

THE EVOLUTIONARY ORIGINS AND CONSEQUENCES OF VARIATION IN FEMALE MATE  
CHOICE PREFERENCES

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## **ABSTRACT**

ALICIA M. FRAME: The Evolutionary Origins and Consequences of Variation in Female Mate Choice Preferences  
(Under the direction of Maria R. Servedio)

In many species, females select males whom they believe will provide them with resources or good genes. To entice females to mate with them, males display their quality via physical traits, such as long tails, bright colors, or elaborate armaments. It has been widely hypothesized that if females always chose males with the best traits, over time the population should become homogenous; eventually, variation in male quality and the utility of female preference should be lost, since females will always select males with desirable traits, which will then be passed on to their offspring. However, in reality, wide variation within male traits and female preferences is well documented. This contradiction is known as the 'paradox of the lek'. In this dissertation, I use mathematical models and simulations to explore alternative explanations for the maintenance of variability in female preferences.

Competition for desirable mates can lead to negative consequences for females. I demonstrate that in the face of intrasexual competition, natural selection can act against female preferences. Nevertheless, female preferences can still evolve under certain circumstances, and competition does not prevent the evolution of additional

preferences. Environmentally determined preferences evolved through sensory bias (eg. preferences for conspicuous males) are known to play a role in the maintenance of male trait variation, and hence I explore whether or not modifiers for increasing preference strength may evolve. I show that unless populations are physically separated, modifiers of female preference do not spread, and that these ecologically determined preferences will neither increase in strength nor be lost via selection. Finally, I demonstrate that temporal variation in female condition and related search costs can alter female preferences. The best policy for a female facing condition-dependent search costs is a threshold for male quality which is determined by her current condition. Such a policy compares favorably with other mate choice policies suggested in the literature, is robust to uncertain information.

This dissertation provides insight into the role of extrinsic factors in shaping sexual preferences, and highlights the importance of thinking beyond the traditional paradigm of sexual selection.

## **DEDICATION**

Dedicated to Alex F. Mills, who put up with hours and hours of whining, plenty of worrying, and too many late nights, and Henry, Scooter, and Princess, our beloved parakeets.

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## CHAPTER I: INTRODUCTION

Sexual selection, defined as selection arising through differential reproductive success, has long been acknowledged to be a potent force in diversification and speciation (West-Eberhard 1983, Panhuis et al. 2001, Ritchie 2007). Access to mates determines whether an individual's genes will be passed on, and the ability to choose the best mate – one of the same species, who is likely to produce healthy offspring – is essential to the survival of a species. Sexual selection is known to lead to rapid, divergent evolution due to the importance of gaining access to mates, the mutual acceleration of preference and trait evolution through linkage disequilibrium, and the wide variety of behavioral and physical characteristics which may be subject to sexual selection (West-Eberhard 1983). In fact, differences in closely related species occur most often in traits related to mating (Ritchie, 2007).

While sexual selection often leads to divergence between species, it may also contribute to homogenization within species. If all females are choosing the most attractive male (e.g., the one with the brightest spots or the longest tail), then all their offspring will inherit genes for attractive appearance, thus reducing variation in appearance in the population. Consequently, if all males look the same, then females can no longer select mates based on appearance and the preference for appearance will gradually be eliminated. More formally, in polygynous species, females often show similar preferences for male traits and a small minority of males gets the majority of

mates, which in time should erode variation in male traits and remove the benefits of choice (Borgia 1979, Kirkpatrick and Ryan 1991). Yet this is not the case in the real world: most species do show variation in male traits, and female preferences persist. This contradiction has become known as the paradox of the lek.

Many hypotheses have been put forth to resolve the lek paradox and explain why preferences are maintained despite sexual selection. Hypotheses about the underlying genetic variation in male traits (Pomiankowski and Moller 1995, Merila and Sheldon 1999), and condition-dependent male traits (Rowe and Houle 1996, Hine et al. 2004, Tomkins et al. 2004) have made significant steps towards explaining processes that maintain variation, but these hypotheses are still centered on male traits, using the maintenance of male preference as the central explanation for the persistence of female preferences.

The bias toward thinking of sexual selection in terms of male traits and female preferences is longstanding. In *The Descent of Man and Selection in Relation to Sex*, Charles Darwin described sexual selection in terms of both the competition for access to mates and the competition to attract mates:

*The sexual struggle is of two kinds; in the one it is between individuals of the same sex, generally the males, in order to drive away or kill their rivals, the females remaining passive; whilst in the other, the struggle is likewise between the individuals of the same sex, in order to excite or charm those of the opposite sex, generally the females, which no longer remain passive, but select the more generally agreeable partners.*

Although nearly 150 years old, this definition still holds today. It also highlights what has long been a central focus of sexual selection: the dichotomy of male traits and female preferences. Under this view, males evolve traits to compete with each other and attract female attention, and female preferences evolve primarily to select the best males to father their offspring. However, just as male traits serve the dual purpose of fighting off rivals and attracting mates, preferences may similarly serve a dual role for females.

When selecting mates, females must balance the benefits of a high quality male, which may include good genes (indirect benefits) or resources such as food, parental care, or territories (direct benefits), with the inherent constraints of natural selection, which include the potential costs involved in finding and mating with such a male, as well as their pre-existing sensory systems and physical composition. When these factors are considered, the maintenance of variation in mating systems becomes much less paradoxical: females are not just picking the best males; they are also looking out for their own best interests.

External pressures on female choice, from search costs to sensory bias, have previously been used to explain the maintenance of variation in male traits and the continuing presence of female preference in spite of sexual selection. An early, and seemingly obvious, explanation for the maintenance of male trait variation and female preference was that natural selection acts directly on females to minimize the cost of mate choice, such as time spent searching for and assessing males, risk of predation and injury, and loss of potential mates to competitors (Reynolds and Gross, 1990). Ryan and

Rand (1993) offered an alternative explanation, proposing that many male traits simply evolved to match pre-existing biases in the female sensory system. I propose a third hypothesis to resolve the lek paradox: that many external factors, including costs and biases, are likely to influence female preferences and drive variability in those preferences. Consequently, the variability in preferences may maintain variability in male traits.

Factors other than choosing the best mate possible, such as search costs, competition, spatial and temporal variation in environments, and female condition, may play an important role in maintaining female preferences while maximizing fitness. These factors can be divided into two categories: preference functions (how a female ranks prospective males) and choosiness (the effort that a female is willing to invest in mate assessment) (Jennions and Petrie, 1997). The fact that these factors may both vary in response to selection, and hence selection is not limited to choosing the best male, is the key to explaining the maintenance and variability of female preferences.

Early genetic models played an important role in verifying claims about sexual selection; for example, by clarifying how female preferences lead to exaggerated male traits (Lande 1981, Kirkpatrick 1982). These models showed that sexual selection alone could drive evolution, and subsequent work has generated many important and testable hypotheses about the origins and maintenance of male traits and female preferences.

In an attempt to formalize the aforementioned qualitative arguments for the persistence of variability in the face of sexual selection, I use mathematical models to

examine three distinct types of variability in female preferences: 1) genetic variation in alleles controlling female preferences, 2) environmentally determined female preferences, and 3) phenotypic plasticity in female preference. In the subsequent chapters, I use population genetic models, numerical and individual-based simulations, game theoretic models and decision theory to address the origins and ultimate outcomes of variability in female choice. Using these models, I generate insights about the long-term trajectory of populations, the effects of different parameters on evolution, and the validity of verbal arguments about female preferences. In the first chapter, I consider a genetic explanation for female preferences in the form of multiple differing preference loci controlling female mate choice for genetically independent male traits. In the second chapter, I explore how female preferences for conspicuous male traits, which evolved through sensory bias, can maintain and drive polymorphisms in heterogeneous environments. In the final chapter I examine how phenotypic plasticity, where a female alters her preferences in response to external cues, can create variation in female preference for a single male trait.

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## CHAPTER II: THE ROLE OF SEXUAL PREFERENCES IN INTRASEXUAL FEMALE COMPETITION

### **Abstract**

While search costs have long been understood to affect the evolution of female preference, other costs associated with mating have been the focus of much less attention. Here I consider a novel mate choice cost: female-female intrasexual competition, that is, when females compete with each other for mates. This competition results in cost to female fecundity, such as a reduction in fertility due to decreased direct benefits, sperm limitation, or time and resources spent competing for a mate. I asked if female-female competition affects the evolution of preferences, and further, if the presence of multiple, different, preferences in a population can reduce competitive costs. Using population genetic models of preference and trait evolution, I found that intrasexual competition leads to direct selection against female preferences, and restricts the parameter space under which preference may evolve. I also examined how multiple, different, preferences affected preference evolution with female intrasexual competition. I found that multiple preferences primarily serve to increase competitive costs and decrease the range of parameters under which preferences may evolve.

## Background

Costs associated with female preferences are often assumed to be directly related to the act of searching for a preferred mate: 1) time spent searching for a mate, 2) the potential for a choosy female to go unmated, or 3) an increased risk of predation (Reynolds and Gross, 1990). These previously considered costs are *viability* costs, where the female's chances of survival and successful mating are affected; here I present an argument for the role of fertility costs and their effect on preference evolution. There is great potential for costs involved in mate choice to be derived from female-female intrasexual competition as well. In general, these costs have not been widely studied or taken into account as potential selective forces driving (or preventing) female preference evolution (Jennions and Petrie, 1997).

In resource-based polygyny, males provide females with resources such as parental care, defense, or territories in which to raise their young. In such scenarios, the cost of competing for a desired male is clear cut: it is well accepted that males may only support a limited number of females, and increasing beyond that threshold leads to decreased female reproductive fitness (Weatherhead and Robertson, 1979). Even in systems where resource limitations are less obvious, reduction in parental efforts can lead to decreased female fitness. For example, in dendrobatid frogs, brood sizes decreased significantly after multiple matings due to decreased male parental effort (Summers 1990). Similarly, in polygynous tree swallows, females mated with polygynous males had reduced fitness because of decreased parental care (Ferretti and Winkler, 2009).

Even in polygynous species where males offer little to females, females may still incur costs simply by waiting to mate with a preferred male, by competing with other females for a preferred male's attention, or by suffering reduced fecundity from male sperm depletion. In lekking birds, dominant females monopolizing preferred males time can lead to delayed breeding and decreased reproductive fitness (Slagsvold and Lifjeld, 1994). Females may also respond to competition for males with direct aggression, potentially injuring competitors (Ahnesjo et al, 1993; Rosenqvist and Berglund, 1992). Sperm depletion and exhaustion, due to males mating multiply, may be costly to females as well (Wedell et al, 2002). Sperm exhaustion has been tied to reduced reproductive fitness for females in insects (Royer and McNeil, 1997), fish (Warner et al, 1995), and crustaceans (Rubolini et al, 2007; Rondeau and Sainte-Marie, 2001; Harris and Moore, 2005). Although these costs are small compared to those suffered by females mating in resource based polygyny, they are all associated with significant decreases in reproductive fitness.

In all of these situations, females are likely to experience a cost for preferring 'popular' males, i.e., those who have many mates. In fact, when females suffer fitness reductions from mating with sperm depleted males, if they can accurately assess the number of mates a male has, they choose males with fewer mates (Harris and Moore, 2005). In general, however, it may be difficult for females to ascertain whether they are likely to suffer competitive costs: for example, in systems where males have large or overlapping territories, females have little or no information about additional mates; in

systems where males provide resources that cannot easily be quantified, the female may have no information about these costs whatsoever.

Without direct knowledge, what can females do to avoid costly competition? One possibility is that multiple preferences may aid in alleviating or preventing competition. Indeed, many of the species discussed previously as examples of costly female competition have multiple male traits and preferences as well (guppies: Brooks, 2002; tree swallows: Bitton et al, 2007; Great Snipe: Fiske et al, 1994). If females have differing preferences, and if males display differing traits, then competition could be reduced. For example, if females of some species may prefer complex song, long tails, or both, and males may have one or both of those traits; females choosing mates with high quality plumage may reduce their cost of competition because they are not competing with those who choose males with a complex song.

Empiricists have found cases of repeatable variability in genetically determined female preferences (Brooks and Couldridge 1999, Marchetti 1998). In such scenarios, females appear to be selecting mates based on multiple independent male traits. Marchetti (1998) found evidence that female yellow browed leaf warblers based their choice of mate on several male characters, and although females preferred high quality males, different females used different traits to distinguish between these males. Brooks and Couldridge (1998) not only demonstrated multiple preferences in female guppies, but demonstrated that they are heritable and genetically independent. The genetic assumptions of my model are built upon these findings.

Although there is ample empirical evidence of intrasexual mate competition in females, to my knowledge it has not been incorporated into evolutionary models. Fawcett and Johnstone (2003) considered the potential for female competition to alter mate choice from a game theoretic point of view, and showed that female competition could alter mating decisions. However, their model ignored genetics and focused primarily on alternative strategies, which is problematic because linkage disequilibrium between genes is a powerful evolutionary force. Furthermore, their model assumed competition would cause a relaxation in preference rather than promote novel preferences, as I suggest.

Here, I argue that competition alone, regardless of the type of trait possessed by males, will impact preference evolution. To address these issues, I first model the evolution of a single female preference in a system with costly intrasexual competition for mates, to determine when preferences may still evolve and the strength of selection acting on preference. Then, I consider whether or not the presence of an additional female preference alleviates competitive costs, and how selection on preferences changes with the introduction of an additional preference. When discussing multiple preferences, I am referring to multiple preferences controlled by independent loci: females may have no preferences, a single preference, or both. As novel preferences evolve to fixation, the result is that the majority of females possess both preferences.

### **Model Specification and Results**

I model mate choice with costly female competition for mates using a population genetic model with haploid loci and discrete non-overlapping generations, based on

previous models of sexual selection via female choice (Kirkpatrick 1982). The model assumes polygyny; all females mate, but males have variable mating success.

For each model, I begin by describing the life cycle in terms of birth, mating, fertility selection, and zygote formation. Using these equations, I can then calculate the strength of direct selection on preference using the notation of Barton and Turelli (1991).

*One Preference, One Trait (two locus model)*

Female preference and male traits are controlled by two haploid loci, each with two alleles: the preferences locus, P, controls female preference, and the trait locus, T, controls male traits. Uppercase letters indicate the presence of a preference or trait, lowercase letters indicate the absence. These two loci yield four genotypes: PT, Pt, pT, and pt. I denote their frequencies as  $x_1$ ,  $x_2$ ,  $x_3$ , and  $x_4$ ;  $X_T$  is used to denote the frequency of the male trait allele ( $x_1 + x_3$ ), and  $X_P$  is used to denote the frequency of the female preference allele ( $x_1 + x_2$ ).

Females choose mates based on their preferences. A female without the preference allele (a p female) will mate randomly with respect to male genotype, whereas a female with the preference allele (a P female) is  $\alpha$  times more likely to mate with a male possessing the trait allele, given that she has evaluated one of each type.

Mate choice results in a 4x4 matrix,  $\mathbf{F}$ , whose elements  $F_{ij}$  represent the proportion of matings taking place between genotypes i and j:

$$F_{ij} = \frac{k_{ij}\alpha \cdot x_i x_j}{Z_i}, \tag{1}$$

Where  $k_{ij}$  is the modifier of preference strength for an  $x_i$  female mating with an  $x_j$  male;  $k_{11}$  and  $k_{13}$  are 1 ( $x_1$  and  $x_2$  females prefer  $x_1$  and  $x_3$  males), all others are 0 ( $x_3$  and  $x_4$  females mate randomly;  $x_1$  and  $x_2$  females do not prefer  $x_2$  and  $x_4$  (traitless) males).  $Z_i$  is a normalization to ensure that all female genotypes have equal mating success;  $Z_1 = \alpha X_T + (1 - X_T)$ ,  $Z_2 = 1$ . The full mating table is given in table 2.1.

**Table 2.1 Mating table for one preference/one trait model.** Females with the preference allele prefer males bearing a trait by a factor  $\alpha$ . Matings are normalized by  $Z$  so that all female genotypes have equal mating success

		Males			
		$x_1$	$x_2$	$x_3$	$x_4$
Females	$x_1$	$\alpha(x_1x_1)/Z$	$(x_1x_2)/Z$	$\alpha(x_1x_3)/Z$	$(x_1x_4)/Z$
	$x_2$	$\alpha(x_2x_1)/Z$	$(x_2x_2)/Z$	$\alpha(x_2x_3)/Z$	$(x_2x_4)/Z$
	$x_3$	$x_3x_1$	$x_3x_2$	$x_3x_3$	$x_3x_4$
	$x_4$	$x_4x_1$	$x_4x_2$	$x_4x_3$	$x_4x_4$

$$Z = \alpha(x_1 + x_3) + x_2 + x_4$$

After females have selected mates, fertility selection is exerted against the offspring of males with a surplus of mates. I denote the intensity of fertility selection by  $\gamma$ . When the mating frequency of a particular male genotype exceeds the population frequency of that male genotype, fertility is reduced proportionally. For genotype  $j$ , fertility selection is determined by

$$\phi_j = \gamma \cdot \left( \frac{\sum_{i=1}^4 F_{i,j}}{x_j} - 1 \right). \quad (2)$$

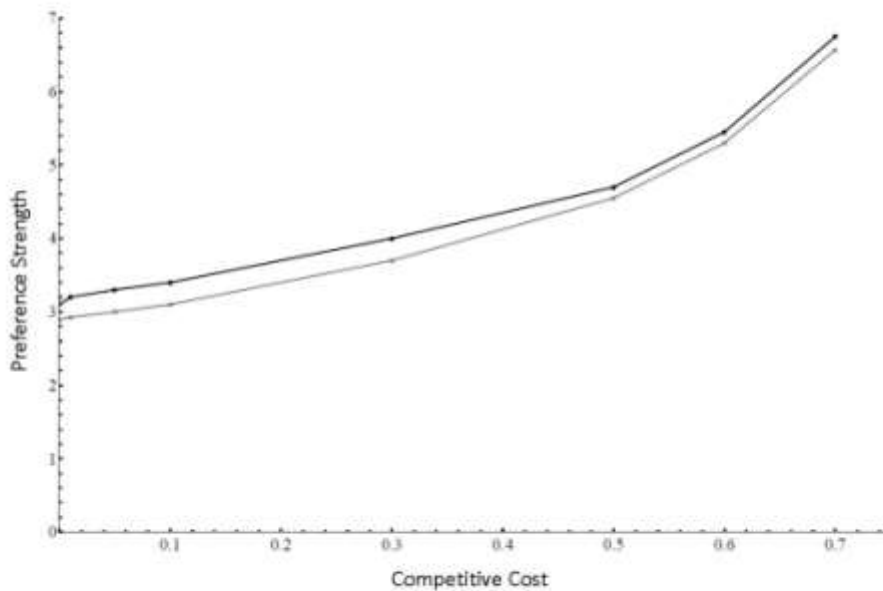
$F^\phi$ , the fertility selection matrix, is calculated by multiplying each column of  $F$  by the corresponding fertility reduction suffered by the male parental genotype. The result is that

$$F_{ij}^\phi = F_{ij}(1 - \phi_j). \quad (3)$$

Recombination follows sexual selection and fertility selection; recombination rates are assumed to be 0.5 between all loci for simplicity (free recombination).

Using these life cycle equations, I first used numerical simulations (run in Matlab) to confirm that it was possible to evolve preferences despite competitive costs. Female preferences may still evolve with competitive costs, although the preference strength needed to overcome selection and fix preferences increases as costs become greater (Figure 1, black line). This confirms that 1) female-female competition does act as a previously unexamined cost of choice, making it likely to cause natural selection against preference evolution, and 2) this cost does not completely bar preference evolution.





**Figure 2.1** Preference strength necessary for preference evolution. This figure shows the minimum preference strength necessary for a female preference allele to evolve to fixation. The x axis shows the competitive cost (the value of  $\gamma$ ) for a given simulation, and the y axis shows the necessary preference strength to be able to evolve female preferences ( $\alpha$ ). As the competitive cost increases, higher preference strengths are necessary to fix female preferences. The black line is the preference strength needed for simulations with a single preference, the grey line is the preference strength required in simulations with two preferences (both introduced at low initial frequencies).

To measure how strong natural selection against costly female preferences is, I applied the methodology of Barton and Turelli (1991) to calculate the strength of direct selection of preference. To illustrate the role of direct and indirect selection, one can write a general equation for the change in the frequency of preference alleles between generations:

$$\Delta p = a_{P,0}C_{PP} + a_{T,0}C_{PT} \quad (4)$$

Here,  $\Delta p$  is the sum of direct selection and indirect selection. For any two loci X and Y,  $a_{X,0}C_{XY}$  measures how the frequency of an allele at locus Y changes due to the selection at locus X ( $a_{X,0}$ ) and the genetic association between locus X and Y ( $C_{XY}$ ). Thus, change in preference is driven by direct selection on preferences,  $a_{P,0}C_{PP}$ , as well as indirect selection via the linkage disequilibrium between preference and trait,  $a_{T,0}C_{PT}$  (from Barton and Turelli 1991, eq 16).

Equation (4) can then be used to partition out how much change in the frequency of a preference allele is due to direct versus indirect selection. The first term represents change due to direct selection:

$$\Delta p_{\text{direct}} = a_{P,0}C_{PP}. \quad (5)$$

This represents direct selection on locus  $P_i$ , favoring preference, with strength  $a_{P,0}$ , multiplied by the genetic variance at the  $P_i$  locus,  $C_{PP}$ .

