

Synthesis

Sensory Bias as an Explanation for the Evolution of Mate Preferences

Rebecca C. Fuller,^{*} David Houle,[†] and Joseph Travis[‡]

Department of Biological Science, Florida State University,
Tallahassee, Florida 32306

Submitted March 5, 2005; Accepted May 23, 2005;
Electronically published August 5, 2005

ABSTRACT: The sensory bias model of sexual selection posits that female mating preferences are by-products of natural selection on sensory systems. Although sensory bias was proposed 20 years ago, its critical assumptions remain untested. This paradox arises because sensory bias has been used to explain two different phenomena. First, it has been used as a hypothesis about signal design, that is, that males evolve traits that stimulate female sensory systems. Second, sensory bias has been used as a hypothesis for the evolution of female preference itself, that is, to explain why females exhibit particular preferences. We focus on this second facet. First, we clarify the unique features of sensory bias relative to the alternative models by considering each in the same quantitative genetic framework. The key assumptions of sensory bias are that natural selection is the predominant evolutionary mechanism that affects preference and that sexual selection on preferences is quantitatively negligible. We describe four studies that would test these assumptions and review what we can and cannot infer about sensory bias from existing studies. We suggest that the importance of sensory bias as an explanation for the evolution of female preferences remains to be determined.

Keywords: direct benefits, sensory exploitation, female choice, Fisherian runaway, good-genes model, sexual conflict.

The sensory bias and sensory exploitation hypotheses of sexual selection attempt to explain why males possess certain types of costly secondary sex traits and why females should prefer males possessing those traits. These similar hypotheses state that female mating preferences are by-products

of the underlying physiology of their sensory systems, which have been molded by natural selection, and that males evolve traits that match those sensory system characteristics (West-Eberhard 1984; Basolo 1990, 1995; Ryan 1990, 1998; Ryan et al. 1990; Endler and Basolo 1998). Endler and Basolo (1998) distinguish between sensory bias and sensory exploitation; for our argument, the two are interchangeable, and we will refer to them as sensory bias for brevity. We distinguish sensory bias from sensory drive, which is a hypothesis about the role of environmental conditions in the evolution of the signaling system and is compatible with all models of sexual selection (Endler 1992, 1993; Endler and Basolo 1998). In contrast, sensory bias has been offered explicitly as an alternative to other models of the evolution of mate choice (West-Eberhard 1984; Basolo 1990, 1995; Ryan 1990, 1998; Ryan et al. 1990; Shaw 1995; Endler and Basolo 1998), and the results from a variety of studies have been interpreted as supporting sensory bias as an explanation for the evolution of female preferences (Basolo 1990, 1995, 1996; Ryan et al. 1990; Proctor 1991; Christy 1995; McClintock and Uetz 1996; Morris et al. 1996; Rodd et al. 2002; Smith et al. 2004).

We contend that the sensory bias model has not been developed rigorously as a genuine alternative to other female preference models and, as a result, has never been tested as such. We develop this argument in stages. First, we discuss the origin of the ambiguity in the sensory bias models. Second, we outline a quantitative genetic framework that defines sensory bias as a distinct alternative to the other models (namely, the Fisherian runaway, good-genes, direct benefits, and sexual conflict models) and facilitates distinctions among them. Subsequently, we discuss which empirical efforts could be developed through this framework as fruitful tests of hypotheses about female preference evolution and whether existing empirical studies do actually test sensory bias as a distinct, alternative model.

Defining and Delimiting Sensory Bias

Sensory bias is a verbal model that looks to natural selection on sensory system function as being responsible

^{*} Corresponding author. Present address: Department of Animal Biology, School of Integrative Biology, University of Illinois, Urbana, Illinois 61801; e-mail: fuller@life.uiuc.edu.

[†] E-mail: dhoule@bio.fsu.edu.

[‡] E-mail: travis@neuro.fsu.edu.

for the origin of female mating preference. Unfortunately, different presentations of the model are not consistent in their descriptions of whether female preference is also molded by sexual selection. For example, Ryan (1990) states that under sensory exploitation, female preferences do not evolve through sexual selection ("current preferences for traits have become established in the population for reasons not related to adaptive mate choice or sexual selection"; Ryan 1990, p. 179). Later text in that same article implies that sexual selection can be responsible ("if a female preference for a male trait in any species is due to sensory exploitation, this need not imply that the sensory bias has never been under selection, even selection for mate choice"; Ryan 1990, p. 185). Different authors espouse different claims about whether current levels of female preference are adaptive; for example, Ryan and Rand (1990) suggest that female mating preferences can be nonadaptive under sensory bias, whereas others claim that the model implies that preferences are adaptive (Dawkins and Guilford 1996; Endler and Basolo 1998). Part of this ambiguity is due to the fact that Ryan and Rand (1990) and Ryan (1990) do not specifically state what they mean by "adaptive," that is, whether preference is molded by sexual selection, natural selection, or both. Similar inconsistency can be found in the comparisons of sensory bias with other models; the conflicting claim that sensory bias is an alternative to the other models of sexual selection and yet consistent with their operation can be found in many presentations of the sensory bias process (West-Eberhard 1984; Basolo 1990, 1995; Ryan 1990, 1998; Ryan et al. 1990; Endler and Basolo 1998).

There are two distinct ideas within the sensory bias literature that must be distinguished. First, much of this literature is aimed at explaining signal design, that is, which signals animals will use, not the content of the signal nor the evolutionary forces that act on signaler and receiver through that content once the pair exists (Endler 1992, 1993). Sensory bias has proved a very productive framework for understanding which traits evolve in males, that is, why some traits evolve as sexual signals instead of others (e.g., traits that elicit greater stimulation of the female sensory system, traits that contrast with background conditions, novel traits that preclude habituation). However, the issue of which specific traits evolve is outside the realm of traditional sexual selection theory. Traditional sexual selection theory begins with the assumption that females exhibit genetic variation in their preference for a male trait, and theory says nothing about the trait for which females exhibit their preference. Traditional sexual selection theories (i.e., Fisher process, good-genes, direct benefits, sexual conflict) all assume that males evolve traits to match female mating preferences to the extent possible, given costs.

The second major theme in sensory bias is the one that concerns us here, and that is the idea that sensory bias can explain the evolution of the quantitative degree of female preference for male traits. The key idea of the sensory bias model is that mating preferences evolve not via sexual selection but by a correlated response of the sensory system to natural selection on other behaviors and/or traits (West-Eberhard 1984; Basolo 1990; Ryan 1990, 1998; Kirkpatrick and Ryan 1991). In this respect, sensory bias can represent a distinct alternative to other models. The critical distinctions among all models of sexual selection are in their explanations for the evolution of female preferences. Despite its ambiguities, we believe that the sensory bias literature does provide a genuinely distinct hypothesis: that the level of female preference in a population evolves as a correlated response to natural selection on other behaviors and/or traits.

