

Sexual conflict and indirect benefits

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Abstract

Recent work on sexual selection and sexual conflict has explored the influence of indirect effects on the evolution of female mating behaviour. It has been suggested that the importance of these effects has been underestimated and that the influence of indirect effects may actually be of relatively greater significance than direct effects. Additionally, it has also been suggested that all indirect effects, both good genes and sexy son, are qualitatively equivalent. Here a counterpoint to these suggestions is offered. We argue two main points: (1) it is unlikely that indirect effects will commonly outweigh direct effects, and (2) that there are important differences between good genes and sexy son indirect effects that must be recognized. We suggest that acknowledgement of these distinctions will lead to increased understanding of processes operating in both sexual conflict and sexual selection.

Introduction

Current literature suggests that sexually antagonistic selection may be an important force driving the evolution of costly female mating traits (Parker, 1979; Holland & Rice, 1998; Chapman *et al.*, 2003). It is increasingly common for authors to argue that these *direct* costs to females of antagonistic male adaptations ('manipulative' mating traits) may be more than compensated for by *indirect* benefits that females gain by producing sons that are similarly good manipulators. Notably, this argument has featured prominently in some recent reviews of sexual conflict (Cordero & Eberhard, 2003; Pizzari & Snook, in press). Further, it has been suggested that, once such indirect effects are included into theory on sexual conflict, its '... main conclusions are called into question'. (Cordero & Eberhard, 2003). This reasoning is founded, in part, on recent theoretical work suggesting that such 'sexy son' indirect benefits of female preference

are qualitatively similar to more traditional 'good genes' benefits (Kokko, 2001; Kokko *et al.*, 2002).

Here we offer a counterpoint to the view that direct costs to females of antagonistic adaptations can easily be balanced by indirect benefits, particularly those attributable to sexy or manipulative sons. Our presentation proceeds along two lines. First, we suggest that there are good reasons to expect that the strength of any indirect benefit (be it through increased offspring viability or increased mating success of sons) will be smaller than that of direct benefits (or costs) to female mating behaviour. As such, it remains to be demonstrated that indirect effects impart any significant effect on the evolution of those female traits that determine mating biases. Second, we point out a fundamental difference between indirect benefits mediated through a sexy son mechanism vs. indirect benefits mediated through more traditional good genes mechanisms. In short, sexy son indirect benefits can never play any role in the maintenance of costly female mating behaviour at equilibrium, whereas traditional 'good genes' indirect benefits can (although its magnitude will depend on the relative strength of direct and indirect selection). Thus, theoretical analyses demonstrate that the direct costs paid by

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females who mate with manipulative males cannot be compensated for through the production of sexy, manipulative sons alone. Importantly, much of what is said is already in the sexual selection literature, but we feel that it has not garnered adequate emphasis in recent research on indirect selection and its effects on sexually antagonistic coevolution.

Before going into the details of the above points, however, we first clarify how the terms 'sexy sons' and 'good genes' will be used throughout. We define the sexy son process as the correlated evolution of male trait and female preference resulting from the linkage disequilibrium that naturally arises between female preference and male trait. This occurs because females carrying genes for a preference will, through assortative mating, produce offspring that contain genes for both the preference and the trait (the former being expressed in daughters while the latter is expressed in sons). Likewise if females prefer to mate with males bearing traits that indicate high fitness (genetic quality or condition), then linkage disequilibrium will naturally develop between the preference and fitness. We refer to this latter process as good genes. In both processes, the preference evolves because it becomes genetically associated with another trait that is under selection (i.e., preference evolves through indirect selection). In sexy sons, the associated trait is the preferred male character, whereas in good genes the associated trait is some summary measure of fitness often referred to as 'quality' or 'condition', and assayed as viability. Notably, quality is always under directional selection for greater values, whether or not the preference is present in the population. This is distinct from sexy sons, where selection for exaggeration of the male trait is entirely dependent upon the presence of the preference. Both processes were part of Fisher's original verbal model of preference evolution (1930), despite the fact that sexy son models are often equated with 'Fisherian' sexual selection. He reasoned that some good genes-like process was required to start coevolution between preference and trait, but that a sexy sons-like effect could then become the primary force.

