Sexual selection favours male parental care, when females can choose

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Explaining the evolution of male care has proved difficult. Recent theory predicts that female promiscuity and sexual selection on males inherently disfavour male care. In sharp contrast to these expectations, male-only care is often found in species with high extra-pair paternity and striking variation in mating success, where current theory predicts female-only care. Using a model that examines the coevolution of male care, female care and female choice, I show that inter-sexual selection can drive the evolution of male care when females are able to bias mating or paternity towards parental males. Surprisingly, female choice for parental males allows male care to evolve despite low relatedness between the male and the offspring. Instead of being disfavoured for male care, females are argued to increase their mating success when they provide parental care. While current theory predicts female-only care, using a model that examines the coevolution of male care, I argue that inter-sexual selection can coevolve with parental effort and favour the evolution of male-only care.

**Keywords:** evolutionary theory; coevolution; sexual selection; mate choice; parental investment

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1. INTRODUCTION

Research has focused on understanding when and why individuals of either sex provide parental care, with a particular focus on why in many taxa, females are more likely to care for their young than males [1–8]. While natural selection and evolutionary history clearly influence parental care evolution [3,4,9,10], recent theory examining sex differences in care has focused on how sexual selection interacts with parental investment. The general conclusion has been that, all else being equal, sexual selection on males disfavours the evolution of paternal care [1–9,11]. For males, uncertainty of paternity is argued to decrease the fitness benefit of caring for offspring (because the male is less related to the young in his care), while successful males are argued to lose mating success when they provide parental care [1–9,11]. Male care is thus argued to evolve when natural selection (in the form of increased offspring survival) favouring parental care is stronger than sexual selection against male care [2–5].

This argument cannot, however, explain the existence of male-only care across diverse taxa, including amphibians [10], arthropods [12], fishes [13] and birds [9] (where it is thought to be ancestral [14]). In the great tinamou, for example, females mate and leave offspring with multiple males, and males care for these offspring alone despite low paternity [15,16]. In the tessellated darter, males will care for completely unrelated young in order to attract females [17], and in sea spiders only males carry the eggs, despite sexual selection on males favouring higher male mating rates [18]. Current theory fails to explain the many species in which male-only care is found in the presence of sexual selection on males. Existing theory has shown, however, that the fitness benefits of paternal care can select for female preferences favouring parental males (the ‘good parent’ process of sexual selection, [19]) and these preferences can select for males to display their parental quality [20–24]. This theory has not, however, considered the way female preferences simultaneously coevolve with both male and female parental effort.

Inspired by this inability of current theory to explain the evolution of male-only care [2,5,25], I developed a coevolutionary model to ask how female preference evolution is predicted to interact with and affect the coevolution of male and female care. The inclusion of female-driven mating or fertilization biases, considered here, is a key departure from both classic and recent theory [2,3,5,26], shown below to have significant effects on both male and female parental care evolution. I examine a situation in which male and female parental care is initially rare, but where paternal behaviour or traits directly associated with male care can be observed. I find that inter-sexual selection owing to the female-driven mating or fertilization biases can coevolve with parental effort and favour the evolution of paternal care and the loss of maternal care.

2. MODEL DESCRIPTION AND RESULTS

(a) **General fitness functions**

I first derive male and female fitness functions, which are then used to predict the direction and the magnitude of selection on three traits: male care, female care and a female preference for parental males. These functions predict how individual traits are expected to evolve and how the evolution of one trait (such as female preference) will influence the evolution of the other traits (such as male and female care [26]). Imagine that there are $M$ potentially reproductive males and $F$ potentially reproductive females in the population. Assume that female fecundity is lower when a female provides care than when she deserts (i.e. $w < W_f$, females pay a fecundity cost of care) and that any differences in the expected reproductive success of offspring can be captured by differences in the probability that offspring will survive and reproduce (represented by $P_0$, $P_1$ and $P_2$) if cared for by none, one or two parents respectively. The equations below represent the expected fitness of an individual male or female that provides care with probability $z_m$ or $z_f$, where $f(z_m)$ and $f(z_f)$ represent...
the relative frequency of males and females (with care behaviour \(z_m\) or \(z_f\)) and \(z'_m\) or \(z'_f\) represent the male or female care behaviour of others in the population. These equations can also be adapted to consider the magnitude of parental effort. Fertilization may be biased towards certain males owing to a variety of factors such as male competition, female mating preferences, fertilization biases and temporal or physiological limitations owing to the costs of mating and care. Here, I consider the evolution of a general female preference that may bias mating or paternity towards certain males and may include pre-copulatory mate choice and/or post-copulatory fertilization biases. If females encounter and potentially mate and sire offspring with \(n\) males on average, the expected relative mating and siring success \(p(z_m)\) of an individual male who provides care with probability \(z_m\) can be represented as:

