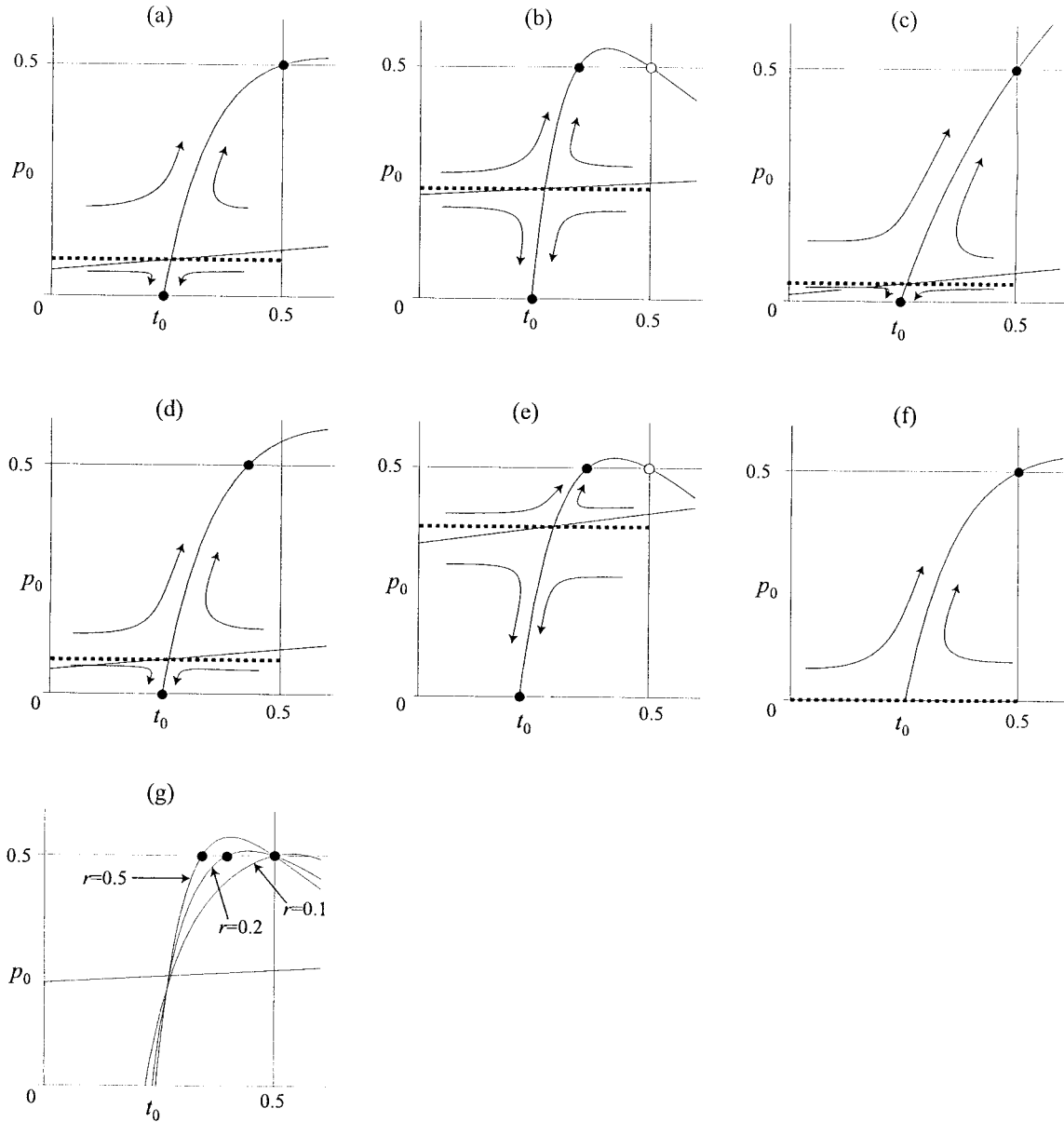
FIG. 3. Parameter dependence on phase planes. Parameter values: (a) $a_0 = 4$, $c_0 = 0$, $s_0 = 0.1$; (b) $a_0 = 2.5$, $c_0 = 0$, $s_0 = 0.1$; (c) $a_0 = 10$, $c_0 = 0$, $s_0 = 0.1$; (d) $a_0 = 4$, $c_0 = 0.1$, $s_0 = 0.1$; (e) $a_0 = 4$, $c_0 = 0$, $s_0 = 0.4$; (f) $a_0 = 4$, $c_0 = 0$, $s_0 = 0$; (g) $a_0 = 2.5$, $c_0 = 0$, $s_0 = 0.1$; $r = 0.5$ for (a–f).

forcing evolution of the values of c_0 and c_2 toward zero, and to attain stable speciation. An important biological implication of this result is discussed in a later section in relation with the speciation and extinction of cichlids in Lake Victoria, east Africa, studied by Seehausen et al. (1997).

Furthermore, other two neutrally stable equilibrium lines are found (Table 2). In the attractive basins of these equilibria, the frequency of either type 0 or type 2 individuals increases quickly in a population and eventually one MRS evolves. Because this is essentially the same phenomenon as trait shift in Higashi et al. (1999), we call these trait shift equilibria. This occurs because asymmetric setting allows unidirectional runaway sexual selection to take place with certain initial conditions.