The relative strength of indirect vs. direct selection

There is considerable empirical evidence that direct costs of antagonistic male adaptations to females are often very large (Chapman *et al.*, 2003). One might suppose, however, that indirect benefits might also be quite large or even larger. While this certainly seems possible, to our knowledge there is no literature suggesting that the influence of indirect effects is greater than the influence of direct effects. For example, in one important review of this area, Moller & Jennions (2001) demonstrated that, for a subset of fitness components and species, the magnitude of direct benefits might be only slightly *larger* than the magnitude of indirect benefits, not that these

effects are actually smaller. Moreover, none of the data analysed included examples of sexual conflict where large direct costs are known.

There are also sound theoretical arguments illustrating why such indirect effects are expected to be small relative to direct effects (Kirkpatrick, 1996; Kirkpatrick & Barton, 1997). The logic can be illustrated with a simple quantitative-genetic model of sexual selection. Using standard notation the change in the mean male trait (\bar{y}) and the mean female preference (\bar{x}) can be expressed as

$$\Delta\bar{x} = G_x\beta_x + B_{xy}\beta_y \quad (1a)$$

and

$$\Delta\bar{y} = G_y\beta_y + B_{xy}\beta_x, \quad (1b)$$

where β_y and β_x are the selection gradients on the male trait and female preference respectively, G_y and G_x are the additive genetic variances of the male trait and female preference, and B_{xy} is the additive genetic covariance between x and y . Often the genetic (co)variance parameters are assumed to be constant in such models, but none of our conclusions below require this assumption. The one assumption that is required (and that has been assumed in virtually all theory on this topic) is that the linkage disequilibrium that generates the covariance between male and female characters does not affect the selection gradient. Mathematically, this means that the selection gradients, β_y and β_x , are not functions of the genetic covariance, B_{xy} .

From equation 1a it is evident that any indirect effect on the evolution of female preference associated with the selection on the male trait (i.e., with β_y) must be weighted by the genetic covariance between x and y (i.e., B_{xy}). Under most conditions the additive genetic variance in female preference is expected to be greater than the additive genetic covariance between it and the male trait. Therefore, indirect effects will be scaled by a factor that is less than the factor scaling the direct effects. Thus, even if the strengths of the selection on male and female characters were equal (i.e., $|\beta_y| = |\beta_x|$) the influence of direct effects will be larger. It is important to note here that whether the direct effects of the preference on female fitness in this model are positive (as in direct benefits models) or negative (as in sexual conflict), the same ideas apply equally regarding the relative size of indirect vs. direct effects.

The sexy sons vs. good genes distinction

It has recently been suggested that the distinction between sexy son and good genes models of sexual selection is relatively insignificant since both postulate the evolution of female preferences through indirect effects (Kokko, 2001; Kokko *et al.*, 2002). The indirect effect in sexy son models arises from the production of sons who thus have higher fitness through an enhanced mating success, whereas the indirect effect in 'good

genes' models arises from the production of sons (and possibly daughters) that have higher viability. In either case, it is indirect selection since genes for female mating preferences spread and are maintained by becoming associated (through linkage disequilibrium) with high fitness alleles at other loci (whose effects might be manifested through higher viability and/or mating success). Linkage disequilibrium between preference and male trait is a natural outcome of assortative mating (e.g., Kirkpatrick, 1985), and linkage disequilibrium between preference and 'good genes' is a likely outcome when preferred traits evolve condition dependence, as is commonly the case (Rowe and Houle, 1996). Thus, both types of indirect effects are likely to be common in many mating systems marked by sexual selection or sexual conflict.

