The Evolution of Female Preferences for Multiple Indicators of Quality

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ABSTRACT: In a variety of species, females exhibit preferences for multiple male ornaments. Several hypotheses have been proposed to explain this phenomenon. Which, if any, of these hypotheses is the most plausible in general remains largely unresolved based on the available empirical data. Yet theoretical studies conclude that the evolution of preferences for multiple signals of male quality is unlikely, especially when the use of an additional cue in mate choice strongly increases the overall cost of choice. This would imply that most male courtship characters do not reflect the male's genetic quality but instead evolved through Fisherian sexual selection. However, the existing models focus on ornaments that signal overall genetic quality and do not address the possibility that different ornaments provide information about different aspects of quality. Therefore, we develop a model in which the ornaments act as signals for distinct quality components. When the ornaments provide overlapping information about these quality components, we retrieve the results of earlier models. However, when the ornaments provide independent information, preferences for multiple ornaments may evolve, even when exhibiting multiple preferences is costly. We discuss our results in relation to the multiple-message and redundant-signal hypotheses for ornament diversity and identify parallels between Fisherian and good-genes mechanisms for the evolution of multiple ornaments.

Keywords: multiple ornaments, good genes, Fisherian runaway.

Male courtship displays often comprise multiple sexual signals involving several behavioral attributes and/or morphological ornaments. What is more, traits such as the peacock's tail, which may appear to be a single ornament to the human observer, may in fact convey a multitude of potentially independent signals encoded by length of the tail, number of ocelli, brightness, symmetry, elaboration, and so on. Despite the numerous examples of complex male courtship displays in natural systems, the reasons for this complexity remain unclear. In particular, two questions are unresolved. First, to what extent are the different components of the male courtship display subject to female choice? Second, to what extent do those components give information about the condition of the male or about direct or genetic benefits expected by the female?

Depending on the answers to these questions, the components of the male courtship display can be classified as follows. Obsolete signals are signals for which female preference has been lost but that are nonetheless maintained because they are not costly (Møller and Pomiankowski 1993) or are needed to achieve threshold levels of stimulation (Holland and Rice 1998). Signals intended for multiple receivers are signals that are only partly intended for females, the other components of the display being used in male-male competition (Andersson et al. 2002). Unreliable signals are signals that do not reflect condition but that are subject to female preferences shaped by Fisher's runaway process (Møller and Pomiankowski 1993). Redundant signals (or back-up signals) are signals subject to female mating preferences shaped by the handicap process, all indicating the same overall condition of the male (Møller and Pomiankowski 1993; Johnstone 1996). Finally, multiple messages are signals subject to female mating preferences shaped by the handicap process, each reflecting a different aspect of the overall condition of the male (Møller and Pomiankowski 1993). Accurate classification thus requires one to determine which of the signals are used in female choice, which ones are used in other contexts (such as male-male competition), to what extent each of the signals is an indicator of quality, and, finally, to what extent the different signals reflect different aspects of quality. Not surprisingly, these questions have only been partly addressed in most empirical studies, and different empirical studies lend support to each of the various hypotheses (reviewed by Candolin 2003).

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A study on red junglefowl (Ligon et al. 1998), for example, demonstrated that females use only one of the ornaments (comb size) to choose mates, suggesting that the other head and plumage ornaments are either obsolete signals or signals that are used in other contexts. Similarly, a study on mallards (Omland 1996*a*, 1996*b*) revealed that females choose males predominantly on the basis of bill characteristics, which are believed to reflect male condition accurately, but that they show only weak preferences for feather ornaments. Evidence for the multiple-receiver hypothesis comes from studies on widowbirds (Pryke et al. 2001; Andersson et al. 2002) and scarlet-tufted malachite sunbirds (Evans and Hatchwell 1992*a*, 1992*b*), in which only one of the feather ornaments appears to be important in female mate choice while the other is used in aggressive interactions between males. In contrast to these examples, in which female choice appears to be restricted to a single male trait, studies on yellow-browed leaf warblers (Marchetti 1998), guppies (Brooks and Couldridge 1999; Brooks 2002), and man (in the context of male rather than female mate choice; Grammer et al. 2001) have demonstrated independent preferences for multiple signals as predicted by the unreliable-signal, redundant-signal, and multiple-message hypotheses.

While the above examples focus on the nature of female mate preferences, other studies have looked into the information content of different male signals. Comparative analysis of feather ornaments in birds (Møller 1993) has been used to support the unreliable- or obsolete-signal hypothesis, and it has been argued that male secondary sexual characters in species with multiple ornaments show far weaker condition-dependent expression than those in species with only a single ornament (Møller and Pomiankowski 1993). Other studies, however, show that multiple male signals involved in female mate choice are dependent on overall condition (redundant-signal hypothesis; Candolin 2003 and references therein) or on different aspects of condition (multiple-message hypothesis; e.g., Møller and Petrie 2002; Doucet and Montgomerie 2003).

Based on the empirical data discussed above, it remains unclear which, if any, of the different hypotheses explaining ornament diversity is the most plausible in general. Accurate discrimination between hypotheses is hampered not only by the lack of data. The interpretation of data is also difficult, due to the fact that it is impossible to distinguish between Fisherian and good-genes sexual selection on the basis of observed patterns of condition dependence (Kokko et al. 2002).

Notwithstanding this, theoretical models (Pomiankowski and Iwasa 1993; Schluter and Price 1993; Iwasa and Pomiankowski 1994) have come to the clear-cut conclusion that the evolution of female preferences for multiple indicators of good genes is less probable than the evolution of multiple preferences by Fisher's runaway process. This is especially true when there are epistatic interactions between the costs of the different female preferences such that the overall cost of choice is greatly increased when females assess an additional male trait. Put differently, when considering multiple ornaments is costly, females should evolve preferences for the single indicator of quality with the highest reliability, honesty, and detectability, and they should disregard ornaments that are less reliable, honest, or detectable. According to existing theory, the multiple components of male courtship displays therefore must be obsolete or unreliable signals that do not (or no longer) reflect condition and are maintained due to low costs or Fisherian runaway selection.

We see reason to reevaluate this conclusion because the existing models have limited applicability. The models assume that all ornaments are indicators of general quality or viability, ignoring the possibility that different ornaments reflect different aspects of condition (but see Johnstone 1996 for an exception). Therefore, most models cannot be used to evaluate the multiple-message hypothesis. Moreover, the models do not take into consideration that different ornaments may provide independent estimates of overall condition, and therefore they are not suited to assess the validity of the redundant-signal hypothesis.

In this article, we attempt to arrive at a more general theory for the evolution of female preferences for multiple ornaments. We extend existing dynamical models for the evolution of multiple sexual ornaments by explicitly considering multiple components of viability. As we demonstrate, by means of individual-based simulations and mathematical analysis, female preferences for multiple male ornaments can evolve, even when multiple preferences are costly, as long as the ornaments provide sufficiently independent information about the underlying quality components.