Critical Dependence on Female Initial Frequencies

We survey over the whole area of the initial frequency space of one sex with the initial frequencies of the other fixed. Whether speciation occurs is determined nearly by female frequencies, whose critical value is the same between symmetric and asymmetric cases. For female initial frequencies at which speciation fails to occur, trait shift appears as the initial female frequencies are strongly asymmetric (Fig. 5a, b). Speciation may also appear in further asymmetric cases. This assures that likelihood of speciation is not reduced by the initial female frequency asymmetry (Fig. 5a, b). If initially there are sufficient females with preference, speciation results regardless of initial male frequencies (Fig. 5c,
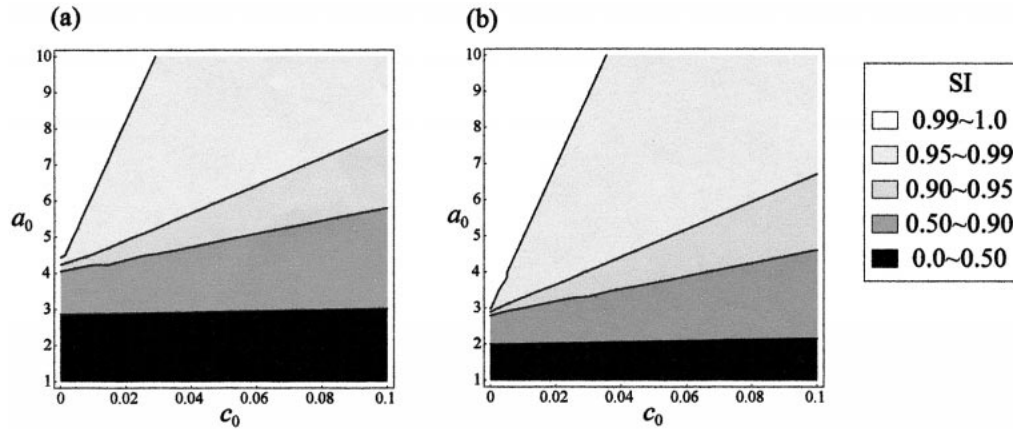
FIG. 4. Parameter dependence of speciation index (SI). SI is defined as $a_0 m_0 / (a_0 t'_0 + t'_1 + c_0 t'_2)$, where m_0 is the frequency of males of haplotype $T_0 T_0 P_0$ after viability selection. SI is the probability with which a type 0 female chooses a $T_0 T_0 P_0$ male as her mate and measures the degree of isolation. (a) $s_0 = 0.3$, (b) $s_0 = 0$. Small a_0 and large c_0 and s_0 mean that the speciation equilibrium is shifted away from the point $t_0 = p_0 = 0.5$.

cf. Fig. 5a, b). Conversely, speciation is not attained with insufficient initial females with preference, unless initial male frequencies are highly skewed (Fig. 5d).

We need to confirm that the results obtained so far do not hinge on the subtle balance of symmetries in parameter values. Parameter asymmetries in a_0 and a_2 and in s_0 and s_2 hardly change the dependence of initial frequencies on speciation, but only slightly shift the boundaries between speciation, trait shift, and failed speciation (Fig. 6a, b, respectively). Parameter asymmetry in c_0 and c_2 has no effect, which can be explained by the fact that, in our symmetric phase plane analysis, the parameter c_0 does not affect the location of the separatrix. Therefore, we conclude that the critical dependence on the initial female frequencies persists as an essential feature of sympatric speciation by sexual selection regardless of the assumption of symmetric initial conditions and symmetric parameter values.

MODEL WITH FEMALE COST ON MATE CHOICE

It has been shown that introducing even a slight cost for mate choice of females prevents the evolution of their preference (Kirkpatrick 1985; Pomiankowski 1987; Bulmer 1989; Iwasa et al. 1991). However, a number of mechanisms have been suggested with which costly female preference can nonetheless evolve (Pomiankowski 1987; Iwasa et al. 1991; Pomiankowski et al. 1991). Because our model does not in-

clude such mechanisms, we need to check the effect of female cost for mate choice.

Female cost for mate choice is incorporated in the same manner as in Pomiankowski (1987). The P_0 and P_2 females with preference incur cost, which reduces their viability to $1 - u_0$ and $1 - u_2$, respectively, compared to one of the P_1 females without preference.

With certain sets of parameters, numerical iterations of the model with small female cost reach speciation. Because our previous analysis by an individual-based model (Higashi et al. 1999) gives the same result, in general, it appears that small female cost does not cancel speciation by sexual selection. Female preference is maintained at the speciation state even in the presence of cost for mate choice, because there is always selection against the females with weaker preference that tend to be engaged in maladaptive interbreeding. In this paper, we further investigate the effect of large female cost and show that it significantly reduces the possibilities for speciation (cf. Fig. 7a and b). Large female cost can cancel out the benefit of having preference or avoidance of the maladaptive interbreeding.

DISCUSSION

Our previous individual-based model has shown that sympatric speciation can occur by sexual selection (Higashi et al. 1999). In this paper, by using a deterministic haploid

TABLE 2. List of equilibria and their stability.

