

Why do females have so few extra-pair offspring?

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Abstract It is generally accepted that if a female can improve her offspring's genetics via extra-pair copulations (EPC), it is by copulating with extra-pair males whose phenotypes are more superior or whose genes are more compatible to hers than those of her bonded male. Here, we present a model that puts together uncertainties about the male genetic quality, a postcopulatory sperm bias in favor of the better or the more compatible genes, and costs that females pay by being choosy about extra-pair male quality. The model's conclusions challenge traditional views of good genes explanations of EPC. When phenotypes give incomplete information about genotypes, a female choosing a phenotypically superior extra-pair male, may nevertheless find herself trading good genes of a bonded male for poor genes of an extra-pair male. Such "unfortunate sperm replacements" can limit the female involvement in EPC even when EPC are otherwise cost-free. The model also shows that even a female bonded to a phenotypically superior male may benefit by EPC, provided that sperm competition is biased toward sperm with more fit or more compatible genes. Furthermore, if choosiness is sufficiently

costly, a female may even do best by copulating with a random extra-pair male.

Keywords Extra-pair copulations · EPC · Female strategies · Costs · Mathematical model · Sperm bias · Old males · Good genes · Compatible genes

Introduction

One of the most intriguing and unexplained phenomena concerning the promiscuity of females in socially monogamous birds is a lack of consistency (Westneat and Stewart 2003). There are great differences in proportions of extra-pair paternity (EPP) among pairs within populations, among populations within species, among related species within clades, and within populations through time (Petrie and Kempenaers 1998; Griffith et al. 2002; Westneat and Stewart 2003; Akçay and Roughgarden 2007). Similarly, there is inconsistency in patterns. Sometimes, certain male phenotypes, presumable superior (old or showy), have higher EPP, and sometimes, they do not (recently reviewed in Akçay and Roughgarden 2007). Successful extra-pair sires sometimes succeed also in within brood paternity, showing consistency in female choice, and sometimes, they do not (Akçay and Roughgarden 2007). It is little wonder that reviews of field studies of extra-pair copulations (EPC) are so often inconclusive about their causes.

If we ignore possible materialistic female benefits (Westneat and Stewart 2003), males clearly have much more to gain by EPC: males benefit primarily by having a good chance for more offspring, whereas females, in addition to a limited gain in fertility (Hasson and Stone 2009), can only gain, by selecting genetically more fit or more compatible fathers, a questionable chance for better

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offspring (Petrie and Kempenaers 1998; Griffith et al. 2002; Westneat and Stewart 2003; Neff and Pitcher 2005; Akçay and Roughgarden 2007). Thus, in accordance with Bateman's principle (Bateman 1948), females are probably the limiting sex in EPC. Therefore, to understand patterns of EPC, one must first and foremost understand constraints and tradeoffs of possible EPC strategies employed by females (see also Arnqvist and Kirkpatrick 2005; Griffith 2007; Eliassen and Kokko 2008).

The model presented here considers potential female benefits by EPC assuming the genetic makeup of male matters (Lehmann et al. 2007; Mays et al. 2008). However, our results contrast with previous predictions of good genes, which state that a female should engage in EPC only when the extra-pair male has a superior phenotype to that of her bonded male (Westneat and Stewart 2003; Akçay and Roughgarden 2007 and many others). We show that under certain conditions a female does best by selecting an extra-pair male whose phenotype is equal to that of her bonded male or even by copulating with a random extra-pair male.

The model is built as a “good genes” model but represents both good and compatible genes. This is achieved by including the perception of genetically good sires as a model variable. The good genes case is represented by assuming that good genes make fit male phenotypes and, hence, can be perceived. This perception is, however, imperfect, due to gene–environment interactions (Kokko and Heubel 2008; Higginson and Reader 2009). There are known examples where compatible genes can also be perceived and judged by phenotypes (Lehmann et al. 2007; Reid 2007; Fromhage et al. 2009; Penn 2009) or indirectly by distances from home territories (Hardy 2003). We treat cases where females base EPC choices on perceivable compatible genes analogous to the imperfect perception of genotypes, as in the good genes case. However, the model also deals with cases where compatible genes cannot be perceived, by assuming no precopulatory perception of genetic merit.

We began to explore potential effects of postcopulatory biases in sperm competition on female EPC strategies by studying patterns of biases toward fertile sperm (Hasson and Stone 2009). Here, we continue this exploration by assuming that all males are fertile (i.e., all eggs get fertilized) and that fertilization may be biased toward the genetically more fit sperm (Evans et al. 2003; Locatello et al. 2006; Pitcher et al. 2007; Hasson and Stone 2009; Puurtinen et al. 2009). Postcopulatory biases seem to be even more plausible when females benefit by selecting compatible genes. For example, biases towards compatible sperm are almost trivially understood as speciation mechanisms that prevent interspecific hybridization (Howard 1999; Puurtinen et al. 2005), which must have arisen,

gradually or abruptly, during periods of isolation between populations. Similarly, processes that occur between insemination and fertilization may expose deleterious mutations and reveal too great a genetic similarity (Puurtinen et al. 2009). Therefore, although data are scarce (e.g., Foerster et al. 2006), there are reasons to believe that sperm biases are not only a feasible evolutionary female strategy (Ball and Parker 2003) but also possibly even a common one. The model shows that postcopulatory biases that favor the genetically more rewarding sperm lead to female EPC tactics that cannot be easily explained otherwise.

The model

The model assumes that females can be choosy, pick up extra-pair males at random, or avoid EPC altogether. It studies the hierarchy of these EPC tactics' payoffs first by assuming EPC are cost free, it then looks for an optimal proportion of extra-pair sperm for each female tactic, and finally studies the effects of costs females pay by being engaged in EPC.

