BRIEF COMMUNICATION

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EVOLUTION BY FISHERIAN SEXUAL SELECTION IN DIPLOIDS

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Most models of Fisherian sexual selection assume haploidy. However, analytical models that focus on dynamics near fixation boundaries and simulations show that the resulting behavior depends on ploidy. Here we model sexual selection in a diploid to characterize behaviour away from fixation boundaries. The model assumes two di-allelic loci, a male-limited trait locus subject to viability selection, and a preference locus that determines a female's tendency to mate with males based on their genotype at the trait locus. Using a quasi-linkage equilibrium (QLE) approach, we find a general equation for the curves of quasi-neutral equilibria, and the conditions under which they are attracting or repelling. Unlike in the haploid model, the system can move away from the internal curve of equilibria in the diploid model. We show that this is the case when the combined forces of natural and sexual selection induce underdominance at the trait locus.

KEY WORDS: **Mathematical model, ornament, preference, ploidy, quasi-linkage equilibrium.**

Sexual selection is considered to be responsible for many striking and bizarre ornaments and mating behaviors found across the animal kingdom. Although there is a large body of theoretical treatment of sexual selection, most studies make simplifying genetic assumptions, such as haploidy or infinitesimally small polygenic inheritance, to make the math more tractable. However, most animal species that exhibit the ornaments attributed to evolution by sexual selection are diploid. This would not concern us if haploid and diploid models behaved identically. However, the small number of studies that have considered sexual selection in diploids have shown that different and unexpected behavior can occur.

Using computer simulations, Heisler and Curtsinger (1990) studied a model of diploid Fisherian sexual selection. Among the cases that they considered is a two-locus diploid model analogous to the haploid model considered by Kirkpatrick (1982) in his seminal paper on sexual selection. Unlike Kirkpatrick (1982) who showed the existence of neutrally stable curves, Heisler and Curtsinger (1990) showed that neutrally stable curves do not exist for any of the parameter sets considered, except under a special case of complete dominance at the trait locus. In some cases, trait and preference frequencies tended toward a curve but then moved slowly along it, whereas in other cases the system appeared to move away from a curve. The latter behavior was associated with heterozygote disadvantage of the trait in the numerical examples considered, but the exact conditions under which these two types of behaviors arise remained unclear, and the authors concluded that there was "a definite need for further analysis of diploid sexual selection models."

Two studies have made analytical progress by describing the behavior of the diploid two-locus model when either the trait or preference locus is nearly fixed. Gomulkiewicz and Hastings (1990) studied dynamics near fixation at the trait locus. They found that the stability properties of the fixation boundaries were similar in their diploid model and the haploid model of Kirkpatrick (1982). One novel feature that they identified in the diploid model, however, was that both fixation states of the trait locus could be simultaneously stable for a given preference frequency, suggesting that if a neutral curve exists, it should be repelling. Otto (1991) analyzed dynamics near fixation at the preference locus.

Like Kirkpatrick (1982), she found that near fixation at both the trait and preference locus, a new preference allele could only rise in frequency through genetic drift or as a correlated response to selection for the rare trait allele. Otto (1991) also considered the fate of novel preference alleles in populations with a polymorphism at the trait locus maintained by overdominance, which of course is impossible in the haploid model. Surprisingly, any new preference allele could invade as long as the trait and preference loci were sufficiently tightly linked, whereas no new preference could invade when the loci were loosely linked. Here, tight linkage allowed invasion because the novel preference allele could remain closely associated with the trait allele that increased the proportion of heterozygous offspring. This example is an exception to the rule that the rate of recombination has little qualitative effect on the dynamics observed in models of sexual selection (Kirkpatrick 1982; Barton and Turelli 1991).

So far no analytical treatment of the dynamics near the internal curve of "equilibria" exists for the diploid two-locus model of Fisherian sexual selection. Although recent multilocus models of sexual selection have been generalized to diploids (Kirkpatrick and Barton 1997; Hall et al. 2000; Kirkpatrick et al. 2002), these studies have focused on the extent of genetic correlations between preferences and traits and on the ability of costly preferences to evolve, rather than on the nature of the internal dynamics. In this article, we assume that genetic associations equilibrate rapidly relative to changes in allele frequencies (discussed below), a simplifying assumption that allows us to paint a more complete picture of the dynamics of sexual selection when both loci are polymorphic. Our results allow us to characterize the nature of the internal curves and to clarify how diploidy alters evolution under sexual selection.

