The role of maternal and paternal effects in the evolution of parental quality by sexual selection

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Abstract

Genetic models of maternal effects and models of mate choice have focused on the evolutionary effects of variation in parental quality. There have been, however, few attempts to combine these into a single model for the evolution of sexually selected traits. We present a quantitative genetic model that considers how male and female parental quality (together or separately) affect the expression of a sexually selected offspring trait. We allow female choice of males based on this parentally affected trait and examine the evolution of mate choice, parental quality and the indicator trait. Our model reveals a number of consequences of maternal and paternal effects. (1) The force of sexual selection owing to adaptive mate choice can displace parental quality from its natural selection optimum. (2) The force of sexual selection can displace female parental quality from its natural selection optimum even when nonadaptive mate choice occurs (e.g. runaway sexual selection), because females of higher parental quality produce more attractive sons and these sons counterbalance the loss in fitness owing to over-investment in each offspring. (3) Maternal and paternal effects can provide a source of genetic variation for offspring traits, allowing evolution by sexual selection even when those traits do not show direct genetic variation (i.e. are not heritable). (4) The correlation between paternal investment and the offspring trait influenced by the parental effects can result in adaptive mate choice and lead to the elaboration of both female preference and the male sexually selected trait. When parental effects exist, sexual selection can drive the evolution of parental quality when investment increases the attractiveness of offspring, leading to the elaboration of indicator traits and higher than expected levels of parental investment.

Introduction

Parents can provide considerably more than genes to their offspring, and parents often vary in the quality of their extra-genetic contributions. This variation in parental quality can significantly affect offspring fitness and thus has been widely investigated by behavioural ecologists, particularly in the context of sexual selection and mate choice (Weatherhead & Robertson, 1979;

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Clutton-Brock, 1991; Andersson, 1994; Westneat & Sargent, 1996; Choe & Crespi, 1997). The focus on the relationship between sexual selection, parental quality and parental investment in offspring is not surprising given taxonomically widespread parental care. For example, nutritional provisioning of offspring by parents occurs in taxa as diverse as mammals, birds, fishes, frogs, insects and arachnids (Clutton-Brock, 1991; Choe & Crespi, 1997). However, parents affect the fitness of their offspring in ways other than care, and variation in parental quality can reflect any variable contribution or characteristic of parents that influences growth, survival or development of their offspring. This includes, but is not limited to, characteristics such as provisioning

offspring other than feeding (e.g. thermoregulation) or prezygotic or postzygotic investment (e.g. nutritional contribution to eggs, nutritive spermataphores).

Models of evolution by sexual selection have considered how variable parental quality influences the evolution of mate preferences and of traits indicative of parental quality (Trivers, 1972; Hoelzer, 1989; Price *et al.*, 1993; Andersson, 1994; Hill, 1994; Westneat & Sargent, 1996; Wolf *et al.*, 1997; Moore *et al.*, 1998; Kokko, 1999). Empirical studies have shown that variation in parental quality contributes to variation in the expression of offspring traits (Westneat & Sargent, 1996; Mousseau & Fox, 1998a,b). Yet parental quality traditionally has been viewed from two separate perspectives: the behavioural ecology perspective of parental investment (Westneat & Sargent, 1996) and the quantitative genetic perspective of parental (maternal, paternal, kin or indirect genetic) effects (Cheverud & Moore, 1994; Moore *et al.*, 1998).

Although considerable progress has been made in understanding the selective factors that could lead to the evolution of parental contributions (Westneat & Sargent, 1996), adopting purely phenotypic analyses of selection can be misleading. Both quantitative genetic models and empirical studies have shown that the presence of parental effects alters the way that parental and offspring characters evolve relative to the expectation for unaffected traits (Cheverud & Moore, 1994; Wolf *et al.*, 1998). Parental effects modify the relationship between individuals' genes affecting parental quality (i.e. the quantity of parental investment provided) and their expression of parentally affected traits. Therefore, models of sexual selection that adopt a quantitative genetic perspective on parental effects may uncover unexpected properties (Cheverud & Moore, 1994).

Our initial investigations of the role of parental effects in sexual selection (Wolf *et al.*, 1997; Moore *et al.*, 1998) showed that parental effects alter the relationship between traits and generate correlations between the expression of an indicator trait and an individual's genes for parental quality. The phenotypic correlation generated by maternal and/or paternal effects between offspring traits and parental quality provides a mechanism whereby females can make adaptive mate discriminations by indirectly assessing the genes that a male possesses for parental quality (Wolf *et al.*, 1997; Moore *et al.*, 1998). Here we investigate how sexual selection on indicator traits and parental quality influences the evolutionary process. We ask, 'What level of parental care or investment should evolve as a result of mate choice? How will this mate choice evolve? Will traits that indicate levels of parental investment or quality evolve, and by what mechanisms?'

We present a model for multivariate evolution that examines the evolution of a potential indicator trait, female preference for that trait and the contributions of males and females as parents (i.e. parental quality). In our model male and female parental quality are allowed to affect the expression of their offspring's indicator trait, both together and separately. We use this framework to examine how parental quality evolves in response to sexual selection on a male trait influenced by parental quality. We also investigate the conditions under which female preference and the male indicator trait are elaborated by sexual selection. We assume female mate choice for simplicity, although the conclusions of the model apply to mate choice by either sex.

