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Quantitative genetic models of sexual selection

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Modeling of R.A. Fisher's ideas about the evolution of male ornamentation using quantitative genetics began in the 1980s. Following an initial period of enthusiasm, interest in these models began to wane when theoretical studies seemed to show that the rapid evolution of ornaments would not occur if there were costs associated with female mate choice. Recent theoretical work has shown, however, that runaway evolution and other kinds of extensive diversification of ornaments and preferences can occur, even when female choice is costly. These new models highlight crucial parameters that profoundly influence evolutionary trajectories, but these parameters have been neglected in empirical studies. Here, we review quantitative genetic models of sexual selection with the aim of fostering communication and synergism between theoretical and empirical enterprises. We also point out several areas in which additional empirical work could distinguish between alternative models of evolution.

The evolution of extravagant male characters (ornaments) has been the subject of debate for much of the history of evolutionary biology. Recent research has conclusively established that such characters (e.g. the tail of the peacock or the song of the nightingale) owe their existence to female mate preference [1]. At the heart of the contemporary debate is the question of whether the preferred traits also indicate overall fitness of the male (survival and reproductive success). Existing theoretical models that explore the evolution of mate preferences and ornaments could constrain the debate by demonstrating what is logically possibility. However, empirical investigation has often become disengaged from the theoretical enterprise. Empirical case studies sometimes focus on subsidiary rather than central issues and often fail to refer to relevant models. On the modeling side, failure to discuss incisive tests of predictions is a common problem. Part of the disengagement also can be attributed to the proliferation of theoretical models and the lack of a recent review.

Evolution by sexual selection has been modeled using game theory, population genetics and quantitative genetics. Our review focuses specifically on quantitative genetic models (see Glossary) of sexual selection. These models explore ideas originally set out by R.A. Fisher [2–4]. In these models, inheritance is quantitative in the sense that both ornaments and preferences are affected by many genes. Our restricted focus has three motivations. First, although population genetic (two-locus) and game theoretic models can provide valuable insights, they cannot capture crucial aspects of evolutionary dynamics that are revealed in the quantitative genetic models. In particular, two-locus models (one locus determines the male ornament, the other determines preference) cannot produce a runaway trait, the most famous aspect of Fisher's proposal. Game theoretic models ignore genetic details and ask if a specified equilibrium can be invaded by new mutants. This approach does not work for sexual selection processes in which the evolutionary outcome is affected by genetic details [5]. A second key virtue of the quantitative genetic models is that they are cast in terms of parameters of inheritance and selection that can be estimated in natural populations. Because two-locus and other types of model cannot describe inheritance and selection for continuously varying traits (such as ornaments and preferences), these models are fundamentally disconnected from the empirical study of sexual selection. Finally, the issues explored in the quantitative genetic models (e.g. the nature of evolutionary outcomes or the mode of selection on preference) span the full range of topics under debate in the sexual selection literature (e.g. good genes and sexual conflict). By contrast, fewer issues have been explored with two-locus models. Our aim here is to examine all sexual selection models that comprise the quantitative genetic family to identify common denominators. We also focus on crucial features in these models that produce different evolutionary outcomes. A particular goal is to facilitate ongoing debates.

Glossary

Direct selection: selection acting on a trait that itself affects fitness.
G-matrix: The additive genetic variance-covariance matrix for a suite of traits.
Good genes theory: females choose mates using criteria that will increase the overall fitness of offspring, rather than just the mating success of their sons.
Indirect selection: evolutionary change in a trait due to genetic correlation with another trait that is under selection.
Quantitative genetic models: models that describe the evolution of continuously distributed traits that are affected by many genes.
Sexual conflict: occurs when characteristics that enhance the reproductive success of one sex reduce the fitness of the other sex.
Sexy son: originally, the proposal that a female chooses males with attractive traits, even though that choice reduced the female's fecundity; incorrectly, female mate choice based on an ornament.

