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POPULATION GENETIC MODELS OF MALE AND MUTUAL MATE CHOICE

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Abstract.—Examples of male mate choice are becoming increasingly common, even in polygynous species. We create a series of population genetic models to examine the evolutionary equilibria and dynamics resulting from male mate choice during polygyny, alone and in the context of mutual mate choice by both sexes. We find that unless males with a preference are able to increase their overall courtship output, male preference will be lost. This loss can be counteracted if males choose females not based on arbitrary traits, but based on a trait that indicates high fertility or viability. We also conclude that if male and female preferences and traits are all controlled by different loci, the male and female mate choice systems are decoupled; the presence of a male preference then has no influence on the equilibria or dynamics of female mate choice. If male and female traits are coupled by pleiotropy, it becomes possible for a male preference to be maintained, regardless of whether preferences between the sexes are pleiotropic or controlled by separate loci.

Key words.—Fecundity selection, mathematical model, pleiotropy, polygamy, polygyny, sexual selection.

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Polygyny, a common mating system in which males can mate with more than one female in a breeding season, while females usually mate with one male (Thornhill and Alcock 1983), is generally associated with male-male competition and female choice (Darwin 1871; Andersson 1994). Increasing numbers of studies have shown, however, that male mate choice, sometimes occurring as part of mutual mate choice by both males and females, may also occasionally occur in polygynous species (Andersson 1994; Cunningham and Birkhead 1998; for reviews see Amundsen 2000; Bondurinasky 2001).

As with female choice, direct fitness benefits accruing to males through mate choice are sometimes not apparent. Males may base their mate choice on ornamental characteristics such as color (e.g., Burley and Coopersmith 1987; Hill 1993; Amundsen et al. 1997; Amundsen and Forsgren 2001) or display plumage (e.g., Jones and Hunter 1993; Romero-Pujante et al. 2002; Kraaijeveld et al. 2004). Male mate choice during polygyny however, is frequently associated with preferences for high-fertility females. Although sometime the indicators of high-fertility are unknown (e.g., Monaghan et al. 1996; Jones et al. 2001), this choice can be based on a correlate of fecundity such as dominance status (Szykman et al. 2001). The most common indicator of high fertility appears to be large female body size; both male preferences for large size and a correlation between size and fertility have been found repeatedly across different taxa (e.g., Olsson 1993; Verrell 1995; Werner and Lotem 2003; Herdman et al. 2004; Saeki et al. 2005). Large female size has also been found to be the target of choice for polygynous males in many taxa where the relationship between size and fertility has not yet been formally assessed (e.g., Ptacek and Travis 1997; Arntzen 1999; Wong and Jennions 2003; for reviews see Andersson 1994, table 6A; Bonduriansky 2001).

The frequent use of traits associated with high fecundity as targets for male mate choice is consistent with expectations that male mate choice may arise when there is large variation in female quality (e.g., Parker 1970; Trivers 1972; Forsberg 1987). Such variation is expected to be one of the predictors of sex role reversal (Owens and Thompson 1994; Johnstone et al. 1996). Many classic studies of male mate choice were performed in species that display sex role reversal (e.g., pipefishes, Berglund et al. 1986a,b; waterbugs, Smith 1979a,b; wading birds, Erckmann 1983; Oring et al. 1991; reviewed in Ridley 1978; Trivers 1985), in which males exhibit parental care and females can mate with multiple males in a breeding season (polyandry; Thornhill and Alcock 1983).

Although male mate choice, when present, may be based on a trait related to female fertility or on a sex-limited character, males may also prefer traits in females that are a reflection of the male's own sexually selected traits. Identical ornaments or colors in both males and females have been documented in birds, mammals, fish, and invertebrates (Amundsen 2000). When the same traits are preferred in both males and females, the traits and potentially the preferences may be pleiotropically controlled between the sexes (e.g., Darwin 1871; Lande 1980; Halliday and Arnold 1987). In this situation, both traits and preferences may be expressed to a different extent between males and females due to the presence of sex-specific modifiers or hormonal control (Kimball and Ligon 1999).

In this paper we consider the consequences of male and mutual mate choice in a polygynous system. Specifically we use a series of population genetic models, based on Kirkpatrick's (1982) model of sexual selection by female choice and Lande et al.'s (2001) model of mutual mate choice, to examine the evolutionary fate of male and female preference and trait alleles. In addition to basic models of male and mutual mate choice, we examine cases where female traits indicate fertility, where males differ in courtship output, where there are costs to preferences, and where traits and/or preferences are pleiotropically controlled between the sexes. Throughout the analyses we are interested primarily in the following questions: Will an allele for male preference spread in models of male and mutual mate choice? What factors will influence whether such an allele will spread? How does male

mate choice affect the dynamics of evolution of a female preference and male trait during mutual mate choice?

Basic Model

We model mutual mate choice using a population genetic model with four haploid loci and discrete nonoverlapping generations. This extends previous population genetic models of sexual selection by female choice (Kirkpatrick 1982) and mutual mate choice (Lande et al. 2001). There are two preference loci, P_f, which controls a female preference, and P_m, which controls a male preference. Each of these loci contains two alleles, designated by subscripts 1 and 2. Alleles with subscript 1 designate random mating, while alleles with subscript 2 designate a mating preference. Preferences are based upon traits determined by the remaining two loci, T_m, expressed in males, and T_f, expressed in females. Each of the trait loci likewise has two alleles. Alleles with subscript 1 are unpreferred, while alleles with subscript 2 are preferred by the opposite sex. These four diallelic loci lead to a model with 16 genotypes with frequencies x_1 through x_{16} at the zygote stage in generation t. These 16 genotypes are $P_{f1}P_{m1}T_{m1}T_{f1}$, $P_{f1}P_{m1}T_{m1}T_{f2}$, $P_{f1}P_{m1}T_{m2}T_{f1}$, $P_{f1}P_{m1}T_{m2}T_{f2}$, $P_{f1}P_{m2}T_{m1}T_{f1}$, $P_{f1}P_{m2}T_{m1}T_{f2}$, and so on. Zygotes proceed through a life cycle consisting of viability selection, sexual selection, and recombination, leading to zygote production in generation t + 1.

During viability selection, individuals with the ornamented trait alleles T_{m2} and T_{f2} suffer a viability cost represented by the selection coefficients s_m and s_f, respectively ($0 < s_m, s_f < 1$). Viability selection against T_{m2} occurs only in males, while viability selection against T_{f2} occurs only in females. Normalizations are performed separately in each sex to determine the genotype frequencies after viability selection, designated by x^*_{f1} though x^*_{f16} in females and x^*_{m1} through x^*_{m16} in males as:

$$x^*_{fi} = \frac{(1 - l_f s_f)x_i}{1 - s_f t_{f2}} \quad \text{and} \tag{1a}$$

$$x^*_{mj} = \frac{(1 - l_m s_m)x_j}{1 - s_m t_{m2}}, \tag{1b}$$

where $l_f = 1$ when i is even, $l_f = 0$ when i is odd, $l_m = 1$ when j mod 4 is 0 or 3, and $l_m = 0$ otherwise. The variables t_{f2} and t_{m2} represent the frequencies of the alleles T_{f2} and T_{m2}, respectively, at the zygote stage.

