Models of selective mating and the initiation of the Fisherian process

KIYOSI TAKAHASI

Department of Biological Sciences, Graduate School of Science, University of Tokyo, Hongo 7-3-1, Bunkyo-ku, Tokyo 113, Japan (k32148@m-unix.cc.u-tokyo.ac.jp)

SUMMARY

The effects of various rules of selective mating on the initial stages of Fisherian sexual selection are investigated. A comparison of three models of selective mating, fixed relative preference, best of N males and absolute preference is provided, with a special emphasis on their mathematical properties. Using a two-locus haploid model of sexual selection in a polygamous population, I show that the absolute preference rule of selective mating may lower the threshold frequency of the preference trait, required for the initiation of the Fisherian process, as low as zero. This was not observed in the previous analyses with fixed relative preference or best of N males rules. It is then argued that absolute preference may cause the initiation of the Fisherian process more easily without introducing additional assumptions such as pleiotropy or random genetic drift. Some problems associated with the mating rule are also discussed.

1. INTRODUCTION

Ever since the pioneering works by O'Donald (see O'Donald (1977*a*) for a review), various genetic models have succeeded in showing that the Fisherian process may cause sexual selection by mate choice in polygamous populations. Fisherian runaway is a self-reinforcing process that may lead to exaggeration of both the deleterious ornamental trait (usually male) and the associated (female) mate preference for the trait (Darwin 1871; Fisher 1915). It has become a standard explanation for the evolution of a mate preference for disadvantageous characters.

By analysing a two-locus system of the Fisherian process based on haploid genetics and polygyny, Kirkpatrick (1982) found that the system exhibits lines, rather than a point, of equilibria that may be locally stable. Such neutral stability was also the case with polygenic modelling (Lande 1981). While these early models assumed that mate preferences do not induce any selective cost, it was later shown that relaxation of the assumption may cause substantial discrepancies in the outcome of the analyses (e.g. Pomiankowski 1987; Bulmer 1989). Costly mate preferences have been a central issue in the sexual selection debate, and there are now plenty of studies, theoretical and empirical, on this subject (see Pomiankowski (1988), Andersson (1994) and Møller (1994) for reviews). Consequently, recent studies have focused much of their attention on other aspects of sexual selection, such as the handicap principle (Zahavi 1975), in addition to the ordinary Fisherian process. However, there still remain uncertainties concerning the pure Fisherian process.

Another less intensively studied issue evoked by

Kirkpatrick's (1982) major gene model is that stable exaggeration of a deleterious ornament occurs only when the equilibrium frequency of the preference exceeds a threshold value (see Pomiankowski 1988, § 4.2; O'Donald 1990). The existence of threshold frequencies, which seems to be a common feature in major gene models of the Fisherian process (Pomiankowski 1988), raises the question of how a preference strength sufficient for the initiation of the Fisherian process is initially established; how can the process get started when preference genes arise at low frequencies by mutation? Fisher (1915) suggested that the secondary sexual characteristics evolve because initially, before they become exaggerated during evolution, they increase the viability of their possessors. On the other hand, the initial survival advantage for the ornament may not be required; pleiotropy or random genetic drift may give rise to the preference. Kirkpatrick (1982) postulated a pre-existing preference already common in the population, and suggested that it might have spread by random genetic drift to a level at which the Fisherian process would immediately start off by itself. Another possibility may be in pre-existing biases inherent in the females' sensory systems (see Ryan (1994) for a review). Without such additional processes, however, initiation of a Fisherian process seems difficult, even with the handicap effects (Pomiankowski 1988).

In this paper I present a comparative study on models of selective mating, and argue that absolute preference (see below) can alone lead to the initiation of a Fisherian process more easily. To show this, I modify a classical haploid two-locus model (see Kirkpatrick 1982; Seger 1985; Seger & Trivers 1986;

Bulmer 1989) to investigate effects of various mating rules on the initiation of the process. The assumption of haploidy is obviously an idealization, and does not have any biological implications. Diploid models of sexual selection are known to show important differences in evolutionary dynamics from the less realistic haploid models, especially when allelic effects are non-additive (Gomulkiewicz & Hastings 1990; Heisler & Curtsinger 1990; Otto 1991).

