Evolutionary Conflicts of Interest: Are Female Sexual Decisions Different?

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q1 abstract: Analyses of reproductive conflicts of interests have yielded important evolutionary insights in many areas of biology. The usefulness of conflict analyses of traits that have been traditionally interpreted as resulting from female choice is controversial, however. This article explores a possible explanation for why conflicts of interest may be ameliorated in female choice situations. In contrast to most other evolutionary contexts in which conflicts of interest are thought to have been important, sexual reproduction usually involves an extensive, irretrievable mixing of the genomes of the participants. Under certain combinations of costs and benefits to females, the genes in the female's genome can benefit, through increased reproduction of her offspring, from the very genes that produce sexually antagonistic traits in the male. In short, females can sometimes gain by "losing." Such Fisherian payoffs are also possible, though probably less important, for males. Gaining by losing is not feasible in most other contexts of evolutionary conflict, except under some conditions in parent-offspring conflict. Some apparent parent-offspring conflicts may instead be parental choice among offspring that is analogous to traditional female choice. Parent-offspring conflict may be relatively common, however, because offspring manipulation of their parents is likely to be damaging to the parents.

Keywords: female choice, sexually antagonistic coevolution, male-female conflict, parent-offspring conflict.

Analyses of evolutionary interactions in terms of conflicts between the reproductive interests of participating parties have a long record of providing useful insights in a wide q2 variety of contexts (Hurst et al. 1996; table 1). These include workers and queens in social animals, embryos and mothers in mammals and angiosperms, organelle and nuclear genomes in eukaryotes, plasmid and chromosome genes in bacteria, parents and their offspring, siblings in the same nest or uterus, parasites in the same host, genetically different cells and tissues in the same multicellular organism, male and female parents over investment in their offspring, rebel meiotic drive genes and chromosomes and the rest of the genome, genes that are imprinted according to their origin in the father or the mother, and genes coding for male and female traits in the same organism. It is thus logical to attempt to apply this same approach in analyzing the reproductive interactions between males and females, focusing on potential conflicts in their reproductive interests (Parker 1979; Holland and Rice 1998; Lessells 1999; Chapman et al. 2003). The realization that genetic imprinting in mammals and angiosperms results from conflicts between males and females over gene expression in their offspring (Haig 2000) is a spectacular example of the dividends of such an approach. But at present there is controversy regarding the importance and ubiquity of such conflict in some other types of prefertilization interactions between males and females that have traditionally been interpreted as evolving under sexual selection by female choice (Cameron et al. 2003; Chapman et al. 2003; Cordero and Eberhard 2003; Córdoba-Aguilar and Contreras-Garduño 2003; Kokko et al. 2003; Pizzari and Snook 2003; Eberhard 2004*a*, 2004*b*). q3

Controversy Concerning Traditional Female Choice and Sexually Antagonistic Selection

The term sexually antagonistic selection will be used here in the sense of Holland and Rice (1998, p. 5) to indicate selection that favors traits that increase the reproduction of individuals of one sex but also reduce the reproduction in terms of surviving offspring of members of the other sex with which these individuals interact ("female attraction to the male display trait reduces her net fitness"). It has long been recognized that a male's reproductive interests are often in conflict with those of some of the females he encounters; males are generally under selection to copulate more readily than females, and many male courtships are rebuffed. This type of conflict, which probably stems from the generally smaller investment made by males than females in their offspring (Darwin 1871; Trivers 1972), is not in question. The controversy concerns why

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Table 1: Evolutionary contexts in which analyses of conflicts of reproductive interest have illuminated understanding, with examples of studies discussing each