The procedure for solving for direct selection,  $a_{P,0}$ , is described in appendix 2.1. The result is that we have an equation describing the strength of selection for (or against) possessing a preference allele:

$$a_{P,0} = -\frac{(\alpha - 1)^2(P - 1)\left((1 - T) + D_{P,T}(1 - 2T)\right) \cdot \gamma}{(\alpha + T - \alpha T)^2}, \quad (6)$$

where  $P$  is the frequency of the preference allele,  $T$  is the frequency of the trait allele, and  $D_{P,T}$  is the linkage disequilibrium between preference and trait.

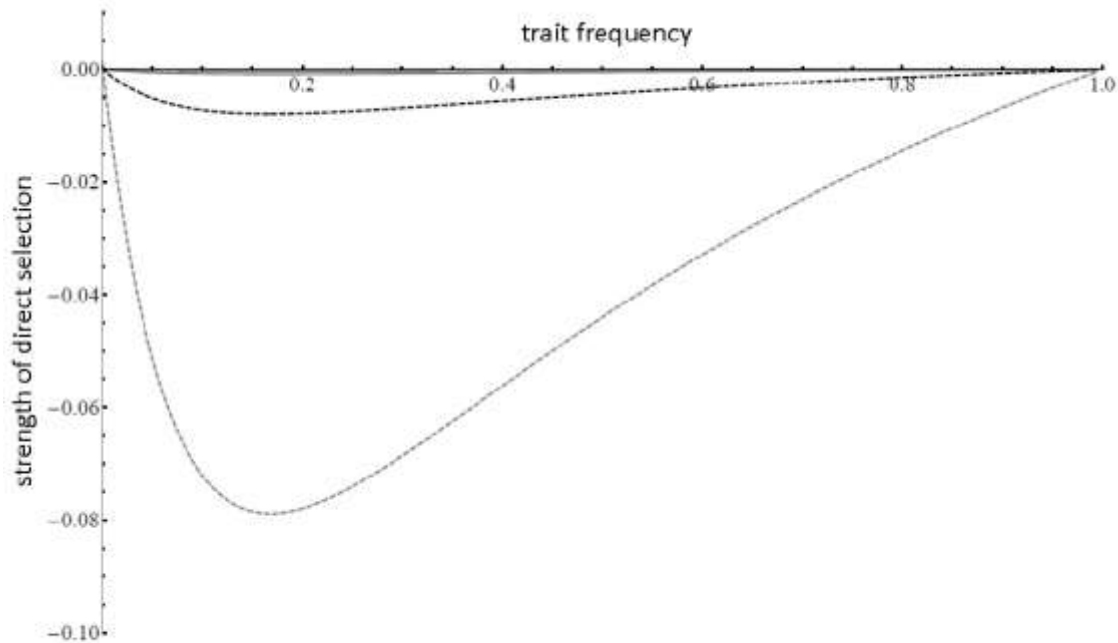
In terms of selective forces, equation (6) demonstrates the selection on the preference locus is a function of preference and trait frequency, as well as preference

strength and the cost of competition – all of which is intuitive from the model description. To understand what (6) means in more concrete terms, first proved that the expression is always negative for realistic values of  $P$  and  $T$  ( $P, T \leq 1$ ). The sign of (6) is negative when  $(1 - T) + D_{P,T}(1 - 2T) > 0$ . Thus,

$$\begin{aligned}
 1 - T + D_{P,T} - 2D_{P,T}T &> 0 \\
 1 + D_{P,T} &> T(1 + 2D_{P,T}) \\
 \frac{1 + D_{P,T}}{1 - 2D_{P,T}} &> T
 \end{aligned} \tag{7}$$

Because  $1 \geq T \geq 0$ , and linkage between preference and trait is greater than or equal to 0, the right hand side of (7) is always positive, and, in turn, (6) is always negative.

I plotted  $\alpha_{P,0}$  for varying frequencies of preference and trait alleles, as well as different cost regimes (Figure 2.2). Because the value of  $\alpha$  does not change the shape of the curve, I only display results with  $\alpha = 5$ . For all scenarios with female competition for preferred males,  $\alpha_{P,0}$  is negative (if  $\gamma = 0$  or  $\alpha = 1$ ,  $\tilde{\alpha}_{P,0} = 0$ ). This means that direct selection *always* acts against female preference if competition is a factor; male traits in this scenario will only evolve if female preferences are sufficiently strong enough that indirect (sexual) selection can outweigh direct selection.



**Figure 2.2 Direct selection for a single preference.** This figure shows the strength of direct selection against female preference ( $\tilde{a}_{p,0}$ ) as male trait frequency increases from 0 – 1. Each line represents direct selection for a different combination of female preference frequency (P) and cost ( $\gamma$ ) – the solid black line indicates P=.01,  $\gamma$ =.01; solid gray indicates P=.01,  $\gamma$ =.1; dashed black indicates P=.5,  $\gamma$ =.01; dashed grey indicates P=.5,  $\gamma$ =.1. For all simulations,  $\alpha$ =5; changing preference strength did not change the shape of the cost curve, but only scaled up the strength of selection against preference. Direct selection always acts against preferences, except when male traits are absent or fixed, in which case,  $a_{p,0} = 0$ .

### *Two Preferences, Two Traits (four locus model)*

Having shown that a single preference is selected against when females compete, I now consider whether or not a second preference is sufficient to alleviate competition, leading to direct selection *for* preferences.

In this model, there are an additional two loci: two preference loci,  $P_1$  and  $P_2$ , control female preference, and two trait loci,  $T_1$  and  $T_2$ , control male display traits.

These four loci yield  $2^4 = 16$  genotypes:  $P_1P_2T_1T_2$ ,  $P_1P_2T_1t_2$ ,  $P_1P_2t_1T_2$ ,  $P_1P_2t_1t_2$ ,  $P_1p_2T_1T_2$ ,  $P_1p_2T_1t_2$ , and so on. I denote their frequencies by  $x_1, x_2, \dots, x_{16}$ .

As before, females select mates based on their preferences.  $P_1$  corresponds to a preference for trait one and  $P_2$  corresponds to a preference for trait 2. For example, a  $P_1p_2$  female prefers males possessing the  $T_1$  trait. When a female possesses both preference alleles,  $P_1P_2$ , she is  $\alpha$  times as likely to mate with a  $T_1t_2$  or  $t_1T_2$  male, and  $1.5 \cdot \alpha$  times as likely to mate with a  $T_1T_2$  male, assuming she has encountered one of each type of male. Mate choice and fertility selection are calculated as described in equations (1), (2) and (3). The full mating table is given in table 2.2.

I first confirmed that multiple preferences evolved in the face of costly competition. Multiple preferences evolve but require stronger preference strengths (i.e. greater  $\alpha$ ) to reach fixation than preferences evolving in the absence of costly competition (figure 1, gray line). Interestingly, the strength of preference necessary to overcome the costs of choice is lower when multiple preferences are present versus a single preference. With simulations alone, however, it is impossible to determine if this is due to a decrease in competitive costs or an increase in indirect selection driven by stronger joint preferences by females with both preferences for males with both traits.

**Table 2.2 Mating table for two preference/two trait model.** Females with preference alleles prefer males with the corresponding traits by a factor  $\alpha$ ; females with both preference alleles ( $P_1P_2$  females;  $x_1$ - $x_4$ ) are **1.5  $\alpha$**  times more likely to mate with males bearing both traits ( $T_1T_2$ ). Matings are normalized by  $Z_i$  so that all female genotypes have equal mating success.

		Males															
		$x_1$	$x_2$	$x_3$	$x_4$	$x_5$	$x_6$	$x_7$	$x_8$	$x_9$	$x_{10}$	$x_{11}$	$x_{12}$	$x_{13}$	$x_{14}$	$x_{15}$	$x_{16}$
Females	$x_1$	$\frac{\alpha p(x_1x_1)}{Z_1}$	$\frac{\alpha(x_1x_2)}{Z_1}$	$\frac{\alpha(x_1x_3)}{Z_1}$	$\frac{(x_1x_4)}{Z_1}$	$\frac{\alpha p(x_1x_5)}{Z_1}$	$\frac{\alpha(x_1x_6)}{Z_1}$	$\frac{\alpha(x_1x_7)}{Z_1}$	$\frac{(x_1x_8)}{Z_1}$	$\frac{\alpha p(x_1x_9)}{Z_1}$	$\frac{\alpha(x_1x_{10})}{Z_1}$	$\frac{\alpha(x_1x_{11})}{Z_1}$	$\frac{(x_1x_{12})}{Z_1}$	$\frac{\alpha p(x_1x_{13})}{Z_1}$	$\frac{\alpha(x_1x_{14})}{Z_1}$	$\frac{\alpha(x_1x_{15})}{Z_1}$	$\frac{(x_1x_{16})}{Z_1}$
	$x_2$	$\frac{\alpha p(x_2x_1)}{Z_1}$	$\frac{\alpha(x_2x_2)}{Z_1}$	$\frac{\alpha(x_2x_3)}{Z_1}$	$\frac{(x_2x_4)}{Z_1}$	$\frac{\alpha p(x_2x_5)}{Z_1}$	$\frac{\alpha(x_2x_6)}{Z_1}$	$\frac{\alpha(x_2x_7)}{Z_1}$	$\frac{(x_2x_8)}{Z_1}$	$\frac{\alpha p(x_2x_9)}{Z_1}$	$\frac{\alpha(x_2x_{10})}{Z_1}$	$\frac{\alpha(x_2x_{11})}{Z_1}$	$\frac{(x_2x_{12})}{Z_1}$	$\frac{\alpha p(x_2x_{13})}{Z_1}$	$\frac{\alpha(x_2x_{14})}{Z_1}$	$\frac{\alpha(x_2x_{15})}{Z_1}$	$\frac{(x_2x_{16})}{Z_1}$
	$x_3$	$\frac{\alpha p(x_3x_1)}{Z_1}$	$\frac{\alpha(x_3x_2)}{Z_1}$	$\frac{\alpha(x_3x_3)}{Z_1}$	$\frac{(x_3x_4)}{Z_1}$	$\frac{\alpha p(x_3x_5)}{Z_1}$	$\frac{\alpha(x_3x_6)}{Z_1}$	$\frac{\alpha(x_3x_7)}{Z_1}$	$\frac{(x_3x_8)}{Z_1}$	$\frac{\alpha p(x_3x_9)}{Z_1}$	$\frac{\alpha(x_3x_{10})}{Z_1}$	$\frac{\alpha(x_3x_{11})}{Z_1}$	$\frac{(x_3x_{12})}{Z_1}$	$\frac{\alpha p(x_3x_{13})}{Z_1}$	$\frac{\alpha(x_3x_{14})}{Z_1}$	$\frac{\alpha(x_3x_{15})}{Z_1}$	$\frac{(x_3x_{16})}{Z_1}$
	$x_4$	$\frac{\alpha p(x_4x_1)}{Z_4}$	$\frac{\alpha(x_4x_2)}{Z_1}$	$\frac{\alpha(x_4x_3)}{Z_1}$	$\frac{(x_4x_4)}{Z_1}$	$\frac{\alpha p(x_4x_5)}{Z_1}$	$\frac{\alpha(x_4x_6)}{Z_1}$	$\frac{\alpha(x_4x_7)}{Z_1}$	$\frac{(x_4x_8)}{Z_1}$	$\frac{\alpha p(x_4x_9)}{Z_1}$	$\frac{\alpha(x_4x_{10})}{Z_1}$	$\frac{\alpha(x_4x_{11})}{Z_1}$	$\frac{(x_4x_{12})}{Z_1}$	$\frac{\alpha p(x_4x_{13})}{Z_1}$	$\frac{\alpha(x_4x_{14})}{Z_1}$	$\frac{\alpha(x_4x_{15})}{Z_1}$	$\frac{(x_4x_{16})}{Z_1}$
	$x_5$	$\frac{\alpha(x_5x_2)}{Z_2}$	$\frac{\alpha(x_5x_2)}{Z_2}$	$\frac{(x_5x_3)}{Z_2}$	$\frac{(x_5x_4)}{Z_2}$	$\frac{\alpha(x_5x_5)}{Z_2}$	$\frac{\alpha(x_5x_6)}{Z_2}$	$\frac{(x_5x_7)}{Z_2}$	$\frac{(x_5x_8)}{Z_2}$	$\frac{\alpha(x_5x_9)}{Z_2}$	$\frac{\alpha(x_5x_{10})}{Z_2}$	$\frac{(x_5x_{11})}{Z_2}$	$\frac{(x_5x_{12})}{Z_2}$	$\frac{\alpha(x_5x_{13})}{Z_2}$	$\frac{\alpha(x_5x_{14})}{Z_2}$	$\frac{(x_5x_{15})}{Z_2}$	$\frac{(x_5x_{16})}{Z_2}$
	$x_6$	$\frac{\alpha(x_6x_2)}{Z_2}$	$\frac{\alpha(x_6x_2)}{Z_2}$	$\frac{(x_6x_3)}{Z_2}$	$\frac{(x_6x_4)}{Z_2}$	$\frac{\alpha(x_6x_5)}{Z_2}$	$\frac{\alpha(x_6x_6)}{Z_2}$	$\frac{(x_6x_7)}{Z_2}$	$\frac{(x_6x_8)}{Z_2}$	$\frac{\alpha(x_6x_9)}{Z_2}$	$\frac{\alpha(x_6x_{10})}{Z_2}$	$\frac{(x_6x_{11})}{Z_2}$	$\frac{(x_6x_{12})}{Z_2}$	$\frac{\alpha(x_6x_{13})}{Z_2}$	$\frac{\alpha(x_6x_{14})}{Z_2}$	$\frac{(x_6x_{15})}{Z_2}$	$\frac{(x_6x_{16})}{Z_2}$
	$x_7$	$\frac{\alpha(x_7x_2)}{Z_2}$	$\frac{\alpha(x_7x_2)}{Z_2}$	$\frac{(x_7x_3)}{Z_2}$	$\frac{(x_7x_4)}{Z_2}$	$\frac{\alpha(x_7x_5)}{Z_2}$	$\frac{\alpha(x_7x_6)}{Z_2}$	$\frac{(x_7x_7)}{Z_2}$	$\frac{(x_7x_8)}{Z_2}$	$\frac{\alpha(x_7x_9)}{Z_2}$	$\frac{\alpha(x_7x_{10})}{Z_2}$	$\frac{(x_7x_{11})}{Z_2}$	$\frac{(x_7x_{12})}{Z_2}$	$\frac{\alpha(x_7x_{13})}{Z_2}$	$\frac{\alpha(x_7x_{14})}{Z_2}$	$\frac{(x_7x_{15})}{Z_2}$	$\frac{(x_7x_{16})}{Z_2}$
	$x_8$	$\frac{\alpha(x_8x_2)}{Z_2}$	$\frac{\alpha(x_8x_2)}{Z_2}$	$\frac{(x_8x_3)}{Z_2}$	$\frac{(x_8x_4)}{Z_2}$	$\frac{\alpha(x_8x_5)}{Z_2}$	$\frac{\alpha(x_8x_6)}{Z_2}$	$\frac{(x_8x_7)}{Z_2}$	$\frac{(x_8x_8)}{Z_2}$	$\frac{\alpha(x_8x_9)}{Z_2}$	$\frac{\alpha(x_8x_{10})}{Z_2}$	$\frac{(x_8x_{11})}{Z_2}$	$\frac{(x_8x_{12})}{Z_2}$	$\frac{\alpha(x_8x_{13})}{Z_2}$	$\frac{\alpha(x_8x_{14})}{Z_2}$	$\frac{(x_8x_{15})}{Z_2}$	$\frac{(x_8x_{16})}{Z_2}$
	$x_9$	$\frac{\alpha(x_9x_2)}{Z_3}$	$\frac{(x_9x_2)}{Z_3}$	$\frac{\alpha(x_9x_3)}{Z_3}$	$\frac{(x_9x_4)}{Z_3}$	$\frac{\alpha(x_9x_5)}{Z_3}$	$\frac{(x_9x_6)}{Z_3}$	$\frac{\alpha(x_9x_7)}{Z_3}$	$\frac{(x_9x_8)}{Z_3}$	$\frac{\alpha(x_9x_9)}{Z_3}$	$\frac{(x_9x_{10})}{Z_3}$	$\frac{\alpha(x_9x_{11})}{Z_3}$	$\frac{(x_9x_{12})}{Z_3}$	$\frac{\alpha(x_9x_{13})}{Z_3}$	$\frac{(x_9x_{14})}{Z_3}$	$\frac{\alpha(x_9x_{15})}{Z_3}$	$\frac{(x_9x_{16})}{Z_3}$
	$x_{10}$	$\frac{\alpha(x_{10}x_2)}{Z_3}$	$\frac{(x_{10}x_2)}{Z_3}$	$\frac{\alpha(x_{10}x_3)}{Z_3}$	$\frac{(x_{10}x_4)}{Z_3}$	$\frac{\alpha(x_{10}x_5)}{Z_3}$	$\frac{(x_{10}x_6)}{Z_3}$	$\frac{\alpha(x_{10}x_7)}{Z_3}$	$\frac{(x_{10}x_8)}{Z_3}$	$\frac{\alpha(x_{10}x_9)}{Z_3}$	$\frac{(x_{10}x_{10})}{Z_3}$	$\frac{\alpha(x_{10}x_{11})}{Z_3}$	$\frac{(x_{10}x_{12})}{Z_3}$	$\frac{\alpha(x_{10}x_{13})}{Z_3}$	$\frac{(x_{10}x_{14})}{Z_3}$	$\frac{\alpha(x_{10}x_{15})}{Z_3}$	$\frac{(x_{10}x_{16})}{Z_3}$
	$x_{11}$	$\frac{\alpha(x_{11}x_2)}{Z_3}$	$\frac{(x_{11}x_2)}{Z_3}$	$\frac{\alpha(x_{11}x_3)}{Z_3}$	$\frac{(x_{11}x_4)}{Z_3}$	$\frac{\alpha(x_{11}x_5)}{Z_3}$	$\frac{(x_{11}x_6)}{Z_3}$	$\frac{\alpha(x_{11}x_7)}{Z_3}$	$\frac{(x_{11}x_8)}{Z_3}$	$\frac{\alpha(x_{11}x_9)}{Z_3}$	$\frac{(x_{11}x_{10})}{Z_3}$	$\frac{\alpha(x_{11}x_{11})}{Z_3}$	$\frac{(x_{11}x_{12})}{Z_3}$	$\frac{\alpha(x_{11}x_{13})}{Z_3}$	$\frac{(x_{11}x_{14})}{Z_3}$	$\frac{\alpha(x_{11}x_{15})}{Z_3}$	$\frac{(x_{11}x_{16})}{Z_3}$
	$x_{12}$	$\frac{\alpha(x_{12}x_2)}{Z_3}$	$\frac{(x_{12}x_2)}{Z_3}$	$\frac{\alpha(x_{12}x_3)}{Z_3}$	$\frac{(x_{12}x_4)}{Z_3}$	$\frac{\alpha(x_{12}x_5)}{Z_3}$	$\frac{(x_{12}x_6)}{Z_3}$	$\frac{\alpha(x_{12}x_7)}{Z_3}$	$\frac{(x_{12}x_8)}{Z_3}$	$\frac{\alpha(x_{12}x_9)}{Z_3}$	$\frac{(x_{12}x_{10})}{Z_3}$	$\frac{\alpha(x_{12}x_{11})}{Z_3}$	$\frac{(x_{12}x_{12})}{Z_3}$	$\frac{\alpha(x_{12}x_{13})}{Z_3}$	$\frac{(x_{12}x_{14})}{Z_3}$	$\frac{\alpha(x_{12}x_{15})}{Z_3}$	$\frac{(x_{12}x_{16})}{Z_3}$
	$x_{13}$	$(x_{13}x_1)$	$(x_{13}x_2)$	$(x_{13}x_3)$	$(x_{13}x_4)$	$(x_{13}x_5)$	$(x_{13}x_6)$	$(x_{13}x_7)$	$(x_{13}x_8)$	$(x_{13}x_9)$	$(x_{13}x_{10})$	$(x_{13}x_{11})$	$(x_{13}x_{12})$	$(x_{13}x_{13})$	$(x_{13}x_{14})$	$(x_{13}x_{15})$	$(x_{13}x_{16})$
	$x_{14}$	$(x_{14}x_1)$	$(x_{14}x_2)$	$(x_{14}x_3)$	$(x_{14}x_4)$	$(x_{14}x_5)$	$(x_{14}x_6)$	$(x_{14}x_7)$	$(x_{14}x_8)$	$(x_{14}x_9)$	$(x_{14}x_{10})$	$(x_{14}x_{11})$	$(x_{14}x_{12})$	$(x_{14}x_{13})$	$(x_{14}x_{14})$	$(x_{14}x_{15})$	$(x_{14}x_{16})$
	$x_{15}$	$(x_{15}x_1)$	$(x_{15}x_2)$	$(x_{15}x_3)$	$(x_{15}x_4)$	$(x_{15}x_5)$	$(x_{15}x_6)$	$(x_{15}x_7)$	$(x_{15}x_8)$	$(x_{15}x_9)$	$(x_{15}x_{10})$	$(x_{15}x_{11})$	$(x_{15}x_{12})$	$(x_{15}x_{13})$	$(x_{15}x_{14})$	$(x_{15}x_{15})$	$(x_{15}x_{16})$
	$x_{16}$	$(x_{16}x_1)$	$(x_{16}x_2)$	$(x_{16}x_3)$	$(x_{16}x_4)$	$(x_{16}x_5)$	$(x_{16}x_6)$	$(x_{16}x_7)$	$(x_{16}x_8)$	$(x_{16}x_9)$	$(x_{16}x_{10})$	$(x_{16}x_{11})$	$(x_{16}x_{12})$	$(x_{16}x_{13})$	$(x_{16}x_{14})$	$(x_{16}x_{15})$	$(x_{16}x_{16})$

$$Z_1 = \alpha p(x_1 + x_5 + x_9 + x_{13}) + \alpha(x_2 + x_3 + x_6 + x_7 + x_{10} + x_{11} + x_{14} + x_{15}) + x_4 + x_8 + x_{12} + x_{16}$$

$$Z_2 = \alpha(x_1 + x_2 + x_5 + x_6 + x_9 + x_{10} + x_{13} + x_{14}) + x_3 + x_4 + x_7 + x_8 + x_{11} + x_{12} + x_{15} + x_{16}$$

$$Z_3 = \alpha(x_1 + x_3 + x_5 + x_7 + x_9 + x_{11} + x_{13} + x_{15}) + x_2 + x_4 + x_6 + x_8 + x_{10} + x_{12} + x_{14} + x_{16}$$