Model

Table 1. Viability of males is determined by their genotype at the T locus. Fixed relative preferences determine the tendency of a female with a particular genotype at the preference locus to mate with a male with a particular genotype at the trait locus. Parameter *s* is the selection coefficient associated with viability selection, *h* is the dominance coefficient, and the $a_{ik,np}$'s measure the strength of female preference.

	T_1T_1	T_1T_2	T_2T_2
Viabilities:	1	$1-hs$	$1-s$
Preferences:			
P_1P_1	$1+a_{T_1T_1\times P_1P_1}$	$1+a_{T_1T_2\times P_1P_1}$	$1+a_{T_2T_2\times P_1P_1}$
P_1P_2	$1+a_{T_1T_1\times P_1P_2}$	$1+a_{T_1T_2\times P_1P_2}$	$1+a_{T_2T_2\times P_1P_2}$
P_2P_2	$1+a_{T_1T_1\times P_2P_2}$	$1+a_{T_1T_2\times P_2P_2}$	$1+a_{T_2T_2\times P_2P_2}$

Our model is a diploid analogue of the haploid Fisherian sexual selection model of a polygynous mating system considered by Kirkpatrick (1982). Initially, we assume no direct fitness consequences for females of being choosy (but see subsection on "Costly preferences"). There are two loci each segregating for two alleles. The T (trait) locus, expressed only in males, encodes a trait that is subject to both viability selection and sexual selection; it has alleles T_1 and T_2 at frequencies t_1 and t_2, respectively. The P (preference) locus, expressed only in females, determines her relative tendency to mate with males of the three possible genotypes at the T locus and is neutral with respect to viability selection; it has alleles P_1 and P_2 at frequencies p_1 and p_2, respectively (see Table 1). Both viability selection and sexual selection are assumed weak (of order ε). The mating tendencies of a given female are given by her so-called "fixed relative preferences" (Kirkpatrick 1982), as shown in Table 1. From these we calculate the frequencies of matings between a given male and female as

$$F_{ij,kl\,\times\,mn,op} = \frac{Y_{ij,kl}X_{mn,op}\left(1 + a_{ik\times np}\right)}{M_{np}}, \tag{1}$$

where $Y_{ij,kl}$ is the frequency of males that inherited haplotype *ij* from their mother and *kl* from their father, where the allele at the T locus is presented first followed by the allele at the P locus (thus, these males have genotype *ik* at the T locus and *jl* at the P locus), $X_{mn,op}$ is the frequency of females that inherited haplotype *mn* from their mother and *op* from their father, $1 + a_{ik\times np}$ is the fixed-relative preference of a female of genotype *np* at the P locus for a male of genotype *ik* at the T locus, and M_{np} is a normalizing constant that ensures that females are equally likely to mate regardless of their preferences

$$M_{np} = \sum_{i,j,k,l} Y_{ij,kl}\left(1 + a_{ik\times np}\right). \tag{2}$$

For example the frequency of matings between T_1T_2 males and P_2P_2 females is

$$\begin{aligned} &F_{T_1-,T_2-\times-P_2,-P_2} + F_{T_2-,T_1-\times-P_2,-P_2} \\ &\qquad = \frac{\left(Y_{T_1-,T_2-} + Y_{T_2-,T_1-}\right)X_{-P_2,-P_2}\left(1 + a_{T_1T_2\times P_2P_2}\right)}{M_{P_2P_2}}, \end{aligned} \tag{3}$$

where the "–" specifies the other alleles carried by these individuals.

We developed recursions using *Mathematica* (available upon request) based on the following lifecycle: viability selection, mating, recombination and gamete production, gamete union within mated pairs and offspring production, followed by the next census when genotype frequencies of offspring were calculated.

To make analytical progress, we assumed that selection and mating discrimination were weak (of order ε) relative to the rate of recombination, *r*, between the two loci. Doing so allowed us to perform a separation of time scales, where we determined processes that equilibrate rapidly and then assumed that the system remains near these “quasi-equilibrium” relationships when assessing the slower evolution of mating preferences. This approach is known as a quasi-linkage equilibrium (QLE) approximation (Barton and Turelli 1991; Kirkpatrick et al. 2002), and it greatly simplifies the analysis of complex evolutionary dynamics.

