E-Article

# Indiscriminate Mating and the Coevolution of Sex Discrimination and Sexual Signals

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ABSTRACT: The presence of same-sex sexual behavior across the animal kingdom is often viewed as unexpected. One explanation for its prevalence in some taxa is indiscriminate mating—a strategy wherein an individual does not attempt to determine the sex of its potential partner before attempting copulation. Indiscriminate mating has been argued to be the ancestral mode of sexual reproduction and can also be an optimal strategy given search costs of choosiness. Less attention has been paid to the fact that sex discrimination requires not just the attempt to differentiate between the sexes but also some discernible difference (a signal or cue) that can be detected. To address this, we extend models of mating behavior to consider the coevolution of sex discrimination and sexual signals. We find that under a wide range of parameters, including some with relatively minor costs, indiscriminate mating and the absence of sexual signals will be an evolutionary end point. Furthermore, the absence of both sex discrimination and sexual signals is always evolutionarily stable. These results suggest that an observable difference between the sexes likely arose as a by-product of the evolution of different sexes, allowing discrimination to evolve.

*Keywords:* indiscriminate mating, mate choice, same-sex sexual behavior, sexual selection.

## Introduction

Evidence that same-sex sexual behavior (SSB) is widespread throughout the animal kingdom continues to accumulate. SSB has been observed in mammals (Vasey 1995, 2002; Vasey and Jiskoot 2010; Furuichi et al. 2014; Sugita 2016), birds (Lombardo et al. 1994; Zuk 2006; MacFarlane et al. 2007, 2010; Young et al. 2008), insects (Van Gossum et al. 2005; Maklakov and Bonduriansky 2009; Hoskins et al. 2015), mollusks (Ambrogio and Pechenik 2008; Hoving et al. 2012; Hoving et al. 2019), echinoderms (Young et al. 1992; Slattery and Bosch 1993; McCarthy and Young 2002), amphibians (Marco and Lizana 2002), and reptiles (Shine et al. 2001). Because same-sex matings require energy expenditure but cannot produce offspring, SSB is often referred to as an evolutionary conundrum (Levan et al. 2009; Scharf and Martin 2013).

Nevertheless, there are many non-mutually-exclusive explanations for SSB (Bailey and Zuk 2009). It is important to distinguish between SSB (i.e., any perceived sexual behavior between members of the same sex) and same-sex sexual attraction (i.e., mating preferentially with one's own sex). Evolutionary explanations for same-sex sexual attraction include non-Mendelian genetic effects, overdominance, and sexually antagonistic selection (Camperio-Ciani et al. 2004; Gavrilets and Rice 2006; Camperio Ciani et al. 2008), social benefits (de Waal 1995; Mann 2006; Vasey et al. 2010), and nongenetic inheritance (Rice et al. 2012; Blanchard 2018; Gavrilets et al. 2018). SSB may also occur in the absence of same-sex sexual attraction (Bailey et al. 2013). For example, SSB may result from aggression against rivals (Hilde and Roden 2006; Preston-Mafham 2006; Kureck et al. 2011; Lane et al. 2016) or may provide a means for extracopulatory insemination (Levan et al. 2009).

A common explanation for SSB is the absence of perfect sex discrimination, such that individuals either attempt matings without determining the sex of their partner or discrimination occurs with errors (the mistaken identity hypothesis; Bailey and French 2012; Macchiano et al. 2018; Sales et al. 2018). This proximate explanation for SSB has a number of potential ultimate causes that all posit that discrimination carries a cost that maintains some degree of SSB, such as a trade-off between number of matings and discrimination (Vasey et al. 2008; Logue et al. 2009; Han and Brooks 2015) or a survival, fecundity, or gamete production cost to discrimination (Parker 2014; Lerch and

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Servedio 2021). Such costs to discrimination can result in a reproductive strategy of indiscriminate mating (i.e., attempting matings without first determining the sex of one's partner). Indiscriminate mating is often attributed to low costs to mating and high costs of missing a mating (Marco and Lizana 2002; McCarthy and Young 2002; Hoving et al. 2012; Monk et al. 2019; Lerch and Servedio 2021).

The broad phylogenetic distribution of species that may mate indiscriminately has led some to argue that indiscriminate mating is a parsimonious ancestral condition for organisms capable of sexual behavior (Monk et al. 2019). Others have challenged the importance of ancestral indiscriminate mating to contemporary SSB, arguing that indiscriminate mating should still be selected against and lost if it is costly (Dickins and Rahman 2020). In other words, explanations are needed for why indiscriminate mating can be maintained through evolutionary time (Clive et al. 2020). Thus, studies are needed to determine what conditions may facilitate the evolution or maintenance of indiscriminate mating.

The conditions favoring indiscriminate mating have seldom been addressed. SSB often appears as a behaviorally plastic strategy in males and is more likely in males that are less experienced (Bailey et al. 2013) or are housed in a male-biased sex ratio (Han and Brooks 2015; Martin et al. 2015; Macchiano et al. 2018). However, the occasional occurrence of SSB due to plasticity is different from the stable persistence of indiscriminate mating through evolutionary time. Insights from experimental evolution in the flour beetle (*Tribolium castaneum*) suggest that a highly skewed female-biased, as opposed to male-biased, sex ratio (9 : 1) may favor the evolution of indiscriminate mating in males (Sales et al. 2018), since males that mate indiscriminately will still most likely mate with females. However, the role of other traits, such as mortality rates, sexual dimorphism, and resource availability (energy budgets), have not been addressed. The evolution of sex discrimination has also been explored in two recent theoretical models. First, Parker (2014) considers a trade-off between mobility and gamete investment in a model that determines whether sex discrimination ("female targeting") will evolve from an indiscriminate mating strategy in a mostly sessile species with external reproduction. Second, Lerch and Servedio (2021) consider a more general case, which includes a search cost to sex discrimination and imperfect signals from the opposite sex, to determine whether indiscriminate mating is ever the optimal strategy. Both of these models find that indiscriminate mating may evolve under a broad range of conditions.

An important component is missing from these models: coevolutionary dynamics. More specifically, the fact that sex discrimination requires some identifying feature of the opposite sex (with which it must coevolve) has been neglected despite the fact that sex recognition (and the resulting behavioral responses) relies on both the presence of sex-specific signals or cues and the chooser's neurological response to these signals (Fernández et al. 2010; Harvanek et al. 2017; Flintham et al. 2018). Furthermore, whether the initial presence or absence of signals or the ability to discriminate has any influence on evolutionary outcomes remains unexplored, but it is of interest given that the likelihood of ancestral indiscriminate mating has been stressed (Monk et al. 2019). This evokes the question of how signals that convey information about an individual's sex arose to be used by potential discriminators in the first place. Finally, imperfect signals of sexual identity (Lerch and Servedio 2021) and the ability to physically move toward the opposite sex (Parker 2014) are known to be important for the evolution of indiscriminate mating.