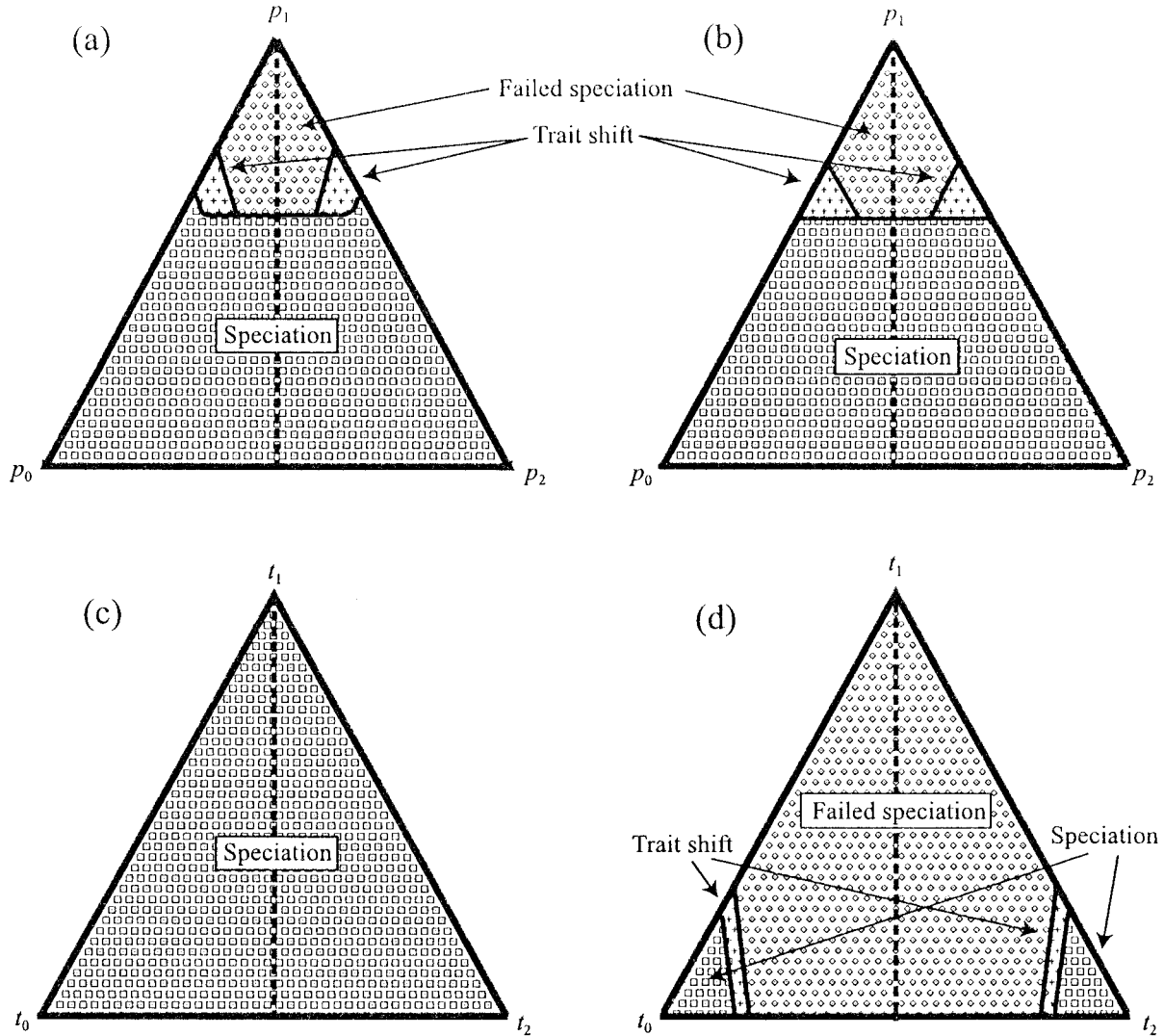| Symmetric model	General (asymmetric) model	
	$c_0 = c_2 = 0$	$c_0 > 0$ and/or $c_2 > 0$
one stable speciation equilibrium point	one neutrally stable speciation equilibrium line	one saddle point equilibrium (speciation)
		two stable extinction equilibrium points
two neutrally stable trait shift equilibrium lines		
one stable failed speciation equilibrium point		

FIG. 5. Effect of asymmetry in initial frequencies. A point in a triangle represents a set of initial frequencies for p_i or t_i. Frequencies p_0 and t_0 are proportional to the distance of the point from the bottom of the triangle, p_1 and t_1 are proportional to the distance from the right side, and p_2 and t_2 are proportional to the distance from the left side. Dotted lines represent symmetric initial frequencies. In (a, b), male initial frequencies are fixed: (a) $t_0 = t_2 = 0.1$, $t_1 = 0.8$; (b) $t_0 = t_2 = 0.4$, $t_1 = 0.2$. In (c, d), female initial frequencies are fixed: (c) $p_0 = p_2 = 0.25$, $p_1 = 0.5$; (d) $p_0 = p_2 = 0.175$, $p_1 = 0.65$. Parameter values: $a_0 = a_2 = 5$, $c_0 = c_2 = 0$, $s_0 = s_2 = 0.3$, and $r = 0.5$, throughout. Nine initial haplotype frequencies are calculated from each initial gene frequencies with $D_1 = D_2 = 0$.

