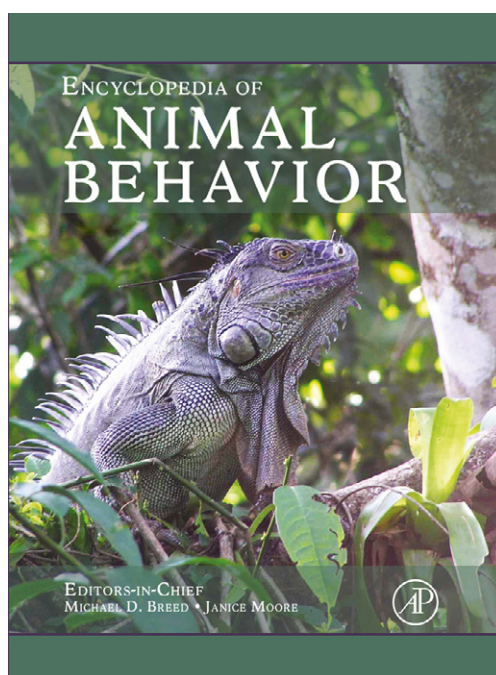


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## Cryptic Female Choice

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Charles Darwin distinguished two contexts in which sexual selection acts on males competing for access to females: Direct male–male battles and female choice. He apparently believed, perhaps because of cultural blinders to thinking about more intimate aspects of copulation, that sexual selection occurred only prior to copulation. He thus thought that a male's success in sexual competition could be measured in terms of his ability to obtain copulations. It is now clear that this view, which prevailed essentially unchallenged for about 100 years, is incomplete, and that males often also compete for access to the female's eggs after copulation has begun. This competition was originally called 'sperm competition' by Parker, but using Darwin's categories, sperm competition is now employed in a more restricted sense to refer to the postcopulatory equivalent of male–male battles; the postcopulatory equivalent of female choice is termed 'cryptic female choice' (CFC) ('postcopulatory' is generally used to refer to all events following the initiation of genital coupling). The word *cryptic* refers to the fact that any selection resulting from female choice among males that occurs after copulation has begun would be missed using the classic Darwinian criteria of success.

The term 'cryptic female choice' was first used in reference to female scorpionflies, which lay more eggs immediately after copulating with large males than after mating with small males (and thus presumably bias paternity in favor of large males). This idea, which is part of a general trend in evolutionary biology to realize that females are more active participants than was previously recognized, is discussed most extensively in two books by Eberhard. CFC has often been invoked to explain the rapid divergent evolution of traits such as male genitalia, as traits under sexual selection are known to tend to diverge rapidly.

In concrete terms, CFC can occur if a female's morphological, behavioral, or physiological traits (for instance, triggering of oviposition, ovulation, sperm transport or storage, resistance to further mating, inhibition of sperm dumping soon after copulation, etc. – see Table 1) consistently bias the chances that particular mates have of siring offspring when she copulates with more than one male. The result is selection favoring males with traits that increase the probability of certain postcopulatory female responses, as they are more likely to obtain fertilizations than others. Male traits associated with such female biases can be morphological (e.g., his genital morphology), behavioral (e.g., his courtship behavior during copulation),

or physiological (e.g., the chemical composition of his semen). There are more than 20 mechanisms by which postcopulatory female-imposed paternity biases can be produced (Table 1), and that have possible example species in which CFC may occur. Some female mechanisms involve the male's genitalia directly (relaxing barriers inside the female reproductive tract to allow the male to penetrate to optimum sites for sperm deposition); some involve manipulating sperm (e.g., discarding, digesting, or otherwise destroying the sperm of some males but not others); some involve her own gametes (e.g., modulation of ovulation, maturation of eggs, oviposition); and some involve postcopulatory investments of resources in particular offspring or resistance to the attempts of other males to mate with her. Still others involve female physiological processes such as hormonal changes that result in ovulation or maturation of eggs. The focus here is on behavioral traits of males and females.