Natural and Sexual Selection

Throughout this article, we draw a distinction between "natural" and "sexual" selection on female mating preferences. By "natural" selection we mean fitness differences that are independent of the identity and number of one's mates, which might also be referred to as nonsexual selection. We use the term "sexual selection" to mean fitness differences arising as a result of both the number and identity of mates (Andersson 1994, p. 7). In contrast, many previous formal definitions of sexual selection depend solely on the number of mates or matings (Endler 1986; Arnold 1994; Shuster and Wade 2003). Unfortunately, this practice neglects the fact that sexual selection can arise as a result of both the numbers and the properties (i.e., quality) of an individual's mating partners. A prime example is found in the Darwin-Fisher mechanism (Kirkpatrick et al. 1990), where males evolve traits via selection generated by variation in mate quality (i.e., males compete for high-quality females with no variation in mate number). Obviously, the same process applies to females, where selection on female mating preferences arises from differences in fitness due to the properties of the males with whom they mate (see Jennions and Petrie 2000 for a review of such effects). Under this definition, the evolution of female mating preferences via the Fisher, good-genes, direct benefits, and sexual conflict models are all forms of sexual selection on female mating preferences because preference affects female fitness via the properties of her mates (see below for the details of these models). Under our definition, the evolution of female preference via sensory bias is a form of natural selection because selection on preference is independent of mate identity. We do not mean to redefine natural selection by our use of the term; we

merely use it as a shorthand for the somewhat awkward phrase “nonsexual selection.”

A Quantitative Genetic Framework for the Evolution of Female Preference

We will consider five basic models for the evolution of female preference: sensory bias, the Fisherian process, good-genes, direct benefits, and sexual conflict. We use the formalism of multivariate quantitative genetics to place all of these in a common explicit framework. To do this, we draw on the many previous quantitative genetic models of female preference (for a review, see Mead and Arnold 2004).

The focus of these models is the vector of changes in the phenotypes during a single generation, denoted $\Delta\bar{\mathbf{z}}$. This change is predicted from the additive genetic variance-covariance matrix, \mathbf{G} , the vector of selection gradients, $\boldsymbol{\beta}$, and the vector of mutational effects, \mathbf{u} , as $\Delta\bar{\mathbf{z}} = \mathbf{G}\boldsymbol{\beta} + \mathbf{u}$. We decompose the total selection gradient $\boldsymbol{\beta}$ into a part due to natural selection ($\boldsymbol{\beta}_N$) and another due to sexual selection ($\boldsymbol{\beta}_S$), selection caused by variation in mate number or quality. Female preference models typically involve a female preference (p) and a male display trait (t), and in some cases they include a residual fitness or viability trait (v). We use the term “viability” to represent variation in naturally selected fitness, including variation in fecundity not affected by mate quality or number.

Expanding \mathbf{G} , $\boldsymbol{\beta}$, and \mathbf{u} to show their constituent elements, for these three traits we have

$$\mathbf{G} \times (\boldsymbol{\beta}_N + \boldsymbol{\beta}_S) + \mathbf{u},$$

$$\Delta\bar{\mathbf{z}} = \begin{pmatrix} V_t & C_{tp} & C_{tv} \\ C_{tp} & V_p & C_{pv} \\ C_{tv} & C_{pv} & V_v \end{pmatrix} \times \left(\begin{bmatrix} \boldsymbol{\beta}_{Nt} \\ \boldsymbol{\beta}_{Np} \\ \boldsymbol{\beta}_{Nv} \end{bmatrix} + \begin{bmatrix} \boldsymbol{\beta}_{St} \\ \boldsymbol{\beta}_{Sp} \\ \boldsymbol{\beta}_{Sv} \end{bmatrix} \right) + \begin{bmatrix} u_t \\ u_p \\ u_v \end{bmatrix},$$

where V represents an additive genetic variance, C represents an additive genetic covariance between a pair of traits, and $\boldsymbol{\beta}$ represents a selection gradient either for mating ($\boldsymbol{\beta}_S$) or for the balance of the life span outside of mating ($\boldsymbol{\beta}_N$).

To characterize each model, we consider the conditions under which it explains the initial evolution of female preference for an exaggerated male trait ($\Delta p > 0$) as well as the equilibrium conditions where an exaggerated preference is maintained within a population ($\Delta p = 0$, $p > 0$).

Sensory bias. Figure 1 shows the forces at work at three stages in the evolution of a female preference and a male display due to sensory bias. Boldface values show the critical assumptions for this model at each stage. The sensory bias model assumes that a change in natural selection on the preference initiates its increase to the level at which it

$$\begin{pmatrix} V_t & C_{tp} & C_{tv} \\ & V_p > 0 & C_{pv} \\ & & V_v \end{pmatrix} \times \left(\begin{bmatrix} \boldsymbol{\beta}_{Nt} = 0 \\ \boldsymbol{\beta}_{Np} > 0 \\ \boldsymbol{\beta}_{Nv} \end{bmatrix} + \begin{bmatrix} \boldsymbol{\beta}_{St} = 0 \\ \boldsymbol{\beta}_{Sp} \equiv 0 \\ \boldsymbol{\beta}_{Sv} \end{bmatrix} \right)$$

$$\downarrow$$

$$\begin{pmatrix} V_t > 0 & C_{tp} & C_{tv} \\ & V_p > 0 & C_{pv} \\ & & V_v \end{pmatrix} \times \left(\begin{bmatrix} \boldsymbol{\beta}_{Nt} = 0 \\ \boldsymbol{\beta}_{Np} > 0 \\ \boldsymbol{\beta}_{Nv} \end{bmatrix} + \begin{bmatrix} \boldsymbol{\beta}_{St} > 0 \\ \boldsymbol{\beta}_{Sp} \equiv 0 \\ \boldsymbol{\beta}_{Sv} \end{bmatrix} \right)$$

$$\downarrow$$

$$\begin{pmatrix} V_t & C_{tp} & C_{tv} \\ & V_p & C_{pv} \\ & & V_v \end{pmatrix} \times \left(\begin{bmatrix} \boldsymbol{\beta}_{Nt} = -\boldsymbol{\beta}_{St} \\ \boldsymbol{\beta}_{Np} = 0 \\ \boldsymbol{\beta}_{Nv} \end{bmatrix} + \begin{bmatrix} \boldsymbol{\beta}_{St} = -\boldsymbol{\beta}_{Nt} \\ \boldsymbol{\beta}_{Sp} \equiv 0 \\ \boldsymbol{\beta}_{Sv} \end{bmatrix} \right)$$

Figure 1: Forces at three stages (initiation, exaggeration, and equilibrium) in the evolution of a female preference and a male trait due to sensory bias. The top set of matrices shows conditions that initiate the exaggeration of female preference from a naturally selected equilibrium where neither preference nor male trait are exaggerated; the middle set of matrices shows intermediate conditions where an increased level of preference has created sexual selection on the male trait; the lower set of matrices shows conditions expected at a new equilibrium with exaggerated preference and trait value. Terms shown in boldface are the critical ones for the sensory bias hypothesis.

can exert sexual selection on the male trait. This is represented by the positive value of $\boldsymbol{\beta}_{Np}$ shown in boldface in the top section of figure 1. At the same time, a critical assumption of the sensory bias model is that sexual selection on female preference is completely absent, or at least negligible. This is represented by the term $\boldsymbol{\beta}_{Sp} \equiv 0$, by which we mean that this selection gradient is assumed to be 0 for every value of p and not just at a local optimum. This means that there are no fitness consequences (positive or negative) to females from choosing particular males.

