A Guide to Sexual Selection Theory

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Abstract

Mathematical models have played an important role in the development of sexual selection theory. These models come in different flavors and they differ in their assumptions, often in a subtle way. Similar questions can be addressed by modeling frameworks from population genetics, quantitative genetics, evolutionary game theory, or adaptive dynamics, or by individual-based simulations. Confronted with such diversity, nonspecialists may have difficulties judging the scope and limitations of the various approaches. Here we review the major modeling frameworks, highlighting their pros and cons when applied to different research questions. We also discuss recent developments, where classical models are enriched by including more detail regarding genetics, behavior, demography, and population dynamics. It turns out that some seemingly well-established conclusions of sexual selection theory are less general than previously thought. Linking sexual selection to other processes such as sex-ratio evolution or speciation also reveals that enriching the theory can lead to surprising new insights.

1. INTRODUCTION

Direct benefits of choice: an increase in fecundity or survival of a choosy female that is unrelated to the genotypes of her offspring

Indirect benefits of choice: an increase in reproductive value of a choosy female that is caused by the genotypes of her offspring

Sexual selection is the process by which individuals compete for access to mates and fertilization opportunities (Andersson 1994, Jones & Ratterman 2009). Darwin (1871) developed the concept of sexual selection to explain the evolution of exaggerated and flamboyant characters such as calls, odors, ornaments, and conspicuous behaviors that are present in one sex only and cannot be easily explained as adaptations to the ecological conditions of a species. Darwin was well aware of the complex nature of sexual selection, "depending as it does, on the ardour of love, the courage, and the rivalry of the males, as well as on the powers of perception, the taste, and will of the female" (Darwin 1871, p. 296). Due to this interdependence of coevolving male and female traits, the essential features of sexual selection are inherently difficult to capture in verbal theories. Yet more than a century would have to pass after Darwin's seminal work before students of sexual selection started to develop mathematical models to capture the complexity of sexual selection in a rigorous fashion. Driven by these models, the empirical study of sexual selection has matured into one of the most active fields in evolutionary biology (Andersson & Simmons 2006).

There are numerous reasons why sexual selection models tend to be more complicated than "standard" models of natural selection. First, whereas models of natural selection often make the simplifying assumption of asexual reproduction or random mating, sexual reproduction and nonrandom mating lie at the heart of sexual selection. Second, natural selection models tend to avoid the intricacies of multilocus genetics. In contrast, sexual selection models are intrinsically multivariate because they reflect the coevolution of mating preferences, ornaments, and, in the case of the "good genes" process, variation in genetic quality. Moreover, the associations (linkage disequilibria) between traits or between preferences and traits are often crucial to understanding the evolutionary outcome (Lande 1981, Iwasa et al. 1991). Third, natural selection models tend to be based on a single fitness component, whereas sexual selection reflects the interplay of viability selection (e.g., costs of ornaments, costs of choosiness), fecundity selection (e.g., trade-offs between parental care and mating opportunities), and selection on mating and fertilization rates. Fourth, sexual selection models have to address sex differences, such as the sex-limited expression of traits and differences in the strength and direction of selection between the sexes. Fifth, as a consequence of sex-differential selection, genetic details may play a more prominent role than they do in other evolutionary models. In particular, autosomal versus sex chromosomal inheritance may strongly affect the outcome of evolution. Sixth, the coevolution between the sexes often takes the form of an evolutionary arms race, resulting in ongoing oscillations or even more complex nonequilibrium dynamics. Accordingly, the analysis of sexual selection often necessitates more refined dynamical approaches than those used in classical equilibrium-oriented methods (Gavrilets & Hayashi 2005, Van Doorn & Weissing 2006). Seventh, sexual selection is intrinsically linked to other processes such as sex-ratio evolution (Trivers & Willard 1973), the evolution of parental care (Trivers 1972), and speciation (Ritchie 2007, Weissing et al. 2011). It is becoming increasingly clear that robust conclusions on the outcome of sexual selection can be obtained only if such processes are explicitly included in the models (e.g., Kokko & Jennions 2008, Fawcett et al. 2011).

Given all these intricacies, it is no wonder that no single model has been able to capture all relevant aspects of sexual selection in a fully satisfactory way. Therefore, various modeling approaches have been developed, each of which has specific strengths and weaknesses. In Section 2, we briefly review these approaches, pointing out their scope and limitations. Section 3 provides an overview of the potential benefits (and costs) of mate choice behaviors. We discuss the relative importance of direct versus indirect benefits of choice and some recent insights, such as the realization that the classical Fisher model can exhibit ongoing oscillations of preferences and ornaments. In Section 4, we address the recent trend of adding mechanistic detail

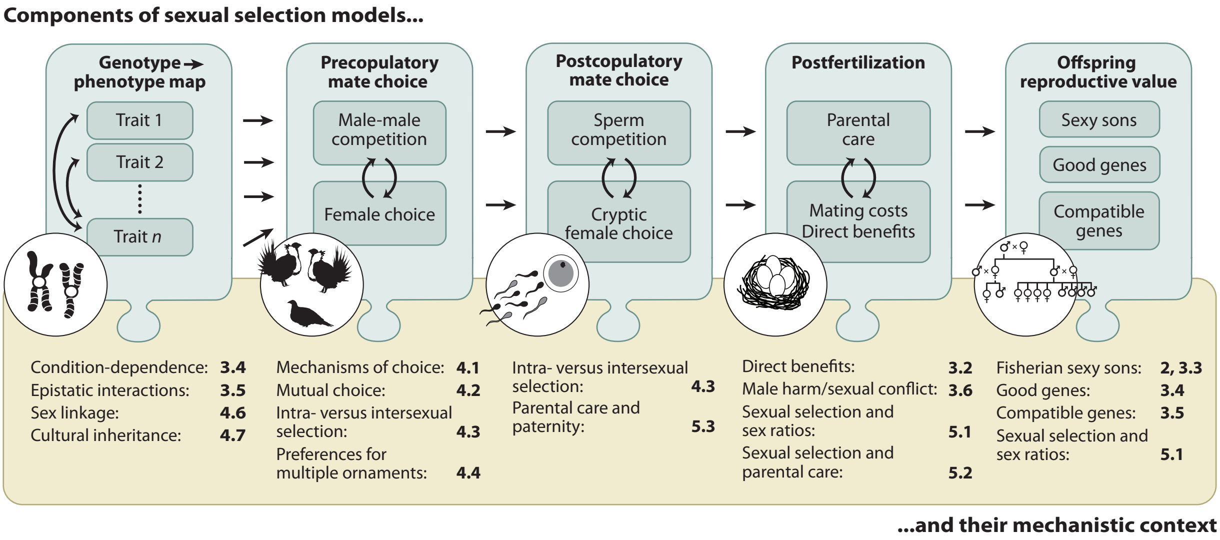

Figure 1

A global overview of the main components of sexual selection theory. Bold numbers refer to corresponding sections of this review.

to the classical models of sexual selection. Research shows that some seemingly well-established results are less robust than anticipated by "standard" theory. Finally, Section 5 discusses the implications of taking a more integrative approach and linking sexual selection to other evolutionary processes such as the evolution of sex, sex-ratio evolution, or speciation. **Figure 1** provides a summary of the various components of sexual selection theory that are discussed here. Throughout this review, the focus is on models that describe the evolution of female preferences for male ornaments, as this comprises the majority of work on the subject. Recent studies that focus on the evolution of male preferences are discussed in Section 4.2.

2. MODELING APPROACHES

The evolutionary process that underlies sexual selection can be mathematically described in a variety of ways (Dercole & Rinaldi 2008, ch. 2). Here we discuss the pros and cons of four of the most widely used descriptions of evolutionary change within the context of sexual selection: population genetics, quantitative genetics, invasion analysis, and individual-based simulations (Pen & Weissing 2000, Fawcett et al. 2007). The sidebar Four Implementations of the Fisher Process and **Figure 2** illustrate the application of the various modeling frameworks to the Fisher process, highlighting the congruencies and differences between the various approaches (for a more elaborate explanation, also see the **Supplemental Text**; for all **Supplemental Material**, follow the link from the Annual Reviews home page at **http://www.annualreviews.org**).

