RUNAWAY SEXUAL SELECTION WHEN FEMALE PREFERENCES ARE DIRECTLY SELECTED

DAVID W. HALL,[1] MARK KIRKPATRICK, AND BRIAN WEST
Section of Integrative Biology C0930, University of Texas, Austin, Texas 78712
[1]*E-mail: davehall@uts.cc.utexas.edu*

Abstract.—We introduce models for the runaway coevolution of female mating preferences and male display traits. The models generalize earlier results by allowing for direct natural selection on the preference, arbitrary forms of mate choice, and fairly general assumptions about the underlying genetics. Results show that a runaway is less likely when there is direct selection on the preference, but that it is still possible if there is a sufficiently large phenotypic correlation between the female's preference and the male's trait among mated pairs. Comparison of three preference functions introduced by Lande (1981) shows that open-ended preferences are particularly prone to a runaway, and that absolute preferences require very large differences between females in their preferences. We analyze the causes of the runaway seen in a model developed by Iwasa and Pomiankowski (1995).

Key words.—Mating preferences, runaway, sexual selection.

Why have females of some species evolved mating preferences for males with extreme secondary sexual traits? A mechanism that has been widely discussed was proposed by Fisher (1958, p. 152) in a famous but obscure passage. In modern terms, Fisher suggested that male display traits and female preferences will naturally become genetically correlated. As a result, further exaggeration of the male trait caused by sexual selection will cause the preference itself to become more exaggerated as a correlated selection response. Because more exaggerated preferences in turn cause stronger sexual selection on the male trait, the preference and trait could coevolve in an explosive "runaway process." Fisher's verbal logic was verified much later by genetic models (O'Donald 1980; Lande 1981; Kirkpatrick 1982).

Theoretical work since Fisher has revealed two key points that he did not discuss (reviewed in Kirkpatrick and Ryan 1991; Andersson 1994). The first regards the outcome of the coevolution between the preference and male trait. Genetic models show that one possibility is that they will arrive at a stable equilibrium point. However, if the genetic covariance between the preference and trait is large enough, the equilibrium becomes unstable. In a landmark paper, Lande (1981) discovered that in such a case, a rapid burst of evolution will follow in which the trait and preference evolve at an exponentially increasing rate until genetic variation is exhausted or the intensity of natural selection becomes very severe. Lande identified this unstable outcome with what Fisher described verbally as the runaway process. Others have used runaway to indicate whether evolution of the male trait leads to exaggerated female preference at equilibrium, regardless of the equilibrium's stability, whereas Fisher did not make that distinction. Generally, however, the term runaway now refers to the outcome discovered by Lande in which a population evolves rapidly away from an unstable equilibrium.

A second development since Fisher is the appreciation of other processes that can establish extreme mating preferences. One important mechanism is natural selection acting directly on the genes underlying a preference (Lande 1981; Kirkpatrick 1982; Bulmer 1989). Direct selection on preference genes happens for many reasons. For example, natural selection acting on the pleiotropic effects of genes that affect mating preferences will also cause those genes to fall under direct selection (Kirkpatrick 1982; 1985). Male parental care generates direct selection on preferences because a female's mate choice affects her fecundity. Search costs may also lead to direct selection on preference (Kirkpatrick 1985; Pomiankowski 1987). These considerations have led to the suggestion that some kind of direct selection may be acting on virtually all preference genes (Kirkpatrick and Ryan 1991; Ryan 1997).

Despite the large amount of work that has been done on the runaway process and on direct selection of preference genes, we do not know how the two mechanisms interact. We do know that if direct natural selection favors a particular value of the preference, then there is an equilibrium in which the preference lies at its favored value. At this equilibrium, the male trait takes a value that is a compromise between the forces of natural and sexual selection acting on the male trait (Lande 1981, eq. (10); Kirkpatrick 1985, eq. (12)). But is this equilibrium always stable, or can an unstable runaway ensue if the genetic covariance becomes sufficiently large? Intuitively, we might suspect that direct selection on the preference will make the equilibrium more stable and therefore make a runaway less likely. That conclusion has not, however, been studied with a genetic model.

Another reason for revisiting the runaway is to learn more about the conditions under which it will occur even when there is no direct selection on the preference. Lande's (1981) conclusions were developed in two stages. The first assumes that females choose males using one of three preference rules, and that the additive genetic and phenotypic values for the preference and trait are normally distributed. He then found the conditions for a runaway given known values for the genetic variances and covariance. A question we consider here is when will a runaway occur if the characters are not normally distributed and females choose their mates by any kind of process. In the second stage of Lande's analysis, he made detailed assumptions about the genes underlying the preference and trait. With those, he found that a runaway occurs when mutation rates at the preference loci are suffi-

ciently large. The genetic assumptions used in this second phase of the analysis, however, have been criticized as biologically unrealistic (Turelli 1988). This paper investigates when a runaway is possible under more general and perhaps realistic assumptions about the genetics.