For the sake of mathematical convenience, we assume that once the bonding stage is over, all of the breeding populations form a “perfect” social monogamy. This refers to a 1:1 sex ratio of breeding adults, where all breeding males are monogamously bonded to all breeding females (Hasson and Stone 2009). During the bonding stage, a random association is assumed between male phenotypes and the female EPC tactics used. Once bonded, however, a female is assumed to be fully informed about her bonded male's phenotype and can employ one of her possible EPC tactics, outlined below. Although phenotypic qualities of females can influence their decisions about EPC (Gowaty 1996), we avoid mathematical complexities that may arise from this by assuming no variations in female phenotypic quality.

EPC in a cost-free setup

Information about genotypes

The model assumes two male genotypes, high quality, G, and poor quality, g, which correspondingly have G and g sperm. By definition, G sperm produces better offspring than g sperm. We assume two distinct male phenotypes: superior, P, whose proportion in the male population is P , and inferior, p, at a proportion of $p=1-P$. We denote the frequency of the better genotype (G) as G in P males, and as g in p males. A fundamental assumption in any “good genes” model is that $0 \leq g < G \leq 1$. As the model assumes that perception of phenotypes is precise, then information that females may have on male genotypes during precopulatory choices is solely represented by the difference between G

and g . A female precopulatory choice can only be perfect when there is a perfect association between genotypes and phenotypes, which happens when all superior phenotypes have good genes and all poor phenotypes have poor genes, i.e., $G=1, g=0$. Similarly, no information about genotypes is represented by $G=g$, such as the case where females benefit by unperceivable compatible genes rather than by good genes.

Sperm bias

The model assumes that EPC are made with a single extra-pair male. The intensity of a female involvement in EPC is measured by the proportion of extra-pair sperm, denoted by μ ($0 \leq \mu \leq 1$), of the total sperm received from both males; μ represents the component of female choice in EPC. We assume a possible bias in sperm competition such that proportions of EPF (extra-pair fertilized zygotes) can be different from μ in favor of G fathers. Assuming both G and g males are fully fertile, any loss of eggs by a g male, as a result of sperm competition, is gained by its G male competitor. The proportions of EPF, therefore, deviate from μ in the only two possible combinations of asymmetric sperm competition: (a) the proportion of EPF when the extra-pair male is G and the bonded male is g, denoted by E_G . (b) The proportion of EPF when the extra-pair male is g and the bonded male is G, denoted by E_g . Sperm bias increases the female’s gain by EPC in case (a), producing $E_G > \mu$, and decreases her losses in case (b), producing $E_g < \mu$.

We assume that sperm bias is most intense when spermatozoa of different origins and qualities are at equal quantities and interact the most. This allows us to use $E_G = \mu + z\mu(1-\mu)$ and $E_g = \mu - z\mu(1-\mu)$ (see Table 1), where z ($0 \leq z \leq 1$) is a coefficient that describes the bias toward G sperm. No bias is described by $z=0$ and strongest bias by $z=1$. The assumption of this nature of sperm bias is not necessarily true, but we prefer to use it here because it produces relatively simple equations, and it is easily tractable. However, in order to test the generality of our conclusions, we have also used an alternative pair of specific EPF equations, computed by assuming that after insemination, a constant proportion z of the g sperm is discarded. This produces new

Table 1 Proportions of eggs fertilized by bonded and by extra-pair males

Pair in competition	Proportion fertilized by extra-pair male (EPF)	Proportion fertilized by bonded male
Extra-pair Male: G Bonded Male: g	$E_G = \mu + z\mu(1-\mu)$	$1 - E_G = (1-\mu) - z\mu(1-\mu)$
Extra-pair Male: g Bonded Male: G	$E_g = \mu - z\mu(1-\mu)$	$1 - E_g = (1-\mu) + z\mu(1-\mu)$

proportions of sperm that are used for the fertilization of all eggs and the following EPF equations: $E_G = \mu/[1 - (1 - \mu)z]$ and $E_g = (\mu - \mu z)/(1 - \mu z)$, where z has the same properties as before. Here, sperm bias intensity is independent on μ ; yet, all of the model’s qualitative conclusions remain intact, including optimality in μ (see below). This allows us to use the first set of EPF equations, without much loss of generality.

EPF proportions are, therefore, in the range of $0 \leq E_g \leq \mu \leq E_G \leq 1$, depending on the proportion of extra-pair sperm, μ , and on sperm bias, z .

Female EPC strategies

We construct a good genes model by assuming all of the female eggs are fertilized and denote a female’s number of surviving offspring as V_G if she copulates exclusively with G males, and as V_g if she copulates exclusively with g males, where $V_G > V_g$. It is, therefore, easy to show that a female receives higher rewards by bonding with a superior male phenotype than by bonding with an inferior phenotype: Let F_p and F_p be the payoffs of sexually monogamous females bonded to a P or to a p phenotype, respectively. This leads to

$$F_p - F_p = GV_G + (1 - G)V_g - [gV_G + (1 - g)V_g] = (G - g)\Delta V \tag{1}$$

where $\Delta V = V_G - V_g > 0$ and, therefore, $F_p > F_p$. Despite preferences that females should exhibit, therefore, toward better phenotypes as mates, we assume no association of such preferences with the different EPC tactics. It is easier to make this assumption for a perfect monogamy (all reproductive females bonded to all reproductive males), with no variations in female phenotypic qualities, as assumed here. Notations used in the model below are summarized in Table 2.

We denote the four mutually exclusive female EPC options, as follows:

- N do not practice EPC.
- P select a phenotypically superior male as an extra-pair sexual partner.
- p select a phenotypically inferior male as an extra-pair sexual partner.
- R select a random male as an extra-pair sexual partner.