For these reasons, to determine whether indiscriminate mating is ever likely to be selected for in nature, we need to evaluate whether it can persist with freely evolving signals. Indeed, one could imagine that indiscriminate mating may be lost as a result of the coevolution of discrimination and signaling in a process analogous to Fisher's model of sexual selection (Fisher 1930). To assess this possibility, we explicitly consider the coevolution of sex discrimination and sexual signals. We find that whenever there is any selective cost to both sex discrimination and sexual signaling, the absence of discrimination and signaling is a stable equilibrium. This suggests that for discrimination and sexual dimorphism to have evolved, one arose as a by-product of the evolution of separate sexes.

## Model

### *Model Overview*

We develop a two-locus, haploid, deterministic population-genetic model for the coevolution of sex discrimination and sexual signals. Note that our model does not consider social interactions/inheritance or same-sex attraction and thus is not relevant to human sexuality. Broadly following Lerch and Servedio (2021), our model considers a scenario with two sexes: the searching sex and the targeted sex. The searching sex actively seeks out mates but suffers an additional search cost (to either viability or fecundity) whenever it attempts to discriminate the sex of potential partners. Each member of the searching sex has equal reproductive effort at each time step but not necessarily equal reproductive success because of the aforementioned search cost and the payment of different opportunity costs depending on the amount of reproductive effort spent on members of the same sex. Depending on their genotype, members of the targeted sex can provide some signal of their sex that gives members of the searching sex an opportunity to successfully

identify them as a target when attempting sex discrimination. This signal is also assumed to come with a cost (although we can set this cost equal to zero to consider cost-free cues). Thus, sexual selection favors both sex discrimination and sexual signaling in our model, whereas natural selection opposes both. We explore two model variants for these costs below.

### *Model Development*

The model assumes overlapping generations (to consider the effect of nonselective mortality; Lerch and Servedio 2021) and thus tracks numbers of individuals instead of frequencies within a single time step. We normalize our variables to sum to 1 at census so they can be treated as frequencies at this point in the life cycle. We note that similar models could be developed with nonoverlapping generations (Otto et al. 2008). The first locus, A, controls sex discrimination and is expressed only in the searching sex. The second locus, S, controls sexual signaling and is expressed only in the targeted sex. Members of the searching sex carrying the $A_i$ allele have discrimination strength $\alpha_i \geq 0$, and members of the targeted sex carrying the $S_j$ allele display a sexual signal with strength $0 \leq \mathcal{s}_j \leq 1$. With a signal of maximal strength, $\mathcal{s}_j = 1$, discrimination success is restricted only by the limitations of the discrimination attempt, whereas a signal with strength $\mathcal{s}_j = 0$ cannot be identified irrespective of discrimination strength. Specifically, the product $\alpha_i \mathcal{s}_j$ represents how much more mating effort a searching-sex individual with the $A_i$ allele spends on a targeted-sex individual with the $S_j$ allele compared with an individual with no signal of sexual identity (either another searching-sex individual or a targeted-sex individual with $\mathcal{s}_j = 0$), given that they encounter one of each. We consider two alleles at each locus, so there are four possible genotypes in each sex. We denote the frequency of genotypes $A_1S_1$, $A_1S_2$, $A_2S_1$, and $A_2S_2$ at the time of zygotes as $x_1^m$, $x_2^m$, $x_3^m$, and $x_4^m$, respectively, where the superscript $m$ denotes the sex ($m = \mathrm{s}$ for the searching sex and $m = \mathrm{t}$ for the targeted sex). Throughout we will use the functions $k(i)$ and $l(j)$ to map genotypes to phenotypes for the searching and targeted sex, respectively. Namely,

$$k(i) = \begin{cases} 1, & i = 1,2; \\ 2, & i = 3,4; \end{cases} \tag{1a}$$

$$l(j) = \begin{cases} 1, & j = 1,3; \\ 2, & j = 2,4. \end{cases} \tag{1b}$$

In words, $k(i) = 1$ means that genotype $i$ is expressed as the $A_1$ allele and $k(i) = 2$ means that genotype $i$ is expressed as the $A_2$ allele. The function $l$ at the S locus behaves analogously.

For completeness, we will provide general equations that assume that both sexes suffer both mortality and fecundity costs to discrimination and signaling, although we never consider mortality and fecundity costs in tandem in our analysis. The first step in the life cycle is mortality (viability selection). We denote the number of surviving individuals from each class using a prime (i.e., $x_i^{m'}$). A proportion $d$ of individuals of each sex with each genotype die as a result of background mortality. The number of surviving individuals of each genotype $i$ is

$$x_i^{m'} = \begin{cases} (1-d)\left(1 - \dfrac{c_v \alpha_{k(i)}}{1 + c_v \alpha_{k(i)}}\right) x_i^m, & m = \mathrm{s}; \\ (1-d)(1 - p_v \mathcal{s}_{l(i)}) x_i^m, & m = \mathrm{t}. \end{cases} \tag{2}$$

The term $c_v \alpha_{k(i)}/(1 + c_v \alpha_{k(i)})$ is the total probability of mortality induced by discrimination; we chose this function because it is 0 with no discrimination ($\alpha_i = 0$) and saturates at 1 as $\alpha_i$ goes to infinity. Saturation occurs more rapidly for larger $c_v \geq 0$, and thus $c_v$ can be interpreted as the mortality (viability) cost to discrimination. Similarly, $p_v \mathcal{s}_{l(i)}$ is the probability of mortality induced by signaling, and thus $0 \leq p_v \leq 1$ is the mortality cost of signaling. With nonzero costs, equation (2) implies that both discrimination and signaling are disfavored by natural selection and that the sex ratio will not be balanced for most parameters.

Following mortality, we assume that each member of the searching sex expends equal effort attempting to mate with conspecifics. As mentioned previously, a member of the searching sex with the $A_i$ allele expends $\alpha_i \mathcal{s}_j$ times more effort attempting to mate with a target with the $S_j$ allele than a conspecific with no signal of sexual identity (either a target with $\mathcal{s}_j = 0$ or any searching-sex individual, since the S locus is not expressed in searchers). Thus, the relative proportion of mating effort that members of the searching sex with genotype $i$ spend on members of the targeted sex with genotype $j$, $M_{ij}$, is

$$M_{ij} = \frac{(1 + \alpha_{k(i)} \mathcal{s}_{l(j)}) x_i^{s'} x_j^{t'}}{z_i}, \tag{3}$$

where

$$z_i = (1 + \alpha_{k(i)\mathcal{s}_1})(x_1^{t'} + x_3^{t'}) + (1 + \alpha_{k(i)\mathcal{s}_2})(x_2^{t'} + x_4^{t'}) + \sum_{j=1}^{4} x_j^{s'} \tag{4}$$

is the normalization factor to ensure all members of the searching sex have equal mating effort (analogous to courtship effort in models of male mate choice; Servedio and Lande 2006). Here, 1 is the effort given regardless of attempted discrimination/sexual signals, and the product $\alpha_i \mathcal{s}_j$ is additional effort due to successful discrimination. Vital to the interpretation of our study, same-sex matings

can also occur between members of the searching sex as a result of indiscriminate mating (seen as the sum at the end of eq. [4]). Such matings carry the opportunity cost that individuals engaging in them spend less effort attempting matings that can produce offspring. This opportunity cost in the searching sex, as well as the increase in received mating effort with stronger signals in the targeted sex, means that both stronger discrimination and stronger signals are favored by sexual selection. Equations (3) and (4) result in same-sex matings occurring more when the sex ratio is biased toward the searching sex or the sexual signal is weaker, but allele frequencies at the discrimination locus A do not change the likelihood that any one searcher engages in a same-sex mating.

