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FEMALE PREFERENCE FOR MALE COURTSHIP EFFORT CAN DRIVE THE EVOLUTION OF MALE MATE CHOICE

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The evolution of male mate choice is constrained by costs of choice in species with a male-biased operational sex ratio (OSR). Previous theoretical studies have shown that significant benefits of male choice are required, for example, by mating with more fecund females, in order for these costs to be offset and a male preference to spread. In a series of population genetic models we show the novel effect that male mating preference, expressed as a bias in courtship, can spread when females prefer, and thus are more likely to mate with, males who court more. We explore two female preference functions for levels of male courtship, one representing a threshold and the other a weighted female preference. The basic finding generally holds for both preference functions. However, the preference function greatly affects the spread of a male preference allele after the addition of competing males who can court more in total. Our results thus stress that a thorough understanding of the response of females to male courtship is a critical component to understanding male preference evolution in polygynous species.

KEY WORDS: Courtship, intrasexual competition, male mate choice, mutual mate choice, sexual selection.

Although originally considered to be less common than female mate choice (Darwin 1871; Andersson 1994), male mate choice is now accepted as being prevalent in many taxa (for reviews see Amundsen 2000; Bonduriansky 2001; Kraaijeveld et al. 2007; Hooper and Miller 2008). The theoretical basis for the prediction that male mate choice should be rarer than female mate choice stems from the fact that, in the majority of species, there is a male-biased operational sex ratio (OSR) (i.e., there are more males "ready to mate" than females, Emlen and Oring 1977; Clutton-Brock and Parker 1992). This may be due to, for example, sex differences in investment in gametes and parental care (Trivers 1972) and/or the spatial and temporal distribution of mates and resources (Emlen and Oring 1977). This led to the assumption that male competition precluded male choice as "beggars can't be choosers" (Emlen and Oring 1977; LeBas 2006). However, an increasingly large number of empirical studies have reported male mate choice in species with apparently intense reproductive competition between males (e.g., Amundsen and Forsgren 2001; Jones et al. 2001; Reading and Backwell 2007; Bel-Venner et al. 2008; Hoefler et al. 2009) and there has therefore been an increasing number of theoretical explorations of the evolution of male and mutual mate choice during the last decade (e.g., Kokko and Johnstone 2002; Servedio and Lande 2006; Servedio 2007; Nakahashi 2008).

These studies have demonstrated that male mate choice is indeed constrained by the OSR and the resulting competition between males, as the costs of mate choice to males will increase with an increasing OSR. These costs include the risk of not finding an alternative mate (Parker 1983; Deutsch and Reynolds 1995; Johnstone 1997b; Venner et al. 2010), increased competition over attractive females who are also preferred by other males (Servedio and Lande 2006; Servedio 2007), and direct costs of

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mate-assessment (Rowe 1994; Watson et al. 1998). It is therefore not surprising that significant benefits of choice that offset these costs must be present in order for male mate choice to evolve in species with intense male–male competition. Such benefits include, for example, gaining matings with more fecund females (Parker 1983; Owens and Thompson 1994; Servedio and Lande 2006; Servedio 2007; Nakahashi 2008) or decreased competition through assortative mating based on quality (i.e., a smaller number of courting males for each female "attractiveness" class) (Fawcett and Johnstone 2003; Härdling and Kokko 2005; Venner et al. 2010). These predictions are consistent with observations, in species with a male-biased OSR and male–male competition, of male mating preferences for more fecund females (Bonduriansky 2001), and of assortative mating based on quality (Burley 1983; Ridley 1983; Crespi 1989; Cézilly 2004).

Here, we further consider the possibility that males may express mate choice by distributing their total courtship effort based on female phenotype. That is, males with a preference would invest an equal total amount of courtship effort as males with no preference, but would differ in how they distribute this effort between preferred and nonpreferred females. Importantly, we explore this possibility under a scenario where females prefer (i.e., are disproportionately likely to mate with) males that court them with a high degree of courtship effort, a form of female preference which is very widespread indeed in a wide range of animal taxa (e.g., Andersson 1994). In such situations, a female preference for high male courtship effort may help males that express a preference overcome the competitive disadvantage that they face by preferentially courting more "popular" females. This effect represents a benefit of male mate choice in the sense that it may offset the cost of increased male–male competition for preferred females. It is especially pertinent to species with a male-biased OSR as males of these species often compete for females' favor through courtship displays (Andersson 1994; Johnstone 1997a). We focus on male courtship that is solely a behavioral display to females (e.g., a courtship dance or call), and thus exclude other precopulatory male traits that can be associated with courtship displays and which confer direct benefits to females (e.g., nuptial gifts). It is widely assumed that females show directional preferences for courtship intensity or duration because courtship is costly (e.g., Cordts and Partridge 1996; Mappes et al. 1996; Clutton-Brock and Langley 1997; Kotiaho et al. 1998; South et al. 2009) and courtship effort can therefore act as an honest signal of male quality (i.e., the handicap principle, Pomiankowski 1987; Johnstone 1995; Lailvaux and Irschick 2006; Seymour and Sozou 2009). Furthermore, evidence that males direct courtship differentially toward, or invest more time in courting, preferred females comes from a number of studies in a range of taxa (e.g., in lizards, Weiss 2002; Ruiz et al. 2010; wolf spiders, Roberts and Uetz 2005; Taylor et al. 2006; cockroaches, Lihoreau et al. 2008; guppies, Herdman et al. 2004; Ojanguren and Magurran 2004; and fiddler crabs, Reading and Backwell 2007).

Servedio and Lande (2006) explored the evolution of male mate choice under polygyny in a series of haploid population genetic models. They assumed, as we do, that all males have an equal amount of effort (energy, time, etc.) that they can put into courtship, biasing the distribution of this effort when they have a preference. Under their scenario, male choice expressed as increased courtship of preferred females leads to increased competition for preferred females and to the subsequent loss of a male preference allele, unless preferred females have sufficiently higher fecundity or mating success (see also Servedio 2007), or unless males can avoid competition by assessing competition strength and shifting their courtship (Rowell and Servedio 2009). Servedio and Lande (2006) also explored the possibility that males with a preference allele were able to court more overall (i.e., they had a higher total courtship effort than males without a preference). Unsurprisingly, this lead to the spread of the male preference as male mating success was proportional to their total courtship effort. However, there are no obvious reasons to believe that males with a preference should simultaneously have a higher total courtship effort, due to trade-offs between signaling and other fitness components (Kokko et al. 2002).

We examine the fate of a male preference expressed as increased courtship by considering the more biologically realistic scenario that males with a preference have an equal total courtship effort to males without a preference, and that they differ solely in how they distribute courtship effort across females. According to the results of Servedio and Lande (2006) and Servedio (2007), a male preference should be lost under this scenario. However, we build on these models by considering the previously unexplored effect of a female preference for extra male courtship on the spread of a male preference allele. We assume that all females are equally sensitive to male courtship effort (i.e., that the female preference for male courtship effort is fixed in the population). Our model is based on the classic model of sexual selection via female choice by Kirkpatrick (1982) and the model of mutual mate choice by Servedio and Lande (2006). As in these models, we assume polygyny, that all females have an equal mating rate, and that all females therefore mate; thus simulating a scenario with male competition for a limited number of females. We explore the following two questions:

1. Can male mate choice evolve if males with a preference bias the distribution of their total courtship effort toward preferred females and females have a preference for males that court more?
2. Is the evolution of male choice affected by nonchoosy males who unbiasedly court more in total?