To distinguish between a decrease in competitive costs and an increase in indirect selection, I again calculated the strength of direct selection (appendix 2.2). As before, selection is a function of trait and preference frequencies. Because of the number of loci, the solution for  $\alpha_{p,0}$  is a complicated expression. For analytical tractability, I performed a weak selection approximation assuming weak preferences and small values for linkage disequilibrium:

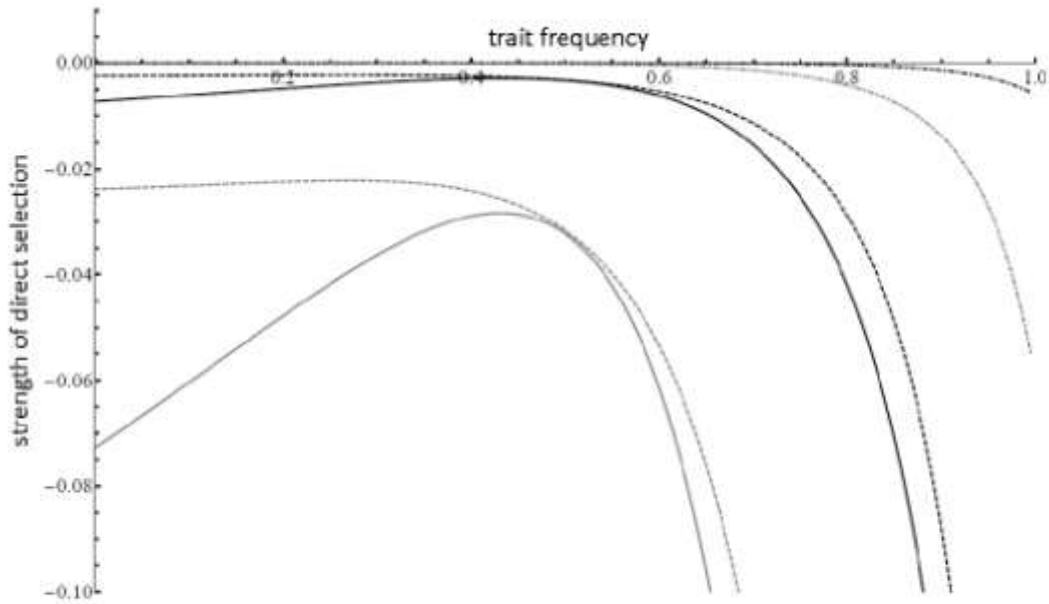
$$\alpha_{p,0} \approx \frac{1}{(T_1-1)^2(T_2-1)^2} \cdot \gamma \left( -P_2(1 - T_1(3 + 2T_2))(P_2 - T_2^2) + P_1(1 - T_1(T_1 + 3)T_2T_2 - 1 + P_2(3T_2T_1 - T_2 - 1 + P_2T_1 - 3T_2(T_2 - 1))) \right) \quad (8)$$

Again, as expected, selection on preference is a function of trait frequency. Without cost, or when both traits are fixed, selection on preference is 0. Under all other conditions, as before, selection is negative. Because of the complexity of (8), proving that it is always negative is not feasible; I used numerical simulations to verify that with two preferences and traits,  $\alpha_{p,0} \leq 0$ .

To visualize the strength of selection, I plotted the original (not weak selection) equation for direct selection for different preference and trait frequencies, and competitive costs (figure 2.3). Just as in the weak selection approximation, all values of  $\alpha_{p,0}$  are negative, except in the case of  $\gamma = 0$  or  $\alpha = 1$ , in which case  $\alpha_{p,0} = 0$ .

Comparing figures 2.2 and 2.3, it is clear that the presence of a second preference alters the strength of direct selection, but does not lead to direct selection for multiple preferences. In general, it appears that the presence of a second preference does decrease costs, but only when preferences are common. When preferences are rare, the presence of a second preference can increase competitive costs drastically.

Thus, a second preference would not directly reduce competitive costs when introduced at a low frequency. When preferences are already at a high frequency, there is a benefit to having multiple preferences (see figure 3), but here I focused on low initial frequencies as an evolutionary realistic scenario.



**Figure 2.3 Direct selection for a single preference; two preference, two trait model.** This figure shows the strength of direct selection against a single female preference ( $a_{p_1,0}$ ) as male trait frequency increases. Each line represents selection against  $P_1$  for a different combination of preference frequencies ( $P_1$  and  $P_2$ ) and cost ( $\gamma$ ) as male trait frequencies ( $T_1$  and  $T_2$ ) increase. The solid black line indicates  $P_1=.95$ ,  $P_2=.01$ ,  $\gamma=.01$ ; solid gray indicates  $P_1=.95$ ,  $P_2=.01$ ,  $\gamma=.1$ ; dashed black indicates  $P_1=.01$ ,  $P_2=.01$ ,  $\gamma=.01$ ; dashed gray indicates  $P_1=.01$ ,  $P_2=.01$ ,  $\gamma=.1$ ; dot-dashed black indicates  $P_1=.95$ ,  $P_2=.95$ ,  $\gamma=.01$ ; and dot-dashed gray indicates  $P_1=.95$ ,  $P_2=.95$ ,  $\gamma=.1$ . For all simulations,  $\alpha=5$ ; changing preference strength did not change the shape of the cost curve, but only scaled up the strength of selection against preference. Regardless of the parameters, direct selection on  $P_1$  is always negative, except when male traits are absent. All the cost curves turn downwards as male trait frequency increases—this is due to selection for multiple preferences ( $P_1P_2$  together) when male trait frequencies are sufficiently high; the curves displayed are for a single preference ( $P_1$ ).



## *Simulation Studies*

To make realistic predictions about the evolution of multiple preferences I used simulation models to explore when multiple preferences could evolve. Using the model framework described above, I looked at the evolution of preferences with female competition. To explore the full range of possibilities for preference and trait evolution, I considered 3 scenarios:

- (1) female preference for arbitrary male traits,
- (2) female preference for male traits favored by natural selection,
- (3) female preference for condition dependent traits, and

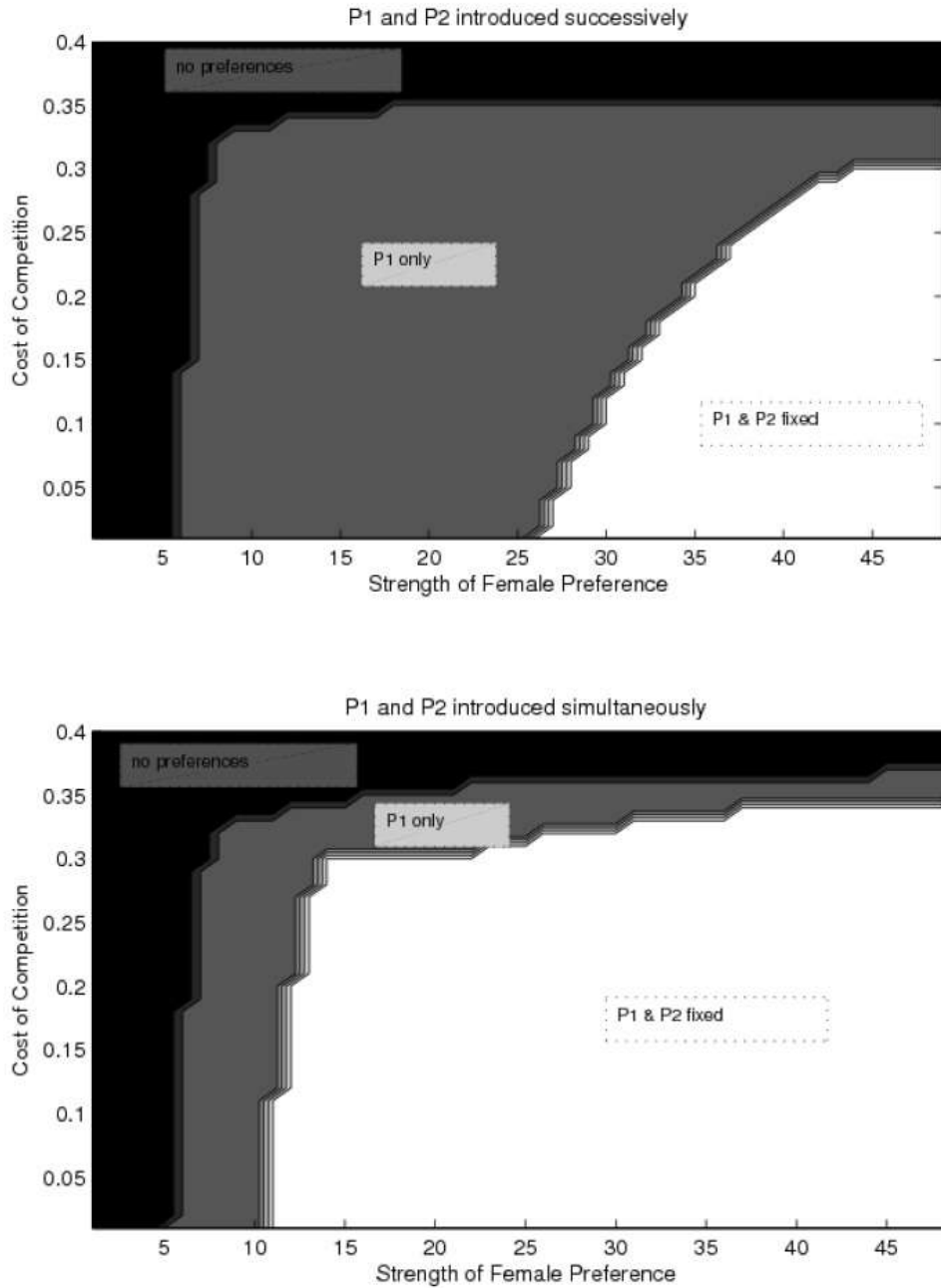
For each scenario, I simulated the evolution of two preferences introduced simultaneously to the evolution of two preferences introduced successively (i.e., the second preference is only introduced after the first one is at equilibrium). I performed numerical simulations in Matlab; equilibrium conditions were found by running recursion equations for genotype frequency, as described above, until trait and preference alleles reached equilibrium. The results presented below are derived from genotype frequencies at equilibrium, which I defined as when the percentage change in genotype frequencies between successive generations was less than  $10^{-16}$

### *1. Female preferences for arbitrary male traits*

I began by simulating a four locus model of female preferences for arbitrary male traits, as described and modeled analytically above. Females gained nothing from mating with preferred males other than producing attractive offspring, and there was no natural selection. With successive introduction of female preference, the initial

female preference evolved to fixation when preference was high enough, despite the cost of competition. When a second preference was introduced, after the fixation of the first, even higher preference strength was needed to overcome competitive costs; competition for the limited pool of males with both traits prevented preference evolution unless preferences for male traits were very strong (figure 4a). When introduced simultaneously, both preferences could fix when the strength of female preference was high and the cost of competition relatively low ( $a > 5, \gamma < 0.35$ , see Figure 4b).

As predicted in figure 2.1, with two preferences introduced simultaneously, the minimum preference strength for preference evolution decreased somewhat. It is also worth noting that the two preferences were able to fix under a broader set of circumstances when introduced simultaneously vs. successively – this replicates the result in figure 2, where direct selection against preference is weaker when two preferences are at low frequencies (dashed lines) than when one is already at a high frequency (solid lines).



**Figure 2.4 Simulation Results for the Evolution of Multiple Preferences for Arbitrary Male Traits.** This figure shows the parameter space, in terms of costs of competition ( $\gamma$ ) and strength of female preference ( $\alpha$ ), where a single preference for an arbitrary trait fixes (gray), both preferences fix (white), and both preferences are lost (black). Top panel is for successive preference introduction, bottom panel shows simultaneous preference introduction. For a preference to fix, preference strength must be sufficiently high, and costs must be relatively low. Introducing preferences successively increases the parameter space where multiple preferences may coexist.

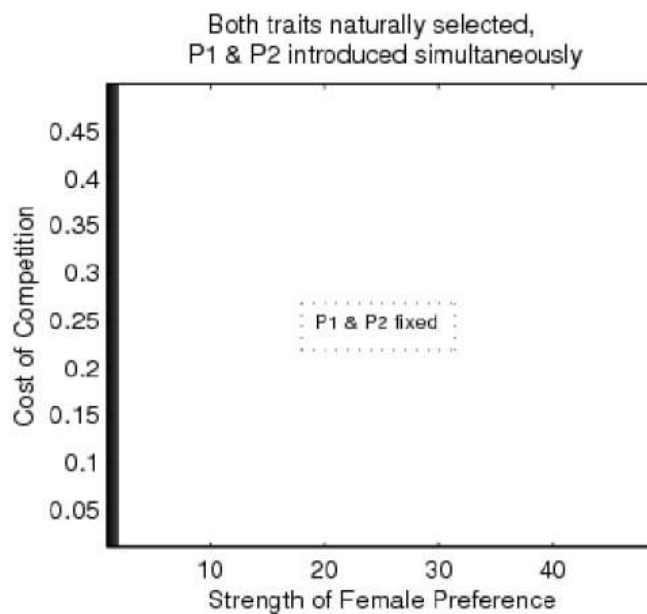
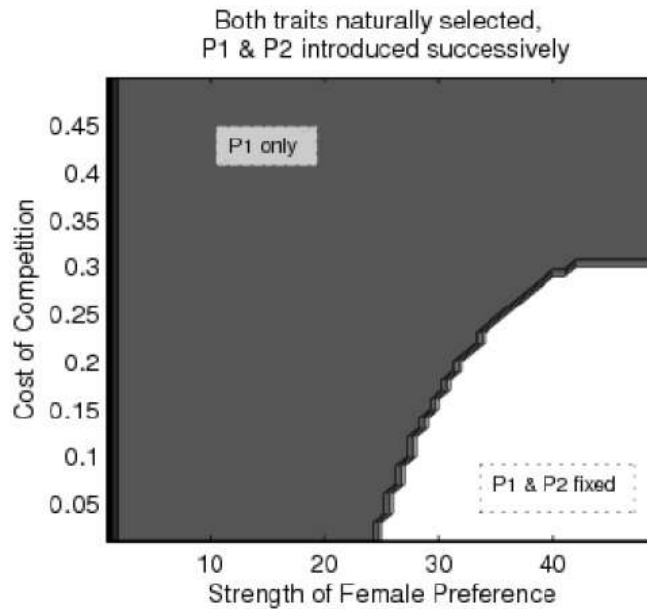
## 2. Female preferences for male traits favored by natural selection

To model honest traits, I first considered male traits favored by natural selection. I altered the four locus model such that following birth, individuals underwent natural selection: individuals of type  $i$  without traits had fitness reduced by a fraction  $s_i$ . Genotype frequency following natural selection was then described by:

$$x_i^\eta = \frac{(1 - s_i)x_i}{\sum_{i=1}^{16}(1 - s_i)x_i} \quad (9)$$

Where  $i \in 4, 8, 12, 16$ . The  $x_i^\eta$  values in (4) replace the  $x_i$  values in (1).

The direct benefits of a male favored by natural selection is sufficient to overcome direct selection against preferences due to female competition—a single preference for naturally selected male traits fixed across a wide range of parameter combinations. Figure 2.5 displays only  $\alpha \in [0, 50]$ , and  $\gamma \in [0, 0.5]$ , but a much wider range was examined for both parameters, and unless  $\gamma$  was unrealistically high (e.g.,  $\gamma > 1.5$ ), a single preference was able to fix. However, direct selection against preferences was able to prevent the evolution of a second preference when the first was fixed—as in figure 2.4, two preferences were able to fix more readily when introduced simultaneously.



**Figure 2.5: Evolution of Multiple Preferences for Naturally Selected Male Traits.** This figure shows the parameter space, in terms of costs of competition ( $\gamma$ ) and strength of female preference ( $\alpha$ ), where a single preference for a naturally selected trait fixes (gray), both preferences fix (white), and both preferences are lost (black, on the far left along the y-axis). The top figure displays results for successive preference introduction, the bottom shows simultaneous preference introduction. Natural selection on traits counterbalances direct selection against preferences due to competition, allowing at least a single preference to fix under most parameter combinations.

### 3. Condition dependent male traits

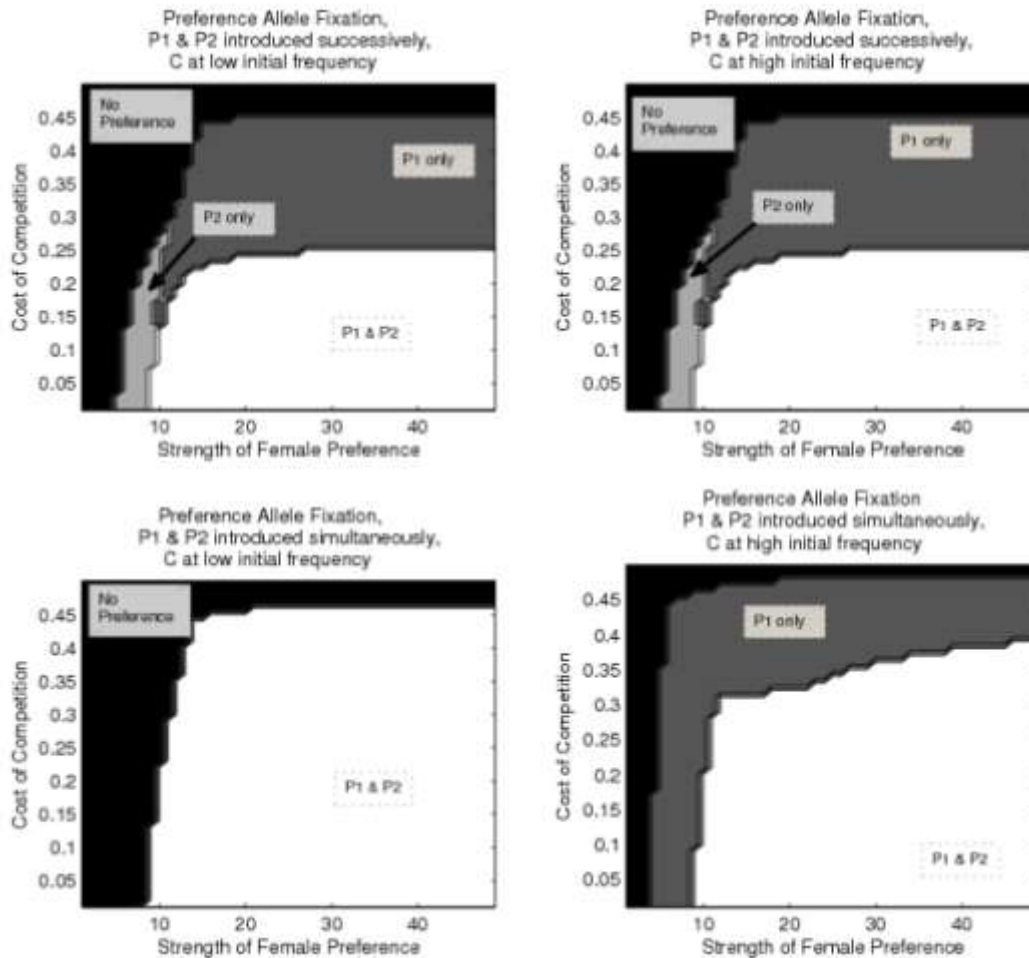
For this scenario, I added a fifth locus C, which denotes an individual's condition. Individuals with c are considered low condition; those with C are high condition, and thus favored by natural selection. The result is  $16 \cdot 2 = 32$  genotypes. I included directional mutation from C to c in order to maintain variation in condition.

The life cycle consists of birth, natural selection, mate choice, fertility selection, zygote formation, recombination and mutation. During natural selection, low quality individuals (those with the c allele), were  $(1 - s)$  times as likely to survive. For mate choice, males displayed traits only if they were also in good condition, ie, females did not prefer low condition males, even if they carried trait genes. Mate choice occurs as described in (1), using  $k_{ij}$  values given in Table 3. After mate choice, fertility selection occurs as in (3) and (4), followed by recombination, mutation, and zygote formation.

Because condition-dependent trait expression leads to increased mate competition because there is a decreased pool of males expressing traits, I considered two regimes for the evolution of condition-dependent preferences:

- (1) evolution of preference along with condition, where preference and condition are introduced at low frequency simultaneously and allowed to evolve together, and
- (2) evolution of preference in a system where the condition allele is at mutation selection balance (mutation rate for c is 0.005) .