We assume that reproductive success of all pairs is directly proportional to mating effort, with the exception that effort spent attempting to mate with other searching-sex individuals does not produce offspring. Thus, the reproductive output between members of the searching sex with genotype $i$ and members of the targeted sex with genotype $j$, $F_{ij}$, is

$$F_{ij} = \left(1 - \frac{c_f \alpha_{k(i)}}{1 + c_f \alpha_{k(i)}}\right)(1 - p_f \mathcal{S}_{l(j)})M_{ij}. \quad (5)$$

The first two parentheses in equation (5) give the fecundity cost to discrimination and signaling, where $c_f$ and $p_f$ are the cost (i.e., control the reduction in the number of offspring produced by each pair with the same functions used as in eq. [2]). Mated pairs between the opposite sexes produce offspring according to the standard assumptions of haploid genetics with free recombination between the two loci. We scale the number of offspring produced to exactly equal the number of deaths from the previous generation, so that $1 - \sum_{i,m} x_i^{m'}$ (eq. [2]) offspring are produced. Offspring are produced with an equal sex ratio and are added to the surviving adults. This returns us to the fixed population size, so that the $x_i^m$ can again be interpreted as genotype frequencies at the start of the next cycle. This set of assumptions for mating and reproduction produces results qualitatively consistent with the alternative formulation in Lerch and Servedio (2021) when we do not allow signals to evolve (sec. S1 of the supplemental PDF).

### *Model Analysis*

We ask two main questions: (1) how does the initial frequency of sexual signals and discrimination affect their coevolutionary dynamics and (2) what levels of discrimination and signaling are evolutionarily stable? To answer these questions, we explore three analyses. The first two assess short-term evolutionary dynamics to determine how the coevolution of discrimination and sexual signals depends on their initial frequencies (question 1).

First, we determined whether coevolutionary dynamics can drive the evolution of sex discrimination and sexual signals from their collective absence. We performed a linear stability analysis about the equilibrium of indiscriminate mating and no signaling ($\alpha_1 = \mathcal{S}_1 = 0$ and the $A_1$ and $S_1$ alleles are fixed; see sec. S2 of the supplemental PDF for a description of change of variables) to determine whether discriminate mating and sexual signaling can invade (evolve).

Second, because bistability is common in our model, we used numerical analyses to find the basins of attraction for indiscriminate mating with no signaling ($\alpha_1 = \mathcal{S}_1 = 0$) and strong discrimination with perfect signaling ($\alpha_1 = 10$; $\mathcal{S}_2 = 1$, corresponding to discriminators being 10 times more likely to attempt to mate with signaling targets than other conspecifics when presented with one of each) when these strategies are competing against one another. We chose these trait values for strong discrimination and signals as a simple initial case, which we relax in multiple ways below. Specifically, we fixed the model parameters and used a range from 0 to 1 for the initial frequencies of the discrimination and signaling alleles $A_2$ and $S_2$. We then iterated the model until it reached an equilibrium. We determined that an equilibrium was reached once none of the genotype frequencies changed by more than $10^{-6}$ between time steps.

Finally, we used an invasion analysis to determine the evolutionary stability of coevolutionary strategies (question 2). We use the convention of $\alpha_1$ and $\mathcal{S}_1$ as the resident, with initial conditions (first residents) of $\alpha_1 = \alpha_0$ and $\mathcal{S}_1 = \mathcal{S}_0$. In section S2 of the supplemental PDF, we derive the invasion fitness assuming that the population is nearly monomorphic for the resident strategy and that the phenotypic difference between the invader and resident is small. We use these expressions for invasion fitness to find the (co)evolutionary stable strategy (which we refer to as the evolutionarily stable strategy [ESS]). In particular, we assume that evolutionary changes occur at a rate proportional to invasion fitness and used the resulting set of differential equations to describe changes through evolutionary time (an approach analogous to Abrams et al. 1993; Dieckmann and Law 1996; Champagnat et al. 2002; Vincent and Brown 2005; see sec. S2 of the supplemental PDF for details). We supported this analysis by confirming that polymorphism is rarely maintained (3% of parameter combinations for discrimination and <1% of parameter combinations for signaling) by checking for mutual invasibility at 5,000 randomly generated parameter combinations (using $d, \mathcal{S}_1, \mathcal{S}_2 \in (0, 1)$; $c \in (0, 0.05)$; $p \in (0, 0.3)$; $\alpha_1, \alpha_2 \in (0, 10)$; Lerch and Servedio 2022). All analyses were carried out using Wolfram Mathematica (Wolfram Research 2019).

## Results

### *Costs to Survival*

We first present results from the model variant with mortality costs but not fecundity costs (i.e., $c_f = p_f = 0$).

*Stability of Indiscriminate Mating and the Absence of Sexual Signals.* In the following analysis, we show that sex discrimination and sexual signals of any strength cannot evolve in a resident population of indiscriminate mating and no signaling under coevolutionary dynamics. The technical details of this subsection can be skipped without missing the biological conclusions. We computed the Jacobian matrix for this system, $\mathbf{J}$, and evaluated it at the indiscriminate mating equilibrium (i.e., $\alpha_1 = \mathcal{s}_1 = 0$, $A_1$ and $S_1$ fixed—thus no linkage disequilibrium—and equal sex ratio; denoted by the shorthand $\mathbf{J}|_0$). Although this can be done analytically, closed-form expressions for the eigenvalues cannot be obtained. We can, however, get meaningful upper bounds on the system's spectral radius (the largest magnitude of an eigenvalue), $\rho(\mathbf{J}|_0)$, using the fact that $\rho(\mathbf{M}) \leq \|\mathbf{M}\|_\infty$ for any square matrix $\mathbf{M}$. Here, $\|\mathbf{M}\|_\infty$ denotes the infinity norm of $\mathbf{M}$ (i.e., the maximum absolute row sum of $\mathbf{M}$). We first assume that the costs $c_v$ and $p_v$ are small. Taking the limit as $c_v$ and $p_v$ go to 0, taking the absolute value of each element, and computing row sums, one of the rows of $\mathbf{J}|_0$ sums to $1 - d/2$, four of its rows sum to $1 - d$, and two of its rows sum to 1. For the first five rows, this implies that we can always choose $c_v$ and $p_v$ to be small enough so that these row sums are arbitrarily close to $1 - d$ or $1 - d/2$ and are thus less than 1. More analysis is needed for the last two columns, as it is unclear whether they approach 1 from above or below. Before imposing low costs, we can rewrite the sums of the absolute values of each element for the final two rows as $1 - dp_v\mathcal{s}_2/2$ and $(1 + c_v\alpha_2(1 - d/2))/(1 + c_v\alpha_2)$, which are both always less than 1 for biologically attainable parameters. Thus, we have that $\rho(\mathbf{M}) \leq \|\mathbf{M}\|_\infty < 1$. That is, indiscriminate mating is always locally stable given low costs. This means that discrimination and signaling will not evolve in a population in which both traits are initially absent. Note that although we assume low costs for most of this analysis, logically one would expect that higher values of $c_v$ and $p_v$ should only make it harder for discrimination and signaling to evolve. Furthermore, we also show in section S2 of the supplemental PDF that neither discrimination nor signaling can invade by mutations of small effect in the absence of sex discrimination and sexual signals.