Sexual selection follows a polygynous mating system. Males are assumed to direct courtship toward specific females, based on the male's preference at the P_m allele. A male with the P_{m2} allele is $1 + a_m$ times as more likely to court a T_{f2} female than a T_{f1} female if he encounters one of each type of female ($a_m > 0$). This can also be thought of as a male courting a preferred female $1 + a_m$ times as vigorously as an unpreferred female. Male courtship produces a 16×16 matrix $\mathbf{M}$, the elements of which are the proportion of time that male genotype j spends in courtship of female genotype i, as follows:

$$\mathbf{M}_{ij} = \frac{x^*_{fi}x^*_{mj}(1 + da_m)}{z_j}, \tag{2}$$

where $d = 1$ if i is even and j is between 5 and 8 or 13 and 16, $d = 0$ otherwise, and

$$z_j = \sum_i x^*_{fi}(1 + da_m). \tag{3}$$

Normalizing by z_j ensures that all males have equal courtship output.

Females choose from among a large number of courting males. A female with the P_{f2} allele is $1 + a_f$ times more likely to mate with a T_{m2} male than a T_{m1} male, assuming one male of each type is courting her with the same amount of effort ($a_f > 0$). Female mate choice results in a 16×16 matrix $\mathbf{F}$, the elements of which are the proportion of matings occurring between each pair of genotypes,

$$\mathbf{F}_{ij} = \frac{\mathbf{M}_{ij}(1 + ka_f)}{y_i}, \tag{4}$$

where $k = 1$ if i is between 9 and 16 and j mod 4 is 0 or 3, $k = 0$ otherwise, and

$$y_i = \sum_j \mathbf{M}_{ij}(1 + ka_f)/x^*_{fi}, \quad \text{given } x^*_{fi} \neq 0. \tag{5}$$

Normalizing by y_i ensures that each female genotype has equal mating success. All female genotypes, even ones that are not preferred by males, are therefore assumed to mate. Likewise, the mating success of females with and without a preference is equal. The assumption that all females mate is likely to be realistic for a polygynous mating system. Violations of this assumption are discussed briefly in the section on fertility selection below. By basing the matrix $\mathbf{F}$ on the matrix $\mathbf{M}$, females choose males not only in proportion to their preference and the frequency of each male genotype, but also in proportion to each male's courtship effort. A male investing twice as much courtship toward a female therefore becomes essentially twice as apparent to her.

Recombination follows sexual selection. Recombination rates are assumed for simplicity to be 0.5 between all loci (free recombination; this assumption is relaxed later in the paper, where pleiotropy is explored). Zygote production follows recombination by summing the appropriate elements of the matrix $\mathbf{F}$, determining the frequencies of all possible progeny genotypes after recombination and segregation. This was done numerically (see below) using an algorithm written in C. Recursion equations are thereby formed for x_1(t + 1) through x_{16}(t + 1).

Male Mate Choice

First we use this model to analyze male mate choice alone. To effectively remove female mate choice from the model, we simply set the female preference strength, a_f, equal to zero. An analytical description of male mate choice becomes possible if we also consider the simplified case where neither of the traits T_m or T_f is under viability selection, $s_m = s_f = 0$. Males with the P_{m2} allele still preferentially court T_{f2} females, and each female still has equal mating success. Under these conditions, it can be shown that the frequency of males in the breeding population with the P_{m2} allele, p^*_{m2}, obtained by summing elements of the matrix $\mathbf{F}$ over the male genotypes 5–8 and 13–16, is

$$p_{m2}^{**} = \frac{p_{m2}t_{f1}}{1 + a_m p_{m1} t_{f2}} + \frac{(1 + a_m)p_{m2}t_{f2}}{1 + a_m(p_{m2} + p_{m1}t_{f2})}, \quad (6)$$

where the designations for t and p on the right side of the equation represent the frequencies of the alleles at the zygote stage. To determine how mating changes the fitness of P_{m2} males, we consider the difference between the proportion of mated males with the P_{m2} allele, p_{m2}^{**}, and the frequency of P_{m2} males at the zygote stage in the same generation, p_{m2}. Simplifying, this can be shown to be

$$p_{m2}^{**} - p_{m2} = -\frac{a_m^2 p_{m1} p_{m2}^2 t_{f1} t_{f2}}{[1 + a_m(p_{m2}t_{f1} + t_{f2})](1 + a_m p_{m1} t_{f2})}. \quad (7)$$

This difference is clearly always negative. Male preference therefore reduces male fitness, causing the allele for male preference, P_{m2}, to decrease in frequency because of competition for mates. This result is general for all starting frequencies of the genotypes (and alleles). It can be seen from expression (7), however, that $p_{m2}^{**} - p_{m2}$ will be very small in magnitude when p_{m2} is small, or in other words, when males with the preference are rare. A low frequency of males with a preference may therefore remain in a population for a long time.

A numerical analysis of $p_{m2}^{**} - p_{m2}$ was also performed, using Mathematica (Wolfram 2004) under conditions where viability selection acted against the T_{m2} and T_{f2} alleles (s_m, $s_f \neq 0$). Analyses over 81 diverse starting conditions for the allele frequencies (0.01, 0.5, and 0.99 for each, assuming linkage equilibrium, here and throughout the paper) and 125 different parameter combinations (spanning 0.01 through 0.99 for s_m and s_f and 0.1 through 20.0 for a_m, over 10,000 runs total) found $p_{m2}^{**} - p_{m2}$ to remain negative under all conditions examined. Allowing viability selection against the preferred traits does not therefore appear to alter the above result.

The simple approach of determining the sign of the change in frequency of male preference due to mating within a generation, $p_{m2}^{**} - p_{m2}$, does not account for selection at other stages in the life cycle. Selection on other loci also could change the frequency of the male preference allele through linkage disequilibrium caused by selection and nonrandom mating. Numerical iteration of the recursion equations (written in C), however, confirms a decrease in frequency of the P_{m2} allele over long-term evolution, using a variety of combinations of parameter values.

These simulations begin with all loci in linkage equilibrium (random combination), here and in all simulations described throughout this paper. The simulations confirm that the frequency of the P_{m2} allele decreases in the first generation, when the P_m locus is not in linkage disequilibrium with any other. During the first generation, before linkage disequilibrium arises, the frequency of the preferred trait allele T_{f2} changes only due to viability selection against it (s_f) and sexual selection favoring it (a_m). After the first generation, linkage disequilibrium arises between the P_m and T_f loci due to nonrandom mating. With linkage disequilibrium between the P_m and T_f loci, the decrease in frequency of the P_{m2} allele causes a concomitant decrease in the frequency of the T_{f2} allele. If the T_{f2} allele is eventually lost, for example, due to strong viability selection against it, the P_{m2} allele stops decreasing and remains at its current frequency. This can also be seen by an examination of equation (7); $p_{m2}^{**} - p_{m2} = 0$ when $t_{f2} = 0$. We therefore infer the existence of a stable line of equilibria where $t_{f2} = 0$.