By examining both the evolution of condition allele with preference, and the introduction of preference into a high condition population, I can better distinguish the interaction between multiple preferences and condition evolution.



**Figure 2.6 Evolution of Multiple Preferences for Condition Dependent Male Traits.** This figure shows the parameter space, in terms of costs of competition ( $\gamma$ ) and strength of female preference ( $\alpha$ ), where a single preference for a condition dependent trait fixes (gray), both preferences fix (white), and both preferences are lost (black). Top row displays results for successive preference introduction, the bottom row shows simultaneous preference introduction. The left column displays results for simulations where the condition allele evolved along with female preference and the right column shows results from simulations where female preference was introduced into a population at mutation selection balance for a high condition allele.

For both regimes, having two preferences evolving simultaneously (as opposed to successively) increased the size of the parameter space where a second preference fixed, allowing it to fix at higher levels of competitive costs (Figure 2.6). Further, as with naturally selected traits, direct selection for preferences for condition dependent male traits balances out direct selection against female preference due to competition, allowing preference to evolve under lower strengths and higher competition.

### **Discussion**

The results from my models indicate that intrasexual competition is costly and, when present, direct selection acts against preference evolution. Multiple preferences change the shape of the cost curve but fail to alleviate costly competition when introduced at a low frequency; direct selection still acts against female preference when multiple preferences are present. This is not to say that intrasexual competition entirely prevents preference evolution; simulation results indicated that preferences may still evolve if they are sufficiently strong enough to overcome natural selection, and that the multiple preferences evolving simultaneously may reduce (but not eliminate) direct selection. Although multiple preferences do not lead to direct (i.e. natural) selection for preference evolution, their presence is likely to increase the strength of indirect selection on preference and trait evolution, creating strong joint preferences in females with both preferences for males with both traits; this leads to a decrease in the initial preference strength required for evolution.

In general, these results are consistent with other models, where costs associated with mate choice have been shown to prevent or restrict the evolution of



multiple female preferences (Kirkpatrick, 1985; Pomiankowski and Iwasa, 1993; Iwasa and Pomiankowski, 1994). Kirkpatrick's (1985) model of the sexy son hypothesis showed that handicap traits, which only lower fitness, do not spread. Models explicitly considering multiple male traits with costly female preference, in terms of search costs/viability selection, also found that female preferences did not evolve due to high joint costs to preference (Pomiankowski and Iwasa, 1993; Iwasa and Pomiankowski, 1994). In these models, if it was more costly for a female to search for and find a mate with multiple preferred traits rather than a male with a single trait, then multiple preferences could not evolve. Similarly, in my model, having multiple preferences served to increase competitive costs when male traits were rare.

My model supports the idea that intrasexual competition is likely to be a significant cost acting against the evolution of female preferences. There are many examples of intrasexual competition: direct aggression between females (Ahnesjö et al 1993, Rosenqvist and Berglund 1992), reduced fecundity due to decreased male parental efforts (Summers 1990, Ferretti and Winkler, 2009), as well as decreased fecundity from male sperm depletion (Warner et al 1995, Royer and McNeil 1997, Rondeau and Sainte-Marie 2001, Wedell et al. 2002, Harris and Moore 2005, Rubolini et al 2007). Yet, in the majority of these species, female preferences have evolved regardless – including multiple preferences. In my models, competitive costs are not an insurmountable obstacle; although multiple preferences fail to alleviate competition, they don't appear to be significantly *more* costly than a single preference, and in fact

serve to increase indirect selection on preferences (see figure 1; the minimum  $\alpha$  required for preference evolution is lower for multiple preferences).

Multiple preferences may in fact serve to alleviate competition, just not in the way modeled here. One possibility is that if individual females have different preferences, controlled by a single locus, instead of multiple preferences controlled by multiple loci, competition could be averted. However, this scenario is unlikely: in most species with multiple preferences, these preferences appear to be controlled by independent genes (Brooks and Coulridge, 1999, Marchetti, 1998). As my model has shown, if preferences are controlled by independent loci, after several generations, many individuals have both preferences leading to increased competition, not avoidance.

Perhaps multiple preferences may not indirectly prevent competition, but instead involve preferences for traits which indicate how many times a male has mated. One study showed that female cockroaches discriminated against males that had mated multiple times, and were able to detect cues on males derived from previous mates, in addition to traits indicating male quality (Harris and Moore 2005). However, it is difficult to imagine how common the ability to detect prior matings is, and there is only one such example in the literature. Another possibility is that females could evolve multiple preferences and switch between preferences when they sense competition for a desired male. This would require knowledge about population wide preference frequencies, but would be possible in lekking species or animals that live in social groups.

When multiple preferences are present, indirect selection on female preference evolution is much stronger. Perhaps instead of relieving competition, multiple preferences allow female choice to evolve by jointly increasing the strength of indirect selection to the point where many weak preferences can overcome natural selection against competition.

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### **CHAPTER III: THE EVOLUTION OF PREFERENCE STRENGTH UNDER SENSORY BIAS: A ROLE FOR INDIRECT SELECTION?**

#### **Abstract**

Evidence suggests that female preferences may sometimes arise through sensory bias, and that males may subsequently evolve traits that increase their conspicuousness to females. Here, we ask whether indirect selection, arising through genetic associations (linkage disequilibrium) during the sexual selection that sensory bias imposes, can itself influence the evolution of preference strength. Specifically, we use population genetic models to consider whether or not modifiers of preference strength can spread under different ecological conditions when female mate choice is driven by sensory bias. We focus on male traits that make a male more conspicuous in certain habitats—and thus both more visible to predators and more attractive to females. We first solve for the rate of spread of a modifier that strengthens preference within an environmentally uniform population; we find that this spread will be extremely slow. Second, we used a series of simulations to consider the role of habitat structure and movement on the evolution of a modifier of preference strength, using male color polymorphisms as a case study. We find that in most cases, indirect selection does not allow the evolution of stronger or weaker preferences for sensory bias. Only in a ‘two island’ model, where there is restricted migration between different patches that favor different male phenotypes, did we find that preference strength could evolve. The

role of indirect selection in the evolution of sensory bias is of particular interest because of ongoing speculation regarding the role of sensory bias in the evolution of reproductive isolation.

## **Introduction**

'Sensory bias,' under its broadest definition, refers to females responding to particular signals from males because their sensory systems are pre-adapted to such stimulation (Dawkins and Guilford, 1996). This definition includes a broad set of female preferences for male traits that resemble important environmental cues (food, Basolo 1990, Proctor 1991, Clark and Uetz 1992; eggs, Egger et al. 2011) as well as for those male signals that simply exploit response to color, auditory transmission, or movement (Ryan and Rand 1990, Boughman 2002, Seehausen et al 2008, Tobias et al 2010). Arnqvist (2006) delineates two possible origins for female sensory bias: *adaptive sensory biases*, where females have evolved under natural selection to respond to particular stimuli (food, predator avoidance, etc.) and these preferences are a target for novel male traits (i.e. males that mimic food), or *hidden preferences*, which are not the result of selection but instead rely on the neutral consequences of an organism's physiology. Less well considered is the issue of whether the strength of sensory biases would be expected to evolve in the context of sexual selection. Although female preferences may originate, via sensory bias, by external sources of selection, can sexual selection in these cases promote the strengthening of these preferences?

Fuller et al. (2005) discuss inconsistencies in the empirical literature regarding whether sexual selection modifies female preferences that are under sensory bias. They

maintain that sensory bias, by definition, does not evolve by sexual selection but instead via natural selection on ecologically relevant perceptual traits. In their model, they present a quantitative genetic framework for the evolution of preferences and traits in which sexual selection on preferences themselves (in terms of a selection gradient on preferences due to variation in mate number or quality) is absent. We are also not interested in sexual selection acting *directly* on preference strength. When sexual selection occurs on male traits, however, preference evolution should follow via *indirect* selection, due to the genetic associations (linkage disequilibrium) that form automatically between female preferences and male traits (e.g., Kirkpatrick 1982). We are interested in the effects that this indirect sexual selection may have on the evolution of the strength of preferences formed by sensory bias, in a variety of ecological contexts.

The strength of sensory biases is of particular interest because of the role that sensory bias has been proposed to play in speciation (Boughman 2002). Environmental adaptation produces and maintains variation in male signaling traits, female sensory systems, or both. When divergence in male traits occurs alongside divergence in preferences, speciation may occur. Boughman (2002) suggested that reproductive isolation could arise as a byproduct of the adaptive divergence of communication systems to different environments (rendering the preference a “magic trait”, wherein a single trait is both naturally and sexually selected, see Servedio et al. 2011). These ideas have been further developed for the maintenance of color polymorphisms by divergent natural selection favoring locally adapted visual systems (Gray and McKinnon 2007) and



for the adaptive divergence of chemosensory systems (Smadja and Butlin 2009). Evolution of the strength of sensory biases both within a single population and in populations with substructure may influence the probability that speciation based on sensory bias can occur.

We focus our analysis on the case, documented in several empirical studies, in which females have a preference for the more conspicuous of alternate male phenotypes in a given habitat (e.g. Boughman 2001, Leal and Fleishman 2004, Uy and Endler 2004, Gray et al. 2008). We are interested specifically in the evolution of the *strength* of preference for the conspicuous male, not in changes in what the females perceives as conspicuous. Mechanistically, evolution in our model may therefore best be thought of as acting on a component of preference comprising the behavioral response of females, for example whether or not to accept a male given a certain level of conspicuousness, rather than on the sensory system of the female per se.

We consider the evolution of preferences in several ecological scenarios. First we consider a single habitat in which sensory bias has led to a preference for a conspicuous male trait, and ask whether mutations for stronger preferences can spread by indirect selection alone. We next use a series of microhabitat models (sensu Chunco et al. 2007) to consider the evolution of stronger (and weaker) preferences for conspicuous males when males with different traits are conspicuous in different micro-environments. In each of these models, we begin with a population where male trait polymorphisms and female preferences of a fixed strength are already present. By starting at an initial equilibrium with a male trait polymorphism, maintained via female preferences, as in

Chunco 2007, we can ignore transient dynamics involved in determining whether or not polymorphisms are maintained, and instead focus on what happens next in terms of preference evolution. We assume in these models that movement of males and females between microhabitats occurs readily at the natural selection and/or sexual selection stages of the life cycle. Finally we consider a two-island model in which two populations are locally adapted and gene flow occurs between them. Although it has previously been argued that sensory biases may coevolve with male traits when specific biases are beneficial to females via direct benefits or decreased search costs (Arnqvist, 2006), we are interested in the previously unaddressed question of whether or not the indirect selection arising from within the system of preferences and traits *alone* can act as a force for change in the strength of female preferences. In order to isolate the effects of this indirect selection on preferences we assume that both direct natural and direct sexual selection on female preferences are absent.

### **Model Description**

We model the evolution of preference strength during sensory bias using a haploid, two locus, two allele population genetic model. Males are polymorphic for a trait with two distinct morphs; although this could be any trait (eg. visual, auditory, or chemosensory), for convenience we refer to the trait as color. Male color polymorphisms are common in fish (e.g. Seehausen and Schluter 2004, Gray and McKinnon 2006) and lizards (eg. Sinervo and Lively 1996), and research on the genetic basis of these color polymorphisms has shown that color expression is controlled in large part by a single locus with multiple alleles (in fish, Baer et al. 1995 and Fuller and

Travis 2004; in lizards, Sinervo and Zamudio 2001). Thus, we model color as a single locus with two alternate alleles; we refer to these as yellow ( $T_Y$  occurring with frequency  $t_y$ ), and blue ( $T_B$  occurring with frequency  $t_b$ ). We assume that color is entirely genetically determined and females do not express color. Although male color does not indicate genetic or phenotypic quality, males are subject to natural and sexual selection based on their coloration. In a given habitat, a male is more or less conspicuous due to his coloration: in the blue habitat, blue males are less conspicuous, and in the yellow habitat, yellow males are less conspicuous. During natural selection, more conspicuous males are selected against (as they are more visible to predators); during sexual selection female prefer conspicuous males because they are more visible. We assume that males of different colors do not have correlated differences in other traits. To maintain variation in male traits, we assume bidirectional mutation between the two alleles (note that in some of the cases with substructure, variation can be maintained even without this assumption).

Females choose mates according to genetically predetermined preferences coded at the preference locus. Because we are interested in the evolution of preference strength, the population is initially fixed for an allele for a baseline preference, referred to as  $M_1$ , which causes a female to be  $\alpha$  times more likely to mate with a conspicuous male than a non-conspicuous male if she encounters one of each. We introduce an allele that modifies female preference,  $M_2$ , which makes females  $\alpha\varepsilon$  times more (or less, if  $\varepsilon < 1$ ) likely to mate with a conspicuous male if encounter rates are equal. We are interested in understanding when, and if, the preference strength modifier  $M_2$  can

spread within the population. The assumptions of our model lead to four genotypes:  $T_B M_1$ ,  $T_B M_2$ ,  $T_Y M_1$ , and  $T_Y M_2$ , whose frequencies are referred to as  $x_1$ ,  $x_2$ ,  $x_3$ , and  $x_4$ .

Because this is a model of sensory bias in which females prefer conspicuous males, we assume that preferred (conspicuous) males experience higher predation rates. If, for example the blue morph is more conspicuous in a certain habitat, then males with the blue allele are selected against during natural selection (because they are more conspicuous to predators), but they are selected for during sexual selection (because they are more conspicuous to females).

Through the following models, we ask whether or not modifiers of preferences which have arisen through sensory bias may evolve within a population. Further, we seek to determine how habitat structure affects the evolution of preference modifiers. For clarity, a listing of all variables and parameters is given in table 3.1.

### **General Model**

In the general model, we consider a single population. Natural selection occurs, selecting against males with a conspicuous phenotype (blue, for convenience) with strength  $s$ :

$$x_j^{ns} = \frac{(1 - ks)x_j}{\bar{w}} \quad (1)$$

where  $\bar{w} = 1 - st_b$  is a normalization that ensures that the genotype frequencies after natural selection sum to 1, and  $k=1$  if  $j=1$  or  $2$ , and  $k=0$  otherwise.

**Table 3.1.** List of variables and parameters used in chapter 3

<b>Variable</b>	<b>Definition</b>
$T_y, T_b$	Yellow and blue trait alleles, respectively
$t_y, t_b$	Frequency of yellow and blue trait alleles
$\alpha$	Strength of female preference
$M_1$	Allele for baseline female preference
$M_2$	Modifier allele for female preference
$\varepsilon$	Strength of modification of $M_2$
$x_1, x_2, x_3, x_4$	Frequencies of the four male genotypes ( $T_bM_1, T_bM_2, T_yM_1, T_yM_2$ )
$x_j^{ns}$	Frequency of male genotype $j$ following natural selection
$s$	Strength of natural selection
$\bar{w}$	Mean fitness of the population
$F$	Mating table
$F_{i,j}$	Frequency of mating between $x_i$ and $x_j$ parental genotypes
$z_i$	Normalization term in a mating table to ensure all female genotypes have equal reproductive success
$\mu$	Mutation rate between blue and yellow morphs
$x_i^z$	Frequency of the $x_i$ genotype in zygotes
$D$	Linkage Disequilibrium
$H_B, H_Y$	Blue and yellow habitats, respectively
$h_b, h_y$	Frequency of blue and yellow habitats
$s_b, s_y$	Selection coefficient against blue males in blue habitat and yellow males in yellow habitat, respectively
$x_j^{HBns}$	Frequency of $x_j$ genotype in the blue habitat following natural selection
$\bar{w}_{HB}, \bar{w}_{HY}$	Normalization terms for blue and yellow habitats during natural selection
$x_{i_{t+1}}^{z\_total}$	Frequency of $x_i$ zygotes across habitats in the two patch model
$x_{i_{t+1}}^{HYz}$	Frequency of $x_i$ zygotes within the yellow habitat in the two patch model
$m$	Migration rate between blue and yellow habitats
$x_i^{m_{Hb}}$	Frequency of $x_i$ genotype in blue habitat after migration
$\delta$	Probability, in the directed movement model, that a male will move to his preferred habitats
$t_b^{HBns}$	Frequency, in the directed movement model, of blue males in the blue habitat following natural selection
$t_b^{HBss}$	Frequency, in the directed movement model, of blue males in the blue habitat following sexual selection

Following natural selection, mate choice occurs. Females with an  $M_1$  allele are  $\alpha$  times more likely to mate with conspicuous (blue) males, and females with an  $M_2$  allele

are  $\alpha\epsilon$  times more likely to mate with conspicuous males (or less likely, if  $\epsilon < 1$ ). The proportion of each type of cross is shown in matrix **F** depicted in Table 3.2. Here,  $F_{ij}$  represents the proportion of matings taking place between an  $x_i$  female and an  $x_j$  male. Female mating frequencies are normalized by  $z_1$  or  $z_2$  to ensure that all female genotypes have equal mating success (thus we assume strict polygyny).

**Table 3.2.** General Model, Mating Table

		Males			
		$T_b M_1^{ns}$	$T_b M_2^{ns}$	$T_y M_1^{ns}$	$T_y M_2^{ns}$
Females	$T_b M_1$	$\frac{\alpha(x_1 \cdot x_1^{ns})}{z_1}$	$\frac{\alpha(x_1 \cdot x_2^{ns})}{z_1}$	$\frac{x_1 \cdot x_3^{ns}}{z_1}$	$\frac{x_1 \cdot x_4^{ns}}{z_1}$
	$T_b M_2$	$\frac{\alpha\epsilon(x_2 \cdot x_1^{ns})}{z_2}$	$\frac{\alpha\epsilon(x_2 \cdot x_2^{ns})}{z_2}$	$\frac{x_2 \cdot x_3^{ns}}{z_2}$	$\frac{x_2 \cdot x_4^{ns}}{z_2}$
	$T_y M_1$	$\frac{\alpha(x_3 \cdot x_1^{ns})}{z_1}$	$\frac{\alpha(x_3 \cdot x_2^{ns})}{z_1}$	$\frac{x_3 \cdot x_3^{ns}}{z_1}$	$\frac{x_3 \cdot x_4^{ns}}{z}$
	$T_y M_2$	$\frac{\alpha\epsilon(x_4 \cdot x_1^{ns})}{z_2}$	$\frac{\alpha\epsilon(x_4 \cdot x_2^{ns})}{z_2}$	$\frac{x_4 \cdot x_3^{ns}}{z_2}$	$\frac{x_4 \cdot x_4^{ns}}{z_2}$

$$z_1 = \alpha(x_1 + x_2) + x_3 + x_4$$

$$z_2 = \alpha\epsilon(x_1 + x_2) + x_3 + x_4$$

We assume that free recombination occurs leading to the production of zygotes. As zygotes are formed, bidirectional mutation takes place at a rate  $\mu$  between Blue and Yellow morphs such that

$$x_i = (1 - \mu)x_i^z + \mu x_{i\pm 2}^z. \quad (2)$$

Where in (2)  $i+2$  is used for  $i=1$  or  $2$  and  $i-2$  is used for  $i=3$  or  $4$ , and  $x_i^z$  is the genotype frequency in zygotes.

To determine if, and how much, a modifier allele will spread, we can calculate the change in the frequency of  $M_2$  between generations:

$$\Delta M_2 = \frac{D(1 - 2\mu)(M_2(1 - s)\alpha(1 - \epsilon) + h_1((1 - s)\alpha\epsilon(1 - \mu) + \mu) + t_y h_1 h_2(1 - 2\mu))}{2(\mu + t_y h_1(1 - 2\mu) + \alpha(1 - s)(1 - \mu))(\mu + t_y h_2(1 - 2\mu) + \alpha\epsilon(1 - s)(1 - \mu))} \quad (3)$$

where

$$\begin{aligned} h_1 &= (1 - (1 - s)\alpha) \\ h_2 &= (1 - (1 - s)\alpha\epsilon). \end{aligned}$$

Here  $D$  represents the linkage disequilibrium between the color and modifier alleles ( $x_1 x_4 - x_2 x_3$ ). In analyzing (3) we are most interested in the case where the frequency of the  $T_y$  allele is nearly 0 or 1; in a single population with an initially fixed preference allele of a given strength maintaining a color polymorphism without mutation is impossible—either natural selection is stronger, favoring the less conspicuous morph, or sexual selection is stronger and favors the more conspicuous morph (see Kirkpatrick 1982). Because of recurrent mutation in our model, we expect low frequencies of the rare morph to remain in the population. The numerator of (3) is scaled by  $D$  (see also Kirkpatrick 1982), which is expected to be very small because there is very little variation in the trait locus (the modifier locus also has very little variation when a new modifier allele is introduced at a low frequency). Substituting allele frequencies for genotypes,  $D = (T_b M_1 \cdot T_y M_2) - (T_b M_2 \cdot T_y M_1)$ . Because  $T_y$  and  $T_b$  are alternative alleles at the same locus, when  $T_y$  approaches 1,  $T_b$  approaches 0 (and vice versa). Thus, in the scenarios we are interested in  $D$  will be very small because both terms are multiplied by  $T_y$ . Because  $D$  is very small, we conclude that the modifier is unlikely to spread at any significant rate. This result was confirmed via numerical simulations.

## Microhabitat Models

To extend our model to additional ecologically relevant sensory bias scenarios, we consider microhabitat population structure, as in Chunco et al (2007). Individuals live in heterogenous environments and experience microhabitats that differ in physical properties that influence color perception, such as light intensity, substrate color and pattern, or visible spectra. Because of their physical differences, male color is perceived differently in each habitat (e.g., Boughman 2001). In one habitat, henceforth referred to as  $H_Y$ , yellow males are more visible – both to predators and potential mates. In  $H_B$ , blue males are more visible. The frequency of the habitats is denoted by  $h_b$  and  $h_y$ .