We first explore question one using a two-locus (female trait and male preference) haploid model. This basic life cycle starts with zygotes and proceeds through: (1) male courtship, in which males distribute their courtship effort by biasing more toward preferred females (the degree of this bias is affected by the strength of male preference); (2) female mate choice, as determined by male apparentness (a reflection of the total courtship effort received by each female from each type of male) and the strength of the female preference for extra male courtship; (3) recombination; and (4) offspring production. We then explore question (2) by adding a third locus that allows increased total courtship effort by males. Under both of these scenarios, we compare two different female preference functions for male courtship effort, one representing a flat preference threshold and the other a weighted female preference. We introduce how these female preferences differ below. Our key finding is that a female preference for males that court them with extra courtship effort can indeed allow the evolution of male preferences. The type of female preference function also plays a role, principally in altering the effects on male preference evolution of the existence of males who unbiasedly court more in total. Finally, direct selection on the female trait and its effects on the spread of the male preference is explored and show largely similar dynamics as reported in Servedio and Lande (2006).

Can Male Mate Choice Evolve When Females Have a Preference for Males That Court More?

To isolate the effect of a female preference for male courtship effort, we first developed a basic two-locus, two-allele haploid model of male choice with no viability or fecundity selection. This model follows many of the assumptions in Servedio and Lande (2006). Females express a trait at locus T; allele T_2 designates a trait preferred by males while T_1 designates a trait not preferred by males. Likewise, allele P_2 at a preference locus P designates a male preference for the female trait T_2, while the allele P_1 designates males showing no preference. There are thus four genotypes under consideration with x_1 through x_4 corresponding to the frequencies of genotypes P_1T_1, P_1T_2, P_2T_1, and P_2T_2.

In this basic model, we assume a simple life cycle starting with zygotes and consisting of male courtship, female mate choice, recombination, and offspring production. We assume that all males have an equal set amount of effort that they can put into courtship, differing solely in how they choose to distribute this total courtship effort between females. When males encounter preferred (T_2) and nonpreferred (T_1) females at equal frequency, males with preference allele P_2 distribute their total courtship effort between preferred (T_2) and nonpreferred (T_1) females at a ratio of $1 + \gamma$: 1, respectively. Males who show no preference (P_1) distribute their total courtship effort (which is equal to the total courtship effort of P_2 males) between T_2 and T_1 females upon encounter at a ratio of 1:1. Here we choose to describe the males' courtship output with the general term "effort," but this could also represent time or energy units. Male courtship thus produces a 4×4 matrix **M** of time spent in courtship between x_j males and x_i females:

$$\mathbf{M}_{ij} = \frac{x_i x_j (1 + d\gamma)}{1 + k\gamma t_2}, \tag{1}$$

where t_2 represents the frequency of T_2 (lowercase letters represent corresponding allele frequencies throughout) and $d = 1$ if $j = 3$ or 4 (i.e., males have the P_2 allele) and i is even (i.e., females have the T_2 allele), $d = 0$ otherwise, $k = 1$ if $j = 3$ or 4, and $k = 0$ otherwise. The normalization ensures that all males have an equal *total* courtship effort, regardless of whether or not they bias their distribution of courtship effort toward T_2 females.

As in Servedio and Lande (2006), we assume polygyny, that females have the ultimate control of mating, and that all females mate. Furthermore, there is an equal mating rate among females. Females mate with males in proportion to how apparent the males are to the female as determined by the male frequency and their courtship effort (i.e., the likelihood that a female will perceive, and therefore mate with, a type of male depends on how much she is courted by that type of male). However, our model differs from Servedio and Lande's (2006) model in that we have included an additional female preference for male courtship effort. Specifically, we assume that all females show a preference for increased male courtship effort (i.e., the preference is fixed in the population, so we do not add a locus for female preference). This means that the probability of a mating occurring depends not only on how much the females are courted by males (i.e., male "apparentness"), but also on the strength of female preference for extra male courtship effort (i.e., male attractiveness as determined by the strength of the female preference for courtship). There are several potential functions by which such a preference could occur. Females may show stabilizing, disruptive, or directional preferences for male traits (e.g., Lande and Arnold 1983; Ritchie 1996; Jennions and Petrie 1997; Wagner 1998). We consider two cases of directional selection, that is, when females prefer males with higher courtship effort. The first represents a female acceptance threshold (e.g., Real 1990, 1991; Weigmann et al. 1996; Jennions and Petrie 1997), which we will call the flat preference function. The second represents a weighted preference function, where the greater a male's courtship effort, the more attractive he is to females (e.g., Janetos 1980; Weigmann et al. 1996; Jennions and Petrie 1997).

Table 1. Flat and weighted female preferences (a) for male courtship effort. The version of the model without males that court more in total (C_2 males courting at rate $1 + c$) is analogous to the first three rows (C_1 males only). In this table $w = 1 + \gamma t_2$, representing the normalization that ensures that males with and without the preference (P_1 males and P_2 males courting preferred T_2 females with effort $1 + \gamma$) have equal total courtship effort (denominators for P_2 males in equation (1) and (9)). Females with a flat preference prefer all males courting above a certain threshold, whereas females with a weighted preference prefer males in proportion to how much they are courted by these males.

Male genotype	Female genotype	Flat female preference	Weighted female preference
C_1P_1	T_2 and T_1	1	$1+a(w-1)$
C_1P_2	T_1	1	1
C_1P_2	T_2	$1+a$	$1+a\gamma$
C_2P_1	T_2 and T_1	$1+a$	$1+a(w(1+c)-1)$
C_2P_2	T_1	$1+a$	$1+ac$
C_2P_2	T_2	$1+a$	$1+a(\gamma+c+\gamma c)$

FLAT FEMALE PREFERENCE

When females have a flat preference, we assume that all females are $1 + a$ times more likely to mate per unit of male courtship with males that court them more vigorously. For simplicity, we assume that females do not discriminate between any male that courts less than a P_2 male courting a preferred, T_2, female (i.e., P_1 males and P_2 males that court T_1 females are both assigned a relative courtship effort of 1; see Table 1). This is analogous to females not discriminating between males below a certain preference threshold for male courtship effort (i.e., preferring any male that courts more than a P_1 male). Female choice thus results in a 4×4 matrix $\mathbf{F}$ of the proportion of matings between each genotype where

$$\mathbf{F}_{ij} = \frac{\mathbf{M}_{ij}(1 + da)}{y_i} \tag{2}$$

and

$$y_i = \sum_j \frac{x_j(1 + d\gamma)(1 + da)}{1 + k\gamma t_2},$$

where the restrictions for d and k are the same as in equation (1). As in Servedio and Lande (2006), by basing matrix $\mathbf{F}$ on the matrix $\mathbf{M}$, we assume that females mate with males in proportion to both the frequency of each male genotype and the amount they were courted by males, such that a male who courts a female with twice the effort is twice as apparent to her. However, our model differs in that we assume that females also express a preference for male courtship (a), such that the mating success of males who court more is $1 + a$ times higher than their mating success due to their frequency and apparentness alone (i.e., females have enhanced sensitivity to male courtship). When females express no preference for male courtship effort ($a = 0$), mating success will be solely determined by how apparent the males are to the female (as determined by male frequency and courtship effort). Note that in this simplified scenario, female preference is not weighted by the level of extra male courtship. Thus, the results of the flat preference version of the model are only biologically relevant for $\gamma > 0$. Normalizing by y ensures that all female genotypes have an equal mating rate.

