

Chapter 1

Cryptic Female Choice and Other Types of Post-copulatory Sexual Selection

William G. Eberhard

Abstract This chapter discusses sexual selection by cryptic female choice (CFC) and other possible types of selection on traits involved in male–female interactions during and following copulation. Morphological, behavioral, and probably also physiological traits all show the typical earmarks of sexual selection: puzzlingly extravagant, apparently non-utilitarian design; and rapid divergent evolution. I discuss ways to attempt to distinguish CFC from other possibilities, and their potential overlap. Differentiating narrow-sense from broad-sense male–female conflict may help clear up some current confusion. The most central differences between the leading hypotheses concern the expected effects of selectively granting paternity on a female’s fitness. Unfortunately, convincing tests of these effects have not been feasible due to technical limitations; published claims regarding such measurements must be treated with caution. Several types of data that provide less direct tests, including defensive designs of females, the presence of female sense organs specialized to sense courtship stimuli from males, physical damage inflicted on the female by the male during copulation, and physical male–female struggles, are discussed. Different types of selection may operate simultaneously in some species, and all may be applicable in particular cases; the major questions concern the relative frequencies of species in which each type of selection occurs. The hypotheses nevertheless provide useful theoretical contexts for understanding multiple aspects of reproductive biology. One promising area for future studies, in which arthropods can provide both experimental and comparative data, is the role of non-genitalic male copulatory courtship structures in stimulating or physically coercing females during sexual interactions.

W.G. Eberhard (✉)

Smithsonian Tropical Research Institute, Panama, Republic of Panama
e-mail: william.eberhard@gmail.com

W.G. Eberhard

Escuela de Biología, Universidad de Costa Rica, San Pedro, Costa Rica

W.G. Eberhard

Biological Sciences and Museum of Natural History,
Louisiana State University, Baton Rouge, USA

1.1 Introduction

Studies of sexual selection broke into new territory with Parker's realization (1970) that the competition among males for chances to fertilize eggs often continues even after copulation has begun. This extension brought Darwin's ideas on sexual selection to bear on a new suite of male–female interactions and offered explanations for many otherwise puzzling male and female traits, such as “post-copulatory” male traits (those brought into play only after copulation has already begun). These often have the typical earmarks of pre-copulatory sexual selection (Darwin 1871): puzzlingly extravagant and apparently non-utilitarian designs; and rapid divergent evolution that often results in species-specific differences, even among closely related species. They include the male's genitalia as well as a multitude of other “contact courtship” structures on various parts of the male body that are also sexually dimorphic and that are specialized to contact females during sexual interactions (Eberhard 1985), and the paradoxical male courtship behavior that often occurs after copulation has already begun (“copulatory courtship” of Eberhard 1994). Still other traits that had not previously been thought to have sexually selected functions include male seminal components that affect female reproductive physiology or that form copulatory plugs, surface molecules on the gametes that are involved in the interactions between sperm and eggs (in animals with both internal and external fertilization); and substances and structures that affect the interactions between pollen and female tissues in plants (Swanson and Vacquier 2002; Swanson et al. 2001, 2003; Karn et al. 2008; Clark et al. 2006; Zigler 2008; Zigler and Lessios 2003; Zinkl et al. 1999; see also Sirot and Wolfner 2015, Chap. 13).

These analyses of post-copulatory sexual selection have spawned a substantial literature that includes several book-length reviews (Smith 1984; Birkhead and Møller 1992, 1998; Eberhard 1985, 1996; Baker and Bellis 1995; Simmons 2001; Arnqvist and Rowe 2005; Leonard and Córdoba-Aguilar 2010), including the present volume. There are several hypotheses for how selection can play a role in the evolution of the morphological, physiological, and behavioral traits involved in post-copulatory events. I will describe these hypotheses and some techniques for distinguishing among them, and then give a brief update of the field and a look into the future.

1.2 Cryptic Female Choice and Alternative Theories Regarding Post-copulatory Selection

1.2.1 *Sexual Selection*

Three classes of post-copulatory sexual selection have been proposed. One of these, cryptic female choice (“CFC”) (e.g., Eberhard 1985, 1996), is the theme of this book. To evaluate the possible importance of CFC, it is necessary to take into account the other two, direct male–male competition (sperm competition or “SC”) (e.g., Simmons 2001) and sexually antagonistic coevolution between males and

females (“SAC”) (e.g., Holland and Rice 1998; Arnqvist and Rowe 2005). Ideally, a discussion of these hypotheses would begin with clear, generally accepted definitions of each. Unfortunately, the hypotheses have changed over time in how they are used, and the oldest criteria for some hypotheses are not necessarily the best. There have also been (and continue to be) widespread applications of terms like “conflict” that employ different meanings and that sometimes stretch ideas beyond their conceptual boundaries (see discussions by Simmons 2001; Jennions 2005; Brennan and Prum 2012; Kokko and Jennions 2014); Kokko and Jennions (2014) have recently advocated combining CFC and SC under SAC *sensu lat.*

I will not try to resolve this apparently intractable tangle (I strongly doubt that there is any set of definitions that would enjoy general acceptance). But there are, however, ways to distinguish CFC from alternative hypotheses which I believe can help guide productive thinking. I will use some examples from other chapters in this book to illustrate this approach.

1.2.1.1 Sperm Competition (SC)

The earliest general discussion of post-copulatory sexual selection was that of Parker (1970), who used the term “sperm competition” to cover all facets. Later authors made the useful distinction (since adopted by Parker) between sperm competition (SC) and CFC, echoing the distinction that Darwin made when he divided pre-copulatory sexual selection into direct male–male combat, and female choice (Table 1.1). SC is now used mostly in this narrower, direct male–male interaction sense. Strictly speaking, SC in this sense does not occur unless temporal and spatial overlap of and interactions among ejaculates from competing males occurs (or potentially occurs) in the female (Simmons 2001). In practice, however, SC is usually expanded to include paternity biases that result from male activities that directly influence the interactions between sperm in the female. SC can occur when a male directly manipulates the sperm of rival males by removing them from the female, packing them into corners in the female, diluting them, killing them, leaving barriers in the female that prevent future inseminations, or removing such barriers. Examples of SC in this book include soldier flies (Barbosa 2015, Chap. 14), depositing and removing mating plugs in Lepidoptera and spiders (Aisenberg et al. 2015, Chap. 4; Andrade and MacLeod’s Chap. 2; Cordero and Baixeras’s Chap. 12; Schneider et al.’s Chap. 3), and sperm removal in spiders and Apachyidae earwigs (Calbacho-Rosa and Peretti 2015, Chap. 5; Kamimura 2015, Chap. 10, Chap. 10).