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The Fisher process

A basic process of sexual selection that produces genetic coupling (the Fisher process) is a common denominator in quantitative genetic models. Fisher's detailed argument for evolution by sexual selection [2–4] was based on Darwin's concept of sexual selection. Darwin [6] argued that sexual selection (selection arising from differences in male mating success) drives the evolution of many of the differences between the sexes in terms of their behavior and structure. Elaborating on this, Fisher argued that the mating preferences of females will evolve, as well as the ornaments of the male that are the focus of female preferences. If there is a heritable basis for both preferences and ornaments, Fisher argued, a female that chooses a male with an extreme ornament will tend to produce daughters with extreme preferences and sons with extreme ornaments. Fisher's most famous prediction was that the ornament (e.g. male tail size) might evolve, together with female preference for the ornament, at ever-increasing speed. In the sexual selection literature, this so-called 'runaway' outcome has become synonymous with Fisher's name. The basic Fisher process involves quantitative inheritance and a genetic coupling between preferences and ornaments that arises from mate choice. The concepts of ornament and preference have subsequently been expanded to include a variety of traits that can become genetically coupled as a consequence of mate choice [7,8].

Quantitative genetic models of sexual selection

Although Fisher [2–4] provided the first verbal models of sexual selection, theoretical work was unable to verify the runaway possibility until Lande [9] formulated a quantitative genetic model of the process. In this model, natural and sexual selection act directly on the ornamental trait to cause evolutionary change (Box 1). Evolution of mate preference occurs by INDIRECT SELECTION through a genetic correlation between the ornament and the preference. The model revealed several key features that were unapparent in Fisher's verbal rendition. In particular, Lande identified the genetic correlation between ornament and preference (Box 2, Figure I) to be the crucial parameter describing genetic coupling. This coupling arises because the combination of assortative mating and sexual selection favoring attractive males produces a correlation between preference alleles and ornament

Box 1. Basic model of Fisherian sexual selection

Fisherian sexual selection describes how female mating preferences can cause evolutionary exaggeration of a male ornament. 'Ornament' and 'preference' are shorthand for a huge range of coevolving male and female traits. The 'ornament' might be a vocalization or visual display of apparently arbitrary origin, or it might be the body size, vigor, athletic ability or some other indicator of overall viability of the male. Less obviously, the 'ornament' might be a pheromone with aphrodisiac-like properties or the genitalia. The crucial common denominator is that 'ornament' and 'preference' interact in sexual dialog and affect the mating success of one or both partners.

The quantitative genetic model introduced by Lande [9] confirmed many of Fisher's predictions, and laid the foundation for future work. Subsequent models add elements to this basic model (Table 1, main text) to accommodate alternative assumptions. The assumptions of the basic model are:

- Male ornament, z, and female preference, y, are autosomally inherited, sex-limited, normally distributed traits with means $\bar{z}$ and $\bar{y}$.
- Additive genetic variances of the ornament and preference (G and H) and the additive genetic covariance (B) between ornament and preference are constant. These genetical concepts are explained in Box 2.
- Every female is inseminated and there is no fecundity selection on females. Because the fecundity and survival of the female are unaffected by her mating preference, there is no selection on preferences. Males do not help to raise offspring or protect or provision mates.
- Average male ornament evolves in response to sexual selection generated by the female mating preferences and viability selection. The total force of directional selection on the ornament is β.
- Average female mating preference evolves as a correlated response to selection on the ornament.

The results of the basic model are:

- The per generation change in the average ornament and the average preference is described by the following standard quantitative genetic equation (Eqn I, II):

$$\Delta\bar{z} = \frac{1}{2}G\beta \qquad [\mathrm{I}]$$

$$\Delta\bar{y} = \frac{1}{2}B\beta. \qquad [\mathrm{II}]$$

- Evolution of the averages occurs along lines of constant slope (dashed lines in Figure I), given by a genetic regression (Eqn III),

$$\frac{\Delta\bar{y}}{\Delta\bar{z}} = \frac{B}{G} \qquad [\mathrm{III}]$$

- Evolution leads toward or away from a line of equilibrium (heavy lines in Figure I), at which the force of sexual selection is balanced by the force of viability selection on the ornament ($\beta(0)$.
- Populations walk towards a line of stable equilibrium at ever decreasing speed if

$$\frac{B}{G} < \alpha + \varepsilon, \qquad [\mathrm{IV}]$$

but runaway from a line of unstable equilibrium at ever increasing speed if

$$\frac{B}{G} > \alpha + \varepsilon, \qquad [\mathrm{V}]$$

α and ε describe the strength of viability selection and the type and strength of mating preference.