The R option is viewed here as the cheapest EPC a female can make. It simply means: “when an opportunity comes by, just pick the first extra-pair male available.” Assuming no special population social structure, this is made at random with respect to the male phenotypes. Each of the female options can be chosen under two mutually exclusive conditions—when the female is

Table 2 Notations

G	A symbol representing high genetic quality, of males or of sperm.
g	A symbol representing poor genetic quality, of males or sperm.
P	A symbol representing high phenotypic quality in males.
P	The proportion of phenotypes with high quality (P) in the male population.
p	A symbol representing poor phenotypic quality in males.
G	The proportion of males with good genes among P males.
g	The proportion of males with good genes among p males.
V_G	The number of a female’s viable offspring surviving when all her offspring are fertilized by G sperm.
V_g	The number of a female’s viable offspring surviving when all her offspring are fertilized by g sperm.
ΔV	The per female potential gain in viability, $V_G - V_g$, by being fertilized by G sperm only instead of by g sperm only.
μ	The proportion of extra-pair sperm.
E_G	The proportion of eggs fertilized by the extra-pair male (EPF) when the extra-pair male is G and the bonded male is g.
E_g	The proportion of eggs fertilized by the extra-pair male (EPF) when the extra-pair male is g and the bonded male is G.
z	Bias intensity coefficient in favor of G sperm when in competition with g sperm.

bonded to a P male or when she is bonded to a p male. This yields eight F_{ij} female tactics, where the subscript i represents the two bonded male’s phenotype, and j , any of the four the female EPC options (Table 3).

Paternal genetics and offspring survival

We can now look for the best female EPC strategy. Here, we follow convention where a “strategy” can be one or more tactics that define everything a female might do under each circumstance that she may encounter. Thus, $\{F_{pN}, F_{pp}\}$ is one possible strategy, while $\{F_{pN}, F_{PN}\}$ is another (see also Dominey 1984). We begin by computing payoffs of a female who uses the N tactic (No EPC) when bonded to an inferior male (F_{pN}) or to a superior male (F_{PN}), correspondingly, as follows:

$$\begin{aligned}
 F_{pN} &= gV_G + (1 - g)V_g = V_g + g\Delta V \\
 F_{PN} &= GV_G + (1 - G)V_g = V_g + G\Delta V
 \end{aligned}
 \tag{2}$$

These two F_{iN} payoff equations, of females who strictly copulate with their ($i=p$ or P) bonded males, are used as a reference. Payoffs, F_{ij} , of each active EPC tactic, is

Table 3 Female EPC tactics

F_{pN}	If bonded to p, do not accept EPC.
F_{pp}	If bonded to p, seek EPC with another p male.
F_{pP}	If bonded to p, seek EPC with a P male.
F_{pR}	If bonded to p, seek EPC with a random male.
F_{PN}	If bonded to P, do not accept EPC.
F_{PP}	If bonded to P, seek EPC with a p male.
F_{PR}	If bonded to P, seek EPC with another P male.
F_{PR}	If bonded to P, seek EPC with a random male.

calculated by taking F_{iN} of a female bonded to an i male, and adding rewards (R_{ij}) and subtracting losses (L_{ij}) that result from the j EPC option she uses:

$$\begin{aligned}
 F_{ij} &= F_{iN} + R_{ij} - L_{ij}, \\
 &\text{given that} \\
 R_{ij} &= r_{ij}E_G\Delta V \text{ and } L_{ij} = l_{ij}E_g\Delta V,
 \end{aligned}
 \tag{3}$$

where r_{ij} and l_{ij} represent, correspondingly, probabilities of rewards and losses of a female who is bonded to a male of type i and uses a j EPC option. Table 4 shows the r_{ij} and l_{ij} that correspond with each EPC tactic.

It is helpful to view r_{ij} and l_{ij} as probabilities of “fortunate” and “unfortunate” sperm replacements, correspondingly, which derive from imprecision of precopulatory choices of

Table 4 Rewards and losses of female EPC tactics

Tactic	Probabilities of rewards	Probabilities of Losses
F_{pN}	$r_{pN}=0$	$l_{pN}=0$
F_{pP}	$r_{pP}=(1-g) G$	$l_{pP}=g (1-G)$
F_{pR}	$r_{pR}=(1-g) [(1-P) g+PG]$	$l_{pR}=g [(1-P) (1-g)+P(1-G)]$
F_{pp}	$r_{pp}=(1-g) g$	$l_{pp}=g(1-g)$
F_{PN}	$r_{PN}=0$	$l_{PN}=0$
F_{PP}	$r_{PP}=(1-G) G$	$l_{PP}=G (1-G)$
F_{PR}	$r_{PR}=(1-G) [(1-P) g+P G]$	$l_{PR}=G [(1-P) (1-g)+P (1-G)]$
F_{Pp}	$r_{Pp}=(1-G) g$	$l_{Pp}=G (1-g)$

For each F_{ij} tactic, the probability of rewards is generated as the probability to replace g genes with G genes. This is computed as the product of two probabilities: (1) the probability that the bonded male’s genotype is g given that his phenotype is i (i.e., either p or P), and (2) the probability that the extra-pair male’s genotype is G given that his phenotype is j (i.e., p, P or a male picked at random, R), depending on the female’s EPC tactic. Probabilities of losses are similarly generated as the probabilities that females replace G sperm with g sperm

genotypes. This is inherent in the fact that genotypes and phenotypes do not perfectly match. Therefore, a female who is bonded to a male whose phenotype is *p* but his genotype is *G*, for instance, may lose some good genes sperm, by unfortunate sperm replacements, if she also copulates with an extra-pair male whose phenotype is *P* but his genotype is *g*. Similarly, a female who is bonded to a *P* phenotype whose genotype is *g* may gain good genes sperm, by fortunate sperm replacements, if she also copulates with a *p* extra-pair male whose genetics happens to be *G*. Sperm bias, $z > 0$, embedded in the EPF equations, E_G and E_g (Table 1), increases rewards and decreases losses (Eq. 3) by enhancing beneficial sperm replacements (*g* with *G*). Unlike mechanisms that create sperm bias, which may have a selective advantage, fortunate sperm replacements, just like unfortunate ones, are random, and depend on proportions of the different sperm types.