If viability selection favors, instead of acts against, the female trait T_{f2}, numerical analysis shows that the change in frequency of male preference due to mating within a generation, $p_{m2}^{**} - p_{m2}$, is still negative (over the same parameter values tested, with T_{f2} being favored by modifying equation [1a] so that s_f acts against the T_{f1} allele). Numerical iteration of the recursion equations over several generations shows, however, that the loss of P_{m2} can be prevented once linkage disequilibrium is established between the P_m and T_f loci. If viability selection favoring T_{f2} is strong enough, T_{f2} can spread, causing P_{m2} to increase due to linkage disequilibrium. In this case if T_{f2} becomes fixed before P_{m2} does, P_{m2} will again stop evolving and remain polymorphic, implying that a stable line of equilibria also exists when $t_{f2} = 1$.

Female Traits Indicate Fertility

Males often prefer traits in females, such as large body size, that indicate high fertility. This is incorporated in the model by introducing fertility selection favoring mated pairs in which the female has the preferred T_{f2} allele. This produces a matrix $\mathbf{S}$ with elements

$$\boldsymbol{S}_{ij} = \frac{\mathbf{F}_{ij}(1 + hf)}{1 + ft_{f2}}. \quad (8)$$

Here f is the fertility advantage gained by pairs involving a T_{f2} female; therefore, $h = 1$ when i is even, and $h = 0$ otherwise. Fertility selection is followed by recombination and zygote production.

To analyze male mate choice when female traits indicate fertility, we start with the simplified case where there is no viability selection acting on male traits ($s_m = 0$) and there is no female mating preference ($a_f = 0$). Under these conditions, we can define a threshold fertility advantage, f_T, as

$$f_T = \frac{a_m p_{m2}(1 - s_f t_{f2})}{1 - s_f t_{f2} + a_m(1 - s_f)t_{f2}(1 - p_{m2})}, \quad (9)$$

where the allele for male mating preference will increase in frequency ($p_{m2}^{**} - p_{m2} > 0$) provided that $f > f_T$. An example of the range of f_T when $s_f = 0$ is shown in Figure 1A. Here the female trait is simply an indicator of high fertility. Figure 1B depicts the more general situation where the female trait also confers low viability ($s_f > 0$); in this case, there is a trade-off between fecundity and viability such that lower viability traits require a larger fertility advantage for a male preference to spread. Simulations including linkage disequilibrium confirm that an alleles for a male preference can spread given sufficiently strong fertility selection. Once again, P_{m2} will stop evolving and remain polymorphic whenever variation is lost at the T_f locus, indicating a line of equilibria.

The assumption that females with higher fertility are preferred by males is mathematically identical to assuming that preferred females have greater mating success (i.e., females mate less if they are not courted as often). The parameter f

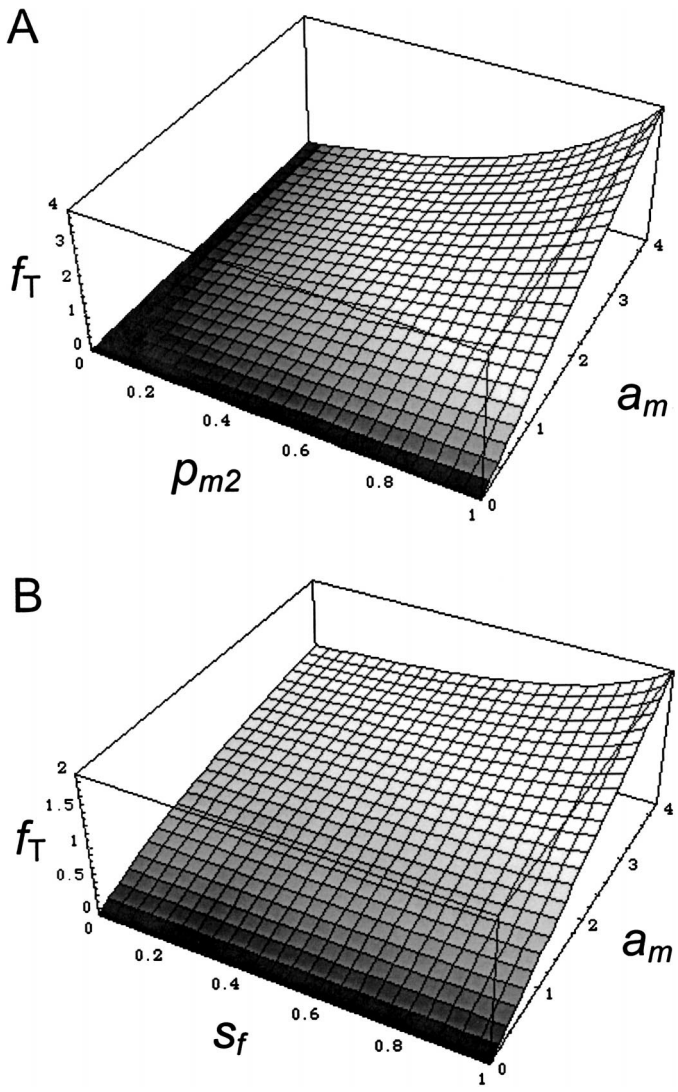

FIG. 1. The surface generated by expression (9) shows the threshold fertility advantage f_T. For $f > f_T$ the male preference allele P_{m2} increases in frequency due to mating within a generation. (A) f_T varies with P_{m2} and a_m, with $T_{f2} = 0.5$ and $s_f = s_m = 0$. (B) f_T varies with s_f and a_m, with $T_{f2} = P_{m2} = 0.5$ and $s_m = 0$.

can therefore also be thought of as a mating advantage conferred on a female genotype that is courted more often.

Males Court Unequally

The basic mutual mate choice model above assumes that all males produce the same total courtship output, regardless of whether they have a preference. It may be, however, that males with a preference can court more than males with no preference. This could potentially occur through several different mechanisms. Males that are able to devote more energy to courtship and hence attract more potential mates may have a greater opportunity to exercise choice. Alternatively, males could be stimulated to exert more courtship effort if they encounter a preferred female. This additional effort could be expressed in a second form of courtship directed only toward preferred females.

We investigated this by assuming that the amount of courtship output increases in proportion to the strength of a male's preference. This was implemented by removing the normalization in equation (2) so that

$$\mathbf{M}_{ij} = x_{fi}^{*} x_{mj}^{*}(1 + da_m), \tag{10}$$

where, again, $d = 1$ if i is even and j is between 5 and 8 or 13 and 16, and $d = 0$ otherwise. The rest of the model proceeds as described above (still assuming that all female genotypes have equal mating success).

Again we can describe analytically the change in frequency of the male preference allele P_{m2} due to mating within a generation in the simplified case where traits are not under viability selection and females do not have a mating preference. Specifically, when males with a mating preference court more it can be shown that

$$p_{m2}^{**} - p_{m2} = \frac{a_m p_{m1} p_{m2} t_{f2}}{1 + a_m p_{m2}}. \tag{11}$$

The difference is always positive. Changing total courtship output of males to be proportional to preference strength therefore reverses the fate of the male preference allele; male preferences then will always spread. This result is confirmed by numerical iteration of the recursions over multiple generations, which include linkage disequilibrium between the loci (numerical simulations in C). P_{m2} remains polymorphic if T_{f2} is lost or fixed.