*Dependence on Initial State.* Relaxing the approximation of low costs (or mutations of small effect), we next investigate the evolutionary dynamics between the strategies of no discrimination ($\alpha_1 = 0$), strong discrimination ($\alpha_2 = 10$), no signals ($\mathcal{s}_1 = 0$), and maximal signals ($\mathcal{s}_2 = 1$). We find that the majority of initial conditions approach either the loss of all discrimination and signals or strong discrimination and maximal signaling (fig. 1). Stable polymorphism is sometimes observed (fig. 1, white regions) but is rare across randomly chosen parameters (see end of "Model Analysis," and note that fig. 1 deliberately uses parameters that show transitions between the regimes and thus are not randomly chosen). Importantly, we find that the complete lack of discrimination and signaling always has a nontrivial basin of attraction (because sexual selection favoring these traits vanishes in this limit and costs are present; fig. 1, green region in bottom left of each panel). This means that if the population lacks sufficient discrimination or signals initially, indiscriminate mating will evolve when discrimination or signals are costly. Many (but not all) parameter combinations display bistability, meaning that given sufficient discrimination and signals, they will evolve to fixation (fig. 1, purple regions). The sizes of these two basins of attraction vary considerably. Discriminate mating is favored by low costs to discrimination and signaling and high mortality (fig. 1; analogous to the case of multiplicative mortality costs in Lerch and Servedio 2021).

An asymmetry naturally arises between the sexes: a greater initial frequency of signaling individuals versus discriminating individuals is needed to escape the basin of attraction for indiscriminate mating (fig. 1). Since the scales for the strengths of discrimination and of signaling are not analogous, this asymmetry cannot readily be interpreted. However, in part it can be accounted for by the targeted sex having greater variance in reproductive success, due to the assumption of equal mating effort by searchers (e.g., a single strongly signaling member of the targeted sex has the potential to mate with more discriminators than vice versa). A similar asymmetry exists in the effect of discrimination costs and signaling costs, with weaker costs to discrimination $c_v$ than costs to signaling $p_v$ being able to prevent sex discrimination and signals from evolving (i.e., costs to discrimination are more detrimental than costs to signaling; figs. S1–S3). An additional reason for the asymmetrical effects of these mortality costs is that stronger discrimination costs skew the sex ratio to be biased toward the targeted sex, whereas stronger signaling costs skew the sex ratio to be biased toward the searching sex (eq. [S1]). A sex ratio biased toward the searching sex favors discrimination, as more indiscriminate matings are with same-sex partners in this case (Lerch and Servedio 2021). Coevolutionary feedbacks mean that the sex ratio also affects whether sexual signals will evolve. Competing indiscriminate mating and no signals against weaker strategies for discrimination ($\alpha_2 = 1$) and signaling ($\mathcal{s}_2 = 0.5$) results in larger basins

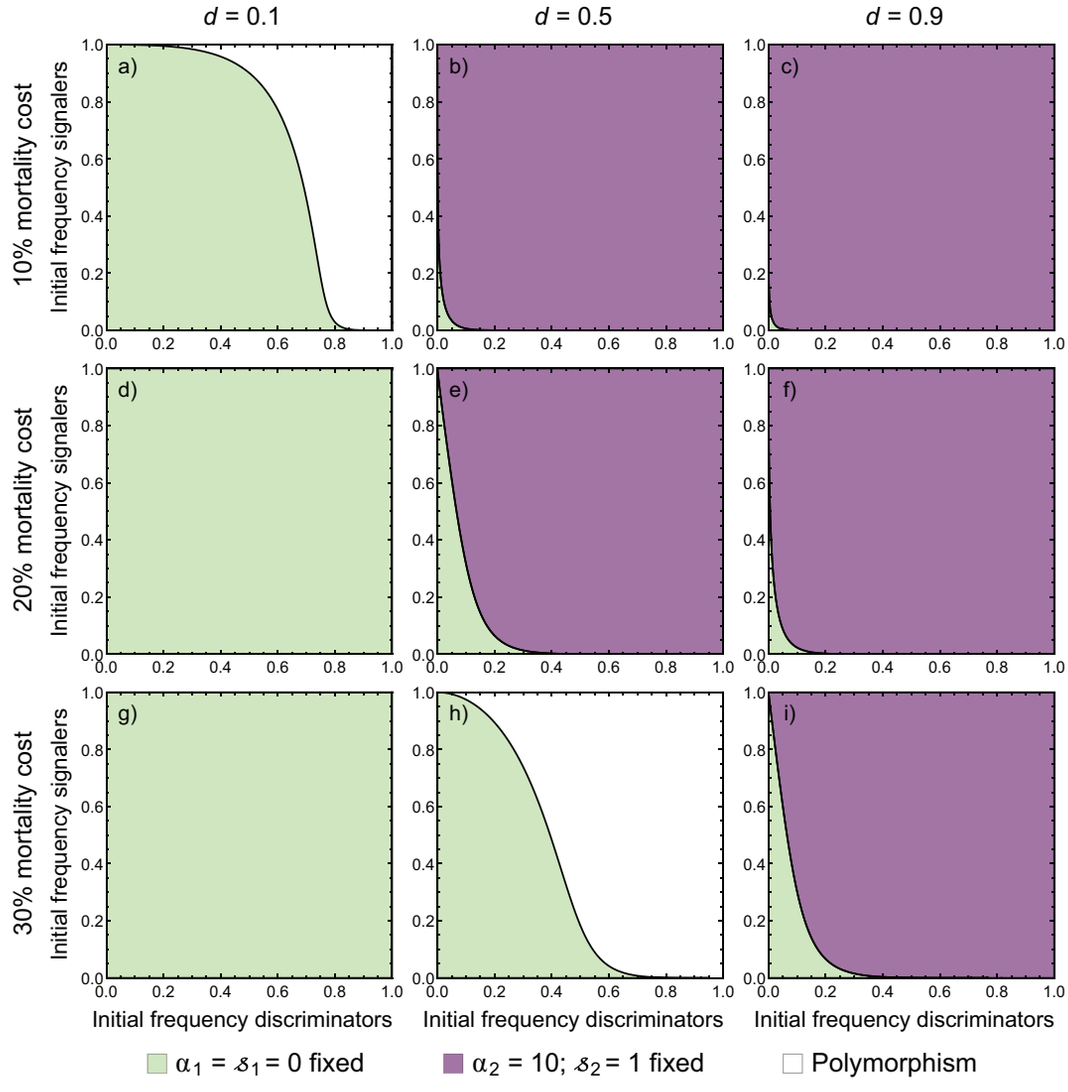


**Figure 1:** Basins of attraction for indiscriminate mating with no signaling ($\alpha_1 = \mathcal{S}_1 = 0$ fixes; green) and strong discrimination with perfect signals ($\alpha_2 = 10$; $\mathcal{S}_2 = 1$ fixes; purple) in the mortality cost model variant with initial frequency of discriminators ($a_2$) and signalers ($s_2$) on the horizontal and vertical axes, respectively, and costs ($c_v$ and $p_v$) increasing down rows within a column (reported as percent mortality) and mortality ($d$) increasing across columns within a row. Discriminate mating is most likely to evolve with high mortality, but there is a basin of attraction for indiscriminate mating and no signaling near $(0, 0)$ for each panel, showing that the analytical results hold with strong selection. Polymorphism can occur in conditions unfavorable to the evolution of discriminate mating. Parameters: for 10% cost, $c_v = 1/90$, $p_v = 0.1$; for 20% cost, $c_v = 1/40$, $p_v = 0.2$; for 30% cost, $c_v = 3/70$, $p_v = 0.3$. Bistability plots were made without fixed grid using RegionPlot in Mathematica (Wolfram Research 2019).

of attraction for indiscriminate mating and no signaling (fig. S4).