Supplemental Material

Fisher process: indirect selection on female preference caused by linkage disequilibrium with directly selected male ornament; leads to self-reinforced runaway selection

2.1. Population Genetics

Population genetics provides a description of evolution in terms of changes in genotype frequencies (see sidebar, Four Implementations of the Fisher Process). In principle, a population genetics framework is the most comprehensive approach to understanding sexual selection, as it directly models the evolutionary dynamics in terms of changing genotype frequencies. Whenever genetic

FOUR IMPLEMENTATIONS OF THE FISHER PROCESS

In a seminal contribution to sexual selection theory, Fisher (1915) predicted that female preferences could evolve through a self-reinforcing runaway process. Fisher argued that, once a female preference for a certain ornament has gained a foothold in a population (for whatever reason), both the preference and the ornament are subject to positive selection, but for different reasons. For the ornament, the argument is simple: Ornamented males will have a mating advantage if sufficiently many females mate preferentially with such males. For the preference, the argument is more sophisticated because selection on the preference is indirect. Because females with a strong preference tend to mate with males with a pronounced ornament, preference and ornament alleles often co-occur in the offspring of such matings, leading to a statistical association among these alleles. As a consequence, positive selection on the ornament will induce correlated positive selection on the preference. Hence, preferences induce the evolution of ornaments and subsequently become selected owing to their association with the ornament. Fisher realized that this self-reinforcing process could explain the huge exaggeration of sexual ornaments observed in many organisms. Interestingly, Fisher's arguments apply to arbitrary ornaments. In other words, ornaments that evolved through the so-called Fisher process do not necessarily indicate any inherent quality of their bearers. Notice that Fisher's argument on the statistical association between preference and ornament genes does not require the physical linkage of preference and ornament loci on the same chromosome.

For many decades, Fisher's ideas were greeted with skepticism. This verbal theory, deriving far-reaching and counterintuitive predictions from indirect processes and the emergence of statistical associations, was in need of a sound quantitative underpinning. Such would not be established until the 1980s, when models from quantitative genetics (Lande 1981) and population genetics (Kirkpatrick 1982) revealed the efficacy of the Fisher process.

Population genetics. Central to the population genetics approach is its ability to track genotype frequencies. Kirkpatrick's (1982) model of the Fisher process is a textbook example of a population genetics model of sexual selection. The model considers two haploid gene loci: (*a*) the female preference locus P with alleles P_0 (no preference; random mating) and P_1 (preference for mating with males carrying an ornament trait) and (*b*) the male trait locus T with alleles T_0 (no ornament) and T_1 (having a costly ornament). The relative allele frequencies of the preference and trait alleles are denoted by p and t, respectively, whereas the linkage disequilibrium parameter D describes the statistical association between alleles P_1 and T_1. As noted in the **Supplemental Text** (see also Bulmer 1994), the change in allele frequencies and genetic association from one generation to the next is described by equations of the form

$$\Delta t = \frac{1}{2} t(1-t)A, \qquad 1.$$

$$\Delta p = \frac{1}{2} DA, \qquad 2.$$

and

$$\Delta D = \text{something complicated}. \qquad 3.$$

A is a function of p and t that describes the net effect of selection on the ornament (a balance between viability selection against the ornament and the mating advantage of ornamented males). Equation 2 shows that p changes only if $D \neq 0$, that is, if there is a statistical association between trait and preference alleles. A detailed analysis of the system represented by Equations 1, 2, and 3 reveals that, starting at zero, D becomes positive. As shown in **Figure 2*a***, the system converges either to loss ($t = 0$) or fixation ($t = 1$) of the ornament or to a line of internal equilibria (given by $A = 0$). The line of internal equilibria corresponds to those combinations of t and p where the costs of carrying an ornament in terms of higher mortality are exactly balanced by the mating advantage of ornamented males. The whole set of equilibria is stable in the sense that selection prevents movements away from it, but each individual equilibrium is only neutrally stable, meaning that stochastic fluctuations can lead to shifts in p and t along the line of equilibria.

Quantitative genetics. Rather than tracking genotype frequencies, the quantitative genetics approach describes evolution in terms of changes of average phenotypic values. In the classical model by Lande (1981), the (phenotypic) values of a male ornament of size t and a female preference of intensity p are autosomally inherited, sex-limited, normally distributed traits with means $\bar{t}$ and $\bar{p}$. As shown in the **Supplemental Text** (see also Mead & Arnold 2004), the change in these means from one generation to the next can be described by the following equations:

$$\Delta \bar{t} = \tfrac{1}{2} G_t \beta_t; \qquad 4.$$

$$\Delta \bar{p} = \tfrac{1}{2} G_{tp} \beta_t. \qquad 5.$$

Here β_t is the total force of directional selection acting on the ornament (which is given by a combination of natural selection against and sexual selection in favor of large ornament size) (see Equation A7 in the **Supplemental Text**). The system does not include a corresponding term for the preference, because $\beta_p = 0$ in the absence of direct costs and benefits of choosiness. G_t is the additive genetic variance of the ornament, and G_{tp} is the additive genetic covariance between trait and preference. Equation 4 describes the evolution of the male trait under direct selection, whereas Equation 5 describes the correlated evolution of the female preference, which is mediated by the (positive) covariance between trait and preference. Like the system represented by Equations 1, 2, and 3, the system noted by Equations 4 and 5 has a line of equilibria. These equilibria correspond to the solutions of $\beta_t = 0$ (where natural and sexual selection are exactly balanced). **Figure 2*b*** shows when the line of equilibria is stable (which happens when the slope of the line of equilibria is larger than G_{tp}/G_t); if the covariance between trait and preference is very large, the line can also be unstable, leading to a never-ending runaway moving from the line with ever-increasing speed.

Invasion analysis. Here we briefly highlight a model of the Fisher process by Pen & Weissing (2000), which combines a reproductive-value approach with methods from adaptive dynamics theory. The model considers a class-structured population consisting of females and two types of males: nonornamented males ($♂_0$) and males expressing an ornament ($♂_1$) reducing their viability by a factor $1 - s$. Evolvable traits are the females' preference p for mating with ornamented males and the tendency t of a male to develop the ornament (i.e., the tendency to become a type-1 male). The aim is to find the evolutionarily stable values p^* and t^* of preference and ornament, respectively. As shown in the **Supplemental Text**, the fitness $W(t, p \mid t^*, p^*)$ of a rare mutant of type (t, p) in a resident population of type (t^*, p^*) can be derived systematically from life-history considerations. Evolutionarily stable strategies can be determined by inspecting the (total) derivatives of the fitness function W with respect to t and p at (t^*, p^*). These are of the form

$$dW/dt = (1 - s)v_{m1} - v_{m0}, \qquad 6.$$

$$dW/dp = b_{pt} \cdot ((1 - s)v_{m1} - v_{m0}), \qquad 7.$$

where v_{m1} and v_{m0} are the reproductive values of ornamented and nonornamented males in the resident population and b_{pt} is the slope of the regression of the female preference on the male trait, which describes the statistical association between trait and preference and is assumed to be positive. At an evolutionary equilibrium, both derivatives in Equations 6 and 7 have to be zero. This is the case when $(1 - s)v_{m1} = v_{m0}$, that is, when viability costs of the ornament are exactly balanced by the mating advantage provided by the ornament. As before, there is a line of equilibria (**Figure 2*c***), and the approach to this line is governed by the canonical equation of adaptive dynamics.

Individual-based simulations. As indicated by **Supplemental Figure 2**, an individual-based simulation keeps track of a finite population of individuals, each of which has a set of properties (e.g., genotypes, sex, degree of preference, degree of ornamentation). Individuals interact, and owing to their properties and chance events, they differ in survival, mating success, and fecundity. During reproduction, individuals transmit (part of) their heritable properties to their offspring. Variation arises as a result of mutation. The simulation then tracks evolutionary change over the course of generations. **Figure 2*d*** shows the outcome of such a simulation resulting from the implementation of the Fisher process by Fawcett et al. (2007). In this simulation model, each individual harbors two loci (both with many alleles): one coding for an ornament of size t and one coding for a preference of intensity p. Making similar assumptions on the mortality costs of the ornament and the mating process as in Lande's (1981) model (see the **Supplemental Text**), the simulated population rapidly converges to a line of equilibria and subsequently drifts along this line. Interestingly, distinct behaviors (ongoing oscillations) can occur in the same model for different parameter settings (see Section 3.3 and **Figure 3*d***).