Table 4 and Eq. 3 make it easy to establish a hierarchy in rewards and losses of the different female EPC tactics. For females bonded to *p* males, it is easy to see that $R_{pP} > R_{pR} > R_{pP}$ and $L_{pP} < L_{pR} < L_{pP}$, and, therefore,

$$F_{pP} > F_{pR} > F_{pP}$$

Similarly, females bonded to *P* males show the same hierarchy:

$$F_{PP} > F_{PR} > F_{PP}$$

Both hierarchies depend on the premise that phenotypic superiority is correlated with quality, $G > g$. These hierar-

chies do not depend on existence or the intensity of sperm bias, and they hold for any $z \geq 0$. Hence, as expected, if a female is engaged in EPC, then regardless of her bonded male's identity, her payoffs are higher if she chooses a phenotypically superior male than if she picks an extra-pair male at random, and lowest, if she chooses to copulate with a phenotypically poor extra-pair male.

It now remains to establish that the two best active EPC tactics, F_{pP} and F_{PP} , are also better than not doing EPC at all, namely that $F_{pP} > F_{pN}$ and $F_{PP} > F_{PN}$. In fact, all that is required is to show, for each of these two tactics, is that rewards are greater than losses (Eq. 3). For a female bonded to a poor male (*p*), it is easy to see that $R_{pP} > L_{pP}$ is always true. For a female bonded to a superior male (*P*), we find that $R_{PP} > L_{PP}$ is only true only if there is sperm bias, $z > 0$ (for then $E_G > E_g$, see Table 1). With no sperm bias ($z = 0$) we get $F_{PP} = F_{PN}$. These conclusions are summarized in Table 5, where each cell shows the best female EPC strategy under the stated conditions.

Cell b in Table 5 exposes an assumption that is often implicit in the conventional view of the good genes hypothesis of EPC. For females bonded to superior males, Cell b shows that $F_{PP} = F_{PN}$, whereas the conventional view maintains that such females should not practice EPC and thus employ F_{PN} . As the conventional view of EPC does not include effects of sperm bias, it must assume that EPC entails costs, which justifies $F_{PP} < F_{PN}$. Thus, according to the conventional view, the only EPC tactic that should be used is F_{pP} , i.e., when the phenotypic quality of the extra-

Table 5 Best cost-free EPC strategies as a function of pre- and post-copulatory biases

Information about	No: $G = g$	Yes: $G > g$
male genotype:		
Sperm bias:	a)	b)
No: $z = 0$	F_{pj} (all tactics have equal payoffs)	F_{pP}
	F_{Pj} (all tactics have equal payoffs)	F_{PP} OR F_{PN}
	c)	d)
	F_{pp} OR F_{pR} OR F_{pP} (all but F_{pN})	F_{pP}
Yes: $z > 0$	F_{pP} OR F_{pR} OR F_{PP} (all but F_{pN})	F_{PP}

Phenotypes may ($G > g$) or may not ($G = g$) provide information about male genetic quality. Likewise, sperm competition may ($z > 0$) or may not ($z = 0$) favor sperm with good/compatible genes. In each cell, the upper row stands for females bonded to poor phenotypes (*p*), and the lower row for females bonded to superior phenotypes (*P*). “OR” is used as a Boolean condition when tactics' payoffs are equally highest. When there are no biases, payoffs of all tactics are equal to each other and to the No EPC tactic (a). Precopulatory biases (right column) give a target to EPC (the better phenotype, *P*), and sperm bias (bottom row) breaks ties between active EPC tactics and No EPC, with an advantage to the active EPC tactics

pair male is higher than that of the bonded male (e.g., Westneat and Stewart 2003; Akçay and Roughgarden 2007). This changes, however, when we add sperm bias (Table 5 bottom row), and even females bonded to best phenotypes benefit by EPC. We show later that this conclusion may hold even when EPC entail costs.

Random EPC

In a cost-free setup with $G > g$, F_{iR} tactics, having EPC with a random male, are less rewarding than their corresponding F_{iP} tactics, where females target phenotypically superior males. However, when costs are assumed, then F_{iR} may become relevant because they are expected to be less expensive than any EPC that involves a choice. It is, therefore, necessary to first establish whether and under what conditions a random EPC tactic is more rewarding than No EPC, namely, that $F_{iR} > F_{iN}$. Equivalently, we might simply examine the rewards and losses balance of EPC, and check that $R_{iR} - L_{iR} > 0$ (Eq. 3).

Firstly, it is easy to see that when bonded to a p male, random EPC are more rewarding than No EPC. This is shown as follows: assume first $z=0$. This gives $E_G = E_g = \mu$ (Table 1) in Eq. 3 and Table 4 and, therefore:

$$R_{pR} - L_{pR} = \Delta V \mu P(G - g) = \delta > 0, \text{ hence, } F_{pR} - F_{pN} = \delta > 0 \tag{4}$$

As F_{pR} increases with z (since E_G , and thus R_{pR} , increase with z , whereas E_g , thus L_{pR} , decrease with z ; Table 1, Eqs. 1, 3), then $F_{pR} > F_{pN}$ is also true for any $z > 0$. When bonded to a P male we find, for $z=0$, that random EPC is less rewarding than no EPC:

$$R_{pR} - L_{pR} = \Delta V \mu (1 - P)(g - G) < 0, \text{ hence, } F_{pR} < F_{pN}. \tag{5}$$