In the second stage of the evolution of female preference, shown in the middle set of matrices in figure 1, female preference has increased to the point from which it exerts directional sexual selection on display. If the male display has additive genetic variation ($V_t > 0$), it will respond immediately to sexual selection. Finally, preference will settle at a local, naturally selected equilibrium point, represented by the term $\boldsymbol{\beta}_{Np} = 0$ in the bottom set of matrices in the figure. Male display is maintained by a balance between natural selection that seeks the return of the display to the original optimum and sexual selection

that favors further exaggeration. This balance occurs in all models of coevolution between preference and display, so we do not show these terms in boldface. In the pure sensory bias model, this balance is particularly simple because the natural and sexual selection gradients on the display should exactly cancel each other's effects.

Fisher process. The first conditions for the Fisher process are that there is genetic variance in both preference and male display (fig. 2; O'Donald 1962; Lande 1981; Kirkpatrick 1982; Pomiankowski et al. 1991). The nonrandom mating that results creates a gametic disequilibrium between p and t ($C_{tp} > 0$). Hence, choosier females produce offspring that inherit alleles producing above-average values of female preference and male display. A Fisher process is initiated when female preference is perturbed away from $p = 0$. The cause of such a perturbation is outside the model, but in a pure Fisher model it might include drift or gene flow. The change in p causes sexual selection on t . Because preference and display have a genetic covariance, this selection on display also results in a response in preference. If $C_{tp} > V_p$, then the response in p will be so large as to perpetuate the sexual selection t , resulting in the "Fisher runaway," where p and t increase or decrease indefinitely. If $C_{tp} < V_p$, then the response in p will quickly return the population to a state where the degree of expression of t matches the level appropriate to p , either larger or smaller than the starting p and t values. If perturbations of p are common, even this nonrunaway process may eventually result in a large shift in preference and display (Lande 1981).

While the above assumptions are sufficient to initiate the Fisher process, the stable exaggeration of preference and trait require that the preference have no cost. This is equivalent to stating that there is no natural selection on preference itself, $\beta_{Np} \equiv 0$. When this is so, preference can be exaggerated at equilibrium (Lande 1981; Kirkpatrick 1982). Display will also be stably exaggerated, again because of an exact balance between positive sexual selection and negative natural selection. This no-cost assumption is generally thought to be unrealistic and therefore to limit the applicability of the Fisher process as an equilibrium explanation of sexual selection (Kirkpatrick 1982; Pomiankowski 1987a; Iwasa and Pomiankowski 1991; Pomiankowski et al. 1991). Note, however, that a costly female preference can be maintained, provided that there is a biased mutation rate against the display ($u_t > u_p$; Pomiankowski et al. 1991).

At equilibrium (fig. 2, *bottom*), the structure of the β gradient on preference under the Fisher model appears superficially similar to that of sensory bias (fig. 1, *bottom*). In actuality, they are quite different. The Fisher process depends on there being no natural or sexual selection of any sort on preference ($\beta \equiv 0$). Sensory bias assumes no

$$\begin{pmatrix} \mathbf{V}_t > \mathbf{0} & \mathbf{C}_{tp} > \mathbf{0} & C_{tv} = 0 \\ & \mathbf{V}_p > \mathbf{0} & C_{pv} = 0 \\ & & V_v \end{pmatrix} \times \left(\begin{bmatrix} \beta_{Nt} = 0 \\ \beta_{Np} \equiv \mathbf{0} \\ \beta_{Nv} \end{bmatrix} + \begin{bmatrix} \beta_{St} > \mathbf{0} \\ \beta_{Sp} \equiv \mathbf{0} \\ \beta_{Sv} \end{bmatrix} \right)$$

↓

$$\begin{pmatrix} \mathbf{V}_t > \mathbf{0} & \mathbf{C}_{tp} > \mathbf{0} & C_{tv} = 0 \\ & \mathbf{V}_p > \mathbf{0} & C_{pv} = 0 \\ & & V_v \end{pmatrix} \times \left(\begin{bmatrix} \beta_{Nt} = -\beta_{St} \\ \beta_{Np} \equiv \mathbf{0} \\ \beta_{Nv} \end{bmatrix} + \begin{bmatrix} \beta_{St} = -\beta_{Nt} \\ \beta_{Sp} \equiv \mathbf{0} \\ \beta_{Sv} \end{bmatrix} \right)$$

Figure 2: Forces at two stages in the evolution of a female preference and a male trait due to the Fisher process. The top matrix shows the conditions necessary for the initial increase in female mating preference, whereas the bottom matrix shows the conditions at equilibrium. Terms shown in boldface are critical to the Fisher hypothesis.

directional selection because preference is at a fitness peak ($\beta_N = 0$) and hence under stabilizing selection.

Good genes. The good-genes process is initiated by positive covariance between male display and genetic variation for residual fitness, v (Hamilton and Zuk 1982; Pomiankowski 1987b; Iwasa and Pomiankowski 1991, 1999). This is equivalent to the existence of condition dependence of the display, for example, if larger individuals have higher v and therefore larger display traits. There is no necessity for display itself (t) to be genetically variable to allow evolution of p . In figure 3, we show a case where genetic variation in v is created by biased mutation (u_v); residual fitness variation could also be created by other means, such as environmental change or gene flow. The good-genes model also assumes genetic variation in preference, which then creates genetic covariance between p and v ($C_{vp} > 0$). On the selection side, p starts at a local, naturally selected optimum ($\beta_{Np} = 0, \partial w^2/\partial p < 0$), but the model is distinguished from those involving direct benefits or sexual conflict by the absence of direct sexual selection on p ($\beta_{Sp} \equiv 0$). Preference then is pushed away from its local optimum by selection for high v . When display is also genetically variable, covariance between p and t is also created; this covariance can accelerate the good-genes process but is not necessary for it to proceed (Houle and Kondrashov 2002).