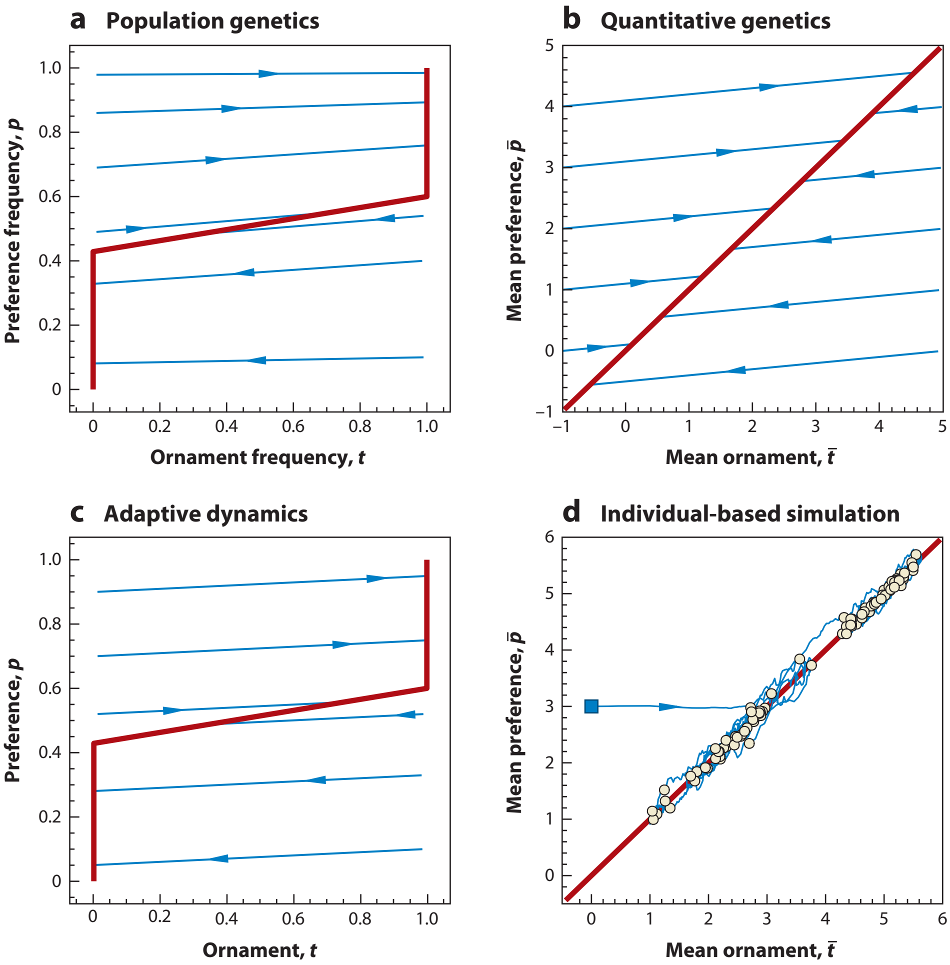

Figure 2

Four implementations of the Fisher process: (*a*) dynamics of Kirkpatrick's (1982) population genetics model, (*b*) dynamics of Lande's (1981) quantitative genetics model, (*c*) adaptive dynamics model by Pen & Weissing (2000), and (*d*) individual-based simulation based on the model by Fawcett et al. (2007). Red lines represent equilibria of the model (line of equilibrium), whereas blue lines with arrowheads indicate representative trajectories of (*a*–*c*) the dynamical systems as well as (*d*) a single simulation, with the square indicating the starting point of the simulation and circles indicating the state of the population at 50 generation intervals.

processes are crucial for a proper understanding of sexual selection, a population genetics model is typically the model of choice. A population genetics framework is often indispensable when studying the implications of a genetic architecture (such as sex linkage, recombination or epistatic gene interactions) on the course and outcome of sexual selection. Moreover, population genetics models are useful for delineating the scope and limitations of less comprehensive frameworks like quantitative genetics or adaptive dynamics.

Although population genetics methods have been very important for theory development, they are less popular in terms of practical applications for at least two reasons. First, despite enormous advances in unraveling the genetic underpinning of sexual characters (Chenoweth &

McGuigan 2010), the genetic basis of traits and preferences is generally not known. Instead of making hypothetical assumptions regarding the underlying genetics, students of sexual selection tend to find quantitative genetics (Section 2.2) and phenotypic approaches (Section 2.3) more appealing because these approaches do not specify the genetics and essentially treat it as a black box. Second, population genetics models quickly become mathematically intractable if several loci with genes of large effects are involved. Therefore, in practice, most population genetics models address only a small number of haploid loci in a setting of discrete, nonoverlapping generations. Perhaps more importantly, mathematical tractability necessitates that investigators make highly simplifying assumptions concerning the phenotypic level. As a result, addressing the mechanisms of behavioral interactions or complex trade-offs between fitness components becomes difficult.

However, the advent of the quasi-linkage-equilibrium (QLE) technique (Barton & Turelli 1991, Kirkpatrick et al. 2002; for a critical appraisal, see Pomiankowski & Bridle 2004) enabled researchers to overcome some of the disadvantages of the population genetics approach. Assuming that selection is weak relative to the rate of recombination, investigators avoid to some extent the intricacies of multilocus genetics by approximating the (high-dimensional) dynamics of genotype frequencies by the dynamics of allele frequencies and lower-level genetic associations (e.g., Kirkpatrick & Hall 2004, Servedio 2004, Greenspoon & Otto 2009). The conclusions obtained are often remarkably robust and not dependent on genetic detail or the mating system (e.g., Kirkpatrick & Barton 1997). However, due to the inherent assumption of weak selection, it is not always clear whether, and to what extent, the predictions of the QLE approach extend to scenarios involving strong selection (e.g., Servedio 2004).

Quasi-linkage-equilibrium (QLE) technique: technique to simplify population/quantitative genetics models by neglecting intricate interaction terms, assuming that selection is weak relative to recombination

2.2. Quantitative Genetics

Quantitative genetics is a widely used technique to model sexual selection (Mead & Arnold 2004). Quantitative genetics describes evolution at the phenotypic level but still takes account of genetics (to a certain extent), thus yielding plausible assumptions on the transmission of phenotypic traits from parents to their offspring. The latter are encapsulated in the so-called G-matrix, the collection of additive genetic variances and covariances of the phenotypic traits in question. As illustrated in the Four Implementations of the Fisher Process sidebar (and in more detail in the **Supplemental Text**), the change of (mean) traits and preferences from one generation to the next is characterized by a relatively simple equation that inspires considerable insights into the dynamics of sexual selection. However, the simplicity and elegance of the quantitative genetics approach comes at a cost, as many assumptions have to be made to justify this approach. Moreover, these assumptions are often implicit and not easily testable. One key assumption of the quantitative genetics approach is that breeding values have a multivariate normal distribution, which has been subject to considerable debate (Barton & Turelli 1991). Another common assumption is that viability costs are given by exponential functions (see the **Supplemental Text**). Assumptions like these are mathematically convenient because they assure that the distribution of phenotypes at the mating stage remains Gaussian. However, they are not always realistic and may be misleading. For example, the Fisher process has a stronger tendency to induce ongoing oscillations of traits and preferences if the costs of choosiness are related to the availability of the preferred males.

Supplemental Material

Quantitative genetics models often treat additive genetic variances and covariances as fixed parameters (e.g., Pomiankowski et al. 1991). However, selection affects the G-matrix entries (for a recent review, see Arnold et al. 2008) both indirectly by shaping the mutation rates and directly via the depletion of additive genetic variation or the buildup of additive genetic covariation (i.e., linkage disequilibria) due to assortative mating. Under certain assumptions regarding mutation, recombination, and the strength of selection, the evolution of the G-matrix can be studied within the quantitative genetics framework by making use of the QLE approach (Barton & Turelli 1991, Pomiankowski & Iwasa 1993, Walsh & Lynch 2013). In most cases, however, individual-based simulations provide a more convenient and versatile tool to assess the evolution of the G-matrix (e.g., Arnold et al. 2008).

Studies of quantitative trait loci (QTL) have shown that quantitative traits are often affected by at least some major genes of large effect. In such cases in which one or more quantitative traits coevolve with large-effect modifiers, a hybrid approach can be taken (Lande 1983). The same type of approach can be used when studying the interplay of sexual selection and segregation distortion or sex-chromosome evolution.