Results

QLE ANALYSIS

From our set of recursions for the genotype frequencies, we calculated an equivalent set of recursions for the allele frequencies and for the genetic associations within and between loci (such as the departure from Hardy–Weinberg equilibrium and linkage disequilibrium; see Barton and Turelli 1991). Assuming that viability selection and mating preferences are weak relative to the rate of recombination, it can be shown that if the association measures, *D*’s, are initially large (of constant order), then they rapidly decline to become small (of order ε). For example, to leading order, cis linkage disequilibrium decays at a rate *r* per generation. Thus, we can separate this rapid process of decay from the slower process of allele frequency change. Specifically, after a relatively short period of time ($\ll 1/\varepsilon$ generations), the system reaches a state in which all disequilibria are small (of order ε). We assume that this state has been attained in the following.

We next track changes at the T and P loci to leading order in ε. From our recursions we find that the T$_2$ and P$_2$ alleles change in frequency across a single generation by

$$\Delta t_2 = t_2' - t_2 = \frac{1}{2}\mathrm{var}_T\left(\left(V_{T_2\bullet} - V_{T_1\bullet}\right) + \left(a_{T_2\bullet} - a_{T_1\bullet}\right)\right) + O(\varepsilon^2) \tag{4a}$$

and

$$\Delta p_2 = p_2' - p_2 = \frac{\Delta t_2}{\mathrm{var}_T}\left(D_{TP} + D_{T,P}\right) + O(\varepsilon^3), \tag{4b}$$

where $\mathrm{var}_T = t_2(1 - t_2)$ is the variance when drawing a random allele from the population at the T locus. $V_{T_2\bullet} = t_2(1-s) + t_1(1-hs)$ is the marginal viability of the T$_2$ allele, $V_{T_1\bullet} = t_1 + t_2(1-hs)$ is the marginal viability of the T$_1$ allele, $a_{T_2\bullet} = t_2\,\bar{a}_{T_2T_2} + t_1\,\bar{a}_{T_1T_2}$ is the marginal preference for males with the T$_2$ allele, and $a_{T_1\bullet} = t_2\,\bar{a}_{T_1T_2} + t_1\,\bar{a}_{T_1T_1}$ is the marginal preference for males with the T$_1$ allele. In turn, these quantities depend on the mean strength of female preference for T$_x$T$_y$ males in populations at (or near) Hardy–Weinberg proportions

$$\bar{a}_{T_xT_y} = {p_2}^2\left(\frac{a_{T_xT_y\times P_2P_2}}{M_{P_2P_2}}\right) + 2p_1p_2 \times \left(\frac{a_{T_xT_y\times P_1P_2}}{M_{P_1P_2}}\right) + {p_1}^2\left(\frac{a_{T_xT_y\times P_1P_1}}{M_{P_1P_1}}\right), \tag{5}$$

where $M_{P_nP_p} = 1 + {t_2}^2(a_{T_2T_2\times P_nP_p}) + 2t_1t_2\left(a_{T_1T_2\times P_nP_p}\right) + {t_1}^2\left(a_{T_1T_1\times P_nP_p}\right)$. Finally, D_{TP} and $D_{T,P}$ are the cis and trans linkage disequilibrium between the T and P loci, respectively. Equation (4b) is a special case of the general multilocus QLE results of Kirkpatrick et al. (2002).

Although the genetic associations rapidly become small (of order ε), the genetic associations then change at a rate that is the same order of magnitude as the changes at the trait locus (O(ε)). Fortunately, the genetic associations do not enter into the recursions for the trait (eq. 4a). On the other hand, the genetic associations are critically important to changes at the preference locus, but because the allele frequencies change slowly at the preference locus (eq. 4b), we can perform a second separation of time scales, with genetic associations changing rapidly (at rates of order ε) and the preference allele changing slowly (at rates of order ε^2). By doing so, we can assume that the genetic associations have reached the quasi-equilibrium values predicted by solving their recursion equations (to order ε)

$$D_{T,P} = D_{TP} = \frac{1}{2}\mathrm{var}_T\,\mathrm{var}_P\left(\Delta a_{T_2\bullet} - \Delta a_{T_1\bullet}\right) + O(\varepsilon^2), \tag{6}$$

where $\mathrm{var}_P = p_2(1 - p_2)$. Here, $\Delta a_{T_2\bullet} = t_1\Delta a_{T_1T_2} + t_2\Delta a_{T_2T_2}$ and $\Delta a_{T_1\bullet} = t_1\Delta a_{T_1T_1} + t_2\Delta a_{T_1T_2}$ are the marginal changes in preference for T$_2$ and T$_1$, respectively, that would come from substituting a P$_1$ allele with a P$_2$ allele; and

$$\Delta a_{T_xT_y} = p_1\left(\frac{a_{T_xT_y\times P_1P_2}}{M_{P_1P_2}} - \frac{a_{T_xT_y\times P_1P_1}}{M_{P_1P_1}}\right) + p_2\left(\frac{a_{T_xT_y\times P_2P_2}}{M_{P_2P_2}} - \frac{a_{T_xT_y\times P_1P_2}}{M_{P_1P_2}}\right)$$

is the average change in female preference for males of genotype T$_x$T$_y$ that would come from substituting a P$_1$ allele with a P$_2$ allele.