\[
p(z_m) = \frac{b(z_m)}{\sum f(z'_m) b(z'_m)},
\]

(2.1)

where \(b(z_m)\) represents the overall degree of bias (i.e. owing to mating and fertilization success) for an individual male with care behaviour \(z_m\). In essence, this formulation assumes that there is an inherent bias for each male phenotype (given by \(b(z_m)\)), where the actual probability of that male phenotype mating and siring offspring is given by the ratio of that absolute bias relative to the average bias among all males in the population and the number of potential competitors per female. Note that if there is no mating or fertilization bias then a male’s expected paternity is \(1/n\), meaning that a female is equally likely to sire offspring with each potential mate she encounters. This bias \(b(z_m)\) captures multiple components of the mating and fertilization process. For example, parental care could decrease the male’s ability to search for mates, biasing mate encounters towards males that tend to desert their offspring, while a female preference for parental males would bias mating or fertilization towards paternal males. Here, I ask whether a female preference will evolve that influences this overall mating and fertilization bias among males.

The reproductive success of both sexes depends on the number of offspring they produce and the survival of their offspring. If females mate with and produce offspring with multiple males, then the probability a male’s offspring will receive male care depends not only on his care behaviour, but also on whether his offspring end up in his care or with other males and whether these other males care for his young. Hence, not only multiple mating but also how females distribute offspring among males will influence the relatedness between a male and the offspring in his potential care as well as the probability that any given offspring will receive paternal care. The importance of female patterns of offspring production and how they distribute offspring among males or reproductive sites is a factor that has received little attention in previous theory on the subject. Male care behaviour and female mating and offspring production patterns together determine the probability that offspring sired by a male with care behaviour \(z_m\) and female care behaviour \(z_f\) will receive paternal care, represented here by \(C(z_m)\). The fitness of a male will depend on his potential mating success, which is based on: (i) the number of females with which he could potentially mate and competition from other males (given here by \(nFM\)) and; (ii) the probability these potential mates will actually mate and sire offspring with him (given for each individual encounter between a male and a female by \(p(z_m)\) above). Given that offspring have been produced, their contribution to the expected fitness of the male will depend on the probability these offspring will receive maternal \((z_f)\) and paternal care \(C(z_m)\) and the associated probability of survival \((P_0, P_1\) or \(P_2\)). A male’s expected reproductive success \(o_m\) (measured in the number of surviving offspring sired in one reproductive bout) can thus generally be represented by:

\[
o_m(z_m, z'_m, b(z_m)) = \left(\frac{nF}{M}\right) \int f(z'_m)p(z_m)z'_mC(z_m)\tau WP_2 + (1 - z'_m)C(z_m)WP_1 + z'_m(1 - C(z_m))\tau WP_1 + (1 - z'_m)(1 - C(z_m))WP_0.\]

(2.2)