The model

Genetics of the system

We define the genetics and evolution of four sex-limited traits: (1) a potential male 'indicator trait', (2) female preference for the male indicator trait, (3) male parental quality (MPQ) and (4) female parental quality (FPQ). For simplicity we refer to the male trait that females use to discriminate among potential mates as an indicator trait, even in cases where it does not reflect MPQ and is therefore not a true indicator. All parameters related to the indicator trait are marked with the letter O, female preference with Y, male parental quality with an S (sire) and female parental quality with a D (dam). We follow the model of Wolf *et al.* (1997) for the inheritance of the indicator trait and FPQ and MPQ, where these traits show Mendelian inheritance and FPQ or MPQ may also influence expression of the indicator trait. We assume pure Mendelian inheritance for female preference. Traits showing only Mendelian inheritance can be partitioned into an additive genetic and an environmental component (the latter of which also contains variance owing to nonadditive genetic effects):

$$z_i = a_i + e_i \qquad (1)$$

where the subscript i is used as a generic label and would take on the values D, S and Y for FPQ, MPQ and female preference, respectively.

Because the indicator trait is influenced by parental quality (i.e. maternal or paternal effect), we can partition the environment into a random component, a component owing to the environment provided by the dam (i.e. the maternal effect) and the environment provided by the sire (paternal effect). The parental quality of a father is $z_{S(t-1)}^*$ and of a mother is $z_{D(t-1)}^*$ (where the asterisk indicates that the individual has survived selection and $t-1$ indicates a trait expressed in the parental generation, i.e. the generation before the focal offspring generation t). We can express an individual's phenotypic value for the indicator trait as:

$$z_{O(t)} = a_{O(t-1)} + S z_{S(t-1)}^* + D z_{D(t-1)}^* \qquad (2)$$

where the S is the paternal effect coefficient and D is the maternal effect coefficient. The parental effect coefficients are partial regression coefficients that represent the

degree to which the phenotype of the offspring is determined by the phenotype of the parent (Kirkpatrick & Lande, 1989).

Most of the influences that maternal and paternal effects have on evolution are a result of the fact that they fundamentally alter the relationship between the genotype (a) and the phenotype (z) (Wolf *et al.*, 1998). This relationship can be expressed as the covariance of the additive genetic value with the phenotypic value, C_{az} (Arnold, 1994). Changes in C_{az} owing to parental effects generate the additional terms (i.e. the terms other than the direct genetic covariance) in the equation for the phenotypic correlation between the indicator trait and paternal quality. Components contributing to C_{az} that result from parental effects also tie the evolution of parental quality to the evolution of the indicator trait (see below). These covariances can be expressed in a matrix, $\mathbf{C}_{az}$, which contains the covariance of the additive genetic value for one trait with the phenotypic value for that same trait or another trait. Based on the model of inheritance in our four-trait system we define the matrix $\mathbf{C}_{az}$ as (taking covariances between a and z in eqns 1 and 2)

$$\mathbf{C}_{az} = \begin{array}{c} \\ a_O \\ a_Y \\ a_S \\ a_D \end{array} \begin{array}{cccc} z_O & z_Y & z_S & z_D \\ G_{OO} + \frac{S}{2}G_{OS} + \frac{D}{2}G_{OD} & G_{OY} & G_{OS} & G_{OD} \\ G_{OY} + \frac{S}{2}G_{YS} + \frac{D}{2}G_{YD} & G_{YY} & G_{YS} & G_{YD} \\ G_{OS} + \frac{S}{2}G_{SS} + \frac{D}{2}G_{SD} & G_{SY} & G_{SS} & G_{SD} \\ G_{OD} + \frac{S}{2}G_{DS} + \frac{D}{2}G_{DD} & G_{DY} & G_{DS} & G_{DD} \end{array} . \quad (3)$$

Natural and sexual selection

We consider the effects of three components of fitness (viability, fecundity and mating success) on the evolution of the four traits. Each trait may influence one or more of these fitness components. For simplicity we utilize a regression approach based on selection gradients in our analysis. The use of selection gradients in our analysis is intended to make this model more amenable to empirical investigation by identifying familiar parameters to measure.

Selection on the indicator trait

Selection on the indicator trait can be separated into two independent episodes, natural and sexual selection (Arnold & Wade, 1984). Natural selection is assumed to result from ecological factors (e.g. predation) that affect viability based on the expression of the indicator trait. Selection resulting from each of these two episodes can be expressed as a selection gradient. The selection gradient is defined as the partial regression of fitness on trait value (Lande & Arnold, 1983). The net selection gradient acting on the indicator trait (β_O^N) is the sum of the natural and sexual selection gradients (β_O^N and β_O^S respectively).

$$\beta_O = \beta_O^N + \beta_O^S. \quad (4)$$

We assume that natural selection favours intermediate trait values. This form of selection can be modelled as a Gaussian function with an optimum corresponding to θ_O. With Gaussian selection it can be shown that the magnitude of the natural selection gradient increases linearly as the mean value of the indicator trait in the population departs from the natural selection optimum (Lande, 1979) such that

$$\beta_O^N = b_O^N(\theta_O - \bar{z}_O) \quad (5)$$

where b_O^N is a scaling factor that determines the rate at which the strength of selection increases as the mean of the population moves away from the optimum. The magnitude of b_O^N is inversely proportional to the width of the Gaussian fitness function (see Lande, 1981, eqn 9). The male trait distributions following viability selection are given in the Appendix.