Seen from another angle, CFC is the result of the difficulties that generally confront a male in his attempts to guarantee that the female's eggs will be fertilized by his sperm. He generally needs the female's help, because males almost never deposit their sperm directly onto the female's eggs in species with internal fertilization; it is also typical that the female, rather than the male or the motility of his sperm, is responsible for transporting the sperm on at least part of their subsequent journeys within her body. Similarly, copulation generally does not automatically result in transfer of sperm to the female, and insemination does not necessarily result in fertilization of all the female's available eggs. A male trait that increases the chances that the female will respond in a way that improves his likelihood of fertilizing her eggs can come under sexual selection by CFC. Thus, for instance, male traits that induce the female to permit the male's genitalia to reach that portion of her reproductive tract where his sperm will have the best chances of surviving and fertilizing eggs, or to refrain from ejecting his sperm from her body, could come under CFC.

### Likelihood of Female-Imposed Postcopulatory Biases

Basic morphology suggests that CFC is probably more common than its better known precopulatory equivalent, classic Darwinian precopulatory female choice. Whereas precopulatory competition among males can occur with

**Table 1** An undoubtedly incomplete list of possible mechanisms that are under at least partial female control which could bias paternity if the female mates with more than a single male, and thus exercise cryptic female choice

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Remate?
Remate sooner rather than later?
Mature more eggs?
Ovulate?
Add more or better nutrients to eggs?
Oviposit more of already mature eggs more quickly?
Transport sperm to optimum sites for eventual fertilization?
Store sperm at different site from other sperm to allow selective use (in species with multiple sperm storage sites)?
Allow male genitalia to penetrate deeply enough to deposit sperm at optimum site for fertilization?
Interrupt copulation before male is entirely finished with sperm and semen transfer and courtship?
Flood reproductive tract with antibodies or other defenses against infections that might damage sperm?
Feed or otherwise nurture sperm received?
Kill sperm received?
Discard sperm from previous male?
Discard sperm from current male?
Abort zygotes from former males?
Resist abortion of zygotes from present male?
Allow male to deposit copulatory plug that impedes future insemination?
Produce copulatory plug that impedes future insemination?
Prepare uterus for implantation (mammals)?
Invest more heavily in rearing offspring prior to their birth?
Invest more heavily in rearing offspring following their birth?
Alter morphology following copulation that makes subsequent copulations difficult or impossible?

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relatively little direct female influence, postcopulatory competition between males is generally played out within the female's own body. Even small changes in her reproductive morphology and physiology, such as the volume and chemical milieu of sites where sperm are stored and where they fertilize eggs, can have consequences for a male's chances of fertilization. The multiplicity of the CFC mechanisms is a result of this basic fact, and their large number and often largely independent controls increase the chances that one or more of these critical processes will come to be affected by males. The extreme power asymmetry between the tiny, delicate sperm, and the hulking, complex female, with her extensive array of morphological, behavioral, and physiological capabilities, also emphasizes the likely importance of female choice as opposed to sperm competition among postcopulatory selective processes. Males and their gametes are of course not completely powerless in determining whether or not fertilization will occur; but females are likely to influence the outcome. In an analogy with human sporting events, the female's body is the field on which males compete, and her behavior and physiology set the rules by which competitors must abide and which strategies will be effective. Even small changes in the female can tilt the competition in favor of males with particular traits.

Another reason to think that sexual selection by CFC is an important evolutionary force is that natural selection on many female reproductive traits is expected to easily lead to CFC. Take, for example, oviposition behavior. In most species, natural selection on females favors repression of oviposition until some stimulus associated with copulation signals that the female has sperm with which to fertilize her eggs. Natural selection on females will thus promote the ability to use cues associated with copulation, such as stimulation by the male or his seminal products, to disinhibit oviposition. Once females have evolved this ability to sense such stimuli and to trigger the processes associated with oviposition (e.g., change feeding behavior, search for oviposition sites, move her eggs from her ovaries to her oviduct), then improvements in male abilities to elicit these responses can come under sexual selection by CFC. If a female mates with more than one male, if her oviposition responses to males are not always complete (i.e., not all her mature eggs are always laid prior to mating with another male), and if some males elicit oviposition better than others, then (other things being equal) those males better able to elicit oviposition will outreproduce the others. Once such variant males appear in a population, selection can favor those females that accentuate this bias in fertilization even further. For example, females with higher thresholds for triggering oviposition would tend to lay eggs only after copulating with especially stimulating males, and would be favored because they would produce male offspring better able to stimulate females to oviposit in future generations. Changes in female thresholds, in turn, could set off a new round of evolution of male abilities to stimulate females. Another important consideration is that the polarity of the female responses expected to be favored by natural selection is consistently in the direction favorable to the male (*increase* chances of oviposition, ovulation, and sperm transport, etc.; *decrease* chances of remating, etc.), thus predisposing these female responses to be subject to further male accentuation.