2. MAJOR GENE MODELS OF THE FISHERIAN PROCESS

(a) *A brief overview*

The Fisherian process of sexual selection has been mathematically formulated by Kirkpatrick (1982) based on two-locus haploid genetics. The model was later investigated more generally by Seger (1985; see also Seger & Trivers 1986). Bulmer (1989) also developed the model to incorporate selective costs of the preference and biased mutation. They studied the joint evolution of a deleterious ornament T_2 and a preference P_2 for it by following changes in their frequencies in the population. Recursions for ornament disequilibrium between the loci (D) were derived as

$$\left. \begin{aligned} t'_2 &= t_2 + A, \\ p'_2 &= p_2 + DA/(t_1 t_2), \\ D' &= (1-r)D[1 + A(1-2t_2)/(t_1 t_2)] \\ &\quad + \frac{1}{2}r(D^2 + t_1 t_2 p_1 p_2)B - DA^2/(t_1 t_2), \end{aligned} \right\} \quad (1)$$

(see equation (1) of Bulmer (1989); see also equation (1) of Kirkpatrick (1982)). Here, $t_1 = 1 - t_2$, $p_1 = 1 - p_2$ and r is the recombination fraction between the loci. Variables A and B are defined as $A = \frac{1}{2}(p_1 t_2^{(m)} + p_2 U_2 - t_2)$ and $B = (U_2 - t_2^{(m)})/(t_1 t_2)$, respectively, where $t_2^{(m)}$ is the frequency of T_2 in males after viability selection; $t_2^{(m)} = (1-s)t_2/(1-st_2)$, with s (less than one) indicating the selection coefficient against T_2 males. U_2 is the proportion of the preferring females who end up mating with males with the ornament. The recursions (1) show that if P_2 females mate non-randomly, so that $U_2 \neq t_2^{(m)}$, a deterministic change in the frequency t_2 (and in p_2 if $D \neq 0$) is observed without the operation of natural selection ($s = 0$), because we still have $A \neq 0$. Hence this is a model of selective mating (Lewontin *et al.* 1968).

In Kirkpatrick's (1982) analysis, where fixed relative preference rule is used, we have $U_2 = a_2 t_2^{(m)} / (t_1^{(m)} + a_2 t_2^{(m)})$, where a_2 (greater than zero) is the preference strength of preferring females for males with the ornament; $a_2 = 1$ implies random mating. With this mating rule he obtained lines of locally stable equilibria (figure 1a), and found that no exaggeration of the ornament is observed (i.e. $\hat{t}_2 = 0$, where a caret indicates an equilibrium value) unless the equilibrium preference frequency $\hat{p}_2$ exceeds a certain threshold given by $Y_K = s/[(a_2 - 1)(1 - s)]$. In cases where disadvantageous ornaments ($s > 0$) are preferred in selective mating ($a_2 > 1$), the threshold frequency Y_K assumes some positive value. If,

Figure 1. Schematic figures of two-dimensional projected space for the haploid two-locus system of Fisherian process with: (a) fixed relative preference model (Kirkpatrick 1982); and (b) better of two males model (Seger 1985). Y_K in figure 1a (or Y_S in figure 1b) indicates the threshold frequency of the preference above which a stable equilibrium with $\hat{t}_2 > 0$ is possible (see also table 1). While the interior equilibrium of Kirkpatrick's model (indicated by a bold line in figure 1a) is locally stable, it is unstable in Seger's model (indicated by a thin line in figure 1b). Arrows indicate approximate directions of the evolution.

then, initially the ancestral population is located at an equilibrium specified by $(\hat{p}_2, \hat{t}_2) = (0, 0)$, a small perturbation will not initiate a Fisherian process, because we still have $p_2 < Y_K$ and the population should eventually converge to a stable equilibrium with $\hat{t}_2 = 0$ (figure 1a).