Conflicting entities	Examples
Transposons vs. rest of genome	Campbell 1981; Eberhard 1990; Hurst et al. 1996
Meiotic driver alleles and chromosomes vs. alternative alleles and the rest of the genome	Trivers 1985; Hurst et al. 1996
Nuclei vs. other nuclei in a syncytium	Buss 1987; Hurst et al. 1996
Plasmids vs. bacterial chromosomes	Eberhard 1990; Hurst et al. 1996
Cytoplasmic vs. nuclear genes in eukaryotes	Eberhard 1980; Cosmides and Tooby 1981; Hurst et al. 1996; Rand 2001
Sex chromosomes vs. autosomes	Rice and Chippendale 2002*
Intracellular bacteria such as *Wolbachia* and their hosts	Weeks et al. 2002
Mother vs. embryo mammals and angiosperms	Haig 1993
Parents vs. offspring	Trivers 1972, 1974; Clutton-Brock 1991
Sibling vs. sibling in the same nest or uterus	Mock and Parker 1997; Gardner 1999; Drummond 2001
Members of family groups	Emlen et al. 1995
Group members in social animals	Hamilton 1964*a*, 1964*b*; West-Eberhard 1975
Cells and tissues in multicellular organisms	Buss and Dick 1992; Dominguez 1995; Pál and Papp 2000; Hudson et al. 2002; Queller et al. 2003
Parasites within the same host organism	Ewald 1994
Parents of species with biparental care of offspring	Lessells 1999
Male-derived vs. female-derived genes in a zygote	Haig and Westoby 1991; Burt and Trivers 1998; Haig 2000
Genes coding for male traits vs. genes coding for female traits in the same organism	Fedorka and Mousseau 2004

females are attracted to and eventually acquiesce to some males and not others.

Traditional female choice explanations of why females accept only some males invoke benefits to the female, either through direct gains (often in terms of greater numbers of offspring produced) or through indirect benefits that result from greater genetic quality of her offspring (Andersson 1994). The new sexually antagonistic selection ideas invoke male-female conflict instead. They propose that selection on females to avoid male-imposed costs that result from sexual interactions could result in a coevolutionary process of antagonistic adaptation and counteradaptation between males and females and that this coevolution would tend to result in rapid, divergent evolution (Holland and Rice 1998; Chapman et al. 2003). Recent discussions of sexually antagonistic selection (and the resulting sexually antagonistic coevolution; Rowe 1994; Holland and Rice 1998) have emphasized the expected payoff to a female from reducing direct male-inflicted costs, and thus increasing the number of offspring she can produce: "the force driving the evolution of the [female] preference is better described as a general female avoidance of male-imposed costs, rather than, as in traditional direct models, acquisition of benefits from preferred males" (Chapman et al. 2003, p. 41).

This debate can be restated as a pair of questions. Does the female gain from allowing (and sometimes even actively facilitating) copulation and fertilization by only the most outstanding, superior males she meets (as proposed by traditional female choice ideas)? Or is she forced or manipulated by some of the males she encounters to copulate and be inseminated against her own best reproductive interests (as proposed by the sexually antagonistic selection hypothesis)?

Traditional female choice with indirect payoffs to the female and sexually antagonistic selection can act on different aspects of female fitness (the fitness of her offspring and her direct output of offspring, respectively). They are thus not strict alternatives, and they may even act simultaneously on the same phenotypic traits (Holland and Rice 1998; Cordero and Eberhard 2003, forthcoming; Kokko et al. 2003). Nevertheless, they have not necessarily played equal roles in the evolution of the male and female traits utilized in sexual interactions. To date, the most extensive observations supporting sexually antagonistic selection has come from two sets of data: seminal products in *Drosophila melanogaster* flies and precopulatory struggles in *Gerris* water striders (summarized in Chapman et al. 2003). Some of this evidence, however, is open to alternative interpretations (Cordero and Eberhard 2003; Córdoba-Aguilar and Contreras-Garduño 2003; Eberhard and Cordero 2003; Pizzari and Snook 2003). For example, consider a male seminal product that increases female resistance to otherwise advantageous rematings. This product could have evolved under sexually antagonistic selection on males despite the fact that it reduced female reproduction. But

female responsiveness to such a product could also result from traditional female choice: by responding to the product, she would be able to obtain sons with superior abilities to inhibit female remating in future generations. As long as any other negative effects on daughters (Chippendale et al. 2003) were not too great, this could be advantageous (Cordero and Eberhard 2003, forthcoming). Similar arguments can be made for other traits (e.g., Moore et al. 2001).