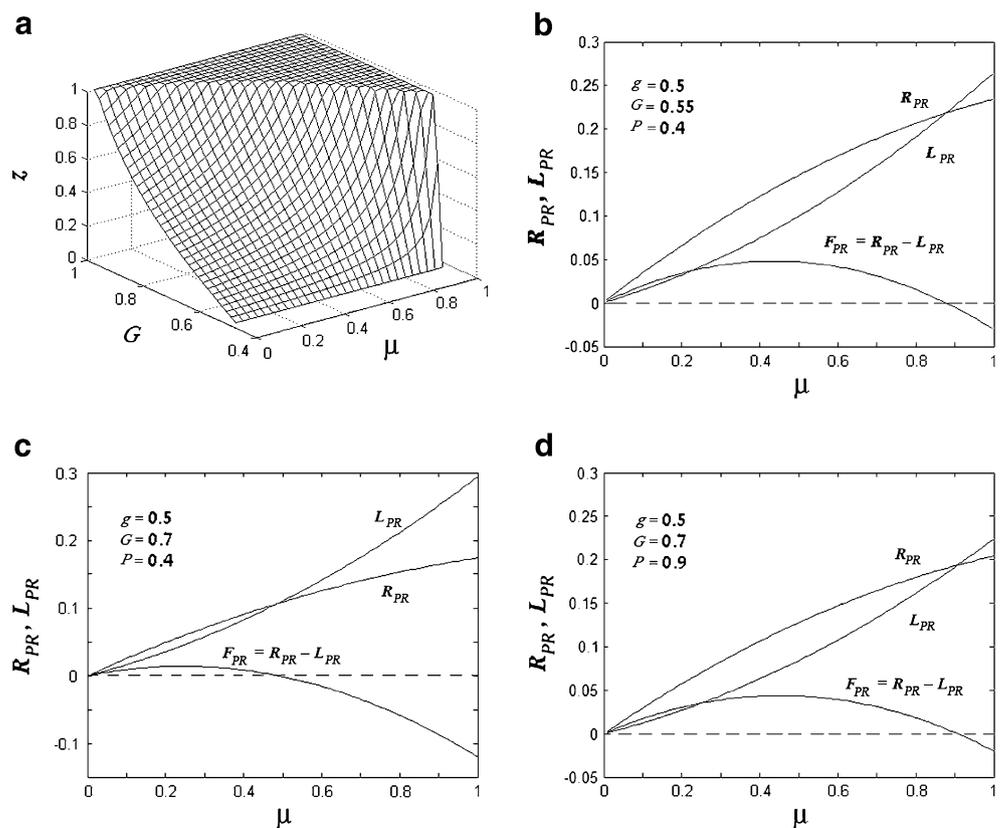
However, we can now show that a sufficiently strong sperm bias can shift the balance toward F_{pR} . By isolating z in the condition $R_{pR} - L_{pR} > 0$ (Table 4), we obtain the condition:

$$z > z^* = \frac{(1 - P)(G - g)}{(1 - \mu)[P(G - g)(1 - 2G) + g(1 - G) + (1 - g)G]} \tag{6}$$

where z^* describes a threshold in sperm bias. When $z > z^*$ then $F_{pR} > F_{pN}$ (Fig. 1).

Figure 1 illustrates the new conclusion drawn from Eq. 6 that a bias for genetically good or compatible sperm can reward females enough, such that even females bonded to best male phenotypes may benefit by random EPC more than they do by sexual monogamy. This happens more easily when the bias is stronger and when phenotypes provide less information about good genes (illustrated by a smaller difference between G and g). By changing one variable at a time, G in 1c and P , the frequency of best phenotypes in 1d, Fig. 1b–d also demonstrate that when

Fig. 1 The surface z^* , in (a), describes the threshold in sperm bias. For $z > z^*$, we get $F_{pR} > F_{pN}$, and for $z < z^*$, we get $F_{pR} < F_{pN}$. It is assumed, in (a), that $g=0.5$ and $P=0.4$. When $z^* \geq 1$, $F_{pR} < F_{pN}$ is always true. Optimality in the proportion of extra-pair sperm, μ , is clearly shown in (b, c, d), by computing $F_{pR} = R_{pR} - L_{pR}$. All three figures assume $z=0.5$



phenotypes provide more information about genotypes, the range of μ for which $F_{PR} > F_{PN}$ decreases. In contrast, this range increases as the superior male class gets more common (higher P). Optimality in μ , another new conclusion of the model shown in Fig. 1b–d, is elaborated in the next section.

Optimality in μ

Uncertainties about male genotypes produce important tradeoffs between two antagonistic probabilistic processes, fortunate and unfortunate sperm replacements (probabilities of rewards and losses in Table 4). In addition, a directional and advantageous process, sperm bias, may also take place between insemination and fertilization. Together, they may produce an optimal intensity of involvement in EPC, $\hat{\mu}$, which satisfies $0 < \hat{\mu} < 1$; $\hat{\mu}$ is computed by taking first and second derivatives with respect to μ , of F_{ij} , payoffs of a female bonded to an i male using an EPC option j (using Eq. 3 and Tables 1). We consider the four tactics that may be, at least sometime, greater than F_{iN} , namely F_{pB} , F_{pR} , F_{PB} , and F_{PR} (ignoring F_{PP} , because F_{pR} always gives higher payoffs and is less prone to costs). The point of maximum payoffs of a tactic F_{ij} with respect to μ is at

$$\hat{\mu} = \frac{1}{2} + \frac{r_{ij} - l_{ij}}{2z(r_{ij} + l_{ij})}, \tag{7}$$

where rewards r_{ij} and losses l_{ij} represent, correspondingly, probabilities of fortunate and unfortunate sperm replacements (Table 4), and z is sperm bias. Using Table 4, we compute Table 6 and Fig. 2 and show $\hat{\mu}$ for all four tactics. Hence, there may exist boundaries to the degree at which a female should be involved in EPC, even when EPC is cost-free.