genetic model, we further elucidate how and why sympatric speciation by sexual selection can happen. In our previous study, female preference was introduced in a model as a parameter, α, the efficiency of male discrimination by females, and it was assumed that as α became large female preference for a particular type of male would increase. In our current model, the preference parameter is decomposed into two independent parameters, a_0 (a_2) and c_0 (c_2). By doing this, we can separate the roles of female preference for the same types of males and against the other types in performing sympatric speciation by sexual selection. As our phase plane analysis reveals (Fig. 3a, b, c), the female preference for the same types (a_0 and a_2) determines the attractive basin for speciation, that is, it has a strong effect in initiating speciation. From the viewpoint of sexual selection theory, the runaway process is more easily triggered with higher female

preference for conspicuous males. In contrast, the female discrimination against the other types of males (c_0 and c_2) has no effect on determining the attractive basin for speciation (cf. Fig. 3a and d), but rather the values determine how much interbreeding is involved when a population has speciated (Fig. 4) and whether the speciation equilibrium is stable.

Our previous individual-based model suggested that the lower the male cost for conspicuous ornaments was, the easier speciation occurred. Our present study makes this trend even more clear by showing that when there is no male cost, speciation results from any initial conditions (Fig. 3f). This critical importance of male cost is somewhat surprising, but assures that sympatric speciation by sexual selection occurs very easily in cases when there is no natural enemy in the environment a population invades.
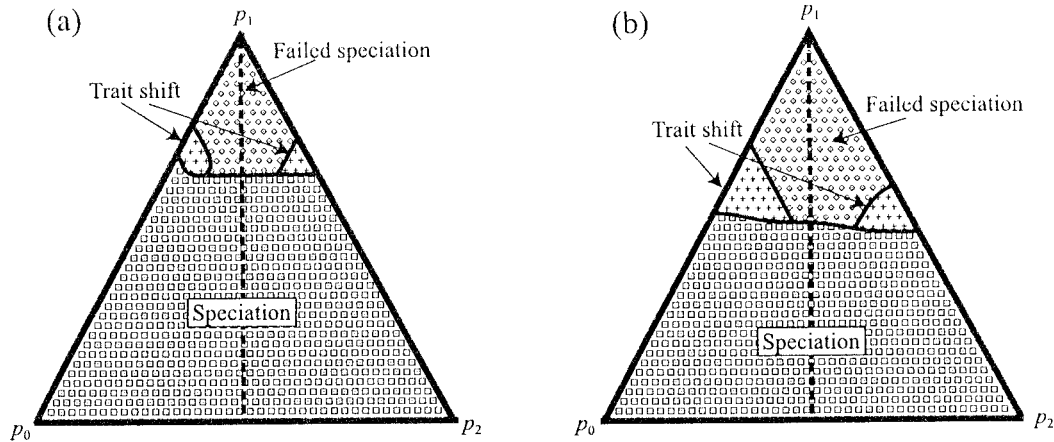
FIG. 6. Effect of asymmetry in parameters. (a) Asymmetry between a_0 and a_2. Parameter values: $a_0 = 5$, $a_2 = 7$, and $s_0 = s_2 = 0.3$. (b) Asymmetry between s_0 and s_2. Parameter values: $s_0 = 0.4$, $s_2 = 0.3$, and $a_0 = a_2 = 5$. Other parameters are fixed throughout: $c_0 = c_2 = 0$, and $r = 0.5$.

Our present study also clearly shows that speciation is initiated when the initial female frequencies exceed a threshold regardless of the male initial frequencies, which was not clear in our previous analysis by the individual-based model. Finally, our current model studies the effects of female cost for preference in more detail than our previous study. Our results not only confirm our previous finding that speciation is robust to introducing slight female cost, but also shows that speciation becomes less possible with larger female cost.

Sympatric speciation is in general driven by disruptive selection that works on a single population. Disruptive natural selection, for example, that associated with host race formation, has prevailed in previous theoretical models on sympatric speciation (e.g., Maynard Smith 1966; Tauber and Tauber 1977; Kondrashov and Kondrashov 1999). This form of disruptive selection, however, is not an assumption in our model. Instead, we assume another form of disruptive selection, namely, disruptive sexual selection. Disruptive sexual

selection operates on male offspring produced from interbreeding. Such males tend to have intermediate secondary sexual characters, which are less successful in acquiring mates from the females with diverged preference. This reinforces the divergence of a population once it starts. There are a few examples of sexually unsuccessful hybrid males (Noor 1997; Vamosi and Schluter 1999), but more experiments are needed. Once confirmed, such cases would greatly support the possibility of sympatric speciation by sexual selection.