For simplicity, we utilize Lande's (1981) model of female preference and sexual selection. Under this model, mating success of a male with a given phenotypic value for the indicator trait is dependent upon both the mean female preference value in the population and the mean value of the indicator trait. Using Lande's (1981) model for sexual selection, it can be shown that an absolute preference function results in a simple linear relationship between the deviation of the mean value of the indicator trait from the mean value of female preference and fitness. This linear relationship results in a simple definition for the sexual selection gradient:

$$\beta_O^S = b_O^S(\bar{z}_Y - \bar{z}_O) \quad (6)$$

where b_O^S is a scaling factor that determines the intensity of sexual selection for a given difference between the mean female preference and mean indicator trait. The value of b_O^S is inversely proportional to the width of the female preference function (Lande, 1981). Although we have assumed an absolute choice preference function, other types of preference functions (i.e. psychophysical, relative; Lande, 1981) give qualitatively similar results to those presented here for absolute choice. Lande (1981, eqn 9) gives a general form of this equation that can be used to generate selection gradients under the assumption of different preference functions and to predict values of b_O^S for different scenarios.

With absolute mate choice, the form of the equation describing sexual selection given in eqn 6 is fundamentally the same as that describing natural selection (eqn 5). However, under sexual selection the optimum changes depending on the value of female preference, unlike natural selection where the optimum is a fixed value determined by the environment. The mean female preference defines the value of the indicator trait with highest mating success, so that as the mean female preference evolves, so does the optimal value for the male trait.

Selection on parental quality

We assume that parental quality reflects parental investment. Further, we assume that due to implicit fitness tradeoffs between parental investment and other traits (e.g. energetic costs owing to parental investment that reduce survival), male and female fitness are maximized by investing an intermediate amount in offspring. Therefore, parental investment is likely to experience optimizing selection and males will have maximal fitness by investing an intermediate amount in each mating. Assuming that the fitness function for MPQ is Gaussian with an optimum θ_S, the selection gradient acting on MPQ can be expressed as a linear function as in eqn 5:

$$\beta_S = b_S(\theta_S - \bar{z}_S) \tag{7}$$

where b_S determines the rate at which the strength of selection increases as a function of the distance that the mean MPQ lies from the optimum. The value of b_S is inversely proportional to the width of the Gaussian selection function.

We assume the same form of optimizing selection on FPQ except that FPQ has an optimum θ_D that may differ from the optimum for MPQ:

$$\beta_D = b_D(\theta_D - \bar{z}_D) \tag{8}$$

Selection on female preference

We assume that there is no direct cost associated with females being choosy (i.e. no viability or mating costs). Selection acts on female preference because it determines what kind of male she mates with and different males may generate variation in female fecundity through their parental quality. We follow Kirkpatrick's (1985) model for selection on female preference except that we assume that the change in female fecundity (where fecundity is number of offspring produced, not just number of eggs laid; Kirkpatrick, 1985) resulting from a mating with a male (Π_S) is an increasing function of his parental quality phenotype z_S:

$$\Pi_S = x_S z_S \tag{9}$$

where the coefficient x_S is a scaling factor that determines the degree to which female fecundity is affected by MPQ. We use this computationally simple linear function because other monotonically increasing functions (such as asymptotic functions, where total fecundity is constrained; e.g. by female body size) give results that are qualitatively similar but equations that are more complex.

Assuming that female fitness is determined solely by her fecundity, female fitness can be expressed as

$$W_{\text{female}} = \alpha + x_S z'_S \tag{10}$$

where α is baseline fitness (i.e. female fitness that is uncorrelated to male quality) and the prime is used to indicate the fact that MPQ is a trait measured in a different individual from the one to which fitness is assigned (cf. Wolf *et al.*, 1999). While the preference phenotype of a female does not directly determine the investment that she will receive from her mates, it does bias the expected indicator trait phenotype of her mates. Because the indicator trait may be phenotypically correlated with MPQ (eqn 3), female mate choice may indirectly create a covariance between the preference phenotype of females and the expected MPQ of their mates. Taking the covariance of female preference with fitness (eqn 10) and solving for the regression of fitness on female preference, the selection gradient acting on female preference is

$$\beta_Y = x_S b_{O \cdot Y'} b^*_{S \cdot O} \tag{11}$$

where $b_{O \cdot Y'}$ is the regression of the male indicator trait on female preference in mating pairs and $b^*_{S \cdot O}$ is the regression of the MPQ on indicator trait measured after selection. Based on our model of inheritance, $b^*_{S \cdot O}$ is defined as (post selection values are given in the Appendix)

$$b^*_{S \cdot O} = \frac{G^*_{OS} + \frac{S}{2}G^*_{SS} + \frac{D}{2}G^*_{SD}}{G^*_{OO} + E^*_{OO} + DG^*_{OS} + S^2 P^*_{SS} + DG^*_{OD} + D^2 P^*_{DD}}. \tag{12}$$

The coefficient $b_{O \cdot Y'}$ gives the degree to which one can predict the phenotype of a female's mate given her preference phenotype while $b^*_{S \cdot O}$ gives the degree to which one can predict the MPQ of a male given the value of his indicator trait. Nonzero values of $b_{O \cdot Y'}$ are due to assortative mating resulting from female preference, and thus are determined by how female preference operates. Wolf *et al.* (1999) present an analogous approach to measuring the force of selection provided by social interactions.