We begin by developing a model of the runaway that allows for direct selection on the preference and that makes fairly general genetical and behavioral assumptions. Following Lande's approach, this section assumes that the critical genetic covariance between the preference and trait has a known value. Analysis shows that direct selection of preference genes does indeed stabilize the equilibrium, but that a runaway can still occur if the genetic covariance is big enough. Next, we use recent theoretical results that allow the genetic covariance to be calculated to determine when the runaway will occur under a broad range of mating behaviors. We then return to the three preference rules introduced by Lande (1981) to find when a runaway will occur under those conditions when there is direct selection on the preference. The analytic results are checked by simulations. Finally, we use these results to study the runaway in a model of cycling sexual selection introduced by Iwasa and Pomiankowski (1995).

THE MODEL

Consider a species with two sex-limited characters, a male trait with mean $\bar{t}$ and a female preference with mean $\bar{p}$. The female preference can be any character that influences her choice of mate. We make no assumptions about how mate choice works or what the mating system is, only that pairing is controlled by the females. Females that differ in their preference differ in the likelihood that they will mate with a male with a given trait value. Thus, for our purposes a ''preference'' is any phenotype expressed by females that affects the probabilities that they will mate with different types of males. Direct selection on preference genes causes a female's preference to affect her survival and fecundity. For simplicity we assume that selection on preferences is not affected by the distribution of the male trait. The model could be easily extended to those situations, however, and we expect that the qualitative conclusions will not be changed. We take the convention that the preference is measured in such a way that larger values of $\bar{p}$ favor larger values of the male trait.

Genetic variation in the preference and trait is caused by genes with additive effects (i.e., no dominance or epistasis). The genes are autosomal, and there can be either haploid or diploid inheritance. There can be any number of loci, and no restriction is made on the distribution of allelic effects or the linkage relations between the loci. The genetic covariance between the trait and preference is denoted G_{tp}. This covariance arises naturally from the nonrandom mating between females with extreme preferences and males with extreme traits. Nonrandom mating produces linkage disequilibrium between loci affecting the trait and those affecting the preference; the trait-preference covariance produced this way is independent of the genetic linkage between the loci (Lande 1981; Kirkpatrick 1982; Barton and Turelli 1991; Kirkpatrick and Barton 1997). At this point we will simply view the

genetic covariance as a known quantity; later in the paper we will calculate its size.

When the population is near an equilibrium, the forces of directional selection acting on the male trait and female preference are weak. In that case, the changes in their means caused by one generation of selection are

$$\Delta \bar{t} = \frac{1}{2} G_t \beta_t(\bar{t}, \bar{p}) + \frac{1}{2} G_{tp} \beta_p(\bar{p}), \tag{1a}$$

$$\Delta \bar{p} = \frac{1}{2} G_p \beta_p(\bar{p}) + \frac{1}{2} G_{tp} \beta_t(\bar{t}, \bar{p}). \tag{1b}$$

Here G_t and G_p are the additive genetic variances and β_t and β_p are the directional selection gradients for the male trait and female preference, respectively. The βs represent the selective force restoring the population to the equilibrium, and are defined as the regression of lifetime relative fitness regressed onto the character value (see Lande and Arnold 1983). At equilibrium the βs are equal to zero (assuming the preference and trait are not perfectly correlated). The selection gradient on the male trait is a function of the mean preference $\bar{p}$ as well as the mean trait $\bar{t}$ because male fitness depends in part on sexual selection caused by the preference. The factors of 1/2 are present due to the sex-limited expression of both characters.

Equations (1) hold for any intensity of selection if the additive genetic values for the trait and preference are normally distributed in the population. They hold much more generally, however, as long as directional selection is weak and the genes affecting the characters have additive effects (T. Johnson and M. Kirkpatrick, unpubl. data). Because we are interested in how the population evolves near an equilibrium, directional selection is necessarily weak and so the following results apply whenever the more general genetic assumptions outlined above are met. Without losing any generality, it is convenient to choose a scale of measurement that sets the equilibrium values of the male trait and female preference equal to zero.

The Runaway Condition

In a runaway process, a population that is close to the equilibrium will move farther away from it. We can determine when that will happen with a linear stability analysis. Linearizing the selection gradients around the equilibrium using a Taylor expansion gives:

$$\Delta \bar{t} = -\frac{1}{2} G_t k_t \bar{t} + \frac{1}{2}(G_t k_{tp} - G_{tp} k_p)\bar{p}$$

$$+ \text{ terms of order } \bar{t}^2, \bar{p}^2, \tag{2a}$$

$$\Delta \bar{p} = -\frac{1}{2} G_{tp} k_t \bar{t} + \frac{1}{2}(G_{tp} k_{tp} - G_p k_p)\bar{p}$$

$$+ \text{ terms of order } \bar{t}^2, \bar{p}^2, \tag{2b}$$

where

$$k_t = -\frac{\delta}{\delta \bar{t}} \beta_t(\bar{t}, \bar{p}), \qquad k_{tp} = \frac{\delta}{\delta \bar{p}} \beta_t(\bar{t}, \bar{p}),$$

$$k_p = -\frac{\delta}{\delta \bar{p}} \beta_p(\bar{p}), \tag{3}$$

and all the derivatives are evaluated at the equilibrium $\bar{t} = \bar{p} = 0$. The sizes of k_t and k_p measure the strength of natural and sexual selection restoring the trait and preference to their equilibrium values. Stabilizing selection on the male trait and female preference implies k_t and k_p are both positive: stronger natural selection occurs against trait or preference values further from the optimum. The value of k_{tp} measures how rapidly a change in the mean preference increases the strength of sexual selection acting on a male trait and is thus assumed to be positive. For there to be a stable equilibrium there must be net stabilizing selection on the preference and/or male trait.