Individual-Based Simulation Model

We simulate the evolution of multiple female sexual preferences and male ornaments in a population consisting of N individuals. Every individual carries alleles for two female preferences and two male ornaments. Expression of these alleles is sex limited. We use p_1 and p_2 to denote the preference values expressed by a female and t_1 and t_2 to denote the amount of energy or resources invested into ornaments by a male. In addition, individuals carry quality alleles determining two independent quality components, A and B. These represent, for example, tolerance to harmful substances in the environment and resistance to parasites. An individual's phenotypic values for the quality components, denoted as q_A and q_B ($0 \le q_A \le 1$, $0 \le q_B \le$

1), affect male and female viability as well as male attractiveness.

Mate Choice

The phenotypic characters t_1 and t_2 are expressed relative to some value optimal for male survival such that negative values of t_1 and t_2 are also biologically meaningful. For the sake of clarity, let us suppose that t_1 and t_2 affect the sizes s_1 and s_2 of two male ornaments, again expressed relative to the value optimal for male survival. As we will explain shortly, the realized size of an ornament is determined not only by a male's investment into this ornament but also by the quality of the male.

Before a female mates, she evaluates the available males based on the size of their ornaments and her own preferences. Females have a higher probability of mating with an "attractive" male, where attractiveness is quantified by a function r. In line with earlier models (Pomiankowski and Iwasa 1993; Iwasa and Pomiankowski 1994), we assume that

$$r = \exp(p_1 s_1 + p_2 s_2). \tag{1}$$

For this mate-choice model, females with larger absolute values of p_1 and p_2 have stronger preferences. Positive values of p_1 and p_2 indicate preferences for larger ornaments, negative values of p_1 and p_2 indicate preferences for smaller ornaments, and females with $p_1 = p_2 = 0$ mate at random. Female preferences are assumed to be nonoverlapping. That is, when females evolve a single preference (e.g., $p_1 \neq 0$ and $p_2 = 0$), only the corresponding ornament (s_1 and not s_2) affects male attractiveness. A female mates only once. The probability that a given male is allowed to sire her offspring is given by his attractiveness relative to the average attractiveness of other males she encounters.

Revealing Indicators of Quality

The male ornaments are revealing indicators of quality. For all males, the realized size of an ornament is proportional to the investment into that ornament. Yet low-quality males must invest more to attain the same level of ornament elaboration and, hence, attractiveness. Specifically, we assume that

$$s_i = t_i \alpha_i \text{ for } i = 1 \text{ or } i = 2, \tag{2}$$

where the coefficient α_i reflects how efficiently male investment into ornament i translates into increased mating success. In accordance with the preceding discussion, the coefficient α_i varies with the male's phenotype for the quality components A and B. Unlike other models (Grafen 1990; Iwasa and Pomiankowski 1994), we do not consider the possibility that t_i, the amount of resources invested into the ornament, is different for males with different qualities. Although biologically relevant, such condition-dependent ornament expression is not essential for a revealing handicap mechanism to work (as formally demonstrated by Iwasa et al. 1991). For the sake of simplicity, condition-dependent ornament expression is therefore presently left out of consideration (see also "Discussion").

An ornament is a revealing indicator when the coefficient α_i increases with male quality q_A and/or q_B. To model this dependency, we define four parameters, α_i^{AB}, α_i^{Ab}, α_i^{aB} and α_i^{ab}, for each ornament ($i = 1$ or 2), which give the efficiency of ornament production for males with the lowest or highest possible value for each of the quality components. For example, we assume that a male with the highest possible value for quality component A ($q_A = 1$) and the lowest possible value for quality component B ($q_B = 0$) expresses the first ornament with efficiency α_1^{Ab} and the second ornament with efficiency α_2^{Ab}. Similarly, $\alpha_i = \alpha_i^{ab}$ for males that have the lowest possible quality on both quality components ($q_A = q_B = 0$). All else being equal, high-quality males are more attractive than low-quality males or, at the very least, equally attractive. This implies $\alpha_i^{AB} \geq \alpha_i^{Ab} \geq \alpha_i^{ab}$ and $\alpha_i^{AB} \geq \alpha_i^{aB} \geq \alpha_i^{ab}$.

For males with intermediate qualities ($0 < q_A < 1$, $0 < q_B < 1$), the efficiency of ornament production is simply given by the weighted average of the efficiencies for extreme males such that, in general,

$$\alpha_i = q_A q_B \alpha_i^{AB} + q_A(1 - q_B)\alpha_i^{Ab} + (1 - q_A)q_B \alpha_i^{aB} + (1 - q_A)(1 - q_B)\alpha_i^{ab}. \tag{3}$$

For example, a male with intermediate quality for both quality components ($q_A = q_B = 1/2$) will be able to express the second ornament with efficiency $(\alpha_2^{AB} + \alpha_2^{Ab} + \alpha_2^{aB} + \alpha_2^{ab})/4$.

The values of the parameters α_i^k ($k = AB, Ab, aB,$ or ab) are determined by a variety of biological factors, such as female perception, the physiology of male ornament production, and the ecology of mate choice. All of these factors affect how rapidly male attractiveness increases with increased male investment into the ornament and how easily females can detect quality differences between males based on an ornament. To illustrate this, let us assume that for a given species and a given ornament the parameters α_i^k are given by

$$\begin{aligned} \alpha_1^{AB} &= 2, \\ \alpha_1^{aB} &= 1, \\ \alpha_1^{Ab} &= 1.98, \\ \alpha_1^{ab} &= 0.99. \end{aligned} \tag{4}$$

With equal investment into their first ornament, a male with a high quality for component *A* will produce an ornament twice the size of that produced by a male with a low quality for the same component. Consequently, even a low level of preference for the first ornament will allow females to discriminate accurately between high- and low-quality males for component *A*. In contrast, the first ornament hardly provides any information about the male's quality for component *B*. Two males that differ only in their quality for component *B* will produce ornaments of roughly the same size no matter how big the quality difference. Therefore, females will not be able to discriminate between high- and low-quality males for component *B* on the basis of the first ornament unless they evolve extremely high levels of preference for this ornament.

As illustrated by the example, ornaments can be reliable indicators for one component of quality but unreliable indicators for another component of quality. This has important consequences. It is possible to order ornaments with respect to their reliability (i.e., the detectability of quality differences) as long as only one quality component is considered. This is impossible, however, when quality is determined by several independent components because the most reliable ornament for one component of quality need not be the most reliable indicator for another quality component. In such a case, the conclusion that females will evolve to ignore everything but the most reliable ornament (Schluter and Price 1993) cannot be applied because it is impossible to identify a single most reliable ornament. Of course, one could attempt to derive alternative ways to order the ornaments, for example, based on the fitness effects associated with the ornaments. However, such a classification would be extremely difficult to establish because it would strongly depend on the frequency distribution of ornaments and preferences in the population. Moreover, as we will demonstrate in this article, evolution will not necessarily lead to a mating preference that is solely based on the ornament with the highest associated fitness benefit.