Importantly, however, indirect benefits via the sexy son mechanism can have no effect on the evolution of female preference (or resistance) at equilibrium, whereas indirect benefits via a traditional 'good genes' mechanism can. This is not a new finding (e.g., Kirkpatrick, 1985, 1996), but it is one that has gone underappreciated in recent studies emphasizing the similarities between sexy son and good genes processes. One implication of this distinction is that, contrary to the suggestions of recent reviews (Cordero & Eberhard, 2003; Pizzari & Snook, in press), the inclusion of sexy son indirect effects into theory on sexual conflict will have no effect on the predicted evolutionary equilibrium (although it might alter the stability properties of equilibria if the indirect effects are strong enough). This finding was briefly noted in the context of sexual conflict in the appendix of Gavrillets *et al.* (2001). Parker (1979) also considered sexy son effects in a model of sexual conflict, but did not explore their effects at equilibrium.

A simple way to appreciate this fact is to determine the equilibria of equations 1a,b (a model in which indirect benefits are mediated by a sexy son mechanism). If there are no indirect benefits (i.e., no sexy son effects) then the genetic correlation between the preference and the trait must be zero (i.e., $B_{xy} = 0$) and the equilibrium occurs where $\beta_x = 0$ and $\beta_y = 0$. In the presence of indirect, sexy son benefits, there is typically $B_{xy} > 0$ (i.e., there is a positive genetic correlation between the female preference and the male trait). In this situation, equilibrium is still reached only when $\beta_x = 0$ and $\beta_y = 0$, except in the case where the genetic covariance matrix is singular (i.e., when there is a perfect genetic correlation between male and female characters). Given that the genetic covariance is generated (at least to some extent) by linkage disequilibrium, such a perfect correlation will never occur. Thus, although sexy son indirect effects might alter stability properties of equilibria (provided the genetic covariance is large enough; Hall *et al.*, 2000) models that include such effects will have the same evolutionary equilibria as those that entirely exclude them. The thesis that

direct costs of mating with manipulative males can be more than compensated for by the production of manipulative sons is essentially a restatement of this 'sexy son' hypothesis (Weatherhead and Robertson, 1979), but where females 'prefer' to mate with males possessing manipulative traits that reduce their survival and fecundity because such losses are compensated for (at equilibrium) by the benefits of producing manipulative (sexy) sons. The above results reveal an important fault with this logic.

Traditional models of good genes effects typically include three variables: (i) female preference, (ii) male display trait and (iii) condition or viability (see, e.g., Iwasa *et al.*, 1991). As has been well-recognized, some mechanism must be in place to maintain variation in the condition (e.g., deleterious mutation), then, under appropriate conditions (i.e., the so-called handicap conditions) a positive correlation between the male display trait and the male viability trait is expected. Thus the male display trait serves as an honest indicator of genetic quality, and hence females who choose mates with large displays will produce sons (and possibly daughters) with alleles for higher viability.

Although not explicitly stated in the literature, this same type of good genes process can occur within a simpler, two-variable model. Consider the sexy son model of sexual selection, (1) but with biased mutation (Iwasa *et al.*, 1991; similar arguments can be made for the case of gene flow when selection varies spatially; Day, 2000). In this model, the male display trait is subject to biased mutation towards smaller size. In other words directional mutation drives the average male trait in the population towards smaller and smaller values. In the absence of sexual selection, the equilibrium male trait value will be below the natural selection optimum, held in balance between upward directional selection and downward mutational pressure. In this way female preference can evolve through a traditional good genes mechanism because preference alleles become associated with trait alleles that are closer to the male optimum. Mathematically there is

$$\begin{pmatrix} \Delta \bar{x} \\ \Delta \bar{y} \end{pmatrix} = \begin{pmatrix} G_x B_{xy} \\ B_{xy} G_y \end{pmatrix} \begin{pmatrix} \beta_x \\ \beta_y \end{pmatrix} + \begin{pmatrix} 0 \\ -w \end{pmatrix}, \quad (2)$$