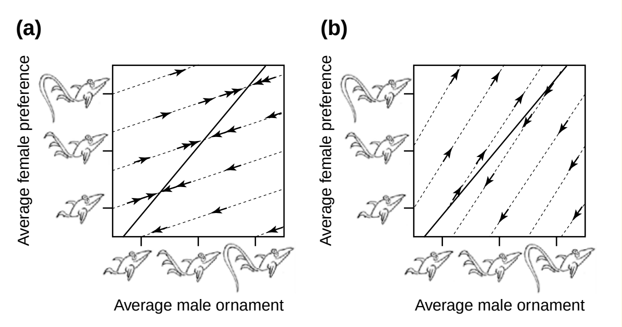

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Figure I. In the basic model, evolutionary outcome can be a stable (walk towards) **(a)** or unstable (runaway) **(b)** line of equilibrium (indicated by the solid line). Dashed lines show evolutionary trajectories. For the type of mating preference depicted here, the vertical axis represents the average value of the ornament (tail size) most preferred by females.

alleles (linkage disequilibrium), even if those alleles are on different chromosomes. Lande also showed that the Fisher process could result in either stable or unstable outcomes (Box 1).

In the ensuing two decades, 20 quantitative genetic models of sexual selection have been produced using Lande's framework. Most of these include the Fisher process. The historical trend in modeling has been to explore the consequences of different types of selection on ornament and preference by adding features to the basic model (Table 1). The earliest basic models assume that mate choice incurred no costs [9–12]. Later basic models specify direct costs to preference [13–18] and show that evolution proceeds to (or away from) a unique point, rather than to (or away from) a line of potential outcomes. SEXY SON models include fecundity selection on both ornament and preference to explore the possibility that evolving preferences reduce the fecundity of females [13,19]. The good genes models explore a 'good genes' or 'indicator' process by including a trait indicating male genetic quality (e.g. viability) that is correlated with the ornament [20,21] and/or with the mating preference [22–24]. Sexual conflict models explore sexually antagonistic coevolution by assuming that selection on females favors an intermediate optimum for mating frequency [25] or mating resistance [26]. Rather than recount the details of each of these subsets of models, we have summarized them in Table 1. Here, we consider the take-home messages from this succession of models using a topical approach, given that multiple subsets of these models have interesting features in common (e.g. runaway selection or perpetual evolution) that cry out for additional empirical work.

Box 2. The G-matrix

Quantitative inheritance as a cloud of genetic values

Ornaments and preferences are continuously distributed traits that are likely to be affected by many genes, most of which might be of small effect. The inheritance of such quantitative traits is described by a statistical model. The ornament of a particular male, for example, is treated as the sum of two parts: a genetic value and an environmental or nonheritable part. The evolution of the population averages for ornament and preference depends on the statistical properties of a bivariate cloud of genetic values. Actual data for the cloud could be obtained by allowing each of a series of males to mate and produce progeny under the prevailing system of mating. The genetic (breeding) values for a particular male would be estimated by taking the average value of ornaments in his sons and the average value of preferences in his daughters. According to the Fisher process, if we plotted both genetic values for the entire series of males, we would expect to obtain a cloud such as that shown in Figure I, indicating genetic coupling between preference and ornament.

The G-matrix summarizes the cloud of genetic values

The cloud of genetic values in Figure I can be summarized by three statistics: G (the genetic variance for the ornament), H (the genetic variance for the preference), and B (the genetic covariance between ornament and preference). These statistics can be assembled in a conventional table known as a variance–covariance matrix. Our variance–covariance matrix describes the statistical dispersion of genetic values and is known as the G-matrix (Eqn I):

$$\begin{bmatrix} G & B \\ B & H \end{bmatrix} \qquad [I]$$

The G-matrix profoundly affects the evolution of ornament and preference. In the basic model (Box 1), only two elements affect evolution (G and B), but, in more complex models, the entire matrix affects evolutionary responses to selection. Furthermore, more complex models specify multiple ornaments and multiple preferences for those ornaments. In those cases, G, H and B represent matrices of values rather than individual values, as in the simple case considered above.