Mate choice is followed by free recombination and segregation to produce zygote genotypes in the next generation. These assumptions lead to the following recursion equation for the frequency of the male preference gene, p_2:

$$\Delta p_2 = \frac{p_1 p_2 t_2 (a(1+\gamma)(1+\gamma(t_2 - p_2)) - \gamma^2 p_2 t_1)}{2(1+\gamma p_1 t_2)(1+\gamma t_2 + a(1+\gamma)p_2 + \gamma p_2 t_1)}. \tag{3}$$

Note that when females do not exhibit a preference for male courtship ($a = 0$), equation (3) reduces to equation (7) of Servedio and Lande (2006) divided by a factor of 2 to account for the fact that equation (3) averages the change in allele frequencies over both sexes. Equation (3) becomes negative under these conditions, confirming that male preferences will be lost when females mate simply in proportion to the frequency of the male genotype and the courtship received.

Note also that equation (3) does not contain the linkage disequilibrium, D, between the male preference and the female trait. Under our assumptions, the male preference does not lead to sexual selection on the female trait. Because there is no direct selection on the female trait in this version of the model, there is no indirect selection on the male preference caused by selection on the female trait (but see Appendix S1 for direct selection on the female trait and its effects on the spread of the male preference). We also note that because the male preference evolves solely due to direct selection, equation (3) (as well as equation (7) for the weighted case below) is valid even when female trait variation is not heritable (e.g., is environmentally determined, as elaborated upon in the discussion).

When females show a preference for male courtship effort ($a > 0$) it can be shown that Δp_2 is positive, leading to the spread of an allele for male preference, when the following two conditions are both met:

$$\gamma(p_2 - t_2) < 1 \tag{4a}$$

and

$$a > \frac{\gamma^2 p_2 t_1}{(1+\gamma)(1-\gamma(p_2 - t_2))}. \tag{4b}$$

Condition (4a) denotes the conditions for the denominator of (4b) to be positive. Under condition (4) the benefit that males with a preference derive from the fact that females prefer high

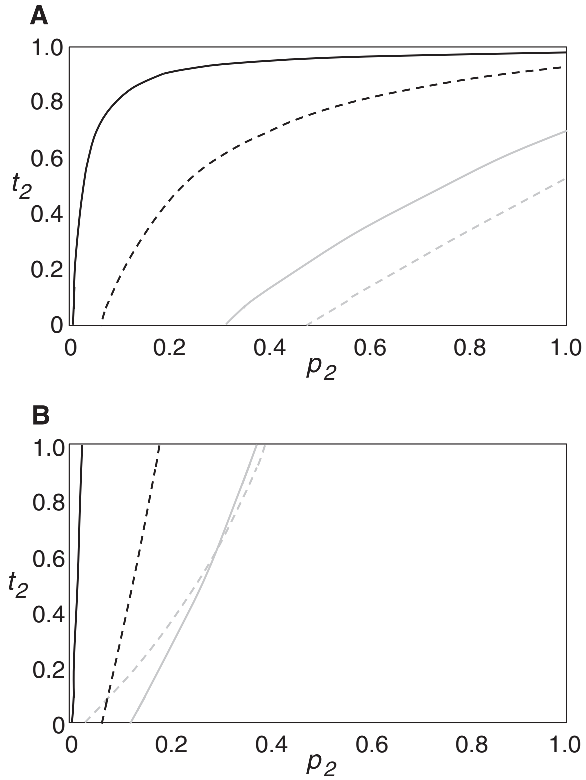

Figure 1. Stable polymorphic equilibria in the two-locus models for the male preference, P_2, and female trait, T_2, alleles (frequencies p_2 and t_2, respectively), for different strengths of female preferences for extra male courtship effort (a). (A) Flat female preferences for male courtship effort. (B) Weighted female preferences for male courtship effort. The evolutionary trajectories to reach these equilibria are very often close to horizontal (very little evolution occurs in t_2). For starting values above each line in (A) the equilibria generally lie along the line $p_2 = 1$ (not shown). Note that when $t_2 = 0$ preferences will not evolve in either model; this is also true for $t_2 = 1$ in the weighted preference model. For all runs $\gamma = 2.0$. The four lines in each graph represent different strengths of female preference for high male courtship effort (black line: $a = 0.01$, black dashed line: $a = 0.1$, gray line: $a = 1$, gray dashed line: $a = 10$). Increasing the strength of the female preference for high male courtship effort (a) generally has a positive effect on the equilibrium frequencies of the P_2 allele for both the flat and weighted female preference functions.

courtship effort by males outweighs the competitive disadvantage inherent to courtship effort biased toward preferred females.

It is clear from the frequency dependence of condition (4) that the initial frequencies of the trait and preference will play a critical role in determining whether the preference allele can spread. For a range of values of the parameter a, there is a line of stable internal equilibria where the frequencies p_2 and t_2 will remain polymorphic (Fig. 1A). We note that this line of equilibrium occurs for a reason that is not analogous to that which produces a line of equilibrium in the classical female choice model of Kirkpatrick (1982). In Kirkpatrick's (1982) model, the line of equilibrium occurs because of a balance struck between natural and sexual selection on a male trait. In our current basic model, there is no natural selection on the female trait; it evolves only because of indirect selection due to the fact that it is genetically correlated with the male preference, which is favored by direct sexual selection. The line of equilibrium in the current model occurs because this direct selection on the male preference is frequency dependent.

A stronger female preference for male courtship (i.e., a higher a) makes it more likely that the male preference allele (P_2) can spread to fixation from a low starting frequency (Fig. 1A). With $a > 0$, a stronger male preference (higher γ) can have a positive effect on the spread of P_2 when the frequencies of both P_2 and T_2 are relatively low (Fig. 2A and B), or have no or very little effect when t_2 is high relative to p_2 (Fig. 2C). This would be the scenario if a new mutation for a male preference entered the population. However, when the frequency of the P_2 allele (p_2) is relatively high or equally high as t_2, a stronger male preference (higher γ) can decrease the spread of P_2 (not shown). Higher trait allele frequencies (t_2) generally lead to both more rapid increases (Fig. 2A–C) and a higher equilibrium level of P_2 (Fig. 1A). With a very high starting t_2, a male preference can reach a high frequency even with a very weak level of a (Fig. 1A).