MUTUAL MATE CHOICE

Although the analyses in the previous section consider only male mate choice, mutual mate choice can be examined in the model by assuming that females also have mating preferences ($a_f \neq 0$). This model is too complex to produce analytical solutions. The behavior of the model can be assessed, however, by numerical analyses and computer simulations. For the basic model, where males have equal courtship output and there is no fertility selection, over 50,000 analyses of diverse genotype frequencies (81 combinations) and parameter values for s_m, s_f, a_m, and a_f (625 combinations; s_m, s_f between 0.01 and 0.99; a_m, a_f between 0.1 and 20.0) consistently arrived at the same conclusion as the analyses of male mate choice alone. The change in frequency of the male preference allele due to mating within a generation was always found to be negative, indicating direct selection against male mating preference. This conclusion was confirmed by numerical iteration of the recursion equations over several generations.

These analyses also indicate that when mate choice is mutual, the dynamics of the male preference and female trait loci have no influence on the dynamics of the female preference and male trait loci. The evolution of the female preference and male trait loci was seen to be exactly the same as that described in Kirkpatrick (1982), regardless of whether a male preference exists. This conclusion is supported by the observation that no linkage disequilibrium forms between the male and female preferences or between the male and female traits in numerical analyses. Both numerical analyses of $p_{m2}^{**} - p_{m2}$ and iterations of the recursion equations over several generations indicate that the male choice and female

choice systems remain decoupled despite additional assumptions of female traits indicating fertility and males courting unequally.

Costs to Preferences

A cost for female preference has been found to qualitatively influence the dynamics of sexual selection models by reducing a line of equilibria to a single equilibrium point (e.g., Pomiankowski 1987). We investigated costs for both female and male preferences in the mutual mate choice model. Our goal was to determine how costs affect the evolution of male preference.

A cost to female preference was implemented in two ways. First, females were assumed to incur a viability cost if they carried the P_{f2} allele. This could happen if choosy females spent more time searching for or evaluating mates. We also evaluated a cost that reduced the fertility of females with the P_{f2} allele. This would be realistic if being choosy depleted energy reserves in a female in a way that caused reduced fertility. As predicted from the uncoupled systems of male and female choice, numerical analyses indicated that neither of these assumptions affected the loss of male preference.

Not surprisingly, a cost of male preference, implemented as reduced viability for males with the P_{m2} allele, accelerated the loss of the P_{m2} allele (larger $p_{m2}^{**} - p_{m2}$, in over 150,000 analyses consisting of 81 genotype frequency combinations and 1875 parameter value combinations). A viability cost of the P_{m2} allele was also implemented for the situation where males do not court equally but in proportion to the strength of their preference (see above). In this case the change in frequency of the P_{m2} allele due to mating within a generation, that occurs with no cost for male preference, can be offset when a cost is added to the model (Fig. 2).

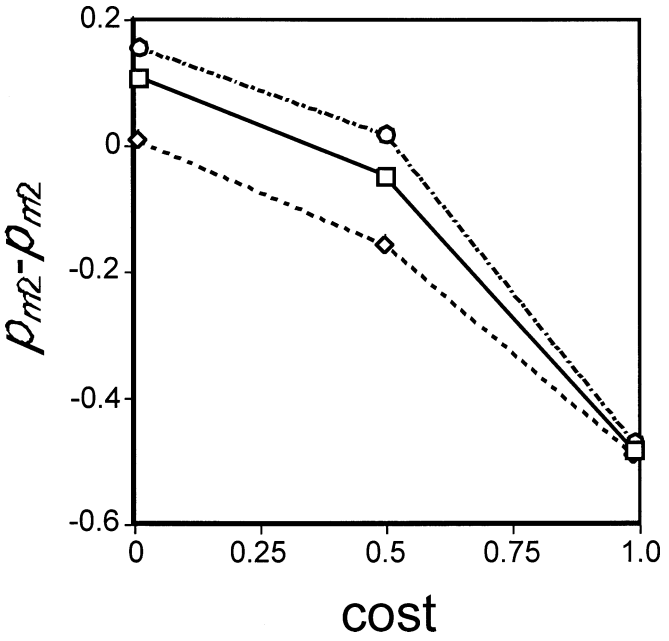

FIG. 2. The value of $p_{m2}^{**} - p_{m2}$ (y-axis) as dependent on male costs (x-axis). Cost indicates the selection coefficient against preference in males with the P_{m2} allele, which occurs simultaneously with viability selection against the male trait. The male preference allele increases due to mating within a generation when $p_{m2}^{**} - p_{m2} > 0$ and decreases when $p_{m2}^{**} - p_{m2} < 0$. All allele frequencies initially equal 0.5 and $s_f = 0.2$ (values of s_m and a_f do not matter, see text). Circles, $a_m = 5.0$; squares, $a_m = 2.0$; diamonds; $a_m = 0.1$.

PLEIOTROPY

Several empirical observations can be explained by pleiotropy of traits or preferences involved in mate choice. For example, females of some species develop rudimentary expression of traits that are sexually selected to an exaggerated degree in males (Darwin 1971; Amundsen 2000). This can be caused by pleiotropic expression of the same trait genes in both males and females (Lande 1980). Likewise, pleiotropic expression of female preference genes in males may create weak male preferences for female traits homologous to male traits.

We explore these pleiotropic effects by further extensions of Kirkpatrick's (1982) model of sexual selection by female choice. This model contains two loci, one for a female preference (P) and one for a male trait (T). Females with allele P_2 prefer males with allele T_2 with a preference strength of a_2. Males with the trait T_2, however, suffer a viability disadvantage, reducing their fitness to $1 - s$. Females with the P_1 allele mate at random. See Kirkpatrick (1982) for a full description of the model.

Male Traits Weakly Expressed in Females

Kirkpatrick (1982) briefly described how the results of this basic model change when the deleterious trait T_2 is expressed equally in both males and females. We concentrate instead on rudimentary expression of the trait in females, using this as a basis of comparison with models that add pleiotropic expression of preferences (below). Following Kirkpatrick (1982) the genotypes T_1P_1, T_1P_2, T_2P_1, and T_2P_2 have frequencies x_1 through x_4 in zygotes. These genotype frequencies are changed by viability selection to

$$x_{vi}^* = \frac{(1 - bs_v)x_i}{1 - s_v t_2}. \tag{12}$$

In females the subscript v is replaced throughout equation (12) by f. The parameter s_f represents the strength of selection against the weakly expressed trait T_2, with the frequency t_2 in zygotes. Because expression of the trait in females is rudimentary, s_f is assumed to be small. Likewise in males the subscript v is replaced by m throughout equation (12), where s_m represents the strength of selection against T_2 when it is fully expressed. Selection in males is assumed to be stronger than or equal to that in females. For both sexes $b = 1$ when i is 3 or 4, and $b = 0$ otherwise.