Once preference starts to increase, it creates sexual selection on display as usual but also sexual selection for high viability, as shown in the middle panel of figure 3. It also creates natural selection to return preference to its starting state. Thus, a number of selective forces are at work in the good-genes process, and they combine to impose direct and indirect selection on all three traits. At equilibrium (fig. 3, *bottom*), natural selection against pref-

$$\begin{array}{c}
\left(\begin{array}{ccc} V_t > 0 & C_{tp} > 0 & C_{tv} > 0 \\ & V_p > 0 & \mathbf{C_{pv}} > \mathbf{0} \\ & & V_v > 0 \end{array} \right) \times \left(\left[\begin{array}{c} \beta_{Nt} = 0 \\ \mathbf{\beta_{Np}} = \mathbf{0} \\ \mathbf{\beta_{Nv}} = \mathbf{u_v/V_v} \end{array} \right] + \left[\begin{array}{c} \beta_{St} = 0 \\ \mathbf{\beta_{Sp}} = \mathbf{0} \\ \mathbf{\beta_{Sv}} = \mathbf{0} \end{array} \right] \right) \\
\downarrow \\
\left(\begin{array}{ccc} V_t > 0 & C_{tp} > 0 & C_{tv} > 0 \\ & V_p > 0 & \mathbf{C_{pv}} > \mathbf{0} \\ & & V_v > 0 \end{array} \right) \times \left(\left[\begin{array}{c} \beta_{Nt} = 0 \\ \mathbf{\beta_{Np}} < \mathbf{0} \\ \mathbf{\beta_{Nv}} > \mathbf{0} \end{array} \right] + \left[\begin{array}{c} \beta_{St} > 0 \\ \mathbf{\beta_{Sp}} = \mathbf{0} \\ \mathbf{\beta_{Sv}} > \mathbf{0} \end{array} \right] \right) \\
\downarrow \\
\left(\begin{array}{ccc} V_t > 0 & C_{tp} > 0 & C_{tv} > 0 \\ & V_p > 0 & \mathbf{C_{pv}} > \mathbf{0} \\ & & V_v > 0 \end{array} \right) \times \left(\left[\begin{array}{c} \beta_{Nt} < 0 \\ \mathbf{\beta_{Np}} < \mathbf{0} \\ \mathbf{\beta_{Nv}} > \mathbf{0} \end{array} \right] + \left[\begin{array}{c} \beta_{St} > 0 \\ \mathbf{\beta_{Sp}} = \mathbf{0} \\ \mathbf{\beta_{Sv}} > \mathbf{0} \end{array} \right] \right)
\end{array}$$

Figure 3: Forces at three stages (initiation, exaggeration, and equilibrium) in the evolution of a female preference and a male display trait, according to the good-genes models. At equilibrium, there is direct selection against the female mating preferences and indirect selection for the preference via the correlation between preference and viability. The status of the covariance between trait and viability is ambiguous. A phenotypic correlation between display and the trait is necessary but need not arise through genes that affect display per se. Terms shown in boldface are critical to the good-genes hypothesis.

erence (i.e., cost of preference) is balanced by indirect selection on preference through the correlation of preference with viability. At equilibrium under the good-genes model, natural selection favors a decrease in preference, while indirect sexual selection favors an increase. This contrasts again with the situation under the sensory bias model, which predicts stabilizing natural selection on preference.

Direct benefits. In the direct benefits model, females acquire fitness benefits by choosing males that provide a fitness benefit to either a female or her offspring (Price et al. 1993; Schluter and Price 1993). Examples include a nuptial gift that enhances fecundity and effective paternal care that increases offspring survival. Increased levels of preference evolve when the male display is correlated with the benefit he can offer a female (fig. 4, *top*). While this process has been described as natural selection on female mating preferences (Kirkpatrick 1987; Reynolds and Gross 1990), in our terminology it involves direct sexual selection ($\beta_{Sp} > 0$) on female mating preferences (fig. 4) because the fitness consequences of preference are functions of the identity and quality of a female's mating partner. Similarly, the costs of mating preference can arise as a function of either sexual or natural selection. In the bottom panel of

figure 4, we show the equilibrium conditions, where the benefits are balanced by natural selection (e.g., Schluter and Price 1993), but the costs of mate choice can also be due to sexual selection, where costs arise from the negative effects of mating with males that have high display levels that balance the benefits they provide (e.g., Kirkpatrick 1985; Price et al. 1993).

Sexual conflict. Sexual conflict scenarios for preference evolution depend on the existence of a female preference for male traits to create the opportunity for sexual conflict to arise (Arnqvist and Rowe 2005). Therefore, sexual conflict models cannot be considered in isolation from the other models. Selection on preference due to sexual conflict arises in our coevolutionary framework whenever male display traits directly affect female fitness. Such effects may occur during the act of mating (Holland and Rice 1998; Gavrillets 2000; Gavrillets et al. 2001), for example, transfer of manipulative or toxic materials in semen or damage to females during mating. In this case, sexual conflict sets up direct sexual selection on female preference to lower the mating rate or choose less damaging mates. Alternatively, conflict may occur whether or not mating occurs. For example, male persistence in courting a female may directly affect her fitness by hampering feeding or attracting predators. In such cases, there may be no selection on preference generated by the male trait.

An example of the sort of pattern expected under sexual conflict is shown in figure 5. We assume that a direct benefits scenario initiates the female preference exaggeration, as shown in the top panel. If males then evolve a level of display that stimulates females to mate more than is optimal for them, sexual selection then favors increasing

$$\begin{array}{c}
\left(\begin{array}{ccc} V_t & C_{tp} & C_{tv} \\ & V_p > 0 & \mathbf{C_{pv}} \\ & & V_v \end{array} \right) \times \left(\left[\begin{array}{c} \beta_{Nt} = 0 \\ \mathbf{\beta_{Np}} = \mathbf{0} \\ \beta_{Nv} \end{array} \right] + \left[\begin{array}{c} \beta_{St} = 0 \\ \mathbf{\beta_{Sp}} > \mathbf{0} \\ \beta_{Sv} \end{array} \right] \right) \\
\downarrow \\
\left(\begin{array}{ccc} V_t > 0 & C_{tp} & C_{tv} \\ & V_p > 0 & \mathbf{C_{pv}} \\ & & V_v \end{array} \right) \times \left(\left[\begin{array}{c} \beta_{Nt} < 0 \\ \mathbf{\beta_{Np}} < \mathbf{0} \\ \beta_{Nv} \end{array} \right] + \left[\begin{array}{c} \beta_{St} > 0 \\ \mathbf{\beta_{Sp}} > \mathbf{0} \\ \beta_{Sv} \end{array} \right] \right)
\end{array}$$