where w denotes mutational bias on the male display trait. The equilibrium of this system is reached when

$$\begin{pmatrix} 0 \\ w \end{pmatrix} = \begin{pmatrix} G_x B_{xy} \\ B_{xy} G_y \end{pmatrix} \begin{pmatrix} \beta_x \\ \beta_y \end{pmatrix}, \quad (3)$$

which can be solved for β_y and β_x to obtain

$$\beta_x = \frac{-B_{xy}w}{G_x G_y - B_{xy}^2} \quad \text{and} \quad \beta_y = \frac{G_x \cdot w}{G_x \cdot G_y - B_{xy}^2}. \quad (4)$$

The denominators in Equation 4 are positive, and thus negative directional selection on the female preference at equilibrium, and positive directional selection on the male trait. Notice that the influence of the indirect effects on

the equilibrium declines as the mutational pressure declines, and it vanishes in the limit when w goes to zero. Thus, despite being referred to as a Fisherian model in the literature (Pomiankowski *et al.*, 1991; Day, 2000) and equated with sexy sons, these sorts of processes actually involve a component of what might be better thought of as traditional good genes.

Intuitively, direct selection against alleles for female mating behaviours can be counteracted by indirect selection for them through their association with favoured alleles at other loci, only when the biased female mating preference that these alleles cause (e.g., preference for larger displays, or a greater susceptibility to male manipulation) results in them mating with a male that has above average fitness. In the case of traditional good genes models, this occurs because the maintenance of genetic variation in fitness ensures that females are always able to choose males with higher viability (by using honest indicators in their decision making). In the above case of mutational bias, this occurs because, in the absence of female preference, this biased mutation is deleterious, again providing females with directional preferences the opportunity to obtain mates with higher than average viability (good genes). In both cases mutation not only introduces new genetic variation into the population, but it imparts a directional force on evolutionary change as well.

In the case of the sexy son mechanism, however, once equilibrium is reached, average males have the highest fitness. Those with slightly larger displays obtain an enhanced mating success, but the extra viability cost outweighs this advantage (and vice versa for males with slightly smaller displays). Thus, any directional female mating preference or resistance cannot be influenced by such indirect effects because random mating yields males of higher fitness at equilibrium. In such cases, mutation still introduces genetic variation into the population, but this variation is typically assumed to be unbiased with respect to its effect on the trait.

Given that sexy son indirect benefits can play no role at equilibrium whereas traditional good genes indirect benefits can, how is it that one can view sexy son and good genes processes as two extremes along a continuum (Kokko *et al.*, 2002)? We suggest that the answer has to do with other (often implicit) processes that are included in such models. To illustrate our argument, suppose that equilibrium is reached at which females have some form preference (or resistance) that does not coincide with their directly selected optimum. Now ask the question, what is required for this equilibrium to result from a balance between direct selection and indirect benefits?

For any indirect benefit to balance the direct selection at equilibrium, female preference (or resistance) must result in females obtaining mates with higher than average fitness. There are many ways in which this

might occur, but it is clear that one underlying feature must be in effect: there must be *the appropriate* variation in males maintained such that those with the preferred traits have higher than average fitness. In particular, the maintenance of purely random variation is not sufficient. There must be some bias in the variation that is introduced (or what is selectively favoured must continually change) so that directional female choice can result in mating with males that have higher than average fitness. This is nothing more than a restatement of issues related to the lek paradox. Such variation is much more likely to be maintained in viability or condition related traits than in display or manipulative traits due to their being larger targets for deleterious mutation (Rowe & Houle, 1996), as well as their being under continual directional selection. Indeed, in the absence of some additional evolutionary force such as mutation bias (Iwasa *et al.*, 1991) or gene flow (Day, 2000), male display or manipulative traits will reach evolutionary equilibrium precisely when the average male has the highest fitness. Thus female preference cannot be maintained through such sexy son processes in the face of direct costs since there is then nothing for females to gain by exercising a preference. In contrast, traditional good genes processes typically have some mechanism for the maintenance of the necessary variation as an inherent part of the process (to avoid the lek paradox).