Evolutionary dynamics

Following the approach of Kirkpatrick & Lande (1989) and Lande & Kirkpatrick (1990) we can derive individual response to selection equations for the four traits in this system. For the three traits with simple Mendelian inheritance

$$\Delta \bar{z}_S = \frac{1}{2}\left[G_{SS}\beta_S + \left(G_{SO} + \frac{S}{2}G_{SS} + \frac{D}{2}G_{SD}\right)\beta_O + G_{SY}\beta_Y + G_{SD}\beta_D\right] \tag{13a}$$

$$\Delta \bar{z}_Y = \frac{1}{2}\left[G_{YY}\beta_Y + \left(G_{YO} + \frac{S}{2}G_{YS} + \frac{D}{2}G_{YD}\right)\beta_O + G_{YS}\beta_S + G_{YD}\beta_D\right] \tag{13b}$$

$$\Delta \bar{z}_D = \frac{1}{2}\left[G_{DD}\beta_D + \left(G_{DO} + \frac{S}{2}G_{DS} + \frac{D}{2}G_{DD}\right)\beta_O + G_{DS}\beta_S + G_{DY}\beta_Y\right]. \tag{13c}$$

In these equations the first term in the bracket describes the response to direct selection on the trait and the other terms describe the correlated response of

the focal trait due to selection acting on other traits. The ½ outside of the brackets reflects sex-limited expression of the traits. Because these traits are not influenced by parental quality, there are no additional terms. Note, however, that the correlated response terms include the indirect genetic effects of parental quality on z_O.

The response to selection of the indicator trait is more complex because of parental effects. Selection acting on the parental traits results in a delayed response to selection in the offspring trait. The response to selection in the indicator trait is

$$\Delta \bar{z}_O = \frac{1}{2} \begin{bmatrix} \left(G_{OO} + \frac{S}{2} G_{OS} + \frac{D}{2} G_{OD} \right) \beta_O + \\ G_{OS} \beta_S + G_{OY} \beta_Y + G_{OD} \beta_D + \\ S \Delta \bar{z}_{S(t-1)} + SP_{SS}[\beta_{S(t)} - \beta_{S(t-1)}] + SP_{SO}[\beta_{O(t)} - \beta_{O(t-1)}] + \\ D \Delta \bar{z}_{D(t-1)} + DP_{DD}[\beta_{D(t)} - \beta_{D(t-1)}] + DP_{DO}[\beta_{O(t)} - \beta_{O(t-1)}] \end{bmatrix}.$$
(14)

In this equation, the first two lines are similar to the previous equations (13a–c). The first line gives the response to direct selection on the indicator trait and the second line gives the correlated response to selection acting on the other traits. The last two lines give the change in the indicator trait resulting from prior selection on MPQ and FPQ, respectively (see Kirkpatrick & Lande, 1989). These terms are included in the evolutionary response because selection on parental quality affects the magnitude of the maternally and paternally inherited portion of the indicator trait.

Results

Below we examine the evolution of each of the four traits to explore the conditions under which traits show either a directional response to selection, evolve to an evolutionary equilibrium point away from their natural selection optimum or evolve to (or remain at) their natural selection optimum. Most of the evolutionary outcomes predicted by our model can be summarized by a series of inequalities that depend on the genetics of the four-trait system (i.e. genetic variances, covariances, and contributions of maternal and paternal effects) and the relative strengths of selection (Table 1). For parental quality and the indicator trait, these inequalities define the conditions under which selection can pull these traits away from their natural selection optima. For female preference (which does not have an optimal value) the

Table 1 Inequalities determining the evolution of the four traits. The first inequality gives the conditions under which the trait evolves away from its optimum (or, in the case of preference, experiences directional selection). These inequalities assume that the terms inside the | | on the two sides of the equation are of opposite sign (i.e. are in opposition). The actual direction of evolution is determined by the sign of the sum these two terms. The second inequality shows the conditions assuming that all traits are heritable and that there are no genetic covariances. Subscript O represents the indicator trait, Y the female preference, S MPQ (sire), D FPQ (dam). Genetic variances (both subscripts the same) and covariances (different subscripts) are symbolized by G. Selection gradients (β) and other coefficients (e.g. $b_{i \cdot j}$, D and S) are defined in the text.

Trait	Inequality	Inequality without genetic covariances	Conditions for evolution
Female preference	$\left\| G_{YY} \beta_Y \right\| < \left\| \left(G_{YO} + \frac{S}{2} G_{YS} + \frac{D}{2} G_{YD} \right) \beta_O + G_{YS} \beta_S + G_{YD} \beta_D \right\|$	$x_S b_{O \cdot Y'} b^*_{S \cdot O} \neq 0$	Preference under directional selection when: (1) MPQ affects female fecundity, (2) females mate nonrandomly with respect to the indicator and (3) the indicator trait predicts the parental quality of a male.
Indicator trait*	$\left\| G_{OO} \beta_O \right\| < \left\| \left(\frac{S}{2} G_{OS} + \frac{D}{2} G_{OD} \right) \beta_O + G_{OS} \beta_S + G_{OY} \beta_Y + G_{OD} \beta_D + S \Delta \bar{z}_{S(t-1)} + D \Delta \bar{z}_{D(t-1)} \right\|$	$\left\| G_{OO}[\beta^S_O + \beta^N_O] \right\| > \left\| S \Delta \bar{z}_{S(t-1)} + D \Delta \bar{z}_{D(t-1)} \right\|$	Force of selection on the indicator trait must be greater than the response due to the evolution of MPQ and FPQ. Balance of natural and sexual selection determines the net force of selection acting on the indicator, and thus determines whether the indicator trait is pulled to or from its optimum.
MPQ	$\left\| G_{SS} \beta_S \right\| < \left\| \left(G_{SO} + \frac{S}{2} G_{SS} + \frac{D}{2} G_{SD} \right) \beta_O + G_{SY} \beta_Y + G_{SD} \beta_D \right\|$	$\left\| \beta_S \right\| < \left\| \frac{S}{2} \beta_O \right\|$	Strength of selection on the indicator must be 2/S times greater than natural selection on MPQ to displace it from its optimum.
FPQ	$\left\| G_{DD} \beta_D \right\| < \left\| \left(G_{DO} + \frac{S}{2} G_{DS} + \frac{D}{2} G_{DD} \right) \beta_O + G_{DS} \beta_S + G_{DY} \beta_Y \right\|$	$\left\| \beta_D \right\| < \left\| \frac{D}{2} \beta_O \right\|$	Strength of selection on indicator must be 2/D times greater than natural selection on FPQ to displace it from its optimum.