Figure 4: Evolutionary forces at two stages (initiation and equilibrium) necessary for the direct benefits model. At an equilibrium shown in the bottom matrix, direct natural selection against the preference (costs of choice) and direct sexual selection for preference (benefits of choice) balance. Terms shown in boldface are critical to the hypothesis.

$$\begin{array}{c}
 \begin{pmatrix} V_t & C_{tp} & C_{tv} \\ & V_p > 0 & C_{pv} \\ & & V_v \end{pmatrix} \times \left(\begin{bmatrix} \beta_{Nt} \\ \beta_{Np} = 0 \\ \beta_{Nv} \end{bmatrix} + \begin{bmatrix} \beta_{St} > 0 \\ \beta_{Sp} > 0 \\ \beta_{Sv} \end{bmatrix} \right) \\
 \downarrow \\
 \begin{pmatrix} V_t & C_{tp} & C_{tv} \\ & V_p & C_{pv} \\ & & V_v \end{pmatrix} \times \left(\begin{bmatrix} \beta_{Nt} < 0 \\ \beta_{Np} < 0 \\ \beta_{Nv} \end{bmatrix} + \begin{bmatrix} \beta_{St} > 0 \\ \beta_{Sp} > 0 \\ \beta_{Sv} \end{bmatrix} \right)
 \end{array}$$

Figure 5: Evolutionary forces at two stages (initiation and equilibrium) necessary for the sexual conflict model. The only difference between this model and the direct benefits model is that there is sexual selection for costly male traits at the start of the process in the first matrix. Terms shown in boldface are critical to the hypothesis.

the level of preference itself to avoid costly interactions with males. The equilibrium situation here is the same as that for the direct benefits model: direct sexual selection for higher preference is balanced by direct natural selection for lower preference. These results are superficially similar to the expectation under sensory bias, in that all three models predict no net directional selection for preference. However, with both sexual conflict and direct benefits, this happens because natural and sexual selection exert conflicting selection, whereas sensory bias assumes only stabilizing natural selection. Scenarios consistent with the joint action of sexual conflict and other types of selection on mate preferences are readily constructed (Arnqvist and Rowe 2005), although the equilibrium pattern of selection might differ from that shown in figure 5.

Although we have discussed each model separately, each of these processes may act simultaneously. Many theoretical studies have modeled conditions where more than one process operates or compared the efficacy of different processes under certain assumptions (e.g., Kirkpatrick 1996; Iwasa and Pomiankowski 1999; Hall et al. 2000). Other attempts to investigate the relationship between models have been misleading. Kokko et al. (2002) claimed to have shown that the Fisher and good-genes models are related, but this claim is based on a misunderstanding of the Fisher process. As outlined above, the Fisher process depends on the genetic covariance between preference and display, which does not appear in Kokko et al.'s evolutionarily stable strategy model. Additional theoretical work on combinations could illuminate the circumstances under which

different processes are likely to have the greatest effects on preference.

Distinguishing Sensory Bias from Other Preference Models in Practice

With this background in mind, which empirical studies could distinguish sensory bias from other models? Which might provide insight into its relative importance in particular situations? The key to the differences between models revealed in figures 1–5 depends on our ability to distinguish between sexual and natural selection. Recall that we have defined sexual selection as the fitness consequences of mate number and mate quality.

The most direct approach is therefore to determine the extent to which natural and sexual selection act on mating preferences. In the strictest sense, sensory bias predicts that selection on preference is independent of the identity and attributes of males, whereas the other models predict that selection on preference follows from the benefits of choosing particular males, regardless of whether those benefits accrue directly or indirectly. Of course, the reality is that a combination of sexual and natural selection may act on preference, and so studies that can assess both facets of selection will be at a premium. One approach is to study selection on preference in natural populations and attempt to decompose the total selection gradient on preference into components due to natural and sexual selection (e.g., Blows and Brooks 2003). This is more easily written than accomplished. For example, to measure sexual selection on preference, we would have to determine whether any selection on preference is a function of the males with whom a female might mate. We would have to mate males with multiple females to determine the statistical effects of individual males on a female's inclusive fitness as well as measure preference independently of the actual mating outcome. This extensive experimental approach will not be feasible in many systems.

A second approach would be to estimate the **G** matrix and look at the variances and covariances important for each model. For example, finding genetic covariances between residual fitness and preference would implicate good genes, and genetic covariances between preference and display a possible role for the Fisher process.

Another powerful approach is to examine the relative roles of multiple models using an elasticity analysis (Caswell 1989; Kirkpatrick 1996). Ideally, one has estimated both the **G** matrix and the **β** vector. An elasticity analysis allows an investigation into which elements have large effects on changes in preference. For example, whenever preference and display trait are genetically variable, there will necessarily be an observed genetic covariance (C_{tp}) between them. However, the observed covariance might

be so small as to be trivial. By examining the effects of small increases and decreases in C_{ip} on changes in preference, one can estimate the importance of the Fisher process (e.g., Kirkpatrick 1996). This is also a daunting empirical task, but the method might profitably be employed in simulation studies that merge these models and can be roughly parameterized from phenotypic data in natural populations. While interpreting the results can be difficult (because some parameters are important in multiple models), many elements are not implicated, particularly in the sensory bias model.

Two types of selection experiments could also be used to assess the sensory bias model. In the first type, experimental populations would be manipulated to enforce random mating in one treatment while allowing mate choice and competition in the other treatment (e.g., Holland and Rice 1999). In both treatments, natural selection would be allowed to operate. Any differences created would accumulate over many generations, increasing the power of the experiment. Under the sensory bias hypothesis, no differences between treatments in female preference would be expected to evolve. All other models that incorporate costs to female mating preferences predict initial decreases in female preference in the enforced random-mating treatment, as long as both the male trait and female preference are genetically variable.

A different type of selection experiment could explore the effects of direct selection on candidate aspects of naturally selected behavior and mate preferences. Under sensory bias, the expectation is that selection on nonmating behavior will strongly affect preference. For example, one could select on foraging behavior, using colored foods of different qualities, and look for correlated responses in female preference and/or male coloration. Alternatively, one could select on mate preferences and look for correlated responses in foraging behavior. If correlated responses are found, it would also be interesting to select simultaneously on both food and mate preferences to see if the correlations can be altered by selection. The closer the association between mating behavior and some aspect of the naturally selected phenotype is, the more likely that natural selection could plausibly overwhelm sexual selection.

Empirical Difficulties in the Current Testing of Sensory Bias

A variety of data have been interpreted as giving support to sensory bias as a model of female preference. This literature has two shortcomings. First, there is considerable misinterpretation of the implications of the various theories for the evolution of preference. Second, there is confusion between the predictions made by sensory bias

about signal design and the predictions made about female choice.