There are also data that do not fit easily with the sexually antagonistic coevolution explanation for why male morphological traits that are specialized for interactions with females tend to show especially rapid divergent evolution. A survey of the comparative morphology of the male genitalia in thousands of species in more than 100 families of insects and spiders found that sexually antagonistic coevolution has not been sufficiently important to leave any trace of the predicted correlation between the mating system (the degree of exposure of the female to male harassment) and rapid divergent evolution of genitalia (Eberhard 2004*a*). A second, taxonomically distinct survey of the functional morphology of species-specific male genitalia and nongenitalic clasping structures in just over 100 genera of insects and spiders failed to confirm another prediction of sexually antagonistic coevolution; even with criteria likely to give overestimates, the predicted coevolution of female structures with possibly defensive functions and species-specific male traits was not common (only about 20% of the genera; Eberhard 2004*b*). In many groups, female structures appear to be either invariant (lacking species-specific resistant capabilities) or selectively cooperative, as expected under traditional female choice. Scattered behavioral observations and experimental modifications also indicate that, at the level of both genitalic and nongenitalic clasping structures, male-female interactions in some species are more accurately described as involving selective female cooperation rather than male-female conflict (Loibl 1958; Belk 1984; Eberhard 2002*a*, 2002*b*).

These survey data do not resolve the controversy. The sexually antagonistic selection hypothesis can be rescued by softening or otherwise limiting its claims; perhaps, for instance, sexually antagonistic selection has acted on male-female interactions involving female physiological responses but not on female morphology (Eberhard 2004*a*, 2004*b*; Hosken and Stockley 2004). Both kinds of selection may have acted at different times. Sexually antagonistic selection may have acted only at certain times during the history of particular traits, providing, for instance, the original "nudges" that set off rounds of traditional Fisherian runaway female choice (Kokko et al. 2003; Eberhard 2004*b*). More data from morphology, as well as from behavior and physiology, will obviously be needed to resolve this controversy. Special attention to the designs of female traits (appropriate to resist the male? to actively cooperate with selected males?) and to the contexts in which they operate (does the behavioral context suggest that conflict is likely or unlikely?) may be helpful.

Nevertheless, the evidence from the surveys raises the possibility that our understanding of female choice interactions with males will not benefit from the usual illumination that has come from emphasizing reproductive conflicts of interest in other evolutionary analyses. Is there something fundamentally different about male-female interactions of this sort compared with the other conflict situations? The objective of this article is not to offer proofs of particular hypotheses but to explore a possible explanation for why such an exception could occur (a partial outline of the basic idea is given in Cordero and Eberhard, forthcoming).

Comparisons with Other Contexts of Conflict of Interest

I will focus on the female, because the key differences between the traditional female choice and sexually antagonistic selection hypotheses concern the selective reasons why females accede to some males but not others (Chapman et al. 2003). I will also focus on female responses to males that can affect the reproductive success of male and female genomes rather than on intralocus or interlocus conflicts (e.g., sexually antagonistic genes; Lessells 1999) because it is at this intergenomic level that the survey data speak against sexually antagonistic coevolution.

What might make female selectivity with respect to males different from the conflicts in table 1? A first possibly important difference is that, in contrast to some cases in which conflict analyses have been fruitful, the female cannot completely avoid interacting with a male without reducing her own reproductive output to zero (unless she is facultatively parthenogenetic). This contrasts, for instance, with an individual of a facultatively social species that can leave the group and go on its own or found or join a new group, a parent that can withhold parental care from the offspring of one uncooperative mate and give it instead to that of another, or a parasite that can leave a host and avoid interacting with other parasites in that host. If a female completely excludes males from participation in her reproduction, her reproductive output will be reduced to zero in all nonparthenogenetic sexually reproducing species. This complete dependence cannot, however, be a general explanation for selective female sexual receptivity because similar dependence also occurs in several other contexts listed in table 1 (e.g., organelle-nucleus, plasmid-chromosome, transposon–rest of genome). Nevertheless, it sets an important limit on the female's options.

A more unusual aspect of sexual interactions is the intimate and generally irretrievable mixing of the female's genome with that of the male in equal proportions in their offspring. Meiosis and the fusion of gametes guarantee not only that the female will have a fixed genetic representation in each of her offspring but also that her genes will be mixed with those of the male; most importantly, they will almost always remain mixed in future generations. This combination of characteristics does not occur in other types of evolutionary interactions in table 1. In many other cases of conflict, the possible genetic payoffs for the interacting parties are variable rather than fixed. For instance, the offspring that could result from the conflicts between workers and queens in social insects and among different workers of the same colony in social insects carry different relative representations of the genomes of the interacting parties; the same is true for the current and future offspring of the parents in conflicts between parents and offspring. Genome mixing also does not occur, at least in the short term, between eukaryote organelles and nuclei, between *Wolbachia* bacteria and their hosts as they struggle over the sex of the organism, between meiotic driver alleles and alternate alleles at the same locus, between driver alleles or chromosomes and the rest of the genome struggling over inclusion in gametes, between plasmid and chromosome genomes in bacteria, between transposons and the rest of the genome, or between parasites and their hosts. In all of these cases, the genetic information of each interacting unit continues to have its own discrete reproductive interests into the immediate future.