Table 1.1 Correspondence between Darwin’s categories of pre-copulatory sexual selection and post-copulatory selection via sperm competition (SC) and cryptic female choice (CFC)

Prior to copulation	Male–Male battles	Female choice
During and following copulation	Sperm competition	Cryptic female choice

Selection of the other two types, SI and SAC, can occur both before and following copulation

1.2.1.2 Cryptic Female Choice

CFC, the post-copulatory equivalent of Darwin's female choice, includes paternity biases which result from differences in the expression of female activities (including morphogenesis) that come into play during and following copulation with different males and that favor males which have particular traits over others which lack these traits. The female is thought to benefit from exercising choice among males by obtaining superior sires for her offspring. Historically, CFC was first discussed as such in relation to biases in oviposition following matings with different males in a scorpion fly (Thornhill 1983) (see Birkhead 1998 for brief earlier mentions). Thornhill defined CFC as female-influenced processes occurring during and/or after copulation that bias offspring production more toward one male than other mates (or potential mates) (Thornhill 1983). More than 20 such female mechanisms have been described (Table 1.2; Eberhard 1996, 2010). Chapters in this book add the possibility of storing sperm from different males in different storage sites and then biasing their use, which may occur in a spider (Andrade and MacLeod's Chap. 2), and several interesting possible mechanisms at the molecular level in Diptera (Sirot and Wolfner 2015, Chap. 13). CFC mechanisms include such basic female reproductive process as sperm transport and dumping, sperm maintenance in storage organs, ovulation, oviposition, and acceptance of mating attempts by future males. Increased performance by the female of any one of these processes (e.g., increased sperm transport, more rapid oviposition) as a result of copulating with some males as compared to others can bias paternity. From the male's perspective, any improvement in his ability to induce the female to alter one of these processes in a way that favors his chances of paternity can result in an advantage in competition with other males who mate with the same female. Though not often emphasized, CFC can be affected by male traits sensed by the female prior to the initiation of copulation (during classic, pre-copulatory courtship) as well as by copulatory courtship traits.

A pair of finer distinctions need to be mentioned. Because the sperm competition interactions listed above are generally played out inside the female's body, the effects of the female on the outcomes of many SC interactions could be considered to constitute CFC in a more inclusive sense than I will use here (Arnqvist 2014). Just as in pre-copulatory sexual selection (Andersson 1994; Wiley and Posten 1996), it can be difficult to draw a line between direct male–male competition and female choice. The importance of making distinctions comes not from application of the names per se, but in understanding the reasons why traits evolved (their functions) (Arnqvist 2014).

A second point concerns the evolutionary diversification of males and females expected under CFC. One of the major lessons for sexual selection of studies of the morphology and physiology of different portions of animal nervous system is their extensive interconnectedness. This interconnectedness opens up diverse possibilities to males that are under sexual selection to stimulate females. Not only are there many female processes (>20), but there are likely many different types of stimuli that influence each of these processes. Arnqvist (2014) missed this point when he supposed that CFC on male genitalia would be unable to explain the evolutionary diversification in male genitalia because male "... genital morphology

Table 1.2 A probably incomplete list of possible mechanisms known to occur in species of arthropods with internal insemination by which a female could exercise CFC by varying the intensity of her response to the male, thus imposing paternity biases favoring the current male copulating with (largely after Eberhard 2010)

1. Permit penetration by the male's genitalia deep enough to allow sperm deposition at the optimum site for storage or fertilization
2. Refrain from terminating copulation prematurely
3. Transport sperm to storage or fertilization sites
4. Modify internal conditions (e.g., pH) inside reproductive tract to reduce defenses against microbial invasion that kill sperm
5. Nourish or otherwise maintain sperm alive in storage sites
6. Nourish or otherwise maintain sperm alive on their way to storage sites
7. Refrain from discarding sperm from current male
8. Discard sperm from previous males
9. Move sperm from previous male to sites where the current male can remove them
10. Accede to male manipulations that result in discharge of his spermatophore
11. Grow more immature eggs to maturity (vitellogenesis)
12. Ovulate
13. Produce eggs with more nutrients
14. Oviposit all available mature eggs
15. Prepare uterus for implantation
16. Refrain from removing copulatory plug produced by male
17. Aid male in the formation of a copulatory plug that impedes future intromissions
18. Produce a copulatory plug that impedes further intromissions
19. Modify morphology following first copulation to make subsequent insemination more difficult
20. Refrain from removing spermatophore before all sperm are transferred
21. Abort previously formed zygotes
22. Refrain from aborting zygotes from current sperm
23. Refrain from mating with other males in the future
24. Invest more in caring for offspring

would be fine-tuned to an 'optimal' genital configuration and there would be little selection for morphological innovation ...". Selection on male morphology and behavior could change when new male variants arose that were able to take advantage of the interconnectedness of female nervous systems to cause further positive stimulation of decision centers for potential CFC processes.

1.2.1.3 Sexually Antagonistic Coevolution (SAC)

SAC can result from coevolutionary races between males and females to control one or more of the many processes in the female that affect the male's chances of paternity. SAC occurs when sexual selection resulting from competition among males favors the male's ability to manipulate or influence the female to respond to him in ways that are advantageous for the male but that are disadvantageous

for the female. The disadvantages to the female are related to traits that are under natural rather than sexual selection. For instance, a female might be induced by the male to lay her eggs sooner after copulation ended (before another male might be able to mate with her) and thereby failed to wait until she had found optimum oviposition sites. Natural selection on the female would favor development of traits that reduced these disadvantages by reducing her susceptibility to the male traits. An example of such female changes would be, for instance, waiting longer before laying eggs, or being more selective while searching for oviposition sites immediately following copulation. Such a female change could then reduce the male's ability to influence females and result in a further round of sexual selection on the males to exert additional influence on the female with respect to oviposition. This could result in an endless coevolutionary race between males and females. Such coevolution would explain the typically rapid and divergent pattern of evolution of the traits involved; it could occur in both pre- and post-copulatory contexts.

Male manipulations are likely to be particularly effective in SAC when the male uses stimuli that function for the female in another, non-sexual context, because female defenses against such stimuli are less likely to be as effective. An example of such a "sensory trap" occurs in the fiddler crab *Uca pugilator* (Christy 1995). Females use objects that project above the flat horizon of the sandy beaches as visual markers for possible shelters where they can hide from predators if attacked; they tend to approach such objects while wandering on the beach while sampling courting males. Males build pillars beside their burrows that utilize this female defensive response to draw them near enough for the male to court.

Unfortunately, the more general phenomenon of male–female conflict of interests has often been mistakenly taken to be equivalent to or an indicator of SAC. In fact, conflict of reproductive interests between the sexes is not limited to cases in which SAC occurs, but will occur any time that a female encounters and is courted by a conspecific male but does not permit him to fertilize all of her eggs; male–female conflict is inherent, for instance, in all classic Darwinian female choice situations (e.g., Kokko and Jennions 2014). Thus, male–female conflict over post-copulatory events includes SC, CFC, and SAC. In practice, conflation of male–female conflict with SAC has blurred the distinction between SAC and other hypotheses (below) and has made SAC seem more important than it would have if the different hypotheses were carefully distinguished. Brennan and Prum (2012) make the useful distinction between "narrow-sense" male–female conflict (corresponding to SAC *sensu stricto*, as I have defined it above, and as I will use it throughout this chapter), and "broad-sense" conflict (corresponding to SAC *sensu lato*) in this wider sense that includes sexual selection in general.

1.2.2 Natural Selection Favoring Species Isolation (SI)

One further, naturally rather than sexually selected function that has been proposed for many species-specific post-copulatory traits is species isolation (SI).