This is also the case with the best of N males rule (Seger 1985), which is specified for the simplest case, $N = 2$, by $U_2 = t_2^{(m)} + c_2 t_1^{(m)} t_2^{(m)}$; c_2 ($-1 \leq c_2 \leq 1$) indicates the preference strength, and P_2 females mate randomly for $c_2 = 0$. The threshold frequency then becomes $Y_S = s/[c_2(1-s)]$ (figure 1b). Since this threshold is greater than zero for $s > 0$ and $c_2 > 0$, a small perturbation will not cause the initiation of the process as in the fixed relative preference model.

The main implication of the previous studies is that under these mating rules, a pure Fisherian process can not lead to stable exaggeration of a deleterious ornament. The same results apply in cases where both P_1 and P_2 females mate preferentially, with different preference strengths (Kirkpatrick 1982; Bulmer 1989). The difficulty concerning the initiation of the Fisherian process has been extensively discussed by Pomiankowski (1988, §4.2) and by O'Donald (1990).

(b) *Absolute preference model*

Maynard Smith (1985) identified three models of selective mating, two of which (fixed relative preference and best of N males) are already discussed above. We now proceed to investigate the third model, namely the absolute preference model. I follow Maynard Smith (1985) emphasizing that this distinction is different in kind from that drawn by Lande (1981). The absolute preference model as discussed in the present study is different from the absolute preference model in Lande (1981); in the present context,

Lande's absolute preference should be classified into the fixed relative preference model.

The absolute preference model, characterized by its mating rule

$$U_2 = m_2 + (1 - m_2)t_2^{(m)}, \quad (2)$$

was first introduced to the study of sexual selection by O'Donald (see O'Donald (1977a) for a review), though he himself referred to models based on this rule as models with complete (or constant) preferences. With this mating rule preferring individuals choose mates with the ornament with a certain probability m_2 ($0 \leq m_2 \leq 1$), and mate randomly with a probability $1 - m_2$; hence m_2 designates the strength of the preference. O'Donald (1973) employed this mating rule to study the evolution of the male ornament in polygynous populations. While this model was rather rarely employed in the analyses based on polygamous mating (Bell 1978; Andersson 1982; Maynard Smith 1985; see also Karlin 1978), the special case $m_2 = 1$ has been the standard rule under monogamy (Bell 1978; O'Donald 1980; Andersson 1982, 1986). Although this rule may lead to an unrealistic situation such as an extreme monopolization of mates by a very small number of individuals (O'Donald 1973; Maynard Smith 1985) some empirical backgrounds have also been reported (O'Donald 1977b; see also § 3).

The effects of the mating rule on the Fisherian process are studied by substituting the rule (2) into the basic recursions (1). Following the straightforward way of ordinary equilibrium analysis, I found that the system exhibits lines of equilibria given by

$$\hat{t}_2 = \left(\frac{\hat{p}_2 m_2}{s} \right), \quad \text{for } 0 \leq \hat{p}_2 < \left(\frac{s}{m_2} \right), \quad (3a)$$

and

$$\hat{t}_2 = 1, \quad \text{for } \left(\frac{s}{m_2} \right) \leq \hat{p}_2 \leq 1, \quad (3b)$$

if $m_2 > s$, or

$$\hat{t}_2 = \left(\frac{\hat{p}_2 m_2}{s} \right), \quad (3c)$$

if $m_2 < s$. These lines are illustrated for the case $m_2 > s$ in figure 2a.

An interesting property of the equilibrium lines (3) is that since the line of internal equilibria (3a) or (3c) passes through the origin $(p_2, t_2) = (0, 0)$, there is no equilibrium that satisfies both $\hat{p}_2 > 0$ and $\hat{t}_2 = 0$. This implies that the threshold required for the initiation of the Fisherian process does not exist under the mating rule; or, in other words, the threshold frequency is zero. Mating rules and their threshold frequencies are summarized in table 1.