In contrast, once a female has committed to having her eggs fertilized by the sperm of a particular male (and, as just noted, she is obliged to use the sperm of at least one male), the reproductive interests of her genome will usually be in general accord with those of the male's genome (possible exceptions are discussed below). Most importantly, both males and females can gain reproductively from the abilities of their partners; these potentially beneficial traits include the very abilities that can provoke apparent reproductive conflict before fertilization. This means that under certain conditions, a female can gain from "losing." For instance, a female may be able to gain from the abilities of her partner to manipulate females into fertilizing their eggs with his sperm (and from her own susceptibility to these male manipulations), if this means that the sons that he sires with her will tend to be more effective manipulators and sire more offspring of their own. Female benefits from having biases can occur even when direct male-male battles and physically forced intromission would seem to have left the female no alternatives (Cox and LeBoeuf 1977; Wiley and Posten 1996). This is the standard argument of indirect benefits to the female in a Fisherian runaway, except that it includes the possibility of male-imposed direct losses to the female.

If the gain to the female in terms of improved quality of her sons is great enough, it can compensate for direct losses in terms of numbers of offspring that the male imposes on her own immediate reproduction (Moore et al. 2001; Cordero and Eberhard 2003, forthcoming) and possible reductions in the quality of her daughters (Chippendale et al. 2003). In such a situation, the best overall tactic for the female could be "selective cooperation" (active cooperation with particular males) rather than resistance (see Eberhard 1997, 2002*b*). Whether or how often such a balance of costs and benefits occurs in nature is an empirical question that depends on the absolute values of gains and losses. At present there is no consensus regarding theoretical predictions of the relative magnitudes of these gains and losses (e.g., Cameron et al. 2003; Kokko et al., forthcoming), and the typical short half-life of theories in this field (Andersson 1994) makes confident pronouncements risky. Determining the selective values of female responses to "antagonistic" male traits will require determining both direct and indirect costs and benefits to the female under at least approximately natural conditions (Parker 1979; Andrés and Morrow 2003; Cordero and Eberhard 2003; Kokko et al. 2003; Pizzari and Snook 2003). In sum, the female gain-by-losing argument, which could explain a relatively reduced role for male-female conflict in possible female choice situations, could be applicable under some balances of costs and benefits; whether such balances occur in nature is unknown.

To a limited extent, the "gain-from-losing" argument can also be applied to males. A male that succeeds in fertilizing the eggs of a particularly selective female may, if female selectivity is favored in future generations, stand to benefit from that very selectivity of the female: the daughters he has with that female would tend to be particularly selective. The best mates for a male may be those females that are most difficult for him to induce to mate and to allow him to fertilize their eggs. Nevertheless, probably the most important limitation on the reproduction of most males is access to females and fertilizable eggs, not the quality of his offspring (Parker 1984; Andersson 1994), so this consideration may be of limited importance for most males. It may often be most advantageous for a male to mate with any female available rather than saving his efforts for only higher quality females.

Most of the conflict contexts in table 1 do not have analogous potential gain-by-losing payoffs to the participants because they do not involve such intimate genome mixing. Take, for instance, a cytoplasmic gene that is able to bias the reproductive investment of the organism in which it occurs toward the sex that most effectively transmits cytoplasmic genes to the next generation. This gene

will lose rather than gain reproductively when it is associated with a nuclear genome that is better able to resist such manipulations. Similarly, when a slime mold cell is induced by a genetically unrelated companion cell to differentiate into a sterile stem cell rather than a reproductive spore, it does not gain reproductively if the companion is particularly good at inducing such conversions. A nucleus in a syncytium that is induced by an unrelated nucleus to remain excluded from tissue that will differentiate into reproductive cells does not gain reproductively. A parasite that allows an unrelated parasite to exploit their common host organism more rapidly and completely does not gain reproductively.

