

Sexual Selection and the Sex Ratio: An ESS Analysis

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Should attractive fathers have more sons? According to widespread verbal arguments, the answer is in the affirmative, but formal models are lacking. We investigate the question by means of an ESS analysis of sexual selection and sex ratio selection. The purpose of this paper is twofold: firstly, we show how an ESS approach can be used to model the coevolution of female mate choice and male secondary sexual traits. In the ESS approach, the genetic covariances of traditional genetic models of sexual selection are replaced by covariances between strategies. In comparison with population genetic and quantitative genetic models of sexual selection, the ESS approach is simpler and yields more insight in the underlying selective forces. Secondly, we show that whether attractive fathers should have more sons depends on the mechanism of sexual selection: sexual selection driven by the Fisherian runaway process alone, without costs of choosiness, does not select for sex ratio specialization according to paternal attractiveness, but the good-genes process causes selection to favor such specialization.

Keywords: Mate choice, runaway, good genes, sex allocation, reproductive value

1. Introduction

Sexual selection driven by female mate choice is held responsible for much male extravaganzas such as conspicuous ornaments and elaborate courtship displays (Darwin, 1859, 1871; Andersson, 1994). Female choosiness itself is favored by selection if it confers a net fitness benefit to females. Those benefits are usually classified as either direct or indirect benefits. Direct benefits of choosiness are improvements of a female's own reproductive success, due to, for example, preferred males having better territories or providing more parental care (Hoelzer, 1989). Indirect benefits are obtained if offspring sired by preferred males have relatively high reproductive success, caused by inheritance of their father's high viability, fecundity, or attraction. Two distinct mechanisms may explain how indirect benefits can accrue to choosy females: Fisher's runaway process (Fisher, 1930) and the good-genes model (e.g. Kirkpatrick, 1996). In Fisher's runaway pro-

cess, choosiness evolves because sons of choosy females tend to have more offspring simply because they are more attractive to other females. According to the good-genes model, choosiness is favored because the preferred male's character signals his good genes, other than those that cause his attractiveness, that he passes on to his offspring.

There is an obvious link between sexual selection and the sex ratio: intrasexual competition for matings is more intense for the sex that is overrepresented in the population. More recently, another link between sexual selection and the sex ratio has been postulated. Based on the idea that the offspring sex ratio should reflect parental quality (Trivers and Willard, 1973), it has been argued that it would be adaptive for attractive males to produce a male-biased sex ratio. Several recent empirical studies, mainly on birds, have investigated the correlation between conspicuousness or phenotypic quality of males and the sex ratio among the offspring of such males (Burley, 1981; Westneat et al., 1995; Ellegren et al., 1996; Sheldon and Ellegren, 1996; Svensson and Nilsson, 1996; Westerdahl et al., 1997). The results were mixed: some studies found a positive correlation, others found no correlation (review in Sheldon, 1998). However, the theoretical status of the

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underlying idea is far from clear yet, being only based on verbal reasoning that can be quite misleading in the context of sexual selection. Therefore here, for the first time, we attempt to analyse this idea by means of formal models.

It is not too surprising that a formal modelling approach has not been attempted thus far. The two most commonly used theoretical methods to study sexual selection, population genetic (PG) and quantitative genetic (QG) models, are not easily adapted to incorporate variable sex ratios. PG models tend to become very complicated, not only because the number of loci to be considered increases, but also because allele frequencies differ between the sexes. Concerning the QG approach, it is not obvious to us how conditional sex allocation can be incorporated into QG models. In contrast, an evolutionarily stable strategy (ESS) analysis has proven to be highly successful in the context of sex ratio evolution (Charnov, 1982; Frank, 1998). For this reason, we first investigate whether, and to what extent, an ESS analysis can also be applied in the context of sexual selection. At first sight, it is perhaps surprising that the ‘‘phenotypic’’ ESS approach (Weissing, 1996) might be useful in the context of a process where genetic variances and covariances play a crucial role for the outcome of selection (Lande, 1981; Kirkpatrick, 1982). However, as we will show below, with some reasonable assumptions, ESS models can be constructed where the genetic covariances of QG are replaced by covariances between strategies. An ESS approach has been used before in the context of sexual selection (Grafen, 1990a, b; Siller, 1998), but without explicitly considering covariances between strategies. Such covariances are important because linkage disequilibrium may cause indirect selection on traits that are not themselves subject to direct selection. Moreover, previous game theory models of sexual selection used rather ad hoc fitness functions. Here we derive fitness consequences from explicit population dynamical models for the life history context of the problem.

First we show that classical results of sexual selection theory can also be obtained by an ESS analysis. We will argue that the ESS approach provides a better insight into the selective forces involved. The power of the method is demonstrated by applying it to the sex ratio problem. We show that, contrary to the standard verbal arguments (e.g. Ellegren et al., 1996), it may crucially depend on the mechanism of

sexual selection whether and how organisms should bias the sex ratio of their offspring in relation to paternal attractiveness.

2. An overview of the method

In this section we give a brief account of the ESS methods we use in the rest of the paper. For a more elaborate treatment, see Taylor and Frank (1996), Frank (1998) and Pen and Weissing (2000).