Viability Selection

After all females have mated, they produce a new generation of offspring. For simplicity, we assume that generations are discrete and nonoverlapping. Viability selection acts at the start of every generation.

Individual survival probabilities vary with the individual's general (i.e., good-genes induced) viability, v, which is taken to depend on the quality components q_A and q_B. As with the procedure followed for the coefficients of attractiveness α_i, we define parameters v_{AB}, v_{Ab}, v_{aB}, and v_{ab}, which correspond to the general viabilities of extreme individuals, that is, individuals with the highest and lowest possible qualities. For individuals with intermediate qualities, v is given by

$$\begin{aligned} v = {} & q_A q_B v_{AB} + q_A(1 - q_B)v_{Ab} + (1 - q_A)q_B v_{aB} \\ & + (1 - q_A)(1 - q_B)v_{ab}. \end{aligned} \tag{5}$$

In addition, individual survival probabilities are affected by the costs associated with the expression of preferences (for females) or ornaments (for males). These factors are assumed to interact multiplicatively with general viability. Consequently, male and female survival probabilities, denoted as h_{m} and h_{f}, respectively, are given by

$$\begin{aligned} h_{\mathrm{m}} &= v(1 - c_{\mathrm{m}}), \\ h_{\mathrm{f}} &= v(1 - c_{\mathrm{f}}), \end{aligned} \tag{6}$$

where c_{m} represents the cost of ornament production and c_{f} represents the cost of choice.

In line with the assumption that the ornaments are revealing indicators of quality, the cost of expressing an ornament is taken to be independent of a male's quality and solely determined by the male's investment of resources into the ornament. Consequently, we take

$$c_{\mathrm{m}} = 1 - \exp(-\beta_1 t_1^2 - \beta_2 t_2^2), \tag{7}$$

such that, in the absence of sexual selection, $t_1 = t_2 = 0$ is the optimal investment into the ornaments. The parameters β_i determine the intensity of stabilizing selection on male investment into the ornament. Note that the costs of expressing the two ornaments interact multiplicatively, implying that the cost of each ornament has an independent effect on fitness.

As mentioned in the introduction to this article, previous studies (Pomiankowski and Iwasa 1993; Iwasa and Pomiankowski 1994) indicate that epistatic interactions between the separate costs of choice can qualitatively affect the evolutionary outcome. Therefore, we assume that

$$c_{\mathrm{f}} = 1 - \exp(-\gamma_1 \theta_{12} p_1^2 - \gamma_2 \theta_{21} p_2^2), \tag{8}$$

where the constants γ_i determine how rapidly the costs of choice increase with the two preferences and where the coefficients θ_{ij} modify the cost of choice for ornament i

depending on the level of preference for the other ornament. In our simulations, we use

$$\theta_{ij} = \exp(\vartheta_i p_j^2). \quad (9)$$

When $\vartheta_i > 0$, the cost of evolving a preference for ornament i increases with the level of choosiness for the other ornament. In that case, females that exert mate choice on the basis of two male ornaments face severe costs. When $\vartheta_i < 0$, by contrast, evaluating an ornament becomes less costly with increasing preference for the other ornament. The preferences have independent effects on fitness when $\vartheta_i = 0$. In all cases, random mating ($p_1 = p_2 = 0$) minimizes the cost of choice.

Genetics

Individuals are diploid. The male traits t_1 and t_2, as well as the female preferences p_1 and p_2, are each separately determined by a single locus. We assume a continuum of alleles at these loci; that is, the phenotypic effect of each allele is a continuous quantity. Male-trait alleles interact additively to determine the phenotypic trait value, as do female-preference alleles to determine the preference value. Mutations at trait and preference loci occur with probability m per allele per generation and are modeled by altering the phenotypic effect of an allele by a number drawn from a normal distribution with narrow width σ_m.

Each of the two quality components q_A and q_B is separately encoded by L diallelic loci. At every quality locus there may be either a high-quality or a low-quality allele. The quality alleles interact additively; that is, every low-quality allele decreases the individual's quality by an amount $1/(2L)$. Hence, the phenotypic qualities q_A and q_B simply represent the fraction of high-quality alleles at loci for quality component A and B, respectively. Variation at the quality loci is maintained through biased deleterious mutations, which occur with probability μ per allele per generation. Beneficial mutations, converting a low-quality allele into a high-quality allele, occur with probability v per allele per generation, where $v \ll \mu$. All genes are unlinked and are transmitted according to normal Mendelian genetics.

Individual-Based Simulation Results

We start by investigating a situation in which both ornaments are equally revealing indicators for both quality components. In this case, the two quality components jointly influence the size of each of the male ornaments, and, crucially, they do so in the same way for both ornaments. In essence, this makes the distinction between the two quality components arbitrary, and, therefore, we would expect the same evolutionary outcome as in a model where only a single quality component is considered.

The individual-based simulations confirm this expectation. When the two ornaments completely overlap in the information they provide about the two quality components, the evolutionary outcome is mainly determined by the joint cost of choice. If the joint cost of choice is low ($\vartheta_i < 0$), such that preference for an ornament becomes less costly as a female exhibits stronger preferences for the other ornament, preferences for multiple ornaments readily evolve (fig. 1*A*). However, when the joint cost of choice is high ($\vartheta_i > 0$), such that the separate costs of choice combine in a supermultiplicative manner and females face severe costs when they consider multiple ornaments, preference for only one of the ornaments evolves (fig. 1*B*).

These results are not surprising. When a single ornament provides full information about all components of quality, a female that exerts a preference for a second ornament will not obtain additional information about the male's genetic quality. Compared with a female that expresses only a single preference, she pays a different price to obtain the same information. Whether or not multiple ornaments evolve will therefore mainly depend on whether or not the costs of multiple preferences are lower than the costs of choice in case of a single preference. This will only be the case if the joint cost of choice is low.

The preceding cost-benefit analysis becomes less straightforward when the two ornaments provide different information about the two quality components. For example, let us suppose that the first ornament provides information about the first quality component but not about the second quality component. Similarly, the second ornament provides information about the second quality component but not about the first. Let us again compare two females, the first one exhibiting preferences for a single ornament, the second exhibiting preferences for both ornaments. It is clear that the two females not only pay different costs but also obtain different benefits. The first female obtains information about one of the quality components only. Hence, she runs the risk of selecting a mate that has low quality on the quality component she neglects to evaluate. The second female, on the other hand, obtains full information about the male's quality. She will always be able to select a high-quality mate.