The most famous example of sympatric speciation by sexual selection comes from the cichlids of the African great lakes. Their male coloration is diverse and there are many sympatric species (Turner 1994; Deutsch 1997; Seehausen et al. 1997; Ritchie and Phillips 1998; Seehausen and Alphen 1998). This suggests the possibility of sympatric speciation by sexual selection (Seehausen et al. 1999). However, there has been much stress on their nich differences, such as jaw morphology, and their role on speciation (e.g., Johnson et al.
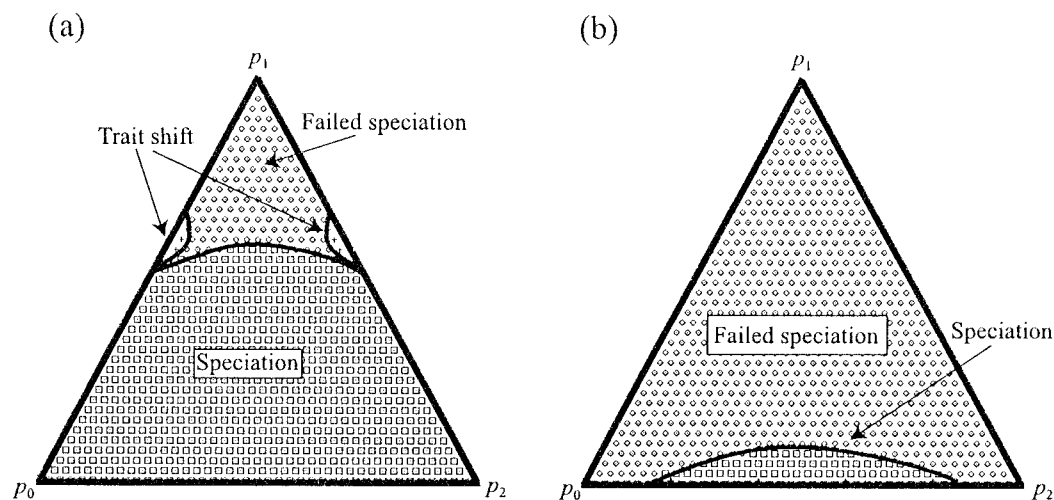

FIG. 7. Effect of female cost on mate choice. Parameter values: (a) $u_0 = u_2 = 0.001$; (b) $u_0 = u_2 = 0.05$. Other parameters: $a_0 = a_2 = 5$, $c_0 = c_2 = 0$, $s_0 = s_2 = 0.3$, and $r = 0.5$ throughout. Male initial frequencies are fixed: $t_0 = t_2 = 0.1$, $t_1 = 0.8$ for both (a) and (b).

1996). This trend has provoked many mathematical models of sympatric speciation by natural selection (e.g., Doebeli 1996; Dieckmann and Doebeli 1999; Kondrashov and Kondrashov 1999). In contrast, our models of sympatric speciation (this paper; Higashi et al. 1999) focus on sexual selection as a driving force of speciation. Recent phylogenetic data has separated the roles of sexual selection and natural selection on the formation of cichlid species flock in Lake Malawi (Albertson et al. 1999). The study suggests that ecological divergence of species occurred in the early stage of flock evolution, whereas the subsequent speciation, which involved little ecological change, must have resulted from other evolutionary forces such as sexual selection. In line with this, the diversity of cichlid fish may well be explained by sympatric speciation models via natural selection and sexual selection.

Turner and Burrows's model is the first that achieved a stable sympatric speciation by sexual selection (Turner and Burrows 1995). As Higashi et al. (1999) noted, the effect of the cost for male secondary sexual character in their model is different from our prediction. In their model, it was a key assumption that males with large ornamentation suffered from high cost, because initial invasion of males with alternative but small ornamentation was promoted by its low cost. In contrast, our prediction is that low male cost on male secondary sexual character promotes speciation. This is clearly shown in our phase plane analysis by the fact that small male cost broadens the attractive basin of speciation equilibrium (Fig. 3f). Turner and Burrows's analysis did not include dependence of outcomes on male cost, which prevents a direct comparison of the predictions from both models.

van Doorn et al. (1998) has recently presented a theoretical model of sympatric speciation and extinction by environment-dependent sexual selection, which is tailored for the case of cichlids in Lake Victoria studied by Seehausen et al. (1997). Their environment-dependent sexual selection assumed that the probability of mating depends not only on male secondary sexual character and female preference, but also on habitat sharing. With this singular sexual selection, they explained the hybridization of once sexually isolated cichlid species observed by Seehausen et al. (1997) in a turbid environment. In contrast, our model can explain the same phenomena without introducing any special mechanism into sexual selection: turbidity will reduce female discrimination by decreasing a_0 (a_2) and increasing c_0 (c_2) in our model. In our phase planes (Fig. 3b, e), this parameter change shifts the speciation equilibrium away from the point of complete isolation ($t_0 = p_0 = 0.5$), which means increased interbreeding (hybridization). Our model makes a further prediction. Recalling that speciation equilibrium becomes an unstable saddle point when c_0 and/or c_2 becomes larger than zero, the turbidity causing such parameter changes drives the smaller population to extinction rapidly in a self-reinforcing manner. Thus, we conclude that simple sexual selection is enough to explain speciation and extinction of cichlid species predicted by Seehausen et al. (1997).

We do not exclude the possibility of allopatric speciation by sexual selection. One of the evolutionary outcomes in our model, trait shift, actually corresponds to this case. According to our results, a population will undergo allopatric divergence (trait shift) if it has sufficient asymmetric parameters and/or trait distribution. Taking this into consideration, our sympatric speciation model could generate great species diversity under various conditions.