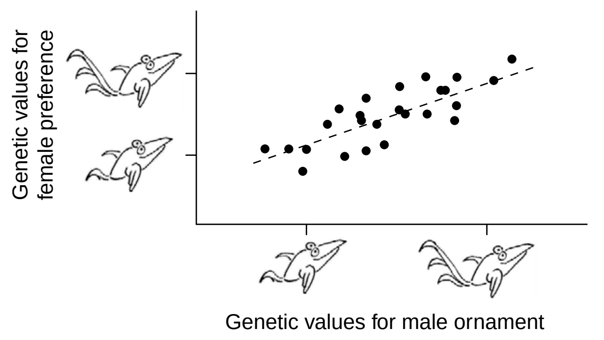

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Figure I. A hypothetical cloud of genetic values representing one trait expressed in males (ornament) and a second trait (preference) expressed in females. The dashed line is the genetic regression B/G, where B is the genetic covariance between ornament and preference, and G is the genetic variance for the ornament.

Joint evolution of female preference and male ornament

Stable versus unstable outcomes

Runaway sexual selection is possible in all scenarios that have been modeled, including good genes situations. The ubiquity of the runaway will surprise many students of sexual selection who have incorrectly viewed the runaway as an alternative to good genes or sexual conflict models. We must be clear about the meaning of 'runaway'. The term is Fisher's characterization [3,4] of an ornament evolving at ever-increasing speed under the force of ever-stronger preference. 'Runaway' has this same meaning in quantitative genetic models of the process, but, more generally, it signifies a category of unstable evolutionary outcome or equilibrium. Equilibrium in these models means that selective forces have reached a balance, but that balance can be unstable (e.g. a ball perched on a ridge) or stable (e.g. a ball resting in a valley) Evolutionary paths lead away from an unstable equilibrium but towards a stable equilibrium (Box 1, Figure I). Remarkably, these two categories of equilibrium (unstable or stable; also termed 'runaway' or 'walk-towards') occur in every model, regardless of the traits that are added or modifications that are made. Either kind of equilibrium can result in exaggeration (or diminution) of the male ornament and female preference. Regardless of the continuing attraction to Fisher's original runaway proposal, stable (walk-towards) sexual selection scenarios might be the most common situation in nature [8], because stable outcomes require less extreme values for genetic parameters.

Prospects for perpetual evolution

The discovery of perpetual evolution is one of the most interesting results in recent models [15,16,21,24,26,27]. In this type of equilibrium (a stable limit cycle), the joint evolution of ornament and preference proceeds endlessly

Table 1. Quantitative genetic models of sexual selection

Type of model	Type of male trait and modes of selection			Type of female trait and modes of selection			Type of equilibrium	Refs
	Type of trait	Natural selection	Sexual selection	Type of trait	Natural selection	Sexual selection		
Basic	Ornament	Stabilizing	All^b	Preference	None	None	Line	[9]
	Ornament with spatial location	Stabilizing	All	Preference with spatial location	None	None	Point or function of geographic location	[10]
	Ornament	Stabilizing	All	Preference	None	None	Line	[11]
				Ornament	Stabilizing			
Basic (monogamy)	Ornament	Stabilizing	Open-ended	Preference	None	None	Line	[12]
				Breeding date	Stabilizing			
Basic	Ornament(s)	Stabilizing	Open-ended	Preference(s)	Cubic^a	None	Point(s)	[14]
	Ornament	Plateau^a	Open-ended	Preference	Stabilizing	None	Point or cycle	[15]
	Ornament(s)	Plateau	Open-ended	Preference(s)	Variable	None	Point(s) or cycle	[16]
	Ornament	Directional	All	Preference	Directional	None	Point	[17]
	Ornament with spatial location	Stabilizing	Open-ended	Preference with spatial location	Stabilizing	None	Point or function of geographical location	[18]
Sexy son	Ornament	Stabilizing	Open-ended	Preference	Stabilizing	None	Point	[13]
	Ornament	Stabilizing	Absolute	Preference	Stabilizing	None	Point	[19]
Good genes	Ornament	Stabilizing	Absolute	Preference	None	None	Line	[22]
	Genetic quality	Stabilizing		Genetic quality	Stabilizing			
	Ornament	Stabilizing	Open-ended	Preference	Stabilizing	None	Point	[29]
	Genetic quality	Stabilizing		Genetic quality	Stabilizing			
	Ornament	Stabilizing	Open-ended	Preference	Stabilizing	None	Point	[20]
	Condition	Directional						
	Ornament	Stabilizing	Open-ended	Preference	Stabilizing	None	Point	[23]
	Genetic quality	Stabilizing		Genetic quality	Stabilizing			
	Ornament(s)	Stabilizing	Open-ended	Preference(s)	Variable	None	Point(s)	[24]
	Genetic quality	Directional		Genetic quality	Directional			
Good genes, good parent	Ornament(s)	Plateau	Open-ended	Preference	Cubic	None	Multiple points or cycle	[21]
	Genetic quality	Directional						
Good genes	Ornament	Stabilizing	Relative	Preference	Stabilizing	None	Point or cycle	[27]
	Genetic quality	Directional		Genetic quality	Directional			
Sexual conflict	Ornament	None	Stabilizing	Resistance	None	Stabilizing	Line	[25]
	Ornament	Stabilizing	Directional	Resistance	Stabilizing	Stabilizing	Point(s) or cycle	[26]