Overall, assuming that both natural and sexual selection are weak, equation (4a) shows that the trait frequency changes at a rate that is order ε and depends on both viability selection (first term) and sexual selection (second term). The coefficient of $^1/_2$ comes from the fact that natural and sexual selection act only on males. Equation (4b) shows that the preference frequency changes much more slowly, at a rate proportional to ε^2. Change at the P locus occurs only as a correlated response to change at the T locus, where the linkage disequilibria measure the strength of that correlation and are given by (6). Consequently, the dynamics of this two-locus diploid model can be understood, to leading order, by tracking only the allele frequencies, allowing us to analyze the behavior of the model more easily.

DIRECTIONAL SELECTION

Because the QLE values of the linkage disequilibria (6) become positive if the P_2 allele causes females to have a stronger preference for males carrying the T_2 allele, equations (4) indicate that both T_2 and P_2 will rise in frequency when directional selection favors the T_2 allele (e.g., when both natural and sexual selection act in the same direction). Thus, as in the haploid model, when females prefer male traits that are also favored by natural selection, both the advantageous trait and the preferences for that trait rise in frequency, as argued by Fisher (1930). This process would lead to the sequential fixation of new trait alleles, until the point is reached at which natural selection opposes any further exaggeration of the trait. In the next section, we consider what happens when this second phase has been reached.

CURVES OF QUASI-NEUTRAL EQUILIBRIA

When natural and sexual selection oppose one another, the two-locus model can exhibit curves of "quasi-neutral equilibria," which are the analog of the truly neutral curves of equilibria observed in Kirkpatrick's (1982) haploid model. We use the term "quasi-neutral equilibria" because movement along these curves is exceedingly slow (Heisler and Curtsinger 1990). We can identify the approximate location of these curves by setting $\Delta t_2 = 0$ and solving for t_2; we will call the resulting quasi-equilibrium $\hat{t}_2$. Once $\Delta t_2 = 0$, change at the preference locus will also cease to leading order (see eq. 4b). When genetic associations are small and can be neglected, a balance between natural and sexual selection is struck at the quasi-equilibrium

$$\hat{t}_2 = \frac{W_{T_1T_2} - W_{T_1T_1}}{2W_{T_1T_2} - W_{T_1T_1} - W_{T_2T_2}}, \tag{7a}$$

where $W_{T_xT_y}$ is the average life-time fitness of male genotype T_xT_y: $W_{T_1T_1} = (1 + \bar{a}_{T_1T_1})$, $W_{T_1T_2} = (1 - hs)\left(1 + \bar{a}_{T_1T_2}\right)$, and $W_{T_2T_2} = (1 - s)\left(1 + \bar{a}_{T_2T_2}\right)$. Equation (7a) assumes only that genetic associations are negligible and is otherwise exact, regardless of the strength of natural and sexual selection. That said, equation (7a) must be solved numerically for $\hat{t}_2$, because the $\bar{a}_{T_2T_2}$ are themselves functions of $\hat{t}_2$ through the mean female preference functions, $M_{P_nP_p}$, in equation (5). Assuming that selection and mating preferences are weak, the quasi-equilibrium can be written explicitly as

$$\hat{t}_2 = \frac{\left(1 - hs + \bar{a}_{T_1T_2}\right) - \left(1 + \bar{a}_{T_1T_1}\right)}{2\left(1 - hs + \bar{a}_{T_1T_2}\right) - \left(1 + \bar{a}_{T_1T_1}\right) - \left(1 - s + \bar{a}_{T_2T_2}\right)} + O(\varepsilon), \tag{7b}$$

where the M_{np} are one, to leading order.

Equation (7a) corresponds to the classic polymorphic equilibrium in a diploid model with fitness $W_{T_xT_y}$; an equivalent relationship was noted by Heisler and Curtsinger (1990) to characterize the quasi-neutral equilibria. This equilibrium is valid when total fitness exhibits either underdominance or overdominance. Because $W_{T_xT_y}$ depends on p_2 via sexual selection, each value of p_2 will have its own corresponding quasi-equilibrium t_2 value. Thus we obtain a curve of quasi-neutral equilibria where viability selection and sexual selection are approximately balanced (see Fig. 1). In general, in the diploid model, the curve of quasi-neutral equilibria is truly curved, unlike the straight lines of equilibria found in the haploid model (Kirkpatrick 1982).