Male fitness is integrated across the frequency distribution of female trait values in the population and weighted by the frequency with which those females will mate with and sire offspring with a male of trait value \(z_m\) (given by \(p(z_m)\)) and the probability these offspring will receive maternal (given by \(z_f\)) or paternal care (given by \(C(z_m)\)), the number of offspring produced by the female \((\tau W\) or \(W)\) and their probability of survival as a function of paternal care (given by \(P_0, P_1\) and \(P_2\)). Assuming female fitness is not limited by access to mates and females only care for their own offspring (i.e. maternity is certain while paternity is not), female expected reproductive success per reproductive bout can be derived in a similar way and is given by:

\[
o_f(z_f, z'_m, b(z'_m)) = \int f(z'_m) p(z'_m) z_m C(z'_m) \tau WP_2 + (1 - z_f) C(z'_m) WP_1 + z_f (1 - C(z'_m)) \tau WP_1 + (1 - z_f)(1 - C(z'_m)) WP_0.\]

(2.3)

Female fitness depends on the probability that she will encounter \((nF(z_m))\) and produce offspring with \((p(z'_m))\) males of differing parental care behaviour (integrated across the distribution of male phenotypes in the population). Female fitness then also depends on the probability that those offspring will receive maternal and/or paternal care (given by \(z_f\) and \(C(z_m)\), respectively), the number of offspring produced by the female \((\tau W\) or \(W)\) and their probability of survival given whether they receive care \((P_0, P_1\) or \(P_2\)).

(b) A specific scenario

Using the equations above, one can ask when selection will favour an increase or decrease in male care, female care and a female preference for parental males. To link reproductive success at one point in time to lifetime expected fitness and selection however, one must make some assumptions about male and female survival and population dynamics (such as age structure and population growth rate). In order to analyse specific equations, it is also necessary to make assumptions about the functional forms of \(b(z_m)\) and \(C(z_m)\), the genetic basis of and correlation among male and female traits, and the distribution of trait values in the population.

For simplicity, the selection gradient analyses presented here assume that there are no sex differences in survival, parental care and mating behaviour do not affect
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adult survival, the population is stable and there are non-overlapping generations such that equations (2.2) and (2.3) can be used to capture the expected lifetime reproductive success of individuals, and to ask when selection will favour changes in parental care behaviour or favour a change in female preference (i.e. the female-driven component of any mating and fertilization bias). In order to determine biologically appropriate functions for $b(z_m)$ and $C(z_m)$, it is necessary to make assumptions about the dynamics of mating, fertilization and care. For simplicity, I assume that males either express a parental phenotype or do not, where $z_m$ represents the probability of expressing the parental phenotype and that the presence or absence of the parental phenotype is detectable by females prior to producing offspring. Any female mating and fertilization bias then depends on the male phenotype observed such that the expected mating and fertilization success of an individual parental male is given by:

$$p_C = \frac{b}{bz_m + (1 - z_m)},$$

and the expected mating and fertilization success of a deserting male is:

$$p_D = \frac{1}{bz_m + (1 - z_m)}.$$

This formulation implies that females may exhibit a bias towards either males exhibiting a parental ($b > 1$) or non-parental ($b < 1$) phenotype, where the strength and the direction of the bias depend on the magnitude of $b$. When females mate with multiple males, the possibility exists that individual males may care for offspring that are both their own and offspring sired by other males. Furthermore, some of the male’s offspring may be potentially cared for by other parental males or not cared for if the female leaves offspring with males that desert. While the exact dynamics of mating and offspring production or egg laying will vary depending on the reproductive biology of particular species, here I examine the situation where a female mate with multiple males and the resulting offspring are in the (potential) care of the male that sired the offspring with probability $p$ and distributed among the other mates of the same female with probability $1 - p$. This means that some of the offspring sired may (or may not) be cared for by their biological father and the rest receive care depending on the probability of parental care in the population at large. In this case, the expected fitness of males per reproductive bout becomes:

$$\omega_m(z_m, z_1, b) = \frac{nF}{M}c(z_m)p_C[[z_1wP_2 + (1 - z_1)WP_1]] + \frac{nF}{M}c(z_m)p_D[[z_1wP_2 + (1 - z_1)WP_1]] + \frac{nF}{M}c(z_m)[p_D(z_1wP_1 + (1 - z_1)WP_0)]$$