Microhabitat ecology, along with sensory bias, has been implicated as an important factor in maintaining male trait polymorphisms (color, Seehausen et al 2008, Gray and McKinnon 2007; auditory signals, Ryan and Rand 1990, Tobias et al 2010). Chunco et al (2007) determined the conditions for polymorphism maintenance under the versions of the microhabitat model we will consider below. We are interested in whether modifiers of preference strength will spread in the each of these scenarios.

As before, the life cycle consists of natural selection, mate choice, and reproduction. However, now that we have microhabitat structure, each step of the life cycle can happen either within a microhabitat or across microhabitats. Because of this, we develop four models: homogenous environment (both natural and sexual selection take place across habitats), Levene soft selection (natural selection occurs within habitats, sexual selection occurs across habitats; Levene 1953), scramble competition (natural selection occurs across habitats, sexual selection occurs within habitats), and a



two-island model (both natural and sexual selection occur within habitats, with migration possible in juveniles).

As in the single population model, the more conspicuous morph is selected against during natural selection. We assume that blue males are selected against in habitat  $H_B$  and yellow males are selected against in habitat  $H_Y$ . Natural selection acting within habitats is equivalent to males remaining in a single microhabitat for the period in which natural selection occurs, for example if males are preyed upon as they remain in a specific microhabitat as juveniles. This also assumes that predators remain in one specific microhabitat at least for each specific prey selection event. In contrast when natural selection occurs across habitats we can envision males moving randomly throughout microhabitats between individual predation events, suffering predation in relation to the frequency of habitats.

When natural selection occurs within habitats, the frequency of genotypes in males can be calculated by modifying equation (1); the frequency of genotypes within each microhabitat is calculated, and the population-wide frequency is simply the weighted average of the two habitats (this assumes that the population density of the focal species between each habitat remains equivalent because of equal densities of predators):

$$x_j^{H_B^{ns}} = \frac{(1 - k_B s_B) x_j}{\bar{w}_{H_B}} \quad (4a)$$

where  $\bar{w}_{H_B} = 1 - s_B f_B$ ,  $s_B$  is the selection coefficient against blue males in habitat  $H_B$ , and  $k_B = 1$  if  $j = 1$  or  $2$  and  $k_B = 0$  otherwise, and

$$x_j^{H_Y ns} = \frac{(1 - k_Y s_Y) x_j}{\bar{w}_{H_Y}} \quad (4b)$$

where  $\bar{w}_{H_Y} = 1 - s_Y t_Y$ ,  $s_Y$  is the selection coefficient against blue males in habitat  $H_Y$ , and  $k_Y = 1$  if  $j = 3$  or  $4$  and  $k_Y = 0$  otherwise. The population-wide frequencies of the genotypes are

$$x_j^{ns} = h_B x_j^{H_B ns} + h_Y x_j^{H_Y ns} \quad (4c)$$

When natural selection occurs across habitats, we do not need to calculate genotype frequencies for habitats independently. Instead

$$x_j^{ns} = \frac{(h_B(1 - k_B s_B) + h_Y(1 - k_Y s_Y)) x_j}{\bar{w}} \quad (5)$$

where  $\bar{w} = 1 - h_B s_B t_B - h_Y s_Y t_Y$  and  $k_B = 1$  and  $k_Y = 0$  if  $j = 1$  or  $2$ , and  $k_B = 0$  and  $k_Y = 1$  otherwise.

Following natural selection, mate choice occurs. Females prefer the more conspicuous male morph;  $M_1$  females are  $\alpha$  times more likely to mate with a conspicuous male, while  $M_2$  females are  $\alpha\epsilon$  times more likely. In our simulations, we consider both symmetric ( $\alpha_y = \alpha_b$ ) and asymmetric ( $\alpha_y \neq \alpha_b$ ) female preferences. Like natural selection, sexual selection can either occur within or between habitats. Sexual selection occurring within habitats assumes that females chose from among males that they see within the microhabitat in which they are present in when they decide to mate. Sexual selection occurring between habitats assumes that females travel between microhabitats at the time of mating, examining males in both before they choose a mate. Within habitats, we consider two independent mating tables, for mate choice

within  $H_Y$  and  $H_B$ : within  $H_B$ , mate choice occurs as in Table 1. Within  $H_Y$ , mate choice favors the yellow males (see Table 3). Thus,  $x_{1t+1}^{Hy} = F_{11}^{Hy} + \frac{1}{2}F_{12}^{Hy} + \frac{1}{2}F_{13}^{Hy} + \frac{1}{4}F_{14}^{Hy} + \frac{1}{2}F_{21}^{Hy} + \frac{1}{4}F_{23}^{Hy} + \frac{1}{2}F_{31}^{Hy} + \frac{1}{4}F_{32}^{Hy} + \frac{1}{4}F_{41}^{Hy}$  (assuming free recombination,  $r=1/2$ ). As with natural selection, total offspring frequencies are calculated as weighted averages of the two habitats:

$$x_{i,t+1}^{z\_total} = h_y x_{i,t+1}^{HyZ} + h_b x_{i,t+1}^{HBZ} \quad (6)$$

Where, for example,  $x_{i,t+1}^{HyZ}$  is the frequency of zygotes at time  $t + 1$  in habitat  $H_y$ .

**Table 3.3.** Mate Choice in  $H_y$

		Males			
		$T_b M_1^{ns}$	$T_b M_2^{ns}$	$T_y M_1^{ns}$	$T_y M_2^{ns}$
Females	$T_b M_1$	$\frac{x_1 \cdot x_1^{ns}}{z_1}$	$\frac{x_1 \cdot x_2^{ns}}{z_1}$	$\frac{\alpha(x_1 \cdot x_3^{ns})}{z_1}$	$\frac{\alpha(x_1 \cdot x_4^{ns})}{z_1}$
	$T_b M_2$	$\frac{x_2 \cdot x_1^{ns}}{z_2}$	$\frac{x_2 \cdot x_2^{ns}}{z_2}$	$\frac{\alpha\varepsilon(x_2 \cdot x_3^{ns})}{z_2}$	$\frac{\alpha\varepsilon(x_2 \cdot x_4^{ns})}{z_2}$
	$T_y M_1$	$\frac{x_1 \cdot x_1^{ns}}{z_1}$	$\frac{x_3 \cdot x_2^{ns}}{z_1}$	$\frac{\alpha(x_3 \cdot x_3^{ns})}{z_1}$	$\frac{\alpha(x_3 \cdot x_4^{ns})}{z_1}$
	$T_y M_2$	$\frac{x_4 \cdot x_1^{ns}}{z_2}$	$\frac{x_4 \cdot x_2^{ns}}{z_2}$	$\frac{\alpha\varepsilon(x_4 \cdot x_3^{ns})}{z_2}$	$\frac{\alpha\varepsilon(x_4 \cdot x_4^{ns})}{z_2}$
		$z_1 = x + x_2 + \alpha(x_3 + x_4)$ $z_2 = x_1 + x_2 + \alpha\varepsilon(x_3 + x_4)$			

If sexual selection instead occurs across habitats, female preferences depend on habitat frequency: the probability of being in a habitat where a given male phenotype is more conspicuous determines her preference (see table 3.4). As before, following mate choice free recombination occurs to produce zygotes. In all models, bidirectional mutation occurs after zygote production between the  $T_B$  and  $T_Y$  alleles (mimicking mutation in the gametes), as described in equation (2).

**Table 3.4.** Across Habitat Mating Table

		Males			
		$T_b M_1^{ns}$	$T_b M_2^{ns}$	$T_y M_1^{ns}$	$T_y M_2^{ns}$
Females	$T_b M_1$	$\frac{(h_b \alpha + (1 - h_b))(x_1 \cdot x_1^{ns})}{z_1}$	$\frac{(h_b \alpha + (1 - h_b))(x_1 \cdot x_2^{ns})}{z_1}$	$\frac{(h_b + \alpha(1 - h_b))(x_1 \cdot x_3^{ns})}{z_1}$	$\frac{(h_b + \alpha(1 - h_b))(x_1 \cdot x_4^{ns})}{z_1}$
	$T_b M_2$	$\frac{(h_b \alpha \varepsilon + (1 - h_b))(x_2 \cdot x_1^{ns})}{z_2}$	$\frac{(h_b \alpha \varepsilon + (1 - h_b))(x_2 \cdot x_2^{ns})}{z_2}$	$\frac{(h_b + \alpha \varepsilon(1 - h_b))(x_2 \cdot x_3^{ns})}{z_2}$	$\frac{(h_b + \alpha \varepsilon(1 - h_b))(x_2 \cdot x_4^{ns})}{z_2}$
	$T_y M_1$	$\frac{(h_b \alpha + (1 - h_b))(x_3 \cdot x_1^{ns})}{z_1}$	$\frac{(h_b \alpha + (1 - h_b))(x_3 \cdot x_2^{ns})}{z_1}$	$\frac{(h_b + \alpha(1 - h_b))(x_3 \cdot x_3^{ns})}{z_1}$	$\frac{(h_b + \alpha(1 - h_b))(x_3 \cdot x_4^{ns})}{z_1}$
	$T_y M_2$	$\frac{(h_b \alpha \varepsilon + (1 - h_b))(x_4 \cdot x_1^{ns})}{z_2}$	$\frac{(h_b \alpha \varepsilon + (1 - h_b))(x_4 \cdot x_2^{ns})}{z_2}$	$\frac{(h_b + \alpha \varepsilon(1 - h_b))(x_4 \cdot x_3^{ns})}{z_2}$	$\frac{(h_b + \alpha \varepsilon(1 - h_b))(x_4 \cdot x_4^{ns})}{z_2}$
		$z_1 = h_b \cdot \alpha(x_1 + x_2) + h_y \cdot \alpha(x_3 + x_4)$			
		$z_2 = h_b \cdot \alpha \varepsilon(x_1 + x_2) + h_b \cdot \alpha \varepsilon(x_3 + x_4)$			

Each combination of natural and sexual selection ecology was analyzed using numerical simulations in Matlab to determine whether or not male polymorphisms could be maintained (reproducing the results of Chunco et al. 2007), and if so, whether preference modifiers could spread. After evolving to an initial equilibrium in trait frequencies, we introduced the modifier allele  $M_2$  at low frequency (.001%) and allowed evolution for 15,000 generations to measure its spread (this number of generations was always found sufficient to determine the alternate outcomes of fixation versus no spread). If a modifier allele fixed, we introduced successively stronger modifiers to determine if there was a limit to evolvable preference strength. Below, the results from each model are described in detail, and are summarized in table 5.

**Table 3.5.** Ecological Model Results

Model	Natural Selection	Sexual Selection	Male Polymorphism	Preference Modifier Spread
Panmictic	Across	Across	No	N/A
Scramble competition	Across	Within	<b>Yes</b>	None
Levene	Within	Across	No	N/A
Two Island	Within	Within	<b>Yes</b>	<b>Rapid</b>
Directed movement	Selection for camouflage	Selection for visibility	<b>Yes</b>	None

*Homogenous Environment model:*

For the homogenous environment model (in which both natural and sexual selection both across microhabitats), we used equation (4) and Table 3 to model the lifecycle. This scenario is analogous to animals that move frequently between microhabitats throughout their lifecycle, and thus experience the selective pressures of both habitats in relation to their frequency. As in the general model, we found that this did not maintain polymorphisms (except in the special case where  $h_y=h_b$  and  $s_y=s_b$ , see Chunco et al. 2007) and as a consequence, preference evolution is not a consideration in this case.

*Scramble competition model:*

In the scramble competition model, individuals experience natural selection throughout their lives as they move between habitats, as in equation (4) but then scramble to find mates as soon as they are available within microhabitats (following tables 1 and 2). We use the term “scramble” to refer to the timing of mating: males are

distributed randomly between microhabitats when mating begins, and females scramble to choose mates as quickly as possible within their current microhabitat. This scenario, the primary one examined by Chunco et al. (2007), preserves male polymorphisms. The introduction of a preference modifier served only to change the equilibrium frequency of male morphs very slightly (due to the perturbation of the introduction), but did not spread further.

*Levene soft selection:*

The Levene model had the opposite assumptions of the scramble model – individuals remain in their microhabitats during natural selection, but mates are chosen across habitats. This is also equivalent to a species where lek mating occurs, and individuals meet in a central location to choose mates. This model leads to the loss of male polymorphism (see Chunco et al. 2007).

*Two-island model:*

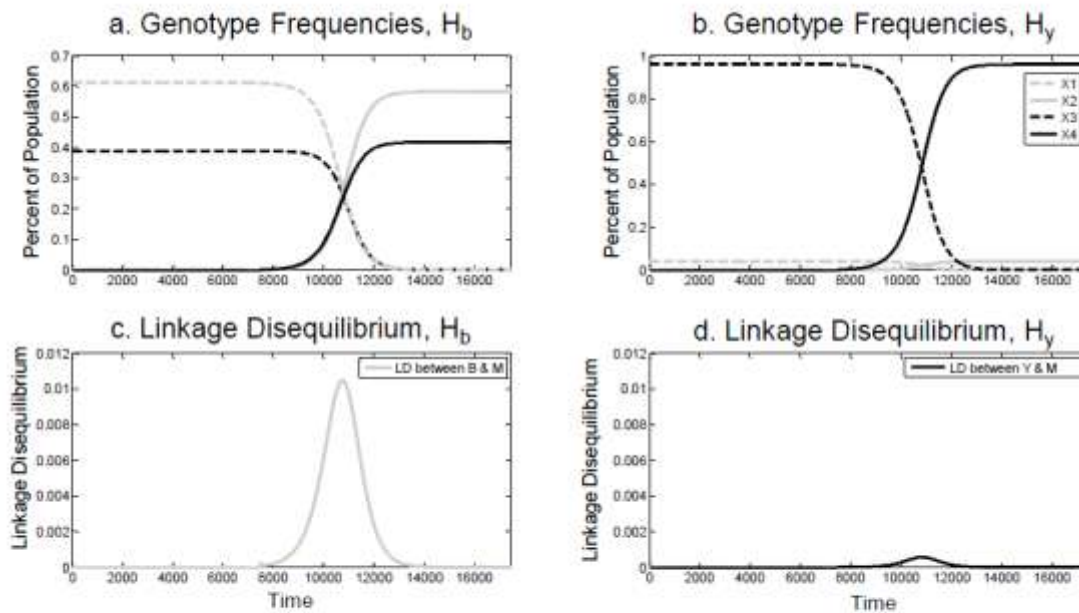
Our two-island model is formally equivalent to the scenario typical of secondary contact between two populations that are locally adapted to different habitats. Individuals are subject to both natural and sexual selection within habitats (see equation 1 and table 3.1) with bidirectional migration as in equation (2). Migration between habitats occurs in juveniles (i.e. after mutation and zygote formation):

$$\begin{aligned} x_i^{m_{h_b}} &= (1 - m)x_i^{H_b} \cdot h_b + m \cdot x_i^{H_y} \cdot h_y \\ x_i^{m_{h_y}} &= (1 - m)x_i^{H_y} \cdot h_y + m \cdot x_i^{H_b} \cdot h_b \end{aligned} \tag{6}$$

where  $m$  is the migration rate between habitats, and  $x_i^{h_b}$  is the frequency of zygotes of genotype  $i$  in habitat  $H_b$  following mating.  $x_i^{m_{h_b}}$  then replaces  $x_j$  in equation 4(a), and

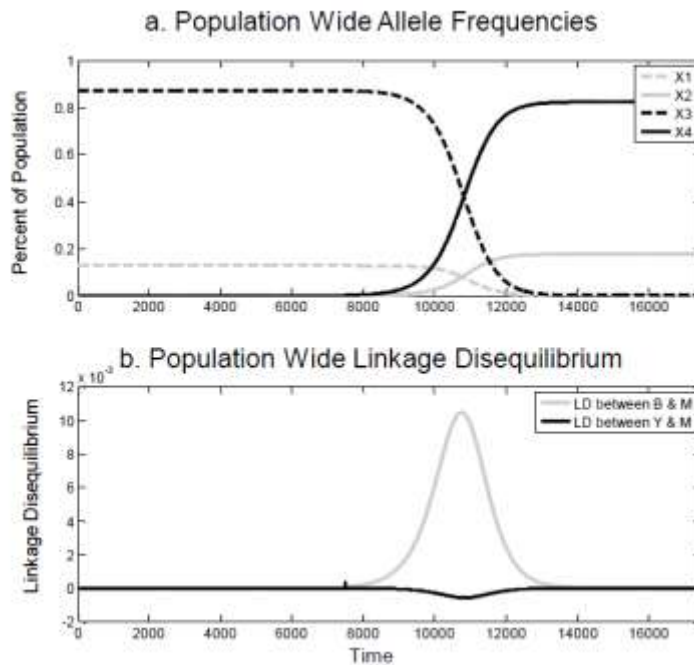
natural selection acts on males within patches. Mating occurs within patches, following table 2, recombination occurs, and the life cycle repeats.

We found that as long as migration is present but not so high as to produce a homogenous environment (tested numerically between .1% and 49%), male polymorphisms could be maintained. When  $m = 0$ , the two island model becomes identical to the general model (and polymorphisms are lost); when  $m > 50\%$ , the model is identical to the homogenous habitat model, where both natural and sexual selection occur across patches. When male color polymorphisms were maintained, successive modifier alleles were able to spread; each habitat fixed the more favored allele type and, due to linkage disequilibrium between the favored allele and the modifier locus, preference modifiers were able to evolve within habitats (example in figure 3.1). Globally, we found that both male morphs could be maintained and preference modifiers fixed (example in figure 3.2).



**Figure 3.1. Within patch allele frequencies and linkage disequilibrium in the two-island model.** This figure shows the simulation results from the two island model with starting conditions  $a_y, a_b = 3$ ,  $s_b, s_y = 0.25$ ,  $m = 0.1$ , and  $h_b = 0.75$ . Panels a and b show allele frequencies within the two habitats (blue and yellow) before and after the modifier is introduced. With this degree of habitat asymmetry, in the blue patch, the blue phenotype (grey lines) makes up the majority, while in the yellow patch, nearly all individuals are yellow (black lines). In both patches, the modifier rapidly fixes after it is introduced (dashed line – original preference, solid line – modified preference; the slight spike at generation 7500 indicates the introduction of the modifiers). Panels c and d show linkage disequilibrium in both patches – as the modifiers are fixing, linkage forms between the blue allele and the modifier in the blue patch, and between the yellow allele and the modifier in the yellow patch.



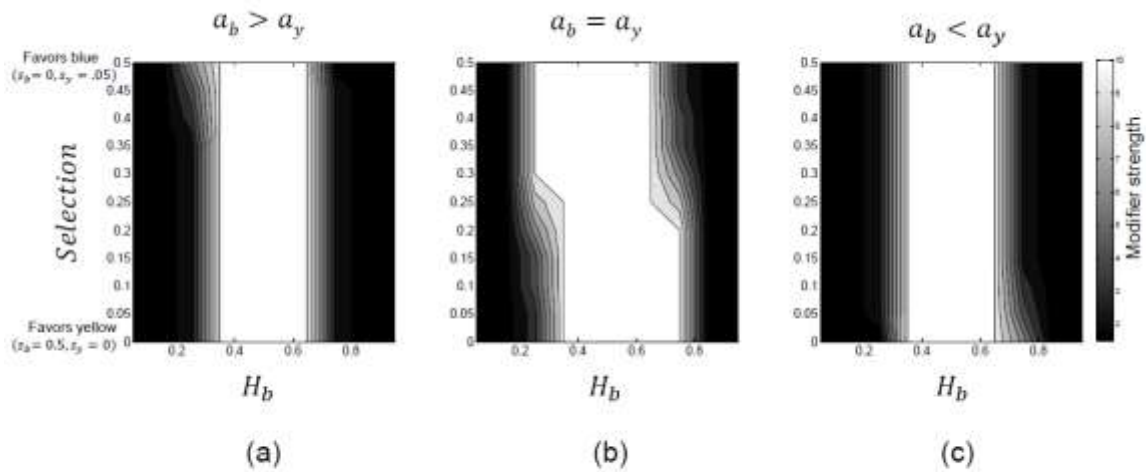


**Figure 3.2. Global allele frequencies and linkage disequilibrium in the two-island model.** Initial conditions  $a_y, a_b = 3$ ,  $s_b, s_y = 0.25$ ,  $m = 0.1$ , and  $h_b = 0.75$ . The top panel, a, shows global allele frequencies before and after the modifier is introduced, where the ancestral genotypes are designated by dashed lines and the genotypes with the modifier are designated by solid lines. When preference strengths are changed, the equilibrium frequency of the blue (grey lines) and yellow (black lines) morphs change, but polymorphism is maintained and the modifier fixes.

We also examined the effects of altering the size of the increase between the initial preference strength and the modifier allele ( $\epsilon$ ), the strength of selection within patches ( $s_B$  and  $s_Y$ ), and the strength of the initial preference ( $\alpha$ ). Larger values of  $\epsilon$  and  $\alpha$  increased the *rate* of modifier spread, but none of these impacted whether or not the preference allele would spread—as long as selection against, and preference for, conspicuous morphs was present modifiers could fix.