Invasion fitness: the exponential growth rate of a rare mutant in an environment determined by the common resident strategy

Reproductive value: the long-term expected genetic contribution of an individual to the population

2.3. Invasion Analysis

Whereas quantitative genetics is based on the assumption that a continuous distribution of phenotypes (and typically also genotypes) is available at all times, evolutionary game theory, adaptive dynamics, and other phenotypic approaches (Weissing 1996) consider the opposite extreme of a monomorphic resident population that is repeatedly challenged by the invasion attempts of rare mutants. The underlying idea is that evolution proceeds by a series of subsequent invasion and trait-substitution events. The dynamics of this process can be described by the canonical equation of adaptive dynamics (Dieckmann & Law 1996), where

$$\frac{\mathrm{d}}{\mathrm{d}\tau}\mathbf{x}^{*} = z\mathbf{M}\nabla W(\mathbf{x}|\mathbf{x}^{*})$$

gives a description of change in the vector of characters $\mathbf{x}^{*}$ over evolutionary time τ through a successive series of invasion-substitution events. z reflects the variation in the rate of occurrence of mutations, whereas the mutational variance-covariance matrix $\mathbf{M}$ describes how a single mutation affects the different traits. $\mathbf{M}$ plays a role very similar to that of the additive genetic variance-covariance G-matrix in quantitative genetics. The direction of selection is given by the invasion-fitness gradient $\nabla W(\mathbf{x}|\mathbf{x}^{*})$ of a rare mutant $\mathbf{x}$ invading in a population of $\mathbf{x}^{*}$ residents. Usually, the exact dynamics of how a mutant coexists with and replaces the resident are not modeled explicitly. Instead, population dynamical considerations are used to derive an expression for the invasion fitness of rare mutants (Metz et al. 1992). This fitness function is then systematically analyzed to identify evolutionarily stable strategies and other potential end points of the evolutionary process (Geritz et al. 1998, McGill & Brown 2007, Dercole & Rinaldi 2008). In a life-history context, it is convenient to frame invasion fitness in terms of reproductive values (Taylor 1996).

Because such phenotypic approaches neglect most genetic intricacies, they can address environmental feedbacks, frequency and density dependence, and age structure in more detail than can other approaches. As a result, recent models investigating the interaction of sexual selection with parental care (Kokko & Jennions 2008) or sex allocation (Fawcett et al. 2011) rely on a phenotypic approach. Nonetheless, the shortcomings of phenotypic models should not be ignored. One key assumption is that populations are nearly monomorphic. Because variation in male ornamentation is essential to the evolution of female choice, additional assumptions are necessary to maintain genetic variation (see the **Supplemental Text**), but the amount of variation that is maintained can alter the outcome in surprising ways (e.g., McNamara et al. 2008). Relaxing the assumption that mutants differ only slightly from the resident can also strongly affect the evolutionary dynamics (e.g., Wolf et al. 2008). Another disadvantage is that phenotypic models do not easily allow for a dynamical description of linkage disequilibria. Furthermore, most of these models assume that evolution proceeds at a much slower timescale than the ecological dynamics, even though it is known that sexually selected characters may evolve rapidly (e.g., Van Doorn et al. 2001, Swanson & Vacquier 2002, Shirangi et al. 2009).

2.4. Individual-Based Simulations

Individual-based simulations (see sidebar, Four Implementations of the Fisher Process) provide a flexible and easily extendable way of modeling complicated scenarios with a high degree of realism [e.g., environmental and demographic stochasticity, spatial population structure (Fromhage et al. 2009), complex genotype-phenotype maps (Ten Tusscher & Hogeweg 2009), a concrete representation of the sensory system (Fuller 2009)]. This is a clear advantage over all the simplifying assumptions made by analytical models. For example, the presence of stochasticity in individual-based simulations allows for a straightforward assessment of the importance of drift (Uyeda et al. 2009), which is much harder to assess in analytical models of sexual selection. On the downside, running complex simulations is often computationally demanding, limiting the number of parameter settings that can be investigated. If the model contains only 10 parameters (most have many more), then $3^{10} \approx 60,000$ simulations are needed to consider all the combinations of only three values for each parameter. Moreover, replicates of each simulation have to be run to cope with the stochasticity inherent in each simulation. Because this is not always feasible, it is often not clear whether and to what extent a given set of simulations is representative. Nonetheless, we believe that the disadvantages of simulation models are often overemphasized (e.g., McElreath & Boyd 2007, p. 8), especially given advantages such as relative ease of implementation and applicability to all kinds of situations. Perhaps most importantly, individual-based simulations can nicely complement an analytical approach. In fact, the theoretical justification of analytical approaches is often restricted to a narrow domain (e.g., weak selection), and simulations are useful for exploring the robustness and general applicability of analytical predictions beyond this domain.

2.5. A Plea for Pluralism

The famous quote that "each disadvantage has its advantage" (by the former Dutch football player Johan Cruijff) also applies to the various modeling frameworks considered thus far (**Table 1**). Accordingly, the choice of approach should depend mainly on the research question being tackled. But how should we deal with the often unrealistic assumptions made by virtually all approaches? Richard Levins's (1966, p. 423) statement that "our truth is the intersection of independent lies" provides an answer: If multiple modeling frameworks with varying underlying assumptions arrive at a similar outcome, we can be confident that this conclusion is robust and not just a result of some limiting assumptions. Hence, the use of multiple modeling frameworks in parallel helps us to delineate the scope and limitations of the predictions of sexual selection theory.

3. THE BENEFITS AND COSTS OF CHOICE

Much debate on sexual selection theory has focused on the benefits driving the evolution of mating preferences. Females can benefit directly from expressing a preference, if the resulting choice of mates gives them a higher viability or fecundity than they would have had without the preference (Møller & Jennions 2001). Alternatively, the particular choice of mating partners may lead choosy females to have offspring with a higher reproductive value (Kokko et al. 2002), for example, through attractive sons (Fisher 1915) or offspring of higher intrinsic quality (Zahavi 1975), in which case benefits are said to be indirect. In this context, offspring reproductive values often refer to offspring lifetime reproductive success, although there may be cases in which the reproductive success of grandoffspring or later generations should also be considered. Here, we highlight the major assumptions underlying models of direct and indirect benefits of sexual selection.

Table 1 Pros and cons of various modeling approaches[a]

	Population genetics	Quantitative genetics	Invasion approaches	Individual-based simulations
Pros	Most comprehensive description of sexual selection; explicit inclusion of genetic aspects (recombination, linkage disequilibrium); transparent model assumptions; provides justification of quantitative genetics approach	Focus on (measurable) phenotypic variation; method applicable to systems with limited information on genetics; model parameters (additive genetic variances and covariances) can be estimated	Minimal assumptions on genetics allow most comprehensive description of phenotypic level; based on transparent fitness concept; fitness function derived from first principles, allowing consideration of demography, class structure, frequency, and density dependence	Most versatile approach; few restrictions on model structure, allowing for complicated genetic architectures and intricate selection scenarios; natural inclusion of demographic and environmental stochasticity
Cons	Mainly suited for discrete variation; tractable only for highly simplified fitness scenarios; limited applicability because the genetic basis of most traits is unknown; analytical tractability limited to a small number of loci with few alleles	Assumptions (e.g., normal distribution of additive effects) often not met; G-matrix often assumed constant; difficult to include complex genetics, complex life histories, and complex fitness scenarios (age structure, trade-offs, etc.)	Assumption of monomorphic population clearly unrealistic; includes only simplistic genetics, although genetic associations may be crucial; multivariate adaptive dynamics theory not well developed	Danger of cherry-picking because only a small part of parameter space can be investigated; interpretation of results often subjective; difficult to judge the generality of conclusions; "coarse" description of simulation programs
Solutions	In the case of weak selection, powerful techniques (e.g., quasi-linkage equilibrium) are becoming available to address complex multilocus problems and fairly complex fitness scenarios	Methods for studying the evolution of the G-matrix are becoming more broadly available; hybrid models combine a quantitative genetic approach with population genetics and adaptive dynamics	Application of adaptive dynamics to genotypic level; combination of adaptive dynamics approach with genetics approaches	Application of simulations to systems in which analytical results are already available as a test case

[a] See Section 2 for a more detailed discussion of these modeling approaches.