Isolation could come about due to mechanical incompatibility between heterospecific pairings (mechanical lock and key), or failure of heterospecific males to trigger essential female reproductive processes (sensory lock and key) (Eberhard 1985; Shapiro and Porter 1989; Simmons 2014). Natural selection on both males and females (especially on females, because of their generally greater investment of time and materials in their gametes and offspring) will favor the ability to avoid wasting these resources as a result of mating with members of other species, because hybrids between species are often selectively inferior in terms of survival and reproduction. SI selection on a female is thought to favor her ability to distinguish conspecific from heterospecific males before her eggs are fertilized (and thus lost) by heterospecific crossing. As in CFC and SAC, multiple pre- and post-copulatory events (accept a copulation or not, transport sperm or not, dump sperm or not, etc.) could be influenced by SI. There are reasons to expect, however, that SI should be most important before copulation begins: it is advantageous to both sexes to distinguish and avoid heterospecific pairings as early as possible in the mating sequence; often this will be before male and female come into physical contact and begin to copulate (Alexander et al. 1997; Peretti 2010). It is nevertheless possible that even when pre-copulatory isolation mechanisms have evolved, post-copulatory selection could still favor additional species-specific, fail-safe devices that further reduce the chances of selectively disastrous cross-specific fertilizations that might result from occasional failures to avoid heterospecific pairings earlier in the mating process. Or it could be supposed (less convincingly) that post-copulatory female discriminations are vestiges of former selection favoring SI, but that have not yet disappeared, even though pre-copulatory isolation mechanisms are now in place (“ghosts of species isolation past”). SI arguments can be confidently rejected, however, as explanations for traits of species that were never in their evolutionary history in contact with closely related species (e.g., cave and island endemics, parasites that mate in isolation from all heterospecific relatives inside their hosts) (Eberhard 1985).

1.3 How to Distinguish Between CFC and the Other Hypotheses

1.3.1 CFC and SC

In some respects, SC is the easiest of the hypotheses to evaluate, because it can be confidently eliminated in many cases in which neither the male nor his semen has direct access to the sperm of rival males. In many of the groups discussed in this book, the traits that are discussed do not involve access by the male or his seminal products to rival sperm. Two additional points need to be made. Failure to eliminate the SC hypothesis is not, of course, conclusive evidence that SC occurs. As already noted, it is sometimes difficult to disentangle SC from CFC (see also Barbosa 2015, Chap. 14; Kamimura 2015, Chap. 10; Sirot and Wolfner 2015, Chap. 13).

For example, SC via dilution of a rival male's sperm by producing larger ejaculates (e.g., Simmons 2001) depends on the design of the sperm storage site in the female, and this can evolve under CFC. By having a voluminous, extensible receptacle (a trait which can obviously vary over evolutionary time, and which could also possibly be altered facultatively by the female in some species by contracting or not contracting particular muscles—see, e.g., Miller 1984, 1990 on odonates), a female can bias paternity via dilution, favoring males with larger volumes of sperm, thus exercising CFC in their favor. The female's body is the playing field on which sperm competition occurs, so changes in a female's morphological, physiological, or behavioral traits can bias the outcomes of SC. In other words, just as there is overlap between direct male–male aggression and female choice in pre-copulatory interactions (e.g., the “passive female choice” of Wiley and Posten 1996), the post-copulatory distinctions between SC and CFC are not always clean. This “female playing field” aspect of SC was recognized early on (Parker 1970), but has been accorded little importance in many (most) discussions of SC.

A second, less well-recognized possibility is that some aspects of SC may produce stimuli that trigger CFC processes. Possible examples include movements during sperm removal, such as the “pumping movements” in some odonates, other movements of sperm-removing structures, and the presence of a mating plug in a female's genitalia. Thus, the seemingly paradoxical presence of “useless” sperm removal penile spines, and the “horns” on aedeagal heads in some odonate species in which the male genitalia do not reach sites in the female where sperm are present (Andrés and Cordero-Rivera 2000; Córdoba-Aguilar 2003; Cordero-Rivera and Córdoba-Aguilar 2010) may be explained as relics of sperm removal movements in which the incidental stimulation of the female eventually came to be the function.

SC and CFC can occur simultaneously, as illustrated by the fact that a male's access to the sperm of rival males is sometimes indirect. For instance, the male of the damselfly *Calopteryx hemorrhoidalis* cannot reach the sperm of rival males stored in the female's spermathecae; but he is able, by rubbing his genitalia against a sensory plate in the oviduct, to induce her to move them to her oviduct, where he is then able to trap and remove them. The male himself actively removes rival sperm, so SC selection has played a role. But the female's responses are biased, as she moves more sperm to the oviduct when the male's penis is thicker, so this aspect of male genitalic morphology is subject to CFC (see Córdoba-Aguilar et al. 2015, Chap. 9). The number of sensory structures in the oviduct plate that the male rubs with his penis is reduced, when compared with the sensory structures of a relative in which the male does not induce females to discard sperm with his penis (Córdoba-Aguilar 2005). This reduction could be due to SAC or to CFC (by reducing her sensitivity, a female under CFC could discriminate more strongly in favor of particularly stimulating males; alternatively, under SAC, she could reduce her reproductively damaging responses to male stimulation).

Proper attribution to the different types of selection in cases like these can be difficult. For instance, in order to adduce a causal role for CFC in addition to that for SC for evolutionary changes in the design of the female's sperm storage

organ in a species in which sperm dilution occurs, one would need to demonstrate that traits of the female storage organ evolved due to the advantage that the female derived from having sons which were particularly effective at diluting rival ejaculates—not an easy task! In general, thorough, rigorous proofs of hypotheses regarding function can be very difficult (Williams 1966, 1997).

1.3.2 CFC and SI

SI has been ruled out pretty convincingly (in my opinion) as a general explanation, at least for the evolution of genitalia. Large accumulations of data in various taxonomic groups do not conform to several general predictions regarding the expected consequences of greater or lesser physical isolation from forming cross-specific pairs (e.g., strict allopatry, host differences in parasitic species) (Eberhard 1985, 2004b). This does not mean, however, that selection for SI can confidently be ruled out for all possible cases. Support for the SI rather than the CFC hypothesis for a particular male trait relies on the supposition that formation of cross-specific pairs is not rare (or, at least, was not rare in the moderately recent past) and that such pairs arrive at the stage in mating when that particular trait comes into play. In some cases, this possibility can be ruled out with reasonable confidence. If species do not overlap both geographically and temporally, heterospecific pairing is not a problem, and selection favoring SI will not occur. Even when there is geographic overlap, SI can sometimes be ruled out. For instance, observation of artificially combined cross-specific pairs in species of the spider *Leucauge* showed that SI selection on the sexually dimorphic male chelicerae, which only come into play after the spiders come into contact, is unlikely: males never even initiate long-distance pre-copulatory courtship and thus cannot be expected to make intimate physical contact with cross-specific females (see Aisenberg et al. 2015, Chap. 4). But in most species strong evidence on this point is lacking. The SI via sensory lock-and-key hypothesis survives some of the types of evidence that weigh against mechanical, lock-and-key SI, but it is also contradicted strongly by some of the others. Thus, it also fails as a general explanation, but must also be considered on a case-by-case basis.