Mating occurs after natural selection. A female with the P_2 allele is $1 + a_f$ times as likely to mate with a T_2 male than a T_1 male if she encounters one of each (Kirkpatrick's $a_2 = 1 + a_f$). Mate choice results in a 4×4 matrix $\mathbf{F}$, with elements

$$\mathbf{F}_{ij} = \frac{x_{fi}^* x_{mj}^* (1 + ca_f)}{y_i}. \tag{13}$$

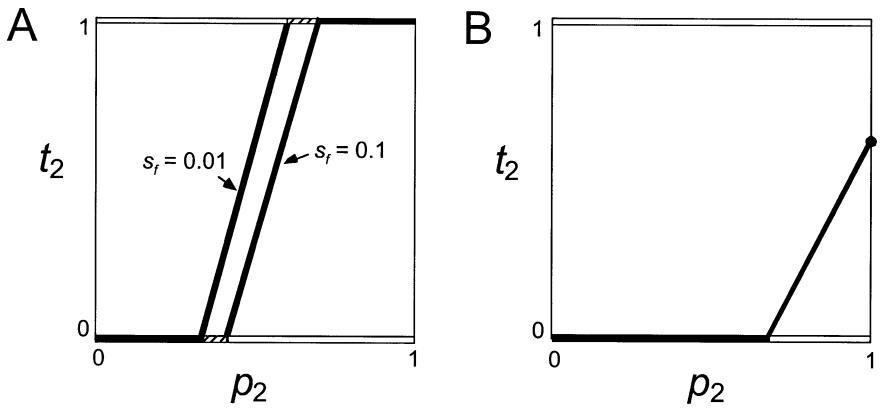

FIG. 3. Equilibria and stability when a trait locus T is expressed pleiotropically in both males and females. (A) Expression in females is weak (s_f is small). Thick black lines indicate neutrally stable equilibria and white (open) lines indicate unstable equilibria. The striped segment on the line where $t_2 = 1$ is stable for $s_f = 0.01$ and unstable for $s_f = 0.1$. When $t_2 = 0$ the striped segment is unstable for $s_f = 0.01$ and stable for $s_f = 0.1$. (B) Expression in females equals that in males ($s_f = s_m = s$). For both panels all results were derived analytically except the stability of the line of polymorphic equilibria, which was confirmed by numerical iterations of the recursions. Parameter values: $a_f = 2.0$ and $s_m = 0.4$.

Here $c = 1$ when i is even and j equals 3 or 4, and $c = 0$ otherwise, and

$$y_i = \sum_j x^*_{mj}(1 + ca_f). \quad (14)$$

Following mating, recombination between the P and T loci occurs at rate r. Zygote production follows recombination as in Kirkpatrick (1982). Recursion equations were determined for the genotype frequencies and used to compute allele frequencies p_2, t_2, and the linkage disequilibria between these loci, D, in the next generation.

Analysis of this model reveals dynamics similar to those with no female expression of the trait. Figure 3 shows the position and stability of the equilibria for the frequencies of the P_2 and T_2 alleles when selection on the trait in females is weak (Fig. 3A) and contrasts these results with the case of equal expression of the trait in both sexes ($s_f = s_m = s$, Fig. 3B). Parameter values in the figure are identical to those used in Kirkpatrick's (1982) figure 1 (where $s_f = 0$), to which Figure 3 can be directly compared. Figure 3 shows a neutrally stable line of equilibria on which both the preference and trait can remain polymorphic. When expression of, and hence selection against, the female trait is weak, the position of the line of equilibria is similar to that when selection against the female trait is absent (Fig. 3A). When the female trait is expressed as strongly as the male trait, this line of equilibria has shifted significantly toward higher frequencies of the preference allele P_2 and lower frequencies of the trait allele T_2 (Fig. 3B; see also Kirkpatrick 1982). The Appendix presents expressions for the intercepts of the line of polymorphic equilibria and conditions for the stability of the edge equilibria (valid for weak and strong selection).

Female Preference Weakly Expressed in Males

Here we assume both that female preference genes are weakly expressed in males and that male traits are weakly expressed in females. This model resembles our mutual mate choice model except that we assume the trait in females and the preference in males are pleiotropic effects of genes primarily expressed in the opposite sex.

Viability selection in the model obeys equation (12). This is followed by mate choice, which proceeds like that in the mutual mate choice model. Males with the allele P_2 preferentially court females expressing the T_2 allele (with preference $1 + a_m$). The proportion of time that each pair of genotypes spends in courtship is described by equation (2), where **M** is now a 4×4 matrix, $d = 1$ if $i = 3$ or 4 and j is even, and $d = 0$ otherwise. Males are again assumed to spend equal time in courtship, as accounted for by the normalization z_j from equation (3), with the current definitions of d.

Females choose from among many courting males, producing the matrix **F** (now 4×4), as expressed by equation (4). Here $k = 1$ if i is even and $j = 3$ or 4, and $k = 0$ otherwise. Normalizing by y_i, using the current definition of k, ensures that females have equal mating success.

Recombination occurs between the P and T loci at rate r, leading to zygote production (following Kirkpatrick 1982). Recursion equations for the genotype frequencies were transformed to allele frequencies p_2 and t_2 and the linkage disequilibrium between the P and T loci, D.

It does not appear possible to maintain a polymorphism for the trait allele in this model (with values of a_m ranging from 0.001 through 10.0). This contrasts with the model in which preferences are expressed only in females. A diagram illustrating the dynamics, equilibria, and stability of the frequencies of the P_2 and T_2 alleles is presented in Figure 4. The line of polymorphic equilibria in Figure 3 has changed to a trajectory of quasi-equilibria along which evolution occurs as the T_2 allele is slowly lost. Loss of the trait occurs more rapidly when P_2 is low enough that the line of quasi-equilibria is not reached. When the preference allele P_2 starts at a high enough frequency, it is possible to avoid this loss, and T_2 can be rapidly fixed.

It can be shown analytically that a male preference does not change the position at which the lines of equilibria at t_2