Here, the first two lines give the expected fitness when the focal male exhibits the parental phenotype and provides care and his offspring either end up in his care (line 1) or with other males (line 2). The second part of equation (2.6) represents the expected fitness from offspring in the situation where the focal male does not exhibit the parental phenotype and either deserts his young (line 3) or his young were left in the potential care of another male (line 4). Female expected fitness can be derived in a similar way such that:

$$\omega_f(z_1, z_m, b) = n\tilde{z}_mPCp([z_1wP_2 + (1 - z_1)WP_1] + n\tilde{z}_mPC(1 - p)[(1 - \tilde{z}_m)z_1wP_1 + \tilde{z}_m(1 - z_1)WP_1] + (1 - \tilde{z}_m)z_1wP_1 + (1 - \tilde{z}_m)(1 - z_1)WP_0]) + n(1 - \tilde{z}_m)p_D[z_1wP_1(1 - z_1)WP_0] + \tilde{z}_m(1 - z_1)WP_1 + (1 - \tilde{z}_m)z_1wP_1 + (1 - \tilde{z}_m)(1 - z_1)WP_0]$$

where the first two terms represent the expected fitness from offspring sired by males exhibiting the parental phenotype and the second two terms represent the expected fitness from offspring sired by males expressing the deserting male phenotype (weighted by the probability males in the population express the parental or non-parental phenotype $z_m$ and the probability $P_C$ or $P_D$ the female produces offspring with parental or non-parental males, respectively). Other possible patterns certainly exist but this formulation captures the general fact that, when females mate with multiple males, some offspring potentially end up in the care of other males and it allows for the consideration of predictions when this is not the case ($p = 1$), or when offspring are distributed randomly among males with respect to parentage ($p = 0$). In this paper, I present the results of analyses conducted on these specific fitness equations (table 1). Below I also discuss the expected evolutionary patterns in general terms, independent of the specific relationships represented by equations (2.6) and (2.7) above.

(c) Coevolutionary dynamics

To consider the coevolution of multiple traits, it can be useful to consider continuous variation in care and female mating preferences to examine the evolution of these traits in a quantitative genetic framework. In general, consider that the male and female fitness functions can be used to yield selection gradient functions, where selection on a trait $z$ is given by $\beta = (1/\omega)(d\omega(z)/dz)$ [27,28]. Selection on male care, female care and female preference are given in table 1. It is also possible to solve $\beta_m = (1/\omega_m)(d\omega_m/dz_m) > 0$ for $b$ to determine at what mating and fertilization bias, male care is favoured ($\beta_m > 0$) or disfavoured ($\beta_m < 0$) by selection.

Given selection gradient functions, it is possible to predict the coevolution of male care, female care and female-driven mating biases (represented by the subscripts $m$, $f$ and $b$, respectively) using standard quantitative genetic methods. Selection on each trait is given by the functions $\beta_m(z_m, z_1, z_0)$, $\beta_f(z_m, z_1, z_0)$ and $\beta_b(z_m, z_1, z_0)$, where the covariance between any two
traits (or genetic variance of a single trait) is given by $G_{ij}$.

The predicted change in trait values is given by:

$$\Delta x_m = \frac{1}{2} \beta_m (z_m, z_r, z_b) G_{mm} + \frac{1}{2} \beta_l (z_m, z_l, z_b) G_{ml}$$

$$+ \frac{1}{2} \beta_b (z_m, z_l, z_b) G_{mb}, \quad (2.8)$$

$$\Delta x_l = \frac{1}{2} \beta_l (z_m, z_l, z_b) G_{lf} + \frac{1}{2} \beta_m (z_m, z_l, z_b) G_{lm}$$

$$+ \frac{1}{2} \beta_b (z_m, z_l, z_b) G_{lb}, \quad (2.9)$$

and

$$\Delta x_b = \frac{1}{2} \beta_b (z_m, z_l, z_b) G_{bb} + \frac{1}{2} \beta_l (z_m, z_l, z_b) G_{lb}$$