STABILITY ANALYSIS

We now find a stability condition for the curve of quasi-neutral equilibria, which allows us to predict when the curve is repelling. The eigenvalues (to linear order in ε) of the Jacobian matrix

$$\left(\begin{matrix} \dfrac{\partial t_2'}{\partial t_2} & \dfrac{\partial t_2'}{\partial p_2} \\ \dfrac{\partial p_2'}{\partial t_2} & \dfrac{\partial p_2'}{\partial p_2} \end{matrix}\right)_{t_2 = \dfrac{W_{T_1T_1} - W_{T_1T_2}}{W_{T_1T_1} - 2W_{T_1T_2} + W_{T_2T_2}}} \tag{8}$$

are $\lambda_1 = 1$ and

$$\lambda_2 = 1 - \frac{1}{2}\frac{\left(W_{T_1T_2} - W_{T_1T_1}\right)\left(W_{T_1T_2} - W_{T_2T_2}\right)}{\left(W_{T_1T_2} - W_{T_1T_1}\right) + \left(W_{T_1T_2} - W_{T_2T_2}\right)}. \tag{9}$$

The second eigenvalue, λ_2, corresponds to the classic eigenvalue governing stability of the polymorphic equilibrium (7) in a one-locus diploid model with fitness $W_{T_xT_y}$.

A point on the curve of quasi-neutral equilibria is unstable whenever $\lambda_2 > 1$. This occurs if $W_{T_1T_2}$ is lower than both $W_{T_1T_1}$ and $W_{T_2T_2}$, that is, whenever underdominance is induced at locus T via the combination of viability and sexual selection (Fig. 1A). Unlike in Kirkpatrick (1982), where all neutral curves were attracting, we find curves of quasi-neutral equilibria that are repelling, consistent with the finding of Gomulkiewicz and Hastings (1990) that, unlike in the haploid model, there exist cases in which both fixation boundaries of the trait locus are stable for a given female preference frequency. Conversely, when overdominance is induced, then the leading eigenvalue becomes $\lambda_1 = 1$ (because $-1 < \lambda_2 < 1$), indicating that any movement along the curve must occur slowly, if at all (to smaller order than ε).

Thus, the diploid model will tend to maintain polymorphisms at the trait and preference loci for long periods of time only when overdominance is induced, whereas the haploid model does so whenever the neutral curve of equilibria is present. The net effect of natural and sexual selection induces overdominance whenever

