Female choice of sexually antagonistic male adaptations: a critical review of some current research

C. CORDERO* & W. G. EBERHARD†

*Instituto de Ecología, Universidad Nacional Autónoma de México, Circuito Exterior, Ciudad Universitaria, Coyoacán, Distrito Federal, México
†Smithsonian Tropical Research Institute, and Escuela de Biología, Universidad de Costa Rica, Ciudad Universitaria, Costa Rica

Abstract

We contrast some recent uses of the concept of male-female conflict, with the type of conflict that is inherent in traditional Darwinian female choice. Females in apparent conflict situations with males may suffer reduced lifetime reproduction, but nevertheless benefit because they obtain sons with superior manipulative abilities. Female defences against male manipulations may not be 'imperfect' because of inability to keep pace with male evolution, but in order to screen males and favour those that are especially good manipulators. We examine the consequences of these ideas, and of the difficulties of obtaining biologically realistic measures of female costs, for some recent theoretical and empirical presentations of male–female conflict ideas, and find that male–female conflict in the new sense is less certain than has been commonly supposed. Disentangling previous sexual selection ideas and the new conflict of interest models will probably often be difficult, because the two types of payoffs are not mutually exclusive.

Introduction

Important theoretical and empirical developments have suggested new interpretations of sexual selection. Some evolutionary phenomena that were previously explained by mate choice or intrasexual competition, may be better explained by coevolution of males and females that result from conflicts of interest between the sexes, in which females evolve to avoid naturally selected costs (e.g. copulations that impose lost time from foraging, increased exposure to diseases or predation, reduced life expectancy) (Rice, 1996; Alexander et al., 1997; Arnqvist, 1997; Holland & Rice, 1998, 1999; Partridge & Hurst, 1998; Rice & Holland, 1999; Johnstone & Keller, 2000; Gavrilets et al., 2001; Moore et al., 2001; Stutt & Siva-Jothy, 2001; Arnqvist & Rowe 2002). Prominent examples are Holland & Rice's (1998) 'chase-away'

Correspondence: Carlos Cordero, Instituto de Ecología,
Universidad Nacional Autónoma de México, Apdo. Post. 70–275,
Circuito Exterior, Ciudad Universitaria,
Coyoacán 04510, Distrito Federal.
e-mail: cordero@miranda.ecologia.unam.mx

model of sexual selection and the sexual conflict model of Gavrilets et al. (2001) that are based on antagonistic coevolution between the sexes. We argue here that when the possible benefits to females of having manipulative sons are included in analyses of sexual conflict models, the model's main conclusions are called into question. Instead of evolving 'resistance' to male antagonistic adaptations, female susceptibility to male manipulations may persist (and evolve) because of the indirect advantage to the female of filtering males according to their abilities to manipulate females; in other words, both the female's degree of resistance and her susceptibility may evolve because of selective female cooperation rather than to male–female conflict. We also discuss how the failure to consider possible female choice benefits in empirical studies documenting sexual conflict has resulted in a lack of measurement of some relevant fitness components. These considerations, together with possible imprecisions in measuring costs and benefits, indicate that further work is needed to determine the importance of male–female conflict in sexual evolution.

What is new in the sexual conflict ideas?

At the outset it is crucial to clarify the meaning of 'conflict' in the phrase male–female conflict, and to distinguish those aspects of the recent ideas regarding conflict between the sexes that are new from those that are not. This is because the classic model of sexual selection by female choice also involves male–female conflicts of interest. A male's interests are best served by fertilizing 100% of the eggs of all the females he encounters. Any female trait that discriminates against one male in favour of another is in conflict with the reproductive interests of the male she rejects.

What is new, and important, in the chase-away and other recent sexual conflict ideas is the explicit (Holland & Rice, 1998; Partridge & Hurst, 1998; Johnstone & Keller, 2000; Gavrilets et al., 2001) or implicit (Alexander et al., 1997) inclusion of additional aspects of conflict that are related to natural rather than sexual selection on the female. Possible direct costs to females from 'antagonistic' male traits include increased mortality because of male seminal products or physical damage, nonoptimal rates of egg production or oviposition, nonoptimal rates of remating, nonoptimal rates of investment in offspring, reduced feeding opportunities, and increased exposure to predation (Chapman et al., 1995; Alexander et al., 1997; Arnqvist, 1997; Holland & Rice, 1998; Partridge & Hurst, 1998; Johnstone & Keller, 2000). In the chase-away model (Holland & Rice, 1998) these costs are expected to result in selection favouring female abilities to counteract the male traits that impose the costs ('female resistance'). Subsequently, coevolution by males to overcome these newly evolved female defences is expected to occur, as a result of selection favouring male abilities to manipulate females. Critics of the chase-away model (Getty, 1999; Rosenthal & Servedio, 1999) did not make the distinction between the types of payoffs that females can obtain when they act counter to male interests; they thus focused on the fact just mentioned that the chase-away model is not novel in predicting increased female thresholds, and neglected the novel reasons that it proposes for the changes in thresholds (Rice & Holland, 1999). Rice & Holland (1999) made this difference explicit when they contrasted previous sexual selection ideas with their new hypothesis regarding the process driving changes: 'obtaining superior genes and/or material benefits vs. intersexual conflict'. Our use of the word conflict in what follows will refer only to the newly considered types of conflict.