Equations (2) can be used to form a stability matrix whose leading eigenvalue is:

$$\lambda = \frac{1}{4}[-G_t k_t + G_{tp} k_{tp} - G_p k_p \\ + \sqrt{(G_t k_t - G_{tp} k_{tp} + G_p k_p)^2 - 4(G_t G_p - G_{tp}^2)k_t k_p}]. \tag{4}$$

The eigenvalue can be real or complex. When it is real, stability is implied whenever $-2 < \lambda < 0$. When it is complex, stability is implied whenever $|1 + \lambda| < 1$. If the stabilizing component of selection acting on the preference and male trait is weak, Equation (4) can be simplified by neglecting the second term under the square root sign. Such an approximation is valid whenever $(G_{tp} k_{tp} - G_t k_t - G_p k_p)^2 \gg 4(G_t G_p - G_{tp}^2)k_t k_p$, and based on our simulation results, seems to work reasonably well even when this inequality is not met. With this approximation, the equilibrium is unstable, and runaway occurs, when:

$$G_{tp} \geq \frac{G_t k_t + G_p k_p}{k_{tp}}. \tag{5}$$

This result shows that a runaway is possible even in the presence of direct selection acting on the preference. A runaway is easy to trigger (i.e., a smaller genetic covariance G_{tp} is required) when stabilizing selection on the male trait and female preference are weak (k_t and k_p are small) and when small changes in the preference have a large effect on the force of sexual selection experienced by males (k_{tp} is large). When there is no direct selection on the preference, then $k_p = 0$ and Equation (5) is identical to the condition obtained by Lande (1981, eq. (12) with $k_t/k_{tp} = \alpha + \epsilon$). Thus, his conclusions about the runaway when preferences are selectively neutral do not depend on his assumption that breeding values for the preference and trait are normally distributed.

These conclusions hold regardless of how the genetic covariance between the preference and trait is maintained. The most interesting (and perhaps common) way that the covariance develops is from the linkage disequilibrium that naturally develops between preferences and male traits. The next section considers this possibility.

Evolution of the Covariance

We now ask when a runaway will occur if the key genetic covariance G_{tp} is caused entirely by the linkage disequilibrium that naturally develops between trait and preference loci. Kirkpatrick and Barton (1997, eq. (10)) found the genetic

correlation between a preference and male trait under the general assumptions about genetics and behavior that we have made in this paper. From that result it follows immediately that the genetic covariance G_{tp} is

$$G_{tp} = \frac{1}{2}\rho_{tp}\frac{G_t G_p}{\sigma_t \sigma_p}, \tag{6}$$

where σ_t and σ_p are the phenotypic standard deviations for the male trait and female preference respectively. The parameter ρ_{tp} is the phenotypic correlation between the preference in females and trait value in males among breeding pairs. This correlation can in principle be measured empirically. It can also be calculated if one assumes particular rules for how females choose males, as we will do below. The approximations leading to Equation (6) assume the correlation is weak ($\rho_{tp} \ll 1$), implying that individual females do not vary greatly in their preferences.

Equation (6) can now be substituted into Equation (5) to give an expression for runaway in terms of the phenotypic correlation between the preference in females and trait value in males among breeding pairs:

$$\rho_{tp} \geq \frac{2\sigma_t \sigma_p(G_t k_t + G_p k_p)}{k_{tp} G_t G_p}. \tag{7}$$

This is a reasonably general result for the conditions under which a runaway will happen. It allows for any form of female choice and direct selection on the preference. It should also hold regardless of what maintains genetic variation in the preference and trait so long as those forces are weak. The main simplifying assumptions leading to Equation (7) are that the genes have additive effects, that the strength of selection returning the population to the equilibrium is weak, and that females do not differ greatly in their preferences.

Our analysis has focussed on the stability of the mean preference and trait. In principle, an analysis of the full genetic system (including all the allele frequencies and linkage disequilibria) could reveal cases where our results suggest an equilibrium is stable when in fact it is unstable. That is, we have found criteria that are sufficient but perhaps not necessary for instability. The simulation results presented below, however, suggest that the the criteria given here are in fact quite accurate.

Runaway with Specific Preference Functions

Lande (1981) analyzed the runaway assuming that females choose males according to one of three specific preference rules. In this section we calculate the correlation ρ_{tp} under these preference rules and combine the results with those from the last section to determine when runaway occurs with direct selection.