Of course, it remains to be shown that the benefits of exhibiting multiple preferences can also outweigh the costs even when the joint cost of choice is high. In figure 1*C*, we simulated the evolution of preferences for two ornaments that, as in our example, provided nonoverlapping quality information with a high joint cost of choice, exactly as in figure 1*B*. Multiple female preferences evolve, illustrating that for the parameters used in this simulation, the

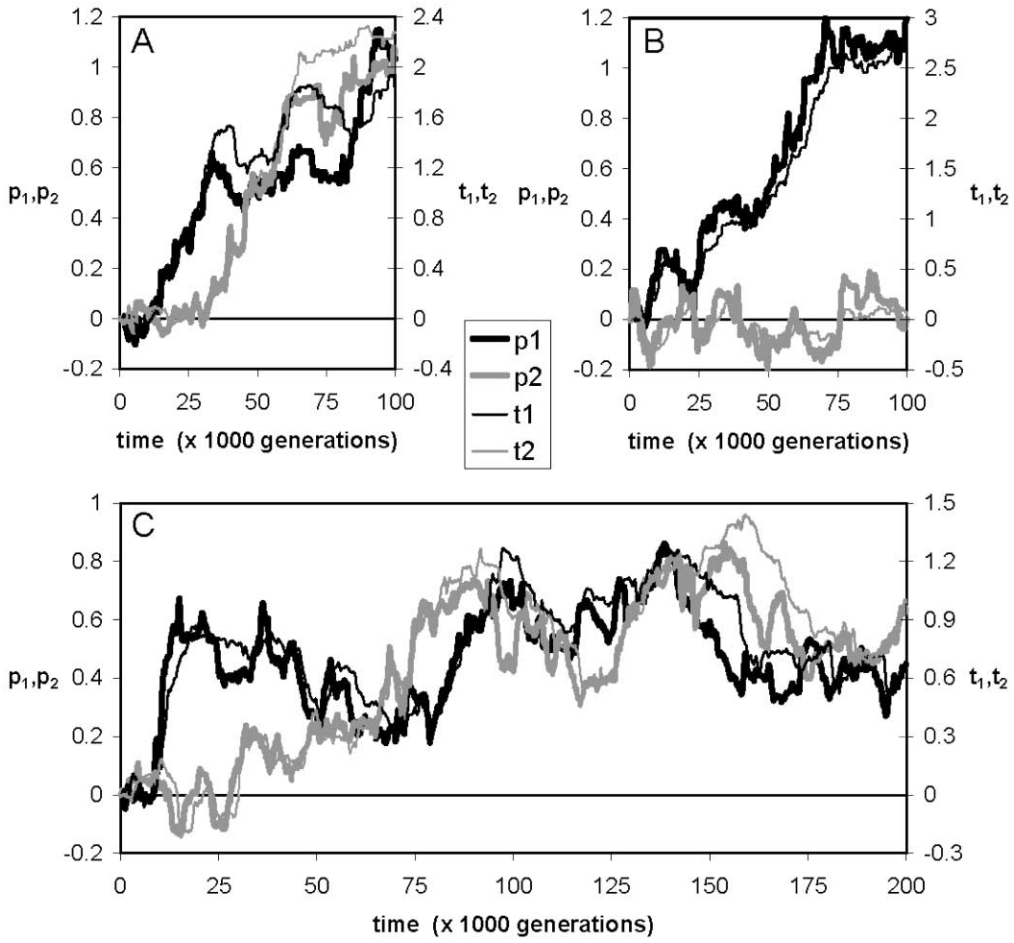

Figure 1: Individual-based simulations. In panels *A* and *B*, the ornaments provide overlapping information about the quality components. Multiple preferences evolve in *A* but not in *B* due to the fact that the joint cost of choice is low in *A* but high in *B*. In panel *C*, the joint cost of choice is high, as in *B*, but the ornaments now provide independent information about the quality components. Despite the high joint cost of choice, multiple preferences evolve. See table 1 for parameter values.

benefit of exhibiting multiple preferences outweighs the high joint cost of choice.

Mathematical Analysis

Due to the stochasticity observed in simulations, it is difficult to characterize thoroughly the behavior of the model for a wide range of parameter conditions. Therefore, we approximate the dynamics of our stochastic individual-based model by deterministic equations. The latter can be analyzed mathematically, yielding further insights into the evolution of multiple female preferences for indicators of independent quality components. To enable this complementary treatment, we make a number of simplifying assumptions.

We concentrate on a genetically simplified version of our simulation model. We assume that individuals are haploid and that each of the two quality components is determined by a single locus with two alleles (*A* and *a* for the first quality component, *B* and *b* for the second). The alleles *A* and *B* confer high quality for their respective quality components; alleles *a* and *b* confer low quality.

The female preferences and the male ornaments may be based on any arbitrary number of loci. However, we do assume that the genes coding for preferences and ornaments mutate only rarely. This allows us to focus on a population with negligible variation for female preference and for male investment into ornaments. Specifically, we assume that almost all individuals carry resident alleles coding for the resident phenotype while a tiny fraction of the individuals carries a mutant allele at one of its preference or ornament loci.

Dynamics of Genotype Frequencies at Quality Loci

Under these simplifications, we need to keep track of four quality genotype frequencies for both resident and mutant individuals. As derived in appendix A in the online edition of the *American Naturalist*, the dynamics of these genotype frequencies can be described by a system of recurrence equations given by

$$\vec{z}_{n+1} = \mathbf{M}\hat{\mathbf{T}}(\vec{z}_n)\vec{z}_n,$$
$$\vec{\varepsilon}_{n+1} = \mathbf{M}\mathbf{T}(\vec{z}_n)\vec{\varepsilon}_n. \quad (10)$$

Here, $\vec{z}_n$ and $\vec{\varepsilon}_n$ represent vectors containing the genotype frequencies in generation n at the viability loci for the resident and the mutant, respectively. The matrix $\mathbf{M}$ incorporates the effects of biased mutations of the quality genotypes. The matrices $\hat{\mathbf{T}}(\vec{z}_n)$ and $\mathbf{T}(\vec{z}_n)$ are transition matrices that incorporate the effects of viability selection and nonrandom mating, exactly as described for the individual-based simulation model. The elements of $\hat{\mathbf{T}}(\vec{z}_n)$ and $\mathbf{T}(\vec{z}_n)$ vary with the quality genotype frequencies of the resident because these determine the availability of mating partners. In addition, the matrix elements vary with female preferences and male investment into ornaments. The mutant transition matrix $\mathbf{T}(\vec{z}_n)$ depends on the mutant phenotype but also on the resident phenotype because mutants interact with resident individuals during mate choice. The resident transition matrix $\hat{\mathbf{T}}(\vec{z}_n)$ depends only on the resident phenotype because resident individuals interact predominantly with other resident individuals.

The system of equations (10) is nonlinear in the resident genotype frequencies but linear in the mutant genotype frequencies. Given that the resident genotype frequencies at the quality loci attain a stable equilibrium distribution $\vec{z}^*$ after some time, we may apply standard stability analysis to find the long-term growth rate of the mutant population. The latter is determined by the dominant eigenvalue λ of the matrix $\mathbf{MT}(\vec{z}^*)$. When $|\lambda| > 1$, the mutant density will increase until, in most cases, the mutant has replaced the former resident. When $|\lambda| < 1$, the mutant will disappear after some time. Hence, λ can be used as a measure for the mutant's invasion fitness (Metz et al. 1996).