The multitude of possible CFC mechanisms, the theoretical expectations that CFC can evolve rapidly, and the frequent finding that females mate with multiple males in nature suggest that it may also be widespread. Perhaps the most convincing indication that postcopulatory biases are of widespread importance involves the behavior of males during copulation. Male behavior was observed carefully during copulation in 131 arbitrarily chosen species of insects and spiders to determine whether males performed courtship during copulation. Using conservative criteria to define courtship behavior, copulatory courtship occurred in >80% of these species. Such behavior is paradoxical under the usual Darwinian interpretation that male courtship functions to induce the female to accept copulation: why should a male continue to court after he is already copulating? There are also reports of similar behavior in other

groups, including nematodes, birds, scorpions, frogs, fish, reptiles, millipedes, mammals, molluscs, and crustaceans. If 80% is anywhere nearly representative, then female-imposed postcopulatory paternity biases are probably very common.

Nonetheless, the question of the general importance of CFC, like Darwin's idea of female choice before it, has been hotly debated. Because CFC was only recently carefully formulated and publicized, relatively few thorough experimental tests for its occurrence have been performed. Convincing rejections are intrinsically difficult to obtain, because there are so many different postcopulatory female processes that might be involved and that thus must be checked. In addition, it is harder to see what goes on inside a female than to observe precopulatory courtship. It can also be difficult to distinguish CFC from alternative explanations such as sperm competition and sexually antagonistic co-evolution.

### **Sexually Antagonistic Co-evolution: An Alternative Hypothesis**

The benefit that a female is thought to derive from exercising CFC (i.e., from rejecting certain mates as sires) is improved quality in her sons. An alternative explanation for these rejections, which could also lead to rapid divergent evolution, is that the female thereby reduces the effects of male manipulations that damage her reproductive interests. For instance (to continue using the example of oviposition), a male ability to induce the female to oviposit more quickly following copulation could result in the female laying some eggs at suboptimal times or places. It is possible that male effects that originally evolved as means to win in competition with other males also incidentally result in a reduction in the female's reproductive output. Arnqvist and Rowe pointed out that rapid diversification could then result from sexually antagonistic co-evolution (SAC) of males and females, with each sex evolving new mechanisms to counteract recent advances by the other sex. Female evolution to reduce the number of offspring she loses due to this male effect could result in another round of male evolution to increase the ability to induce females to oviposit. Distinguishing SAC from CFC with direct observations is extremely difficult (and impossible in popular lab species such as *Drosophila* fruit flies and *Tribolium* flour beetles, in which natural habitats are unknown, and it is thus not possible to determine the natural reproductive payoffs of different behaviors). In addition, CFC and SAC are not mutually exclusive, and can act simultaneously or in sequence on the same traits.

There are two different versions of the SAC hypothesis. One emphasizes physical coercion by the male, and has been tested by looking for the predicted species-specific

mechanisms of physical or chemical male coercion of the female and species-specific resistance by the female. There is substantial evidence against such races, including the frequent lack of interspecific differences among females that correspond to the differences among males of the same species; a strong trend in allometric scaling of genitalia of insects and spiders that is opposite in direction to the trend predicted by SAC; the lack of the predicted correlation between coercive male mating attempts and rapid divergent evolution of male genitalia; and a general lack of female structures with mechanically appropriate designs for combating or repelling males. There are some female genital structures that mesh with species-specific male genitalia as predicted by SAC, but these are generally 'selectively cooperative' structures, such as pits, slots, or grooves that facilitate male coupling, rather than 'defensive' structures (such as erectile walls or poles that would prevent male coupling). The female structures are selective in that they facilitate coupling only with males that possess certain structures or forms (as expected under CFC).