Genetic correlations. Verbal models of sensory bias repeatedly emphasize the idea that male secondary sex traits and female mating preferences do not “coevolve” and therefore that they do not result in a genetic correlation between male trait and female preference (Basolo 1990; Ryan 1990, 1998). This has led to the idea that the absence of a correlation implicates sensory bias. Neither of these premises is correct. In general, when both display and preference are genetically variable, there will be some level of genetic covariance between them within populations, regardless of the mechanism by which the mean preference and display evolved. Conversely, the lack of genetic correlation between display and preference need not imply a pure sensory bias mechanism. The Fisher process cannot act without such a correlation, but none of the other models depends critically on this correlation. Direct benefits (Kirkpatrick and Ryan 1991; Schluter and Price 1993; Iwasa and Pomiankowski 1999), good genes (Houle and Kondrashov 2002), and sexual conflict (Gavrilets 2000) have all been modeled with no genetic covariance between the display and preference.

Sensory bias and genetic variation in female mating preferences. A more controversial inference from presentations of the sensory bias model is that an absence of variation in female mating preference within a population is evidence that the sensory bias process is operating (Reeve and Sherman 1993; Basolo and Endler 1995; Christy and Backwell 1995; Sherman and Wolfenbarger 1995; Endler and Basolo 1998; Jennions and Petrie 2000). This follows from the argument that female mating preference arises from such fundamental properties of the sensory system that it is constrained in its response to any selective pressure. One might argue further along these lines that nearly all mutations in the sensory system are likely to be deleterious and that the standing level of genetic variation in sensory systems will be near 0, which of course would obviously prevent further evolution of preferences via any form of sexual selection.

We do not believe that the level of preference variation carries any information that would falsify any model of female preference. Genetic variation in preference is necessary for preferences to evolve by any of the five models. Furthermore, all of the models can accommodate situations where the relative amount of variation in preference is much smaller (or much larger) than that for the display trait. Even proponents of sensory bias do not require that female preferences are fixed (e.g., Basolo and Endler 1995; Endler and Basolo 1998). Under any model of mate preference, the variation in preference could be absent at some times. None of the models depends on variance in pref-

erence to maintain exaggerated male traits; the mean of the preference is the source of selection on display.

Historical biases and initial levels of preference. Some presentations of the sensory bias model emphasize that historical patterns of selection produce a “sensory bias” that leads to a measurable preference (Ryan and Rand 1993; Phelps and Ryan 2000; Jennions and Brooks 2001; Ryan et al. 2001). This is an important hypothesis that may inform us about the starting conditions for exaggerated preferences and display. To be sure, the initial value of preference (p_0) can have large effects on the predicted preference equilibrium under the Fisher process (Kirkpatrick 1982; Lande 1981) and under some good-genes models (Pomiankowski 1987b; Payne and Pagel 2001). However, “sensory bias” in this sense does not refer to a full model of preference evolution. Instead, it simply refers to a situation where the initial preference differs from 0 ($p_0 > 0$). The sensory bias, direct benefits, and sexual conflict models can cause an initial increase in preference away from 0 (Kirkpatrick and Ryan 1991; Gavrillets et al. 2001).

Phylogenetic evidence for sensory bias. Many authors have suggested that the sensory bias model predicts that female mating preferences precede the evolution of male traits that exploit those preferences and that this sequence is a unique signature of the sensory bias mechanism (Basolo 1990; Ryan 1990, 1998; Ryan and Keddy-Hector 1992; Shaw 1995; Endler and Basolo 1998). The classic example is that of swordtail fishes (*Xiphophorus*), in which Basolo (1990, 1995, 1996) found the preference for males bearing swords to be ancestral to the evolution of the swords themselves. If the preference is assumed to be for a sword per se, then preference cannot have evolved by sexual selection in taxa without the male trait, and therefore sensory bias must be responsible.

The dilemma is in defining what female preference means, that is, what a preference is “for.” The more narrowly the preference is defined, the more likely we might be to misinterpret the phylogenetic evidence (Sherman and Reeve 1999). The critical assumption is that preference is for swords rather than a more general feature of the male, such as length. In *Xiphophorus helleri*, Rosenthal and Evans (1998) have demonstrated that female preference for males with swords is actually an expression of a more general preference for large males. A preference for overall size has been proposed for many poeciliids (Marler and Ryan 1997; Ptacek and Travis 1997; but see Basolo 1998). If this is generally true, then the phylogenetic pattern is not conclusive, because the more general preference may have evolved via either natural or sexual selection. Many authors consider the evolution of specific displays to match more general preferences as consistent with sensory bias (Basolo 1990; Ryan et al. 2003). However, this argument

is really focused on the evolution of the specific male display and not on the reasons for the evolution of preference.

Assuming that preferences do evolve via the sensory bias mechanism, comparative data will only support the hypothesis provided that speciation events occur between the evolution of the preference and the evolution of the male display (Endler and Basolo 1998). However, most models predict the rapid evolution of male displays, provided that genetic variation exists (for a review, see Mead and Arnold 2004). Such a scenario would most likely give the appearance of coevolution of preference and display across taxa, even if sensory bias is responsible.

Ornaments as mimics. Some of the best evidence for sensory bias is that male secondary sex traits sometimes resemble important objects or cues that function in non-mating contexts (Proctor 1991; Christy 1995; Weller et al. 1999; Greenfield and Weber 2000; Porter et al. 2002; Rodd et al. 2002; Smith et al. 2004). Important as this sort of evidence is, it does not refute the other models of sexual selection. Guppies provide a particularly good example. Rodd et al. (2002) have presented intriguing data that suggest that male color patterns are food mimics. This is based on data showing that variation among populations in female mating preference for males with orange spots can be explained by the attraction of both sexes to inanimate orange objects. Given that these animals frequently eat orange food items, the implication is that selection for easy detection of orange food items results in selection for preferences for orange males.

On the other hand, a long program of research also suggests that female choice for males with orange spots is adaptive because males must ingest carotenoids to produce these colors (Houde 1997). Carotenoid coloration could be an honest indicator of male quality (Kodric-Brown and Brown 1984; Kennedy et al. 1987; but see Grether et al. 2001). Hence, there are three scenarios that can explain the pattern of mating and foraging preferences in guppies: selection on foraging preferences has resulted in a correlated response in mating preferences (sensory bias); mating and foraging preferences are independent traits, and each have evolved to their respective fitness optima; or female mating preferences have evolved via sexual selection and have resulted in correlated responses in foraging preference in both males and females.

Finally, there is a great deal of work directed at the question of why particular display traits are utilized rather than others, which is often included under the rubric of sensory bias. Some works focus on the evolution of sensory systems (West-Eberhard 1984; Ryan 1990; Arak and Enquist 1993; Ghirlanda and Enquist 2003), while others focus on the interaction of environment with the sensory system (Endler 1992, 1993; Schluter and Price 1993). We agree that these are fascinating areas of research where

much empirical work is needed. However, as pointed out by others (Endler and Basolo 1998), such work is best seen as being concerned with signal design rather than signal content. Models of female preference are dependent on the nature of signal content rather than signal design.