*Inequality assumes constant force of selection on MPQ and FPQ.

inequality gives the conditions where preference will experience directional selection.

Genetic covariances between a focal trait and other traits being selected can contribute to the response to selection and help determine multivariate evolution (see Arnold, 1994, for a review). In our model, genetic correlations have additional and unexpected roles and we limit our discussion to these. Table 2 lists when each of the six possible genetic covariances is likely to occur and the expected influence on evolutionary dynamics.

Evolution of female preference

Evolution by direct selection
Female preference evolves when the direct response to selection does not equal the correlated responses to selection (assuming no cost to the preference; Table 1). If there are no genetic correlations between traits, this inequality reduces to the conditions under which female preference experiences direct selection. First, the MPQ of a female's mate must affect her fecundity ($x_S \neq 0$). Second, females must be able to discriminate among mates based on the indicator trait, resulting in a predictable relationship between the indicator trait and female preference (i.e. $b_{O \cdot Y'} \neq 0$). Finally, the indicator trait must predict the male's value of MPQ (i.e. $b^*_{S \cdot O} \neq 0$). The conditions under which the regression of the MPQ on the indicator trait is not zero (which depends on

the existence of a phenotypic covariance between the indicator and MPQ) are given in eqn 12 and discussed elsewhere (Wolf *et al.*, 1997). A relationship between MPQ and the indicator trait can exist even when the indicator trait is not heritable (i.e. $G_{OO} \neq 0$). Thus if females can choose higher quality mates, and mate quality affects her fitness, female preference will evolve.

Correlated evolution and the runaway process
Genetic covariances between the indicator trait and female preference (Table 2) can contribute to a runaway process, as envisaged by Fisher (1915). The runaway process described by Lande (1981) also describes the runaway process in our system. In our model, a correlated response to selection on the indicator results in the evolution preference and produces a self-reinforcing process. The importance of the Fisherian runaway process for the current model is primarily as a source of sexual selection on the indicator trait (below). This runaway process simply relies on the presence of genetic covariances for the self-reinforcing process to continue and makes no assumption about the honesty of the indicator trait.

Our model allows for runaway to occur under two conditions in addition to those that result in the usual runaway process. These conditions arise from the altered relationship between the genotype and the phenotype that result from maternal and paternal effects. The

Table 2 Genetic covariances that contribute to evolutionary dynamics. Standard correlated responses to selection (i.e., those expected in the absence of parental effects or sexual selection) are not listed in the consequences for multivariate evolution because all covariances contribute to the correlated response to selection of traits involved in the covariance. Subscripts as in Table 1.

Genetic covariance (traits)	Likely origin	Consequences for multivariate evolution
Preference & indicator (G_{YO})	Linkage disequilibrium built up by assortative mating based on the indicator trait	Preference-indicator covariance plays an important role in runaway sexual selection (e.g. Lande, 1981)
Preference & MPQ (G_{YS})	Linkage disequilibrium built up by assortative mating based on the indicator trait when paternal effects exist	Will enhance the correlated response of female preference to selection on the indicator trait when paternal effects exist. Can enhance the runaway process due to this effect
Preference & FPQ (G_{YD})	Linkage disequilibrium built up by assortative mating based on the indicator trait when maternal effects exist	Contributes to the correlated response of female preference to selection on the indicator trait when maternal effects exist. Can result in runaway sexual selection because assortative mating can build this covariance
MPQ & indicator (G_{SO})	Linkage disequilibrium built by epistatic selection (e.g. Wolf & Brodie, 1998) or owing to pleiotropy where factors such as hormonal state affect the expression of both male characters	Enhances the response of the indicator trait to direct selection when paternal effects exist because the covariance contributes to $C_{a_o z_o}$ (eqn 3). Contributes to honest signalling of the indicator trait (eqn 12; Wolf *et al.*, (1997)
MPQ & FPQ (G_{SD})	Pleiotropic effects of loci contributing to parental quality in both sexes. Loci affecting hormonal state in both sexes are one possible source of this pleiotropy (e.g. Horseman & Buntin, 1995)	Can contribute to honest signalling (Wolf *et al.*, 1997) when maternal effects exist. Can contribute to the correlated response of MPQ or FPQ to selection on the indicator trait
FPQ & indicator (G_{DO})	Linkage disequilibrium built by epistatic selection (e.g. Wolf & Brodie, 1998) or owing to pleiotropy between maternal and direct effect loci	Enhances response of the indicator trait to direct selection when maternal effects exist because the covariance contributes to $C_{a_o z_o}$ (eqn 3)

inequality associated with the evolution of female preference when either maternal or paternal effects exist (Table 1) indicates that female preference can respond to selection acting on the indicator trait when there is a covariance between FPQ (or MPQ) and female preference.