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APPENDIX

Variable Transformation

Through the variable reduction in the text, we now have a set of four recursive equations of variables z_i ($i = 0, \ldots, 3$):

$$z_{i,n+1} = f_i(z_{0,n}, z_{1,n}, z_{2,n}, z_{3,n}) \qquad (i = 0, \ldots, 3), \qquad \text{(A1)}$$

where $z_{i,n}$ stands for z_i of generation n. The frequencies of type 0 males (t_0) and females (p_0) are written using z_i ($i = 0, \ldots, 3$):

$$t_0 = z_0 + z_1 + z_2, \quad \text{and} \qquad \text{(A2)}$$

$$p_0 = z_0 + z_3 + z_6 = z_0 + z_3 + z_2. \qquad \text{(A3)}$$

We define two linkage coefficients D_1 and D_2:

$$D_1 = \frac{(z_0 + z_2)z_4 - 2z_1z_3}{2}$$

$$= \frac{(z_0 + z_2)\{1 - 2(z_0 + z_1 + z_2 + z_3)\} - 2z_1z_3}{2}, \quad \text{and} \qquad \text{(A4a)}$$

$$D_2 = \frac{z_0 - z_2}{2}. \qquad \text{(A4b)}$$

These relationships among variables can be rewritten as:

$$z_0 = t_0p_0 + D_1 + D_2, \qquad \text{(A5a)}$$

$$z_1 = t_0(1 - 2p_0) - 2D_1, \qquad \text{(A5b)}$$

$$z_2 = t_0p_0 + D_1 - D_2, \quad \text{and} \qquad \text{(A5c)}$$

$$z_3 = (1 - 2t_0)p_0 - 2D_1. \qquad \text{(A5d)}$$

Substituting (A5a–d) for (A1) yields the model (1a–c) and (A10).

Drawing Null-Isoclines and Equilibria

Setting the right side of model (1a–c) equal to zero yields multidimensional null-isoclines. From $\Delta p_0 = 0$, we have, $D_1 = 0$ or $W_0 = 1$. From the definition of D_1, we know that $p_0 = 0$ and $p_0 = 0.5$ yield $D_1 = 0$. Therefore, the sufficient conditions for $\Delta p_0 = 0$ are $W_0 = 1$, or

$$p_0 = 0, \quad \text{or} \qquad \text{(A6)}$$

$$p_0 = \frac{1}{2}. \qquad \text{(A7)}$$

From $W_0 = 1$, we have the line

$$p_0 = \frac{1 + \{(a_0 + c_0)(1 - s_0) - 2\}t_0}{(a_0 + c_0)(1 - s_0)}. \qquad \text{(A8)}$$

When either $D_1 = 0$ or $W_0 = 1$, we can eliminate D_2 from $\Delta t_0 = \Delta D_2 = 0$ and obtain a relationship between t_0 and p_0, which is a curve where $\Delta t_0 = \Delta D_2 = 0$. The expression of this curve is complicated and not shown here, but is named (A9).

Therefore, the intersection of (A6–8) and (A9) (Fig. 2a) is the point where $\Delta t_0 = \Delta p_0 = \Delta D_2 = 0$. Numerical analysis finds that the two intersections of (A6) and (A9) and (A7) and (A9) are the stable equilibria of the model (1a–c) and (A10). It is also confirmed that, at the equilibrium on (A7), $z_0 (=z_8) \cong 0.5$ when the equilibrium is sufficiently close to the point $t_0 = p_0 = 0.5$, which means that the population is dominated by type 0 and 2 individuals of both sex. This state represents speciation. At another equilibrium on the line $p_0 = 0$, female population is occupied by type 1 individuals, that is, only random mating is taking place. No speciation occurs in this state.

The Exact Equation of ΔD_1

The exact equation for ΔD_1 is expressed as follows:

$$\Delta D_1 = \frac{1}{8}\{(1 - r)^4\alpha + r(1 - r)^3\beta + r^2(1 - r)^2\chi + r^3(1 - r)\delta + r^4 + \epsilon\} - D_1, \qquad \text{(A10)}$$

where

$$\alpha = \left(1 + UV\frac{1 - s_0}{1 - 2s_0t_0}\right)D_1, \qquad \text{(A11)}$$

$$\beta = \frac{2}{1 - s_0t_0}[2Z(t_0p_0 + D_1)\{1 - (1 + s_0)t_0\} + 2\{(X_1 + Y_1 - Z)(1 - s_0)t_0 + (X_2 + Y_2 - Z)(1 - 2t_0)\}\{(1 - 2t_0)(1 - 2p_0) + 4D_1\}$$

$$- 2Z\{(1 - 2t_0)p_0 - 2D_1\}\{1 - (1 + s_0)t_0\} - (t_0p_0 + D_1 + D_2)\{(X_3 + Y_1 - Z)(1 - s_0)t_0 + (X_2 + Y_2 - Z)(1 - 2t_0)\}]$$

$$+ \frac{2}{(1 - 2s_0t_0)^2}[(1 - s_0(t_0p_0 + D)U\{2(X_3 + Y_1)(1 - s_0)(t_0(1 - 2p_0) - 2D_1) + 2(X_2 + Y_2)((1 - 2t_0)(1 - 2p_0) + 4D_1)\}$$

$$+ \{(X_1 + Y_1)(1 - s_0)(t_0p_0 + D_1 + D_2) + 2(X_2 + Y_2)((1 - 2t_0)p_0 - 2D_1) + (X_3 + Y_1)(1 - s_0)(t_0p_0 + D_1 - D_2)\}$$