When conditions are asymmetric ( $H_b \neq H_y$ ,  $s_b \neq s_y$ ,  $a_b \neq a_y$ ), the spread of the modifier alleles can be damped (figure 3.3). As long as polymorphisms are present,

at least one modifier allele can fix despite asymmetric selection strengths and habitat frequencies. However, the range of successive modifiers which are able to spread is moderated by asymmetry – in scenarios where one morph is much favored over the other, or one habitat is much more common than the other, there is a limit to the eventual preference strength that can evolve. Figure 3.3 shows the combined effects of unequal selection, habitat asymmetry, and asymmetric initial preference strengths: each panel shows habitat frequency, from all  $H_Y$  through all  $H_B$ , on the x axis, and selection strength, ranging from favoring the yellow morph to favoring the blue morph, on the y axis, and each panel displays the results of preference evolution under different preference regimes. In 3.3a, the initial preference for blue is greater, in 3.3b, preferences are equal, and in 3.3c, preference for yellow is stronger. Comparing across the three panels, we see that increased asymmetry, from any source, can either prevent polymorphism from evolving (black regions) by favoring one morph too strongly over the other, or damp the spread of modifier alleles (grey regions). When all three parameters (habitat, natural selection, and sexual selections) favor one morph, predictably, polymorphism is lost (3.3a and 3.3c).



**Figure 3.3 The effect of asymmetry on modifier spread in the two island model.** The x-axis is the frequency of blue habitat, going from 0 (all yellow) to 100% (all blue). The y-axis shows selection asymmetry, as the values increase, the asymmetry between selection in the two patches increases as follows:  $s_y = y, s_b = 0.5 - y$ . For example, at 0,  $s_b = 0.5, s_y = 0$ , and at 0.25,  $s_y, s_b = 0.25$ . For this figure  $m = 0.1$  and  $\epsilon = 0.5$ . Each panel shows a different preference scenario, is (a) preference is stronger for the blue morph with  $a_b = 10, a_y = 5$ ; in (b) preference is equal, with  $a_b, a_y = 5$ . And in (c), yellow is preferred more strongly than blue with  $a_b = 5, a_y = 10$ . The shading indicates the final value of  $M_2$  that was able to fix in the population going from black (no modifier fixed) to white (10 successive modifiers fixed; simulation terminated at this point).

Finally, we examined the potential for preference loss via the spread of a modifier for weaker preferences, i.e.  $\epsilon < 1$ . In these cases, we found that in the two-island model such modifiers failed to spread. When a modifier increases preference strength for the more visible male phenotype in a given microhabitat, linkage disequilibrium between the modifier and the male color allele forms and allows the spread of the modifier. In the case of a modifier for weaker preference, linkage disequilibrium cannot develop, and the modifier fails to spread.

*Directed movement:*

Finally we considered the possibility of directed movement, where males could choose to move to the habitat where they suffered reduced predation during natural selection, and then move to the habitat where they were more attractive to females when they were ready to mate. Thus, after natural selection, the frequency of blue

males in  $H_b$  will be  $t_b^{HBns} = \frac{(1-\delta)t_b}{(1-\delta)t_b + \delta t_y}$ , and the frequency of blue males in  $H_y$  will be

$t_b^{HYns} = \frac{\delta t_b}{\delta t_b + (1-\delta)t_y}$ , where  $\delta$  represents the probability that a male will select the

correspondingly colored habitat. Prior to sexual selection, males move to the habitat where they are more visible, such that after natural selection the frequency of blue

males in  $H_b$  will be  $t_b^{HBss} = \frac{\delta t_b}{\delta t_b + (1-\delta)t_y}$ , and the frequency of blue males in  $H_y$  will be

$t_b^{HYss} = \frac{(1-\delta)t_b}{(1-\delta)t_b + \delta t_y}$ .

These assumptions allowed the maintenance of polymorphisms under a broad range of environmental conditions, as long as males were likely to select the correct habitat ( $\delta > 0.5$ ) but preference modifiers again failed to evolve.

## **Discussion**

We set out in this study to determine the evolutionary pressures placed on the strength of female preferences during sensory bias – not from natural selection on the sensory system – but from the action of sexual selection that arises from sensory bias itself. Selection placed on female preferences from within a Fisherian system such as this one is indirect; natural and sexual selection changing male trait frequencies leads to changes in the frequencies of female preference (and/or preference modifier) alleles

due to linkage disequilibrium between trait and preference loci. We considered several ecological scenarios, all characterized by the assumption, consistent with sensory bias, that different male phenotypes were conspicuous in specific habitats in which females (and predators) preferred them. We found that under the majority of scenarios examined, indirect selection will not lead to any notable amount of evolution of preference strength when preferences arise from sensory bias. This is true for the evolution of preference strengths within a single population, in a variety of microhabitat models, and when males can direct their movement to minimize predation events and maximize their chances of being chosen as a mate. The only scenario in which preference strength can evolve is when the biological scenario falls under the assumptions of a two-island model. The reason for these differences in the ability for modifiers of preference strength to spread, as we describe below, has to do with the ability for linkage disequilibrium to build up between traits and modifiers of preference strength in the different scenarios examined.

When there is sensory bias within a single population, preference (as opposed to the lack of any preference) is likely to be initially fixed; if preferences are a product, for example, of the physiology of the sensory system they will likely be present in all females. The initial conditions of this scenario will result in the subsequent fixation of one of the trait alleles in this two-locus system. Although we altered this condition in our model by allowing bidirectional mutation at the trait locus, so little variation in the trait is maintained that it is impossible for significant linkage disequilibrium between a trait and modifier of preference strength to build, especially when the modifier is

introduced at a low frequency. A modifier of preference strength will therefore not spread in a realistic time frame under these conditions. In natural populations, however, significant trait variation is often present despite the existence of female preferences. We caution therefore that under natural conditions the spread of a modifier may be somewhat greater than found here, although it will still be limited by the strength of linkage disequilibrium, which will be low if the modifier is initially rare.

In the microhabitat models considered there is an even more fundamental reason why modifiers of preference strength will not spread, namely that linkage disequilibrium will not build between the trait and modifier loci. When there is microhabitat structure, female preferences under sensory bias are not simply present or absent based on a genetic cue (e.g., consistently for a specific male trait), rather they are always for the more conspicuous male phenotype, which is determined by an interaction of the trait genotype with the environment. In other words, the male trait in this system can be thought of not as just color, but as the property of conspicuousness itself. Thus, non-random mating causes a genetic association to be formed between the modifier of preference strength and a different trait allele within different microhabitats. Because at some point in the life cycle in these models the male phenotypes re-assort randomly between microhabitats, this linkage disequilibrium dissolves. The scenario of sensory bias thus inherently prevents the buildup of linkage disequilibrium in these types of microhabitat models, and modifiers of preference strength cannot spread.

Only in the two island model does linkage disequilibrium between the color and modifier loci evolve, and only in that case because individuals do not move between habitats enough to break up the linkage disequilibrium that builds – females in the yellow habitat, for example, always prefer yellow males over blue, and because their offspring remain in that habitat, sufficient linkage disequilibrium builds over generations for the modifier to spread (the same is true in the blue habitat). If individuals in our simulations were to be allowed to migrate freely between habitats, the linkage disequilibrium would be lost and preference modifiers would fail to spread further. Interestingly, polymorphism maintenance and the evolution of preference strength are more robust to high migration rates in this model than in two-island models of reinforcement (e.g., Servedio 2000). In contrast to a traditional model of reinforcement, our models have no frequency dependent sexual selection; natural and sexual selection are always acting in opposite directions in the patches, as determined by the property of conspicuousness, thus preventing loss of variability in the male trait.

Although we only found increases in preference possible in the two-island model, it is important not to discount this possibility. We found modifiers spreading when migration was below 50% -- although this is technically a ‘two island model’, that is something of a misnomer. Typically, migration between ‘island’ populations is very low, e.g., 1% (Pinho and Hey, 2010). Our models support the spread of modifiers with much higher contact rates, which could potentially correspond to scenarios of parapatry and mosaic sympatry (Mallet et al, 2009).

It is important to remember, however, that the goal of these models was to identify evolutionary forces on preferences during sensory bias that arise through indirect selection specifically; these are not likely to solely determine the fate of modifier alleles in nature. It is possible, for example, that there may be direct selection against modifiers that increase preference due to the fact that stronger preferences sometimes cause females to incur greater search costs (e.g., Alatalo et al. 1988; Hedrick and Dill 1993; Gotthard et al. 1999; see also Real 1990; Reynolds & Gross 1990). It is also expected that if preferences are set by sensory biases, the natural selection that initially established the preference is likely to still be acting. This leaves open the possibility that such selection may also affect preference strength. Either of these sources of selection would act directly on female preference; such direct selection is expected to be substantially stronger than indirect selection (Kirkpatrick and Barton 1997). We found very little to no indirect selection on modifiers of preference strength in our single population and microhabitat models; in these cases there is no force to counteract any direct selection that may be present on preferences in the system. We would expect that in the two-island model the indirect selection that we found on modifiers of preference strength will combine with any existing direct selection to determine the ultimate strength of preferences.

Our models imply that speciation involving sensory bias is unlikely to be facilitated by the indirect evolutionary forces that sensory bias itself places on preference strength, provided that sensory bias simply generates general preferences for conspicuous phenotypes. Sensory bias is most likely to be involved in speciation



when preferences diverge due to divergent natural selection on the underlying sensory system (e.g., Boughman 2002). If such preferences were to be strengthened, speciation may be more likely. We note that this is not true when the preference is simply for conspicuousness itself. We found in our microhabitat model that modifiers of preference strength will not spread in this scenario. Even if preferences were infinitely strong, however, speciation would not result in our microhabitat scenarios because, as described above, there is no possibility for linkage disequilibrium to build between preferences and traits; since different males are preferred in different environments and males and females both assort randomly between microhabitats during the life cycle, no isolation is possible. In our two-island model we find that stronger preferences can evolve. Once again, however, females with a strong preference for conspicuous males will shift the specific male trait allele that they prefer if they are in a different environment, precluding speciation by the Biological Species Concept (Mayr 1942). Finally, even in allopatric populations, our single population model shows that selection generated by sensory bias itself has a very limited effect of the spread on modifiers of preference. True isolation involving sensory bias cannot therefore rely on simply strengthening a preference for conspicuous males, but must instead involve genetic changes that will cause preferences not to change when females relocate (e.g. Van Doorn et al. 1998).

Finally, we would like to emphasize that in addition to finding that the indirect forces generated by sensory bias are unlikely to cause preferences to strengthen, we also found that they cannot *decrease* the strength of sensory biased preferences. Once

present, these preferences will not be lost even if other selective forces on them are removed, in the scenarios modeled here.

To sum, when we isolate the evolutionary forces on the evolution of preference strength that arise during sensory bias, we find that this indirect selection is only likely to be notable when migration is restricted at all points in the life cycle, as in a two-island model. In such scenarios it would be interesting to examine in more detail whether indirect selection will alter the strength of preferences from an optimum set by natural selection on preferences. Within a single population or in microhabitat scenarios, however, our results suggest that preference strength will not be altered by the action of sensory bias itself.

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## **CHAPTER IV: CONDITION DEPENDENT MATE CHOICE: A STOCHASTIC DYNAMIC PROGRAMMING APPROACH**

### **Abstract**

We study how changing female condition during the mating season and condition-dependent search costs impact female mate choice, and what strategies a female could employ in choosing mates to maximize her own fitness. We address this problem via a stochastic dynamic programming model of mate choice. In the model, a female encounters males sequentially and must choose whether to mate or continue searching. As the female searches, her own condition changes stochastically, and she incurs condition-dependent search costs. The female attempts to maximize the quality of the offspring, which is a function of the female's condition at mating and the quality of the male with whom she mates. The mating strategy that maximizes the female's expected reward is a quality threshold. We compare the optimal policy with other well-known mate choice strategies, and we use simulations to examine how well the optimal policy fares under imperfect information.

### **Introduction**

How females choose their mates has long been a central question in the study of sexual selection. Ultimately, females seek to mate with a high quality male, where quality is measured either in terms of direct benefits to the female, good genes, or

attractive offspring (Kirkpatrick 1987). However, the proximate mechanism of female mate choice, i.e., how an individual female actually goes about choosing a mate, has received much less attention (Gibson and Langen 1996). When choosing a mate, a female must balance her ultimate desire for a male with high fitness with the proximate concerns of search costs, male availability, and her own condition. We develop a model of female mate choice that considers the tradeoff between offspring quality and search costs. In our model, we consider female condition as a stochastically changing variable, and search costs as a function of female condition. We find that the optimal strategy is a condition-dependent threshold, and that it outperforms previously identified strategies, e.g., best-of- $n$  (Janetos 1980), under changing conditions.

Previous models of mate choice decisions typically tried to determine policies that would maximize the quality of a female's eventual mate. Such models have generally resulted in strategies that can be divided into three categories: best-of- $n$ , threshold, and comparative Bayes. Note that throughout this paper, we use the term 'policy' to refer to a specific decision rule used to determine mate choice, while 'strategy' refers more broadly to a type of policy. The best-of- $n$  strategy states that females should assess a fixed number ( $n$ ) of males and then return to and choose the option with the highest quality; the optimal value of  $n$  depends on assessment costs and the variance of male quality (Janetos 1980), and such a strategy assumes the ability to return to a previously encountered male. A threshold strategy states that females set a quality threshold and mate with the first male they encounter who exceeds the threshold. As with the parameter  $n$  in the best-of- $n$  strategy, the optimal threshold

depends on the mean and variance of the distribution of male traits (Real 1990). Comparative Bayes is a dynamic search algorithm that involves sampling males and learning about the distribution of male traits to develop a threshold that improves with each observation (Luttbeg 1996).

Earlier models of mate choice generally neglect to account for female condition as a factor. While some models include search costs (Real 1990, Luttbeg 1996, Collins et al 2006), these are assumed to be fixed; all females experience the same search costs, and these search costs do not change over time. However, there is ample empirical evidence that female search costs are a function of female condition; in general, poor condition females suffer higher search costs (Alatalo et al 1988, Milinski and Bakker 1992, Woodgate et al 2010). Cotton (2006) highlighted the role of condition dependent search costs in mate choice, emphasizing that female preferences can change plastically in response to condition. Previous models also assumed that a female's offspring quality was solely dependent on the quality of her mate (Anetos 1980, Real 1990, Collins et al 2006), when it is actually a function of the quality of both parents (Eshel 1984). By overlooking female condition and variability in search costs, prior models of optimal mate choice failed to explore an interesting problem.

In this chapter, we develop a mathematical framework that describes condition-dependent mate choice and explicitly models dynamic female condition and condition-dependent search costs. We consider the reward function to be offspring quality, rather than mate quality, and thus calculate it as a function of the quality of both parents. We find that a condition-dependent threshold policy is optimal, and confirm that it



outperforms the oft-cited best-of- $n$  strategy under changing conditions. We also test the robustness of the optimal policy to limited information about male quality, and confirm that even with limited information, a condition-dependent threshold policy maximizes expected offspring quality.

## Methods

We model the process by which a particular female searches for a mate. We assume that the female may have a range of conditions and that she encounters males of varying quality. More formally, let  $S = \{1, 2, \dots, N_S\}$  be the set of conditions for the female and  $Q = \{1, 2, \dots, N_Q\}$  be the set of possible male qualities. Let  $f(q)$  be the probability that a randomly-encountered male has quality  $q$  and define  $F(q) = \sum_{q' \leq q} f(q')$ , that is,  $F$  is the probability that a randomly encountered male has quality at most  $q$ . For a given female of condition  $s$  and male of quality  $q$ , denote the expected fitness of their offspring by  $G(s, q)$ , and assume that better condition (of the female) and better quality (of the mate) both lead to better offspring; that is,  $G$  is non-decreasing in both  $s$  and  $q$ . Because  $G$  is non-decreasing in  $q$ , we can also define its inverse: let  $G^{-1}(\cdot)$  be the minimum mate quality required to obtain an offspring of fitness at least  $g$  when the female is in condition  $s$ . Specifically,  $G^{-1}(s, g) = \min\{q: G(s, q) \geq g\}$ . Our model does not require any additional assumptions about the function  $G(s, q)$ ; in our experiments, we will employ a concave function for  $G(s, q)$ , based on empirical evidence Luttbeg1996.

We assume that the female's condition evolves according to a Markov chain. This means that the female's condition at the next decision point depends on her past

history only through her present condition, and is independent of everything else in the problem. Therefore, we can represent the changing condition by a probability transition matrix  $P = [p_{st}]$ , where  $p_{st}$ , for  $s, t \in S$ , is the probability that the condition will be  $t$  when next encountering a potential mate, if the condition is currently  $s$  and the female continues to search. By assuming that the condition evolves according to a Markov chain, we can formulate the mate choice problem as a Markov decision process. A Markov decision process (MDP) is a type of dynamic program where costs, rewards, and state transitions are affected by decisions. In this case, the future expected reward will depend on the decision to mate or continue searching. If the individual decides to mate, then the reward  $G(s, q)$  is earned. If the individual decides to continue searching, she pays a state-dependent search cost  $c(s)$  and then experiences a state transition according to  $P$ . Both rewards and costs are allowed to be state-dependent in the MDP formulation.

#### *Markov decision process formulation*

A complete MDP formulation includes states, actions, and rewards. The state space is  $S \times Q$ ; that is, all combinations of female condition and male quality. The action set  $A$  consists of two actions, mate or continue; we denote this by  $A = \{M, C\}$ . A stationary policy for a MDP is a function that maps each state to one of the actions. In this article, we assume that the mate choice strategy must be a stationary policy. Let  $\pi$  denote any such policy; that is,  $\pi: (S \times Q) \rightarrow A$ .

Let  $V^\pi(s, q)$  be the expected reward earned under policy  $\pi$  if the current state is  $(s, q)$ . Then  $V^\pi(\cdot)$  must satisfy

$$V^\pi(s, q) = \begin{cases} G(s, q), & \text{if } \pi(s, q) = M \\ -c(s) + \sum_{t \in S} \sum_{r \in Q} p_{st} f(r) V^\pi(t, r), & \text{if } \pi(s, q) = C. \end{cases} \quad (1)$$

In other words, if policy  $\pi$  prescribes mating in state  $(s, q)$ , then the offspring fitness  $G(s, q)$  is earned. Otherwise, cost  $c(s)$  is incurred and we calculate the expected reward over all future states  $(t, r)$ . Our objective is to maximize  $V^\pi(\cdot)$  over all possible policies  $\pi$ . We denote this maximum by the function  $V(s, q)$ , the optimal expected reward when starting in state  $(s, q)$ , and note that  $V(\cdot)$  must satisfy

$$V(s, q) = \max\{G(s, q), -c(s) + \sum_{t \in S} \sum_{r \in Q} p_{st} f(r) V(t, r)\}, \quad \forall s \in S, q \in Q. \quad (2)$$

Note that the equations given in (2) are known as Bellman's equations. Because the distribution of future male qualities (which are denoted in the above by  $r \in Q$ ) is independent of the current state, we can simplify (2) by defining  $V(s) = \sum_{r \in Q} f(r) V(s, r)$  for all  $s$ .  $V(s)$  is the expected reward earned starting in condition  $s$  if the optimal policy is followed for any encountered mate. Then

$$V(s, q) = \max\{G(s, q), -c(s) + \sum_{t \in S} p_{st} V(t)\}, \quad \forall s \in S, q \in Q. \quad (3)$$

We will use this simplified version of Bellman's equations throughout the rest of the paper.

Using the formulation that we have defined above, we can show that for each female condition, the optimal policy is a threshold policy in terms of the male quality; i.e., for each  $s \in S$  there exists  $q^*$  such that the optimal action is to mate if and only if  $q \geq q^*$ .

To see why this is the case, consider a finite-horizon version of this problem where  $V_M(s, q)$  is the expected reward earned starting in state  $(s, q)$  if there are  $M$  decision points remaining. In this formulation, if the female chooses to continue

searching at the last decision point, the problem ends and a reward of zero is earned. For all practical purposes,  $G(s, q)$  will be non-negative, and hence the female will always mate at the last decision point. Then it must be the case that

$$V_M(s, q) = \max\{G(s, q), -c(s) + \sum_{t \in S} p_{st} V_{M-1}(t)\}, \quad \forall s \in S, q \in Q, \quad (4)$$

with the conventions that  $V_{-1}(s, q) = 0$ , for all  $s \in S, q \in Q$  and  $V_i(s) = \sum_{q \in Q} V_i(s, q)$  for all  $i$ . Note that the difference between (3) and (4) is that the solution to (4) can be calculated recursively, by first calculating  $V_0(s, q)$ , then calculating  $V_1(s, q)$ , etc.; while in (3),  $V(s, q)$  appears in both the left and right hand side of the equations, so such a calculation is not possible.

Then the optimal action to take when  $M$  decision points are remaining is to mate if and only if  $G(s, q) \geq -c(s) + \sum_{t \in S} p_{st} V_{M-1}(s)$ , or in other words, if and only if

$$q \geq G^{-1}(s, -c(s) + \sum_{t \in S} p_{st} V_{M-1}(t)). \quad (5)$$

The right hand side of (5) does not depend on the optimal action taken at decision point  $M$ , so it is simply a threshold policy where the action depends on the quality of the encountered mate. Since  $M$  is arbitrary, by taking the limit as  $M \rightarrow \infty$ , we conclude that the optimal policy must be a threshold policy where every action depends on  $q$ , regardless of how many decision points remain.

An important point is that while the optimal policy to this problem is a threshold policy in the male quality, the threshold is dynamic; that is, it changes according to the female's condition, taking into account the probability of transitions from one condition to another.