On the other side of the coin, evidence that females reject cross-specific males on the basis of male stimulation, as in the male claspers of *Enallagma* damselflies (Robertson and Paterson 1982; McPeck et al. 2008, 2009), is not sufficient to demonstrate SI. Female ability to make such a discrimination could have evolved under sexual selection, and only incidentally also impede heterospecific pairing. There is evidence favoring a sexually selected CFC function for similar stimulation in another damselfly, *Hetaerina americana*; females grasped (and thus stimulated) with the claspers of a conspecific male lay more eggs when the male releases her (A. Córdoba-Aguilar, personal communication). Similarly, morphological incompatibility of female and male genitalia in carabid beetles (Sota and Kubota 1998; Kamimura and Mitsumoto 2012) is also not sufficient to demonstrate SI by

lock-and-key arguments. In these beetles, the expected evolutionary sequence of genital changes under SI, beginning with females which have erected barriers to heterospecific males being favored, seems not to have occurred, because females suffer mechanical damage when they couple with heterospecific males. The resulting barrier to gene flow appears likely instead to be an incidental consequence of some other types of selection. Evidence of intra-specific uniformity and interspecific differences in genital morphology (McPeck et al. 2008, 2009 on odonate clasping organs) is also unconvincing, because such patterns are not incompatible (as is sometimes claimed) with other hypotheses. Sexual selection does not necessarily imply intra-specific divergence (though this could occur). In addition, there could be divergence in copulation behavior resulting from sexual selection, even when there is no intra-specific divergence in morphology (Eberhard 1985).

1.3.3 CFC and SAC

1.3.3.1 Direct Measurements of Fitness Effects

The crucial difference between CFC and SAC concerns the sizes of the payoffs that a female is presumed to obtain from failing to cooperate with some males. CFC focuses on the possibility that the females gain from favoring some males over others because she obtains sons that will have better abilities to induce positive CFC responses by females in the following generation. In contrast, SAC focuses on the possibility that the female gains from avoiding losses in her naturally selected abilities (in the current generation) to produce offspring. Each hypothesis supposes that the payoffs that accrue from the type of benefit that it emphasizes are greater under natural conditions (where the animals evolved) than those from the alternative type of benefit. In other words, a sexual conflict explanation for a male trait will prevail when the benefit to the female from reducing costs imposed by the male trait is greater than the genetic benefit that the female obtains from acquiring superior genes for that trait in her sons when she accepts some males but not others as sires. Vice versa, the CFC hypothesis supposes that the indirect genetic benefits are larger than the direct, naturally selected costs imposed by the male. The difference between the two hypotheses depends on the relative magnitudes of these quantities.

Unfortunately, it is generally impossible, because of practical limitations, to make quantitative measurements in nature of these two types of variable that are precise enough to compare the relative sizes of these two alternative payoffs convincingly. It seems to me undeniable, for instance, that some kinds of sexual interactions must lower the female's fitness, as in the wounds in the walls of the female's reproductive tract produced by the male genitalia of *Drosophila* spp. (Kamimura 2007, 2010; Yassin and Orgogozo 2013; Masly and Kamimura 2014) and *Callosobruchus* spp. beetles (Crudgington and Siva-Jothy 2000; Hotzy et al. 2012). But the crucial question in these cases of whether the size of this reduction in the fitness of the female is greater or less than the reproductive payoff she

obtains in terms of her sons' abilities to sire offspring under natural conditions remains unknown. It cannot be simply assumed (as is sometimes the case) that just because the female is physically damaged by the male, the costs of this damage are greater than the benefits to the female from his siring her offspring (see B.II below).

Similarly, the elegant studies of Tallamy and colleagues (Tallamy et al. 2002, 2003) demonstrated that a female of the beetle *Diabrotica undecimpunctata howardi* gains from exercising CFC in favor of males that perform superior copulatory courtship (more rapid antennal vibrations) when she relaxes her oviduct muscles and allows the male to inflate his genitalia inside her and transfer sperm only when the male has vibrated his antennae more rapidly. She obtains superior sons, which execute more effective copulatory courtship. Nevertheless, the magnitude of this gain, taking into account population densities and male–female encounter rates in the wild, is not known. Nor is the relation of this magnitude known with respect to the potential costs to the female's reproduction of her rejection of some males (e.g., delay in acquiring sperm due to rejection of some males, metabolic costs of rejection behavior, possible increased susceptibility to predation during copulation). It is possible that the same trait can result in both types of effects on the female's fitness, and selection from SAC and CFC can even sometimes reinforce each other (Cordero and Eberhard 2005). Again, the absolute magnitudes of the costs and benefits are crucial; knowledge of whether or not a cost or benefit exists is not enough. Demonstrating that one type of selection has occurred does not justify discarding the other. Similarly, Arnqvist (2014) points out the difficulty of disentangling selection on putative CFC traits.

An additional, important problem is that even though direct measurements of these variables can be made in captivity, the data are not adequate for testing CFC versus SAC because the captive conditions (e.g., *Drosophila* culture bottles) undoubtedly have large effects on the magnitudes of both types of payoffs. For instance, demonstration that a male seminal product increases the female's oviposition rate and reduces her lifespan in captivity does not solve the question of whether the earlier oviposition does or does not compensate for a reduced lifespan in nature, or even whether females ever live long enough in nature for the longevity effects to manifest themselves (and of course, it also fails to give any indication of whether the magnitude of a possible net loss to the female in ovipositions is or is not large enough to compensate the gains she may derive in nature from genetically superior sons). Or, to balance this comment with a study that arrived at different conclusions, the substantial indirect benefit to females of the cricket *Acheta domesticus*, may balance or overshadow the female survival costs of mating with more attractive males under captive conditions. But despite the authors' care in employing captive conditions at least somewhat similar to those used for immediately preceding generations, doubt remains regarding the ecological realism of these experiments. The upshot of all this uncertainty is that the relative importance of SAC and CFC is very difficult or perhaps impossible to judge by direct measures (see Eberhard 2009, 2010 for further discussion).

Can the controversies concerning CFC be resolved? For the reasons just given, I believe that the jury is out regarding direct measurements of the crucial variables

relating to the central point of the CFC–SAC conflict, the question of whether females gain or lose in total reproductive output (in terms of both quantity and quality of offspring) from particular aspects of their responses to interactions with males in nature; and I believe it is likely to remain out for the indefinite future. The necessary data on female fitness under ecologically realistic conditions are simply too difficult to obtain. I am thus pessimistic regarding measuring the crucial variables that would be required to resolve the theoretical conflicts via direct measurements. Claims that one or the other hypothesis has been definitely confirmed by direct observations of reproductive payoffs should be critically examined in light of the potential problems discussed here.

1.3.3.2 Indirect Tests

One contrast between CFC and SAC concerns the degree of active female cooperation with the male. Under CFC (and classic Darwinian female choice in general), the female will often promote and facilitate pairing and paternity for certain preferred males. Under SAC, females (except possibly virgin females) are expected to resist males until further resistance is more costly than giving in. Thus, CFC predicts, in contrast to the “antagonistic coevolution” of SAC, that there will be “synergistic male–female coevolution” (West-Eberhard 2014). This active selective female cooperation that is predicted under CFC could be manifested in both morphological and behavioral traits.