3.1. No Benefits: Sensory By-Products

Female preferences can evolve in the absence of any benefits related to mate choice, for example, as a pleiotropic by-product of natural selection on the sensory system (Kirkpatrick 1987, Kirkpatrick & Ryan 1991). This is confirmed by models employing evolving neural networks (mimicking a simple sensory system), which often lead to mating preferences (e.g., in favor of symmetric mates) as a by-product (reviewed in Enquist & Ghirlanda 2005 and Phelps 2007). Whereas early models based their conclusions on highly simplified network architectures (Arak & Enquist 1993; for a critique, see Dawkins & Guildford 1995), more recent models are tailored to the sensory system of particular organisms. For example, Fuller's (2009) model based on the sensory system of guppies (*Poecilia reticulata*) reveals that details of the sensory architecture, such as the number of output neurons, can strongly affect the evolution of sensory biases. It remains to be seen which types of sensory architecture are most conducive to the evolution of preferences as sensory by-products, on which external conditions (i.e., the sensory environment) certainly have a large influence (Endler & Basolo 1998). In addition, there are few predictions on the long-term evolution of preferences that evolve as by-products of natural selection. Will pleiotropy in preferences always decay over time (when pleiotropic preferences lead to suboptimal female mating decisions) (Arnqvist 2006), or can we find situations in which the coevolutionary dynamics of both natural and sexual selection enhance the maintenance of pleiotropic preferences?

3.2. Direct Benefits

Direct selection on female choosiness occurs whenever the degree of choosiness is related to a female's survival and fecundity. Choosiness is often costly; for example, the search for mates can expose the female to predators, or females may risk ending up unfertilized (Kokko & Mappes 2005). As discussed below, even slight costs can override indirect benefits of choosiness, leading to the theoretical expectation that sexual selection driven only by indirect benefits of choosiness is rare in nature (Kirkpatrick & Barton 1997, Cameron et al. 2003).

The evolution of female preferences can most easily be explained if females gain direct benefits from being choosy. One likely mechanism is when females prefer males that advertise their quality to provide paternal care: Illuminating models on this good-parent process have been made by Price et al. (1993) and Iwasa & Pomiankowski (1999). Direct-benefit models have received relatively little attention in the theoretical literature presumably because the underlying mechanisms seem transparent and not too challenging (or sufficiently counterintuitive) to modelers. However, a number of recent results indicate that direct-benefit mechanisms are not as straightforward as previously thought. For example, males may differ not only in parental ability but also in genetic quality, and these aspects of quality are not necessarily related. Hence, it matters what aspect of quality is being signaled and how to interpret male signals (Kokko 1998, Alonzo 2012). Moreover, mating with a male of high parental quality may not assure a high level of paternal care if such males tend to mate with many females and therefore have to distribute their care over many offspring (Cotar et al. 2008, Tazzyman et al. 2012). In addition, females can be expected to change their own care level depending on their choice of mates (Ratikainen & Kokko 2010). All this leads us to conclude that the theory of direct benefits of sexual selection deserves more attention than currently is devoted to it.

3.3. Indirect Benefits: The Fisher Process

The Fisher process relates to the scenario in which female preferences are maintained as a result of self-reinforcing selection (see sidebar, Four Implementations of the Fisher Process). The key benefit associated with the Fisher process is a greater number of grandoffspring: According to this theory, choosy females will produce attractive sons, which in turn will have a higher mating rate. These benefits are relatively small: The slightest costs of choosiness break down the line of equilibria and costly choosiness disappears from models of the Fisher process (Kirkpatrick 1982, Pomiankowski 1987, Bulmer 1989) (see **Figure 3*a***). However, the Fisher process can be rescued if additional mechanisms, such as a mutation bias (mutations that have mainly negative effects on male ornamentation) (Pomiankowski et al. 1991) (**Figure 3*b***) or migration bias (influx of migrant males with smaller ornaments) (Day 2000) (**Figure 3*c***), are included in the model. Even in the absence of such mutation or migration biases, the exaggeration of sexually selected traits beyond the naturally selected optimum is possible if the costs of choosiness and ornamentation are sufficiently weak (Hall et al. 2000). When this is the case, traits and preferences do not converge to equilibrium but oscillate forever on a limit cycle (B. Kuijper, L. Schärer, and I. Pen, unpublished manuscript)

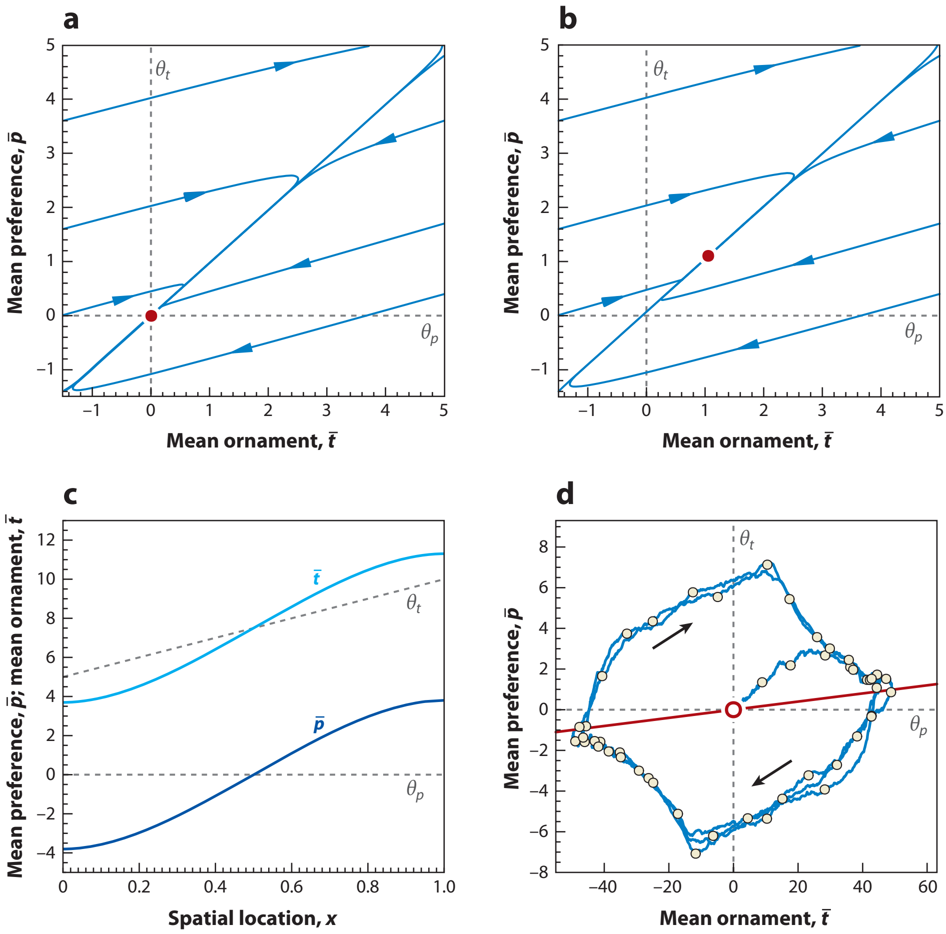

Figure 3

Costs of choice and the Fisher process. (*a*) In the presence of costly choice, the line of equilibria (see **Figure 2*b***) collapses to a single equilibrium point, coinciding with the naturally selected optima θ_t and θ_p of trait and preference, thus eliminating costly exaggeration of sexually selected traits (Pomiankowski 1987, Bulmer 1989). (*b*) Biased mutations tending to reduce ornamentation can "rescue" sexual selection, giving rise to an equilibrium point away from the naturally selected optimum (Pomiankowski et al. 1991). (*c*) Spatial variation and the influx of migrants with smaller ornaments can also lead to the exaggeration of trait t (*light blue line*) and preference p (*dark blue line*) beyond their naturally selected optima (*dotted lines*), which now vary along a spatial gradient (x axis) (Day 2000). (*d*) When the viability costs of preferences and traits are small, the equilibrium in panel *a* becomes unstable (indicated by the *red*, *open circle*) and the system converges to a limit cycle, corresponding to indefinite cycling of traits and preferences around the naturally selected optimum. Small circles indicate the state of the population in intervals of 200 generations.

(**Figure 3*d***). Similar cyclic dynamics were previously described in variants of the Fisher process with a curvilinear set of equilibria that ignored the costs of choice (Iwasa & Pomiankowski 1995).