2.1. Evolutionary stability of a single trait

A trait x^* is considered evolutionarily stable (an ESS, Maynard Smith, 1982) if a population exhibiting this trait cannot be invaded by any mutant with an alternative trait $x \neq x^*$. In other words: x^* is an ESS if it yields a higher fitness than any alternative x :

$$W(x, x^*) < W(x^*, x^*) \quad (1)$$

where $W(x, x^*)$ denotes the fitness of a mutant trait x in a monomorphic resident population with trait x^* . This implies the equilibrium condition

$$\left. \frac{\partial W}{\partial x} \right|_{x=x^*} = 0. \quad (2)$$

Higher-order conditions must be checked to see if x^* corresponds to a local maximum or minimum and to see if x^* has additional stability properties (see Geritz et al., 1998).

The fitness function $W(x, x^*)$ is derived from a population dynamical model for a subpopulation of mutants embedded in a resident population. Populations generally consist of several classes of individuals, classified according to sex or age or any other interesting property. Transitions between different classes of mutants from one time unit to the next are summarized by the square matrix $\mathbf{A} = \mathbf{A}(x, x^*)$, where each matrix element $a_{ij} = a_{ij}(x, x^*)$ represents the per capita contribution of a class j individual mutant to the class i individuals mutants one time unit later. The asymptotic growth rate $\lambda = \lambda(x, x^*)$ of the subpopulation of mutants, given by the dominant eigenvalue of \mathbf{A} , is a proper measure of fitness (Metz et al., 1992), but is usually hard to calculate.

An alternative fitness function can be obtained by a reproductive value approach (e.g. Taylor, 1996; Pen and Weissing, 2000). This fitness function identifies the same evolutionarily stable strategies as λ , but it is easier to calculate and often provides more insights into the underlying selective forces. Formally, this fitness function is given by

$$W(x, x^*) = \sum_{i,j} v_i^* u_j^* a_{ij}(x, x^*), \quad (3)$$

where the u_j^* are the class frequencies of the resident population in demographic equilibrium and the v_i^* are the reproductive values of the different classes of resident individuals. Formally, the vectors \mathbf{u} and \mathbf{v} are dominant right and left eigenvectors of the matrix $\mathbf{A}(x^*, x^*)$. The equilibrium condition (2) is then given by

$$\left. \frac{\partial W}{\partial x} \right|_{x=x^*} = \sum_{i,j} v_i^* u_j^* \left. \frac{\partial a_{ij}}{\partial x} \right|_{x=x^*} = 0. \quad (4)$$

2.2. Evolutionary stability of multiple traits

In studying the coevolution of several traits, such as the coevolution of female sexual preferences and male secondary sexual traits, one has to consider the possibility that correlations between traits occur, such as a correlation between the degree of female preference and the degree of male exaggeration. Suppose, for example, that we are interested in the coevolution of traits x and y . Selection on x is not only governed by the “direct” effect of x on fitness, quantified by $\partial W/\partial x$, but also indirectly by the effects of y on fitness, quantified by $\partial W/\partial y$, which have to be taken into account if y is correlated with x . If y were a function of x , the total effect of selection on x would be quantified by the total differential of W with respect to x :

$$\frac{dW}{dx} = \frac{\partial W}{\partial x} + \frac{dy}{dx} \frac{\partial W}{\partial y}. \quad (5)$$

In the context considered here, y is not a function of x but only correlated with x . To take this correlation into account, it is convenient to replace dy/dx in (5) with β_{yx} , the statistical regression coefficient of y on x (Taylor and Frank, 1996). In this way, the total selection differentials on x and y are given by

$$\frac{dW}{dx} = \frac{\partial W}{\partial x} + \beta_{yx} \frac{\partial W}{\partial y} \quad (6a)$$

$$\frac{dW}{dy} = \frac{\partial W}{\partial y} + \beta_{xy} \frac{\partial W}{\partial x}, \quad (6b)$$

where the derivatives are evaluated at $x = x^*$ and $y = y^*$. The identification of the derivatives with the regression coefficients is not exact in general, but if x and y are from a bivariate normal distribution, then it is “exact” (see Lande, 1976) because in that case $E(y|x) = E(y) + \beta_{yx} [x - E(x)]$.

At an evolutionarily stable pair (x^*, y^*) both selection differentials have to be equal to zero:

$$\frac{\partial W}{\partial x} + \beta_{yx} \frac{\partial W}{\partial y} = 0 \quad (7a)$$

$$\frac{\partial W}{\partial y} + \beta_{xy} \frac{\partial W}{\partial x} = 0, \quad (7b)$$

evaluated at $x = x^*$ and $y = y^*$.