$$- (1 - s_0)(t_0(1 - 2p_0) - 2D_1)V\{(X_3 + Y_1)(1 - s_0)(t_0p_0 + D_1 + D_2) + 2(X_2 + Y_2)((1 - 2t_0)p_0 - 2D_1)$$

$$+ (X_3 + Y_1)(1 - s_0)(t_0p_0 + D_1 - D_2)\}$$

$$- 2U\{(X_1 + Y_1)(1 - s_0)(t_0(1 - 2p_0) - 2D_0) + (X_2 + Y_2)((1 - 2t_0)(1 - 2p_0) + 4D_1)\}((1 - 2t_0)p_0 - 2D_1)], \qquad (A12)$$

$$\chi = \frac{1}{1 - 2s_0t_0}\Bigg[2(t_0p_0 + D_1)(1 - 2t_0)(1 - 2p_0) + \frac{(a_0 + c_0)(1 - 2s_0t_0)}{\{(1 - s_0)(a_0 + c_0) - 2\}t_0 + 1}(1 - 2p_0)(1 - s_0)t_0\{(1 - 2t_0)(1 - 2p_0) + 4D_1\}$$

$$+ 4\{(X_1 + Y_1 - Z)(1 - s_0)t_0 + (X_2 + Y_2 - Z)(1 - 2t_0)\}Z\{1 - (1 + s_0)t_0\}$$

$$- 2(t_0p_0 + D_1 + D_2)p_0\frac{(a_0 + c_0)(1 - 2s_0t_0)}{\{(1 - s_0)(a_0 + c_0) - 2\}t_0 + 1}(1 - 2t_0)$$

$$- 4Z\{1 - (1 + s_0)t_0\}\{(X_3 + Y_1 - Z)(1 - s_0)t_0 + (X_2 + Y_2 - Z)(1 - 2t_0)\}$$

$$- 2(1 - 2p_0)(1 - s_0)t_0\{(1 - 2t_0)p_0 - 2D_1\}\Bigg]$$

$$+ \frac{1}{(1 - 2s_0t_0)^2}[2(t_0p_0 + D_1 + D_2)U\{2Y_1(1 - s_0)(t_0(1 - 2s_0) - 2D_1)_0 + Y_2((1 - 2t_0)(1 - 2p_0) + 4D_1)\}$$

$$+ 2\{(X_1 + Y_1)(1 - s_0)(t_0p_0 + D_1 + D_2) + 2(X_2 + Y_2)((1 - 2t_0)p_0 - 2D_1)$$

$$+ (X_3 + Y_1)(1 - s_0)(t_0p_0 + D_1 - D_2)\}$$

$$\times \{2(X_3 + Y_1)(1 - s_0)(t_0(1 - 2p_0) - 2D_1) + 2(X_2 + Y_2)((1 - 2t_0)(1 - 2p_0) + 4D_1)\}$$

$$+ \{X_1(1 - s_0)(t_0(1 - p_0) - D_1 + D_2) + X_2((1 - 2t_0)(1 - p_0) + 2D_1) + X_3(1 - s_0)(t_0(1 - p_0) - D_1 - D_2)\}$$

$$\times ((1 - 2t_0)(1 - 2p_0) + 4D_1)V - 2(1 - s_0)((t_0(1 - 2p_0) - 2D_1)V\{2Y_1(1 - s_0)(t_0p_0 + D_1) + Y_2((1 - 2t_0)p_0 - 2D_1)\}$$

$$-4\{(X_1 + Y_1)(1 - s_0)(t_0(1 - 2p_0) - 2D_1) + (X_2 + Y_2)((1 - 2t_0)(1 - 2p_0) + 4D_1)\}$$

$$\times \{(X_3 + Y_1)(1 - s_0)(t_0p_0 + D_1 + D_2) + 2(X_2 + Y_2)((1 - 2t_0)p_0 - 2D_1) + (X_3 + Y_2)(1 - s_0)(t_0p_0 + D_1 + D_2)\}$$

$$- 2\{(X_1 + Y_1)(1 - s_0)(t_0(1 - 2p_0) - 2D_1) + (X_2 + Y_2)((1 - 2t_0)(1 - 2p_0) + 4D_1)\} \times ((1 - 2t_0)p_0 - 2D_1)U], \qquad (A13)$$

$$\delta = \frac{2}{(1 - 2s_0t_0)^2}\Bigg[\{(X_1 + Y_1 - Z)(1 - s_0)t_0 + (X_2 + Y_2 - Z)(1 - 2t_0)\}(1 - 2p_0)(1 - 2t_0)$$

$$+ 2\frac{(a_0 + c_0)(1 - 2s_0t_0)}{\{(1 - s_0)(a_0 + c_0) - 2\}t_0 + 1}p_0(1 - s_0)t_0Z\{1 - (1 + s_0)t_0\}$$

$$- 2Z\{1 - (1 + s_0)t_0\}p_0\frac{1 - 2s_0t_0}{\{(1 - s_0)(a_0 + c_0) - 2\}t_0 + 1}(1 - 2t_0)$$

$$- (1 - 2p_0)(1 - s_0)t_0\{(X_3 + Y_2 - Z)(1 - s_0)t_0 + (X_2 + Y_2 - Z)(1 - 2t_0)\}\Bigg]$$