*Evolutionarily Stable Mating Strategies.* Although the analyses presented above give some sense of whether indiscriminate mating or discriminate mating is favored, they do not consider evolutionary stability. We use an invasion analysis (see sec. S2 of the supplemental PDF for details) to solve for a local ESS that is also convergent stable. Because of the bistability seen above, the stable strategies reached depend on the starting conditions. Since no discrimination and the absence of sexual signals is always stable, we use nonzero initial signaling strength to permit the possibility of nontrivial evolutionary end points. We find two qualitative outcomes for ESS: (1) completely indiscriminate mating ($\alpha_1 = 0$) and no signals of sexual identity ($\mathcal{S}_1 = 0$) or (2) discrimination ($\alpha_1 > 0$) and "perfect" signals of sexual identity ($s = 1$) as the ESS

(fig. 2). In the former case, the population mates indiscriminately, and the proportion of same-sex matings is given by the sex ratio (fig. S5*a*–S5*c*). In the latter case, the frequency of same-sex matings is limited by discrimination, and the resulting imperfect discrimination may lead to very little or very frequent SSB, depending on parameters (fig. S5*a*–S5*c*). Same-sex matings are common in most of parameter space, but when costs are low, there can be a considerable increase in relative reproductive effort spent on the targeted sex at equilibrium (fig. S5*d*–S5*f*; i.e., discrimination can be highly successful).

High mortality rates favor the evolution of discriminate mating (fig. 2). Intuitively, this can be understood as multiplicative mortality costs causing the net selective effect of costs to discrimination and signaling to be the lowest at high mortality (because each individual is already at high risk of nonselective mortality; Lerch and Servedio 2021). Unsurprisingly, we also find that weak costs to either discrimination $c_v$ or signals $p_v$ favor the evolution of discriminate mating (fig. 2). There are cases, however, where increasing the cost to signaling $p_v$ can drive the evolution of stronger discrimination (moving upward on fig. 2 can lead to darker purple). This occurs because increasing the cost to signaling $p_v$ relative to discrimination $c_v$ skews the sex ratio to have fewer members of the targeted sex, in turn favoring discrimination.

The ESS depends considerably on initial conditions. When the initial strength of signals $\mathcal{S}_0$ is higher, more of parameter space ends at the ESS with discrimination and signaling maintained (fig. 2). Put another way, discrimination and signaling can evolve in the face of higher costs when the initial amount of signaling in the population is higher. This occurs because when signaling is stronger ($\mathcal{S}_0$ is higher), higher discrimination is more likely to evolve quickly. Conversely, in the absence of discrimination ($\alpha_1 = 0$), signaling is always disfavored. This creates a "race" between discrimination becoming high enough that signaling is favored before signaling evolves to be so weak that discrimination is

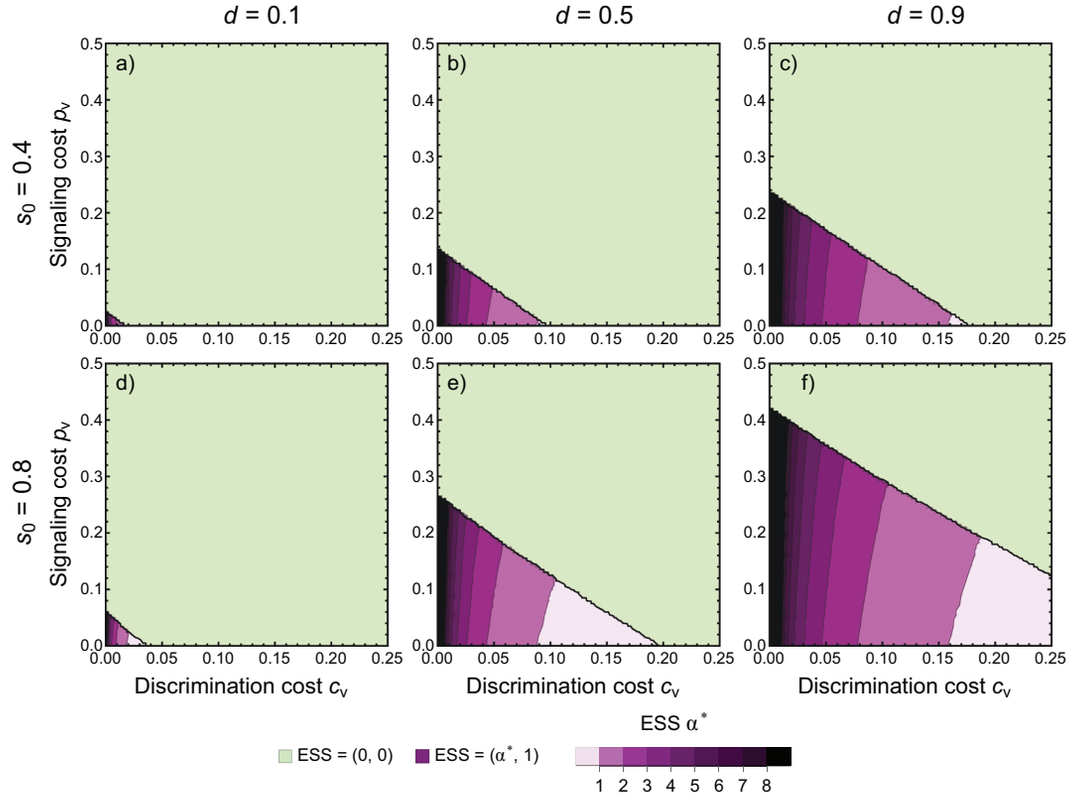


**Figure 2:** Evolutionarily stable strategy (ESS) in the model variant with mortality costs, with discrimination cost $c_v$ on the horizontal axes, signaling cost $p_v$ on the vertical axes, and mortality $d$ increasing across columns within a row. Initial residents were no discrimination $a_0 = 0$ and some signaling ($\mathcal{S}_0 = 0.4$ in the first row and $\mathcal{S}_0 = 0.8$ in the second row). Much of the parameter space has coevolutionary ESS of indiscriminate mating and no signals ("ESS $= (0, 0)$"; green [see key]). Parameters resulting in discriminate mating at the coevolutionary ESS have perfect signaling ($\mathcal{S}^* = 1$) with an intermediate value for discrimination $\alpha^*$ ("ESS $= (\alpha^*, 1)$"; purple). In this case, we show the value of the stable discrimination strategy $\alpha^*$ as the different shades of purple (see rightmost key below figure). Discriminate mating is most likely to be the ESS with high mortality and stronger initial signals.

selected against (fig. S6). Clearly, one way to bias this race in favor of discriminate mating is for there to be stronger signaling initially. Because initial discrimination is more valuable than initial signaling for the evolution of discriminate mating, using initial conditions of no initial signaling and initial discrimination results in more of parameter space maintaining discrimination and signaling at ESS (fig. S7).