We will consider β_{xy} and β_{yx} as constants and assume that they satisfy the non-degeneracy condition $\beta_{xy}\beta_{yx} \neq 1$. This implies that the equilibrium conditions (7a) and (7b) coincide with the conditions

$$\left. \frac{\partial W}{\partial x} \right|_{x=x^*} = 0 \quad (8a)$$

$$\left. \frac{\partial W}{\partial y} \right|_{y=y^*} = 0. \quad (8b)$$

Hence, the pairs (x^*, y^*) can be found by finding the equilibria of x and y separately, without knowledge of the coefficients β_{xy} and β_{yx} . However, whether (x^*, y^*) corresponds to a maximum, as determined by higher-order conditions, may depend on the values of β_{xy} and β_{yx} . A special case obtains if there is no direct selection on one of the two traits, say x : $\partial W/\partial x = 0$. In that case the equilibrium condition is given $\partial W/\partial y = 0$, and since W is a function of x and y , the equilibrium is usually a continuum (often a “line of equilibria”).

In general, for n traits x_1, \dots, x_n , the equilibrium condition can be written as

$$\beta \nabla W = 0, \quad (9)$$

where ∇ is the gradient-operator $(\partial/\partial x_1, \dots, \partial/\partial x_n)$ and β is the $n \times n$ matrix of “regression” coefficients. If β has nonzero determinant, the equilibrium condi-

tion is equivalent to $\nabla W = 0$. An equilibrium corresponds to a maximum if the matrix $\nabla(\beta \nabla W)$, evaluated at the equilibrium, is negative definite (has only negative eigenvalues, see Lancaster, 1969).

3. ESS models of sexual selection

Below we present two ESS models that try to capture the essence of the two processes thought to be most important in the evolution of female choice: the Fisherian runaway process and the good-genes process. In the next section we expand these models to allow for variable sex ratios.

3.1. Fisherian runaway

There are two types of males: type 0 and type 1. Type 1 males invest more than type 0 males into some conspicuous trait. Males have mixed strategy y , which is the probability that they will develop in type 1 males. Males that develop into type 1 pay a survival cost c , that is, their survival to adulthood relative to type 0 males is given by $1-c$.

Females have a certain preference x for type 1 males, which translates into them giving a proportion α of matings to type 1 males, $\alpha = \alpha(x)$ being an increasing function of x . The number of matings per type of male depends on the frequency of types and the preference of females in the resident population because mutant males and females are assumed to be rare. Let there be u_f^* females in the resident population, and u_{m0}^* , respectively, u_{m1}^* males of type 0 and 1. The per capita number of matings per type of male are then given by

$$Q_0^* = \frac{(1 - \alpha^*)u_f^*}{u_{m0}^*} \quad (10a)$$

$$Q_1^* = \frac{\alpha^* u_f^*}{u_{m1}^*}. \quad (10b)$$

The two conditions taken together imply the constraint that the total number of matings by all males must equal the total number of matings by all females:

$$u_f^* = Q_0^* u_{m0}^* + Q_1^* u_{m1}^*. \quad (11)$$

Assuming nonoverlapping generations and an even sex ratio, the transitions between the different

classes of mutant individuals from one generation to the next are summarized by the matrix

$$\mathbf{A} = \frac{1}{2} \begin{pmatrix} 1 & Q_0^* & Q_1^* \\ 1-y & (1-y)Q_0^* & (1-y)Q_1^* \\ (1-c)y & (1-c)yQ_0^* & (1-c)yQ_1^* \end{pmatrix}. \quad (12)$$

The first column represents females' contribution to the next generation, the second and the third the contributions by type 0 and type 1 males, respectively. The factor $1/2$ reflects the fact that offspring inherit $1/2$ of each parent's genes, as we assume here.

It is easy to verify that the growth rate of the resident population (the dominant eigenvalue of \mathbf{A} when $x = x^*$ and $y = y^*$) is given by $\lambda^* = 1$. In other words, we assume that the resident population is stationary, females producing exactly one daughter on average. The relative sizes of the three classes in the resident population are given by the equation $\mathbf{A}\mathbf{u}^* = \lambda^*\mathbf{u}^*$, where $\mathbf{u}^* = (u_f^*, u_{m0}^*, u_{m1}^*)$. Since the rows of \mathbf{A} are constant multiples of each other, the solution is proportional to the multipliers:

$$\mathbf{u}^* = (1, 1-y^*, (1-c)y^*) \quad (13)$$

Note that these are the frequencies after viability selection.

The reproductive values of the three classes are given by $\mathbf{v}^* \mathbf{A} = \lambda^* \mathbf{v}^*$, where $\mathbf{v}^* = (v_f^*, v_{m0}^*, v_{m1}^*)$. Because the columns of \mathbf{A} are constant multiples of each other, a solution is easily seen to be

$$\mathbf{v}^* = (1, Q_0^*, Q_1^*). \quad (14)$$

In English: the reproductive values of males are just their average number of successful matings times the reproductive value of a female.

There is clearly no direct selection on female preference (there is no x in the matrix), since there are no costs of choice (but see below) and the success of a female's sons depends on the strategy of resident females. Hence $\partial W / \partial x = 0$.

Inserting (11) into (4) yields the direct effect of selection on the male trait y :

$$\left. \frac{\partial W}{\partial y} \right|_{y=y^*} = (1-c)v_{m1}^* - v_{m0}^* \quad (15a)$$

$$= (1-c)Q_1^* - Q_0^*. \quad (15b)$$

In other words, as long as the expected reproductive success (viability times number of mates) of attractive sons is larger than that of unattractive sons, $(1 - c)Q_1^* > Q_0^*$, selection favors an increase in y , and vice versa.