$$+ \frac{1}{(1 - 2s_0t_0)^2}[2\{(X_1 + Y_1)(1 - s_0)(t_0p_0 + D_1 + D_2) + 2(X_2 + Y_2)((1 - 2t_0)p_0 - 2D_1) + (X_3 + Y_1)(1 - s_0)(t_0p_0 + D_1 - D_2)\}$$

$$\times \{(Y_1 + Y_3)(1 - s_0)(t_0(1 - 2p_0) - 2D_1) + Y_2((1 - 2t_0)(1 - 2p) + 4D_1)\}$$

$$+ \{2X_1(1 - s_0)(t_0(1 - p_0) - D_1) + X_2((1 - 2t_0)(1 - 2p_0) + 4D_1)\}$$

$$\times 2\{(X_3 + Y_1)(1 - s_0)(t_0(1 - 2p_0) - 2D_1) + (X_2 + Y_2)((1 - 2t_0)(1 - 2p_0) + 4D_1)\}$$

$$- 4\{(X_1 + Y_1)(1 - s_0)(t_0(1 - 2p_0) - 2D_1) + (X_2 + Y_2)((1 - 2t_0)(1 - 2p_0) + 4D_1)\}$$

$$\times \{2Y_1(1 - s_0)(t_0p_0 + D_1) + Y_2((1 - 2t_0)p_0 - 2D_1)\}$$

$$- 2\{(X_1 + Y_1)(1 - s_0)(t_0(1 - 2p_0) - 2D_1) + X_2((1 - 2t_0)(1 - 2p_0) + 4D_1)\}$$

$$\times \{2(X_3 + Y_1)(1 - s_0)(t_0p_0 + D_1) + 2(X_2 + Y_2)((1 - 2t_0)p_0 - 2D_1)\}], \qquad (A14)$$

$$\epsilon = \frac{1}{(1 - 2s_0t_0)^2}\left[\frac{(a_0 + c_0)(1 - 2s_0t_0)}{\{(1 - s_0)(a_0 + c_0) - 2\}t_0 + 1}(1 - s_0)p_0t_0(1 - 2p_0)(1 - 2t_0) - UV(1 - s_0)\{t_0(1 - 2p_0) - 2D_1\}\{(1 - 2t_0)p_0 - 2D_1\}\right.$$

$$+ \{(X_1 + X_3)(1 - s_0)(t_0(1 - 2p_0) - 2D_1) + X_2((1 - 2t_0)(1 - 2p_0) + 4D_1)\}$$

$$\times \{2Y_1(1 - s_0)(t_0p_0 + D_1) + Y_2((1 - 2t_0)p_0 - 2D_1)\}$$

$$- 2\{X_1(1 - s_0)(t_0(1 - p_0) - D_1 + D_2) + X_2((1 - 2t_0)(1 - p_0) + 2D_1) + X_3(t_0(1 - p_0) - D_1 - D_2)\}$$

$$\left. \times \{2Y_1(1 - s_0)(t_0p_0 + D_1 + D_2) + Y_2((1 - 2t_0)(1 - 2p_0) + 4D_1)\}\right], \tag{A15}$$

$$X_1 = \frac{(1 - 2s_0t_0)\{a_0(t_0p_0 + D_1 + D_2) + c_0(t_0p_0 + D_1 - D_2)\}}{\{(1 + s_0)(a_0 + c_0) - 2\}t_0 + 1} + t_0(1 - 2p_0) - 2D_1, \tag{A16}$$

$$X_2 = \frac{2(1 - 2s_0t_0)(t_0p_0 + D_1)}{\{(1 + s_0)(a_0 + c_0) - 2\}t_0 + 1} + t_0(1 - 2p_0) - 2D_1, \tag{A17}$$

$$X_3 = \frac{(1 - 2s_0t_0)\{c_0(t_0p_0 + D_1 + D_2) + a_0(t_0p_0 + D_1 - D_2)\}}{\{(1 + s_0)(a_0 + c_0) - 2\}t_0 + 1} + t_0(1 - 2p_0) - 2D_1, \tag{A18}$$

$$Y_1 = \frac{(a_0 + c_0)(1 - 2s_0t_0)((1 - 2t_0)p_0 - 2D_1)}{\{(1 + s_0)(a_0 + c_0) - 2\}t_0 + 1} + (1 - 2t_0)(1 - 2p_0) + 4D_1, \tag{A19}$$

$$Y_2 = \frac{2(1 - 2s_0t_0)((1 - 2t_0)p_0 - 2D_1)}{\{(1 + s_0)(a_0 + c_0) - 2\}t_0 + 1} + (1 - 2t_0)(1 - 2p_0) + 4D_1, \tag{A20}$$

$$Z = (1 - t_0)(1 - 2p_0) + 2D_1, \tag{A21}$$

$$U = \left[\frac{(a_0 + c_0)(1 - 2s_0t_0)}{\{(1 + s_0)(a_0 + c_0) - 2\}t_0 + 1} - 2\right]p_0 + 1, \quad \text{and} \tag{A22}$$

$$V = 2\left[\frac{1 - 2s_0t_0}{\{(1 + s_0)(a_0 + c_0) - 2\}t_0 + 1} - 1\right]p_0 + 1. \tag{A23}$$