Female Sense Organs and Responses to Their Stimulation

One contrast concerns the evolution of the female sense organs that receive male stimuli. Under the SAC hypothesis, females are predicted not to have sense organs and responses to stimulation of these organs whose only function is to receive and respond to manipulative stimuli from the male (she would produce more surviving offspring if she received and/or responded less, not more). Rather the male is expected to stimulate preexisting female sensory receptors and to exploit the responses to stimulation of these receptors that evolved to perform other functions for the female; the male takes advantage of this combination of female sensitivity and responses to manipulate her for his own ends (e.g., via “sensory traps”).

Under CFC (and SI via sensory lock and key), in contrast, a female gains from distinguishing among males by modulating her responses to the stimuli that she receives from the male. One mechanism by which such female discrimination could evolve is through acquiring specialized organs to sense particular male signals. Contrary to some discussions (e.g., Arnqvist 2014), CFC is not necessarily expected to be associated with female sensitivities and responses that under natural selection. To be sure, the early stages of the evolution of a male’s use of particular stimuli in CFC would depend on the existence of female sense organs that can sense the male’s signal, and on female responses to such stimulation. But

subsequent evolution under CFC could favor both changes in her responses (e.g., changes in thresholds) and modifications of the sense organs themselves that function to improve her perception of differences in the morphology and behavior of males.

Arthropod species with specialized male contact courtship organs are especially interesting in this context, because it is possible to distinguish specialized female tactile sense organs predicted by CFC and sensory lock and key, such as modified setae (Aisenberg et al. 2015, Chap. 4), campaniform organs (Eberhard 2001), or peg-like basiconica mechanoreceptors (Robertson and Paterson 1982), and to check whether they are restricted to the area contacted by the male's specialized organ. In some cases, these female sense organs might coevolve with the form or behavior of the male contact courtship organs, differing between species in concert with differences in the design or behavior of the male's contact courtship organs. Morphological coevolution of female receptors of this sort is not the only possible female mechanism by which a female could carry out CFC, however; for instance, she could alter her CNS to change the process of analyzing stimuli or criteria for executing responses. Thus, the CFC (and SI) prediction is that sometimes but not always there will be female tactile sense organs specially modified to sense male contact courtship devices.

The existence of specialized female sense organs whose only apparent function is to sense the species-specific stimuli of the male constitutes strong evidence against SAC, which predicts that they will not occur. One possible female receptor organ of this type is the sexually dimorphic, elongate setae on sternum of a female spider (Aisenberg et al. 2015, Chap. 4), but experimental tests of the role of these setae in male–female interactions are still lacking. A more completely studied example is the species-specific arrays of female sensillae on the pronotum, whose stimulation is known to be crucial for copulation to occur in *Enallagma* damselflies (Robertson and Paterson 1982). There are, on the other hand, at least two cases in which species-specific female sense organs of this sort were searched for but do not occur (on the chelicerae of female *Leucauge* spiders, the wings of female *Archiseptis* flies) (Aisenberg et al. 2015, Chap. 4; Eberhard 2001). These data are too sparse to reveal whether there is a general pattern; an extensive SEM survey of male–female dimorphism in tactile receptors in the areas of the female body that are contacted by male courtship devices (e.g., the species surveyed in Eberhard 2004a) would be very interesting.

SAC also predicts that the areas near female sense organs stimulated by males will often show signs of previous coevolutionary conflict; one form would be potentially defensive structures whose designs are appropriate to fend off or protect against male contact courtship devices. Such female structures could be, for instance, erectable spines or retractable covers that would hold the male's structure away from her body (Eberhard 2004a). A concrete example of a defensive structure of this sort (though it functions in a male–male rather than a male–female context) is the set of large flanges on the midline edges of the prothoracic mesostigmal grooves in male (but not female) *Enallagma* damselflies, which probably defend the male from being grasped by other males (Robertson and Paterson 1982).

In addition, SAC predicts that male contact courtship devices should often have designs that are appropriate to increase the male's ability to overcome (push aside, pry under, etc.) such female defenses. In contrast, as explained above, under CFC the female could gain by sensing the male's contact courtship structures, so neither female defensive designs nor male offensive designs to overcome female defenses are expected (though female choice by mechanical fit might sometimes result in somewhat similar designs). Again, female discrimination could also occur via changes in her CNS rather than her morphology, so the predictions of both SAC and CFC are for trends rather than consistent presence or absence.

These predictions were tested in a broad survey of insects and spiders. Contrary to SAC predictions, lack of obvious female defensive designs was the rule (Eberhard 2004a, b). This same lack of apparent female morphological defenses also occurs in a spider and in tsetse flies discussed in this book (Aisenberg et al. 2015, Chap. 4; Briceño and Eberhard 2015, Chap. 15). The recent discovery of subtle female modifications in *Drosophila* associated with potentially damaging male genital structures (e.g., Kamimura and Mitsumoto 2012; Yassim and Orgogozo 2013) (see next section) introduces a note of caution, however, regarding lack of morphological female defenses. In this genus previous reliance on male rather than female genitalia to distinguish species in taxonomic studies (Lachaise et al. 2000) gave a misleading impression of a lack coevolution of female structures that are adjusted to the elaborate male genitalia.

Even when there are female defenses against male-inflicted damage, interpretation of SAC versus CFC is not simple. A female defense does not rule out CFC: females could gain indirectly, through improved offspring quality, by imposing paternity biases with defensive structures. The crucial question regarding function hinges again on the relatively sizes of the costs and benefits. It must also be kept in mind that the predictions concern relative frequencies, not presence/absence. Thus, the SAC prediction is for female defensive structures to be present in some but not all groups, this is because there are other, non-mechanical ways such as changes in the female's CNS for females to overcome male manipulations. In contrast, CFC predicts that female fending-off structures that would prevent males from making contact with the female's sense organs may be rare. The female's best interests would seem to usually but not always be served by evaluating the stimuli from males, not by excluding the male non-selectively from her sense organs (unless the female's choice criterion is the male's ability to circumvent such a barrier).

Physical Damage to the Female

Several types of data have been used in discussions of SAC to argue that male genitalia and seminal products damage the reproductive output of females. Some types of evidence are weak because the male effects on female reproduction have only been measured in captivity and do not deal with the possibility that these effects may be selectively irrelevant in nature; even such basic effects as reductions in life expectancy or total egg production in captivity could be irrelevant under natural

conditions if predation or difficulty in finding suitable oviposition sites impose important limitations (see discussion in Eberhard 2010). Another type of evidence, physical damage to female structures, such as hole in the lining of her reproductive tract due to abrasive or perforating male genitalia or harmful seminal products, is more convincing. Damage of this sort (“traumatic” copulation or insemination) has been documented in various animal groups (summarized in Arnqvist and Rowe 2005; Lange et al. 2013; Masly and Kamimura 2014; Arnqvist 2014; for an additional case in a different taxonomic group, see Eberhard 1992). If such holes in her reproductive tract were advantageous to the female, the expectation is that she would not seal them up again following copulation, as is often the case (Crudginton and Siva-Jothy 2000; Flowers and Eberhard 2006; Kamimura 2010; Yassin and Orgozo 2013). Measuring the magnitude of the damage, in terms of lost offspring, has the same practical problems as do other such measurements in captivity (e.g., the rate of female infections that result from wounds under the typically highly crowded but also otherwise relatively aseptic conditions of captivity may not be representative of those in nature). Nevertheless, it seems reasonable to deduce that the effect of these traumas on the female is negative rather than positive or neutral.