This can be expressed in a more formal way. Consider two regions, I and II, on the p_2 - t_2 plane that are separated by the line of internal equilibria. These regions are defined, respectively, as

$$t_2 > p_2 m_2 / s, \quad \text{for region I,} \quad (4a)$$

Figure 2. Figures of two-dimensional projected spaces for the haploid two-locus system of a Fisherian process with the absolute preference rule of selective mating. Parameters are (a) $m_1 = 0$, $m_2 = 0.2$ and $s = 0.1$; and (b) $m_1 = 0.02$, $m_2 = 0.2$ and $s = 0.1$. Equilibria are illustrated with bold lines, and arrows in the figures indicate the signs (+ or -) of Δp_2 and Δt_2 assuming that the linkage disequilibrium D is positive. In figure 2a, the line of internal equilibria defined by equation (3a) in the text separates the p_2 - t_2 plane into regions I and II (see inequalities (4) in the text). Since this line of internal equilibria passes through the origin $(p_2, t_2) = (0, 0)$, the threshold frequency required for the initiation of the Fisherian process does not exist with this mating rule. This is also the case for figure 2b; the internal equilibria, defined by equation (6) in the text, passes through the origin.

and

$$t_2 < p_2 m_2 / s, \quad \text{for region II,} \quad (4b)$$

with $0 \leq p_2, t_2 \leq 1$ (figure 2a). Then assuming the initial population located at $(\hat{p}_2, \hat{t}_2) = (0, 0)$, there are two possible perturbations: (i) a perturbation that leads the population into region I; and (ii) a perturbation leading to region II (figure 3). Some investigations of the basic recursions (1) will tell us that in region I, we have $\Delta t_2 < 0$ (where Δ designates a change within a generation) and $\Delta p_2 < 0$ if $D > 0$, which should be reasonable for the present situation. In region II we have $\Delta t_2 > 0$, and if $D > 0$, $\Delta p_2 > 0$ (figure 2a). Hence while perturbation (i) will not cause further exaggeration of the trait, perturbation (ii) may eventually initiate the Fisherian process, without introducing additional assumptions, by leading the population to a new equilibrium with $\hat{t}_2 > 0$. This was not observed in the previous models of selective mating.

(c) When both types P_1 and P_2 mate preferentially

The above analysis can be generalized so that both types P_1 and P_2 mate preferentially, with different preference strengths. Such cases have been discussed for the fixed relative preference in Kirkpatrick (1982) and for the better of two males in Bulmer (1989). This generalization can be made for the absolute preference model by redefining the mating rule functions as

$$U_{11} = m_1 + (1 - m_1)t_1^{(m)}, \quad (5a)$$

Table 1. *Models of selective mating*

(Parameters and variables are defined in the text.)

model	mating rule (U_2)	threshold frequency
fixed relative preference	$a_2 t_2^{(m)} / (t_1^{(m)} + a_2 t_2^{(m)})$	$Y_K = s / [(a_2 - 1)(1 - s)]$
better of two males	$t_2^{(m)} + c_2 t_1^{(m)} t_2^{(m)}$	$Y_S = s / [c_2(1 - s)]$
absolute preference	$m_2 + (1 - m_2) t_2^{(m)}$	$(Y_0 = 0)$

Figure 3. Two possible directions of perturbations to the initial population with $(\hat{p}_2, \hat{t}_2) = (0, 0)$. Parameters are $m_1 = 0$, $m_2 = 0.2$ and $s = 0.1$, as in figure 2a. Third possibility that the population is perturbed along the line of equilibria is not considered. The regions I and II as defined in the text by inequalities (4) are separated by the line of internal equilibria which is indicated by a bold line in the figure (see also figure 2a). As discussed in the text, the perturbation (i) that leads the population into region I will not cause the exaggeration of the traits, while the perturbation (ii) leading to region II may initiate a Fisherian process.

and

$$U_{22} = m_2 + (1 - m_2) t_2^{(m)}, \quad (5b)$$

instead of equation (2), where U_{ij} ($i, j \in \{1, 2\}$) is the proportion of P_i females who end up mating with T_j males; obviously, $U_{i1} + U_{i2} = 1$. The recursions, (1), can also be applied to the present case if we redefine the variables A and B as $A = \frac{1}{2}(p_1 U_{12} + p_2 U_{22} - t_2)$ and $B = (U_{22} - U_{12}) / (t_1 t_2)$. Note that the previous definitions of A and B (and of the mating rule functions also) can be recovered if we assume that $m_1 = 0$ so that P_1 females mate randomly ($U_{1j} = t_j^{(m)}$). Substituting the mating rule, (equation (5)), into the basic recursions, (1), I found that at equilibrium we have

$$\begin{aligned} \hat{t}_2 = & \langle (1 - s)m_1 \hat{p}_1 + m_2 \hat{p}_2 + s \\ & - \{[(1 - s)m_1 \hat{p}_1 + m_2 \hat{p}_2 + s]^2 - 4sm_2 \hat{p}_2\}^{1/2} \rangle / (2s). \end{aligned} \quad (6)$$