As with the covariance between the indicator and preference, covariances between parental quality and preferences can be built by assortative mating. For example, when paternal effects exist there is necessarily a covariance between a male's phenotypic value for the indicator and his genetic value for MPQ (eqn 3). Thus, assortative mating owing to female preference will build an association between the genetic value for preference and the genetic value for MPQ in the population. The same holds for FPQ. Thus, when maternal and paternal effects exist, genes contributing to MPQ (or FPQ) appear as if they were genes for the indicator trait (eqn 3). This latter point implies that evolution by the runaway process can occur even in the absence of a genetic covariance between the indicator trait and female preference. A lack of a genetic correlation will occur when the indicator trait is not heritable (i.e. has no direct additive genetic variation; see below).

Evolution of parental quality

When parental quality affects the expression of the indicator trait, the evolution of parental quality is determined by the combination of direct selection and indirect selection on the indicator (eqns 13a,c). These forces are expected to be in opposition. Assuming optimal parental quality before selection, selection on the indicator trait will always act to displace parental quality from its optimum (i.e. $\Delta \bar{z} \neq 0$ in eqns 13a,c when $\beta_O \neq 0$ and parental effects occur). This results in a direct selection gradient on parental quality (eqns 7 and 8) that is opposite in sign to the indirect selection acting through the indicator trait. As a result of these conflicting selection pressures, parental quality is expected to reach an equilibrium where the relative strength of natural selection acting directly on parental quality balances the correlated selection acting on the indicator trait (Table 1). The distance that parental quality is displaced from its optimum by a given strength of selection on the indicator will be determined by the rate at which fitness declines away from the optimum (eqns 7 and 8). The displacement of parental quality from the optimum is not due to the standard correlated response to selection that occurs purely as a result of genetic covariances. Genetic covariance can contribute (Table 2) but is not necessary for parental quality to be displaced from its optimum by selection on the indicator (Table 1).

Evolution of FPQ by adaptive mate choice
Variation in FPQ permits adaptive mate choice when two conditions are met (eqn 12): FPQ must result in a maternal effect on the indicator trait and it must be genetically correlated with MPQ. Under these conditions FPQ may evolve due to selection on the indicator trait (Table 1). Thus, whenever maternal effects provide the opportunity for adaptive mate choice they can also result in the evolution of FPQ away from the natural selection optimum. Maternal effects appear to be ubiquitous (Mousseau & Fox, 1998a,b), but there is a paucity of genetic studies of parental quality to evaluate the covariance between MPQ and FPQ (Cheverud & Moore, 1994). Genetic correlations across the sexes for parental quality may be common. For example, FPQ and MPQ can be under similar hormonal control (e.g. Horseman & Buntin, 1995).

Evolution of MPQ by adaptive mate choice
Adaptive mate choice may also occur as a result of paternal effects. When paternal effects exist the indicator trait is expected to be an honest indicator of MPQ under nearly all conditions (eqn 12; see also Wolf et al., 1997). Therefore, paternal effects will result in adaptive mate choice and drive the evolution of mate preference, of indicator traits (via sexual selection) and of MPQ (through correlated response to selection). The same conditions that allow adaptive mate choice result in the evolution of MPQ away from its optimum. MPQ evolves until natural selection and indirect sexual selection balance (Table 2).

Maternal effects also permit adaptive mate choice based on the indicator trait, driving MPQ away from its natural selection optimum as a correlated response due to selection on the indicator. This is because one of the conditions necessary for adaptive mate choice due to maternal effects is the presence of a genetic covariance between MPQ and FPQ (above). The conditions for MPQ to evolve away from its optimum as a correlated response are (rearranging the inequality equation for MPQ in Table 1)

$$[(D/2)G_{SD}]\beta_O > G_{SS}\beta_S + G_{SD}\beta_D. \tag{15}$$

The strength of selection on the indicator trait must be stronger than both direct selection on MPQ, as well as the selection acting on genetically correlated FPQ, to pull MPQ away from its natural selection optimum (assuming that β_O is in opposition to β_S and β_D as expected).