### *Costs to Fecundity*

We next consider the case of a fecundity cost to discrimination but no costs to mortality (i.e., $c_v = p_v = 0$). Our general conclusions from the analyses with mortality costs hold, except that nonselective mortality $d$ does not affect the results with only a cost to fecundity.

*Stability of Indiscriminate Mating and the Absence of Sexual Signals.* Checking the stability of indiscriminate mating is now straightforward, as the sex ratio is fixed at 1 : 1. The eigenvalues at the indiscriminate mating equilibrium (with $\alpha_1 = \mathcal{s}_1 = 0$) can be found in closed form. Each is less than 1 in magnitude, meaning that indiscriminate mating is always a stable equilibrium and discrimination and signaling will not evolve from indiscriminate mating and no signals.

*Dependence on Initial State.* Again, we find that there is always a nontrivial basin of attraction for indiscriminate mating (fig. 3). With costs to fecundity, however, the sizes of the basins of attraction do not change noticeably with changing mortality rates (compare fig. 3 with fig. S8). The asymmetry between signaling and discrimination remains: more initial signalers than initial discriminators are required for discrimination and signaling to evolve. Since fecundity costs do not alter the sex ratio, the degree of the asymmetry in discrimination and signaling fecundity costs is smaller than with mortality costs, but discrimination costs are still more detrimental than signaling costs to the evolution of discrimination and signaling (fig. 3). Furthermore, fecundity costs are more likely to permit discrimination to evolve than are mortality costs. That is, an $x$% reduction in mortality is more costly to the evolution of discrimination than is an $x$% reduction in fecundity (note that fig. 1 and fig. 3 have different panels and axes, so care must be taken in visual comparison).

*Evolutionarily Stable Mating Strategies.* Consistent with the results from the analyses of the basins of attraction, a relatively larger region of parameter space has discrimination and signaling as the ESS when there are fecundity costs as opposed to mortality costs (fig. 4). There is still dependence on the initial conditions, as high initial signaling considerably expands the region where complete discrimination and signaling evolves (fig. 4*b*). The ESS is insensitive to changing mortality rates when costs are to fecundity rather than mortality (sec. S2 of the supplemental PDF).

## Discussion

Examination of the coevolution of both sex discrimination and sexual signals shows that any costs to survival or fecundity cause populations to retain an indiscriminate mating strategy if they do not discriminate or signal ancestrally. More specifically, we find that coevolutionary dynamics typically lead to positive feedback with either indiscriminate mating and the absence of sexual signals evolving or signals evolving to maximal strength while maintaining discrimination; the former strategy, in particular, is always a local attractor. Coevolutionary dynamics between indiscriminate mating and signals that facilitate discrimination can thus either promote or hinder the evolution of discrimination and signaling. The fact that neither discrimination nor signaling can evolve from their shared absence suggests that readily detectable differences between the sexes most likely arose as a by-product of the evolution of two sexes rather than for the initial function of sexual identification.

Our results are generally insensitive to whether costs are paid to mortality or fecundity. An exception is that high nonselective mortality rates $d$ favor discrimination with mortality costs, but nonselective mortality has no effect when costs are to fecundity. The role of nonselective mortality is analogous to that in Lerch and Servedio (2021), who additionally found that with additive mortality costs to discrimination (a model variant that we do not consider an analog to here) intermediate mortality favors sex discrimination. Overall, mortality costs are more likely to prevent the evolution of sex discrimination than are fecundity costs. Furthermore, discrimination costs are more likely to prevent the evolution of sex discrimination than are signaling costs, in part because sex ratios biased toward the searching sex generate stronger selection for sex discrimination (a result seen in experimental evolution; Sales et al. 2018).

In contrast, a number of studies have shown either that exposure to females decreases the incidence of male SSB or that male-biased sex ratios increase its prevalence (Bailey et al. 2013; Han and Brooks 2015; Martin et al. 2015; Macchiano et al. 2018). Since males are typically considered searchers in the context of SSB (Parker 2014; Han and Brooks 2015; Sales et al. 2018), ostensibly this stands at odds with our model and that of Lerch and Servedio (2021), which showed that male-biased sex ratios favor the evolution of discrimination in males. However, the studies that appear to conflict with the model are considering plastic rather than evolved responses.