This equilibrium curve has a simple (and important) property that it passes through the origin $(p_2, t_2) =$

$(0, 0)$ (and also through $(p_2, t_2) = (1, 1)$) in the p_2 - t_2 plane (figure 2b). Then, following the same procedure as in the special case $m_1 = 0$, we find that a perturbation that moves the initial population into region II (see figure 2b) will lead to a new equilibrium with $\hat{t}_2 > 0$, eventually initiating the Fisherian process also in the present generalized situation.

3. DISCUSSION

(a) *General remarks*

This paper presents a comparative study on models of selective mating based on polygamous mating, and argues that the absolute preference rule may initiate the Fisherian process of sexual selection more easily without introducing additional assumptions such as pleiotropy or random genetic drift. While previous studies of absolute preference in polygamous populations (e.g. O'Donald 1973; Bell 1978; Karlin 1978; Andersson 1982; Maynard Smith 1985) could either follow the evolution of the secondary sexual trait, assuming that the associated preference does not evolve, or study the joint evolution of the traits only numerically, the present paper provides a complete coevolutionary analysis that is not constrained to a simulation study. It also generalizes the previous treatments by allowing the probability, m_2 , of selective mating to vary, and more importantly, this seems to be the first to show in explicit terms that the absolute preference model alone can cause the initiation of a Fisherian process. Such results have not been obtained in previous studies with fixed relative preference (Kirkpatrick 1982) or best of N males rule (Seger 1985).

This is best illustrated by comparing the threshold frequencies of the preference required for stable exaggeration of the ornament in respective models of selective mating. While both the fixed relative preference model and best of N males model have positive threshold frequencies, the absolute preference rule can lower the threshold as low as zero (table 1); hence a small perturbation away from the initial state $(\hat{p}_2, \hat{t}_2) = (0, 0)$ may initiate the Fisherian process, if the initial population is perturbed in a manner that leads the population into region II (figures 2 and 3).

Such invasion of the mutant phenotypes is observed because, for one reason, the ancestral population is initially located on a neutrally stable equilibrium. O'Donald (1990) argued that if a new mutant that arose in a population at a low frequency

could then invade the population, the population must initially be located on an unstable point. He then raised the question of how this unstable point was reached; what was the initiating event that produced the unstable point from which the new phenotype could then invade the population? This study provides a possible answer to this question; the initial state does not have to be an unstable point but should instead be neutrally stable. It has been argued that stochastic processes such as random genetic drift may relocate the population onto another neutrally stable point so that the mutant may eventually invade the population (Kirkpatrick 1982). The present study shows that the evolution proceeds in a more deterministic manner, and that certain types of perturbation may cause the invasion of the mutant phenotype if initially the population is located on a neutrally stable point.

(b) Polygenic models of sexual selection

Ever since Lande's (1980) polygenic inheritance model of sexual selection, various studies have assumed that both the ornament and the preference are continuous characters that, respectively, follow Gaussian distributions. The evolutionary dynamics are then studied by following changes in the average (population mean) phenotypic values. The main implication of this assumption is that the initial stages of the Fisherian process (in the sense as used in the present paper) cannot be studied by this type of polygenic model. Since small changes in the average value may mean substantial changes in allele frequencies, ordinary polygenic models fail to formulate the initial evolution of a trait that arises in a population at a low frequency by mutation, in a manner I have discussed in previous sections (see also Heisler 1984). Therefore, while with polygenic modelling the difficulties in the initial stages of Fisherian sexual selection may be overcome by certain types of handicaps (Iwasa *et al.* 1991), this does not mean that the same thing applies in major gene models (Pomiankowski 1988).