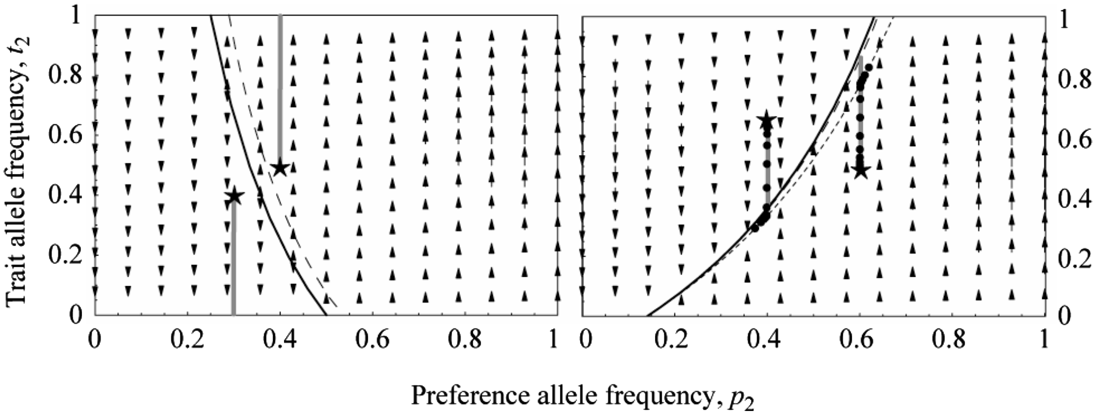

Figure 1. Quasi-neutral equilibria (solid curves) are repelling (left panel) if underdominance is induced at the trait locus and attracting (right panel) if overdominance is induced. In both panels, additivity was assumed at the preference locus, P_1P_1 females were assumed to mate at random ($a_{--\times P_1P_1} = 0$), and $r = 0.5$. Parameters in the left panel: $h = 0.5$, $s = 0.05$, $a_{T_1T_1\times P_2P_2} = 0.05$, $a_{T_1T_2\times P_2P_2} = 0.1$, and $a_{T_2T_2\times P_2P_2} = 0.2$. Parameters in the right panel: $h = 0.1$, $s = 0.007$, $a_{T_1T_1\times P_2P_2} = 0$, $a_{T_1T_2\times P_2P_2} = 0.005$, and $a_{T_2T_2\times P_2P_2} = 0.015$. The arrows describe the change in allele frequencies predicted by equations (4), and the solid curves illustrate the quasi-neutral equilibria (7b); the direction of the arrows and the position of the quasi-neutral curve are both unaffected by the strength of selection (i.e., by multiplying all of the s and $a_{ik\times np}$ terms by a common factor). The long-dashed curves give the more exact quasi-neutral curve (7a). Starting at the stars, the full set of recursion equations was numerically iterated (gray curves). In the left panel, the system rapidly reached fixation on the T_1 or T_2 allele, depending on the starting position. In the right panel, the system reached the quasi-neutral curve by about 50,000 generations but then moved extremely slowly along it for the next eight million generations (imperceptible on figure). To exaggerate this movement, we multiplied the strength of selection (the s and $a_{ik\times op}$ terms) in the right panel by five (dots: with the ith dot giving the position after 2^i generations). With stronger selection, the more exact equation (7a) is needed to describe the position of the curve (short-dashed curves), and the slow movement can now be seen ($2^{24} = 16.8$ million generations are shown).

$W_{T_1T_2} > W_{T_1T_1}$ and $W_{T_1T_2} > W_{T_2T_2}$ or, to leading order,

$$-h\,s + d\,\left(\bar{a}_{T_2T_2} - \bar{a}_{T_1T_1}\right) > 0 \text{ and}$$
$$(1-h)\,s - (1-d)\,\left(\bar{a}_{T_2T_2} - \bar{a}_{T_1T_1}\right) > 0, \qquad (10)$$

where d is a measure of the dominance of the male trait with respect to sexual selection, $\bar{a}_{T_1T_2} = d\,\bar{a}_{T_2T_2} + (1-d)\,\bar{a}_{T_1T_1}$, assuming Hardy–Weinberg proportions at the P locus with allele frequency p_2. d equals one if the females within the population perceive T_1T_2 males as equivalent to T_2T_2 males and equals zero if females perceive T_1T_2 as equivalent to T_1T_1. Assuming that viability selection acts against T_2 and sexual selection favors it, the balance will result in overdominance if viability selection acts weakly against heterozygous males (h sufficiently low) and sexual selection strongly favors heterozygous males (d sufficiently high). Specifically,

$$h < \min\left[\frac{d}{s}\left(\bar{a}_{T_2T_2} - \bar{a}_{T_1T_1}\right),\; 1 - \frac{(1-d)}{s}\left(\bar{a}_{T_2T_2} - \bar{a}_{T_1T_1}\right)\right]. \qquad (11)$$

If both conditions in (10) are reversed (i.e., h is greater than the maximum of the bracketed terms in eq. 11), underdominance is induced.

RUNAWAY SELECTION FOR DISADVANTAGEOUS TRAITS WHEN THE PREFERENCE FOR THEM IS RARE

Takahasi (1997) emphasized the fact that, in the haploid model of Kirkpatrick (1982), the female preference must reach a threshold frequency, perhaps through genetic drift, before a runaway can occur when the rare male trait is disadvantageous. This presents a challenge to the effectiveness of the fixed-relative preference scheme in generating conditions for runaway sexual selection, restricting runaway selection to cases in which the initial exaggeration of the male trait is favored by natural selection. Takahasi's point is generally true in the diploid model, except when the fitness of T_1T_2 heterozygotes approaches the fitness of T_1T_1 homozygotes (i.e., h approaches 0 and $a_{T_1T_2\times P_1P_1}$ approaches $a_{T_1T_1\times P_1P_1}$). In this case, the intercept of the quasi-neutral curve of equilibria approaches the corner at $t_2 = p_2 = 0$ (Fig. 2). Given that viability selection acts against the T_2 allele, trajectories along the $p_2 = 0$ axes will always point down, indicating that the curve is attracting in this region. Consequently, even the introduction of a small initial frequency of the P_2 allele can result in the system moving to the right of the curve, leading to the rise of the trait and preference (Fig. 2).