Recall that  $\pi$  maps each combination of female condition and male mate quality to an action (mate or continue), i.e.,  $\pi: (S \times Q) \rightarrow A$ . However, we have now established that the optimal policy can be expressed in a simpler form,  $\theta: S \rightarrow Q$ . That is, the optimal policy  $\theta$  maps each condition  $s \in S$  to a single quality  $\theta(s) \in Q$ , such that a female in condition  $s$  will mate if and only if the encountered male's quality is at least  $\theta(s)$ . It is not possible to write the function  $\theta$  in closed form. However, the optimal thresholds can be computed using the value iteration algorithm. The value iteration algorithm calculates  $V_M(s, q)$  using (5) for  $M = 1, 2, \dots$ . The algorithm stops when the change in the optimal values  $V(s, q)$  is less than a pre-specified value of  $\varepsilon$ , and then solves (2) to determine the values of  $\theta$ .

We can also give analytical lower bounds for the optimal mating thresholds by examining a one-step version of the mate choice problem. The one-step version of the mate choice problem assumes that if the female continues searching, she will always mate at the next decision point. That is, the reward earned by the one-step mate choice is  $V_1(s, q)$ . Let  $g_s$  denote the expected reward from mating with a randomly selected male, if the female is in state  $s$ , and note that  $g_s = \sum_{q \in Q} f(q)G(s, q)$ . Therefore, if the female continues searching, she will earn a future expected reward of  $\sum_{t \in S} p_{st}g_t$ . Hence, the female's optimal expected reward is  $\max\{G(s, q), -c_s + \sum_{t \in S} p_{st}g_t\}$ . Note that according to (3),  $\theta(s) = G^{-1}(s, -c_s + \sum_{t \in S} p_{st}V(t))$ . By definition, the optimal policy always gives the largest possible reward. Therefore,  $V(t) \geq g_t$  for all  $t \in S$ , because  $V(t)$  is the reward earned by following the optimal policy in state  $t$  while  $g_t$  is

the reward earned by following the always-mate policy in state  $t$ . Then because  $G^{-1}(s, q)$  is non-decreasing in  $q$ , we can conclude that

$$\theta(s) \geq G^{-1}(s, -c_s + \sum_{t \in S} p_{st} g_t). \quad (6)$$

The above equation states that the mating threshold obtained from the one-step version of the mate-choice problem is a lower bound on the optimal mating threshold. While this result does not completely characterize the optimal policy, it does show that if the male quality is below the threshold resulting from the one-step problem, the female should definitely choose to continue searching. Moreover, when conditions (such as high search costs) make the female very likely to mate in the optimal policy, then the one-step threshold turns out to be a good approximation of the optimal threshold.

#### *Evaluating best-of- $n$ with changing conditions*

In the literature, best-of- $n$  strategies are widely believed to be desirable for mate choice. A best-of- $n$  strategy involves evaluating  $n$  males and then returns to mate with the best male encountered Janetos1980. To better understand the behavior of the policies developed in this article (the optimal threshold and the one-step threshold), we must be able to compare their expected rewards to the expected reward for best-of- $n$  under the same regime of search costs and dynamic conditions.

To derive the expected reward for a female in condition  $s$  utilizing the best-of- $n$  strategy, we calculate the expected reward for mating using this strategy, which we denote by  $R_n$ , and then subtract the cost of sampling  $n$  males and returning to the highest quality male encountered, which we denote by  $D_n$ . We calculate the expected

reward for a female using best-of- $n$  by averaging twice, first over the female's final condition  $t$  after  $n$  steps and then over the highest mate quality  $q$  encountered. To compute the probability of each possible final condition, we begin by noting that the  $k$ -step probability transition matrix for female fitness is  $P^k$  (that is, matrix  $P$  multiplied by itself  $k$  times). Let  $p_{st}^k$  denote the  $(s, t)$ th element of matrix  $P^k$ ; this quantity is the probability of transitioning to state  $t$  over  $k$  steps when starting in state  $s$ . To compute the probability that the highest-quality male encountered is of quality  $q$ , first note that each encounter is assumed to be independent. Hence,  $F(q)^n$  is the probability that all  $n$  males encountered had quality at most  $q$ . However, this expression includes the event where all  $n$  males encountered had quality strictly less than  $q$  (i.e., it does not guarantee that a quality- $q$  male was actually encountered). Therefore, we subtract  $F(q - 1)^n$ , which is the probability that all  $n$  males encountered had quality at most  $q - 1$ . Hence,

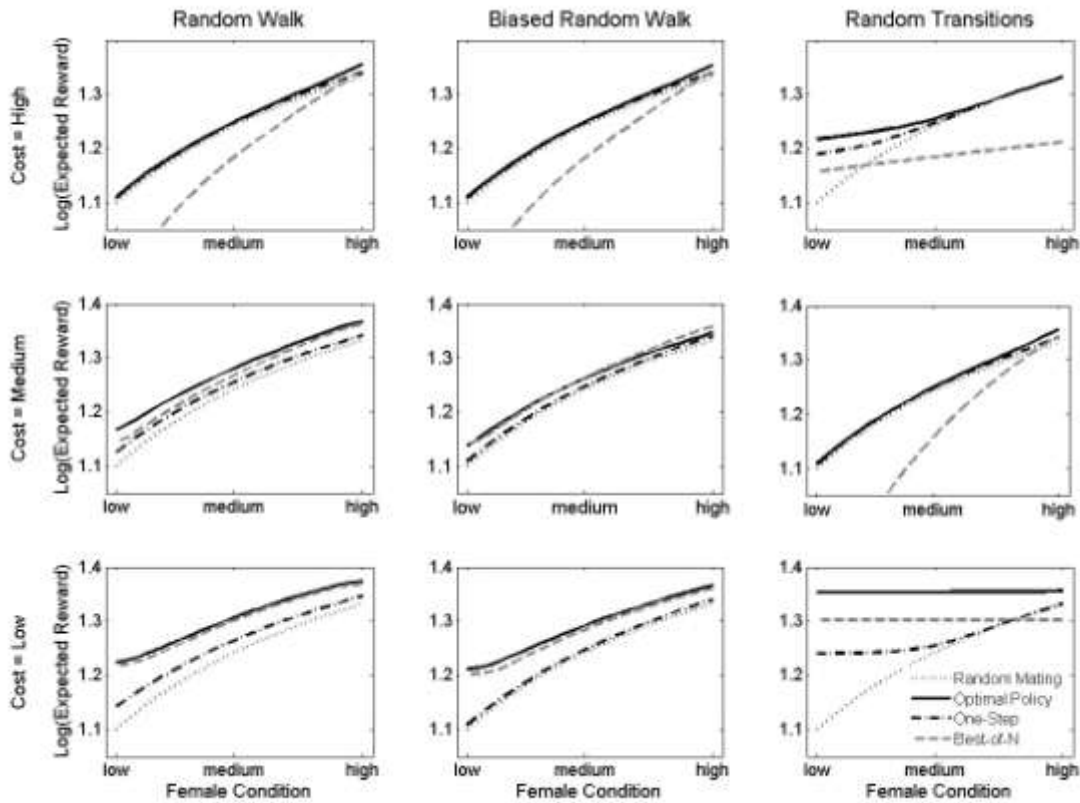
$$E[R_n|s] = \sum_{t \in S} p_{st}^n \sum_{q \in Q} [F(q)^n - F(q - 1)^n] G(t, q).$$

The expected cost of using the best-of- $n$  strategy is calculated similarly, by averaging over the possible states at each of the  $n$  time steps; as a result,  $E[D_n|s] = \sum_{k=1}^n \sum_{t \in S} p_{st}^k c(t)$ . Here, we do not need to average over qualities because search costs do not depend on mate quality. Thus, the net reward for a female in state  $s$  using best-of- $n$  is  $E[R_n|s] - E[D_n|s]$ , the expected reward of minus the expected cost of employing a best-of- $n$  strategy.

### *Policy comparison*

To test how well the optimal policy (found via the value iteration algorithm) performs, we performed a numerical study to calculate the expected reward under the optimal threshold, the one-step threshold, and the traditional best-of- $n$  model. As a baseline, we also calculated the expected reward for random mating,  $g_t$ . We considered three probability transition schemes: (1) a random walk, where condition is equally likely to increase or decrease; (2) a biased random walk, where condition is more likely to decrease over time to approximate aging; and (3) uniformly random transitions, where an individual is equally likely to transition to any possible condition. We considered low, intermediate, and high nominal search costs; intermediate search costs were 10 times as large as low and high search costs were 100 times as large. In all scenarios, search costs increased as condition decreased, and we used a concave reward function (see Appendix 4A for the full set of parameters used in the numerical study).



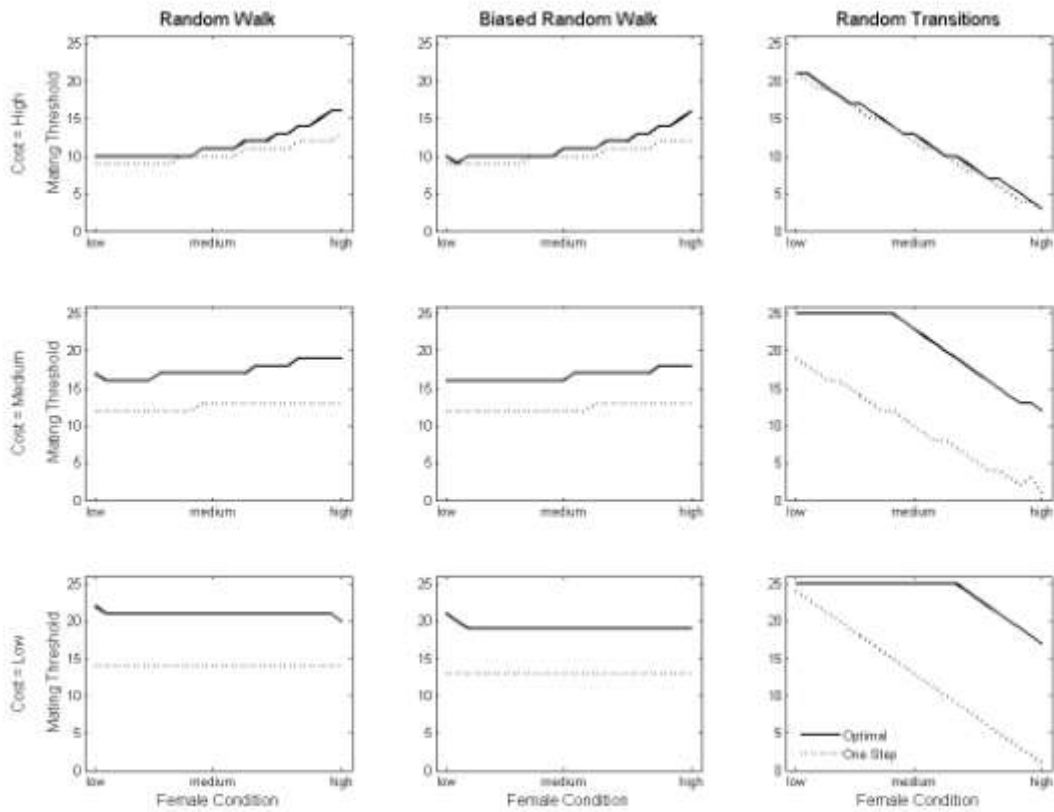


**Figure 4.1. Expected rewards for different mate choice policies.** We calculated the expected rewards for the optimal policy, the one step look ahead policy, and best-of- $n$ . The rows, from top to bottom, show high, medium, and low search costs. The columns each represent a different transition matrix,  $P$ . For this plot,  $N_s = N_Q = 25$ . On the x axis, female fitness ranges from 1 (the lowest) to 24 (the highest).

The expected rewards for the optimal threshold policy, the one-step threshold policy, random mating, best-of- $n$  were computed for all combinations of the parameters described above, and plotted in Figure 4.1. When presenting the expected reward for best-of- $n$  strategies, we assume that the female uses the value of  $n$  with the highest expected reward, given her transition scheme, costs, and initial state. That is, the optimal value of  $n$  is always used; if a fixed  $n$  were used, then the resulting expected

reward would be lower. In all scenarios, the numerical results confirm that the optimal policy performs best. When search costs are high, the one-step policy is a close approximation of the optimal policy. The optimal policy outperforms best-of- $n$  in every scenario except the biased random walk with medium costs, where they perform equally. Best-of- $n$  performs particularly poorly with high search costs. It is also important to note that although the expected reward increases for all strategies with improving female condition, the differences between the strategies increase with decreasing female condition.

Mate quality thresholds, i.e., the minimum male fitness required for the female to choose to mate, are plotted in Figure 4.2. As one might expect, higher costs and less predictable environments lead to lower thresholds. Consistent with (6), the one-step thresholds are a lower bound on the optimal thresholds. When females can expect that there is a good chance their condition will increase in time, and do not suffer greatly from mating, low condition females have higher thresholds than high condition females (see, e.g., low costs and random transitions), because they can benefit from waiting for their own condition to improve. When costs are high and females are likely to decrease in condition over time (see, e.g., biased random walk and high cost), low condition females have lower thresholds than high condition females, because the potential benefit from waiting to find a better mate is offset by the likelihood that their own condition will decrease and in the meantime they will accrue high search costs. These results are consistent with empirical evidence of condition-dependent variability in female preferences (Cotton 2006).



**Figure 4.2: Mating thresholds for females under the optimal policy and the one step look ahead policy.** Here,  $N_S = N_Q = 24$ . From left to right, we plotted low, medium, and high search costs. The thresholds for the two policies are generally similar, where thresholds are lower with high costs or a high probability of decreasing in condition, and high thresholds when searching is inexpensive

### *Incomplete Information*

In a real system, it is unlikely that a female can accurately assess the true state of a potential male. Instead, she is likely to have a general idea of a male's condition, which may be more or less accurate depending on the honesty of the signals he is using to advertise to potential mates. To assess whether our optimal threshold policy would be viable in such a scenario, we tested its performance under varying degrees of

uncertainty about a male's true condition and compared the average reward values to those obtained through mating randomly.

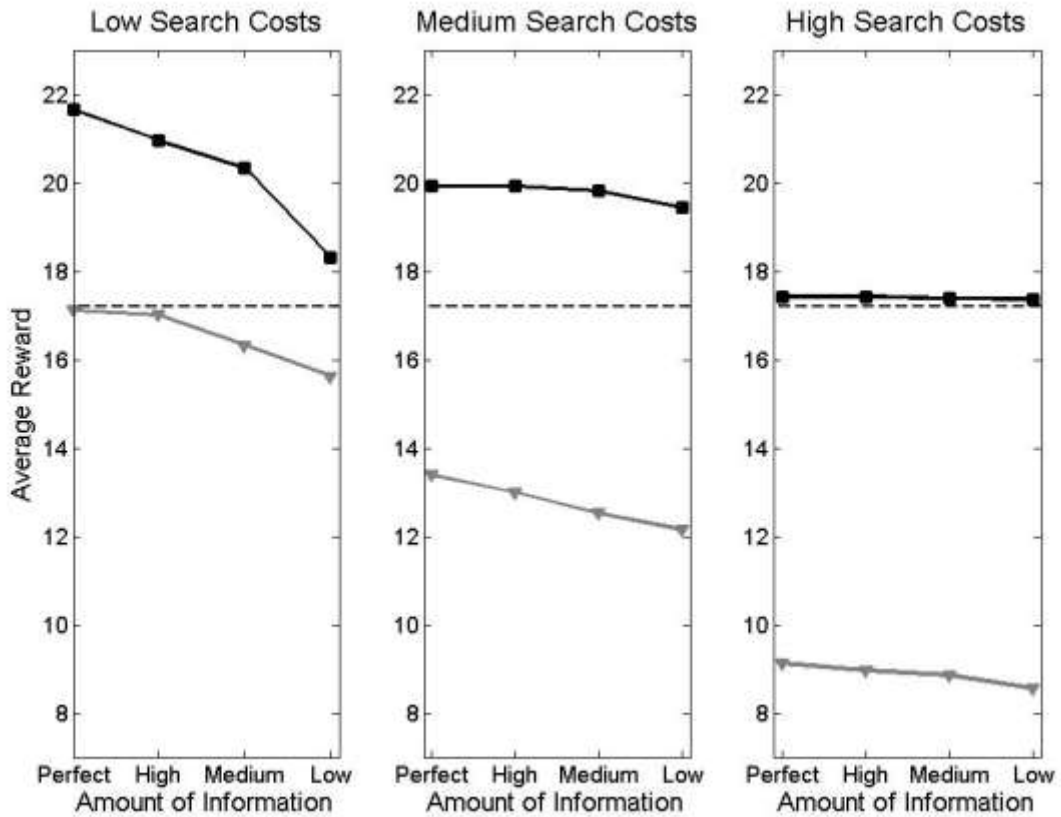
We used an individual based model to simulate mate choice and rewards for females employing either random mating or an optimal threshold. Male traits and female condition were assigned according to a discretized normal distribution with 24 bins, and changed via a biased random walk. We examined three levels of imperfect information, approximated by decreasing granularity: high (12 visible states), medium (6 visible states), and low (3 visible states). We compared these results to those derived from mating with perfect information, i.e., where females could observe all 24 male states. In each case, the female perceives the quality of the male to be the weighted average of all males in the same perceived state. For each level of information, we repeated the simulations with low, medium, and high search costs.

In the simulation, each female sampled males until she found a male exceeding her condition-dependent threshold value. After all females selected mates, each female's net fitness was calculated as  $G(s, w) - C_{\text{total}}$ , and after each simulation average female fitness was calculated. In order to compare the simulation results to previous works, we also simulated best-of- $n$  mate choice for each level of information, using the optimal value of  $n$  for each female given her starting condition. In these simulations, females sampled  $n$  males, and returned to the highest (perceived) quality male they encountered. As a control, we calculated the expected reward for random mating. Complete details on the simulation are described in Online Appendix .

In all simulations, the optimal policy outperformed both random mating and best-of- $n$  mate choice (see Figure 4.3). The best-of- $n$  strategy performed surprisingly poorly, but this can be explained because we are looking at the average reward over a population of females; recall that in Figure 1, we saw that best-of- $n$  performed much worse than the optimal policy for lower condition females. In the simulations, the extremely poor rewards for females with low condition bring the average reward down substantially.

As the granularity of information about male quality decreases, the expected reward decreases for both best-of- $n$  and the optimal threshold. Because best-of- $n$  ignores changing condition and search costs, females actually search longer (i.e., the optimal value of  $n$  is larger) when they have less information. However, because the optimal threshold adapts to female state, females can stop searching when it becomes costly.

This result shows the surprising robustness of the optimal threshold policy in making the best decision given the available information, and its adaptability to changing conditions. With perfect information and low costs, the optimal threshold policy performs about equally with a best-of- $n$  policy. However, when information is imperfect the optimal threshold policy is the clear winner: intuitively, there is no use in sampling a large number of males when the female cannot clearly tell the difference between them, and this fact becomes even more pronounced as costs increase. The optimal policy outperforms random mating (the dashed line in each figure) in all scenarios, even when mate choice is costly and information is poor.



**Figure 4.3. Comparison of simulation results for policy performance under uncertainty about male quality.** The three panels, from left to right, show the expected rewards under low, medium, and high search costs. In each figure, the  $x$  axis depicts the amount of information about male quality, going from poor information (at the left) to perfect information (at the right) In these simulations,  $n_s = n_q = 24$ ,  $\mu = 12$ , and  $\sigma = 1.67$ . With high information, females perceived **12** male classes, with medium information, **6**, and with poor information, **3**.

## Discussion

In this paper, we have constructed a model of female mate choice where female condition changes stochastically over time, search costs are a function of female condition, and the ultimate reward of mating (i.e., offspring quality) is a function of both maternal and paternal fitness values. We proved that the optimal policy to maximize a

female's expected reward is a condition-dependent threshold, analytically derived lower bounds on the optimal thresholds, and demonstrated that the optimal threshold can be found using a value iteration algorithm. We showed that the optimal threshold policy outperforms best-of- $n$  and random mating under a broad range of parameters. The optimal policy converges with random mating when costs are very high, and does equally well as best-of- $n$  when costs are low. Finally, we showed through simulation that our policy is robust to imperfect information, outperforming other strategies even with very little information about male quality.

Optimal mate choice strategies have been a relatively well studied. Early models considered simple heuristics in constant environments (eg Janetos 1980), while more recent models have dealt with incorporating search costs Real 1990, and complex problems such as learning (Luttbeg 1996) and stochasticity in male quality (Collins et al 2006). However, the model presented in this article is unique in that we consider the impact of female condition on mate choice decisions: the offspring quality is a function of both male and female fitness, and female fitness changes stochastically during the search process.

The model presented in this paper predicts fairly simple thresholds based on a female's state. Many policies that have been shown to perform well rely on complex calculations involving differential equations and prior probability distributions. Our policy calculates thresholds based solely on male trait distribution, female search costs, and state transition probabilities; given those values, an optimal threshold can be calculated for each female state, and no dynamic updates need to be made. Generally, a

female in poor condition with little hope for improvement has weaker preferences than a high quality female that can take the extra time to find a better mate. Interestingly, Janetos (1980) did suggest that an 'optimal one-step process' would be a useful strategy: if females had a finite time horizon for mating, they should be very picky at the beginning of their search, and gradually decrease their threshold. This is analogous to our finite time horizon model where  $N_s = 1$  and  $P = [1]$ .