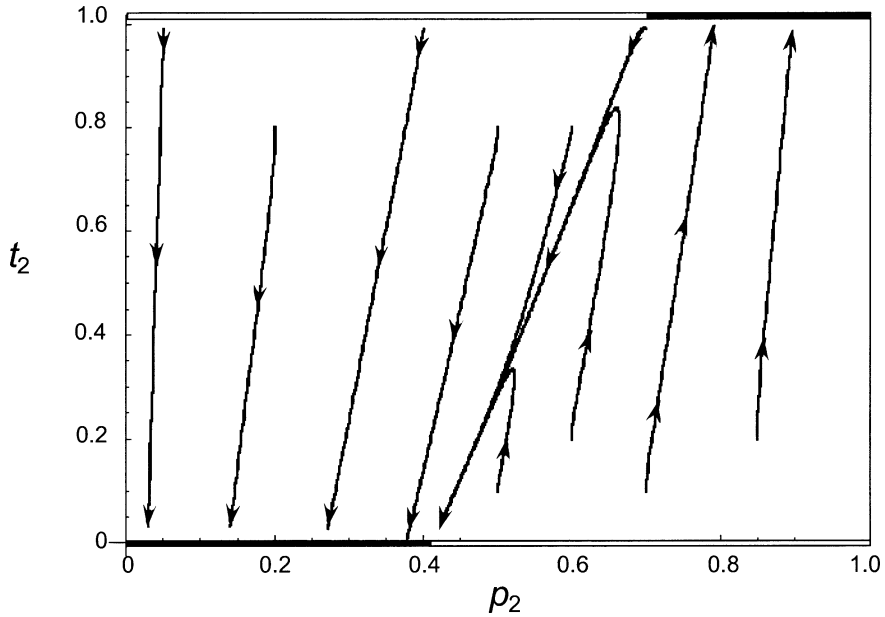

FIG. 4. Diagram presenting the dynamics, equilibria, and stability of the model with female preferences expressed weakly in males and male traits expressed weakly in females. Thick black lines indicate neutrally stable equilibria and white (open) lines indicate unstable equilibria. The position and stability of the edge equilibria was determined analytically and internal dynamics were determined by numerical iteration of the exact recursion equations. Parameter values: $a_f = 2.0$, $a_m = 0.1$, $s_m = 0.4$, and $s_f = 0.1$.

$= 0$ and $t_2 = 1$ switch from being stable to unstable. These results hold for both weak and strong viability and sexual selection. These points are still described by expressions (A1) and (A2) in the Appendix. The stability conditions (A3) and (A4) likewise still hold, regardless of selection strength.

Three Loci: Female Preference, Male Preference, Pleiotropically Controlled Trait

The final model contains separate loci for male and female preferences (P_m and P_f; respectively) but a pleiotropic trait (T) that is expressed equally in both sexes. The variables x_1 through x_8 represent the zygotic frequencies of genotypes $P_{f1}P_{m1}T_1$, $P_{f1}P_{m1}T_2$, $P_{f1}P_{m2}T_1$, $P_{f1}P_{m2}T_2$, $P_{f2}P_{m1}T_1$, and so on. Viability selection therefore alters the frequencies of the genotypes in both sexes to

$$x_i^* = \frac{(1 - es)x_i}{1 - st_2}, \tag{15}$$

where $e = 1$ if i is even and 0 if i is odd.

Viability selection is followed by sexual selection, again using the assumptions of the mutual mate choice model. P_{m2} males preferentially court T_2 females (preference $1 + a_m$). Equation (2) gives the proportion of time that each pair of genotypes spends in courtship, where **M** is now an 8×8 matrix, $d = 1$ if i is even and j mod 4 is equal to 0 or 3, and $d = 0$ otherwise. The normalization in equation (3) ensures that males spend equal time in courtship. Females with the P_{f2} allele are assumed to prefer T_2 males (preference $1 + a_f$). Matrix **F** from equation (4) shows the proportion of mating pairs of each genotype after females choose from among courting males. **F** is now an 8×8 matrix, where $k = 1$ if $i > 4$ and j is even, and $k = 0$ otherwise. Normalizing by y_i ensures that females have equal mating success.

Recombination occurs between all loci at rate $r = 0.5$. Recursion equations for the genotype frequencies were calculated by summing the appropriate elements of the matrix **F** after recombination and segregation.

Pleiotropy of the trait in this model, as in some of the other pleiotropic models above, is a necessary condition for reciprocal mate choice in which males preferentially court females who in turn prefer them (see Lande et al. 2001). This occurs when the pleiotropy in the trait is augmented by positive linkage disequilibrium that arises between the male preference and the trait and between the female preference and the trait. Numerical iteration of the recursion equations indicates that, in contrast to the male mate choice or mutual mate choice models above, the male preference allele P_{m2} can sometimes increase in frequency. Its spread, however, appears to be quite modest over all parameter values examined (e.g., Fig. 5). The P_{m2} allele ceases to spread when variation is lost at the T locus, which generally occurs rapidly (T_2 was always fixed when P_{m2} spread, but could be either fixed or lost in other cases).

DISCUSSION

Analyses of models of male and mutual mate choice have allowed us to reach several conclusions regarding the evolution of mate mating preferences for female traits and their influence on the dynamics of the classical sexual selection system involving a female preference and a male trait. Our conclusions for the evolution of male preference are summarized in Table 1.

One of our primary findings is that male preferences for arbitrary female traits cannot be maintained in a polygynous mating system, provided that a preference does not increase the total courtship output of a male. When such males prefer

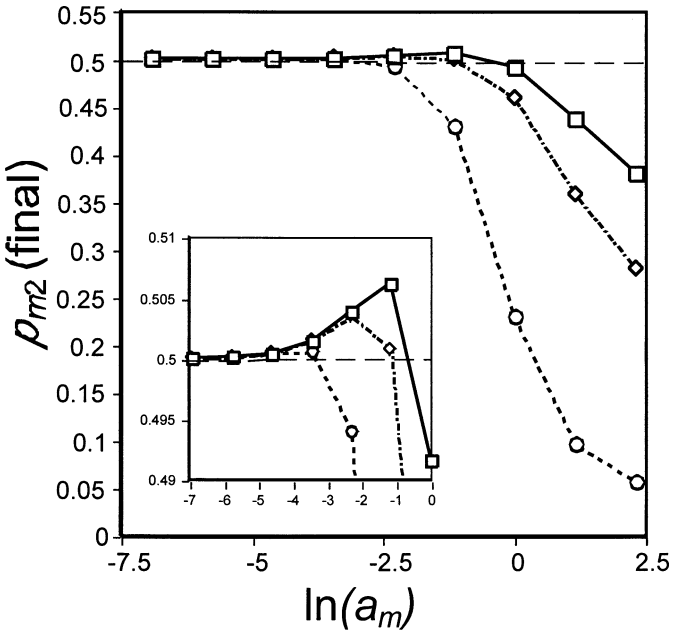

FIG. 5. Equilibrium frequency of the P_{m2} allele given the strength of male preference for T_2 females (a_m, on a log scale). The inset shows a closeup of the region below $a_m = 1.0$. The fine dashed line at $p_{m2} = 0.5$ shows the starting frequency for p_{m2}; equilibria above this frequency represent an increase in p_{m2}, while equilibria below represent a decrease in p_{m2}. For all lines $s = 0$ (higher s caused P_{m2} to be less likely to spread and lowered the equilibrium frequency). Parameter values: $a_f = 5.0$ (squares), $a_f = 1.0$ (diamonds), and $a_f = 0.1$ (circles).

female traits that are selectively neutral or reduce female viability, male preference will disappear. This contrasts sharply with the parallel situation of female preferences for showy male traits, which can spread under a wide variety of conditions (Lande 1981; Kirkpatrick 1982).

The difference occurs because when all male genotypes have equal total courtship output and all female genotypes have equal mating success, female preference is selectively neutral, whereas male preference is directly selected against (see also Lande et al. 2001). Males with a preference court some females more and other females less. If each female genotype chooses a mate in proportion to the amount of time she is courted by each type of male, males courting preferred females will face much stiffer competition than males courting females that are unpreferred. This gives a direct selection advantage to males with no mating preference, who benefit from the lower competition in courting unpreferred females. This frequency-dependent selection against males with a preference is lower when males with a preference are rare, but still acts to eventually eliminate male preference.