Females exhibiting *psychophysical preference* have open-ended preferences for males with more extreme trait values. Specifically, a female with preference value p has a preference for a male with trait value t that is proportional to $\exp\{tp\}$. Females with *absolute preference* most prefer males that match their pre-existing search image, and their preference falls off symmetrically on either side of this most preferred male. Specifically, a female's preference is proportional to

TABLE 1. The phenotypic correlation ρ_{tp} of the preference in females and the trait in males across mating pairs for Lande's (1981) three preference functions. The genetic covariance G_{tp}, obtained from Equation (6), is also given. These are weak selection approximations that assume $\sigma_t^2 \ll \nu^2$.

	Psychophysical	Absolute	Relative
ρ_{tp}	$\dfrac{\sigma_t \sigma_p}{\sqrt{1 + \sigma_t^2 \sigma_p^2}}$	$\dfrac{\sigma_t \sigma_p}{\sqrt{\nu^4 + \sigma_t^2 \sigma_p^2}}$	$\dfrac{\sigma_t \sigma_p}{\sqrt{\nu^4 + \sigma_t^2 \sigma_p^2}}$
G_{tp}	$\dfrac{G_t G_p}{2\sqrt{1 + \sigma_t^2 \sigma_p^2}}$	$\dfrac{G_t G_p}{2\sqrt{\nu^4 + \sigma_t^2 \sigma_p^2}}$	$\dfrac{G_t G_p}{2\sqrt{\nu^4 + \sigma_t^2 \sigma_p^2}}$

TABLE 2. The values for the ks that determine stability of the equilibrium for each of the three preference functions (see eq. (3)). These are weak selection approximations that assume $\sigma_p^2 \ll \omega_p^2$ and $\sigma_t^2 \ll \omega_t^2, \nu^2$.

	k_t	k_{tp}	k_p
Psychophysical	$\dfrac{1}{\omega_t^2}$	1	$\dfrac{1}{\omega_p^2}$
Absolute	$\dfrac{\nu^2 + \omega_t^2}{\nu^2 \omega_t^2}$	$\dfrac{1}{\nu^2}$	$\dfrac{1}{\omega_p^2}$
Relative	$\dfrac{1}{\omega_t^2}$	$\dfrac{1}{\nu^2}$	$\dfrac{1}{\omega_p^2}$

$\exp\{-(t - p)^2/2\nu^2\}$, where p is the trait value she most prefers and ν measures the range of trait values around p that a female will readily accept. Females exhibiting *relative preference* base their preference on the distribution of males in the population. A female with preference p most prefers males whose trait value t is p above the average male. Her preference is proportional to $\exp\{-[t - (p + \bar{t}^*)]^2/2\nu^2\}$, where $\bar{t}^*$ is the mean trait among males that are available to mate and ν again reflects the range of males around her most preferred type that a female will readily accept.

For all three preference functions, the frequency of females with preference p mating with males with trait value t is bivariate normally distributed, and the correlation coefficient for this distribution is readily obtained. This coefficient is the correlation between the male trait and the female preference among mated pairs, ρ_{tp}. Table 1 gives its value for the three preference functions as well as the genetic covariances that they produce.

To determine when a runaway will occur, we also need the ks that appear in Equation (7). To do that, we need to make an assumption about the form of natural selection. Lande (1981) assumed there is stabilizing natural selection on the male trait that takes the form of a gaussian function with variance ω_t^2. To that we will add the assumption that the fitness function acting on the preference in females is proportional to a gaussian function with variance ω_p^2. Thus the intensity of stabilizing natural selection on the female preference and male trait becomes stronger as the values of ω_p^2 and ω_t^2 decrease, respectively. With these assumptions and results in Lande (1981), the selection gradients β_t and β_p can be calculated directly, and from them the ks. These results are given in Table 2. (These results can be generalized to fitness functions that are not gaussian. The ω_p^2s that appear in the following expressions are replaced by $-1/\{(d^2/dp^2) \ln[w_p(p)]\}$, where w_p is the fitness function for the preference and the derivative is evaluated at the preference equilibrium. The ω_t^2s are replaced by the analogous expression for the male trait.)

The conditions for runaway under the three preference rules are found by substituting the ks into equation (6), which gives

Psychophysical:

$$0 < \frac{1}{2} G_t G_p - \frac{G_t}{\omega_t^2} - \frac{G_p}{\omega_p^2} \qquad (8a)$$

Absolute:

$$0 < \frac{G_t G_p}{2\nu^4} - \frac{G_t(\nu^2 + \omega_t^2)}{\nu^2 \omega_t^2} - \frac{G_p}{\omega_p^2} \qquad (8b)$$

Relative:

$$0 < \frac{G_t G_p}{2\nu^4} - \frac{G_t}{\omega_t^2} - \frac{G_p}{\omega_p^2} \qquad (8c)$$

These results show that a runaway is possible with all three preference functions even when there is direct selection on the preference. As one would anticipate, however, runaway becomes increasingly less likely as the strength of stabilizing natural selection on the preference and male trait become stronger (that is, ω_p^2 and ω_t^2 become smaller). A runaway is possible if the genetic variances of the trait and preference are sufficiently large. This is the fundamental explanation for Lande's (1981) finding that a runaway will occur if the mutation rate at preference loci is sufficiently large.