If one is willing to include some additional evolutionary force (e.g., mutation bias) in the sexy son process to maintain the necessary variation, then it is certainly possible for females to gain indirect benefits through the production of sexy sons at equilibrium. It is important to recognize, however, that this occurs only when the strength of direct selection on female preference is very weak relative to the input of variation (e.g., through mutation; Iwasa *et al.*, 1991; Day, 2000). If selection against female preference is strong, then little preference will evolve, and the male trait will reach equilibrium below its natural selection optimum. In this case, the indirect benefit acquired by females with preference then comes from having sons that are closer to the natural selection optimum (i.e., good genes, as described earlier). In this way, provided such additional evolutionary forces are at play, one can move from a situation largely dominated by good genes indirect effects when direct selection on females is strong, through to one dominated by sexy son indirect effects when direct selection on females is very weak. Nevertheless, without such additional evolutionary factors, the outcome of evolution under these two forms of indirect selection is qualitatively different, and this warrants making a clear distinction between the two.

Conclusions

We provide a counterpoint to recent studies that suggest indirect benefits to females will often counterbalance the

direct costs of sexually antagonistic traits in males, and against the increasing trend of treating all indirect effects as equivalent is cautioned against.

To close, we suggest that there are two quite distinct issues at hand in current discussions about this subject.

The first issue is whether or not it is reasonable to try to distinguish the good-genes process from the sexy son process empirically by asking whether the indirect benefit comes from offspring mating success or viability. Our view is that the recent research by Kokko and others (Kokko, 2001; Kokko *et al.*, 2002) clearly illustrates that such approaches are often untenable. For example, good genes benefits, which females may derive from mating with genetically higher quality (condition) males, are typically thought to appear as higher offspring viability (Andersson, 1994; Møller & Alatalo, 1999). However, if individual males can allocate condition from viability to attractive (or manipulative) ornaments, then this high quality could manifest itself as an elevated mating success but reduced survivorship of male offspring. In such cases, a good genes mechanism could easily be incorrectly rejected. These two processes are not mutually exclusive alternatives (e.g., elements of the sexy son process will always occur when there are mating preferences), and natural systems are likely to be much more complex, with both processes interacting with one another. Indeed it is doubtful that male traits conforming solely to the sexy son process occur in natural populations since most traits are significantly affected overall by condition or vigour. This perspective is fruitful in that it emphasizes how an individual's fitness consists of multiple components (e.g., mating success, viability), and how one must consider all such components and allocation decisions among them, when determining whether preferred males have superior genotypes.

The second issue is whether or not the sexy son process (often referred to as the Fisherian process) will have qualitatively similar effects as the good genes process on the equilibrium values of female preference (resistance) and male trait. This is an entirely separate question, and one for which we suggest the answer is no. Mechanistically, one can see the important difference by considering what each process supposes is maintaining the presence of costly female mating behaviour alleles. Under both processes, certain female alleles are costly (selection acts directly against them), but they are maintained at appreciable frequencies because they become associated with alleles at other loci that are beneficial. Under sexy son, however, these beneficial alleles at other loci are beneficial only because of the presence of the costly preference alleles themselves. Their selective advantage depends entirely on the presence of these costly female preference alleles that are in need of explanation in the first place. In a sense, the costly female preference alleles rely on the presence of themselves in other females for their own maintenance. Under good genes this is not true because the beneficial alleles at other loci are beneficial

regardless of which female mating behaviour alleles are present in the population. As a result, it is not surprising that these two processes have fundamentally different evolutionary dynamics and outcomes.

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