There are several situations under which this conclusion does not hold. The first is when males with a preference are able to court more. This was investigated by changing the normalizations during mating to remove the assumption that all male genotypes have equal total courtship output. When males with a preference court proportionally more, they are able to spend the same amount of time as males without a preference in courting unpreferred females. Males with a preference therefore lose their disadvantage with unpreferred females, and they gain an advantage by being chosen more often by preferred females. Under these conditions, male preferences will spread. It is questionable, however, whether these conditions are realistic for polygynous species.

Male mating preferences can also spread when these males prefer females with high fitness. This may occur most commonly when a female trait is an indicator of high fertility, as is often the case for large female body size (e.g., Olsson 1993; Verrell 1995; Werner and Lotem 2003; Herdman et al. 2004; Saeki et al. 2005; see also Andersson 1994, table 6A; Bonduriansky 2001). Male preferences also can spread when the preferred female trait is an indicator of high viability. Evidence for female traits improving survival or being genetically associated with high fitness traits (good genes) comes from many taxa (e.g., Yamazaki et al. 1976; Lenington 1983; Hill 1993; Wynn and Price 1993; Johnsen et al. 1996; Potti and Merino 1996; Linville et al. 1998; Hansen et al. 1999; Roulin et al. 2000, 2001; Jawor et al. 2004). In both cases of female fertility and viability advantages, the strength of selection determines whether the selective disadvantage of male preference will be overcome, allowing the preference to spread.

These conclusions for male mate choice also apply in our basic model of mutual mate choice by both sexes. This is a consequence of male mate choice and female mate choice

TABLE 1. Conclusions for the evolution of male preference.

Model	Variant	Male preferences
Four unlinked loci P_m, P_f, T_m, T_f	Males have equal courtship output.	Lost.
	Female traits indicate high fertility but potentially low viability.	Can increase given high fertility advantage ($f > f_T$).
	Female traits indicate high viability.	Can increase given high-viability advantage.
	Preferred females are more likely to mate.	Can increase given large advantage to preferred females.
	Males' courtship output is proportional to their preference.	Increase.
	Cost to female preference.	No effect on male preference.
	Cost to male preference.	More rapid loss.
Two loci: pleiotropy of preferences and traits P, T		Preferences can remain polymorphic, lost, or fixed; traits will be lost or fixed.
Three loci: pleiotropy of traits P_m, P_f, T		Male preferences can spread a small amount under certain conditions.

systems being completely decoupled, provided that both male and female preferences as well as male and female traits are controlled by unlinked loci (as in our four-loci model). Under these conditions, male preference has no influence on the evolution of female preferences and male traits.

The decoupling of male and female mate choice systems means that costs to female preferences have no influence on the evolution of male preference. Not surprisingly, a cost for male preference can accelerate the loss of male preference or prevent its spread even when males with a preference court more. Costs of male preferences, including those arising from searching (e.g., Duetsch and Reynolds 1995) or seasonal time constraints (Johnstone 1997) have been shown in previous models to prevent male mate choice from evolving. While our results support this role of costs to choice, we also show that costs are not necessary to prevent the evolution of male mate choice; male preferences often will be lost because of the direct selection against them described above.

Female secondary sexual characters often are complete or partial expressions of exaggerated traits that are sexually selected in males (Darwin 1871; Amundsen 2000). A leading hypothesis for the existence of these traits is that genetic correlations between the sexes may lead to nonadaptive trait expression (Lande 1980; Kirkpatrick 1982; Lande and Arnold 1985). Some evidence, however, contradicts the existence of strong genetic constraints (Price and Birch 1996; Bleiweiss 1997; Omland 1997; Burns 1998). Other mechanisms leading to the evolution of malelike traits in females include female contest competition (West-Eberhard 1983) or selection to avoid intrasexual competition by masking sexual identity (e.g., Burley 1981).

The presence of pleiotropy, causing strong genetic correlations between the sexes in traits (and potentially preferences), changes our main conclusions. Male and female mate choice systems are then no longer independent, and male preferences can be maintained even with equal courtship output among males. We began our investigation of pleiotropy using a model where only females express preferences, to contrast weak pleiotropic expression of a male trait in females with the case of trait expression in males alone. From Kirkpatrick's (1982) analysis of equal expression of a trait in both sexes, pleiotropy is expected to allow a neutrally stable line of polymorphic equilibria of the preference and trait, just as when trait expression only occurs in males. Our analysis of weak expression of female traits confirms this expectation, showing that the position of the line of equilibria changes with the degree of expression (affecting the magnitude of viability selection) of the female trait.

The pleiotropy model becomes more interesting when male preferences are introduced. We analyzed two kinds of male preference, first as a pleiotropic effect of female preferences (e.g., Halliday and Arnold 1987), and secondly controlled by a separate locus. Female and male traits were assumed for both analyses to be pleiotropic effects of a single trait locus. When male preference is a pleiotropic effect of female preference, the line of polymorphic equilibria for trait and preference collapses. Although preference alleles can remain polymorphic, trait alleles are either fixed or lost. Due to the coupling of male and female mate choice systems, male preferences are no longer always lost as in the four-loci model, but can be maintained by the Fisherian system operating on female mate choice. Male preference also can be maintained in some cases when the coupling between the male and female mate choice systems is a function of pleiotropy in the trait alone. In this situation, a combination of pleiotropy and linkage disequilibrium will cause males to prefer females that in turn prefer these same males. This reciprocal mate choice will occur regardless of whether male and female preferences are also pleiotropically controlled or are controlled by different loci. When preferences are controlled by different loci, we found that male preferences could spread under some parameter values, but this spread would be rather restricted.

Our models, which analyze the consequences of male mate choice in polygynous species, differ from several other models of male mate choice that concentrate on predicting the causes of sex role reversal. Early consideration of conditions for male mate choice predicted that parental investment (Trivers 1972), energetic costs of copulation (Dewsbury 1982), and variance in mate quality (Parker 1983) were instrumental in determining whether males or females were the choosy sex. More recent models incorporate these same factors as well as additional constraints on choosiness and costs of breeding attempts, and they assess how these factors influence and compare with measures such as the operational sex ratio and potential reproductive rate in predicting sex roles (e.g., Owens and Thompson 1994; Deutsch and Reynolds 1995; Johnstone et al. 1996; Johnstone 1997; Kokko and Monaghan 2001; see also Bonduriansky 2001). These models primarily use game theory, assuming optimality. Our population genetic models add additional factors, such as arbitrary (neutral or deleterious) or advantageous female traits and equal (or unequal) total courtship output among male genotypes, to the list of conditions that can potentially prevent (or allow) male mate choice to evolve in polygynous species.