(c) Problems associated with the absolute preference model

The discrepancy regarding the initial evolution between the absolute preference and the other two models can be ascribed to the mathematical properties of the respective mating rules. Taking a limit $t_2 \rightarrow 0$, we have $U_2 \rightarrow m_2$ (greater than zero) with the absolute preference model, whereas $U_2 \rightarrow 0$ with the fixed relative preference or better of two rule. Hence in fixed relative preference and better of two models, terms containing U_2 are ignored in the local stability analysis and do not contribute to the condition for the initial evolution. Mathematically, this is the very reason why the absolute preference model may lead to the initiation of the Fisherian process while the other two do not.

This mathematical property of the absolute preference model may, however, lead to unrealistic re-

sults in practice, such as extreme monopolization of mates, as previously pointed out by Maynard Smith (1985). A number of studies have argued that a certain type of handicap may cause sexual selection by mate choice in polygamous populations (e.g. Bell 1978; Andersson 1982). It seems, however, that this may in part be an artifact due to the unrealistic nature of the absolute preference model. Its mathematical properties are also discussed in detail by O'Donald (1973). With this mating rule the males take part in the same number of preferential matings when they are rare as when they are common (see equation (2)); individually, therefore, they mate more often when they are rare. Hence the frequency dependence is strongly negative. This indicates why perturbations that lead the population into region I (see figures 2 and 3) do not cause stable exaggeration of the ornament, while perturbations leading to region II may initiate the Fisherian process; in region I, too few preferring individuals exist in the population, compared to individuals with the ornament (see equation (4a)), to start off the process. In the extreme case of $t_2 = 0$ (and hence $t_2^{(m)} = 0$), we have $U_2 = m_2$, implying that even though the ornament does not exist in the population, a certain number of individuals must nevertheless mate with the non-existent mates. Strictly then, the mating rule for the absolute preference model should be defined as

$$U_2 = m_2 + (1 - m_2)t_2^{(m)}, \quad \text{for } t_2 > 0, \quad (7a)$$

and

$$U_2 = 0, \quad \text{for } t_2 = 0, \quad (7b)$$

instead of the rule, (2), above. Note that this problem does not occur in monogamous populations where by definition each individual gets only one mate.

Although the absolute preference rule may produce unnatural situations, this is only when t_2 is very small relative to p_2 and hence there is a possibility of strong monopolization of mates by a small number of individuals; otherwise the mating rule seems to have some empirical backgrounds in nature (O'Donald 1977b; see also O'Donald 1973). Then what type of mate-choice processes in nature could be an example of the absolute preference? Since the mating rule (equation (2) or (7)), implies that a certain proportion m_2 of preferring individuals should choose mates with the ornament irrespective of the frequency of the ornamental trait in the population, it should arise if some individuals respond only to the courtship of individuals of the opposite sex that possess a particular character. I suspect that such may be the case in chemically mediated communication systems, where sex pheromones of one sex act as a mating signal required to elicit the response of potential mates (see Andersson 1994, ch. 15; Svensson 1996 for a review). It should also be noted that the mating rule has a formal resemblance to ordinary assortative mating (O'Donald 1973; Karlin 1978). It has been argued that assortative mating or interaction of individuals occurs in socially or spatially structured

populations (e.g. Eshel & Cavalli-Sforza 1982; Aoki & Feldman 1994). Then it may be inferred that the absolute preference type of selective mating should also occur in (socially or spatially) structured populations.

I note, to conclude, that absolute preference may also be important in cultural processes. I have argued elsewhere that cultural processes may exhibit dynamics similar to Fisherian runaway, if transmission of cultural information occurs between individuals who meet and interact selectively (Takahasi 1997). Due to the formal resemblance between sexual and cultural selection, I find that the absolute preference type of selective interaction initiates the cultural runaway more easily (analysis not shown). It would be interesting to know how non-random interaction of organisms can be expressed in mathematical terms. It then becomes possible to investigate the nature of non-randomness in a more quantitative manner.

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