With psychophysical and relative preferences, Equations (8a) and (8c) show that as long as there is genetic variation for the preference and trait a runaway will be triggered if natural selection on the characters is sufficiently weak. The propensity of psychophysical preferences to trigger runaways was noted by Lande (1981). A runaway is much more difficult to initiate, however, when preferences are absolute. The reason is that absolute preferences exert stabilizing selection on the male trait.

Even in the absence of any natural selection on the preference or male trait, Equation (8b) shows that absolute preferences require $G_p > 2\nu^2$ for a runaway to happen. That implies that differences among females in the males that they most prefer are much larger than the range of males that any single female will find acceptable. Although possible, it seems on biological grounds that this is probably very rarely the case. The conditions only become less plausible when the stabilizing effects of natural selection on the male trait and preference are included in the model. In short, a runaway may be implausible in species that have absolute preferences.

Simulations

To test the accuracy of our analytic approximations, we compared them with results from a simulation model. This simulation is based on the ''infinitesimal model'' of inheritance (Fisher 1918; Bulmer 1971). Genetic variation in the preference and male trait is assumed to be caused by a large (effectively infinite) number of unlinked loci with equivalent

TABLE 3. Comparison of analytic approximations and simulation results for the conditions leading to a runaway. The simulation is based on the infinitesimal model of inheritance, as described in the text. The genetic variances for the male trait and preference, G_t and G_p, were determined by simulation and account for linkage and Hardy-Weinberg disequilibria. Females have psychophysical preferences (and so k_{tp} = 1). The analytic approximation for the genetic covariance, G_{tp}, is based on Equation (6). Approximations for the minimum strength of stabilizing selection on the preference (threshold k_p) that will prevent a runaway, k_p (1) and k_p (2), are based on Equations (4) and (5), respectively, using the analytic approximation for the genetic covariance. In all simulations we assume that the heritability of the male trait and female preference are both equal to 0.5. An asterisk indicates that the equilibrium is predicted to be stable for all values of k_p.

Parameters			Analytic approximations			Simulation results	
k_t	G_t	G_p	G_{tp}	k_p (1)	k_p (2)	G_{tp}	k_p (3)
0.01	1.26	0.108	0.055	0.40	0.39	0.061	0.43
0.01	1.19	0.085	0.043	0.37	0.36	0.046	0.38
0.01	1.13	0.063	0.031	0.32	0.32	0.033	0.33
0.01	1.08	0.041	0.020	0.24	0.24	0.021	0.24
0.01	1.04	0.020	0.010	*	*	0.010	*
0.01	0.96	0.107	0.043	0.32	0.31	0.046	0.33
0.01	0.68	0.105	0.032	0.24	0.24	0.033	0.25
0.01	0.43	0.103	0.021	0.16	0.16	0.021	0.16
0.01	0.21	0.102	0.010	*	0.08	0.010	0.08
0.02	1.25	0.109	0.055	0.28	0.27	0.061	0.30
0.02	1.18	0.086	0.043	0.23	0.22	0.046	0.24
0.02	1.12	0.063	0.031	0.14	0.14	0.033	0.15
0.02	1.07	0.042	0.021	*	*	0.021	*
0.02	1.03	0.020	0.010	*	*	0.010	*
0.02	0.95	0.107	0.043	0.23	0.22	0.046	0.24
0.02	0.68	0.105	0.031	0.17	0.17	0.033	0.18
0.02	0.43	0.103	0.020	0.12	0.12	0.021	0.12
0.02	0.21	0.102	0.010	*	0.06	0.010	0.06

effects. Exact recursion equations can be derived that account for the evolution of the genetic variances for the preference and male trait as well as the genetic covariance between them (Kirkpatrick 1996).

The simulation results presented in Table 3 are chosen to make two comparisons. First, the analytic approximation for the genetic covariance G_{tp} between the female preference and male trait from Equation (6) shows good agreement with the simulation results. The analytic approximation improves as the genetic variance in the male trait or female preference declines. Second, the analytic approximation for G_{tp} is then used with Equations (4) and (5) to find the minimum strength of stabilizing selection (threshold k_p) on the preference needed to prevent a runaway. The predicted threshold k_p is compared to the value obtained from the simulation. These predictions are more accurate when the error in the covariance is small and when selection on the male trait is weak. The third result from the simulations, for which data are not shown, is that for parameter combinations that give a threshold k_p close to zero, the analytical approximation does less well. This is because the error in the estimation of the covariance becomes large relative to the absolute value of the threshold k_p. From these results, we conclude that the analytic approximations are performing well throughout most of the region of the parameter space where they are predicted to do well (weak selection and small genetic covariance).