Table 1: Parameter values used in the simulations

Figure	α_1^{AB}	α_1^{Ab}	α_1^{aB}	α_1^{ab}	α_2^{AB}	α_2^{Ab}	α_2^{aB}	α_2^{ab}	ϑ_1	ϑ_2
1*A*[a]	3.0	1.5	1.5	.5	3.0	1.5	1.5	.5	−.25	−.25
1*B*	3.0	1.5	1.5	.5	3.0	1.5	1.5	.5	.25	.25
1*C*	2.0	2.0	.5	.5	2.0	.5	2.0	.5	.25	.25
2*A*[b]	2.0	2.0	2.0	…[c]	3.0	3.0	3.0	…	1.0	1.0
2*B*	2.0	2.0	2.0	…	3.5	3.0	3.0	…	1.0	1.0
2*C*	3.0	2.0	2.0	…	4.5	3.0	3.0	…	1.0	1.0
2*D*	4.0	2.0	2.0	…	4.5	3.0	3.0	…	1.0	1.0
2*E*	4.0	3.0	2.0	…	4.5	1.5	4.0	…	1.0	1.0
2*F*	3.2	3.2	.0	…	2.0	.8	.2	…	1.0	1.0

[a] Other parameters in figure 1 were $N = 1{,}000$, $\beta_1 = \beta_2 = 0.5$, $\gamma_1 = \gamma_2 = 0.01$, $v_{AB} = 1.0$, $v_{Ab} = v_{aB} = 0.5$, $v_{ab} = 0.0$, $m = 0.001$, $\sigma_m = 0.05$, $L = 10$, $\mu = 0.01$, $v = 0.0001$.

[b] Other parameters in figure 2 were $\mu_A = 0.06$, $\mu_B = 0.05$, $\beta_1 = 0.4$, $\beta_2 = 0.6$, $\gamma_1 = 0.07$, $\gamma_2 = 0.04$, $v_{AB} = 1.0$, $v_{Ab} = 0.7$, $v_{aB} = 0.8$.

[c] The parameters α_i^{ab} are irrelevant for the analytical model.

Evolutionary Dynamics

Under suitable assumptions (Weissing 1996), evolution can be described as a sequence of mutation and trait-substitution events. The invasion fitness may be used not only to predict the outcome of a single step in this sequence but also to predict the direction and rate of the process as a whole. In other words, from the mutant's invasion-fitness function, we may derive equations describing the evolutionary dynamics of the phenotypic characters of our model. Starting from equation (10), this procedure is outlined in detail in appendix B in the online edition of the *American Naturalist*. Here, we only give the end result, consisting of two equations for the evolutionary rate of change in male investment into the ornament and two equations for the evolutionary rate of change in female preference. The former are as follows:

$$\frac{dt_i}{d\tau} = \frac{1}{2}\frac{\partial \ln[(1 - c_m)r_{AB}]}{\partial t_i} \text{ for } i = 1 \text{ or } i = 2, \quad (11)$$

where τ represents evolutionary time. Male ornament sizes will change until a stable equilibrium is reached. At equilibrium, $dt_i/d\tau = 0$, which, in view of equation (11), implies that the equilibrium amount of resources invested into the ornaments maximizes the product of male survival (represented by $1 - c_m$) and attractiveness for the most viable males (represented by r_{AB}; cf. eqq. [1]–[3]). The attractiveness of low-quality males (r_{Ab}, r_{aB}, and r_{ab}) does not enter into the equations for male investment into ornaments because low-quality males occur at low frequencies only.

The equation for the evolutionary rate of change in female preference is given by

$$\frac{dp_i}{d\tau} = \frac{1}{2}\frac{\partial \ln(1 - c_f)}{\partial p_i} + \mu_A w_A \frac{\partial \ln(R_A)}{\partial p_i} + \mu_B w_B \frac{\partial \ln(R_B)}{\partial p_i}. \quad (12)$$

In this equation, μ_A and μ_B denote the rate of deleterious mutations for quality components A and B, respectively. The coefficients w_A and w_B denote the reproductive values of males carrying a deleterious mutation at one of the quality loci. The functions R_A and R_B, which vary with the

preferences present in the resident population, represent the attractiveness of high-quality males relative to the attractiveness of males carrying a deleterious mutation; that is,

$$R_A = \frac{r_{AB}}{r_{aB}},$$

$$R_B = \frac{r_{AB}}{r_{Ab}}. \tag{13}$$

According to equation (12), female choosiness evolves to a level at which the costs and benefits of choice are balanced. When there is no variation among males (no mutation bias, $\mu_A = \mu_B = 0$), female preference will evolve to maximize $1 - c_f$; that is, the cost of choice will be minimized. When mutation bias creates variation among males, the female preferences will evolve away from their respective viability-selection optima to a point where $\partial \ln (1 - c_f)/\partial p_i$ is negative provided that $\partial \ln (R_A)/\partial p_i$ and $\partial \ln (R_B)/\partial p_i$ are sufficiently larger than 0.

The terms $\partial \ln (R_k)/\partial p_i$ ($k = A$ or B) have an interesting biological interpretation. For females that mate randomly, low-quality males are, by definition, as attractive as high-quality males. To females that exhibit stronger preferences, however, high-quality males will appear increasingly attractive. Therefore, R_A and R_B are monotonically increasing functions of p_1 and p_2. Ornaments may differ in the rates at which R_A and R_B increase with female preference. Precisely these differences are quantified by the terms $\partial \ln (R_k)/\partial p_i$, which represent the rate at which the relative attractiveness of high-quality males (for quality component k) increases with female preference for ornament i. If $\partial \ln (R_k)/\partial p_i$ is only slightly larger than 0, the relative attractiveness of high-quality males increases only slowly with preference, and females must evolve high levels of choosiness before they can accurately distinguish high-quality from low-quality males. In this situation, we say that the information content of ornament i is low for quality component k, meaning that the ornament i is a poor revealing indicator for quality component k. However, when $\partial \ln (R_k)/\partial p_i$ is large, even low levels of choosiness will allow females to select males with high quality for quality component k. In this case, we say that the ornament i has a high information content for quality component k.

It is a direct consequence of equation (12) that a female preference p_i will converge on its viability selection optimum (maximal $1 - c_f$) when the corresponding ornament is not a revealing indicator for at least one component of quality (i.e., when $\partial \ln (R_A)/\partial p_i = \partial \ln (R_B)/\partial p_i = 0$).