3.4. Indirect Benefits: Good Genes

In good-genes scenarios of sexual selection, there is an evolution of female preferences for male indicators of heritable quality. Heritable "quality" is typically interpreted as enhanced offspring survival, but it should actually be interpreted to indicate enhanced offspring reproductive value (Kokko 2001, Kokko et al. 2002). Even if offspring inherit genes intrinsically favoring their viability, their survival may actually be lower than that of lower-quality offspring (for example, owing to intense signaling). This focus on reproductive values, in combination with the notion that all models of sexual selection, including the good-genes process, contain some element of the Fisher process, has led researchers to conclude that differences between the Fisher process and good-genes sexual selection are small and superficial (Kokko 2001, Kokko et al. 2002). However, good-genes sexual selection is conceptually different from the Fisher process in several ways. First, the dynamics of both processes are different: Whereas the Fisher process requires only coevolving preference and ornament genes, good-genes processes include at least one additional dimension (corresponding to heritable quality). Second, the evolution of a genetic correlation between trait and preference is a crucial aspect of the Fisher process (see sidebar, Four Implementations of the Fisher Process). In contrast, good-genes sexual selection still works (and, in fact, leads to a runaway process) even when such a correlation cannot be established (e.g., when preferences inherit exclusively through the matriline, in contrast to ornaments inherited exclusively through the patriline). In cases like this, preferences can evolve through a genetic correlation with alleles related to heritable quality. Third, in the Fisher process, ornaments and preferences are directly coupled; by definition, the ornament is the target of the preference. Discussions of whether the ornament can act as a reliable indicator of genetic quality (i.e., male attractiveness) are irrelevant for the Fisher process, even though they have played a dominant role in the context of good-genes processes. Hence, although it is important to point out the similarities between indirect-benefit models of sexual selection (Kokko et al. 2002), the conceptual differences between the Fisher process and good-genes processes should not be neglected.

Good-genes sexual selection: indirect selection on female preference caused by linkage disequilibrium with directly selected male ornament; leads to self-reinforced runaway selection

Another debate regarding good-genes models of sexual selection has centered on the question of how females can reliably distinguish between males of different quality. According to Zahavi's (1975) handicap hypothesis, signals are reliable indicators of male heritable quality only if costs are associated with these signals. However, not all costly signals are reliable indicators of quality (Getty 2006). To separate the sheep from the goats, signals have been classified into different categories (Maynard Smith 1985; for formal definitions, see Van Doorn & Weissing 2006). Signals are condition dependent when the expression of a given signal is less costly for males of higher quality. Alternatively, signals are designated as revealing if for a given level of resource allocation into the development of an ornament high-quality males produce ornaments that are more pronounced than those of low-quality males. Whereas condition-dependent and revealing signals can evolve as reliable indicators of heritable quality (Andersson 1994), epistatic signals (which are neither condition dependent nor revealing) are usually considered unreliable and therefore cannot lead to the evolution of costly female preferences. However, several studies have reported the contrary. In a general model, Kirkpatrick & Barton (1997) show that—irrespective of the type of signal—the buildup of a correlation between male ornamentation and heritable quality can lead to indirect selection on the female preference (although this effect is weaker in the case of epistatic signals) (see also Siller 1998). Van Doorn & Weissing (2006) show that female preferences for epistatic signals can evolve if the coevolution of ornaments and preferences leads, not to a stable equilibrium, but to a limit cycle (as shown in **Figure 3*d***).

Another problem for good-genes sexual selection is that female preference for high-quality males can lead to the depletion of genetic variation in quality, commonly referred to as the lek paradox (for a review, see Kotiaho et al. 2008). A potential resolution to the lek paradox is the genic capture hypothesis (Rowe & Houle 1996). The central tenet of this hypothesis is that an individual's condition is determined by a large number of genes, providing a large mutational target so that some genetic variation in condition always exists. Indeed, sexual selection may cause the number of genes that underlie a signal to increase, giving rise to genic capture (Lorch et al. 2003).

Directional preferences: when all females prefer similar male phenotypes instead of basing their preference on their own genotype or state

3.5. Indirect Benefits: Compatible Genes

Whereas good-genes models assume that genetic quality is an intrinsic property of the genetic makeup of an organism, reality may not be that simple (Hunt et al. 2004, Puurtinen et al. 2009). For example, males may signal local adaptation (Proulx 2001, Reinhold 2004) or adaptation in contexts of frequency-dependent, disruptive selection (Van Doorn et al. 2009). In addition, offspring performance may not directly reflect the genetic quality of the parents if it is affected by epistatic interactions between paternally and maternally inherited genes. Epistatic interactions are a complicating factor for sexual selection theory: Depending on their own genotype, different females may prefer different types of males. The existence of sexually antagonistic variation (Albert & Otto 2005, Arnqvist 2011) or selection on heterozygosity and other forms of epistatic variation are further examples of such compatible-allele effects (Puurtinen et al. 2009). In general, such effects weaken the selection for preference alleles. However, recent models show that directional preferences can nevertheless evolve if certain conditions, such as biased mutations (Lehmann et al. 2007) or spatial variation in finite populations (Fromhage et al. 2009), are met.

3.6. Avoiding Male-Induced Costs: Sexual Conflict

A large body of literature has revealed that females may have to endure mating-related costs, such as seminal toxins or damage by male genital spines (e.g., Rice 1996, Arnqvist & Rowe 2005). Thus, resistance to harmful mating may be thought of as a mating preference, because it can restrict the potential set of mating partners (Halliday 1983). Importantly, selection for female resistance is direct, because any female that evolves higher levels of resistance reaps the benefits in terms of increased fecundity or survival (Kokko et al. 2006).

The most influential coevolutionary models envisage female resistance as a threshold character that causes females to mate only with those males that have harm-trait values that surpass the female's threshold (Gavrilets et al. 2001). Females that accept too many males will incur a fecundity cost on top of the mortality cost of developing a resistance trait. Depending on these costs, the course of evolution varies, but exaggeration of male harm and female resistance is a common outcome. The situation is substantially different when female resistance evolves in the form of insensitivity, making a female reluctant to mate with any male phenotype (Rowe et al. 2005). In this case, male harm is effectively neutralized by female insensitivity, and an evolutionary standstill is a likely outcome, showing that mechanisms with which female resistance is realized can strongly change conclusions. Sexual conflict models have to account for the further complication that females mating with the most persistent males may accrue indirect benefits because they will tend to produce more persistent sons. Although these indirect benefits are unlikely to recoup the direct costs of harm for the reasons stated above, they may nonetheless alter the coevolutionary dynamics substantially (Härdling & Karlsson 2009).

3.7. Multiple Costs and Benefits

Whereas a single benefit or cost component has been the focus of most models, the co-occurrence of multiple costs and benefits has hardly been explored (but see Iwasa & Pomiankowski 1999, Van Doorn & Weissing 2004, Härdling & Karlsson 2009). One particular aspect that deserves attention is the potential for trade-offs between direct and indirect benefits. For example, in the good-parent process, females may incur more direct benefits (i.e., more care) by mating with unattractive males that have few mating opportunities and, hence, can focus their care on a small number of offspring (e.g., Cotar et al. 2008, Tazzyman et al. 2012). These direct benefits are associated with indirect costs, as the sons sired by these males will not be attractive and thus have a limited mating rate. Such trade-offs may lead to condition-dependent choices (Cotton et al. 2006) in which some females prefer males that provide direct benefits and others prefer males with indirect benefits.

4. ADDING MECHANISTIC DETAIL TO SEXUAL SELECTION MODELS

Traditionally, sexual selection models incorporated the processes under study in an abstract and seemingly general way. Recent models tend to include more mechanistic detail, thereby making the models more specific but also more easily applicable to real systems. Here we highlight how seemingly general insights of traditional models can change when the mechanisms underlying sexual selection are explicitly incorporated.

4.1. The Mechanisms of Mate Choice

Mate-choice behaviors refer to any behavior that limits an individual's set of potential partners (Halliday 1983). Although any review on mate choice is eager to point out the behavioral and social complexities involved (Cotton et al. 2006), little has been done to integrate these notions with formal models of sexual selection. In practice, most models assume that females sample from an effectively infinite pool of males in which attractive males are more "apparent" to choosy females and are thus more easily encountered (e.g., Lande 1981, Kirkpatrick 1982). Because slight changes to these assumptions can dramatically affect an outcome (e.g., Seger 1985), the question of how females should optimally sample males in the face of costs and constraints arises. Optimal-sampling models predict that females should evaluate males sequentially and stop sampling when they sample a male that matches a certain threshold (Real 1990, Wiegmann et al. 2010), such that the value of this threshold may depend on the particular way females acquire information about the male phenotype distribution (e.g., Dombrovsky & Perrin 1994, Luttbeg 1996). Houle & Kondrashov (2002) show that sequential sampling in a good-genes model enhances sexual selection. By contrast, in classical models, the costs of preferences increase with the level of exaggeration beyond an abstract survival optimum. Thus, sampling costs allow a female to have very strong preferences as long as she is likely to encounter a suitable male within a limited number of samples. In general, this finding by Houle & Kondrashov (2002) shows that there is much to say for a further integration of mechanistic aspects of mate choice within models of sexual selection.