[a] See Figure 2.

[b] All three modes of preference described by [9]: open-ended, absolute and relative.

along an elliptical path in which periods of ornament exaggeration alternate with periods of diminution (Figure 1a). The result is intriguing because it might explain the striking radiations of male ornaments in newts, jumping spiders and lekking birds. Perpetual evolution outcomes have been found in basic, good genes and sexual conflict models. The common denominator is a stabilizing mode of selection on both preference and

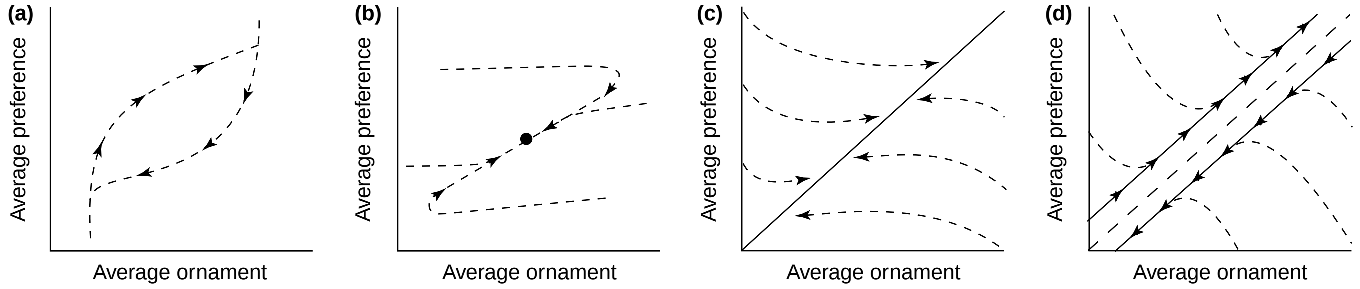

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Figure 1. Evolutionary paths and equilibria in quantitative genetic of models of sexual selection. Evolutionary paths (dotted lines with arrows) show evolutionary change in average preference and average ornament. **(a)** Preference and ornament cycle between periods of elaboration and periods of diminution. **(b)** Alternatively, costly preferences can cause preference and ornament to evolve to a stable equilibrium point, shown as a solid circle. In sexual conflict models [25,26], the evolutionary outcome can be stable **(c)** or unstable **(d)**. In the stable case (c), populations evolve towards a line of equilibrium (solid line). Selective forces balance once a population reaches the equilibrium line, but populations can move along the line by genetic drift. In the unstable case (d), populations evolve towards but do not reach an unstable line of equilibrium (dashed line). Once a population nearly reaches the equilibrium line, it continues to evolve along a path parallel with the line, with a constant rate of change in average preference and ornament.