Figure 2 shows expected patterns of division of paternity between males when EPC are cost free and unconstrained. For females bonded to poor phenotypes (tactics F_{pB} and F_{pR}), most or all copulations are expected to be with extra-pair males ($\hat{\mu} > 0.5$). For these females, No EPC is not an option. Division of paternity for females who are bonded to superior phenotypes depends on their options for EPC tactics. If they can only choose between random EPC (F_{PR}) or No EPC, then most ($\hat{\mu} < 0.5$) or all ($\hat{\mu} = 0$) of their

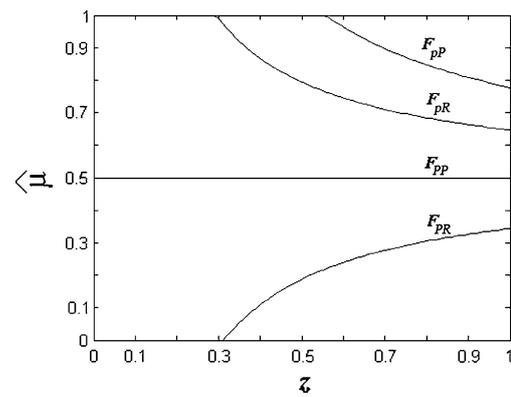


Fig. 2 Optimal proportions of extra-pair sperm, as a function of sperm bias and female EPC tactics, given the constraints $0 \leq \hat{\mu} \leq 1$. Calculations were made using $g=0.4$, $G=0.7$, $P=0.5$

sperm is expected to be obtained from their bonded males. When the phenotype of an extra-pair male is equal to that of their bonded male (F_{PB}), then paternity should be equally divided.

It is easy to see in Table 6 that except for the F_{PB} tactic (but only if it is cost free), paternity should only be divided if there is at least some sperm bias ($z > 0$). It is expected more often and more equally when there is little information about phenotypes and hence precopulatory biases are relatively weak (G closer to g ; see numerators in Table 6) and when postcopulatory biases (z) are strong (Fig. 2). The difference between the perceivable “good genes” and “unperceivable compatible genes” explanations of EPC now stands out. As information about genotypes declines, then $\hat{\mu}$ in F_{pB} , F_{pR} , and F_{PR} converges to $\hat{\mu} = 0.5$ (using the model’s assumption of a single extra-pair male). Two cases, for which females have absolutely no information about male genotypes, represent females’ benefits by unperceivable genetic compatibility: (1) when phenotypes cannot predict certain paternal genotypes ($G=g$), and (2) when females use the tactic F_{PB} , i.e., both bonded and extra-pair males are phenotypically alike (Table 6, Fig. 2). Indeed, both show an optimal extra-pair sperm proportion of $\hat{\mu} = 0.5$ but require $z > 0$ in order to produce payoffs higher than those of the No EPC tactic (Table 5).

Costs and constraints

We introduce costs by recalling that V_G and V_g (Eqs. 2, 3) represent the number of a female’s successful offspring, had the female been inseminated by only one type of sperm, either G or g , respectively. Reproductive costs are introduced by a viability coefficient, $0 \leq v \leq 1$, and we replace V_G and V_g with vV_G and vV_g . Reproductive costs may represent costs on the female potential productivity when females

Table 6 Optimal proportions of extra-pair sperm

Tactic	Optimal μ
F_{pB}	$\hat{\mu} = \frac{1}{2} + \frac{G-g}{2z[(g+G-2gG)]} > \frac{1}{2}$
F_{pR}	$\hat{\mu} = \frac{1}{2} + \frac{P(G-g)}{2z[P(g+G-2gG)+2(1-P)g(1-g)]} > \frac{1}{2}$
F_{PB}	$\hat{\mu} = \frac{1}{2}$
F_{PR}	$\hat{\mu} = \frac{1}{2} - \frac{(1-P)(G-g)}{2z[(1-P)(g+G-2gG)+2PG(1-G)]} < \frac{1}{2}$

divert resources to EPC, as well as costs on offspring viability that result from reduced paternal care. By this, we generalize the cost free model above, which now represents the special case $v=1$.

To find the payoffs F'_{pp} , when there are costs, we insert v into the payoffs equation of tactic F_{pp} as follows (using Eqs. 2, 3 and Table 4):

$$F'_{pp} = gvV_G + (1-g)vV_g + (1-g)GE_Gv\Delta V - g(1-G)E_gv\Delta V = vF_{pp} \quad (8)$$

It is easy to show that by incorporating costs in the other F_{ij} equations of active EPC tactics, we similarly obtain $F'_{ij} = vF_{ij}$. We can now ask: can costs ($v<1$) lead females to switch to their second best tactics, EPC with a random male, F_{pR} and F_{PR} ?

Case 1: costs paid equally in all active EPC tactics

By assuming that v is equal in all EPC tactics, we can easily see that the same hierarchy of payoffs shown in Table 5 for $v=1$ holds also for $v<1$. The only exception is the relative status of the No EPC tactic, F_{iN} , which entails no such costs.

Equation 8 shows that costs on reproduction can theoretically reduce the female payoffs F'_{pp} to zero (namely, for $v=0$), i.e., lower than F_{iN} . More generally, there must exist, therefore, for any tactic and condition for which $F_{ij}>F_{iN}$ when $v=1$ (see Table 5), a certain $0<v^*<1$ that gives $v^*F'_{ij}=F_{iN}$. Hence, it pays to use EPC whenever

$$v > v^* = \frac{F_{iN}}{F_{ij}} \quad (9)$$

Applying Eq. 9 to the best active EPC tactic of females bonded to superior males, F_{pP} , where extra-pair males sought are equally superior, gives:

$$v^* = \frac{F_{pN}}{F_{pN} + 2zG(1-G)\mu(1-\mu)\Delta V} \quad (10)$$

As shown before, when $v=1$, sperm bias, $z>0$, is necessary for obtaining $F_{pP}>F_{pN}$. However, v^* decreases monotonically with z . Therefore, a strong sperm bias makes it easier to satisfy $v>v^*$ and maintain $F'_{pP}>F_{pN}$ for greater costs on offspring's viability.