According to (9), the total selection differentials on x and y are given by

$$\frac{dW}{dx} = \beta_{yx} [(1 - c)Q_1^* - Q_0^*] \quad (16a)$$

$$\frac{dW}{dy} = (1 - c)Q_1^* - Q_0^*. \quad (16b)$$

An internal equilibrium, if it exists, is therefore given by

$$*(1 - c)Q_1^* = Q_0^*. \quad (17)$$

At this point the mating advantage of type 1 males is exactly counterbalanced by their viability disadvantage. Because Q_0^* and Q_1^* are functions of both x^* and y^* , the equilibrium determined by (17) will usually not be unique.

Whether an internal equilibrium actually exists depends on details of the choice process. In Kirkpatrick's (1982) 2-locus population genetic model, choosy females give a proportion $p = au_{m1}/(u_{m0} + au_{m1})$ of their matings to type 1 males, whereas non-choosy females give a proportion $q = u_{m1}/(u_{m0} + u_{m1})$. Type 1 males are preferred over type 0 males if and only if $a > 1$. Our model yields the same line of equilibria if we let the females' strategy x be such that type 1 males get a proportion $\alpha = xp + (1 - x)q$ of matings. This gives the following line of equilibria:

$$y^* = b_0 + b_1 x^* \quad (18)$$

with intercept $b_0 = -[a(1 - c) - 1]^{-1}$ and slope $b_1 = -(1 - c)(1 - a)c^{-1}b_0^{-1}$. The line of equilibria is stable if and only if the regression of y on x is sufficiently small: $\beta_{yx} < 1/b_1$.

Alternatively, we can equate the female strategy x with a and we get $\alpha = xu_{m1}/(u_{m0} + xu_{m1})$. In this case there is again a (vertical) line of internal equilibria, given by $x^* = 1/(1 - c)$, which is always unstable: if initially $x > 1/(1 - c)$, then $y \rightarrow 1$ and $x \rightarrow \infty$; if initially $x < 1/(1 - c)$, then both y and x go to zero.

The main message of this and other models of the Fisherian runaway process is that female preference

and exaggerated male traits can coevolve despite natural selection against such male traits. Evolution comes to a halt when the sexual selection advantage of the male trait is exactly counterbalanced by the natural selection disadvantage.

However, other models of the Fisherian runaway process that yield a line of equilibria (Lande, 1981; Kirkpatrick, 1982; Seger, 1985) are structurally unstable in the sense that a small cost of choosiness destroys the line of equilibria (Bulmer, 1989). The same is true for our model, in which costs of choice are easily incorporated: the first row of the matrix (12) can be multiplied by a factor of, say, $1 - k$, where k is an increasing function of choosiness x . The outcome of this model is that there is no stable internal equilibrium and female preference and the costly male trait go to zero. Fisherian runaway models are therefore most relevant when female preference preexisted for some reason not present in the model.

3.2. A good-genes model

The other main idea about how females might get indirect benefits from being choosy is the good-genes process. Females prefer males whose trait signals their possession of genes that enhance the fitness of their offspring. The main difficulty with this idea is that natural selection tends to eliminate variation in fitness (Charlesworth, 1987) and that some other force must be invoked to conserve such variation. Such forces may include biased mutation (Bulmer, 1989; Pomiankowski et al., 1991), and temporal/spatial fluctuation in the direction of natural selection such as in cyclical host-parasite dynamics (Hamilton and Zuk, 1982).

To model such a situation we again assume there are two types of male (type 0 and type 1, the latter carrier of the "good genes"). Type 1 males have a viability advantage of $1 + b$ relative to type 0 males. Types inherit true from father to son, except that a fraction ε of sons of type 1 males are of the inferior type 0. This might be interpreted as mutation bias. Females again give a proportion α of matings to type 1.

Our assumptions translate into the following transition matrix:

$$\frac{1}{2} \begin{pmatrix} 1 & Q_0^* & Q_1^* \\ 1 - (1 - \varepsilon)\alpha & Q_0^* & \varepsilon Q_1^* \\ (1 + b)(1 - \varepsilon)\alpha & 0 & (1 + b)(1 - \varepsilon)Q_1^* \end{pmatrix} \quad (19)$$

The growth rate of the resident population is again given by $\lambda^* = 1$, and the relative class frequencies in the resident population are given by

$$\mathbf{u}^* = (1, 1 - (1 - \varepsilon)\alpha^*, (1 + b)(1 - \varepsilon)\alpha^*). \quad (20)$$