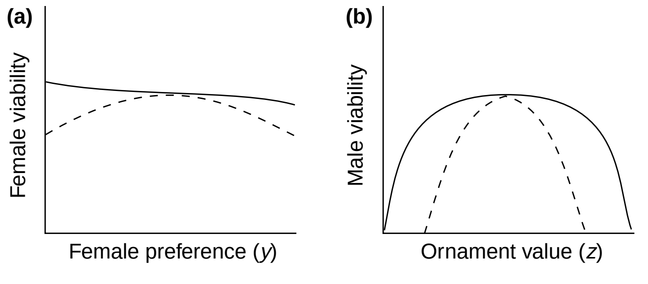

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Figure 2. Modes of selection on preferences and ornaments. Two forms of viability selection on female preference with large impacts on evolutionary dynamics are shown in **(a)**. Female viability is graphed as a function of female preference, y. The dashed line illustrates a standard model of stabilizing selection with an intermediate optimum, viability $= \exp(-by^2)$, with *b,* a constant, $=0.0125$. The solid line illustrates a more complex, nonlinear mode of selection in which stronger preferences are disfavored, viability $= \exp(-by^3)$, $b = 0.0004$. **(b)** Two forms of stabilizing viability selection on male ornaments. Male viability is graphed as a function of ornament value, *z.* The dashed line shows a standard model for stabilizing selection in which viability $\propto \exp(-z^2)$. The solid line shows a selection model with a plateau shape, viability $\propto \exp(-z^4)$.

ornament. Cycling dynamics can be produced in the basic or good genes framework by invoking special (cubic or plateau) forms of natural selection on preference and ornament [15,16,21] (Figure 2). But cycles can also occur under standard forms of stabilizing selection [27] (Figure 2). In the sexual conflict framework, cycles can occur in the absence of good genes effects [26].

The discovery of perpetual evolution with three different kinds of model and under varying sets of conditions suggests that it might occur in the natural world. The best test for perpetual evolution would be to follow natural or experimental populations and determine whether ornaments follow a cyclic pattern of evolution. Instances of extreme geographic variation in ornaments might also reflect cyclical dynamics and should be investigated from this point of view.

Consequences of costly mating preference

One of the earliest and continuing criticisms of the basic model focused on the consequences of costly female preferences. The basic model assumes that preference has no effect on female fitness, and so is selectively neutral [9]. The addition of DIRECT SELECTION on preference, either in the form of fecundity selection [19] or viability selection [13,20,22,23] can cause the line of possible equilibria to collapse to a single point (Figure 1b). This single point sometimes corresponds to no exaggeration of the ornament and an absence of mating preferences. Thus, direct selection on preference can limit the evolution of both preference and trait. Recent models show, however, that a diversity of outcomes is nevertheless possible if selection acts directly on preference [23,27]. In particular, the diverse outcomes are possible when selection on preferences has a typical stabilizing form rather than the unusual cubic form assumed in some earlier models (Figure 2a) [14,21].

Good genes

That ornaments are indicators of male genetic quality was alluded to by Fisher [3,4] but brought to center stage by Zahavi [28]. Under this scenario, females might enhance the overall quality of genes that they pass on to offspring by choosing the right male. In the quantitative genetic models, this possibility is captured by positing a genetic correlation between the ornaments and overall viability of males [14,22,23,29]. Less commonly, a genetic correlation between mating preference and female viability is proposed [24]. Recent formulations have shown that the good genes scenario can promote the evolution of ornaments [14,20,22–24,27,29,30]. This conclusion, however, is subject to two important qualifications. First, it is unlikely that the good genes situation exists separately from the basic Fisherian condition of a genetic correlation between ornament and preference. Consequently, it is misleading to paint the basic Fisher process and good genes as alternative explanations for ornament exaggeration, as is common in many textbook accounts. Rather, the issue is whether good genes do their work along side the inevitable Fisher process. Second, even when the genetic correlations that are necessary for the good genes process are present, the supplementary exaggeration of the ornament as a result of good genes might be relatively small [29,30]. The key empirical issues in deciding whether the good genes effect is small (and likely to be overwhelmed by direct selection on preferences) are the relative magnitudes of indirect and direct selection on preferences [27,30]. A plausible argument has been made here that indirect selection on preferences is weak [30]. The good genes effect, according to this argument, is likely to be weak because it depends upon a long causal pathway, from preference to ornament to total fitness. A weak link anywhere in the pathway means that the whole pathway will also be weak. Furthermore, the use of available estimates of inheritance and selection parameters also indicates that the good genes effect is probably small [30]. The issue is by no means settled, however. Houle and Kondrashov [27] have argued that organisms are capable of evolving specificity in mating preferences such that direct costs are avoided. The most tractable empirical data that bear on this controversy are estimates of direct selection on preferences, an almost completely unexplored territory.