Female choice of antagonistic male adaptations

An important omission in conflict models is the possible positive payoff to a female from increased abilities in her male descendants to manipulate females of subsequent generations. By mating with a male who manipulates her, a female could simultaneously both lose fitness because of reduced survival and reproduction, and gain fitness because of her superior male descendants if the male is a particularly good manipulator (Byrne & Roberts, 2000) (also see Kokko, 2001; p. 324, for a similar argument involving 'attractive' instead of 'manipulative' males). Benefits through the quality of the female's sons can be important whether the male's negative effects on the female are a necessary part of the benefits he gains (e.g. damaging the female during mating as a means to induce females to avoid or to delay rematings; Johnstone & Keller, 2000; Crudgington & Siva-Jothy 2000), or whether the male's negative effects are only incidental (e.g. a seminal factor that gives the male an advantage in sperm competition with other males, and that incidentally also has negative effects on female survival; Chapman et al., 1995).

The crucial point is that even if a female's survival is reduced by mating, this does not necessarily imply that her overall fitness was reduced, and it thus does not necessarily mean that conflict between male and female interests was the only factor driving the evolution of the female's reproductive traits. By the same token, a female's direct gains through resisting male manipulations would also be complemented by indirect gains she obtains through having more resistant daughters (B. Holland, pers. comm.). Questions of causality can only be resolved by determining the quantitative balance between female gains and losses that include both direct and indirect effects. (If the net effect on female fitness is positive because of the indirect benefits obtained via male offspring, then terms such as 'male manipulation' and 'damage' are no longer appropriate. However, we use these words to emphasize the contrast between our ideas and other studies on sexual conflicts.) The chase-away and other male–female conflict of interests models are incomplete, because they fail to include the possible positive effects on her offspring's quality that result from a female's biases in determining paternity. A recent theoretical analysis suggested that such indirect payoffs are likely to be small compared with direct ones (Kirkpatrick & Barton, 1997), but noted that more data are needed on the quantities identified as crucial in the model and on direct selection before it will be possible to decide the relative importance of direct and indirect payoffs. In contrast, a recent empirical survey emphasized that the two types of benefits may be of similar magnitude (Møller & Jennions, 2001). Thus the issue of the relative importance of the two types of payoff is not settled, and the possible importance of indirect payoffs should not be ignored.

Generalizing, we are suggesting that female susceptibility to male manipulations may persist despite the existence of female mutants with the ability to counteract these manipulations when females derive an indirect advantage from being partially susceptible to the male (see next section). Female susceptibility to potentially

damaging male manipulations could thus be maintained not as a result of male–female antagonistic coevolution, but by selective female cooperation to obtain high-quality sons (see next section). Again, our basic point is that it is not reasonable to argue that a given trait evolved only as a result of male–female conflict until the possible benefits that a female can derive, through her offspring, from being manipulated by a male are balanced against the direct costs she pays. This idea is not original, and was considered by Parker in a simple genetic model of 'conflict thresholds' (Parker, 1979). Although he found that in his model females may experience an overall gain through their sons by mating with males that have antagonistic traits under certain conditions, this possibility has been virtually ignored by most subsequent authors.