WEIGHTED FEMALE PREFERENCE

Our second preference function is a weighted preference. Here we assume that all females compare the courtship that they are receiving from a given male with that of males using the basal rate of courtship, defined as the lowest amount of courtship that a male in this population will give to the least preferred female. All females weight their preference, a, by the difference between these courtship values. For example, the lowest rate of courtship in a population in this model will be given by P_2 males that have a preference but are courting the unpreferred T_1 females (see Table 1). In our particular implementation of a weighted preference, we scale a female's preference so that her preference for this lowest courting male is 1. We then multiply the difference between the additional scaled courtship of a particular type of male and 1 by the preference parameter a. If equation (1) is rewritten as $M_{ij} = x_i x_j b_{ij}$, then the coefficients of the weighted preference are thus defined as:

$$f_{ij} = 1 + a\left(b_{ij}(1 + \gamma t_2) - 1\right). \qquad (5)$$

These assumptions lead to a 4 × 4 matrix **F** of the proportion of matings between a female of genotype i and a male of

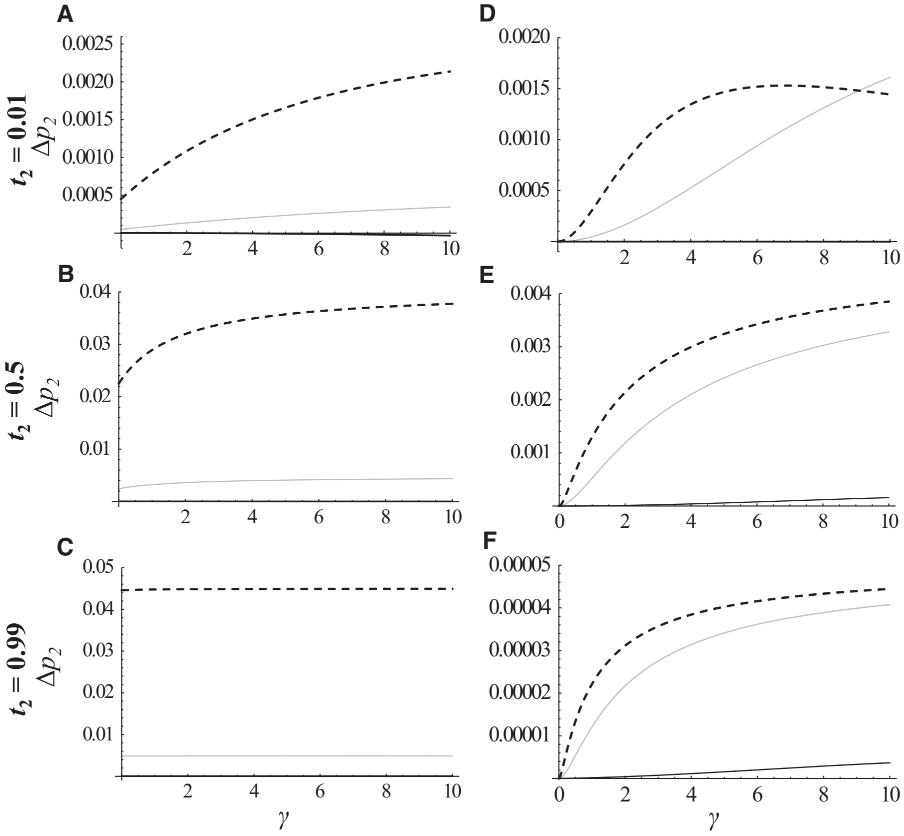

Figure 2. The relationship between the spread of the male preference allele (Δp_2) and the strength of male preference (γ) for the two-locus models. Different starting frequencies of the female trait allele (t_2) are shown for both flat (A–C) and weighted (D–F) female preferences for male courtship effort. The three lines in each graph represent different strengths of female preference for high male courtship effort (black line: $a = 0.01$, gray line: $a = 1.0$, black dashed line: $a = 10.0$). For all plots, the initial starting frequency of the male preference allele (p_2) is set at 0.01 to explore the spread of the allele after the occurrence of a new mutation. Note that the scale on the y-axis varies between plots and that $a = 0.01$ (black lines) fall on the x-axis (Δp_2 near zero) for plots A–D. Under this scenario, where the starting frequency of the male preference allele (P_2) is low, increasing the preference strengths of both females (a) and males (γ) generally increases the spread of P_2.

genotype j,

$$\mathbf{F}_{ij} = \frac{\mathbf{M}_{ij} f_{ij}}{z_i}, \tag{6}$$

$$\Delta p_2 = \frac{p_1 p_2 t_1 t_2 \gamma^2 \left(a(1 + t_2\gamma - p_2(2 + \gamma + 2t_2\gamma)) - a^2(1 + t_2\gamma)(p_2(1 + \gamma + t_2\gamma) - t_2\gamma) - p_2\right)}{2\left(1 + (1 + a)p_1 t_2 \gamma + a p_1 t_2^2 \gamma^2\right)((1 + t_2\gamma)(1 + a t_2 \gamma) + p_2 t_1 \gamma(1 + a(1 + \gamma + t_2\gamma)))}. \tag{7}$$

where $z_i = \sum_j x_j^* f_{ij}$. Because the matrix **F** is based on the matrix **M**, females are thus mating in proportion to the frequency with which they are courted (as in the case of flat preferences), but now their preference for courtship is weighted by the amount of courtship they are receiving, as described above. Normalizing by z leads to an equal mating rate for all females. We note that with this weighted function when $\gamma = 0$, females will mate solely in proportion to the frequency and apparentness of males.

Mating is again followed by free recombination and segregation, leading to recursion equations for the allele frequencies and disequilibria. The recursion equation for the frequency of the male preference allele p_2 is now

As is the case with the flat preference, this equation does not include linkage disequilibrium because male preferences change only due to direct selection.

The conditions for the spread of P_2 (when Δp_2 in equation (7) is positive) are more complicated than with the flat preference function. We can again show graphically (Fig. 1B) that for a range of the female preference parameter a there will be a line of stable internal equilibria where the frequencies p_2 and t_2 will remain polymorphic due to the frequency dependence of direct selection on the male preference (see section Flat Female Preference above). A stronger female preference for male courtship (i.e., a higher a) leads to higher equilibrium frequencies of the P_2 allele unless a is very high ($a = 10$) and the starting frequency of T_2 is low (Fig. 1B).

With weighted preferences, the effects of the interaction between the strength of the male preference (γ) with the strength of female preference for male courtship effort (a) is also more complicated than for the flat female preference function. With $a > 0$, a stronger male preference (higher γ) can have a positive effect on the spread of P_2 when the starting frequency of P_2 is low (p_2 initial $= 0.01$) (Fig. 2D–F), although this relationship is once again more complicated with high a ($a = 10$) (Fig. 2D), due to the ratio of weightings for preferences for P_2 males versus P_1 males. We consider these positive effects of a and γ on the spread of the P_2 allele when the starting frequency of P_2 is low to be the most biologically relevant, as it portrays the fate of a new mutation for a male preference entering the population. When the starting frequency of P_2 is higher ($= 0.5$ or 0.99), stronger male preferences (higher γ) can decrease the spread of the male preference allele P_2 (not shown). This negative relationship between γ and the spread of P_2 is heightened with an increasing a. In contrast to the flat female preference function, intermediate starting frequencies of T_2 generally lead to less rapid increases in p_2 when it starts at a low frequency (Fig. 2E; it also lead to decreases in the spread of P_2 when it starts at a high frequency, not shown). However, as with the flat preference function, higher t_2 relative to p_2 leads to a higher equilibrium level of P_2 (Fig. 1B), although this effect is not as pronounced.