Our results complement the empirical findings that female condition impacts preferences, and that females may exhibit plasticity in their preferences in order to maximize reproductive success (Cotton 2006). Observational studies have correlated decreased preferences strength with poor condition (Rintamaki et al 1995, Bakker et al 1999). Experimentally, both condition (Burley and Foster 2006, Hunt et al 2005, Hingle et al 2001) and variation in search costs (Milinski and Bakker 1992, Alatalo et al 1988) have been shown to moderate female preferences.

Unlike some previous works, we did not use a Bayesian model, wherein females have a prior belief about male quality which is updated during their search. This type of model can significantly increase the complexity of the strategy that the female would have to employ. In reality, it is likely that females can acquire social information about the distribution of male quality prior to mate choice (Doligez et al 2002, Valone and Templeton 2002, White 2004). Furthermore, our simulations with imperfect information show that the optimal threshold policy under our model is robust to scenarios where females know very little about male quality. We also made the assumption that females



would have some awareness of their own condition, based on the evidence of condition-dependent mate choice (Cotton 2006).

Our findings, that females are likely to alter their preferences in response to changes in condition and related search costs, have important implications regarding the maintenance of genetic variation in populations and the lek paradox. If females adaptively alter their preferences, then male trait variation will be maintained because lower condition females will decrease their threshold for mating. Empirically, we would like to stress the need for increased awareness of female condition in experimental studies of mate choice, and the importance of sequential mate choice tests.

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## CHAPTER V: CONCLUSIONS

In this dissertation, I sought to understand what factors could drive variability in female preferences, and what impacts variation in female preference could have on evolutionary outcomes. To achieve this goal, I considered both proximate (competition, search costs) and ultimate (ecological adaptation, evolved strategies to maximize fitness) explanations, and found that variation in preferences could come from many different sources. I also found that female preferences may play an important evolutionary role in maintaining variability in male traits.

In the second chapter of my dissertation, *The Role of Sexual Preferences in Intrasexual Female Competition*, I asked if female competition for mates, resulting in decreased fertility, could lead to direct selection against female preferences. I found that moderate to high levels of competition could lead to direct selection against female preferences, but that this could be overcome by indirect selection when female preferences for male traits was strong enough. I then asked if the presence of multiple female preferences, for orthogonal male traits, could decrease competition and thus alleviate selection against preference. I found that, while the presence of multiple preferences within a population changed the strength of direct selection against preference evolution, it still persisted. Nevertheless, the presence of multiple preferences did serve to expand the parameter space under which multiple preferences could evolve by increasing the strength of indirect selection.

In the third chapter of my dissertation, *The Evolution of Preference Strength Under Sensory Bias: A Role for Indirect Selection?*, I ask if female preferences that originate via sensory bias can evolve to become stronger or weaker via modifier alleles. I assumed that female preferences for conspicuous male traits were already present due to natural selection acting on the sensory system, such that females preferred to mate with male phenotypes that were more visible in the environment. Recapitulating the results of Chunco (2007) I first confirmed that female preferences for conspicuousness can maintain male polymorphisms in a heterogeneous environment. I then looked at whether or not modifiers of preferences could evolve, and considered how their evolution was impacted habitat structure. I found that in most scenarios, gene flow prevented the evolution of stronger or weaker preferences – a preference that has evolved via sensory bias will not be altered further through indirect selection. The only exception was in the case of the ‘two island model’ where two populations, where different male phenotypes were differentially visible, were connected only via migration.

In the fourth chapter, *Condition Dependent Mate Choice: A Stochastic Dynamic Programming Approach*, I consider how proximate factors – search costs and changing female fitness during her mate search – can affect mate choice, and what strategies a female should use while searching for mates when faced with these challenges. I found that a threshold policy, where females had male-quality thresholds based on their own fitness and search costs, was the best strategy to maximize fitness. Because female

condition varies in a population, when this strategy is employed, preference strength will vary as well.

Taken together, the elements of my dissertation provide insight into variability in female preferences, but also serve to highlight the importance of thinking beyond the traditional male trait/female preference dichotomy that has dominated sexual selection theory. The most widely cited alternative force in sexual selection is male-male competition for access to females or the resources to attract females (eg. Berglund 1996, Moore and Moore 1996, Hunt 2008). However, this view is unnecessarily restrictive and fails to take into account many important alternative factors in evolution through sexual selection.

Females do not necessarily choose males based on some absolute measurement of quality. By considering sexual selection only as an interaction between males and females, in which all females are a homogenous group with the same goal of choosing the best mate, important factors driving variability in female preferences and the maintenance of variability in male traits are overlooked. Empirically, it has been noted that female-female competition (Clutton-Brock 2009), condition dependent preferences (Cotton et al. 2006), and facultative changes in female preferences (Jennions and Petrie 1997) can drive changes in the strength and direction of female preferences.

Proximate consequences of female preferences include competition for mates, the impacts of where and when mating takes place, and the costs of actually finding a mate. In the short term, competing for attractive males can lead to decreased fertility (Wedell et al, 2002), decreased parental care (Ferretti and Winkler, 2009), or physical

harm inflicted by other females (Ahnesjo et al. 1993, Rosenqvist and Berglund 1992). In an attempt to maximize fitness over the long term, this may lead to the evolution of alternative strategies or weakening of preferences in order to prevent undue competitive costs. The process of actually *finding* a mate can be costly as well – females spend time and energy searching for mates instead of foraging for food, protecting themselves against predators, or caring for themselves (Reynolds and Gross, 1990). These costs can lead to reduced fertility (as I demonstrated in Chapter 2), and negatively impact females. To moderate these costs, females can evolve strategies that maximize their own fitness during mate choice and help mitigate search costs (chapter 4), or preferences may be purged from the population as a result of natural selection.

Natural selection interacts with sexual selection as an ultimate driver of female preferences, which can shape the evolution of both male traits and female preferences. The impact of natural selection on sexually selected traits in males well explored, especially in the context of producing indicator traits which can advertise how well adapted a particular male is (see, for example Kodric-Brown and Brown 1984, Rowe and Houle 1996, Cotton et al 2004), as well as in the classic case of sexual and natural selection opposing each other (Andersson 1982). However, the interplay of natural selection and female preferences is equally important. The female counterpart to sexually selected male traits which increase mortality can be thought of as costly preferences that decrease a female's fitness through high search costs (eg. Pomiankowski et al 1991, Iwasa et al 1991). Just as natural selection can prevent the

evolution of male traits, or modulate their expression, it can also prevent or modulate female preferences, as I showed in my second chapter.

Natural selection can also shape female sensory systems in ways that males can later exploit (Ryan 1990). All animals evolve sensory systems and neurological pathways that allow them to sense their environments, forage for food, avoid danger, and perform numerous other tasks necessary for survival. However, females use these same sensory systems to choose mates. Males, in turn, can develop traits that exploit female senses (Fuller et al. 2005). Because their sensory systems are maintained via natural selection, these preferences won't be lost due to being costly, and linkage disequilibrium is unlikely to develop and alter preference strengths (as demonstrated in chapter 3). Further, when females live in heterogeneous environments, ecological adaptations can lead to functional preference polymorphisms (eg. for conspicuousness, Gray et al 2008, or audibility, Tobias et al. 2010). In this scenario, instead of restricting female preferences, natural selection acts to maintain them.

Each chapter incorporates natural selection as a potent force acting on female preferences. I examine the role of sexually selected preferences leading to natural selection against female preference, I consider how preferences arising through sensory bias can evolve, and I look at how females can balance the costs of mate searching with changes in their own condition to maximize fitness. Incorporating factors beyond the simple male trait, female preference pairs that have dominated models of sexual selection has allowed me to address a diverse set of topics and propose novel solutions



to the ongoing conundrum of the origins and maintenance of variation in female preferences, and their evolutionary consequences.

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## APPENDIX 2.1: $A_{p,0}$ EQUATIONS FOR A SINGLE PREFERENCE AND TRAIT

The relative fitness of female preference and male traits is:

$$W(X_p, X_{t^*}) = \frac{(1 - X_p)(1 - X_{t^*}) \phi_1}{Z_1} + \frac{(1 - X_p)X_{t^*} \phi_2}{Z_1} + \frac{X_p(1 - X_{t^*}) \phi_3}{Z_2} + \frac{X_p X_{t^*} \phi_4}{Z_2} \quad (\text{A1})$$

where  $X_p$  represents the presence of preference alleles in females;  $X_p = 1$  if a female has allele P, and 0 if she does not. Likewise,  $X_{t^*} = 1$  if a male has allele T, and 0 if he does not.  $z_i$  is the normalization for sexual selection (as described in equation 2).  $\phi_i$  is the fertility selection against male genotype  $i$  (see equation 3 in the text). For example, for an  $x_1$  individual (PT),  $X_p = 1$  and  $X_{t^*} = 1$ , and  $X_p, X_{t^*} = \frac{\phi_4}{Z_2}$ .

Equation (A1) can be used to calculate the  $a$  terms present in equation (4) in the text. To calculate the  $as$ , the fitness equation for a model (here, A1) is set equal to a generic equation for fitness in terms of  $as$  and  $Cs$ , and a function of the  $Xs$ . Terms are then matched to solve for  $a$  in the model under consideration. This procedure is described fully in appendix B of Kirkpatrick and Servedio (1999).

**APPENDIX 2.2:  $A_{P,0}$  EQUATIONS FOR A DIRECT SELECTION ON PREFERENCE AND TRAIT  
IN THE FOUR LOCUS MODEL**

The relative fitness of a female possessing a preference allele in the four locus model is:

$$W(X_{P_1}, X_{P_2}, X_{T_1}, X_{T_2}) = \tag{A2}$$

$$\begin{aligned} & \frac{(1-X_{P_1})(1-X_{P_2})(1-X_{T_1}^*)(1-X_{T_2}^*) p \alpha \phi_1}{Z_1} + \frac{(1-X_{P_1})(1-X_{P_2})(1-X_{T_1}^*)X_{T_2}^* \alpha \phi_2}{Z_1} + \\ & \frac{(1-X_{P_1})(1-X_{P_2})X_{T_1}^*(1-X_{T_2}^*) \alpha \phi_3}{Z_1} + \frac{(1-X_{P_1})(1-X_{P_2})X_{T_1}^*X_{T_2}^* \phi_4}{Z_1} + \\ & \frac{(1-X_{P_1})X_{P_2}(1-X_{T_1}^*)(1-X_{T_2}^*) \alpha \phi_1}{Z_2} + \frac{(1-X_{P_1})X_{P_2}(1-X_{T_1}^*)X_{T_2}^* \alpha \phi_2}{Z_2} + \\ & \frac{(1-X_{P_1})X_{P_2}X_{T_1}^*(1-X_{T_2}^*) \phi_3}{Z_2} + \frac{(1-X_{P_1})X_{P_2}X_{T_1}^*X_{T_2}^* \phi_4}{Z_2} + \\ & \frac{X_{P_1}(1-X_{P_2})(1-X_{T_1}^*)(1-X_{T_2}^*) \alpha \phi_1}{Z_3} + \frac{X_{P_1}(1-X_{P_2})(1-X_{T_1}^*)X_{T_2}^* \phi_2}{Z_3} + \\ & \frac{X_{P_1}(1-X_{P_2})X_{T_1}^*(1-X_{T_2}^*) \alpha \phi_3}{Z_3} + \frac{X_{P_1}(1-X_{P_2})X_{T_1}^*X_{T_2}^* \phi_4}{Z_3} + \frac{X_{P_1}X_{P_2}(1-X_{T_1}^*)(1-X_{T_2}^*) \phi_1}{Z_4} + \\ & \frac{X_{P_1}X_{P_2}(1-X_{T_1}^*)X_{T_2}^* \phi_2}{Z_4} + \frac{X_{P_1}X_{P_2}X_{T_1}^*(1-X_{T_2}^*) \phi_3}{Z_4} + \frac{X_{P_1}X_{P_2}X_{T_1}^*X_{T_2}^* \phi_4}{Z_4} \end{aligned}$$

As in appendix one,  $X_{P_i}$  represents the presence of preference alleles in females, where  $X_{P_i} = 0$  if a female has preference  $i$ , and 1 if she does not. Likewise,  $X_{T_i}^* = 0$  if a male has trait  $i$ , and 1 if he does not.  $Z_i$  is the normalization for sexual selection ( $Z_1, Z_2$ , and  $Z_3$  are described in table 2;  $Z_4=1$ ).  $\phi_i$  is the fertility selection against male genotype  $i$  (see equation 3 in the text). As with female preference, there are only four unique male

genotype combinations such that  $\phi_1$  is the discount for  $T_1T_2$  males,  $\phi_2$  is for  $T_1t_2$  males,  $\phi_3$  is for  $t_1T_2$  males, and  $\phi_4$  is the discount for  $t_1t_2$  males.

As in appendix 2.1, equation (A2) is used to calculate the  $\alpha$  terms present in equation (5) in the text. Because of the complexity of equation (A2), I applied a weak selection approximation to get a shorter, analytically tractable expression for  $\alpha_{P,0}$ : I assumed that costs were low, preferences weak, and linkage disequilibrium small (confirmed via simulations), and performed a Taylor series expansion of  $\alpha_{P,0}$ . This method yielded equation (8), a considerably shorter expression for direct selection on preferences. To confirm the validity of the weak selection approximation, I compared it to the original expression and confirmed that, as  $\alpha$ ,  $\gamma$ , and  $D_{i,j}$  decreased, the two expressions converged. For the sake of comparison to (6), the equation used in figure (3) is the original formulation of  $\alpha_{P,0}$ , not the weak selection approximation.

### APPENDIX 3.1: DETAILS OF THE NUMERICAL STUDY AND SIMULATION

**Parameters used in numerical study:** To calculate the expected rewards and mate quality thresholds for each of the policies examined in figures 1 and 2 we used the following parameters:

**Number of States:**  $N_s = N_q = 24$ .

**Male Trait Distribution:** Normal distribution with  $\mu = 12.5$  and  $\sigma = 4.1667$ , discretized into 24 states.

**Transition Matrix for Random Walk:**  $p_{1,1} = p_{24,24} = 0.9, p_{1,2} = p_{24,23} = 0.1$ ; otherwise,

$$p_{i,j} = \begin{cases} 0.1, & \text{if } j = i - 1 \\ 0.8, & \text{if } j = i \\ 0.1, & \text{if } j = i + 1 \\ 0, & \text{otherwise.} \end{cases}$$

**Biased Random Walk:**  $p_{1,1} = .95, p_{24,24} = 0.85, p_{1,2} = 0.05$ , and  $p_{24,23} = 0.15$ ;

otherwise,

$$p_{i,j} = \begin{cases} 0.15, & \text{if } j = i - 1 \\ 0.8, & \text{if } j = i \\ 0.05, & \text{if } j = i + 1 \\ 0, & \text{otherwise.} \end{cases}$$

**Random Transitions:** In this case, all states are equally likely, such that  $p_{i,j} = \frac{1}{n_s}$  for all

$i, j$ . In this case,  $p_{i,j} = 0.0417$  for all  $i, j$ .

**Search Costs:** See Table A1 for values used for  $C$ .

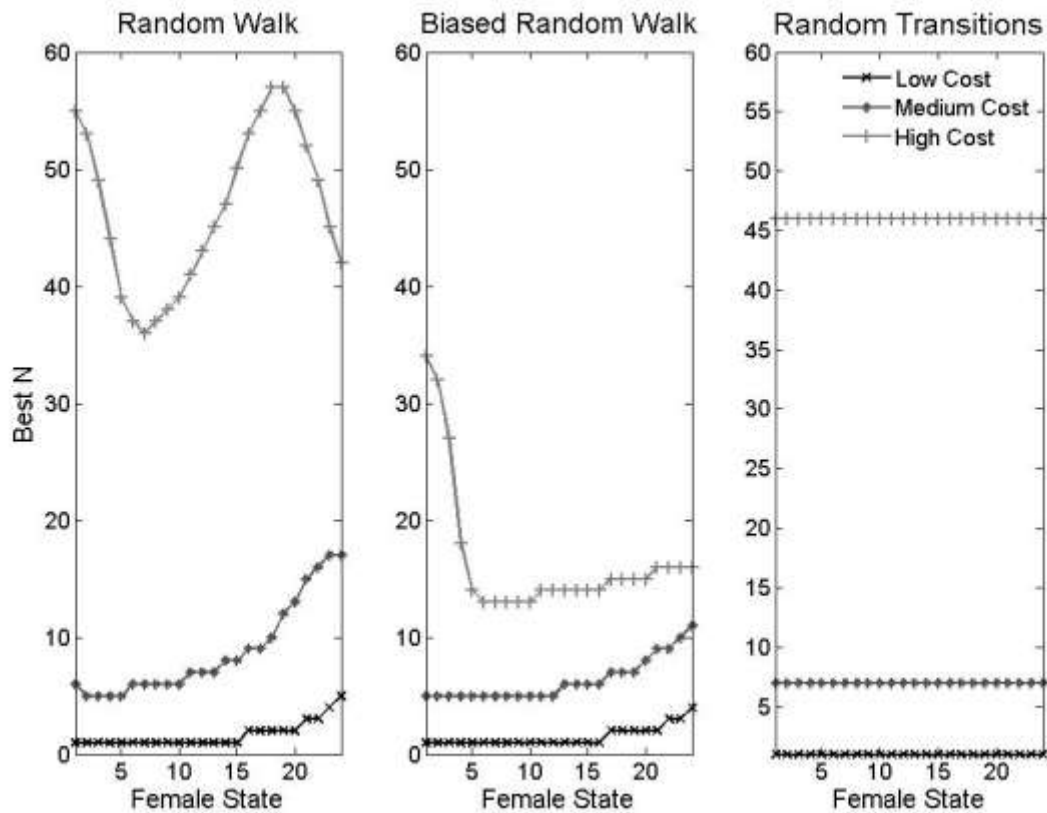
**Table A3.1.** Search costs used in numerical experiments

<b>Condition</b>	<b>Low Cost</b>	<b>Medium Cost</b>	<b>High Cost</b>
1	0.0200	0.2000	2.0000
2	0.0192	0.1917	1.9167
3	0.0183	0.1833	1.8333
4	0.0175	0.1750	1.7500
5	0.0167	0.1667	1.6667
6	0.0158	0.1583	1.5833
7	0.015	0.1500	1.5000
8	0.0142	0.1417	1.4167
9	0.0133	0.1333	1.3333
10	0.0125	0.1250	1.2500
11	0.0117	0.1167	1.1667
12	0.0108	0.1083	1.0833
13	0.0100	0.1000	1.0000
14	0.0092	0.0917	0.9167
15	0.0083	0.0833	0.8333
16	0.0075	0.075	0.7500
17	0.0067	0.0667	0.6667
18	0.0058	0.0583	0.5833
19	0.0050	0.0500	0.5000
20	0.0042	0.0417	0.4167
21	0.0033	0.0333	0.3333
22	0.0025	0.0250	0.2500
23	0.0017	0.0167	0.1667
24	0.0008	0.0083	0.0833



**Number of Males Sampled in Best-of-N:** We calculated the  $n$  with the largest expected reward for each female state and for each combination of search costs and transitions.

These values are shown in Figure A1.



**Figure A3.1:**  $n$  values used in numerical experiments. We iteratively calculated the  $n$  with the highest expected reward for each initial female condition (on the  $x$  axis, from 0--24), and combination of transition matrix and search costs. This figure plots the the best  $n$  for each combination, which was then used in the presentation of the results of the best-of- $n$  policy in

**Reward Function:** For the figures presented in the policy comparison section (Figures 1

and 2),  $G(s, q) = 3.5355 \sqrt{(s - 0.5) \frac{25}{24} + (q - 0.5) \frac{25}{24}}$ . We also tested other reward functions, and they produced results consistent with those presented.

### **Details of the simulations with incomplete information.**

Each simulation was initialized with 10000 males and 10000 females, each of which was assigned a fitness value from a discretized normal distribution with a mean of 12.5, and a standard deviation of 4.1667. Individuals were separated into 24 equally sized bins, each of which contained  $1/4$  of a standard deviation: an individual in bin 1 had a fitness value 3 standard deviations below the mean, bin 2 had a fitness 2.75 standard deviations from the mean, and so on. We used the same costs and reward function as described above, and used the biased random walk described in that section.

To model imperfect information, males were assigned perceived fitness values, based on how well a female was able to gauge fitness in a given simulation. For a simulation of mate choice with poor information about male quality, males had only three perceived fitness values, which were the weighted average of the fitness of males in the bottom, middle, and top third of fitness values respectively. For intermediate information, females were able to perceive 6 male states, and with good information females could observe 12 male states. Under perfect information, females could observe all 24 male states.

Female mate choice thresholds were calculated offline, using the optimal policy as calculated using the value iteration algorithm with  $\epsilon = 10^{-4}$ . In calculating this

policy,  $Q$  was the set of observed male states, and  $f(q)$  was equal to the observable pmf of  $Q$ . For example, with poor information, a female believed that males had 3 possible conditions and were distributed such that approximately 16% of males were in high or low condition and 68% were in medium condition.

To simulate mate choice, each female drew a mate randomly from the population. If the male's condition was greater than or equal to her threshold for mating, she selected that male as her mate; otherwise, she chose to search again. When a female decided to continue her search, she paid a search cost relative to her fitness ( $c(s)$ ) and her fitness transitioned based upon the probabilities described by  $P$ . Females continued to search until they either selected a mate or their total search costs exceeded their condition (i.e., they died before choosing a mate).

To estimate the true reward with imperfect mate choice, monte carlo simulations were used, wherein each simulation (low, medium, high, and perfect information) was run 10000 times. The average reward over the 10000 runs was calculated and is presented in figure 3.

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