4.2. Mutual Choice and Sex-Role Reversal

The focus on female choice within many models denies the observed variation in choosiness between the different sexes that exists across taxa; this varies from exclusive female choice to male or mutual choice (Clutton-Brock 2007). In general, mutual choice evolves when both sexes exhibit sufficient variation in quality, but it is hampered by the possibility that choice may be more costly for the sex that competes most intensely for matings (Johnstone et al. 1996). Moreover, the intensity of competition among members of one sex may be a function of the amount of choice exerted by the opposite sex, indicating that the evolution of sex differences in mate choice is the result of a complicated feedback between choice and competition (see Kokko & Johnstone 2002, Kokko & Jennions 2008). To disentangle this, recent models have taken a self-consistent approach whereby individuals of each sex are considered to be either breeding (time out) or busy acquiring matings (time in). The time and mortality costs of each activity feed back on the densities of individuals that breed or that compete for mates, which subsequently influences the evolution of mate choice in each sex (Kokko & Jennions 2008). Using a version of this framework, Kokko & Johnstone (2002) found that mutual choice evolves only under restrictive conditions because choosiness in one sex immediately reduces the mean mating rate of the other sex, which subsequently becomes more competitive and less likely to evolve choice (see also Servedio & Lande 2006). Only when both the cost of breeding and the mate-encounter rates are high for both sexes does it pay for both males and females to be choosy (Kokko & Johnstone 2002).

4.3. Intrasexual versus Intersexual Selection

In addition to ornamentation that has evolved in the context of mate attraction, males may also evolve weapons or signals (i.e., badges of status) in the context of male-male competition. Although male ornaments may be used for both mate attraction and male-male competition, they have been the subject of little formal attention to date despite considerable empirical support (Berglund et al. 1996). A recent model by Veen (2008), however, considers the coevolution of female preferences for male signals that signal both dominance in male-male competition and quality to a female. Interestingly, whereas mate choice and male-male competition in isolation may lead to the evolution of such signals only under particular conditions (see Sections 2 and 3), the interaction between both processes appears to be particularly conducive to the evolution of male signals.

Focusing on the postcopulatory stage, a sound body of theoretical predictions on intrasexual selection (i.e., sperm competition) exists (Parker & Pizzari 2010). In addition, recent efforts have started to consider trade-offs between male investment in traits that increase a male's mating rate and his success in sperm competition (e.g., Tazzyman et al. 2009). However, the role of female choice in these contexts is only starting to be assessed (Ball & Parker 2003, Fromhage et al. 2008), and we know of no formal studies on the coevolution between female choice and heritable male traits that are directly related to ejaculate investment.

4.4. Preferences for Multiple Ornaments

Even though the vast majority of sexual selection models typically focus on single, univariate display traits, sexual displays often involve many different components (for recent reviews, see Candolin 2003, Bro-Jørgensen 2010). Most models that have formally investigated multiple ornaments are based on the redundant-signal hypothesis (Møller & Pomiankowski 1993) in which preferences evolve for multiple indicator traits reflecting the same quality. The widely accepted view is that there is only a limited scope for preferences based on these backup signals because females should always favor the most honest and reliable ornaments; preferences for any additional ornament will be tolerated only when its costs are sufficiently low (Schluter & Price 1993, Iwasa & Pomiankowski 1994) (**Supplemental Figure 1*a*** versus **Supplemental Figure 1*b***). Nonetheless, these analyses rely on equilibrium arguments, whereas more dynamical analysis shows that females can easily maintain preferences for multiple redundant ornaments through conflicts between males and females over the honesty of signaling (Van Doorn & Weissing 2006) (**Supplemental Figure 1*c***). Moreover, preferences for multiple ornaments can also easily evolve when each ornament signals a different aspect of quality (multiple messages) (Johnstone 1995, Van Doorn & Weissing 2004) (**Supplemental Figure 1*d***). Hence, in contrast to more classical models (e.g., Schluter & Price 1993), various studies note that the evolution of multiple indicators of quality does not appear as restrictive as previously thought. Yet, these recent studies generate as many new questions as they resolve: Can external factors, such as context dependence, also

Supplemental Material

be responsible for the maintenance of multiple preferences? For multiple ornaments, how much more likely is it that reproductive isolation a result of drift (e.g., Pomiankowski & Iwasa 1998)? These and other questions await further investigation.

4.5. Individual Variation in Ornamentation

Along with the inheritance of sexually selected characters, the large developmental variation and plasticity observed in sexually selected characters are also poorly understood (Pomiankowski & Møller 1995). To date, how sexual selection affects developmental variation has been investigated only in the context of condition-dependent indicator traits. In particular, a number of theoretical studies have investigated how indicator traits develop over an individual's life span (Kokko 1997, Rands et al. 2011). Interestingly, these studies find that low-quality males may express larger ornaments than do high-quality males because their higher mortality rate induces them to make a terminal investment to achieve matings. It remains to be seen if such dishonest signals are more widespread and extend to contexts in which individual variation is expressed in aspects other than variation in life span.

4.6. Genetic Architecture: Sex Linkage

Based on the observation that organisms with Z-W sex chromosomes (e.g., birds, butterflies) tend to have more strongly exaggerated ornaments than organisms with X-Y sex chromosomes (e.g., mammals, flies) (Hastings 1994), the sex-linked inheritance of sexually selected traits is recently receiving much attention (Reinhold 1998, Reeve & Pfennig 2003). This research also takes into account a growing number of concrete examples of sex-linked sexually selected traits (Qvarnström & Bailey 2009). Although simple haploid inheritance models apply to cases of Y or W linkage, other patterns of sex linkage require a diploid locus in one sex (i.e., XX or ZZ), requiring a more complex model. Multilocus approximations such as QLE can considerably simplify such models. Using these techniques, Kirkpatrick & Hall (2004) confirmed that, compared with X-Y systems, Z-W systems are more conducive to sexual selection. For example, Z-linked preferences are favorable to Fisherian sexual selection: When present in males, such preferences endure indirect selection two-thirds of the time. By contrast, when present in females, such preferences are found one-third of the time, where they endure no or negative selection. Z-W systems are also more conducive to sexual selection in the presence of sexual antagonism: when females express a costly male ornament (i.e., owing to a lack of sex-limited expression) (Albert & Otto 2005). Z linkage of the ornament ensures that an ornament endures net positive sexual selection (i.e., is present in males two-thirds of the time), whereas costs due to expression in females are minimized (present in females one-third of the time). Besides ornaments and preferences, other traits such as genetic quality may be sex linked and thus can also affect sexual selection (Connallon 2010), illustrating the importance of the genetic architecture when making predictions about the strength of sexual selection.

4.7. Cultural Imprinting

Cultural inheritance may also play an important role in the evolution of sexually selected characters. Examples include song imitation in passerine birds and mate-choice copying in guppies (Dugatkin 1996). In principle, cultural evolution can be understood by the frameworks described in Section 2, with the modifications that transmission may occur horizontally and that genetic and culturally inherited traits may evolve independently on separate timescales (Lachlan & Feldman 2003). As a result, imitation often leads to positive frequency dependence, given that the most prevalent variant is also most likely to be imitated (Laland 1994). Thus, the cultural variants and genotypes that are initially present in a population have a large impact on the eventual outcome because any novel and rare variant is unlikely to invade in regimes of positive frequency dependence (e.g., Kirkpatrick & Dugatkin 1994, Lachlan & Feldman 2003). As a consequence, drift may play a crucial role in the eventual fixation of sexually selected characters, suggesting a large scope for population divergence when imitation is important (Lachlan & Servedio 2004). In general, aspects such as learning and imitation as well as the social context in which they occur (Vakirtzis 2011) should play a more central role in sexual selection theory.