What can be learned regarding SAC versus CFC in species in which females are damaged by males? A recent burst of elegant studies, with especially well-documented details of the morphological interactions between male and female genitalia in several species of *Drosophila* (Kamimura 2007, 2010; Kamimura and Mitsumoto 2012; Yassin and Orgogozo 2013; Masly and Kamimura 2014), offers interesting illustrations of possible evolutionary responses of females to damage. In three of nine species that were checked, there were strong female sclerites (hypothesized to be “vaginal shields”) in areas contacted by the male’s cerci during copulation (Yassin and Orgogozo 2013), as would be predicted by SAC. One other “shield” also occurs on the vulva and another in the uterus (one species each); both are contacted by other potentially damaging male genital structures.

Apparently the male’s cercal teeth do not normally produce wounds, however, in either these or other *Drosophila* species which lack “shields” at these sites (Kamimura 2010). Should one take the presence of possible female defensive structures in some species as confirmation of SAC? Or should their absence in other species in which males have genital structures with spines and pointed processes be taken as refutation of SAC? And what about the likelihood that the female is stimulated by the process of producing this damage (below)? Or the possibility that areas of thickened cuticle have other functions, such as providing as substrates on which the male can tap or vibrate, or as a filter that makes the female less sensitive to stimuli from the male and thus better able to bias her responses in favor of those males which are especially good at producing such stimulation? Surely labeling a female structure with a suggestive term like “shield,” which implies that the function has been established, is not helpful. I am not suggesting that I understand the functions of these fascinating male and female structures. Rather I wish to emphasize that such understanding will require keeping the different possible explanations clearly in mind, and avoiding the temptation to rush to judgment before there is good reason to choose between them.

A similarly open mind is needed to understand the most common type of female “defensive” structures in *Drosophila* spp.—the membranous furrows and pouches of the female tract, where spiny or abrasive portions of the male genitalia rest during copulation (Kamimura 2010; Kamimura and Mitsumoto 2012; Yassin and Orgogozo 2013; Masly and Kamimura 2014). Crosses of female *D. sechellia* with males that had posterior genitalic lobes of different sizes and shapes suggest that these pouches can have defensive effects (Masly and Kamimura 2014), probably because they reduce the force with which the male structure presses against the lining of the female tract and thus reduce the damage that it can inflict. But there are complications with this interpretation. In female *D. sechellia*, smaller rather than larger male posterior lobes were more likely to cause wounds (Masly and Kamimura 2014). In addition, paradoxically, the walls of the female pouches in *Drosophila* are generally very thin and membranous (Kamimura 2007, 2010; Yassin and Orgogozo 2013; Masly and Kamimura 2014); in this respect, the pouches seem designed to *allow* rather than prevent wounding. An effective female defense could be accomplished by a simple thickening or hardening of the portion of wall that is contacted by the male’s genital structure. Perhaps such hardening would make the lining stiffer and thus impede oviposition, a second function of the female reproductive tract. But a small female compensation, such as extending the nearby oviduct wall slightly, would be so simple and cheap that it seems reasonable to expect such a defense. In any case, I do not see how to eliminate the possibility that the pouches represent filters; they could function to allow the female to favor the males that have mechanically compatible lobes (Yassin and Orgogozo 2013), or those that have the greatest abilities to stimulate or penetrate the walls of these pouches.

Finally, it seems that stimulation of the female occurs nearly inevitably, while the male is in the process of wounding her. It is remarkable that a stimulating function has not been considered for these male genital structures in *Drosophila*, nor in those of other insects with abrasive male genitalia such as seed beetles (Hotzy et al. 2012). In the context of possible stimulation, it is also striking that some other *Drosophila* male genital structures are spinous (the aedeagus) or sharply peaked (the ventral branches), but do not make wounds in the female (Kamimura 2010). These structures could serve as stimulators, as hold-fast devices (Kamimura 2010), or both. The lack of transfer of male material through the wounds made by the male genitalia in one species, (*D. melanogaster*) (Kamimura 2010), also favors these possibilities over a “wounding to introduce seminal products into the female body cavity” interpretation, which is more appropriate in other species in which such transfer actually occurs (Hotzy et al. 2012). This transfer function also seems improbable with respect to the perforations produced by the posterior lobes *D. sechellia* (Masly and Kamimura 2014), because these male structures are basal with respect to his aedeagus, which is introduced much deeper into the female and near whose tip the ejaculate emerges. The function of producing perforations in the female is thus not clear in these species, and stimulation has not been ruled out. In sum, the exciting discovery of various types of genital wounds in *Drosophila* spp. (and other animals) presents a complex panorama in which various interpretations in combination with or instead of SAC are feasible.

Male–Female Behavioral Struggles

Another easily misunderstood trait related to the relative importance of SAC and CFC involves using direct observations of physical struggles between males and females. Struggles preceding and during copulation are often taken as indicators that sexual conflict hypotheses should be applied. But this kind of evidence must be considered carefully, for at least two reasons. In the first place, an overt male–female struggle is not a reliable indicator of SAC. Take, for example, the sepsid fly *Archisepsis diversiformis*. The male jumps onto the female at feeding and oviposition sites, usually with little or no preliminary interactions, and clamps the bases of the female’s wings firmly with elaborate species-specific modifications of his front femur and tibia. Almost invariably, the female immediately shakes her body violently, as if to throw the male off. Most mountings (some of which last for 5 min or more) end with the male dismounting after having failed to copulate (Baena and Eberhard 2007). At first glance, this looks like a classic case of a male forcing the female to mate by wearing down her resistance: Stronger, more vigorous males would be able to resist the female’s attempts to dislodge them, and by imposing the cost of staying mounted, eventually force females to mate. But the details of the interaction speak clearly against this interpretation. In those pairs in which mating occurred, copulation generally began within about 30 s of the mounting; in none of the cases in which the male stayed mounted for a long time while the female shook, did he succeed in mating. In addition, video recordings showed that the male was almost never thrown off physically; rather he stepped off of the female during a break in her shaking (Baena and Eberhard 2007). And finally, studies of the genital mechanics of this species (and other sepsid flies, where female shaking behavior is also the rule) showed that the male is physically incapable of forcing his genitalia into the female’s body. At nearly all times during a female’s life, the distal-most segments of her abdomen (her “proctiger”) rest on the dorsal surface of her vulva, covering the opening to her reproductive tract. In order for a male to achieve intromission, the female must first lift her proctiger, allowing him physical access to her vulva. The male has no genital structure capable of prying up this female “door,” so he must rely entirely on active female cooperation to gain intromission (Eberhard 2002). In sum, copulations in this species are not reasonably attributed to the male overcoming female resistance, despite the forceful male–female struggles that consistently precede copulation, and the timing of her cooperation shows that it is not appropriately attributed to physical coercion by the male. Rather copulation results only in those cases in which the female cooperates actively with the male.