$$+ \frac{1}{2} \beta_m (z_m, z_l, z_b) G_{bm}, \quad (2.10)$$

where the first term represents the change owing to direct selection on the trait of interest and the second two terms represent the correlated selection on the trait owing to genetic covariances among traits. As above, selection on each trait is given generally by:

$$\beta_m = \frac{\partial \omega_m}{\partial x_m} \quad \beta_l = \frac{\partial \omega_l}{\partial x_l} \quad \text{and} \quad \beta_b = \frac{\partial \omega_l}{\partial x_b} \quad (2.11)$$

where specific results are found in Table 1. Since male and female fitness depend on mating patterns and the care behaviour of other males and females in the population, these selection gradients are functions of the other trait values in the population. Taking, for example, the evolution of female-driven mating or fertilization biases, the equations above imply that female preferences may evolve either through direct selection because female-driven mating or fertilization biases lead to an increase in female fitness if females are able to sire offspring more frequently with parental males and offspring sired by parental males, or owing to correlated selection on care behaviour (and genetic covariances among traits, for example, in females). However, the strength and even the direction of selection depend on the population mean trait values for male care, female care and female mating biases as well. Finally, the predicted direction and rate of trait evolution will depend on assumptions about the genetic variances and covariances of the three traits given in equations (2.8)–(2.10) above.

Imagine that males are more likely to provide care if their expected paternity is higher (i.e. $C(z_m)$ is an increasing function of $p(z_m)$ such that $\partial C(z_m)/\partial z_m > 0$). As long as parental care increases offspring survival, female fitness will always increase with an increase in paternal care in this model. However, this fact alone will not drive direct selection on male care if paternal care comes at a net fitness cost to males. However, if a female’s current offspring will be more likely to receive paternal care if they bias their mating towards parental males (or males bearing indicator traits that are correlated with paternal quality), then selection will favour female preferences that favour parental males (in the likely case that any costs of exhibiting a preference is less than the benefit of care received from parental males). Furthermore, a female preference for parental males will be favoured as long as they increase the mating or fertilization success of parental males (even if other factors lead to a net loss of fitness for parental males). However, as long as female-driven mating or fertilization biases can continue to increase in strength (i.e. female control over mating or fertilization is not limited by other reproductive or genetic constraints in the species) then the female preference will eventually increase to the point where there is a net mating or fertilization advantage for paternal males and thus favour the evolution of increased paternal care. Furthermore, if maternal care is costly for females (e.g. $w < W$) and offspring survival with male-only care is relatively high, the equations above predict that selection will favour female-drive mating biases that favour the evolution of paternal care and the loss of maternal care. Finally, if females are more likely to mate with parental males, a genetic correlation between female bias and
male care will be generated, which will strengthen the coevolution of female preference and male paternal care as a sexually selected trait.

(d) Model predictions

Using the specific forms of the general equations above, it is possible to determine the relative bias threshold (degree of mating and fertilization bias) at which paternal care would be favoured or disfavoured by selection (figure 1). These analyses confirm that paternal care will be generally disfavoured if paternal care comes at a net cost to mating and fertilization success, unless natural selection owing to low offspring survival favours paternal care (figure 1, \( b < 1 \)). Yet, these analyses also show that sexual selection on males can favour the evolution of paternal care despite uncertainty of paternity, if a female preference favours parental males (figure 1, \( b > 1 \)). This will be the case as long as both traits have positive genetic variances (i.e. are heritable) and a negative genetic covariance does not limit their evolution. A positive genetic correlation between female preference and male paternal care will only increase the rate at which these two traits coevolve. It is thus the assumption that parental males always lose mating success that drove previous predictions arguing that sexual selection inherently disfavours paternal care when females mate multiply. The evolution of paternal care will of course also depend on the strength of natural selection on parental investment, which will depend on a multitude of social, ecological and phylogenetic factors [2–4,10, 12–14]. Theory reported here shows, however, that when parental care is favoured generally, sexual selection is not an essential predictor of whether male care will evolve per se. Instead, paternal care evolution will depend on whether a female preference for parental males can evolve, which depends both on whether females can observe or predict paternal care and whether females can bias mating or fertilization. Furthermore, when a female preference favours paternal care (figure 1, \( b > 1 \), top half), the relatedness between the male and the offspring in his care (\( \rho \)) no longer influences the direction of selection on paternal care.