It is concluded, then, that costs of EPC, when applied equally to all active EPC tactics, maintain the predictions about most rewarding female strategies summarized by Table 5, with the exception that with sufficiently intense reproductive costs females should avoid EPC.

Case 2: costs are paid only by choosy females

We now assume that costs on productivity, $v<1$, are expressed only in the two choosy EPC tactics, F_{pP} and F_{pB} , tactics that lead females to copulate only with extra-pair males superior to their bonded males. These two tactics were shown to be the most rewarding tactics for $v=1$. We compare their payoffs with those of the females' second best EPC tactics, F_{pR} and F_{PR} , those that lead females to copulate with a random male, and which we continue to assume are cost free ($v=1$). The random EPC tactics are considered only under conditions that satisfy $F_{iR}>F_{iN}$, i.e., that they are better than not doing EPC at all. For females bonded to inferior phenotypes, $F_{pR}>F_{pN}$ is always true (see Eq. 4). However, for females bonded to superior phenotypes, $F_{pR}>F_{pN}$ is only true when sperm bias is sufficiently strong, $z>z^*$ (Eq. 6, Fig. 1).

Similarly to the analysis surrounding Eq. 9, we find that it pays more to make EPC with a random male than with best males when an offspring's viability as a result of female choosiness decreases below v^* :

$$v < v^* = \frac{F_{pR}}{F_{pP}} \quad \text{and} \quad v < v^* = \frac{F_{PR}}{F_{pP}} \quad (11)$$

Given that $F_{pP}>F_{pR}$ is always true, there always exists a certain $0<v<v^*$ that gives $F_{pR}>F_{pP}$. Because $F_{pR}>F_{pN}$ (EPC at random are more rewarding than No EPC) is also true, then $0<v<v^*$ is enough to make females bonded to poor phenotypes switch from choosing best extra-pair phenotypes, to make EPC at random, i.e., using F_{pR} .

The same argument holds for females bonded to phenotypically superior males, and $0<v<v^*$ gives $F_{PR}>F'_{pP}$. However, $F_{PR}>F_{pN}$ is only true for a sufficiently strong sperm bias in favor of good genes, $z>z^*$ (Eq. 6, Fig. 1). Hence, a random choice of an extra-pair male can be a female's best tactic when both of these two conditions are simultaneously met.

Information about male genotypes and the frequency of P males are also important in influencing the choice of random EPC. It is easy to show, using Table 4 and Eq. 14, that as the difference between G and g gets smaller, so is the difference in payoffs of F_{iR} and F_{iP} . As a result, v^* increases and lower costs (higher v) are sufficient to satisfy $v<v^*$ and lead to random EPC. It is also easy to show, using Table 4, that the exact same argument holds for a high frequency of the superior male phenotypes in the population, P . In fact, by setting z to 0 (no sperm bias), we get, for females bonded to inferior males, the simple condition $v^*=P$.

Hence, when there is little information in phenotypes about genotypes, and when the frequency of best phenotypes in the male population is high, females become more

likely to copulate with random extra-pair males, even if bonded to superior males. This states, in fact, that as conditions assumed for “good genes” get more similar to conditions assumed for unperceivable “compatible genes,” at least in terms of the perception of males’ genetics, one should expect to find more females engaging in EPC at random.

Case 3: constraints

Very similar conclusions can be reached when EPC are constrained, say, if males guard their mates rather than entail direct reproductive costs. Constraints can be introduced in the model by a freedom coefficient, f (where $0 \leq f \leq 1$), which describes the female freedom to obtain an optimal proportion of extra-pair sperm, $\hat{\mu}$. The actual proportion of extra-pair sperm obtained becomes $f\hat{\mu} < \hat{\mu}$, which leads to a suboptimal use of EPC, hence to lower payoffs (i.e., lower reproductive success).

Conclusions of the model with constraints, not shown here, are, therefore, largely similar to the analysis of costs on viability described above in details. Most importantly, if males increase their guarding efforts in the presence of attractive males (Slagsvold and Lifjeld 1997), then choosiness entails additional costs. For a sufficiently low f , females may then switch from EPC with best phenotypes, F_{IB} , to random EPC, F_{IR} . However, costs on viability, at their maximum ($v=0$), give no payoffs. In contrast, maximum constraints ($f=0$) give payoffs that are equal to those of a female who is strictly monogamous, F_{IN} . Significant constraints, therefore, produce limited EPC benefits, and female EPC decisions become sensitive to small reproductive costs inflicted by EPC or to individual differences in availability of resources of either female (Gowaty 1996) or male (Eliassen and Kokko 2008) origin.

Discussion

A simple statement of the model’s conclusions is that if females can efficiently detect genetic quality at the postcopulatory stage, then it may pay them to mate multiply and even randomly. Precopulatory mate choice may become then less important where females benefit by good or compatible genes, and male phenotypes give imperfect information about genotypes. To put it simply, even if the social mate looks good, he might not actually be good as a sire, or, using the same argument, even if he looks bad, he might actually be a good sire. If sperm competition gives additional information about genes, then it pays to accept sperm from different origins and let sperm competition do the final screening of good genes. Such a postcopulatory choice, however, has to work quite efficiently to overcome

the cost of unfortunate sperm replacements, i.e., unwillingly replace good genes with bad genes, plus other, direct costs.

Predictions, weak and strong

The good genes explanation of female EPC is based on two fundamental assumptions: (1) that females improve their offspring’s fitness if they copulate with males who have better genes than those of their bonded males and (2) that qualities of phenotypes and genotypes strongly correlate. These assumptions make three predictions upon which most tests of the good genes function are based:

1. Extra pair offspring (EPO) should have, on average, better fitness than within pair offspring (WPO) (Griffith et al. 2002; Westneat and Stewart 2003; Akçay and Roughgarden 2007; Brommer et al. 2007).
2. Only females bonded to poor quality males should be engaged in EPC (Griffith et al. 2002; Westneat and Stewart 2003; Akçay and Roughgarden 2007).
3. These females should only do it with extra-pair males who are phenotypically superior to their bonded males, namely, only the F_{PP} tactic is expected (Griffith et al. 2002; Westneat and Stewart 2003; Akçay and Roughgarden 2007; Brommer et al. 2007).