An illustrative conceptual model

A simple model shows how a female could gain from being 'manipulated' by a male. Suppose that (a) males vary in the amount of seminal protein (SP) that they transfer to the female during copulation; (b) that SP has dose-dependent positive effects on both female mortality and on female oviposition rate soon after copulation, before the female is likely to remate and (c) that females do not have any mechanism to counteract the negative effects of SP (we refer to these females as E^0). One possibility is that at time 1, a mutant female (E^1) arises, that produces a small amount of an enzyme that deactivates both effects of SP, and whose action is also dose-dependent and occurs soon after copulation. This mutant can be favoured both by natural selection on females (because of the increased survivorship of herself and her female offspring), and by sexual selection (because E^1 will bias paternity, via higher oviposition rates, in favour of males that produce higher than average amounts of SP, and the male descendants of such males will have increased abilities to manipulate females). Subsequent mutations that gradually increase the amount of enzyme could be favoured for both reasons, until a mutant (E^*) arises which produces an amount of enzyme that optimizes the sum of the advantages from increased survivorship of the mutant female and her female offspring and increased male offspring quality, balanced against the costs of production of the enzyme. The indirect benefits that females obtain through their male descendants depend on the ability of these to manipulate females, and thus depend on the amounts of enzyme produced by the females in the population (i.e. they are frequency-dependent; note that the greater the range of variation in the amounts of SP transferred, and the greater the amount of genetic variation in males that affects this quantity, the greater the indirect benefits to the female from biasing paternity). The most important point is that when indirect benefits are relatively large, E^* will produce an amount

of enzyme that is smaller than the amount necessary to deactivate the largest amounts of SP transferred by males, and it will suffer some mortality because of SP. A female mutant (E^M) that produces the amount necessary to deactivate the largest amounts of SP transferred in the population could not prosper in a population of E^* females, despite her increased survival, because she would be unable to reap the genetic benefits of biasing paternity in favour or males that produce larger amounts of SP.

A second possibility is that at time 1 the mutant E^M arises. If the fitness of E^M is higher than that of E^0, then E^M females will replace all others. If subsequent female mutants arise with lower amounts of the enzyme, they will not be able to invade, because their sons will be unable to manipulate any females in the population. A third possibility is that the initial increase in frequency of E^1 in a population of E^0 is entirely due to increased longevity. For example, if E^1 produces only a small amount of enzyme, the mutant female would have a slightly longer lifespan that might be especially advantageous if it passes some threshold value (e.g. long enough for a second clutch), but she may not produce a perceptible paternity bias in favour of males producing larger quantities of SP. Further mutations that increase the amount of enzyme could eventually result in females that, in addition to having an increased lifespan, produced enough enzyme to obtain indirect benefits. Thus it is possible that an originally antagonistic female trait that evolved because of greater payoffs in male–female conflicts could later evolve to become a selectively cooperative trait due to increased payoffs from intersexual selection.

Quantifying gains and losses in sexual interactions

Many recent studies that have attempted to quantify the costs to the female of sexual interactions with different males and have concluded that male–female conflict is important (e.g. Chapman et al., 1995; Rice, 1996; Arnqvist, 1997; Holland & Rice, 1999; Stutt & Siva-Jothy, 2001) suffer from a second, 'ecological' problem. The measurement of costs and benefits that were made in captivity (typically with unlimited access to food and oviposition sites, absence of predators and parasites, high population densities of similarly aged individuals) are not necessarily appropriate to quantify costs and benefits that would occur under natural conditions where these organisms evolved. For instance, it is not clear whether reductions in female lifespan, such as 29 to 21 days in *Drosophila* (Chapman et al., 1995), or from 147 to 111 days in bedbugs (Stutt & Siva-Jothy, 2001) are of any selective consequence under natural conditions. Perhaps females in nature never live this long, or perhaps if they do they are no longer reproductive. Similarly, the advantage of having sons capable of inducing the female

to lay more eggs during the 2 days immediately following copulation (Holland & Rice, 1999) would be reduced if females in the field are often mated by older males when they are newly emerged and do not have mature eggs (Markow, 2000).

A female's fitness undoubtedly depends on many ecological factors. Demonstration of a cost under the highly artificial conditions of a culture bottle or a constant temperature and humidity chamber is surely not equivalent to demonstrating that such a cost occurs in nature (Eberhard, 1998). The magnitude of this problem may be less in the studies of *Drosophila* than in those of other species, because it is uncertain what conditions should be considered 'natural' for a strain that has spent many generations in culture (Harshman & Hoffmann, 2000a, 2000b; Matos *et al.*, 2000; Ackerman *et al.*, 2001). But even relatively small differences in conditions in captivity can affect selection on such important traits as female fecundity (Ackerman *et al.*, 2001). Presumably some traits in present day lab strains are tuned to conditions in nature, others to conditions in cultures, and still others to neither. Two general conclusions are clear: one cannot make confident statements regarding reproductive costs and benefits to females until both natural and artificial rearing conditions are carefully analysed; and such studies are yet to be performed.

Holland & Rice (1999) responded to some ecological-type criticisms (e.g. Chapman & Partridge, 1996) with arguments that do not really address applicability in nature. They argue that several trends in their data on the effects of monogamy imply that their cost assessments were an appropriate basis for evolutionary interpretations. But their conclusions involving quantification of the impact of increased female oviposition and mortality rates in response to male stimuli in captivity may not be appropriate for the conditions under which female responses evolved. This does not prove that their conclusions are necessarily wrong, only that they were not convincingly demonstrated.