A Specific Example

For the sake of concreteness, let us now choose, as in the individual-based simulation model,

$$\begin{aligned} r_k &= \exp (\alpha_1^k p_1 t_1 + \alpha_2^k p_2 t_2), \\ c_m &= 1 - \exp (-\beta_1 t_1^2 - \beta_2 t_2^2), \\ c_f &= 1 - \exp (-\gamma_1 \theta_{12} p_1^2 - \gamma_2 \theta_{21} p_2^2), \end{aligned} \tag{14}$$

with $k = ab, aB, Ab$, or AB. For simplicity, we consider only nonnegative values of preference and male investment into ornaments from here on; that is, $p_1 \geq 0$, $p_2 \geq 0$, $t_1 \geq 0$, and $t_2 \geq 0$. As in the individual-based simulations, the costs of exhibiting a preference for one of the ornaments may depend on the level of choosiness for the other ornament. Therefore, the baseline costs of choice, γ_i, are modified by the coefficients for the joint cost of choice, θ_{12} and θ_{21}, which are allowed to vary with p_2 and p_1, respectively (as in eq. [9]).

Equation (11) now reduces to a simple equation with equilibrium solutions (denoted by tildes):

$$\tilde{t}_i = \frac{1}{2} \frac{\alpha_i^{AB}}{\beta_i} \tilde{p}_i. \tag{15}$$

Substituting these equilibrium solutions into equation (12) eventually yields two equations from which the equilibrium values for the female preferences can be solved (see app. C in the online edition of the *American Naturalist*). With $i = 1$ or 2, $j = 1$ or 2, and $j \neq i$, these equations are given by

$$\tilde{p}_i \gamma_i \theta_{ij} + \vartheta_j \gamma_j \tilde{p}_i \tilde{p}_j^2 \theta_{ji} = \mu_A \tilde{w}_A \kappa_i^A \tilde{p}_i + \mu_B \tilde{w}_B \kappa_i^B \tilde{p}_i. \tag{16}$$

The left side of this equation represents the costs of choice, the right side the benefits of choice. As indicated by the tilde, the reproductive values $\tilde{w}_A$ and $\tilde{w}_B$ are functions of the equilibrium preference values. The constants κ_i^k ($k = A$ or B) derive from the terms $\partial \ln (R_k)/\partial p_i$. They measure the information content of the ornaments, that is, the amount of information that ornament i gives about quality component k. To be exact,

$$\kappa_i^A = \frac{\alpha_i^{AB}(\alpha_i^{AB} - \alpha_i^{aB})}{2\beta_i},$$

$$\kappa_i^B = \frac{\alpha_i^{AB}(\alpha_i^{AB} - \alpha_i^{Ab})}{2\beta_i}. \tag{17}$$

Equilibria and Their Stability

The solutions of the equilibrium conditions (15) and (16) fall into three categories. We always find a trivial equilibrium ($\tilde{p}_1 = \tilde{p}_2 = \tilde{t}_1 = \tilde{t}_2 = 0$) at which females mate at random. In addition, we may find boundary equilibria, at which females exhibit a preference for just one of the ornaments, and internal equilibria, at which females exhibit preferences for multiple ornaments.

The trivial equilibrium is stable when the information content of both ornaments is low (app. C), such that the benefits of mate choice (right side of eq. [16]) do not outweigh the costs of choice (left side of eq. [16]). A representative phase portrait for this case is shown in figure 2*A*. Figure 2 depicts projections of the four-dimensional phase space of our model, in which information about the dynamics of the male characters t_1 and t_2 is not shown. These projections, however, provide nearly complete information about the dynamics because the male characters evolve on a timescale much faster than that on which female preferences change (provided that the mutation biases and the costs of choice are small). Consequently, t_1 and t_2 are always close to a quasi-equilibrium value, defined by equation (15).

When the information content of the ornaments is sufficiently high (app. C), the trivial equilibrium loses its stability, and the system may evolve to a boundary equilibrium, at which females exert a preference for one ornament only. We find one (fig. 2*B*) or two (fig. 2*C–E*) boundary equilibria, depending on whether the benefits of choice outweigh the costs for only one ornament or for both ornaments. In figure 2*C*, female preferences always evolve to the same boundary equilibrium, as one would expect for the situation in which one of the ornaments is a superior indicator of quality (Schluter and Price 1993). Indeed, for the parameters used in figure 2*C*, the second ornament has a higher information content for both quality components.

When both ornaments provide comparable net benefits (as in fig. 2*D*, 2*E*), we find an internal equilibrium. It is already known that multiple preferences can be stable when the joint cost of choice is low ($\vartheta_i < 0$), even when the two ornaments provide completely overlapping information about quality (fig. 1*A*; Iwasa and Pomiankowski 1994). Therefore, we assume, from here on, that the joint cost of choice is high ($\vartheta_i > 0$). Under these conditions, multiple preferences are unstable if the ornaments provide overlapping information about the two quality components (figs. 1*B*, 2*D*; Iwasa and Pomiankowski 1994). However, as soon as the ornaments provide sufficiently independent information about the two quality components, the internal equilibrium becomes stable, and multiple preferences can evolve (figs. 1*C*, 2*E*). If an internal equilibrium exists, it is unique in most cases. For a narrow range of parameters, however, we may find a phase portrait such as that in figure 2*F*, with multiple internal equilibria. Multiple internal equilibria occur when one ornament (ornament 1 in this case) is a highly reliable indicator for one quality component but a poor indicator for the other quality component, whereas the other ornament (ornament 2 in this case) is a mediocre indicator for both quality components. Depending on the initial conditions, the population will then either end up in a boundary equilibrium, where females assess only the mediocre indicator for both quality components, or in an internal equilibrium, where females assess both ornaments.

Clearly, the existence of an internal equilibrium, its stability, and the stability of the two boundary equilibria depend on the costs and benefits of choice, particularly on the joint cost of choice and the degree of overlap in the information content of the two ornaments (app. C). To investigate further the conditions under which multiple preferences are stable, we systematically varied the information contents of the two ornaments, thereby changing the benefits of choice for the two ornaments as well as the extent to which they provide independent information about quality. This analysis revealed that multiple preferences are stable for a wide range of parameter conditions (app. D). Even when the ornaments provide considerably different benefits of choice, females may evolve preferences not only for the superior ornament (as predicted by Schluter and Price 1993) but also for the inferior ornament as long as the ornaments provide sufficiently independent information. This conclusion holds not only for the specific model studied in this article. Under quite weak and general assumptions, it can be shown that our conclusions apply to more complex mate-choice scenarios (app. E in the online edition of the *American Naturalist*).

Discussion

Our analysis demonstrates that the scope for the evolution of multiple female preferences is wider than previously reported. Female preferences for multiple indicators of quality may evolve not only when the joint cost of choice is low but also when the different ornaments provide information about different components of quality. In addition to these possibilities (app. E), multiple preferences can evolve when increasing preferences yield diminishing returns in terms of the benefits of choice, as would be the case when the costs of ornament production rise sharply (Johnstone 1996). We therefore conclude that there is no a priori reason to rule out the multiple-message hypothesis as a suitable hypothesis for the evolution of female preferences for multiple male ornaments.