We use (10a) and (10b) to obtain the mating frequencies of the two types of male in the resident population:

$$Q_0^* = \frac{1 - \alpha}{1 - (1 - \varepsilon)\alpha^*} \quad (21a)$$

$$Q_1^* = \frac{1}{(1 + b)(1 - \varepsilon)}. \quad (21b)$$

Normalizing the reproductive value v_f^* of females to unity we obtain the following reproductive values for the two types of male in the resident population:

$$v_{m0}^* = Q_0^* \left(1 - \frac{\varepsilon\alpha^*}{1 - (1 - 2\varepsilon)\alpha^*} \right) = \frac{1 - \alpha^*}{1 - (1 - 2\varepsilon)\alpha^*} \quad (22a)$$

$$\begin{aligned} v_{m1}^* &= Q_1^* \left(1 + \frac{\varepsilon(1 - \alpha^*)}{1 - (1 - 2\varepsilon)\alpha^*} \right) = \\ &= \frac{1 - \alpha^* + \varepsilon + \varepsilon\alpha^*}{(1 + b)(1 - \varepsilon)(1 - (1 - 2\varepsilon)\alpha^*)}. \end{aligned} \quad (22b)$$

The direction of selection on choosiness x is then given by

$$\left. \frac{\partial W}{\partial x} \right|_{x=x^*} = \alpha'(1 - \varepsilon)[(1 + b)v_{m1}^* - v_{m0}^*] \quad (23a)$$

$$= 2\alpha' \frac{\varepsilon}{1 - (1 - 2\varepsilon)\alpha^*}. \quad (23b)$$

The right-hand side is clearly positive, indicating selection for increasing preference for type 1 males. This process can be halted at an internal equilibrium for a sufficiently high cost of choosiness. Such a cost can be incorporated in the model by multiplying the first row by $1 - k$, where k increases with choosiness

x . In equilibrium, the left-hand side of (23b) would then be equal to $k'/(1 - k^*)$.

For simplicity, we have assumed that females are able to distinguish between males bearing high-viability genes and males bearing low-viability genes. In other words, we have not addressed the important topic whether and how male traits can serve as reliable indicators of “good” genes with respect to natural selection. We have neglected these aspects in order to keep our models simple, but indicator mechanisms (handicaps, Zahavi, 1975, 1977) can easily be incorporated in an ESS model (see also Grafen, 1990a, b; Siller, 1998). Our model also makes the simplifying assumption that only male, and not female, offspring have a survival benefit $(1 + b)$. The benefits of choosiness would of course be larger if both, sons and daughters, would profit from the good genes of their father. This could easily be addressed by splitting the female stage into two stages (type 0 and type 1 females). However, to keep our models simple, we will not consider this extension here.

4. Sexual selection and the sex ratio

In this section we extend the models of the previous section to analyse the verbal claim that it would be adaptive for attractive fathers to have more sons. The main result is that it may depend crucially on the mechanism of sexual selection whether this is to be expected.

We assume that females are in control of the sex ratio, but the results are the same under paternal control. Females mated with a type 0 male (which happens with probability $1 - \alpha$) produce a sex ratio (proportion sons) of s_0 , mated with a type 1 male (probability α) a sex ratio of s_1 . The average sex ratio is given by $S = (1 - \alpha)s_0 + \alpha s_1$.

4.1. Fisherian runaway

The Fisherian runaway model of the previous section is easily extended to allow for variable sex ratios. The transition matrix (12) becomes

$$\mathbf{A} = \frac{1}{2} \begin{pmatrix} 1 - S & (1 - s_0^*)Q_0^* & (1 - s_1^*)Q_1^* \\ S(1 - y) & s_0^*(1 - y)Q_0^* & s_1^*(1 - y)Q_1^* \\ S(1 - c)y & s_0^*(1 - c)yQ_0^* & s_1^*(1 - c)yQ_1^* \end{pmatrix}. \quad (24)$$

The population growth rate is $\lambda^* = 1 - S^*$, but we assume that offspring survival is scaled in such a way that the population is stationary. The class frequencies in the resident population are proportional to

$$\mathbf{u}^* = (1 - S^*, S^*(1 - y^*), S^*(1 - c)y^*). \quad (25)$$

To calculate the reproductive values we use the fact, verified in the appendix, that in populations with non-overlapping generations, the average reproductive value of all females equals the average reproductive value of all males. For the present model, this means

$$u_f^* v_f^* = u_{m0}^* v_{m0}^* + u_{m1}^* v_{m1}^*. \quad (26a)$$

Using (25), this is equivalent to

$$1 - S^* = S^* [(1 - y^*) v_{m0}^* + (1 - c)y^* v_{m1}^*] \quad (27)$$

where we have normalized v_f^* to unity. It is then easy to verify that

$$v_{m0}^* = \frac{1}{2} Q_0^* \left(\frac{1 - s_0^*}{1 - S^*} + \frac{s_0^*}{S^*} \right) \quad (28a)$$

$$v_{m1}^* = \frac{1}{2} Q_1^* \left(\frac{1 - s_1^*}{1 - S^*} + \frac{s_1^*}{S^*} \right) \quad (28b)$$

The direct effect of selection on female choice and male exaggeration is given by

$$\begin{aligned} \left. \frac{\partial W}{\partial x} \right|_{x=x^*} &= \frac{\partial S}{\partial x} \Big|_{x=x^*} \times [-1 + (1 - y^*) v_{m0}^* + (1 - c)y^* v_{m1}^*] \\ &= \alpha' (s_1^* - s_0^*) \frac{1}{S^*} (1 - 2S^*) \end{aligned} \quad (29a)$$

$$\left. \frac{\partial W}{\partial y} \right|_{y=y^*} = 2S^* [(1 - c)v_{m1}^* - v_{m0}^*]. \quad (29b)$$