A second SAC version emphasizes male stimuli which act as sensory traps. The male produces a stimulus that elicits a particular female response; this female response exists because previous natural selection in another context favored such a response to the same (or a similar) stimulus. An example would be the female oviposition responses to male stimuli during or following copulation that, as noted earlier, originally evolved to prevent the female from wasting eggs by ovipositing before she has copulated. By accentuating or elaborating the oviposition-eliciting stimulus, the male could obtain greater or more consistent female responses and thus win in competition with other males that copulated with the same female. But the female could lose offspring because of precipitous oviposition, and thus suffer net damage from the male manipulations.

The sensory trap version of SAC is less easy to distinguish from CFC, because it does not predict defensive morphological co-evolution in females. It seems less probable a priori, however, because it depends on the female not being able to evolve an effective defense against the male manipulation and thus eliminate the costs she suffers in reduced numbers of surviving offspring. Such a female defense would seem to be via easily evolved as a simple change in her stimulus response threshold, or a modification of her tendency to respond to the stimuli depending on the context in which she receives them. It also supposes that the inevitable benefit from a paternity bias that produces sons better able to stimulate females is consistently overbalanced by the male-produced damage, an empirically very difficult condition to demonstrate convincingly.

Of course, a priori arguments of this sort are less satisfying than conclusions based on data. The strongest empirical argument against this version of SAC is again

from genitalia – the lack of the predicted correlation between coercive male mating attempts and rapid divergent evolution of male genitalia that was mentioned earlier. In a survey of many thousands of species of insects and spiders, the male genitalia showed no sign of a trend to diverge more rapidly in groups in which males control (or at least attempt to control) access to resources that are needed by females, and attempt to force or convince reluctant females which arrive to mate in order to gain access to the resources (i.e., in groups in which male reproductive interests are more likely to be in conflict with those of females).

## Male Behavioral Traits Probably Under Cryptic Female Choice

### Genitalic Morphology and Behavior

One of the most widespread trends in animal evolution is that the male genitalia of species with internal fertilization often evolve especially rapidly and divergently. The most probable explanation involves postcopulatory sexual selection, probably CFC. Data on genitalia are especially important and permit powerful tests because they are extremely abundant. This is because the taxonomists of many different groups discovered long ago that genitalia are useful in distinguishing closely related species, and detailed descriptions of genitalia are available in the extensive primary taxonomic literature on many groups.

Much of the diversity in genital morphology is probably intimately related to genital behavior. But genital behavior during copulation and the functional consequences of such behavior are neglected topics, long overdue for further research. Most studies of the functional morphology of genitalia are distressingly typological, often giving 'the' position of the male without taking into account the probability (given their often complex genital musculature) that the male structures move during copulation. Many surprising phenomena (such as the ability to sing to the female during copulation recently documented in a crane fly, and perforation of the female tract with long spines found in some beetles) probably remain to be discovered. Many details of genital behavior are normally hidden inside the female, but direct observations utilizing both copulating pairs and beheaded male insects (thus removing inhibition by the brain of posterior ganglia), and morphological studies of the genitalia of flash-frozen pairs and of muscle attachments and articulations, can give surprising amounts of information. Recent extension of these observations with X-ray imaging can give even more detailed ideas of genital function.

Probably the most complete studies of genital behavior to date with relation to CFC involve tsetse flies. One portion of the male's genitalia remains outside the female's body and delivers powerful squeezes to the tip

of her abdomen that show species-specific differences in frequency and duration. Earlier studies concluded that stimulation from some aspect of male copulation behavior (rather than chemical cues) induced the critical female responses of ovulation and rejection of future males. They were recently confirmed and extended by surgically removing and altering certain male genital structures, and blocking the female receptors contacted by these genital structures during copulation. These manipulations resulted in reduced sperm transport, reduced ovulation, and greater female acceptance of copulation with subsequent males. The morphology of these male structures varies between closely related species, while that of the portions of the female that they contact are uniform, favoring the cryptic female choice explanation over the sexually antagonistic co-evolution explanation for this case of rapid divergent genital evolution.