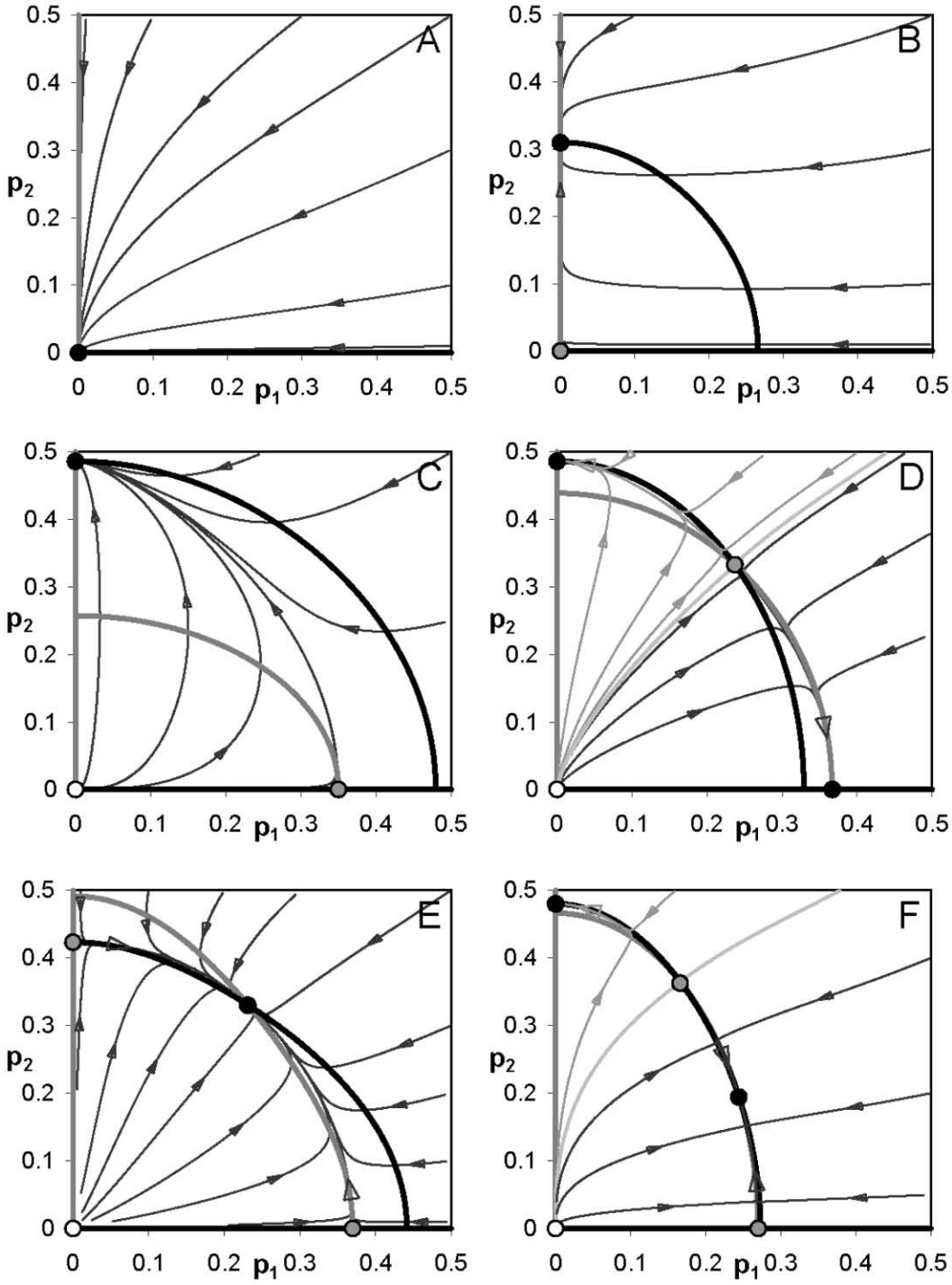

Figure 2: Qualitatively different outcomes of the model. The panels *A–F* represent projections of the four-dimensional trait space of our model in which information about the male characters is not shown. Each phase portrait shows projected trajectories computed for the full four-dimensional system (*lines with arrows*); null clines, computed using a quasi–steady state assumption for the male characters (*thick gray lines*: p_1 isocline; *thick black lines*: p_2 isocline); and equilibria (*open circles*: unstable nodes; *gray-filled circles*: saddle points; *black-filled circles*: stable nodes). If there exist multiple stable equilibria (*D*, *F*), a thick light-gray line indicates the boundary between the basins of attraction of the equilibria. See table 1 for parameter values.

Redundant Signals and Multiple Messages

Throughout this article, we have interpreted the two quality characters *A* and *B* of our model as independent components of an individual's quality. Under this interpretation, ornaments that reveal nonoverlapping information about the quality characters convey multiple messages as proposed by the multiple-message hypothesis. At the same time, however, the two quality characters *A* and *B* jointly determine an individual's general viability, and they might therefore be interpreted as independent estimates of an individual's overall genetic quality, as proposed by the redundant-signal (or back-up-signal) hypothesis.

This illustrates that it is almost impossible to distinguish between a multiple-message and a redundant-signal mechanism. Indeed, in the original formulation of the two hypotheses (Møller and Pomiankowski 1993), the distinction between these hypotheses is blurred, and it depends on the level of description whether ornaments should be considered as multiple messages or as redundant signals. In fact, one can distinguish between the two hypotheses only if one is able to demonstrate that different females weigh the information provided by the different ornaments in a different manner (this would be indicative of a multiple-message mechanism). On the basis of the current model, which does not address this level of complexity, we may therefore extend our conclusions to encompass the redundant-signal hypothesis; that is, multiple preferences can evolve—even when the joint of choice is high—when the ornaments provide independent estimates of an individual's overall genetic quality.

This conclusion may have implications for the interpretation of empirical results. First, the extensive evidence for the multiple-message hypothesis could as well be interpreted as evidence in support of the redundant-signal hypothesis, for which evidence is scarce (Candolin 2003). This is because it is usually impossible to distinguish between the case in which the viability components defined by the human observer are functionally relevant for the choosing female (multiple-message hypothesis) and the case in which they merely serve as correlates of some underlying quantity the female wishes to estimate (redundant-signal hypothesis).

Second, the redundant-signal hypothesis has predominantly been tested by investigating whether different components of the male courtship display are positively correlated with one another (Candolin 2003). The presence of such a positive correlation among male courtship traits is then interpreted as supporting the redundant signal hypothesis, whereas the absence of such a correlation, or even a negative correlation, is interpreted as evidence against the redundant signal hypothesis. Our results indicate that multiple ornaments can evolve as redundant signals but only when the ornaments are independent indicators of quality. Under a redundant signal mechanism, we would therefore expect the expression of any individual male courtship trait to be correlated with overall quality. However, we would expect a weak correlation or no correlation at all among the different traits. We would not expect to find strong positive correlations among traits because this would imply that the male indicator traits do not provide independent estimates of overall quality. This suggests that testing the redundant signal hypothesis based on the pattern of correlations among male courtship traits, as discussed above, may be problematic.