ACCURACY OF THE QLE APPROXIMATION

The approach that we have taken assumes weak selection relative to the rates of recombination. With stronger selection, we find

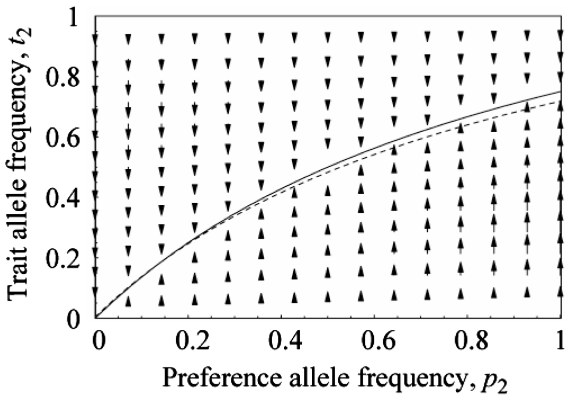

Figure 2. When the fitness of T_1T_1 males in the presence of P_1P_1 females is the same as the fitness of T_1T_2 males ($h = 0$ and $a_{T_1T_1\times P_1P_1} = a_{T_1T_2\times P_1P_1}$), the quasi-neutral equilibrium curve passes through the origin $\{0,0\}$ (dashed: eq. 7a; solid: eq. 7b). Thus a small perturbation to the right will cause the trait to rise in frequency, with a correlated increase in the preference. Additivity was assumed at the preference locus, and P_1P_1 females were assumed to mate at random ($a_{\_\_\times P_1P_1} = 0$). Parameters: $h = 0$, $s = 0.05$, $a_{T_1T_1\times P_2P_2} = 0$, $a_{T_1T_2\times P_2P_2} = 0.075$, and $a_{T_2T_2\times P_2P_2} = 0.1$.

numerically that equation (7a) continues to describe the position of the quasi-neutral curve of equilibria, whereas the weak selection approximation (7b) becomes increasingly inaccurate (e.g., Fig. 1B). In addition, we explored the consequences of reducing the rate of recombination (Supporting Fig. S1). Except near the quasi-neutral curve, the behavior of the system was unaffected by the rate of recombination. Even though linkage disequilibrium is critically important for the evolution of female preferences, recombination acts both to destroy disequilibrium and to create it (by placing maternally inherited preference alleles together onto the same chromosome as the paternally inherited trait allele that was preferred by the mother). These two roles balance and explain why recombination does not affect the linkage disequilibrium (6) to leading order. Near the quasi-neutral curve, however, lower order terms begin to dominate, and recombination does influence the dynamics. For example, with overdominance, we found that the direction of the very slow movement along the quasi-neutral curve depends on the rate of recombination (Supporting Fig. S1C), in a manner consistent with Otto (1991).

COSTLY PREFERENCES

Finally, we explored the impact of costly female preferences on the Fisherian runaway process by assuming that females bearing the P_2 allele have stronger preferences but are directly selected against. Specifically, P_2P_2 females suffer a fixed reduction in fitness of z, whereas P_1P_2 females suffer a fitness reduction of h_f z, regardless of the composition of the population. If the cost, z, is of the same order as the preferences themselves, $a_{ik\times np}$, then at QLE, selection acts to eliminate the p_2 allele at rate

$$\Delta p_2 = \mathrm{var}_P \frac{\left(\left(1-h_f\right)\, p_1 + h_f\, p_2\right)\, z}{2} + O(\varepsilon^2), \qquad (12)$$

which does not depend on the preferences, only on the costs. If we assume that the cost of being choosy is weak relative to the preferences (i.e., z is of order ε^2), then the frequency of the preference allele changes according to the sum of (4b) and (12).

This result has interesting implications. Whenever the trait is evolving and Δt_2 is large enough that equation (12) is small relative to (4b), the dynamics will be relatively unaffected by costly preferences. Over time, however, trait evolution will slow down, either because the system reaches trait fixation or the quasi-neutral curve of equilibria (7). Once it does, the costs will dominate the dynamics (eq. 12 will overwhelm eq. 4b once Δt_2 becomes too small). Female preferences will then decline over time, moving the system left along the preference axis (if the trait is fixed) or sliding down the quasi-neutral curve (if the curve is attracting). (If the curve is repelling, as in Fig. 1A, and $t_2 \approx 1$, the system will move to the left [weaker preferences] until the quasi-neutral curve is reached and then down [trait reduction].) Metaphorically, the system behaves much like the child's game "chutes and ladders," where costly preferences can invade and spread as long as the male trait is changing, only to shoot back down toward the origin once the trait equilibrates. For preferences to persist over the longer term under this model, either the trait must continually change or preferences must evolve to be cost-free or even beneficial while the trait is changing (e.g., by allowing species or kin recognition).