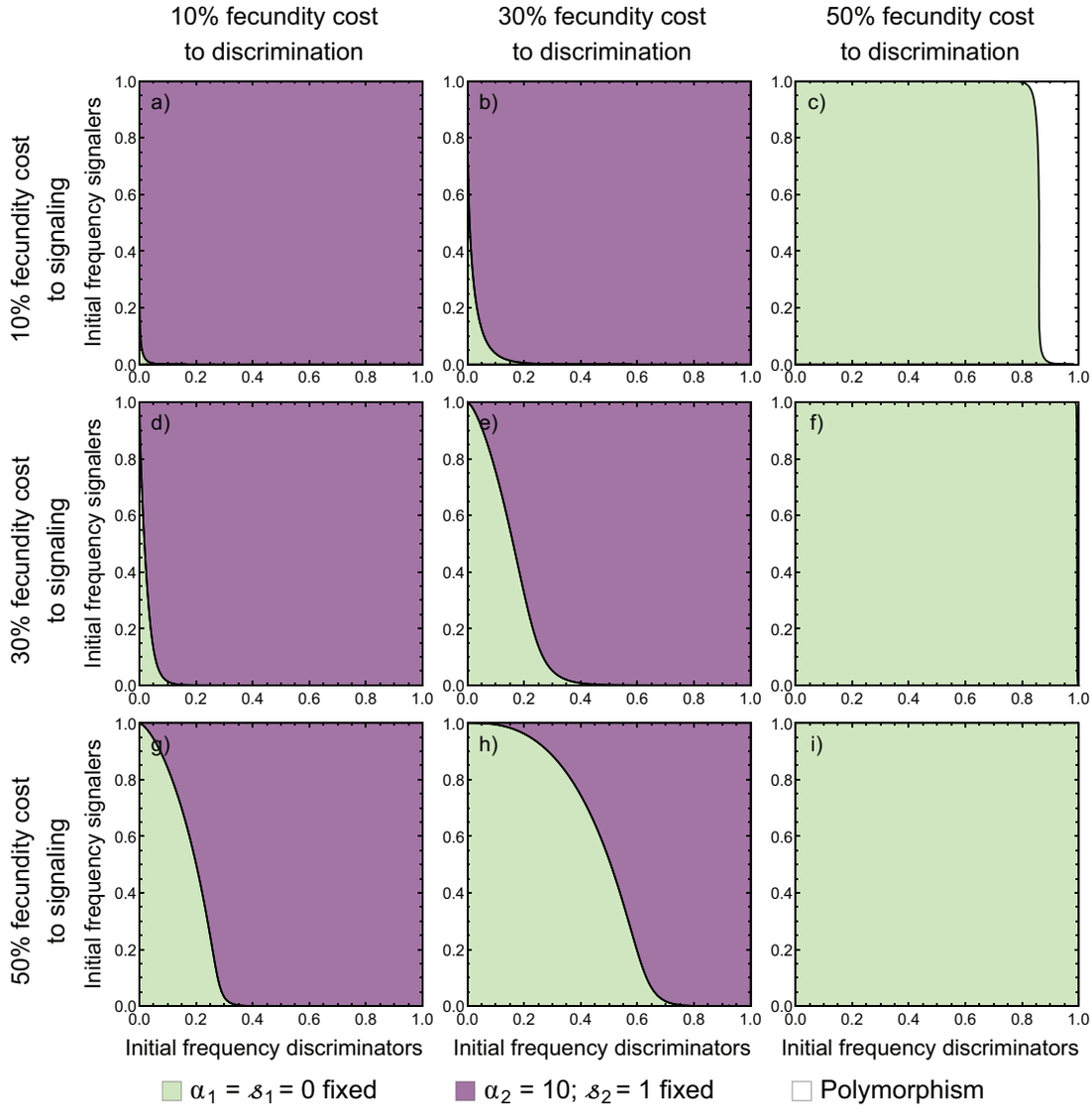


**Figure 3:** Basins of attraction for indiscriminate mating with no signaling ($\alpha_1 = \mathcal{S}_1 = 0$ fixes; green) and strong discrimination with perfect signals ($\alpha_2 = 10$; $\mathcal{S}_2 = 1$ fixes; purple) in the fecundity cost model variant with initial frequencies of $a_2$ and $s_2$ on the horizontal and vertical axes, respectively, and signaling costs ($p_i$) increasing down rows within a column and fecundity costs ($c_i$) increasing across columns within a row. Once again, we see that there is always a basin of attraction for indiscriminate mating and no signals near $(0, 0)$, and discrimination costs are more likely than signaling costs to prevent the evolution of discrimination and signaling. Mortality of $d = 0.9$ is used here but does not influence the results (see fig. S8). Parameters: for 10% cost, $c_f = 1/90$, $p_f = 0.1$; for 30% cost, $c_f = 3/70$, $p_f = 0.3$; for 50% cost, $c_f = 0.1$ , $p_f = 0.5$.

They suggest that temporal or spatial variation in conditions affecting the costs and benefits of discrimination and signaling (e.g., the sex ratio or population density) could favor displaying weak or no discrimination as a plastic response to the current conditions. Experimental evolution has confirmed our result that male-biased sex ratios result in the evolution of higher discrimination (Sales et al. 2018). More work is needed to connect our theoretical results with past empirical work on plasticity.

Since, as mentioned above, studies of SSB typically only consider male-male matings, it is natural to interpret the searching sex as males in connection with this work. However, this assignment of male and female roles in our model will not hold in all systems. Different evolutionary effects of the costs to signalers and discriminators arise in our model in part because the targeted sex has greater variance in reproductive success. Since in polygynous species males are expected to have higher variance in reproductive success,

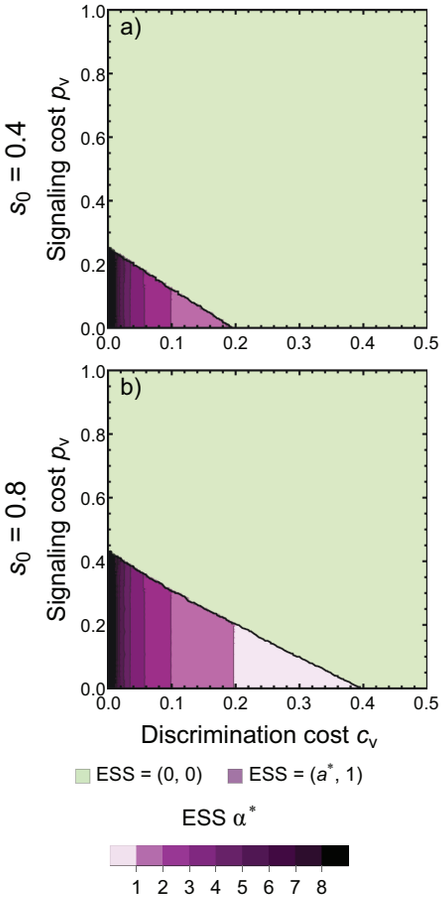


**Figure 4:** Evolutionarily stable strategy (ESS) in the model variant with fecundity costs, with discrimination cost $c_f$ on the horizontal axes and signaling cost $p_f$ on the vertical axes. Initial residents were no discrimination $\alpha_0 = 0$ and some signaling ($\mathcal{S}_0 = 0.4$ in the first row and $\mathcal{S}_0 = 0.8$ in the second row). Green indicates an ESS of indiscriminate mating and no signaling, and purple indicates perfect signaling with discrimination maintained in the population. Mortality of $d = 0.9$ is used here but does not influence the results (see sec. S2 of the supplemental PDF), and thus these panels can be compared with figure 2 for any value of mortality $d$ (note that the axes on these two graphs are different).

they would resemble the targeted sex rather than the searching sex in this regard. Notably, however, the general expectation that males have greater variance in reproductive success is less pronounced in broadcast spawners (often considered proxies for early sexually reproducing animals) than it is in species with internal fertilization (Levitan 2004, 2005; Evans and Lymbery 2020). Overall, the sex roles in our model depend on somewhat arbitrary assumptions and thus should not be treated as general predictions. Our focus has thus been on coevolutionary dynamics between discrimination and signaling (especially the dependence on initial conditions, such as the stability of indiscriminate mating and no signaling). We believe these conclusions will hold regardless of the specifics of sex roles in a given system.

A potentially interesting future avenue for exploring sex roles in our model would be to allow both sexes to signal or discriminate simultaneously. Nontrivial coevolutionary dynamics may result in this situation from the fact that the act of mating is costly in some species that engage in SSB (Fowler and Partridge 1989; Cordts and Partridge 1996; Kuijper et al. 2006; Maklakov and Bonduriansky 2009). For instance, the searching sex may benefit from signaling their sexual identity so that other searchers do not attempt to mate with them. If the searching sex provides such a signal, then there may be no selection on the targeted sex to signal their sexual identity because the absence of the signal will identify targeted-sex individuals. On the other hand, if having too many matings is costly to the targeted sex, then the targeted sex may actually evolve to conceal their sexual identity to prevent overmating (Rowe et al. 2005; Scharf and Martin 2013). This could be another path to indiscriminate mating persisting through evolutionary time even without search costs.