In addition to sex role reversal and choice of high fecundity females, there are other situations in which male mate choice has traditionally been expected to appear. Two of these are monogamy and sex-ratio selection. Male mate choice is expected to arise in monogamous species as part of a mutual mate choice process engaged in by both males and females (e.g., Darwin 1871; Fisher 1930; Mock 1985; Andersson 1994). Mutual ornamentation in putatively monogamous species has recently been associated with a high ''divorce'' rate, causing increased competition for mates of both sexes (Kraaijeveld 2003). Mutual mate choice in monogamous species has been considered theoretically by several researchers (e.g., Ihara and Aoki 1999; Bergstrom and Real 2000; Almeida and Abreu 2003; see also; O'Donald 1980; Kirkpatrick et al. 1990).

Ihara and Aoki (1999) studied male mate choice using a population genetic approach that, like ours, is based upon the female mate choice model of Kirkpatrick (1982). Ihara and Aoki assumed two loci, one for a male preference and one for a female trait. Their model assumed that males differ in resources; resource-rich males are more likely to be able to act upon their preferences. Furthermore, females mated to resource-rich males have higher fertility than other females. This causes direct selection on male preference that tends to be expressed in matings with high-fertility females. In a monogamous version of this model, Ihara and Aoki concluded

that male preference and a female trait will coevolve only if the fertility benefit to females that mate resource-rich males is sufficiently high. This resembles our conclusion that male preferences will be more likely to spread if female traits indicate high fertility. Ihara and Aoki also concluded that a polygynous version of their model would restrict the coevolution of male preferences and female traits, where polygyny is incorporated by assuming that resource-rich males have more mates than resource-poor ones. Their polygyny model differs from ours in that males do not court equally, and all females do not have equal mating success (due to the inclusion of resources in their model). The conclusions are therefore not directly comparable between the two models.

A different approach to mutual mate choice models is seen in studies that pair choosy males and females using a game theory technique called two-sided matching (Bergstrom and Real 2000; Almeida and Abreu 2003). This assumes both male and female mate choice and then assesses the stability of pairings. Bergstrom and Real (2000) concluded by extension of an analysis by Gale and Shapley (1962) that stable matchings would be very difficult to maintain in a polygamous system (although easy to achieve under monogamy). Almeida and Abreu (2003) used a two-sided matching model to point out that mutual mate choice can lead to sympatric speciation. In their model, mismatched pairs suffer a cost because their pairing is inherently unstable. Fitness in this model is negatively frequency dependent, which promotes sympatric speciation instead of one genotype going to fixation. Our models, in which females all have equal mating success, do not incorporate inherent costs to female choice. Preferences are also unidirectional in our models. Assortative mating between choosy and nonchoosy individuals, however, would tend to occur in some of our pleiotropy models when polymorphisms are maintained in both preferences and traits. Similar stable polymorphisms may occur if two opposing preferences were present (as seen in Kirkpatrick 1982). The maintenance of polymorphisms in secondary sexual characters and assortative mating based on these traits may be important first steps toward sympatric speciation (e.g., Higashi et al. 1999; Kondrashov and Kondrashov 1999).

Assortative mating is also a consequence of the male choice models of Fawcett and Johnstone (2003) and Härdling and Kokko (2005; see also Sozou and Seymour 2005). These studies use game theory models to analyze the courtship choices of males when both male and female quality varies. They predict that poor-quality males, with low competitive ability, may do best to forsake courting high-quality females in favor of low-quality females. Courtship of low-quality females involves less competition, giving low-quality males a greater chance of success than if they compete with other males for high-quality females. These males are thus avoiding the competition cost that ultimately reduces the frequency of the male preference in our models. The authors find that high-quality males, on the other hand, would do best to court high-quality females, leading to assortative mating based on quality. This assortative mating could lead to speciation if quality is partially heritable (e.g., based on size), rather than an environmentally determined condition.

The evolution of male mate choice due to sex-ratio selection also has implications for speciation. Seehausen et al. (1999) suggested for a Lake Victoria cichlid fish species that a region of reduced recombination on the sex chromosomes can help to maintain an association between sex determining genes and phenotypic traits that mediate mate choice, leading to an interaction between sex-ratio distortion and sexual selection. In this situation, the association of preference genes with sex-determining genes can create indirect sex-ratio selection on mating preferences. This, in turn, can lead to assortative mating between incipient species. Lande et al. (2001) investigated the impact of such selection on male and female mate choice, assuming these to be pleiotropic, using a model generalized by our current analyses.

In conclusion, researchers since Darwin (1871) have observed that male mate choice is generally weak or absent in polygynous species, which make up the vast majority of animals (Andersson 1994). Our basic model provides an explanation for this observation: if males with a preference are not able to court proportionally more, they will face greater apparent competition, causing male preference to be lost. Further analyses demonstrate that this loss can be offset if males prefer a trait that indicates high fertility or viability of females; this result is also in accord with empirical observations of male mate choice when it does occur. Other primary conclusions from the models indicate that pleiotropy of traits and of preferences between the sexes also can provide conditions for male preference to increase in frequency. Advances in studies of the genetics of preferences may provide opportunities to test these predictions about pleiotropy.

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Appendix

Stability of the model where the male trait is expressed weakly in females was determined by performing a linear stability analysis on the set of recursion equations for p_2, t_2, and D. The position of the intercept of the line of polymorphic equilibria with the axis for $t_2 = 0$ was determined to be

$$p_2 = \frac{s_m + s_f}{a_f(1 - s_m)}. \tag{A1}$$

When p_2 is less than or equal to the intercept defined by expression (A1) the line of equilibria at $t_2 = 0$ is neutrally stable, otherwise it is unstable (see Fig. 3A). As pointed out by Kirkpatrick (1982), when the expression of the trait is equal in females and male ($s_f = s_m = s$; Fig. 3B) this reduces to the expression shown in Kirkpatrick's equation (2) where $\hat{p}_2$ is replaced by $\hat{p}_2/2$.

The line of polymorphic equilibria has an intercept with the axis for $t_2 = 1$ when

$$p_2 = \frac{(1 + a_f)[s_m + s_f(1 - 2s_m)]}{a_f(1 - s_f)}. \tag{A2}$$

The line of equilibria at $t_2 = 1$ is unstable when p_2 is less than the intercept defined in expression (A2) and neutrally stable otherwise. Again expression (A2) reduces to the corresponding expression in Kirkpatrick's equation (2), with $\hat{p}_2$ replaced by $\hat{p}_2/2$ when $s_f = s_m = s$ (this intercept is not seen in Fig. 3B because of the parameter values used).

It also can be shown that there will be some segment on the line $t_2 = 1$ that is stable provided that

$$a_f > \frac{1 - s_f}{(1 - 2s_f)(1 - s_m)} - 1 \tag{A3}$$

or $a_f > 2s/(1 - 2s)$ for the case where selection coefficients are equal in each sex. Otherwise stability will be maintained only on the line of polymorphic equilibria (which will not intersect the axis at $t_2 = 1$) and part of the line of equilibria at $t_2 = 0$. The entire line of equilibria at $t_2 = 0$ will be stable if

$$a_f < \frac{s_f + s_m}{1 - s_m} \tag{A4}$$

or $a_f < 2s/(1 - s)$ when selection coefficients are the same in both sexes.