Runaway in the Iwasa-Pomiankowski Model

Iwasa and Pomiankowski (1995) introduced a model of the runaway that includes biased mutation that exerts a directional force on the mean male trait. The model is interesting because it shows unusual dynamics. Under some conditions, a population will rapidly runaway from the equilibrium, then slowly return. This cycle repeats indefinitely.

A major conclusion of the paper is that biased mutation can stabilize an equilibrium that would otherwise show runaway. In this section we show that the underlying reason for their finding has nothing to do with biased mutation per se. Instead, it depends on the strength of stabilizing selection, in accord with the results developed above. Biased mutation shifts the location of the equilibrium, which in turn changes the intensity of stabilizing natural selection acting on the preference and male trait. It is the change in stabilizing selection that affects the stability of the equilibrium.

First we will show that the analysis developed above correctly predicts the stability properties of the Iwasa-Pomiankowski model. They assumed a particular natural selection fitness function in which the male trait is selectively neutral at its viability optimum but is very strongly selected when it deviates from the optimum:

$$w(t) = \exp\{-ct^4\} \tag{9}$$

They further assumed psychophysical preferences, weak selection on the preferences, and small phenotypic variances. The per generation change in the mean trait caused by mutational bias is denoted u.

Using their assumptions, we can determine the equilibrium and then calculate the ks and the genetic covariance G_{tp} at the equilibrium. Substituting those values into Equation (5) gives the conditions required for the equilibrium to be unstable. Runaway occurs when the mutational bias is less than a critical threshold:

$$u < \frac{1}{12\omega_{\bar{p}}^2}\sqrt{\frac{G_p^3}{6c}}. \tag{10}$$

This is exactly Equation (6) of Iwasa and Pomiankowski (1995) (albeit with two trivial changes in notation).

Two conclusions follow. First, this exercise serves as a check on our work, as we can rederive a previous result using our framework. Second, it reveals the underlying cause of why biased mutation affects stability in the Iwasa-Pomiankowski model. Equation (10) was found by considering only the strength of stabilizing selection on the preference and trait at the equilibrium. Biased mutation exerts a directional force on the male trait, which changes its equilibrium value. It also generates indirect selection on the preference, changing the preference equilibrium, which in turn affects the shape of the sexual fitness function for males. The net result in some cases is to move the equilibrium from a point where stabilizing selection prevents a runaway to one where it does not. These effects are illustrated in Figure 1.

Under the fitness function of Equation (9), increasing mutational bias will inhibit a runaway. However, the opposite result can occur: biased mutation can actually trigger a runaway. With a male fitness function that has a different shape than Equation (9), increasing mutation can shift the equilib-
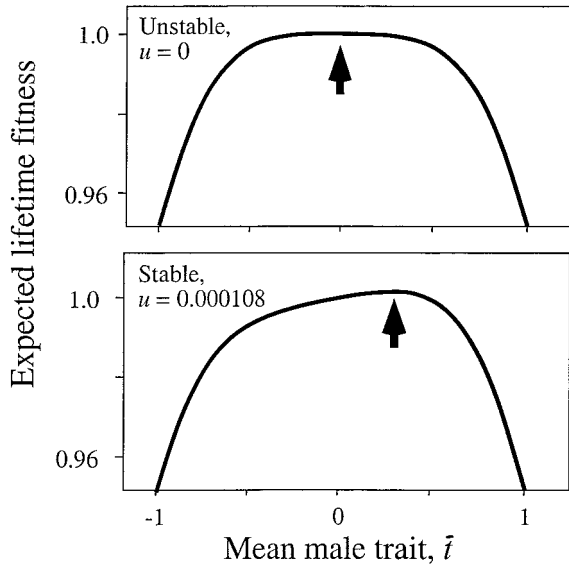
FIG. 1. The fitness function for males (including both natural and sexual selection) when the mean male trait is at equilibrium in the model of Iwasa and Pomiankowski (1995). (Top) The fitness function when there is no biased mutation, $u = 0$. The arrow shows the location of the unstable equilibrium. Note that the fitness function is neutral (flat) at the equilibrium. (Bottom) The fitness function with biased mutation, $u = 0.000108$. The arrow shows the position of the stable equilibrium. Note that the fitness function is stabilizing (concave downward) at the equilibrium. Other parameter values are taken from Iwasa and Pomiankowski (1995, fig. 1): $k_p = 0.002$ (from $b = 0.001$), $c = 0.05$, $G_t = 0.5$, $G_p = 0.5$. Stability was determined by finding the equilibrium and its corresponding eigenvalues numerically.
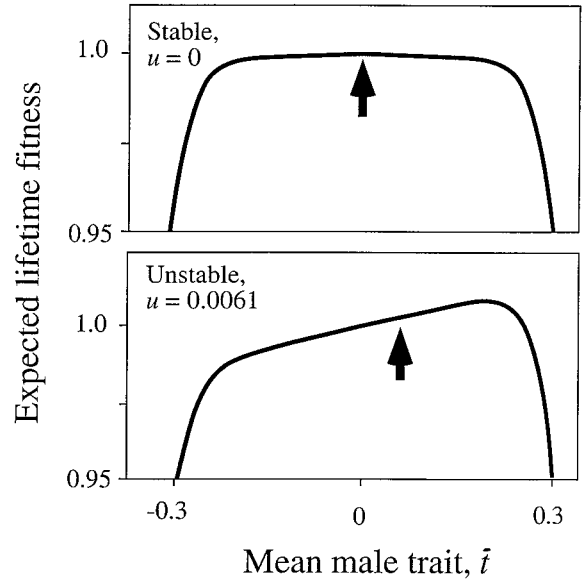