Even in the absence of costs of choice, there is now direct selection on female choice if there is sex ratio differentiation ($s_0^* \neq s_1^*$) and a biased average sex ratio ($S^* \neq 1/2$). If the average sex ratio is male-biased ($S^* > 1/2$), then selection favors a preference for type 1 males if type 0 males have more sons than type 1 males ($s_0^* > s_1^*$) and vice versa. Conversely, if the average sex ratio is female-biased, then selection favors a preference for type 1 males if type 0 males have more daughters ($s_0^* < s_1^*$) and vice versa. Comparison with (15b) shows that the direction of selec-

tion on the male strategy y is not affected by sex ratio differentiation.

The selection differentials for the sex ratios are

$$\left. \frac{\partial W}{\partial s_1} \right|_{s_0=s_0^*} \propto (1 - \alpha^*) \frac{1}{S^*} (1 - 2S^*) \quad (30a)$$

$$\left. \frac{\partial W}{\partial s_1} \right|_{s_1=s_1^*} \propto \alpha^* \frac{1}{S^*} (1 - 2S^*). \quad (30b)$$

Clearly, both selection differentials have the same sign and selection on both sex ratios tends to restore an even sex ratio. In other words, there is no selection for sex ratio specialization depending on the attractiveness of males. The reason is that the sexual selection advantage of attractive sons is exactly counterbalanced by their viability disadvantage when the Fisher process has reached an equilibrium. Some degree of sex ratio specialization may nevertheless persist, as long as the average sex ratio is close to evenness, but its direction is unpredictable and governed by non-deterministic forces such as genetic drift. This is confirmed by simulations (Weissing et al., in prep.).

4.2. Good-genes model

Allowing for variable sex ratios, the transition matrix (19) of the good-genes model in the previous section becomes

$$A = \frac{1}{2} \begin{pmatrix} 1 - S & (1 - s_0^*) Q_0^* & (1 - s_1^*) Q_1^* \\ s_0(1 - \alpha) + s_1 \varepsilon \alpha & s_0^* Q_0^* & s_1^* \varepsilon Q_1^* \\ s_1(1 + b)(1 - \varepsilon) \alpha & 0 & s_1^*(1 + b)(1 - \varepsilon) Q_1^* \end{pmatrix} \quad (31)$$

The growth rate of the resident population is $\lambda^* = (1 - S^*)$ and the class frequencies in the resident population are proportional to

$$\mathbf{u}^* = (1 - S^*, s_0^*(1 - \alpha^*) + s_1^* \varepsilon \alpha^*, s_1^*(1 + b)(1 - \varepsilon) \alpha^*). \quad (32)$$

Using (10a) and (10b), the mating frequencies of the two types of male are

$$Q_0^* = \frac{(1 - S^*)(1 - \alpha^*)}{s_0^*(1 - \alpha^*) + s_1^* \varepsilon \alpha^*} \quad (33a)$$

$$Q_1^* = \frac{1 - S^*}{s_1^*(1 + b)(1 - \varepsilon)}. \quad (33b)$$

Normalizing the reproductive value v_f^* of females to unity, the reproductive values of the two types of males in the resident population are given by

$$v_{m0}^* = \frac{(1 - \alpha^*)(1 - s_0^*)}{s_0^*(1 - \alpha^*) + 2s_1^*\varepsilon\alpha^*} \quad (34a)$$

$$v_{m1}^* = \frac{(1 - s_1^*)(s_0^*(1 - \alpha^*) + 2s_1^*\varepsilon\alpha^*) + s_1^*\varepsilon(1 - \alpha^*)(1 - s_0^*)}{s_1^*(1 + b)(1 - \varepsilon)(s_0^*(1 - \alpha^*) + 2s_1^*\varepsilon\alpha^*)}. \quad (34b)$$

The direction of selection on choosiness is now

$$\left. \frac{\partial W}{\partial x} \right|_{x=s^*} = 2\alpha' \left[s_0^* - s_1^* + \frac{(1 - s_0^*)s_1^*\varepsilon}{s_0^*(1 - \alpha^*) + 2s_1^*\varepsilon\alpha^*} \right]. \quad (35)$$

Note that for $s_0^* = s_1^* = 1/2$ this reduces to (23b).