Sexual selection and speciation

Recent models have also helped to identify and clarify connections between sexual selection and speciation, topics that were historically estranged until ~20 years ago.

Lines of equilibria and potential for diversification

Speciation depends on diversification in mating behavior and other traits that promote reproductive incompatibility between populations. One important connection between the quantitative genetic models and speciation is supplied by equilibria that, by their very nature, generate diversity (in the form of equilibrium lines, multiple points and stable limit cycles). The positive feedback process resulting in the runaway could rapidly lead to a new species if divergence in ornaments leads to sexual isolation. Even when the line of equilibrium is stable, evolution along this line can occur rapidly (through the interaction of random genetic drift with natural and sexual selection) because populations

Table 2. Future directions for research

Direction	Approach	Main effect(s)	Empirical evidence	Refs
Quantify magnitude of genetic variance for ornament(s) (*G*)	Measure ornaments in father and sons	Determines equilibrium dynamics (runaway versus walk-towards) in all models	Fruit fly Flour beetle	[44] [45]
Quantify magnitude of genetic variance for preference (*H*)	Measure preference in mothers and daughters.	Affects rate of evolution of preference in good genes and sexual conflict models	Fruit fly	[52,53]
Quantify magnitude of genetic covariance between the sexes (*B*)	Measure ornaments in fathers and preference in daughters OR preference in mothers and ornaments in sons	Affects equilibrium dynamics (runaway versus walk-towards) in basic, good genes, and sexy son models	Fruit fly Stalk-eyed fly Cricket Guppy Stickleback	[46,52] [47] [48,49] [50] [51]
Quantify stability of genetic variances and covariances	Compare G, H, and B sampled from populations with a known phylogeny	Affects runaway versus walk-towards dynamics in all models	No empirical data for ornaments and preferences	
Determine incidence of indirect selection on preference	Measure preference of mothers and fitness in offspring	Affects evolution of preference	No empirical data	
Determine mode of preference (open-ended, absolute, relative, etc.)	Measure preference as a function of the ornaments of potential mates	Affects runaway dynamics in all models	Open-ended Absolute Relative Other	[56,57] [58] [59] [60]
Determine prevalence of costly, beneficial, and neutral preferences	Measure costs as a function of preference	Affects whether equilibrium is a line or a point in good genes and sexual conflict models	Fruit fly Flour beetle Arctiid moth Cricket Fish	[53] [45] [54] [49] [50,51]
Determine strength of direct selection on preference	Measure female fitness as a function of preference	Affects whether equilibrium is a line or a point in good genes models	No empirical data	
Determine sexual selection gradient for females	Measure female fecundity as a function of mate number	Indicator of sexual conflict	Waterstrider Dung fly	[61] [62]

starting from the same point might drift to different sides of the line of equilibrium and be selected in opposite directions [9]. Turelli *et al.* [31] argued that drift along the line will be an inefficient mechanism for producing the sexual incompatibilities upon which speciation depends. One way to test arguments of this type is to use models that translate differences produced by sexual selection into measures of sexual isolation [32], so that progress towards speciation can be evaluated. Such models provide an explicit interface between the quantitative genetic models and speciation. In addition, these models provide an avenue for evaluating the contribution of drift to the evolution of sexual isolation and, hence, to speciation. So far, this avenue is not well traveled.

Multiple ornaments and preferences

Sexual selection for multiple ornaments can also generate extensive divergence leading to sexual isolation. Models with multiple ornaments are especially relevant to speciation in groups in which sexual communication involves many characters and sensory modalities (e.g. birds of paradise, pheasants and grouse). The models indicate that, even when there is direct selection on preferences, the basic Fisherian process can easily lead to the evolution of multiple ornaments and preferences [14]. When a good genes element is added to the models, an interesting result is obtained. The evolution of one indicator ornament can block the evolution of other indicators, suggesting that the multiple ornaments of lek-breeding birds are probably not all indicator traits [24]. Furthermore, multiple ornaments and preferences are prone to perpetual, cyclic evolution under some conditions [16]. Because different ecological situations can send populations on different cyclical pathways of ornament elaboration and diminution, there might be much potential for the evolution of sexual isolation [16]. The message for field workers is that the sexual selection models make direct predictions about diversification and speciation, and these specific predictions could be used to test the models.