Is the Evolution of Male Choice Affected by Nonchoosy Males Who Unbiasedly Court More in Total?

In the model above, males with a preference benefit from the fact that females prefer to mate with males who court more. We next analyze how this relationship is affected by the addition to the model of another way that courtship can be increased. We thus introduce a third locus that allows males to increase their total courtship effort without expressing a preference toward any specific type of female. Allele C_1 at locus C designates a basal level of total courtship effort while allele C_2 designates a higher level of total courtship. Specifically, C_2 males unbiasedly court both types of females $(1 + c)$ times more than C_1 males do, but they pay a survival cost that reduces their relative fitness to $(1 - s_c)$.

With the addition of locus C there are now eight genotypes, where x_1 through x_8 represent the frequencies of the genotypes $C_1P_1T_1$, $C_1P_1T_2$, $C_1P_2T_1$, $C_1P_2T_2$, $C_2P_1T_1$, etc. Viability selection occurs before male courtship; in this version of the model it reduces the viability of C_2 males as described above, yielding

$$x_j^* = \frac{(1 - g s_c) x_j}{1 - s_c c_2}, \tag{8}$$

where $g = 1$ if $j = 5$ through 8 and $g = 0$ otherwise, as the frequency of the male genotype x_j after natural selection.

The time spent in male courtship between a male of genotype j and female of genotype i can now be described by the 8 × 8 matrix as follows:

$$\mathbf{M}_{ij} = \frac{x_i x_j^* (1 + d_1 c)(1 + d_2 \gamma)}{1 + k_1 \gamma t_2}, \tag{9}$$

where $d_1 = 1$ if j equals 5 through 8 (C_2 males), $d_1 = 0$ otherwise, $d_2 = 1$ if i is even and j mod 4 is 0 or 3 (P_2 males courting T_2 females), $d_2 = 0$ otherwise, $k_1 = 1$ if j mod 4 is 0 or 3 (P_2 males), and $k_1 = 0$ otherwise. This matrix is normalized so that males with the preference alleles P_1 versus P_2 have equal total courtship effort, as in the two-locus model described above. That is, P_2 and P_1 males invest an equal total amount of effort or time in courting females, differing solely in how they distribute this total courtship effort between preferred (T_2) and nonpreferred (T_1) females. P_2 males distribute their total courtship effort between T_2 and T_1 females upon encounter at a ratio of $1 + \gamma$: 1, while P_1 males distribute their total courtship effort between T_2 and T_1 females upon encounter at a ratio of 1:1. This is in contrast to males with the C_2 allele, who have a higher total courtship effort than C_1 males. We again explore two types of female preferences, flat and weighted, following the same assumptions as above.

FLAT FEMALE PREFERENCE

As in the two-locus model, the assumption of a flat preference function implies that all females are $1 + a$ times as likely to mate with a male that courts them above the basal level of courtship in the population (that of C_1P_1 males). That is, the mating success of C_2 and P_2 males who court a type of female more than the basal level is $1 + a$ times higher than their mating success due to their frequency and apparentness alone (see Table 1). Mating again occurs following strict polygyny, where females perceive males in proportion to how often they are courted by them. With a flat preference, the proportion of matings between x_i females and x_j males is represented by the 8 × 8 matrix $\mathbf{F}$ where

$$\mathbf{F}_{ij} = \frac{\mathbf{M}_{ij}(1 + a d_3)}{z_i} \tag{10}$$

and

$$z_i = \sum_j \frac{x_j^*(1 + d_1 c)(1 + d_2 \gamma)(1 + d_3 a)}{1 + k_1 \gamma t_2},$$

where d_1, d_2, and k are identical to those in equation (9), and $d_3 = 1$ if either d_1 or d_2 is equal to 1. The normalization z_i ensures that all females have an equal mating rate. After mate choice, free recombination and segregation occur to produce zygotes in the next generation.

It is of interest to compare the evolution of the male preference allele P_2 with and without the presence of the locus that allows increased total courtship effort, C. The expression for Δp resulting from the three locus model is very complicated. A weak selection approximation of Δp in the two and three locus cases (see Appendix S2) shows that at quasi-linkage equilibrium (when the associations between loci have stabilized but the allele frequencies of those loci have not) the difference between the values for Δp with and without the allele for extra courtship can be approximated to the first order by

$$\Delta p_{C\_\mathrm{approx}} - \Delta p_{\mathrm{no}C\_\mathrm{approx}} \approx -\tfrac{1}{2} a c_2 t_2 p_1 p_2. \qquad (11)$$

Under the conditions of weak selection and weak preferences, the addition to the model of an allele leading to increased total courtship effort, c_2, thus leads to a smaller increase, or a greater decrease, in the frequency of the p_2 allele than if c_2 were not present. A stronger preference for extra courtship on the part of females (higher a) will magnify this effect. Note that the difference shown in expression (11), which does not include expressions for the disequilibria, is due to the effects of direct selection on the preference allele.

To examine the effect on the preference allele of the addition of the locus for increased total courtship effort, C, under assumptions of strong selection, we derived an expression for the net strength of direct selection placed on the preference allele ($\tilde{a}_{P,0}$), using the notation of Barton and Turelli (1991) (see Appendix S3). With a flat female preference, the addition of males who have an increased total courtship effort (C_2) has a negative effect, decreasing net direct selection favoring the male preference allele (P_2) (Fig. 3). This is because C_2 males not only compete for a female's preference with P_2 males that are preferentially courting T_2 females, but, unlike P_2 males, they also do not suffer from becoming less apparent to T_1 females, as they court unbiasedly. As in the two-locus version, the effect of the female preference for extra male courtship (a) on selection on the P_2 allele is positive (see y-axis values on Figs. 3 and 4). The effects of a stronger male preference (higher γ) are more complicated, being positive, negative, or having little effect depending both on the starting frequencies of P_2 and T_2 as in the two-locus version and on the level of a (Fig. 3). Increasing the total courtship effort of C_2 males (higher c) has a negative effect on net direct selection favoring the P_2 allele, as C_2 males become increasingly apparent to females and outcompete P_2 males (Fig. 4).

WEIGHTED FEMALE PREFERENCE

As with flat preferences, the basic assumptions of the weighted preference models are identical between the two- and three-locus models. In the three-locus model, all females again compare the courtship that they are receiving to a basal (the lowest) rate, and scale their preference accordingly. The coefficients of the weighted preference are thus defined again by equation (5) (also see Table 1), where now the coefficients b_{ij} are obtained by rewriting equation (9) as $M_{ij} = x_i x_j^* b_{ij}$. These assumptions again yield a matrix $\mathbf{F}$ described by equation (6). Once more we assume free recombination and segregation to complete the recursion equations.