5. SEXUAL SELECTION AND OTHER PROCESSES

5.1. Sexual Selection and Sex-Ratio Evolution

Trivers & Willard (1973) predicted that females mated to attractive males should bias their sex allocation toward sons. Formal models confirm this (Pen & Weissing 2000, Fawcett et al. 2007) but also find that females mated to unattractive males almost exclusively produce daughters. Moreover, a more inclusive coevolutionary model in which sex allocation feeds back on the evolution of ornaments and preferences shows that sex allocation undermines sexual selection (Fawcett et al. 2011): By producing only daughters (which are certain to reproduce) but no unattractive sons, females mated to unattractive males have a fitness level that approaches that of females mated to attractive males. As a result, mating with attractive males ceases to yield any advantage to choosy females, thereby eliminating sexual selection and sex allocation based on it (Fawcett et al. 2011). This example is a clear demonstration of how more inclusive coevolutionary models can change our insights. Research has yet to determine whether sex allocation based on male attractiveness can be maintained in the presence of mate choice, for example, in cases in which sex allocation is based on sexually antagonistic alleles (Alonzo & Sinervo 2007, Blackburn et al. 2010).

5.2. Sexual Selection and Parental Care

Conventional sexual selection models assume females provide care and males compete over females. Although parental care is more commonly provided by females than males, substantial taxonomic variation in sex biases in parental care exists and is poorly explained by conventional theory (Kokko & Jennions 2008). Modeling the evolution of parental care is complicated: The decision of one parent to provide care versus to compete for matings depends not only on the behavior of its current partner but also on the opportunity to gain future matings, which, in turn, is a function of the population-wide density of members of its sex that are competing for matings as opposed to caring for their young (Houston et al. 2005, Kokko & Jennions 2008). To understand this better, investigators need more inclusive modeling approaches that take into account both the evolutionary dynamics (evolution of ornaments, preferences, care decisions) and the ecological dynamics (acting at a much faster timescale) in which individual decisions feed back on the densities of caring and competing individuals.

McNamara et al. (2000) provide one of the first models to take such a dynamical approach. These authors found that high population-wide levels of care select for individuals to desert their brood more rapidly (because they are likely to have mated with a partner providing care) and pursue more matings. However, as desertion rates increase, individuals face more competition for future matings, making it less worthwhile to desert and more preferable to continue caring. The authors also showed that alternations in patterns of care may result, such that bouts of biparental care may alternate with uniparental or no care. The feedback between desertion and competition also cautions researchers against attributing sex differences in care to biases in the operational sex ratio (OSR): For example, male-biased OSRs are widely assumed to lead to increased male-male competition and, hence, less male care (Trivers 1972). As reviewed by Kokko & Jennions (2008), a male-biased OSR may actually select for increased parental care by males because males now face increased competition over matings, thereby increasing the relative value of parental care. Hence, the co-occurrence of male-biased OSRs and female-biased patterns of parental care requires more specific explanations that consider the intricacies of the sexual selection processes or species-specific differences within costs of competition.

Operational sex ratio (OSR): the ratio of male versus female individuals that are available for mating at any given time

5.3. Sexual Selection and the Evolution of Sex

Despite recent theoretical progress on the evolution of sex along various lines, we still have a limited understanding of the various factors that can overcome the costs of sexual reproduction (Lehtonen et al. 2012). Sexual selection, which requires sexual reproduction, may positively feed back on the maintenance of sex (for a recent review, see Whitlock & Agrawal 2009). Specifically, if females choose males with the fewest mutations, the load of deleterious mutations is reduced in comparison with asexual populations (Siller 2001, Agrawal 2001). The twofold cost of sex is also overcome for those individuals that bear high-fitness offspring (e.g., attractive sons), which will result in a larger number of grandoffspring (Hadany & Beker 2007).

However, sexual selection may also work against the evolution of sex (Whitlock & Agrawal 2009). For example, the evolution of male harm or costly competition can reduce the mean fitness of sexual populations. The expected population size of sexual, as opposed to asexual, organisms is further reduced by the increased variance in male reproductive success, which may lead to an increased load of deleterious mutations due to drift. Last, the presence of divergent selection pressures in the two sexes (i.e., sexually antagonistic selection) also disfavors sexual reproduction (Roze & Otto 2012). To determine whether sexual selection defies the evolution of asexual reproduction, a more inclusive approach is required.

5.4. Sexual Selection and Speciation

Closely related species often differ most dramatically in their mating traits, suggesting that sexual selection plays an important role in speciation. Indeed, sexual selection has been ascribed a prominent role in virtually all processes related to speciation. For example, Lande (1981) has described how the Fisher process contributes to the divergence of mating preferences in geographically isolated populations and, hence, to the evolution of reproductive isolation mechanisms (Uyeda et al. 2009). Such divergence can be strongly enhanced when the driving force is sexual conflict, leading to antagonistic coevolution of the two sexes (Hayashi et al. 2007). Sexual selection can contribute to the low fitness of hybrids (and, hence, postzygotic reproductive isolation) if hybrids are less attractive as mates. Mating preferences may be a potent mechanism underlying reinforcement (selection against the occurrence of deleterious hybridization), for example, when individuals tend to mate with genetically compatible partners (Servedio & Noor 2003, Servedio 2004) (Section 3.5). In fact, reinforcement can give rise to particularly strong selection of female preferences for signals that indicate low degrees of hybrid incompatibility (Kirkpatrick & Servedio 1999). Sexual selection can also lead to the evolution of prezygotic isolation, which may occur in sympatry, when two diverging Fisher processes co-occur in populations with a broad variation in female preferences (Higashi et al. 1999; Van Doorn et al. 2001, 2004). A more likely scenario, however, is the evolution of preferences for indicators of local adaptation (Proulx 2001, Reinhold 2004) (Section 3.5) that, under parapatric conditions, can strongly enhance disruptive natural selection (Van Doorn et al. 2009). For recent reviews of the role of sexual selection in speciation, readers are referred to Ritchie (2007), Weissing et al. (2011), and the Marie Curie Speciation Network (2012).

FUTURE ISSUES

Despite the hundreds of models on sexual selection presented over the past four decades, we feel that the field is only at the beginning of a more integrative theory of sexual selection. In particular, the following aspects should receive major attention in future models:

1. Research needs to apply a more robust approach to the study of mating traits, which are typically modeled in a rather simplistic manner. In nature, preferences as well as traits are often conditional strategies, depending on an individual's position within the overall mating market. Virtually no models consider the possibility that individuals reallocate resources from ornamentation to the provisioning of direct benefits like parental care (or vice versa) in a dynamic way, which may be of particular relevance for species with mates with mutual choosiness. The evolution of preferences when different types of benefits are at stake has also not received much theoretical attention. Current models (e.g., Kirkpatrick & Barton 1997) lead to the clear-cut prediction that direct benefits play a role more prominent than that of indirect benefits. However, if this is true, why do many females engage in extrapair copulations (yielding only indirect benefits), which may endanger their social mate's investment in their joint clutch (thereby risking the loss of direct benefits)? Questions like these have hardly been considered by sexual selection theory.
2. The interplay between natural and sexual selection is still poorly understood: Are mating preferences and natural selection typically antagonistic (as often envisaged), or do they more often act in concert (Proulx 2001, Van Doorn et al. 2009)? How do ecological conditions affect the perception (and evolution) of sexually selected signals (Endler & Basolo 1998)? Under which conditions do preferences evolve as a pleiotropic by-product of natural selection (Kirkpatrick & Ryan 1991), and will such preferences be maintained in the long term? How do more explicit formulations of ecological interactions (predation, host-parasite interactions) (Hamilton & Zuk 1982) and environmental dynamics influence male quality and the benefits of choice?
3. An integrative theory of sexual selection should highlight inclusive models in which ecological aspects (i.e., density-dependent feedbacks, resource dynamics) are modeled dynamically in combination with evolving preferences and ornaments. Such an approach also requires that the models explicitly account for the coevolutionary interaction of female preferences, male ornaments, and traits involved in other processes, such as parental care, sex allocation, and male-male competition.
4. Most current predictions regarding the evolution of sexually selected traits are based on equilibrium situations, whereas several lines of evidence indicate that such traits exhibit rapid turnovers and strong interpopulation divergence (Wiens 2001, Bro-Jørgensen 2010). More effort is needed to understand when nonequilibrium dynamics occur and how aspects such as the genetic architecture (e.g., Van Doorn & Weissing 2006) or environmental dynamics (Bro-Jørgensen 2010) affect the continuous evolution of sexually selected traits.

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