The inverse problem also exists: lack of overt female resistance is not a reliable signal of lack of male–female conflict (Kokko and Jennions 2014). For instance, as noted by Arnqvist and Rowe (2005), sexual conflict can be “hidden” when male and female interactions are evenly balanced. One illustrative image is the static pose of evenly matched arm wrestlers, who are fighting intensely but hardly moving (Jennions 2005). I would argue, however, that this limitation is not always severe, because of the potential power of resolution of well-focused, detailed

behavioral observations to resolve questions of this sort (Peretti and Córdoba-Aguilar 2007). It would be easy, for instance, to discriminate a photograph of a true, evenly matched arm wrestling battle from photographs of “battles” in which the participants’ arms were linked but their torsos were not positioned appropriately to apply force to the opponent, or their legs were positioned inappropriately (e.g., legs were crossed) and did not give support and power to the torso and arm. In the same way, additional details of male–female interactions can sometimes be used to evaluate the SAC prediction of a history of male–female coevolution. One type of indirect evidence of SAC would come from the mechanical designs of females. Females should show signs of having evolved previous defenses against males, while the species-specific traits in modern males should be designed to enable them to overcome these female defenses (see Eberhard 2004a).

This technique for evaluating these SAC predictions has at least two important limitations. Firstly, recognizing the “defensive” nature of a design in the female is not always easy, because the effectiveness of a defense depends on the design of the males (see the discussion of female pouches and male genital spines in *Drosophila* above). Secondly, a female’s defense may sometimes occur in her nervous system rather than in her external morphology, as noted above. This type of defense leaves no easily read vestige in the behavior or external morphology of the female. Nevertheless, there are general classes of relatively inexpensive and effective defensive structures (e.g., derived, moveable devices that can cover the portion of the female that needs to be defended when she is accosted by a male), and they should be common under SAC. The data on insects and spiders clearly do not fit this prediction. Female devices with designs appropriate to facultatively protect areas of the female’s body that are contacted by species-specific male “copulatory courtship structures” seem to be rare (Eberhard 2004a); the most common female characteristic in a survey of 106 structures in 84 taxonomic groups was a complete lack of any possibly defensive female structure (seen in 54 % of the groups). This argues against the generality of SAC.

1.4 The Current State of Affairs

It is now clear that post-copulatory interactions between a female and the male and products from the male have important impacts on the relative reproductive success of males, and result in sexual selection. No single-species study will be enough to resolve questions regarding the importance of CFC relative to alternative hypotheses for explaining post-copulation events (e.g., Arnqvist and Rowe 2005; Jennions 2005). SC surely exists in some cases, though the possible additional role of CFC in these cases has generally not been explored adequately (see Kamimura 2015, Chap. 10; Sirot and Wolfner 2015, Chap. 13). SI via mechanical lock and key is surely not a generally applicable explanation of genital diversity, but nevertheless, it cannot be ruled out a priori, and cases must be examined one by one. SI via sensory lock and key survives some of these types of evidence, but not others, so is also an

unlikely general explanation but must be tested case by case. The greatest uncertainty surrounds the controversy between CFC and SAC interpretations. To judge by perusing the literature and scanning titles in recent congresses, conflict-based interpretations appear to have prevailed in the minds of many. At a very superficial level of analysis, this emphasis is reasonable: “broad-sense” male–female conflict (Brennan and Prum 2012) is almost trivially true for male–female interactions in nature. Male and female reproductive interests are seldom identical.

At the more interesting narrow-sense level of conflict, however, I believe that the controversy between SAC and CFC has not been resolved. It is possible that the selection on males to win out over other males has produced profound conflict between the sexes, favoring traits that inflict damage to the female’s naturally selected reproductive interests, and that the most important payoff to females from rejecting some males is from avoiding this damage. It is also possible that the most important payoff to the female is obtaining superior survivorship or signaling genes for her offspring and that many cases of apparent male–female conflict are better understood as selective female cooperation with some males but not others. I thus believe that the current popularity of conflict-based hypotheses is largely due to a lack of appropriate analyses. The fact that both kinds of selection could act simultaneously on the same trait and that different traits of the same animal could evolve due to different types of selection (Cordero and Eberhard 2005; Kokko et al. 2003; Kokko and Jennions 2014; Barbosa 2015, Chap. 14) emphasize the likelihood that different hypotheses are correct in different cases.

1.5 Peering into the Future

Perhaps a little simplified history can help illuminate the future. I believe that this book marks a typical “middle age” in the ontogeny of a possibly fruitful scientific idea. CFC was born as an extension or refinement of the transformative realization of Parker (1970) that sexual selection can occur even after copulation has begun. The basic addition of CFC to Parker’s original insight is that female choice can occur in many different forms after copulation has begun, in addition to direct male–male battles via sperm competition.

The first general discussions of CFC and its derivatives (Thornhill 1983; Eberhard 1985, 1996) were based mostly on suggestive evidence that had been collected in other contexts (as also occurred in early discussions of SC and SAC—Arnqvist and Rowe 2005; Jennions 2005). Some early doubts regarding CFC (e.g., Møller 1997), emphasized this inevitably incomplete and “cobbled together” nature of much of the evidence. The obvious way to evaluate such doubts was (and is) to gather further observations, using techniques and experimental designs specifically designed to test both the criticisms and the hypothesis itself.

The first general presentations of CFC were convincing enough to earn the hypothesis a place in the standard list of possible explanations that are currently proposed by specialists in the field with respect to post-copulatory selection

(it is sometimes less thoroughly explored than some other hypotheses, however—see Eberhard 2012). Nevertheless, the acceptance of CFC at a more general level among evolutionary biologists has lagged behind. For example, CFC is still a very poor sister to SC and SAC in one large recent evolution textbook (Zimmer and Emlen 2013), where it is not even mentioned in the index.

Some of this neglect is probably related to the recurrent “amnesia” among biologists in thinking about the importance of social rather than environmental factors in sexual selection, and the reasons given by Darwin to distinguish between sexual and natural selection (West-Eberhard 2014). CFC, in contrast with SAC and SI, has a relatively weak logical connection with the ability of the animal to deal with its external environment. For instance, the size of a male’s genitalia, a likely candidate for the action of CFC (Eberhard 1985), shows relatively little response in size to changes in nutrition; male genitalia are likely to be poor signals of a male’s size or health (Eberhard et al. 1998; Emlen et al. 2012). The male copulatory courtship behavior that is favored by CFC by females in the beetle *Diabrotica undecimpunctata howardi* has no perceptible association with hatching rate, survivorship, developmental rate, size, age at first maturity, or fecundity of the offspring, but is nevertheless correlated with the copulatory courtship behavior of her male offspring (Tallamy et al. 2003). In general, undue emphasis on natural rather than sexual selection can lead one to miss the importance of sexually selected payoffs.

Another possible problem for general acceptance of CFC may be its emphasis on the female’s sometimes potentially invincible powers to control post-copulatory sexual events, in contrast to the perhaps more intuitively appealing views of male control (SC) or male–female battles over control (SAC). In his book on sperm competition, for instance, Simmons (2001, p. 279) doubted even the possibility of sorting out male and female effects: “Interpretations of male versus female control can rarely be more than a point of view, neither of which can be said to be right or true.” This seems to me to fly in the face of common sense. A male may, in the end, have little or no ability to impose his own reproductive interests after he has done all he can in terms of courtship, seminal products, etc. If, for instance, the female nevertheless fails to open up her reproductive tract for him and he has no morphological structure with which he can force his way in (Tallamy et al. 2002; Baena and Eberhard 2007), or if she unceremoniously dumps his ejaculate from her body as soon as he withdraws his genitalia (for an easily intuited example, see Baker and Bellis 1995 on humans), she will have the decisive last word (see also Kokko and Jennions 2014).