We can again derive an expression for the effect of the C locus on male preference evolution by looking at the conditions of quasi-linkage equilibrium, assuming weak selection and weak courtship and mating preferences (Appendix S2). We find that with weighted preferences

$$\Delta p_{C\_\mathrm{approx}} - \Delta p_{\mathrm{no}C\_\mathrm{approx}} \approx \tfrac{1}{2} a \gamma c_2 t_2 p_1 p_2. \qquad (12)$$

This difference, again due to direct selection, is now to the second order in the selection and preference parameters. With weighted preferences, the addition of the allele for increased total courtship effort, c_2, increases the evolution of the male preference allele p_2. This increase is heightened by stronger male preferences (γ) and stronger female preferences for extra courtship (a). Under weak selection the type of female preference function, weighted versus flat, thus changes the effect that extra unbiased courtship will have on the spread of the male preference allele.

To examine similar effects under assumptions of strong selection, we again used the notation of Barton and Turelli (1991) to obtain an expression for the net strength of direct selection placed on the preference locus (Appendix S3). In contrast to the flat female preference, with a weighted female preference the addition of the C locus generally has a positive effect, increasing net direct selection favoring the male preference allele (P_2) (Fig. 3). However, when the strength of the female preference for extra male courtship (a) is high, this pattern can be reversed with a low starting frequency of T_2 and low γ (Fig. 3). The changing effects of the strength of selection on the P_2 allele with and without the C_2 allele are due to the relative preference weights females give to each type of courting male, which differ both with the male genotypes at the P and C loci as well as with the genotype of the female herself at the T locus (see Table 1). As in the two- and three-locus flat preference versions of the model, the effect of the female preference for extra male courtship (a) on selection on the P_2 allele is positive (Figs. 3 and 4). The effects of a stronger male preference (higher γ) are also generally positive (Fig. 3). This is intuitive as males who court more are preferred proportionately

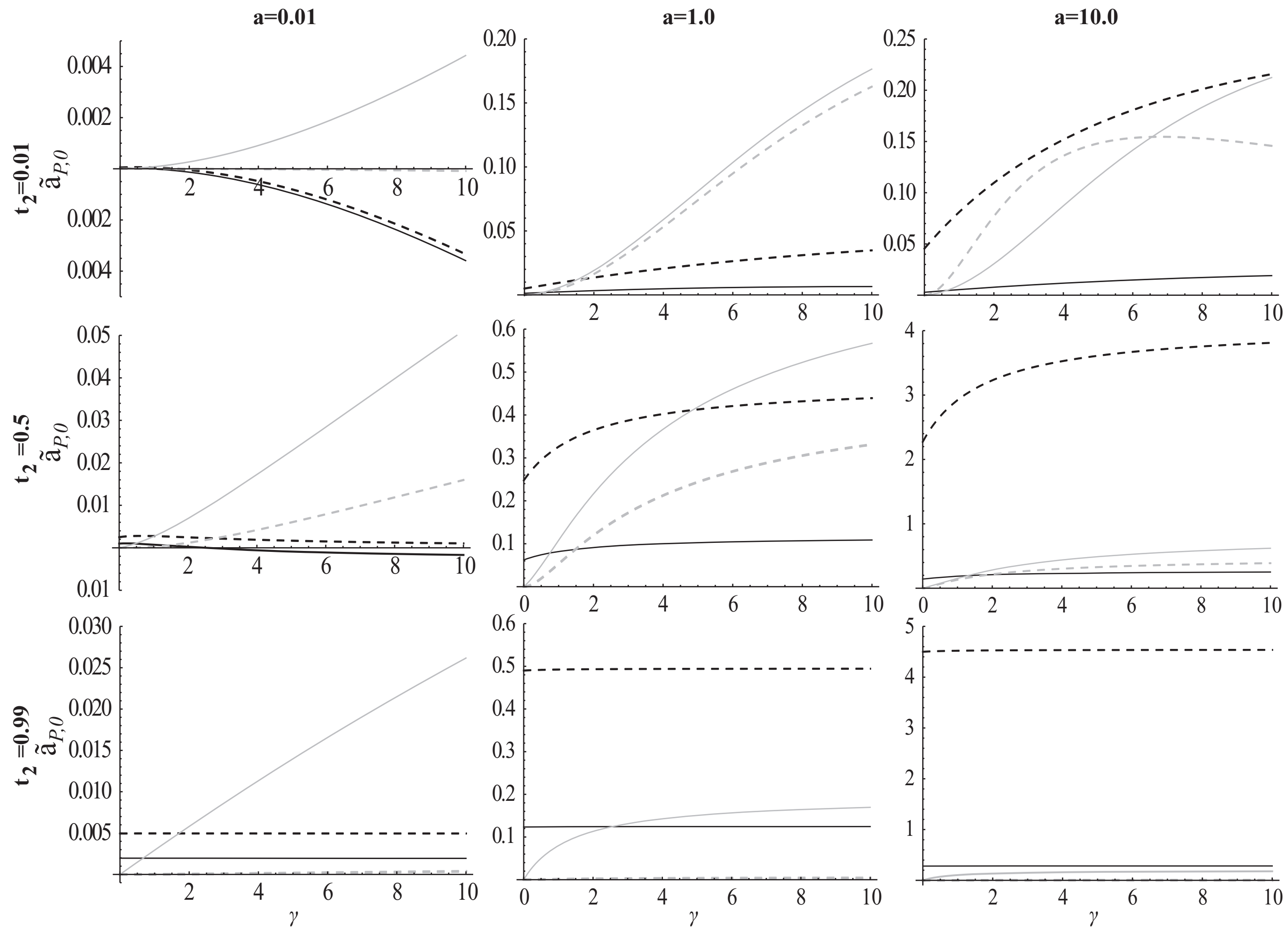

Figure 3. The relationship between the net measure of direct selection on the male preference allele ($\tilde{a}_{P,0}$) and the strength of the male preference (γ) for both the two- and the three-locus models with the increased total courtship effort locus C. Three different levels of female preference for male courtship effort (*a*) are shown. The black lines represent values for the flat female preference function (solid: with C, dashed: without C). Gray lines represent values for the weighted female preference function (once again, solid: with C, dashed: without C). For all plots $s_c = 0.5$, $c = 2.0$, and the starting value of $p_2 = 0.01$. For the flat female preference function, the addition of males who unbiasedly court more in total (C_2) leads to weaker net direct selection on the male preference allele (P_2) (black dotted lines higher than black solid lines). In contrast, for the weighted preference function this pattern is reversed, with the addition of C_2 males generally leading to stronger net direct selection on P_2 (gray dotted lines lower than gray solid lines). Note that increasing *a* increases selection on the P_2 allele.

more by females. However, for high values of *a* and γ, and low starting frequencies of T_2, increasing γ can have a negative effect (see also above). Increasing the total courtship effort of C_2 males (higher *c*) shows more complex dynamics, having a negative effect on net direct selection on the P_2 allele when *a* is high as in the flat preference version of the model (Fig. 4). However, when *a* and/or γ is very low, increasing *c* generally has a positive effect on net selection on the P_2 allele.