Evolution of FPQ by nonadaptive mate choice
When maternal effects exist, the net force of selection acting on the indicator trait always produces a force of selection affecting FPQ. When nonadaptive mate choice occurs and results in Fisherian runaway evolution, mothers of higher parental quality have more attractive offspring due to the maternal effect. Because males inherit genes for FPQ from their mothers, there is a covariance between males' genes for FPQ and the expression of the indicator trait (eqn 3). The corresponding fitness gain associated with the genes for FPQ in those males may keep FPQ away from its optimum.
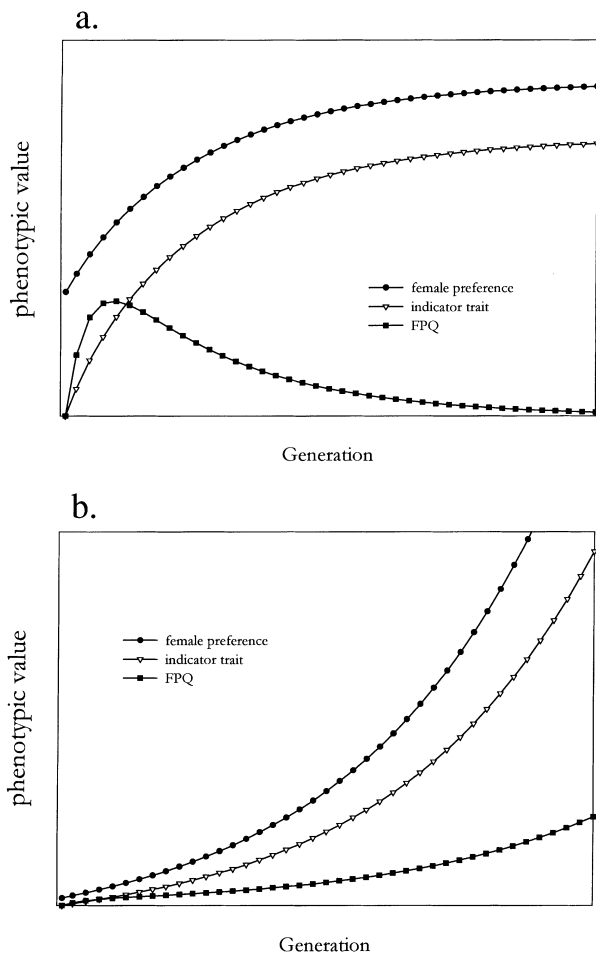
a.

b.

Fig. 1 Evolution by the runaway process when maternal effects are present. (a) Evolutionary trajectories when the system evolves to an equilibrium point. For this example, and in the case shown in (b), $b_O^N = 0.01$, $b_O^S = 0.05$, $b_D = 0.1$, the optima (θ_O and θ_D) are set at zero and $m = 1$. In this first case all additive genetic variances have a value of 1 and the covariance between the indicator and preference (G_{OY}) has a value of 0.75. (b) Evolutionary trajectories when the runaway process does not reach an equilibrium. In this case the additive genetic variances for the indicator (G_{OO}) and FPQ (G_{DD}) have a value of 1, while preference has an additive genetic variance (G_{YY}) of 2. The genetic covariance between the indicator and preference has a value of 1.5.

Figure 1 illustrates two possible outcomes of the runaway process (following Lande, 1981). In Fig. 1(a), an equilibrium is reached when natural selection counterbalances the force of sexual selection. In this case, as the runaway process slows and the net force of selection acting on the indicator trait approaches zero, the force of selection pulling FPQ away from its optimum also approaches zero (i.e. the benefit of increased maternal investment goes to zero). Once the process has reached

its endpoint, there is no net benefit to males that have a more elaborate indicator trait because these same males have lower viability. FPQ does not experience indirect selection and is found at its natural selection optimum. Figure 1(b) illustrates the case in which the runaway process does not reach an equilibrium value. In this case, preference and the indicator trait evolve to more elaborate values at a geometrically increasing rate (Lande, 1981). The continuously increasing rate of sexual selection results in an ever-increasing strength of selection on the indicator trait, which then results in continuously accelerating evolution of FPQ. These results suggest we should find FPQ displaced from its natural selection optimum only in systems in which sexual selection is ongoing (i.e. has not reached an equilibrium).

Evolution of MPQ by nonadaptive mate choice

Because the presence of paternal effects always produces adaptive mate choice under our model, purely nonadaptive mate choice is not expected to drive the evolution of MPQ. However, when adaptive mate choice occurs as a result of the presence of paternal effects, assortative mating by female based on the indicator trait is expected to build a covariance between preference and MPQ. The resulting covariance between MPQ and preference can accelerate the evolution of MPQ when adaptive mate choice occurs (because adaptive mate choice produces selection on preference), and may result in a runaway process as envisaged by Fisher (1915), where initially adaptive mate choice instigates runaway.

Evolution of indicator traits

The net selection gradient experienced by the indicator trait (eqn 4) is determined by the distance that the mean value lies from both the natural selection and the sexual selection optima. The natural selection optimum (eqn 5) is assumed to be fixed, determined by ecological factors, whereas the sexual selection optimum is determined by the mean female preference phenotype in the population (eqn 6). Because female preferences evolve, the mean value of the indicator trait will track a moving sexual selection optimum, but will always be checked by the increasing strength of natural selection as the mean moves further from the natural selection optimum.

Under adaptive mate choice, the elaboration of female preference due to direct benefits determines the evolution of the indicator trait. The evolution of female preference is determined by the ability of females to mate assortatively based on the indicator trait, the degree to which MPQ affects female fitness and the covariance between the indicator and MPQ (Table 1). Thus all three of these factors will indirectly influence the evolution of the indicator trait because they determine how the sexual selection optimum changes. As long as female preference continues to evolve by adaptive mate

choice, sexual selection will continue to act on the indicator trait (eqn 6). Thus, we expect to see directional evolution of the indicator trait as it follows the mean preference.

When runaway sexual selection occurs, we do not expect maternal effects to alter the equilibrium values predicted by Lande (1981) since they do not alter the point at which sexual selection and natural selection counterbalance (i.e. eqns 4–6 do not contain expressions that are affected by maternal effects). However, maternal effects do alter the response to selection for the indicator trait (eqn 14) and can therefore impede or accelerate the rate of runaway and, when applicable, the approach to the equilibrium.