Somehow unnoticed stands a fourth prediction of the good genes hypothesis, which might have been a logical consequence of the very same two fundamental assumptions that produce predictions 1–3:

4. Females who are engaged in EPC (i.e., those who use the F_{PP} tactic) should have all of their offspring fathered by extra-pair males (i.e., $\hat{\mu} = 1$).

Predictions 1–3 are explicitly stated in discussions of good genes benefits by EPC. In contrast, prediction 4 is not, but it has also not been seriously considered. Generally speaking, the logic seems to be that if data do not support prediction 4, then EPC must entail costs or be constrained or both. A limited use of EPC, in turn, stabilizes social monogamy (Kokko 1999). The assumption of costs is, therefore, always in the background in most discussions of EPC, which solves theoretical and empirical problems that would have been arisen by prediction 4.

The assumption of direct (reproductive) costs of EPC also takes us back to the old distrust in good genes in sexual selection, that originated from Fisher’s fundamental theorem of natural selection as well as from his runaway explanation of male sexual displays (Fisher 1930): indirect benefits by good genes have never been believed to be strong enough to compensate for noticeable direct costs (e.g., Kirkpatrick 1986; Griffith et al. 2002; Arnqvist and Kirkpatrick 2005). This explains why the central question

asked has been why females seek EPC at all, rather than why they do not do it more (Westneat and Stewart 2003).

Prediction 1 is the ultimate test of whether EPC benefits females via the improvement of their offspring's genetics (Akçay and Roughgarden 2007). However, no study has completed the comparison between EPO and WPO using all aspects of their reproduction (Schmoll et al. 2009), and more than one study is needed to establish a general trend. Unlike prediction 1, predictions 2 and 3 have been commonly tested but have not been consistently validated, nor have they shown to be powerful trends. Based on their meta-analysis of 36 studies, Akçay and Roughgarden (2007), therefore, tend to reject the good genes hypothesis.

However, our model finds that predictions 2 and 3 do not seem to be as strong predictions of good genes models as assumed by Akçay and Roughgarden or by other previous studies. This is mainly because our model questions some of the fundamental assumptions of the good genes hypothesis. The first is the strong correlation assumed between good genes and male phenotypic quality, that is $g=0$, $G=1$. Our model assumes good genes cases fall somewhere in between ($0 < g < G < 1$). When the correlation is relaxed, predictions 2 and 3 are less robust, and sensitive to other factors such as sperm biases and costs of EPC, in particular costs that are higher for choosy females. Neither of these has previously been included in models of EPC. As these can alter predictions 2–4, there should be no wonder why field tests often fail to verify them. Our model shows that female EPC strategies can be more complex than previously assumed.

Random EPC?

One of the two most important conclusions of the model is that EPC may not only occur between females who are bonded to phenotypically inferior males, p , and extra-pair males who are phenotypically superior, P (violating prediction 2). If EPC are more constrained or costly to choosy females, and if phenotypes and genotypes do not perfectly match, then females bonded to p males can benefit more by copulating with random extra-pair males (using the F_{PR} tactic).

Moreover, even females bonded to phenotypically superior males can benefit by EPC. If EPC is cost-free, information about genotypes is incomplete, and sperm competition is biased toward the genetically better sperm, then females benefit by dividing copulations with other phenotypically superior males (using F_{PP}). Furthermore, if choosiness is particularly costly (Petrie and Kempenaers 1998), information about genotypes is sufficiently poor and the frequency of phenotypically better males is sufficiently high, then females bonded to superior males may switch to selecting extra-pair males at random (using F_{PR}). If these factors affect females bonded to phenotypically superior

males, their effect is stronger on females bonded to phenotypically inferior males. Hence, one cannot rule out good genes benefits simply because predictions 2 and 3 are found only intermittently.

How much EPC?

The model's conclusions challenge the view that costs of EPC or constraints by guarding males are necessary to explain small proportions of EPP. The model shows that when information about genotypes is incomplete, females may find themselves trading good genes of bonded males who happen to be phenotypically inferior, with poor genes of extra-pair males who happen to be phenotypically superior. This cost, of unfortunate sperm replacements, together with sperm bias for good genes, can limit the female involvement in EPC, and result in an optimal proportion of extra-pair sperm that is $0 < \hat{\mu} < 1$. Indeed, entire EPP broods are expected more often when the F_{PP} tactic is used. However, as the association between phenotypic and genotypic qualities decreases, and as sperm bias increases, chances are higher to find broods that are divided between the males (Table 6, Fig. 2).

When females benefit by unperceivable compatible genes, i.e., when precopulatory information is completely absent ($G=g$), extra-pair sperm is expected to be equally divided between the two males (assuming a single extra-pair male and cost free EPC). In such cases, sperm bias must exist or females should avoid EPC for even slight costs, and females are not expected to be choosy about extra-pair males.

Male age

Akçay and Roughgarden (2007) also show that older male age is the main predictor of success in EPC, while male size comes second. This may correspond with a good genes explanation, if one assumes that natural selection weeds out, at a younger age, more males of poor genetic quality than males of high genetic quality (Kokko 1998; Brooks and Kemp 2001, but see Hansen and Price 1995; Radwan 2003). Akçay and Roughgarden's results also show that male "attractiveness" is even less associated with EPC than male size. Whether this shows inherent real biological differences between age, size, and attractiveness, or of a greater human objectivity determining age as opposed to the assessment of relevant showy characters selected by females, currently remains to be tested.

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