Discussion

We find that a female preference for males that court more elevates the mating success of males who choose to distribute a larger proportion of their total courtship effort toward preferred females, and that this can lead to the spread of a male preference allele. To our knowledge, this is the first time that this effect of female choice on the evolution of male mate choice has been explored, and we show that it provides a novel way of offsetting the high costs associated with male preferences under a male-biased OSR (Parker 1983; Rowe 1994; Deutsch and Reynolds 1995; Johnstone 1997b; Watson et al. 1998; Servedio and Lande 2006; Servedio 2007; Venner et al. 2010). This is likely to be a widespread effect as females of such species often show preferences for male courtship effort (Andersson 1994; Johnstone 1997a). Furthermore, there are increasing reports of males expressing their preferences for females as increased courtship (e.g., Weiss 2002; Herdman et al.

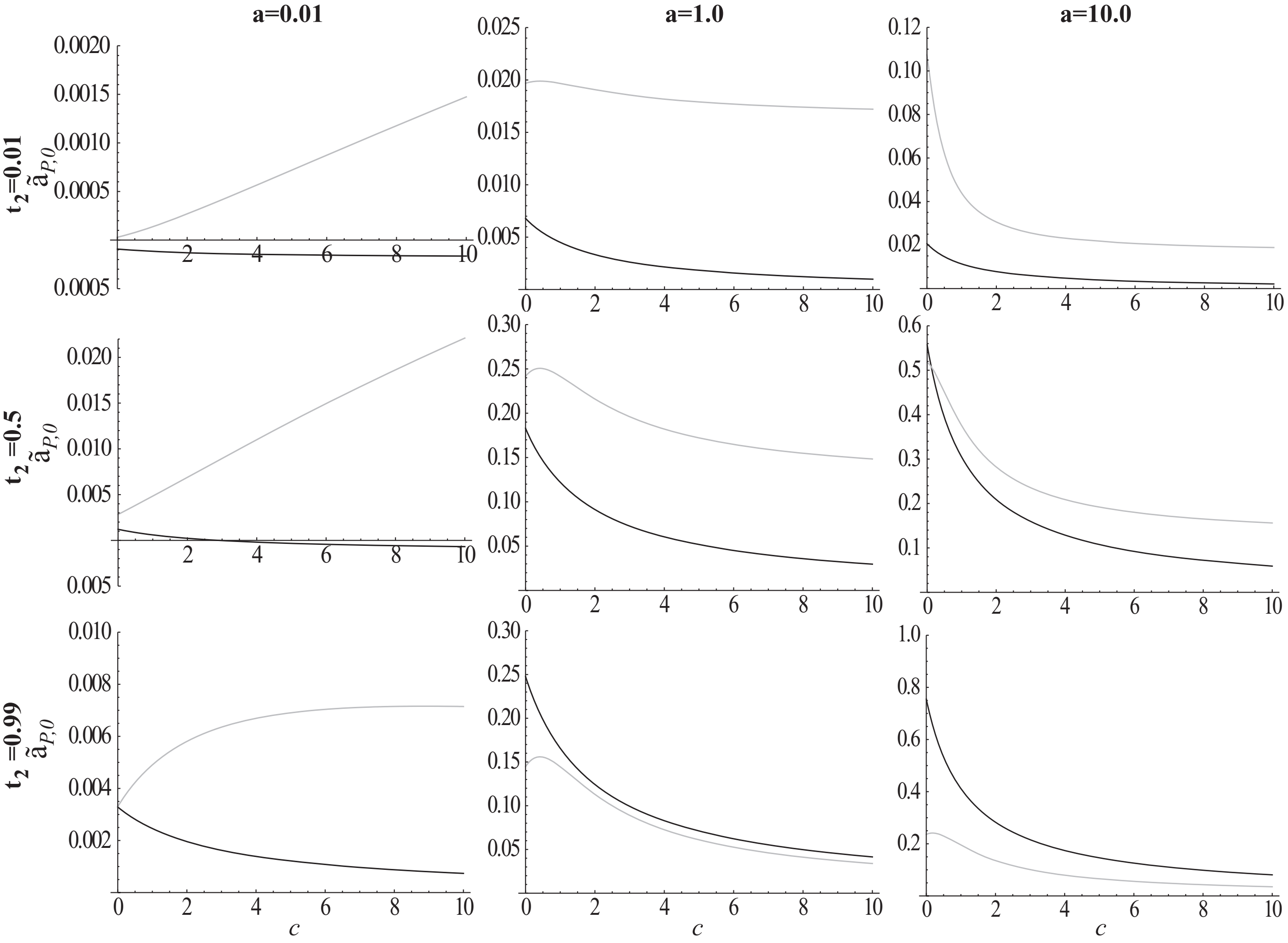

Figure 4. The relationship between the net measure of direct selection on the male preference allele ($\tilde{a}_{P,0}$) and the increased total courtship effort of C_2 males (c) for the three-locus model. Black lines represent the flat female preference function and gray lines represent the weighted female preference function. Three different levels of female preference for male courtship effort (a) are shown. For all plots $s_c = 0.5$, $\gamma = 2.0$, and the starting frequency of $p_2 = 0.01$. For the flat female preference function, increasing the total courtship effort of C_2 males (c) always decreases selection favoring P_2 males. In contrast, for the weighted female preference function increasing c increases selection favoring P_2 when a is low. However, with a higher a this relationship becomes negative with increasing c. Note that increasing a increases selection on the P_2 allele.

2004; Ojanguren and Magurran 2004; Roberts and Uetz 2005; Reading and Backwell 2007; Lihoreau et al. 2008; Ruiz et al. 2010).

We find that the evolution of the male preference is contingent upon the starting frequencies of both the preferred female trait allele and the male preference allele. The negative effect of the starting frequency of the male preference allele makes intuitive sense when one considers that the costs of competition experienced by males courting preferred females will be higher when a larger proportion of males show a preference. Consideration of the competitive costs that males with a preference face when courting preferred females also accounts for the fact that the spread of the male preference allele is facilitated by higher frequencies of the preferred females, as the more preferred females relative to males with a preference, the less the competition.

The female preference function plays an important role in determining the fate of the male preference allele. The positive effects of increasing the strength of the female preference for male courtship effort generally held with both a flat and weighted female preferences. However, with high levels of female preference the relationships became more complicated when females used a weighted preference. High levels of the weighted female preference did not have as strong an effect on the spread of the male preference allele as more moderate female preferences did, when the female trait had a low starting frequency.

The effects of the addition to the system of nonchoosy males who unbiasedly court all females more and thus have a higher total courtship effort are also highly dependent on the female preference function. When females exhibit a flat preference for extra male courtship, the addition of males who unbiasedly court all females more in total constrains the spread of the male preference allele by increasing competition for the favor of females. In contrast, when females exhibit a preference that is weighted by the amount that males court, the addition of nonchoosy males who unbiasedly court all females more in total generally has a positive effect on spread of the male preference allele. This is due to the sexual selection that the specific weightings of female preferences in this model place on males with and without the preference; with weighted preferences, the relative preference of females for males with versus without the P_2 allele is generally higher when those males also carry the allele for extra-unbiased courtship (C_2). The type of preference function present can thus be critically important for determining the way in which various alleles that alter courtship in males may affect each other's evolution. Our results showing that the evolution of male preferences can be affected by the specific female preference function also join previous reports highlighting the important role that female preference functions play in determining the fate of male traits (e.g., Janetos 1980; Real 1990; Weigmann et al. 1996; Jennions and Petrie 1997).