FIG. 2. A male fitness function that produces a stable equilibrium when there is no mutation bias but that causes a runaway when mutation bias is introduced. The male trait viability function is $w(t) = \exp\{-0.07t^2 + 2.5t^4 - 1000t^8\}$ in place of Equation (9). (Top) The fitness function with no biased mutation, $u = 0$. The arrow shows the location of the stable equilibrium. (Bottom) The fitness function with biased mutation, $u = 0.0061$. Arrow indicates the unstable equilibrium; the fitness function is less strongly stabilizing here than at the equilibrium in the top panel. Other parameter values are $k_p = 0.02$, $G_t = 0.01$, and $G_p = 0.01$. Stability was determined by finding the equilibrium and its corresponding eigenvalues numerically.

rium from a point where stabilizing selection is strong to one where it is weak. Under some situations, this shift will cause stabilizing selection to become so weak that a runaway begins. An example is shown in Figure 2. Although the example is contrived, it shows that we cannot say whether biased mutation (or other evolutionary forces) will generally stabilize or destabilize an equilibrium.

The point is that the role of mutation bias, and by extention other evolutionary forces that influence the runaway, can be understood terms of stabilizing selection using the framework developed here. Mutation bias can either stabilize or destabilize an equilibrium, depending on the shape of the fitness function.

DISCUSSION

An unstable runaway in which female mating preferences and a male trait rapidly coevolve away from an equilibrium is possible even when stabilizing natural selection acts on the preference. Direct selection acting on female preference makes a runaway less likely. When there is no pleiotropy between the preference and trait, conditions for a runaway depend on a relatively small number of factors: the strength of stabilizing selection on the preference and trait, the phenotypic and additive genetic variances for the trait and preference, the phenotypic correlation between the preference and trait among mating pairs, and the rate at which an increase in the preference intensifies sexual selection on males (see

Eq. (7)). Many other variables, such as the number of loci and their linkage, do not enter.

These results corroborate and extend those of Lande (1981), who first discovered that a preference-trait equilibrium can become unstable. The main generalizations we have made are to allow for any form of female preference, natural selection acting on the preferences, and more general genetic assumptions. Our results agree with his for the cases where there is no selection on the preference, and females choose males according to one of his three preference rules.

Some preference functions make a runaway much more likely than others (Lande 1981). Psychophysical (or open-ended) preferences are the most prone for three reasons. First, they generate a strong correlation between mating pairs (large ρ_{tp}). Second, they exert strong sexual selection whose intensity accelerates rapidly with small changes in the mean preference (large k_{tp}). Third, variation among females with psychophysical preferences generates disruptive selection on the male trait which further destabilizes the equilibrium. Absolute preferences, in which each female has a fixed search image of her most preferred male, are much less likely to begin a runaway. Even when natural selection on both the preference and the male trait is very weak, a runaway with absolute preferences requires very large differences between females in the males they most prefer.

Direct natural selection on mating preferences can arise many ways. Mating preference genes, like other genes, are likely to have pleiotropic effects that are subject to selection.

A second source of selection on preferences appears when females receive a direct benefit (or cost) from mating with certain males. Examples include when males provide parental care or when diseases are transmitted between mates. A third type of direct selection on preferences is caused by female search costs (Kirkpatrick 1985; Pomiankowski 1987). Search costs might favor females with no preference or alternatively might favor females with extreme preferences if being sensitive to certain signals makes it easier to locate males. Females might, for example, find a male more easily in an environment rich in distracting stimuli if they are strongly tuned to conspicuous colors and sounds. These examples suggest that some form of direct selection acts on most if not all female mating preferences (Kirkpatrick 1985; Kirkpatrick and Ryan 1991). Support for this view comes from selection experiments in which mating preferences frequently evolve as a side effect of selection directed at other traits (for review see Rice & Hostert 1993).

Direct selection of preferences has two important effects on the outcome of sexual selection. First, it determines where the equilibrium for the female mating preference lies (Lande 1981; Kirkpatrick 1982; Bulmer 1989). In many cases, direct selection will favor preference for extreme males. When that happens, the equilibrium for the preference is determined by natural selection, and the male trait evolves to a compromise between what the preferences favor and what maximizes survivorship (Kirkpatrick 1985). This may be a very common way in which strong preferences and extreme male displays evolve. Some have argued that Fisherian runaway does not operate in models with direct selection on female preference because the equilibrium is such that the cost of preference is minimized (Iwasa et al. 1991; Pomiankowski et al. 1991; Andersson and Iwasa 1996, Higashi et al. 1999). However, this argument confuses the position of the equilibrium with its stability, and it is the latter that is of interest with respect to Fisherian runaway (see introduction). That is, the equilibrium indeed minimizes female costs but that equilibrium can be unstable, resulting in a runaway.