Conclusions drawn from incomplete tests of CFC are still another problem. Take as an example a case that is deservedly well known, in which exquisitely fine experimental modifications were made of the spines on one male genital structure (the ventral cercal lobe) of *Drosophila* flies (Polak and Rashed 2010) that grasps the female oviscapts (Eberhard and Ramirez 2004; Kamimura and Polak 2010). The conclusion that these structures do not function to influence CFC, on the basis of the lack of any effect of removing this genital structure on whether sperm is transferred and is or is not used preferentially with respect to the sperm of other males in the same female, failed to take into account many other possible mechanisms of CFC (increased resistance to further mating, greater numbers of eggs matured and

laid after copulation before another copulation, reduced delay in laying eggs already mature, etc.). CFC, because of the multitude of possible mechanisms by which it can occur, is an especially difficult hypothesis to test experimentally.

Whatever the reason for lingering doubts, future resolution of the question of whether CFC is of wide general importance will be determined by the accumulation of relevant data that test the predictions that CFC and rival hypotheses make. Perhaps the major role of the present book is to show that a surprising amount of scattered observations have accumulated in which CFC was specifically tested and supported. The current book complements another recent, taxonomically more wide-ranging compilation (Leonard and Córdoba-Aguilar 2010). It is especially interesting to see the applicability of these ideas at the level of molecules and genes (Sirot and Wolfner 2015, Chap. 13). The difficulties in resolving the relative importance of different theories that were discussed above do not mean that there are not exciting new directions for empirical study of the phenomena that these theories aspire to interpret. In fact, as noted by Jennions (2005), perhaps the greatest payoff from these controversies will be to provide motives for studying exciting topics in reproductive biology in the context of testing theories, rather than simply describing esoteric phenomena.

I will close by emphasizing one topic that I find particularly promising, that of “non-genital contact courtship devices” in arthropods (Fig. 1.1) (Eberhard 1985). These are mentioned in several chapters in this book. They are male structures that are specialized to contact the female on her outer surface, and they often bear the typical signatures of sexual selection: puzzlingly ornate designs that are not obviously functional, and rapid divergence between closely related species (Eberhard 1985, 2004a). I believe that these structures hold special promise for improved understanding of sexual selection in general for several reasons. The sense organs that females use to perceive male tactile stimuli are located at specific, spatially localized sites on her body, and they probably often function more or less exclusively in the single task of sensing the male. The sites of these female sense organs are easily determined in many arthropods and can thus provide insights into female choice criteria in different species (e.g., Robertson and Paterson 1982). The numbers and locations of female tactile sense organs can be compared to see whether they mirror differences in the sizes, shapes, and locations of male contact courtship organs in these species. And in each species, the female’s sense organs can also be compared with the homologous tactile sense organs of conspecific males. Do females evolve special receptors to sense the species-specific aspects of male contact courtship structures (as is expected to be common under CFC, but not under SAC)?

Furthermore, it is often possible to experimentally mask or cripple the particular female tactile receptors that are sensitive to male contact courtship stimuli, impeding the female’s ability to sense the male but leaving her otherwise intact and able to respond normally to most other stimuli. Such selective blinding of the female to the male’s tactile charms has powerful effects in tsetse flies (Briceño and Eberhard 2015, Chap. 15), an orb-weaving spider (Aisenberg et al. 2015, Chap. 4), and a sepsid fly (Eberhard 2002). When combined with experimental alterations of the corresponding male morphology, strong conclusions can be obtained with respect to function.

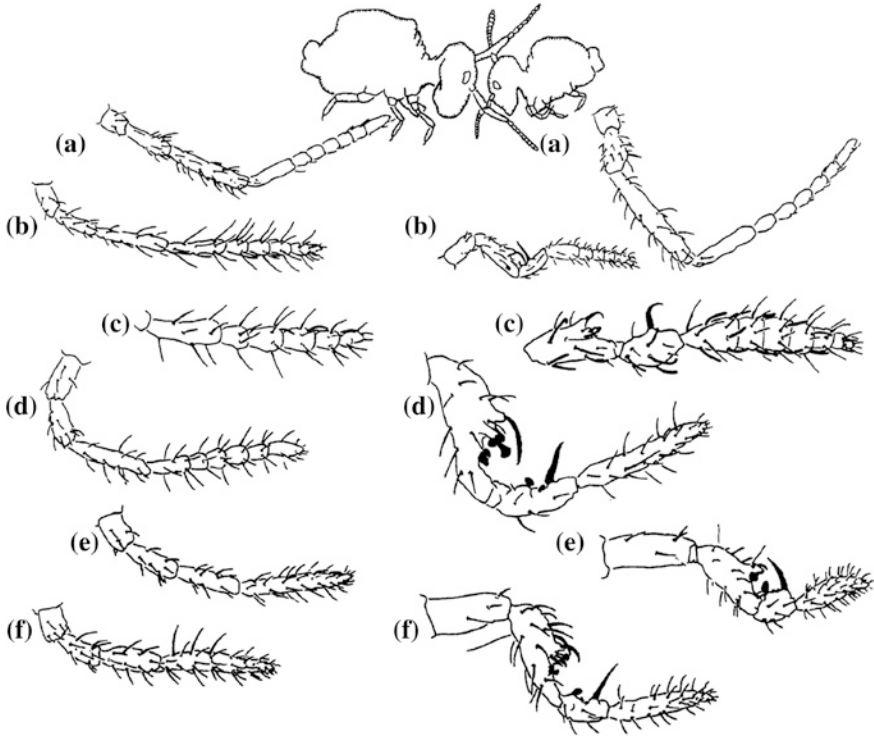


Fig. 1.1 An illustration, in the male contact courtship organs in symphyleona collembolans, of the common trend for females to lack morphological adjustments to the species-specific modifications in male structures. The male uses the basal segments of his antenna to grasp the female's antennae (*upper drawing*). In each pair of drawings below, the female antenna is on the *left*, and the male on the *right*. **a** *Bovicornia greensladei*, **b** *Yosiides himachal*, **c** *Smithuridia sphaeridioides*, **d** *Debouttevillea marina*, **e** *Denisiella* sp., **f** *Jeannenotia stachi*. The lack of differences in the female antennae that correspond to the differences in the male antennae is not in accord with predictions of the mechanical lock and key species isolation or sexually antagonistic coevolution hypotheses concerning coevolution in female morphology. *Upper drawing* after Mayer (1957); *lower drawings*, to different scales, after Massoiud and Betsch (1972)

The study of non-genital contact courtship devices is especially feasible in arthropods, because many of their surface tactile sense organs—setae and cuticular stress sensors such as campaniform organs and lyriform organs—are easily seen and can be easily masked or inactivated experimentally in highly specific ways. A survey of such female-specific sense organs among closely related species (as in Robertson and Paterson 1982), combined with a known phylogeny and experiments to determine the effects of experimental “blinding” females (e.g., Krieger and Krieger-Loibl 1958 on damselflies), could yield exciting insights into the evolution of post-copulatory sexual selection, and sexual selection in general.

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