By calculating the selection gradient \( \beta_b \) on the female preference, it is possible to show that selection will favour an increase in a female preference for parental males (i.e. \( \beta_b \geq 0 \) for all parameters values as long as \( \rho > 0 \) and \( \bar{z}_m > 0 \), table 1 and figure 2). Hence, selection will very generally favour the evolution of a female preference for parental males, as long as females can bias mating or fertilization towards parental males (and the trait is heritable and free to evolve, e.g. not limited by a negative correlation with parental care). Most surprisingly, however, these analyses also show that inter-sexual selection can affect the evolution of paternal care patterns through the coevolution with paternal care (figure 3). If a female preference evolves that biases mating or fertilization towards parental males (figure 2), then inter-sexual selection can favour an increase in paternal care (figure 1) and the loss of maternal care (figure 3).

These equations predict the evolution of paternal care unless: (i) there is no selection for females to prefer parental males (or stronger selection on females to prefer males for other indirect or direct benefits), (ii) observable traits associated with paternal care do not exist, (iii) some aspect of the reproductive biology limits the evolution of female-driven mating or fertilization biases, or (iv) genetic variances or covariances limit the capacity for these traits to evolve (i.e. they are not heritable or negative genetic correlations constrain their evolution). In general, this implies that explaining the prevalence of maternal care and the absence of paternal care requires more than evoking the presence of sexual selection on males. Instead, one must also explain the absence of a female preference for parental males or a female's inability to control mating or fertilization.
3. CONCLUSIONS

Here, I show that inter-sexual selection can explain the evolution of male-only care in the presence of sexual selection on males and female promiscuity (in species where natural selection favours uniparental care). Male-only care is predicted in species where females can tell which males might provide care and bias mating or fertilization towards these males. For example, this would arise if females can observe male care behaviour directly (such as by observing a nest or the presence of healthy offspring) or if there is something about the phenotype of the male that is correlated with paternal care on average (allowing females to infer the likelihood of male care, [29–31]). These predictions are consistent with the observed occurrence of male-only care in species where females can identify potentially parental males and offspring sired by parental males are more likely to receive care than those sired by deserting males (i.e. $\beta_f > 0$ as long as $\rho > 0$). These contour plots represent the strength of selection on a female preference for parental males ($\beta_f$) as a function of the female care pattern $z_f$ and the probability a male will receive and can care for his own offspring ($\rho$). Two scenarios are presented: (a) biparental care conditions, where two parents are required for high offspring survival ($P_2 = 0.9$, $P_1 = 0.4$), (b) uniparental conditions where offspring survival is relatively high with a single parent ($P_2 = 0.9$, $P_1 = 0.8$). The strength of selection on the female preference for parental males increases as female care decreases and as the probability a male receives his own offspring increases. Results shown for $F = M = 1$, $b = 1$, $w = 0.5$, $W = 1$, $z_m = 0.1$, $P_0 = 0.1$. Parameter values affect the quantitative but not qualitative predictions.
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care. For example, in fishes, females often prefer males based on their nests and/or the presence of healthy eggs [32], and in some arthropods males must accept eggs from females in order to mate [12] such that parental males have higher mating success owing to female mating preferences. Rigorous comparative tests will be needed, however, to test these predictions fully. While sexual selection may disfavor the evolution of paternal care when care comes at a net loss to fertilization success, inter-sexual selection can also strongly favor the evolution of paternal care and the loss of maternal care. Predicting which will arise requires understanding the coevolution of male display traits and female mating and fertilization patterns with parental effort in both sexes. These analyses further show that it is not sufficient to argue that sexual selection explains the prevalence of maternal care. When female choice coevolves with parental care patterns, inter-sexual selection can favor the evolution of paternal care. Explaining its absence thus requires knowing why females in many species are unable or unwilling to bias mating and fertilization towards parental males.

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