A second effect of direct selection on preferences, and the one addressed here, is to stabilize that equilibrium and inhibit a runaway process. It is difficult to evaluate the importance of this role in nature. As little as is known about what just type of preference is most favored by direct selection, we know nothing from natural populations about how *strongly* selection favors the optimal preference. If preference phenotypes could be directly measured on females, then in principle one could use existing methods to estimate the strength of stabilizing selection acting on them (e.g., Lande and Arnold 1983; Schluter 1988). That would be an important contribution to our understanding of preference evolution and sexual selection.

If preference genes experience direct selection because of their pleiotropic effects on other traits, then they may be selected in males as well as females. The models above assume that preference genes are selected only in females, but they can be easily modified to allow for selection on both sexes. If preference genes are selected the same way in both sexes, then runaway becomes even more difficult, as one would expect. Quantitatively, the k_p term in the $\Delta\bar{p}$ equation

in Expression (2) would no longer be multiplied by 1/2, since it would now be expressed in both sexes.

What is the ultimate fate of a population if a runaway is triggered? The results developed here tell us about the local stability of the equilibrium, but nothing about what will happen to it if it does run away. Several outcomes are possible. One is that the population will arrive at a new equilibrium. A second possibility is that the trait and preference will become entrained in coevolutionary cycles (Iwasa and Pomiankowski 1995). It is impossible at this time to evaluate either empirically or theoretically which outcome is likely to be more common.

LITERATURE CITED

Andersson, M. 1994. Sexual selection. Princeton Univ. Press, Princeton, NJ.

Andersson, M., and Y. Iwasa. 1996. Sexual selection. Trends Ecol. Evol. 11:53–58.

Barton, N. H., and M. Turelli. 1991. Natural and sexual selection on many loci. Genetics 127:229–255.

Bulmer, M. G. 1971. The effect of selection on genetic variability. Am. Nat. 105:201–211.

———. 1989. Structural instability of models of sexual selection. Theor. Popul. Biol. 35:195–206.

Fisher, R. A. 1918. The correlation between relatives on the supposition of Mendelian inheritance. Trans. R. Soc. Edinb. 52:399–433.

———. 1958. The genetical theory of natural selection. 2d ed. Dover Publications, New York.

Higashi, M., G. Takimoto, and N. Yamamura. 1999. Sympatric speciation by sexual selection. Nature 402:523–526.

Iwasa, Y., and A. Pomiankowski. 1995. Continual changes in mate preferences. Nature 377:420–422.

Iwasa, Y., A. Pomiankowski, and S. Nee. 1991. The evolution of costly mate preferences II. The ''handicap'' principle. Evolution 45:1431–1442.

Kirkpatrick, M. 1982. Sexual selection and the evolution of female choice. Evolution 36:1–12.

———. 1985. Evolution of female choice and male parental investment in polygynous species: the demise of the ''sexy son.'' Am. Nat. 125:788–810.

———. 1996. Good genes and direct selection in the evolution of mating preferences. Evolution 50:2125–2140.

Kirkpatrick, M., and N. H. Barton. 1997. The strength of indirect selection on female mating preferences. Proc. Natl. Acad. Sci. USA 94:1282–1286.

Kirkpatrick, M., and M. J. Ryan. 1991. The evolution of mating preferences and the paradox of the lek. Nature 350:33–38.

Lande, R. 1981. Models of speciation by sexual selection on polygenic traits. Proc. Natl. Acad. Sci. USA 78:3721–3725.

Lande, R., and S. J. Arnold. 1983. The measurement of selection on correlated characters. Evolution 37:1210–1226.

O'Donald, P. 1980. Genetic models of sexual selection. Cambridge Univ. Press, Cambridge, U.K.

Pomiankowski, A. 1987. The costs of choice in sexual selection. J. Theor. Biol. 128:195–218.

Pomiankowski, A., Y. Iwasa, and S. Nee. 1991. The evolution of costly mate preferences. I. Fisher and biased mutation. Evolution 45:1422–1430.

Rice, W. R., and E. E. Hostert. 1993. Laboratory experiments on

speciation: What have we learned in 40 years? Evolution 47: 1637–1653.

Ryan, M. J. 1997. Sexual selection and mate choice. Pp. 179–202 *in* J. R. Krebs and N. B. Davies, eds. Behavioural ecology, an evolutionary approach. 4th ed. Blackwell, Oxford, U.K.

Schluter, D. 1988. Estimating the form of natural selection on a quantitative trait. Evolution 42:849–861.

Turelli, M. 1988. Population genetic models for polygenic variation and evolution. Pp. 601–618 in B. S. Weir, E. J. Eisen, M. M. Goodman and G. Namkoong, eds. Proceedings of the second international conference on quantitative genetics. Sinauer, Sunderland, MA.