Parent-Offspring Conflict and Nondamaging Male Manipulations

Parent-offspring conflicts over parental investment in current offspring do not easily fit the arguments just presented. On the one hand, several types of evidence indicate that conflict in parent-offspring interactions has been evolutionarily important (Trivers 1985; Lessells 1999; Haig 2000). Nevertheless, the gain-from-losing argument could apply to parents under certain conditions. A parent with a particularly manipulative offspring could enjoy increased representation in future generations because this offspring is likely to produce offspring that will be particularly effective manipulators in future generations. Similarly, a q15 queen in a social insect might gain from ceding some reproductive opportunities to workers that are especially good at resisting the queen's attempts to repress worker reproduction under certain quantitative conditions of gains and losses (see West-Eberhard 1983 for a general discussion of social competition of this sort). As with male-female interactions, the outcome is expected to be determined by the quantitative balance between losses (in terms of current reproduction) and gains (through offspring quality that will affect future reproduction). While the elaborate and escalated traits of some parent-offspring interactions (e.g., mother-fetus interactions in mammals) have generally been discussed as examples of conflict (Haig 1993), they could also be favored by selection on parents to bias provisioning in favor of particularly manipulative offspring. Parent-offspring conflict is complicated by the fact that a manipulative offspring will later have to pay a cost for its own manipulative abilities when it becomes a parent and is confronted with its own manipulative offspring. Inactivation via genetic imprinting of genes that produce manipulation in an individual's own offspring is a solution to this problem that has evolved in taxa with large maternal investments (Haig and Westoby 1991; Haig 2000).

This leaves a question. Why might conflict have more evolutionary impact on parent-offspring interactions than on male-female conflict over female selectivity among possible mates, despite the fact that both females and parents share the possibility of gaining from losing? As just noted, the relative magnitudes of gains and losses probably affect the importance of possible conflict in both cases, so perhaps there is a difference in this balance in the two contexts. Precise, biologically realistic measurements of such values are extremely difficult to obtain (and in fact, lack of biological realism in some previous studies where selection was measured only in fruit fly culture bottles weakens claims regarding sexually antagonistic selection in *Drosophila melanogaster*; Cordero and Eberhard 2003). I see no easy answer to this empirical question. I can only offer a tentative hypothesis based on a basic difference between male-female and parent-offspring interactions.

In male-female interactions, male manipulations are ultimately designed to obtain access to the female's eggs, and manipulations that favor the male but do not do direct damage to the female (i.e., reduce her expected numbers of offspring) are probably both feasible and common. For instance, a male may sing or perform visual displays that are effective at drawing the female's attention but have no negative effect on her production of offspring. Nondamaging manipulations of females will also often be more favorable to the male, other things being equal, than potentially damaging manipulations. After all, the male needs the female to propagate his genes. In the parent-offspring context, on the other hand, innocuous manipulations by the offspring of their parents may be less feasible. This is because the offspring's needs (i.e., to acquire resources or protection) are likely to often have direct negative effects on production of other offspring by its parents. More resources going to one offspring will generally mean less resources going to other offspring. Thus, innocuous manipulation by the offspring, which does not negatively affect direct reproduction of its parents, may be less feasible. This could result in a more pervasive evolutionary importance of conflicts between parents and offspring.

Possible Tests

Several empirical questions arise from this discussion that might yield further insights. Do the designs of physiological traits involved in female responses to male seminal products show, in contrast to the morphological traits in the surveys (Eberhard 2004*a*, 2004*b*), indications of being q16 derived from defensive responses (e.g., are they derived from her immune system, as occurs in the female paragenitalia of bugs with traumatic insemination; Carayon 1966)? Are traits expected under sexually antagonistic selection more common in species in which male and female genomes are less completely mixed in their offspring, at

least in the short term (e.g., species with especially low rates of crossing over, especially those in which linkage has a larger effect on the genome because of low numbers of chromosomes)? Does facultative hermaphroditism (removal of a female's strict need of males to reproduce) lead to the expected increase in traits likely to evolve under sexually antagonistic selection? Does selective elimination of the father's chromosomes in male offspring, as occurs in some mites and scale insects (Bull 1983), thus postponing possible reproductive benefits to the female from her mate's manipulative abilities until her grandsons, lead to increased occurrence of traits expected under sexually antagonistic selection? Do males sometimes bias courtship efforts toward females that are especially difficult to convince in order to obtain reproductive payoffs from more selective daughters?

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