The selection differentials for the sex ratios are given by

$$\left. \frac{\partial W}{\partial s_0} \right|_{s_0=s_0^*} = (1 - \alpha^*) \frac{(1 - \alpha^*)(1 - 2s_0^*) - 2\varepsilon\alpha^*s_1^*}{s_0^*(1 - \alpha^*) + 2s_1^*\varepsilon\alpha^*} \quad (36a)$$

$$\left. \frac{\partial W}{\partial s_1} \right|_{s_1=s_1^*} = \alpha^* \frac{(1 - \alpha^*)(1 - 2s_1^*)s_0^* + 2\varepsilon s_1^*(1 - s_0^* - s_1^*\alpha^*)}{s_1^*[s_0^*(1 - \alpha^*) + 2s_1^*\varepsilon\alpha^*]}. \quad (36b)$$

It can be shown that there are two possible sex ratio equilibria (assuming $\varepsilon < 1/2$):

$$(s_0^*, s_1^*) = \begin{cases} \left(0, \frac{1}{2\alpha^*} \right) & \text{if } \alpha^* \geq 1 - \varepsilon \\ \left(\frac{1 - \alpha^* - \varepsilon}{2(1 - \alpha^*)(1 - \varepsilon)}, \frac{1}{2} \frac{1}{1 - \varepsilon} \right) & \text{if } \alpha^* < 1 - \varepsilon \end{cases} \quad (37)$$

For both equilibria a male-biased sex ratio is produced by females with attractive males, and a female-biased sex ratio by females with unattractive males. The second equilibrium requires that type 0 males are preferred over type 1 males, hence the first equilibrium would be observed if females prefer type 1 males. Note that in this equilibrium females with unattractive males produce a more biased sex ratio than females with attractive males. Selection on choosiness, as measured by (35) tends to vanish as the sex ratio equilibria are approached, because sex ratio specialization tends to reduce the variation in genetic quality of offspring for sexual selection to act on. The end result would be a slightly weaker sex

ratio trend than predicted by the two equilibria. These results are confirmed by a computer simulation study (Weissing et al., in prep.).

5. Discussion

5.1. Comparison with other methods

Most models for the coevolution of female sexual preferences and male secondary sexual traits are either quantitative genetic models or population genetic models. Here we briefly discuss the pros and cons of these approaches and our ESS approach.

5.1.1. Population genetic models

The most important advantage of population genetic (PG) models (Kirkpatrick, 1982; Seger, 1985) is that they are “closed”: correlations between female preference and male traits are not introduced as fixed parameters but are “explained” by the model itself.

The main drawback of PG models is their complexity. Even the simplest two-locus haploid models yield intimidating formula's that are difficult to interpret. Diploid models are even worse in this respect (Tomlison, 1988; Gomulkiewicz and Hastings, 1990; Heisler and Curtsinger, 1990). Moreover, it is not clear whether the results of PG models are robust with respect to genetic assumptions. It is, for example, not clear under what circumstances diploid models lead to the same conclusions as haploid models. Another disadvantage of PG models is that they can harbor only a very limited amount of genetic variation. As a consequence, no real “run-away” can be simulated.

5.1.2. Quantitative genetic models

The quantitative genetic (QG) approach has the advantage that the models are easier to handle than PG models. Plus, the assumption that male traits and female preferences are multifactorial is more realistic than the few-loci assumption of most PG models. On the downside, most QG models of sexual selection (e.g. Lande, 1981; Pomiankowski et al., 1991; Twasa et al., 1991; but see Barton and Turelli, 1991; Kirkpatrick, 1996) assume constant genetic variances and covariances, while it is obvious that such parameters change “in reality” (Turelli, 1984; Roff, 1997; Lynch and Walsh, 1998).

Another disadvantage of the QC methodology is the assumption of normally distributed traits. This permits only a certain class of fitness functions to be used, namely those that maintain normality in the population (Lande, 1976; but see Turelli and Barton, 1994), usually exponential functions with simple exponents (see Pomiankowski et al., 1991; Iwasa et al., 1991). Such “phenomenological” fitness functions make it hard to implement specific mechanisms of sexual selection.

5.1.3. ESS models

The ESS approach used here has the advantage that by neglecting the underlying genetic processes the models become relatively simple and transparent. This allows a greater emphasis on a biologically interpretable description of the selection process. Moreover, the method is applicable to relatively complex life histories for which a well-developed theory of fitness functions exist, based on demographic matrix models and reproductive values. For example, in our models there is a direct link between female fitness and male fitness because the reproductive value of a parent is a weighted sum of the reproductive values of its sons and daughters. Such a direct link is missing in the QC models of Iwasa et al. (1991), where male and female fitness are linked only through the correlations between traits. It is possible to combine the QC approach with the fitness function approach of an ESS analysis where reproductive values are explicitly derived from population dynamical and demographic considerations (Day and Taylor, 1996), but in the context of sexual selection this has not been done yet.

Another advantage of the ESS approach is that it is relatively easy to incorporate specific mechanisms of mate choice or sex ratio control. Especially in vertebrates where the chromosomal mechanism of sex determination is likely to interfere with perfect sex ratio control (Krackow, 1995), an explicit mechanistic approach may yield additional insight (e.g. Pen et al., 1999).

A disadvantage of our ESS approach, shared with the QG approach, is the introduction of unexplained variance and covariance coefficients. However, in principle it is possible to set up a model for these terms, as is common practice for ESS models in a kin selection context, where the regression coefficients represent coefficients of relatedness (see Tay-

lor and Frank, 1996; Frank, 1998; Pen, 1999). Kirkpatrick (1996) has done just this for a QG model of sexual selection.