One final note: costs of choosiness might not be fixed as assumed here but might depend on the composition of the male population. For example, females might be able to detect when the male trait is monomorphic and accept any male, without suffering a fitness reduction. In this case, costs of female preferences will again cause the system to shoot down the quasi-neutral curve, but once the trait locus is fixed, relative costs would disappear, allowing female preferences to remain indefinitely. Thus, the ultimate outcome of the process of sexual selection depends on the nature of the costs of being choosy.

Discussion

Neutral curves or curves of quasi-neutral equilibria have appeared in haploid, polygenic, and diploid models of Fisherian sexual selection that lack costs to being choosy (Kirkpatrick 1982;Lande 1981; Heisler and Curtsinger 1990; Takahasi 1997). Here we consider the diploid case and, using a QLE analysis, analytically derive general equations for the curves of quasi-neutral equilibria and specify the conditions under which they are attracting or repelling. Added to the work of Gomulkiewicz and Hastings (1990) and Otto (1991), which consider dynamics near fixation at the trait locus and preference locus, respectively, this work helps to paint a more complete picture of the diploid two-locus model of Fisherian sexual selection.

The most important qualitative result is that the balance between the dominance imposed by natural selection and the dominance imposed by sexual selection determines whether the quasi-neutral curve of equilibrium is repelling (net underdominance) or attracting (net overdominance). The position of these curves is, to leading order, given by the standard one-locus polymorphic equilibrium (7), with fitness given by the net effect of natural and sexual selection within a population with preference allele frequency p_2. In cases in which overdominance is induced, the diploid model of fixed relative preferences, like the haploid model, predicts the maintenance of polymorphism at the trait and preference loci for long periods of time, once evolution reaches the point where the costs of the trait due to natural selection balance the benefits due to sexual selection. When underdominance is induced, polymorphism is not maintained, however, and instead we see a repelling curve of internal equilibria. These repelling curves are potentially of biological interest, because very small amounts of drift could lead isolated populations to different sides of these curves, selecting against exaggeration on one side and for further exaggeration on the other. Furthermore, much more rapid changes in the trait and preference occur when the curve becomes repelling, causing a runaway process (Lande 1981; Hall et al. 2000). For example, in Figure 1A, when the trait allele T_2 is rare, a slight change in p_2 from just below 0.5 to just above it is enough to drive selection on the trait in opposite directions, potentially contributing to reproductive isolation between populations.

Whether attracting or repelling curves of equilibria are exhibited in the fixed mating preference model of sexual selection is thus sensitive to the ploidy of the organism involved and to the nature of dominance with respect to viability and mating success. Previous work has also shown that the repelling/attracting nature of the internal curves is sensitive to the exact type of preference model used, the pleiotropic nature and frequency of mutations affecting traits and preferences, and the fitness costs of mating preferences (Lande 1981; Seger 1985; Takahasi 1997; Hall et al. 2000).

In our analysis, we have only kept the leading order terms in the QLE analysis, and we have not addressed the dynamics that occur over the much longer time periods once a population reaches the quasi-neutral curve. We know from simulations (Heisler and Curtsinger 1990; Otto 1991; see also Fig. 1) that trajectories that hit the quasi-neutral curves do not stop. Rather they move very slowly near the curve. For example, in the cases considered in Figure 1B, the full set of recursions was iterated for millions of generations, and yet movement along the curve is so slow as to be imperceptible to the eye over this time period (gray curve) unless we strengthened selection (dots). With such slow movement, it is likely that other evolutionary forces not considered in this model (mutation, migration, environmental change, and genetic drift) will govern the long-term changes in trait and preference in the vicinity of the quasi-neutral curves. Furthermore, as discussed at the end of the Results section, even very weak costs of female preferences dominate the dynamics once trait evolution slows down near these quasi-neutral curves, driving the loss of costly female preferences.

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Supporting Information

The following supporting information is available for this article:

Figure S1. Recombination between the preference and trait loci has little effect on the dynamics of the diploid model of sexual selection except near the quasi-neutral equilibria (solid curves based on eq. 7b; dashed curves based on eq. 7a).

Supporting Information may be found in the online version of this article.
(This link will take you to the article abstract).