Interpreting studies showing female preferences for males from different populations or taxa

Another type of evidence that has been cited as favouring male–female conflict ideas rather than traditional female choice ideas is that in some species females show less preference for the signals of males with which they normally mate in nature (conspecific males, or males from the same populations) than for those of males with which they normally would not mate (nonconspecifics, males from other populations; Holland & Rice, 1998). But similar preferences could evolve under sexual selection by female choice. If females are exposed to males of differing abilities as stimulators, they will be under selection to filter potential mates so as to get the very best sires. So they are expected to put up stiffer and stiffer

filters, as males get better and better at stimulating them. By having a stiffer filter, a female will be better at obtaining as fathers just those males which are the very best stimulators in her population. In terms of the thresholds of female responses to male stimuli, this can mean that females will evolve to have higher and higher thresholds for responses to male signals designed to induce female acceptance (other outcomes are also possible – for instance pay more attention to particular 'new' stimuli which some males have added to their displays, and less to old ones). Higher thresholds in females will look just like female countermeasures against males of their own population (of course they are countermeasures, but not countermeasures designed to exclude all males as in the new male-conflict models, but only to exclude those males which are less able to stimulate). Thus this type of bias does not constitute convincing evidence that favours the male female conflict hypothesis over traditional sexual selection by female choice (or vice versa).

Conclusions

Male-female conflict over the naturally selected costs to females associated with mating is both feasible and possibly important, but a net cost to the female has not been convincingly demonstrated in experiments with insects. For some of the same reasons, the conflict models of selection are also incomplete. For many male stimuli, females would seem to be free to evolve new response thresholds to male manipulations that either reduce their costs or increase their own benefits (for a specific morphological example see Eberhard, 1998), so the inevitability that females must pay the costs of being antagonistically seduced is by no means obvious. Our examination of male-female conflict ideas and data in combination with classic sexual selection ideas shows that possible benefits to the female from higher quality male descendants will also need to be balanced quantitatively against ecologically realistic costs of mating before it will be possible to evaluate whether sexually antagonistic coevolution is an appropriate model for any given case.

Disentangling previous sexual selection ideas and the new conflict of interests models as driving forces in the evolution of reproductive traits will probably often be difficult. The two types of payoffs are not exclusive. For instance, females that derive a net benefit from mating with manipulative males (through superior sons) may often nevertheless evolve increased resistance to the male's manipulations. A female could derive a naturally selected payoff, such as increased survival, from resisting mortality associated with a male's increased ability to win out in sperm competition (Wolfner, 1997), and at the same time she could derive payoffs from improved offspring quality, because decreased female sensitivity to male manipulations would in effect raise the female's

threshold and make her respond only to males capable of especially potent manipulations. Female reproductive traits thus could be driven by both classic sexual selection and conflict of interests at the same time. The balance may be complex, and the relative importance of different payoffs could change over time. After all, sex is both cooperative and antagonistic (Snook, 2001).

One unfortunate consequence of the recent emphasis on possible male-female conflict is the temptation to try and evaluate whether males or females are 'winning' or 'in control' in this supposed evolutionary arms race (Birkhead & Møller, 1998; Birkhead, 1998; Holland & Rice, 1998; Rice & Holland, 1999). This vision of sexual interactions is misleading, because the influence (control) that results from any given trait in one sex is determined (controlled) by traits in the other sex (Wiley & Poston, 1996; Eberhard, 1998; Getty, 1999). Take, for instance, the popular (though probably seriously misleading; Gomendio et al., 1998) image of a long female reproductive tract that serves as a race course for sperm. Paternity can only be decided by such races if, on the male side, sperm cells are mobile, if they are capable of surviving and swimming in the right direction in the particular chemical milieu that occurs inside the female's duct, and if they have sufficient endurance to swim the length of the duct. However such a sperm cell's superior swimming ability can serve to bias paternity in its favour over other sperm only under certain female-determined conditions, such as the length of the duct, contractions of the walls, currents produced by cilia, and the chemical (e.g. pH) and biotic (e.g. phagocytes) environment within the duct that make swimming ability correlate with fertilization success. Male traits control the effects of female traits, and vice versa. It is the effects of the traits themselves on fertilization that are interesting and useful to study (as, in fact, is clear in the careful description given by Rice & Holland (1999) when they describe what they consider to constitute winning), rather than the nonquestion of which sex is in control.

Acknowledgments

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