Our first goal in writing this article is to distinguish between the use of the term “sensory bias” as an explanation for signal design and as an explanation for mate preference evolution. Second, we have tried to clarify what the sensory bias hypothesis for mate preference evolution is and how it differs from other mate preference models. Finally, we have outlined testable predictions for sensory bias as an alternative to other models for the evolution of mate preference. Unfortunately, our analysis makes it clear that none of the models have been adequately tested, including sensory bias. While we recognize that the tests we have described are daunting tasks, we believe that they are the critical ones for evaluating the power of the sensory bias idea for explaining the most perplexing feature of sexual selection: why do females have such strikingly strong preferences for costly, elaborated male traits?

Acknowledgments

We thank J. Endler, M. Enquist, H. Rodd, and an anonymous reviewer for helpful comments on the manuscript.

Literature Cited

- Andersson, M. B. 1994. *Sexual selection*. Princeton University Press, Princeton, NJ.
- Arak, A., and M. Enquist. 1993. Hidden preferences and the evolution of signals. *Philosophical Transactions of the Royal Society of London B* 340:207–213.
- Arnold, S. J. 1994. Bateman principles and the measurement of sexual selection in plants and animals. *American Naturalist* 144(suppl.): S126–S149.
- Arnqvist, G., and L. Rowe. 2005. *Sexual conflict*. Princeton University Press, Princeton, NJ.
- Basolo, A. L. 1990. Female preference predates the evolution of the sword in swordtail fish. *Science* 250:808–810.
- . 1995. Phylogenetic evidence for the role of a preexisting bias in sexual selection. *Proceedings of the Royal Society of London B* 259:307–311.
- . 1996. The phylogenetic distribution of a female preference. *Systematic Biology* 45:290–307.
- . 1998. Evolutionary change in a receiver bias: a comparison of female preference functions. *Proceedings of the Royal Society of London B* 265:2223–2228.
- Basolo, A. L., and J. A. Endler. 1995. Sensory biases and the evolution of sensory systems. *Trends in Ecology & Evolution* 10:489.
- Blows, M. W., and R. Brooks. 2003. Measuring nonlinear selection. *American Naturalist* 162:815–820.
- Caswell, H. 1989. *Matrix population models: construction, analysis, and interpretation*. Sinauer, Sunderland, MA.
- Christy, J. H. 1995. Mimicry, mate choice, and the sensory trap hypothesis. *American Naturalist* 146:171–181.
- Christy, J. H., and P. R. Y. Backwell. 1995. The sensory exploitation hypothesis. *Trends in Ecology & Evolution* 10:417.
- Dawkins, M. S., and T. Guilford. 1996. Sensory bias and the adaptiveness of female choice. *American Naturalist* 148:937–942.
- Endler, J. A. 1986. *Natural selection in the wild*. Princeton University Press, Princeton, NJ.
- . 1992. Signals, signal conditions, and the direction of evolution. *American Naturalist* 139(suppl.):S125–S153.
- . 1993. Some general comments on the evolution and design of animal communication systems. *Philosophical Transactions of the Royal Society of London B* 340:215–225.
- Endler, J. A., and A. L. Basolo. 1998. Sensory ecology, receiver biases and sexual selection. *Trends in Ecology & Evolution* 13:415–420.
- Gavrilets, S. 2000. Rapid evolution of reproductive barriers driven by sexual conflict. *Nature* 403:886–889.
- Gavrilets, S., G. Arnqvist, and U. Friberg. 2001. The evolution of female mate choice by sexual conflict. *Proceedings of the Royal Society of London B* 268:531–539.
- Ghirlanda, S., and M. Enquist. 2003. A century of generalization. *Animal Behaviour* 66:15–36.
- Greenfield, M. D., and T. Weber. 2000. Evolution of ultrasonic signalling in wax moths: discrimination of ultrasonic mating calls from bat echolocation signals and the exploitation of an anti-predator receiver bias by sexual advertisement. *Ethology Ecology and Evolution* 12:259–279.
- Grether, G. F., J. Hudon, and J. A. Endler. 2001. Carotenoid scarcity, synthetic pteridine pigments and the evolution of sexual coloration in guppies (*Poecilia reticulata*). *Proceedings of the Royal Society of London B* 268:1245–1253.
- Hall, D. W., M. Kirkpatrick, and B. West. 2000. Runaway sexual selection when female preferences are directly selected. *Evolution* 54:1862–1869.
- Hamilton, W. D., and M. Zuk. 1982. Heritable true fitness and bright birds: a role for parasites. *Science* 218:384–387.
- Holland, B., and W. R. Rice. 1998. Perspective: chase-away sexual selection: antagonistic seduction versus resistance. *Evolution* 52:1–7.
- . 1999. Experimental removal of sexual selection reverses intersexual antagonistic coevolution and removes a reproductive load. *Proceedings of the National Academy of Sciences of the USA* 96:5083–5088.
- Houde, A. E. 1997. *Sex, color, and mate choice in guppies*. Princeton University Press, Princeton, NJ.
- Houle, D., and A. S. Kondrashov. 2002. Coevolution of costly mate choice and condition-dependent display of good genes. *Proceedings of the Royal Society of London B* 269:97–104.
- Iwasa, Y., and A. Pomiankowski. 1991. The evolution of costly mate preferences. II. The handicap principle. *Evolution* 45:1431–1442.
- . 1999. Good parent and good genes models of handicap evolution. *Journal of Theoretical Biology* 200:97–109.
- Jennions, M. D., and R. Brooks. 2001. A sense of history. *Trends in Ecology & Evolution* 16:113–115.
- Jennions, M. D., and M. Petrie. 2000. Why do females mate multiply? a review of the genetic benefits. *Biological Reviews* 75:21–64.
- Kennedy, C. E. J., J. A. Endler, S. L. Poynton, and H. McMinn. 1987. Parasite load predicts mate choice in guppies. *Behavioral Ecology and Sociobiology* 21:291–295.
- Kirkpatrick, M. 1982. Sexual selection and the evolution of female choice. *Evolution* 36:1–12.
- . 1985. Evolution of female mate choice and parental in-