5.2. Implications for sex ratio control

It has been argued verbally on several occasions that it would be adaptive for parents to produce more sons when the father is relatively attractive (e.g. Burley, 1981; Ellegren et al., 1996; Westerdahl et al., 1997). However, our results suggest that whether parents are expected to adjust the sex ratio of their offspring in relation to paternal attractiveness may depend on the mechanism of sexual selection underlying the evolution of male attractiveness.

Under a purely Fisherian runaway process biased sex ratios are not necessarily expected, because in equilibrium the mating advantage of attractive males is offset by their viability disadvantage. Sons may inherit the attractiveness of their father, but they also inherit the associated handicaps.

Our model of Fisherian runaway assumes that female choice is not costly. According to some models, the Fisherian process by itself does not lead to stable exaggeration of male characters when female choice is costly (Pomiankowski, 1987). If it is true that costly choice can only be maintained if the sons of choosy females have higher fitness than the sons of less choosy females, then it seems possible that some degree of sex ratio specialization will be selected for. Explicit models are required to test this logic.

Under the good-genes process, our results suggest that it is possible that selection favors attractive males to have more sons than unattractive males. In our model we have assumed that only sons benefit from having an attractive father. If daughters would also benefit from the good genes passed on by their father, it seems likely that selection for biased sex ratios will be weaker and might even be reversed if daughters benefit more than sons.

The empirical evidence (reviewed by Sheldon, 1998) is mixed: sometimes attractive fathers do produce more sons, sometimes they do not. This might reflect differences in the underlying process of sexual selection, as our models suggest, but the data to test this possibility are not available yet. It might be interesting to test the logic of our results in a laboratory setting where the regime of sexual selection

would be under experimental control, and where genetic variation in the sex ratio is available.

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APPENDIX

Equality of male and female reproductive values

Here we show that in populations with non-overlapping generations and symmetric genetics the average reproductive value of females equals the average reproductive value of males.

There is an arbitrary number of discrete classes of females and males. The matrices \mathbf{F} and \mathbf{M} represent the contributions, measured in numbers of individuals, by females in the current generation to the females and males of the next generation. Now consider a focal genetic locus and let π_{ij} ($i, j \in \{f, m\}$) represent the proportion of genes at that locus a sex- i offspring inherits from its sex- j parent. Then $\pi_{ff}\mathbf{F}$ and $\pi_{mf}\mathbf{M}$ represent, respectively, the genetic contribution by females to the females and males of the next generation. Likewise, $\pi_{fm}\tilde{\mathbf{F}}$ and $\pi_{mm}\tilde{\mathbf{M}}$ denote the genetic contribution of males to the females and males of the next generation. Note that $\pi_{jf} + \pi_{im} = 1$, that is, an offspring's gene must come from one of its parents. The total genetic flow from one generation to the next can then be represented by the block matrix

$$\mathbf{A} = \begin{pmatrix} \pi_{ff}\mathbf{F} & \pi_{fm}\tilde{\mathbf{F}} \\ \pi_{mf}\mathbf{M} & \pi_{mm}\tilde{\mathbf{M}} \end{pmatrix} \quad (\text{A1})$$

Under symmetric genetics, all π_{ij} are identical to $1/2$, and the total contribution to each sex by females equals the total contribution to each sex by males:

$$\mathbf{F}\mathbf{u}_f = \tilde{\mathbf{F}}\mathbf{u}_m \quad (\text{A2a})$$

$$\mathbf{M}\mathbf{u}_m = \tilde{\mathbf{M}}\mathbf{u}_f \quad (\text{A2b})$$

where \mathbf{u}_f and \mathbf{u}_m denote the class-frequencies in demographic equilibrium of females and males, respectively.

The reproductive values \mathbf{v}_f and \mathbf{v}_m of females and males, respectively, are given by

$$\lambda\mathbf{v}_f = \frac{1}{2}\mathbf{v}_f\mathbf{F} + \frac{1}{2}\mathbf{v}_m\mathbf{M} \quad (\text{A3a})$$

$$\lambda\mathbf{v}_m = \frac{1}{2}\mathbf{v}_f\tilde{\mathbf{F}} + \frac{1}{2}\mathbf{v}_m\tilde{\mathbf{M}} \quad (\text{A3b})$$

where λ denotes the population growth rate, the dominant eigenvalue of \mathbf{A} . Hence,

$$\lambda\mathbf{v}_f\mathbf{u}_f = \frac{1}{2}\mathbf{v}_f\mathbf{F}\mathbf{u}_f + \frac{1}{2}\mathbf{v}_m\mathbf{M}\mathbf{u}_f \quad (\text{A4a})$$

$$\lambda\mathbf{v}_m\mathbf{u}_m = \frac{1}{2}\mathbf{v}_f\tilde{\mathbf{F}}\mathbf{u}_m + \frac{1}{2}\mathbf{v}_m\tilde{\mathbf{M}}\mathbf{u}_m. \quad (\text{A4b})$$

But by (A2a) and (A2b) the two right-hand sides are identical and it follows that

$$\mathbf{v}_f\mathbf{u}_f = \mathbf{v}_m\mathbf{u}_m \quad (\text{A5})$$

which is what we wanted to show.

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