Sexual conflict and the possibility of rapid divergence

A third connection to speciation is made by recent models of chase-away sexual selection [33]. There is the potential for rapid, antagonistic coevolution in these sexual conflict models [25,26]. Consequently, different initial conditions (e.g. geographical differences in ecology) can send populations along divergent evolutionary paths (Figure 1c,d), resulting in sexual isolation and speciation. Under restricted circumstances, perpetual (cyclic) coevolution of male ornaments and female resistance also is possible, even when resistance is costly. These models [25,26] indicate that the runaway and other speciation-promoting features of Fisherian evolution could prevail under a very wide range of circumstances.

How can we test for the presence of sexual conflict? One signature feature of sexual conflict is an intermediate optimum for mate number in females. In the models, the fecundity of a female initially increases with her number of mates, but then sexual conflict causes a decline in fecundity as mate number continues to increase [26].

The relationship between fecundity and mating success in males and females is a central aspect of mating systems [34]. A test for curvilinearity in the fecundity-mating success relationship of females could be conducted using standard techniques for measuring stabilizing selection [35].

Constancy of the G-matrix

Constancy of genetic variances and covariances (the G-MATRIX, Box 2) is an assumption in most models of sexual selection. A model for evolutionary change in the G-matrix becomes particularly important when ornament and preference undergo extensive evolution [36]. Because the G-matrix itself might evolve if the traits evolve to a great extent, some models [29] have allowed evolution of genetic variances and covariances. More commonly, the G-matrix is assumed to remain constant, based on the assumption that there is balance between input from mutation and recombination and erosion by selection [9,37]. Long-term stability of the G-matrix is then a consequence of constancy in processes of mutation and selection. How plausible is such long-term stability? Intractable analytical solutions to the problem of stability suggest that the issue must be approached either empirically [38] or by computer simulations [39]. The overriding message from empirical studies over the past two decades is that some features of the G-matrix are notably stable, although instances of instability have also been discovered [40–42]. Recent computer simulations show that the G-matrix is relatively stable under some circumstances (e.g. under particular, stable regimes of selection and pleiotropic mutation in large populations), but prone to erratic wobbling (significant changes in the correlations between traits) under other conditions (e.g. small population size) [43]. The bottom line is that G-matrix constancy can be expected on some timescales, for some kinds of character and in some kinds of population. In the realm of sexual selection, we need comparative studies of the G-matrix to tell us whether the circumstances that promote stability are either common or rare.

Prospects: assessing assumptions and testing predictions

The importance of particular key model parameters, as highlighted here, suggests directions for future empirical work. The key issues (Table 2) include: types and modes of selection on preference, the magnitude of the genetic covariance between the sexes, and the presence of sexual conflict. Empirical work (Table 2) has provided estimates of some parameters (e.g. ornament heritability [44,45], of genetic correlation between the sexes [46–52], and of costs associated with preferences [49,53,54]; also see review [55]). However, such studies have lagged behind theoretical modeling in quantifying many other aspects of sexual selection (e.g. viability selection on the male trait, direct and indirect selection on preference, magnitude and stability of genetic variances and covariances). We are not arguing for quantification for the sake of quantification. In numerous instances, the values of parameters (singly and in combination) have qualitative effects on the evolutionary paths and outcomes. Empirical work focusing on parameter estimation will provide an opportunity to test predicted outcomes of the sexual selection process and determine which models, if any, are relevant in particular circumstances. For example, sampling mated pairs and estimating the phenotypic correlation between preference and ornament would enable us to evaluate the potential role of indirect selection in preference evolution [30]. Similarly, measuring and assessing direct selection on preference could determine the pervasiveness of costly preferences, which has implications for evolutionary outcome. More modeling also is needed to clarify particular conceptual issues. The connection between sexual selection and speciation, for example, is often made by hand waving rather than by explicit modeling. An additional need is to extend current models so that they make explicit, contrasting predictions about rates and patterns of radiations in ornaments and preferences. Most current models stop well short of this goal.

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