- vestment in polygynous species: the demise of the “sexy son.” *American Naturalist* 125:788–810.
- . 1987. The evolutionary forces acting on female mating preferences in polygynous animals. Pages 67–82 in J. W. Bradbury and M. B. Andersson, eds. *Sexual selection: testing the alternatives*. Wiley, Chichester.
- . 1996. Good genes and direct selection in evolution of mating preferences. *Evolution* 50:2125–2140.
- Kirkpatrick, M., and M. J. Ryan. 1991. The evolution of mating preferences and the paradox of the lek. *Nature* 350:33–38.
- Kirkpatrick, M., T. Price, and S. J. Arnold. 1990. The Darwin-Fisher theory of sexual selection in monogamous birds. *Evolution* 44:180–193.
- Kodric-Brown, A., and J. H. Brown. 1984. Truth in advertising: the kinds of traits favored by sexual selection. *American Naturalist* 124:309–323.
- Kokko, H., R. Brooks, J. M. McNamara, and A. I. Houston. 2002. The sexual selection continuum. *Proceedings of the Royal Society of London B* 269:1331–1340.
- Lande, R. 1981. Models of speciation by sexual selection on polygenic traits. *Proceedings of the National Academy of Sciences of the USA* 78:3721–3725.
- Marler, C. A., and M. J. Ryan. 1997. Origin and maintenance of a female mating preference. *Evolution* 51:1244–1248.
- McClintock, W. J., and G. W. Uetz. 1996. Female choice and pre-existing bias: visual cues during courtship in two *Schizocosa* wolf spiders (Araneae: Lycosidae). *Animal Behaviour* 52:167–181.
- Mead, L. S., and S. J. Arnold. 2004. Quantitative genetic models of sexual selection. *Trends in Ecology & Evolution* 19:264–271.
- Morris, M. R., W. E. Wagner, and M. J. Ryan. 1996. A negative correlation between trait and mate preference in *Xiphophorus pygmaeus*. *Animal Behaviour* 52:1193–1203.
- O’Donald, P. 1962. Theory of sexual selection. *Heredity* 17:541–552.
- Payne, R. J. H., and M. Pagel. 2001. Inferring the origins of state-dependent courtship traits. *American Naturalist* 157:42–50.
- Phelps, S. M., and M. J. Ryan. 2000. History influences signal recognition: neural network models of túngara frogs. *Proceedings of the Royal Society of London B* 267:1633–1639.
- Pomiankowski, A. 1987a. The costs of choice in sexual selection. *Journal of Theoretical Biology* 128:195–218.
- . 1987b. Sexual selection: the handicap principle does work—sometimes. *Proceedings of the Royal Society of London B* 231:123–145.
- Pomiankowski, A., Y. Iwasa, and S. Nee. 1991. The evolution of costly mate preferences. I. Fisher and biased mutation. *Evolution* 45:1422–1430.
- Porter, B. A., A. C. Fiumera, and J. C. Avise. 2002. Egg mimicry and allopaternal care: two mate-attracting tactics by which nesting striped darter (*Etheostoma virgatum*) males enhance reproductive success. *Behavioral Ecology and Sociobiology* 51:350–359.
- Price, T., D. Schluter, and N. E. Heckman. 1993. Sexual selection when the female directly benefits. *Biological Journal of the Linnean Society* 48:187–211.
- Proctor, H. C. 1991. Courtship in the water mite *Neumania papillator*: males capitalize on female adaptations for predation. *Animal Behaviour* 42:589–598.
- Ptacek, M. B., and J. Travis. 1997. Mate choice in the sailfin molly, *Poecilia latipinna*. *Evolution* 51:1217–1231.
- Reeve, H. K., and P. W. Sherman. 1993. Adaptation and the goals of evolutionary research. *Quarterly Review of Biology* 68:1–32.
- Reynolds, J. D., and M. R. Gross. 1990. Costs and benefits of female mate choice: is there a lek paradox? *American Naturalist* 136:230–243.
- Rodd, F. H., K. A. Hughes, G. F. Grether, and C. T. Baril. 2002. A possible non-sexual origin of mate preference: are male guppies mimicking fruit? *Proceedings of the Royal Society of London B* 269:475–481.
- Rosenthal, G. G., and C. S. Evans. 1998. Female preference for swords in *Xiphophorus helleri* reflects a bias for large apparent size. *Proceedings of the National Academy of Sciences of the USA* 95:4431–4436.
- Ryan, M. J. 1990. Signals, species, and sexual selection. *Oxford Surveys in Evolutionary Biology* 7:157–195.
- . 1998. Sexual selection, receiver biases, and the evolution of sex differences. *Science* 281:1999–2003.
- Ryan, M. J., and A. Keddy-Hector. 1992. Directional patterns of female mate choice and the role of sensory biases. *American Naturalist* 139(suppl.):S4–S35.
- Ryan, M. J., and A. S. Rand. 1990. The sensory basis of sexual selection for complex calls in the túngara frog, *Physalaemus pustulosus* (sexual selection for sensory exploitation). *Evolution* 44:305–314.
- . 1993. Sexual selection and signal evolution: the ghost of biases past. *Philosophical Transactions of the Royal Society of London B* 340:187–195.
- Ryan, M. J., J. H. Fox, W. Wilczynski, and A. S. Rand. 1990. Sexual selection for sensory exploitation in the frog *Physalaemus pustulosus*. *Nature* 343:66–67.
- Ryan, M. J., S. M. Phelps, and A. S. Rand. 2001. How evolutionary history shapes recognition mechanisms. *Trends in Cognitive Sciences* 5:143–148.
- Ryan, M. J., W. Rand, P. L. Hurd, S. M. Phelps, and A. S. Rand. 2003. Generalization in response to mate recognition signals. *American Naturalist* 161:380–394.
- Schluter, D., and T. Price. 1993. Honesty, perception and population divergence in sexually selected traits. *Proceedings of the Royal Society of London B* 253:117–122.
- Shaw, K. 1995. Phylogenetic tests of the sensory exploitation model of sexual selection. *Trends in Ecology & Evolution* 10:117–120.
- Sherman, P. W., and H. K. Reeve. 1999. Sexual selection and sensory exploitation. *Science* 283:1083a.
- Sherman, P. W., and L. L. Wolfenbarger. 1995. Genetic correlations as tests for sensory exploitation. *Trends in Ecology & Evolution* 10:246–247.
- Shuster, S. M., and M. J. Wade. 2003. *Mating systems and strategies*. Princeton University Press, Princeton, NJ.
- Smith, C., L. Barber, R. J. Wootton, and L. Chittka. 2004. A receiver bias in the origin of three-spined stickleback mate choice. *Proceedings of the Royal Society of London B* 271:949–955.
- Weller, S. J., N. L. Jacobson, and W. E. Conner. 1999. The evolution of chemical defences and mating systems in tiger moths (Lepidoptera: Arctiidae). *Biological Journal of the Linnean Society* 68:557–578.
- West-Eberhard, M. J. 1984. Sexual selection, competitive communication and species-specific signals in insects. Pages 283–324 in T. Lewis, ed. *Insect communication*. Academic Press, New York.