When expression of the preferred female trait confers a cost to female viability or female fecundity, the female trait allele is quickly lost in the population in our basic model (Appendix S1). Once the female trait is lost, the preference remains at its current level because it becomes selectively neutral. When males instead favor females whose traits reflect either high viability or high fecundity selection (akin to males favoring high-condition females), the female trait rapidly goes toward fixation. The male preference can only spread as long as there is polymorphism at the female trait locus. Indirect selection will contribute to the spread of the male preference in these situations due to the fact that the male preference becomes genetically correlated with the female trait. However, the effect of indirect selection is slight in comparison to the effect of direct selection on the male preference due to a female preference for male courtship effort. Our results therefore support the general prediction that males must reap significant direct benefits of choice to offset the direct costs of male mate choice under polygyny, and that male preferences for traits which detract from the possible direct benefits of male choice are unlikely (Fitzpatrick et al. 1995).

Our exploration of direct selection on the female trait provides insight into the relative effects of indirect selection due to a genetic correlation with the female trait and direct selection via a female preference for extra male courtship on the evolution of the male preference. However, the scenario of complete loss or fixation of the female trait is unlikely as genetic variation in sexually selected traits in nature is often maintained even in the face of strong directional selection (an aspect of the so-called lek paradox, Borgia 1979; Pomiankowski and Møller 1995). The maintenance of such genetic variation in sexually selected traits has been suggested to occur through the process of "genic capture" (Rowe and Houle 1996), which is a good genes indicator model. Through this process, the condition-dependent expression of traits reflects not only environmental variation but also the myriad of genes that are likely to contribute to condition (Rowe and Houle 1996; Lorch et al. 2003; Hunt et al. 2004; Tomkins et al. 2004). The maintenance of genetic variation in the female trait through genic capture would allow the persistence of indirect selection on the male preference. Nonetheless, as mentioned above, this effect of indirect selection would be slight in comparison to that of direct selection on the male preference due to a female preference for male courtship effort (see also Kirkpatrick and Barton 1997).

Variation in a female trait preferred by males can also be maintained when the female trait is phenotypically plastic and the environment is variable during development. This situation includes cases where the trait is condition dependent and solely reflects environmental effects upon, for example, the amount of resources available or the length of the season during development (i.e., nonheritable factors) (Iwasa and Pomiankowski 1999; Cotton et al. 2004). Under these scenarios, there would be no opportunity for linkage disequilibrium to arise between the male preference and expression of the nonheritable preferred female trait. Interestingly, many of the results of our basic model are robust to the possibility that the female trait preferred by males is solely environmentally determined. As shown by the recursion equations describing the spread of the male preference under both a flat (equation (3)) and weighted female preference (equation (7)), there is an absence of linkage disequilibrium, D, between the male preference and the female trait. Thus, in the basic model, there is no indirect selection leading to the evolution of the male preference. The recursion equations (3) and (7) are therefore independent of whether or not female trait variation is genetically determined and would still hold if the frequency of the trait were unchanging. As described in the legend to Figure 1, the lines of equilibrium reached in these models from a variety of starting conditions involve evolutionary trajectories that are almost horizontal in our figures; negligible evolution occurs in the direction described by the frequency of the trait. For these reasons, the evolution of the male preference allele described by Figure 1 will be very similar even if trait variation is solely due to the environment and changes very little between generations. These facts provide a set of conditions that allow preference evolution while circumventing the problem of the loss of trait variation that constitutes the lek paradox (a problem that is apparent in the version of our model with direct selection on the trait). In cases where trait expression reflects high environmental quality, any further direct benefits that males gain from preferring these nonheritable condition dependent female traits would further accelerate the spread of the male preference (Parker 1983; Owens and Thompson 1994; Servedio and Lande 2006; Servedio 2007; Nakahashi 2008).

This study also provides support for the prediction that the evolution of costly female traits used solely to attract males is unlikely under polygyny and a male-biased OSR. We find that indirect selection favoring the female trait, which occurs because the female trait becomes genetically associated with the male preference when it spreads, is insufficient to overcome the costs of expressing the trait (Kirkpatrick and Barton 1997). This is because all females are likely to mate due to the male-biased OSR, and their fitness will largely reflect their fecundity rather than their mating rate (Bateman 1948). Thus, females will not reap sufficient benefits from attracting males to offset the costs of expressing the trait (Maynard et al. 2003).

However, there is increasing evidence of apparently costly female traits evolving under directional selection via male mate choice (e.g., LeBas et al. 2003; Siefferman and Hill 2005; Bitton et al. 2008; Doutrelant et al. 2008; Simmons and Emlen 2008; Wright et al. 2008). In a recent review, Rosvall (2011) highlighted that, based on empirical evidence to date, females appear to compete most often for high-quality mates that confer direct and indirect benefits rather than the number of mates. Thus, females may signal to attract high-quality males, a possibility also under this scenario where females mate once only. Additionally, females may also benefit through attracting many males, thereby facilitating simultaneous assessment of male quality (Bradbury 1981; Shuster and Wade 2003) and reducing the costs of choice to females. Interestingly, a Härdling and Kokko (2005) model exploring assortative mating when both sexes can mate multiply showed that female quality may be negatively correlated with female mating rate. This is due to increased competition for high-quality females resulting in only a subset of males courting them. We therefore agree that further theoretical models exploring the benefits of signaling to females beyond total number of mates and fecundity will provide valuable insights. Further empirical studies may identify additional factors (e.g., additional benefits to females of signaling to attract mates) that may lead to departures from the predictions of current theoretical models.

In addition to being more likely to be accepted by females, males may also benefit from courting preferred females more through differential maternal allocation to offspring. This is possible as females have been shown to increase reproductive investment when mated to males perceived as more attractive, for example, through increased investment in eggs (Burley 1988; Sheldon 2000; Loyau and Lacroix 2010).

In conclusion, our model provides evidence that directional female preferences for costly male traits such as courtship can facilitate the evolution of male mate choice. This model does not present a novel set of predictions for empiricists to test, as the data required to support our model already exists (i.e., male preferences expressed as biased courtship effort and female preferences for higher male courtship). Instead, we provide a novel pathway that can explain the evolution of male preferences in polygynous species with male-biased OSRs.

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Supporting Information

The following supporting information is available for this article:

Appendix S1. How is the evolution of male mate choice and the female trait affected by direct selection on the female trait?
Appendix S2. A weak selection approximation of Δp in the two- and three-locus cases.
Table S1. Accuracy of the approximations in expressions (B2), (B3), and (11) for the flat preference model.
Table S2. Accuracy of the approximations in expressions (B5), (B6), and (12) for the weighted preference model.
Appendix S3. The net strength of direct selection placed on the preference allele ($\tilde{a}_{P,0}$) for the three-locus version of the model.

Supporting Information may be found in the online version of this article.