Our results have implications for the feasibility of the hypothesis that indiscriminate mating is the ancestral mode of sexual behavior (Parker 2014; Monk et al. 2019). Although indiscriminate mating may be more widespread than appreciated (Monk et al. 2019), sex discrimination seems to be common. Our model suggests that sex discrimination would be unlikely to be common if both indiscriminate mating and the absence of sexual signals were ancestral (since this is always a local evolutionary attractor). As such, our results suggest that either discrimination or sexual signals were likely ancestral for any phylogenetically independent origin of sexual reproduction that led to sex discrimination. We believe that the most likely scenario is that indiscriminate mating is indeed ancestral in these cases; however, so too are readily discernible differences between the sexes. Such differences (in the language of our model, signals) could be physiological by-products that resulted from sexual differentiation. As by-products, they may have arisen as cost-free cues and became costly later in evolutionary time, or they may have been costly signals trading off with, for example, anisogamy, increasing in frequency owing to selection favoring the evolution of two sexes. It is for these reasons that we have computed our ESS with initial signaling but no initial discrimination in figures 2 and 4. If signals of sexual identity are indeed by-products of anisogamy, there may actually be constraints on their evolution even after the origin of two sexes that are connected to maintaining two sexes, in which case it is possible that they could not be lost (only elaborated), in contrast to how we have modeled them here. Although our model has

implications for the ancestral state of discrimination and signaling, it does not rely on a specific ancestral state to explain stable SSB in modern populations, since discrimination is shown to readily evolve in both directions under some conditions. This is noteworthy because the ancestral state may have no bearing on the contemporary prevalence of SSB (Clive et al. 2020; Dickins and Rahman 2020).

Parker (2014) has argued that a series of six transitions drove the evolution of behaviorally complex multicellular sexual organisms from unicellular asexual organisms in the process known as the sexual cascade. The "key event" of this process is the evolution of advanced mobility leading to female targeting (Parker 2014; in our language, sex discrimination). To support this argument, Parker (2014) developed a game-theoretic model for the evolution of sex discrimination. Notably, this model assumes that males (the searching sex) are always capable of discerning differences between the sexes. It would be interesting to determine how these results change when allowing coevolution between discrimination and signaling: female targeting is expected to evolve less frequently given an imperfect ability to recognize females (Lerch and Servedio 2021). More broadly, incorporating sexual signals into the conceptual model of the sexual cascade could enhance an understanding of the origin of sexual complexity. Explicitly allowing for coevolutionary dynamics with detectable differences between the sexes could also be considered in explanations for sexual reproduction, such as work showing how anisogamy drives differences in mate search allocation (Lehtonen et al. 2016).

While the coevolution between discrimination and signaling in our model is reminiscent of the coevolution between mating preferences and mating traits in sexual selection models, there are important differences. In many classic sexual selection models, the evolution of preferences is enabled solely by the linkage disequilibrium that forms between neutral (female) preferences and (male) traits; this results in coevolution between sexually selected traits and the preferences that evolve as a result of indirect selection through this genetic association (the Fisher process; Lande 1981; Kirkpatrick 1982). In cases where there is a search cost (as in our model), the evolution of preferences from low frequencies generally cannot occur (Pomiankowski 1987*a*; Bulmer 1989) unless there are other factors involved, such as the traits being honest indicators of good genes (Pomiankowski 1987*b*) or mutation pressure (Pomiankowski et al. 1991). In our case, discrimination has a direct sexually selected fitness benefit in the form of obtaining mates capable of producing offspring. Discrimination thus evolves primarily through direct sexual selection (rather than indirect selection, as in classic sexual selection models), which more readily counters search costs (here a form of natural selection), rendering them less of a barrier than in classic sexual selection models.

With the bulk of past work on SSB considering males as searchers or choosers (Parker 2014; Han and Brooks 2015; Sales et al. 2018), it may be tempting to compare our model to a male mate choice model. However, in models of male mate choice under polygyny, females generally mate with equal reproductive success. This assumption does not match our model (if we interpret males as the searching sex), since the targeted sex has higher variance in reproductive success than the searching sex. In male mate choice models, preferences are directly selected against because males that bias their courtship (attempted matings) toward particular female phenotypes are at a competitive disadvantage compared with males that have no bias, since they are underrepresented in their matings with unpreferred females (Servedio and Lande 2006; reviewed in Fitzpatrick and Servedio 2018). In contrast, in our model one analog of unpreferred females (if we assume females are the targets) would be other males, which searching males would not gain a fitness advantage from mating with regardless of variation in the number of successful matings. Thus, direct selection against male preferences in our models results only from search costs and not additional opportunity costs (which favor discrimination in our model, since time spent attempting to mate with same-sex individuals could instead be spent on opposite-sex individuals).

Our model also relates to another popular theoretical framework: the acceptance threshold hypothesis (Reeve 1989). The acceptance threshold hypothesis is a general model considering an individual choosing whether to interact with preferred or unpreferred partners but incapable of perfectly determining the quality of any one potential partner. Reeve (1989) showed that the choosiness of an individual depends on differences between these two classes as well as the cost of interacting with an undesirable partner. The acceptance threshold hypothesis has been explicitly considered as an explanation for SSB (Engel et al. 2015; Han and Brooks 2015) and relates to other hypotheses proposing that SSB may occur because of the low chances of encountering a conspecific (Hoving et al. 2012) or the low costs of attempting copulation (Marco and Lizana 2002). More recently, the acceptance threshold hypothesis has been extended to consider the coevolution of discrimination and signals (Miller et al. 2020; Tibbetts et al. 2020). Miller et al. (2020) find that both initial signals and recognition ability are required to prevent the total loss of these two traits from the system (analogous to our results). The coevolution of signals and responses to those signals is expected to be quite general and has been considered in seemingly disparate cases, such as sexual selection (e.g., Kirkpatrick 1982; Thom and Dytham 2012), kin recognition (e.g., Johnstone 1997; Axelrod et al. 2004), and mimicry (e.g., Gavrilets and Hastings 1998). Empiricists have directly measured the interplay between signaling and recognition

in brood parasitism (Hauber et al. 2006), sexual selection (Hurst 2009), self-recognition (Lightfoot et al. 2019), and individual recognition (Sheehan et al. 2016). A notable gap, however, has been the lack of consideration and measurement of coevolutionary dynamics in understanding SSB and indiscriminate mating. Empirically studying signals of sexual identity as they relate to SSB would be a valuable contribution.

Our study emphasizes the importance of realizing that there are two steps to discrimination: (1) the presence of a signal or cue that can be observed and (2) the attempt to discern the signal or cue. Although much recent effort has gone into analyzing the second step, studies and discussions of indiscriminate mating have paid little attention to the first step: that a signal or cue must exist for discrimination to occur. We have shown that there are important coevolutionary dynamics between discrimination and signals under the assumption that each is costly. Underscoring this is the fact that most parameter combinations in our model evolve either to no discrimination and no signaling or to discrimination and maximal signaling. Our results demonstrate that without both sufficient initial signaling and initial discrimination, the population will retain the strategy of indiscriminate mating.

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## Statement of Authorship

B.A.L. conceived of the project, led the analyses, and wrote the first draft of the manuscript. Both authors aided in conceptualization and model formulation, and both provided edits and comments on the manuscript.

## Data and Code Availability

A Mathematica notebook that allows users to replicate results has been uploaded to Zenodo (https://doi.org/10.5281/zenodo.7116167; Lerch and Servedio 2022).

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