### Nongenital Male Courtship During and Following Copulation

Male courtship behavior that involves structures other than his genitalia and occurs during or following copulation is common, but also poorly studied. 'Copulatory courtship' behavior patterns include waving, rubbing the female, licking, squeezing rhythmically, kicking, tapping, jerking, rocking, biting, feeding, vibrating, singing, and shaking. If these male behaviors function as courtship, the prediction is that they affect postintromission female responses that increase the male's chances of fertilizing her eggs. Very few studies have tested the prediction.

Tallamy and colleagues studied nongenital copulatory courtship in the cucumber beetle, *Diabrotica undecimpunctata*. The male waves his antennae rapidly over the female's head during the early stages of copulation, when the tip of his genitalia has penetrated to the inner portion of her vagina. If he waves them rapidly enough, the female relaxes the muscles surrounding this portion of her vagina, thus allowing the male to inflate a large membranous sac at the tip of his genitalia and deposit a spermatophore containing his sperm. If she does not relax these muscles, he is unable to inflate the sac and eventually withdraws his genitalia without having transferred a spermatophore. Some females mate with up to ten males before finally permitting a male to inflate his sac and transfer sperm. Females gain superior male offspring by screening males this way, as predicted by CFC. The sons of males which vibrate their antennae more rapidly also tend to vibrate their own antennae more rapidly when they copulate. Studies of three other insects have confirmed that nongenital copulatory courtship induces the female to favor the male's reproduction, by inducing the female to oviposit soon after copulation in a fly, to remain still rather than walking around during copulation in a flea, and to use the current male's sperm rather than that

of previous males in a beetle (the female mechanism was not determined).

Again, there are indications, though less definitive than in the case of genitalia, that nongenital copulatory courtship is not the result of coercive coevolutionary arms races between males and females. Male copulatory courtship behavior is generally noncoercive, and inappropriately designed to force the female to continue copulation or to perform other responses leading to fertilization. Indeed, the sites where most possible female processes occur that could prevent fertilization are deep within the female's body, seemingly inaccessible to direct male manipulation via copulatory courtship.

### Other Male Traits Possibly Under CFC

An apparently widespread trend for seminal products derived from male accessory glands to frequently affect female reproductive processes in insects and ticks suggests selection on male abilities to affect postcopulatory female reproductive processes via chemicals in their semen. Over 70 species have been studied, with the nearly uniform finding that male seminal products induce one or more of the following female responses: oviposit eggs that are already mature; ovulate or otherwise bring immature eggs to maturation; resist further mating; and (less frequently studied) transport his sperm. Such male products could evolve via CFC or SAC. Some studies in *Drosophila* suggest, though not conclusively, that the effects of seminal products may damage female reproductive interests (remaining doubts stem from the question of whether it is appropriate to draw conclusions regarding why given traits evolved based only on data obtained in fruit fly culture bottles).

CFC may affect the evolution of other nonbehavioral male traits, including sperm morphology, sperm proteins, and the egg molecules with which they interact, and CFC may also occur in plants, affecting both the properties of pollen tubes that influence their ability to grow down the style and find the ovules, and the ability of young zygotes to induce the mother to refrain from aborting them.

### Summary

CFC and sperm competition extend the classic Darwinian context of sexual selection to include events that occur after copulation has begun. CFC has been demonstrated in a number of species, and there are reasons to expect

that it can evolve readily. Several types of indirect evidence suggest that it may be a widespread and important evolutionary phenomenon, but there are as yet only a few direct demonstrations that it occurs. Further tests, preferably in a variety of different taxonomic groups, will be needed to determine the generality of its importance.

**See also:** Compensation in Reproduction; Invertebrates: The Inside Story of Post-Insemination, Pre-Fertilization Reproductive Interactions; Sexual Selection and Speciation; Social Selection, Sexual Selection, and Sexual Conflict.

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