The runaway process is not limited to situations in which a genetic covariance between the indicator and preference occurs. Mate choice based on the indicator trait can result in a genetic covariance between preference and either MPQ or FPQ when maternal and paternal effects exist. This genetic covariance can contribute to the runaway process in the same way that the covariance between the indicator and preference does in existing models of runaway (Lande, 1981). In effect, the genes contributing to MPQ of FPQ can replace the genes that directly contribute to the indicator trait in the sexual selection process. When maternal or maternal effects exist, the indicator trait can show a response to selection even when the indicator trait shows no direct genetic variance (i.e. is not heritable [$G_{OO} = 0$]). These results imply that runaway sexual selection is possible even when the indicator trait is not heritable, as long as it is influenced by genetically based maternal or paternal effects.

Discussion

Because parents provide both an environment and genes to their offspring, researchers have recognized that mates may choose partners nonrandomly with respect to both types of contributions. However, there is not a clean separation of environmental and genetic contributions (Wolf et al., 1998). When genes affect the expression of parental quality, the parentally provided environment can have a genetic basis and should be considered an indirect genetic effect (Cheverud & Moore, 1994; Moore et al., 1998; Wolf et al., 1998). Thus, the environment provided by the parents can be inherited and is itself subject to evolution. As a result of these indirect effects, sexual selection can drive male and female parental quality beyond their optima under natural selection, cause the evolution of male traits that are not directly heritable and generate situations under which parental quality itself evolves through a runaway process.

Indicator traits and parental quality show nonindependent evolution because offspring inherit genes that control the environment they experienced, generating a covariance between individuals' genes for parental quality and their expression of the indicator trait (eqn 3). The expression of the indicator trait will always reflect, to some degree, the genes that an individual harbours for parental quality. Thus, when mates are chosen based on such traits, the force of sexual selection will act indirectly on genes for parental quality. In addition, because the expression of the indicator trait can reflect the genes for MPQ harboured by a male, the indicator trait may be viewed as an honest indicator for MPQ (Wolf et al., 1997).

The relationship between parental quality and the indicator trait produced by indirect genetic effects implies that parental quality may often be influenced by sexual selection. Because variation in parental quality can generate honest signals for MPQ, it can result in the evolution of female preference. Female preference for the indicator in turn generates sexual selection that can displace parental quality from its natural selection optimum, because of the influence of parental quality on indicator traits. This scenario implies that certain patterns of parental effects will be associated with nonoptimal parental quality because of their associated effects on sexual selection. The conditions under which parental effects result in adaptive mate choice can be seen in eqn 3 and are discussed in Wolf et al. (1997).

In addition to cases where parental effects result in adaptive mate choice, female preference may evolve by nonadaptive processes such as runaway sexual selection (Fisher, 1915). In this situation, nonoptimal investment by mothers (i.e. greater or less than optimal with respect to their own fitness) in their male offspring is favoured because it can increase the attractiveness of those sons. Furthermore, due to assortative mating, such a process can generate a self-reinforcing covariance between female preference and FPQ (Table 2) that promotes a runaway process driving the evolution of FPQ beyond its natural selection optimum.

Maternal and paternal effects also can allow for sexual selection to result in the evolution of indicator traits that lack underlying additive genetic variation (i.e. $G_{OO} = 0$). Evolutionary change can still occur because maternal and paternal effects function as heritable sources of environmental variation in sexually selected traits. Indicator traits can evolve under either adaptive mate choice or runaway sexual selection because of changes in other characters (parental effects) that are heritable and affect the expression of the indicator trait (e.g. eqn 14). This result may be a partial solution for the Lek paradox, where one expects lower direct heritability for traits under sexual selection (Kirkpatrick & Ryan, 1991).

Our model highlights the synergy between parental effects and sexual selection, suggesting that not only do parental effects greatly influence sexual selection, but that sexual selection in turn may drive parental quality beyond its natural selection optimum. Given the large

number of species for which both parental care and sexual selection co-occur (Clutton-Brock, 1991; Westneat & Sargent, 1996), we suspect that our model may have wide applicability. To evaluate the importance of our model to natural systems, we need to begin to measure the salient genetic parameters, including the effects of parental care on indicator traits (S and D) and the heritability of and genetic covariance between MPQ and FPQ (G_{SD}). Coupled with estimates of female preference and selection on indicator traits, these quantitative genetic parameters would provide novel and, based on our model, probably surprising results and insights into evolutionary process.

Acknowledgments

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Appendix

Male trait distributions after viability selection on the indicator trait

Because we assume that mate choice occurs following a bout of viability selection on the indicator trait, it is necessary to determine the distribution of male phenotypes following selection. Although z_O is the only trait under viability selection, correlated changes in the phenotypic distribution of z_S (the other trait expressed by males) may occur. Following weak viability selection, both male phenotypes are normally distributed with new means and variances calculated as:

$$\bar{z}_O^* = \bar{z}_O + \beta_O^N P_{OO} \tag{A1a}$$

$$P_{OO}^* = P_{OO} - \left(\beta_O^N\right)^2 P_{OO}^2 \tag{A1b}$$

$$P_{OS}^* = P_{OS} - \left(\beta_O^N\right)^2 P_{OO} P_{OS} \tag{A1c}$$

$$\bar{z}_S^* = \bar{z}_S + \beta_O^N P_{OS} \tag{A1d}$$

$$P_{SS}^* = P_{SS} - \left(\beta_O^N\right)^2 P_{OS}^2. \tag{A1e}$$

See Tallis & Leppard (1988) and Falconer & Mackay (1996) for additional details on this approach.