Handicaps versus Fisherian Traits

In their articles on the evolution of multiple ornaments, Pomiankowski and Iwasa (1993; Iwasa and Pomiankowski 1994) argue that sexual traits in species with multiple ornaments evolved predominantly through Fisherian runaway sexual selection and not via the handicap process. This idea is based on their conclusion that multiple female preferences can evolve for Fisherian traits but not for handicaps (assuming that the joint cost of choice is high). Given the fact that the distinction between Fisherian and handicap models of sexual selection is merely conceptually useful (Kokko et al. 2002), this conclusion is surprising.

Iwasa and Pomiankowski's conclusion derives from a comparison between a Fisherian (Pomiankowski and Iwasa 1993) and a handicap model (Iwasa and Pomiankowski 1994) for the evolution of multiple preferences. Together with the difference in the mechanism of sexual selection (Fisherian vs. handicap sexual selection), these models differ also in another aspect: in the Fisherian model, two male characters are subject to independent biased-mutation processes, but in the handicap model, a single biased-mutation process, acting on general viability, causes variation in the expression of both male ornaments. Although it is biologically reasonable to suppose that mutation acts differently on Fisherian traits versus handicaps, it is desirable, from a mathematical point of view, to decouple the assumptions on the mechanism of sexual selection from the assumptions on the mutation process. This allows one to determine whether the different outcome of the two models is explained by the mere fact that one is a Fisherian model and the other a handicap model or whether perhaps the different assumptions on the mutation process are responsible for the observed difference in the outcome of the models.

In this article, we have demonstrated that female preferences can evolve for multiple handicaps if the male ornaments provide independent information about different components of quality. In this scenario, expression of the male ornaments is subject to independent biased-mutation

processes—exactly as in the Fisherian runaway model of Pomiankowski and Iwasa (1993)—due to the fact that the quality components underlying those ornaments are separately and independently affected by mutation bias. Along the same lines, an appropriate Fisherian counterpart of the handicap model of Iwasa and Pomiankowski (1994) would model a situation in which both male characters are affected by the same biased-mutation process. Such a situation is, in fact, approximated by a special case of our model, namely, the case in which the two ornaments provide completely overlapping information about quality. In this case, only a single preference can evolve (fig. 1*B*; fig. 2*C*, 2*D*). This result also holds in the special case in which an individual's viability is independent of its quality components (i.e., when $v_{AB} = v_{Ab} = v_{aB} = v_{ab}$). Under these conditions, the quality components A and B can be reinterpreted as sets of genes that merely modify the expression of the male ornaments. Our model then becomes a Fisherian model in which females benefit from being choosy only through a sexy-son mechanism. Because the two ornaments are equally affected by the two sets of modifier genes, the distinction between these two sets of genes is arbitrary, implying that the variation in the expression of male ornaments is essentially created by a single biased-mutation process. Crucially, one would expect that only a single preference would evolve in this Fisherian model, exactly as in the handicap model of Iwasa and Pomiankowski (1994), which also considers only a single biased-mutation process.

We conclude that ornament diversity is predominantly determined by the number of independent components of variation about which the ornaments provide information. Whether or not these components of variation correlate with fitness components other than attractiveness (as assumed in good-genes models) seems not to affect the outcome in a qualitative fashion (cf. Kokko et al. 2002). However, these conclusions do not eliminate the possibility that, as suggested by Pomiankowski and Iwasa (1993; Iwasa and Pomiankowski 1994), sexual traits in species with multiple ornaments have evolved predominantly through Fisherian runaway sexual selection and not via the handicap process. For example, sexual traits that are only weakly associated with quality traits (i.e., Fisherian traits) may be more likely to experience independent biased mutations than traits that are strongly associated with quality traits (handicap traits). Such an effect would produce the pattern as proposed by Iwasa and Pomiankowski, not due to a fundamental difference between Fisherian and handicap traits but due to a correlated difference in the genetic architecture underlying Fisherian and handicap traits.

Methodological Remarks

Our analytical model is a hybrid model consisting of a population-genetical model for the genotype frequencies at the quality loci and an adaptive-dynamics model for the female preferences and male sexual characters. An important advantage of this approach is that it allows us to express directly the fitness gradients in terms of parameters of the model without the need to keep track of genetic variances and covariances, as in quantitative-genetic models (e.g., Iwasa and Pomiankowski 1994). Although it is possible to estimate the values of genetic (co)variances as functions of model parameters (Pomiankowski and Iwasa 1993, using theory developed by Barton and Turelli 1991), this procedure is quite complex and involves restrictive assumptions.

The adaptive-dynamics method describes evolution as a mutation-limited process. This assumption allowed us to derive fitness functions relatively easily but at the same time forced us to assume that there is negligible genetic variation in the resident population for the characters under consideration. This assumption is clearly problematic for the quality components because the handicap principle relies on the continual presence of genetic variation in quality. Therefore, we used a simple explicit genetic model to keep track of the frequencies of quality genotypes. For the female preferences and male sexual characters, the assumption of mutation-limited evolution has the important consequence that we cannot address the effects of genetic covariances between preferences, between the male sexual characters, and between preferences and male characters. The latter covariances are instrumental in driving Fisher's (1930) runaway process of sexual selection.

In view of the above, we made an effort to check our analytical results against individual-based computer simulations, which do not rely on the assumptions needed in analytical phenotypic models of evolution. Despite the restrictions imposed by our method of analysis, we found good qualitative agreement between the simulations and our analytical results. We found no differences in the number of equilibria or their stability properties, but we did observe small quantitative differences in the exact location of equilibrium points or transient dynamics. Apart from this, it is reassuring to find, for the special case in which the ornaments provide overlapping information about genetic quality, that the results of our model fit with previous models (Schluter and Price 1993; Iwasa and Pomiankowski 1994), realizing, of course, that the existing models rely on similarly restrictive assumptions (e.g., assumptions of weak selection; Taylor 1996*b*).

Condition-Dependent Trait Expression

In this study, we have treated the information content of an ornament as a fixed parameter of the model. This approach excludes the possibility that males adjust their investment into ornaments depending on their quality in order to realize an optimal pattern of condition-dependent ornament expression (Grafen 1990). An obvious next step is to extend our model to allow for this.

Analysis of such an extended model (G. S. Van Doorn and F. J. Weissing, manuscript in preparation) reveals that condition-dependent trait expression does not lead to results that are qualitatively different from the results of the present article unless females adjust their preferences more rapidly than males can fine-tune their trait expression pattern. In this case, females may be continually forced to direct their preferences to novel ornaments because evolution in males will tend to lower slowly the information content of any ornament on which female preference is acting. This process of sexual conflict over the information of content of ornaments may lead to the continual change of sexual preferences and male ornament expression.

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