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Sexual Conflict in Nonhumans



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what the important variables are that shape the way in which it is expressed (and can be measured). We subsequently analyze the causes of sexual conflict following Tinbergen's four questions, with a special emphasis on the ontogenetic level, the latter with the specific aim to provide a more integrative view of sexual conflict and its evolution.

Synonyms

[Conflict between the sexes](#); [Precopulatory sexual selection](#); [Postcopulatory sexual selection](#); [Sexual selection](#)

Definition

Sexual conflict is the disagreement over investment that ensues because males and females adopt or develop strategies that are only aimed at increasing their own fitness, but that impose a cost on the mating partner.

Introduction

Males and females differ in their reproductive investment, resulting in what is called “sexual conflict”. In this review we start by offering a brief description of what sexual conflict is and

What Is Sexual Conflict?

Tregenza et al. (2006) noted that there is no clear or widely accepted definition of sexual conflict, pointing out that “biologists are often reluctant to commit themselves to narrow definitions of concepts” in order to avoid limits in their thinking (p. 229), something that can be easily verified when looking at different publications on sexual conflict in which no definition whatsoever is provided. However, we consider that providing a definition, even if it is tentative and subject to future modifications as research progresses, is the very first step for constructing a solid theoretical framework in any research field. In the few papers on sexual conflict where a definition is adopted, authors most commonly cite what was put forward by Parker (1979, p.124): sexual conflict is “a conflict between the evolutionary interests of individuals of the two sexes.” Although this definition serves as a good starting point for evolutionary questions, we feel it is not

completely accurate since males and females do not have themselves evolutionary interests as such but rather individual interests with evolutionary consequences. Moreover, the interest of males and females when they mate is actually the same: obtaining the highest benefits with the lowest costs (i.e., maximum fitness). One way to increase one's reproductive fitness is by developing different strategies that increase the likelihood of being chosen by a given partner or by adopting high-quality mate-choice criteria, which result in what is called intrasexual competition for mates (e.g., males competing for access to a female) and mate choice mechanisms. Yet another possibility to increase one's benefits while keeping costs low is to induce the other partner to increase his/her investment. Such a strategy will then imply a cost for the partner, who is expected to counter-adapt to avoid being manipulated. These two possibilities lead to two different types of conflict: one among subjects of the same sex, which is generally referred to as intrasexual competition, and the other one between the two mating partners, which represents actual sexual conflict. It is crucial to note here that the two can be intricately intertwined, making it difficult to disentangle them fully (see Brennan and Prum 2012).

Thus, sexual conflict is the disagreement over investment that ensues because males and females adopt or develop strategies that are only aimed to increase their own fitness but that imposes a cost on the mating partner. In other words, what is beneficial for one is detrimental for the other. Such conflict stems from the unequal or differential investment in reproduction of a particular male and female when they mate. This differential investment is already seen at the very early stages of the reproductive cycle due to the fact that the cost of producing gametes is assumed to be different between males and females, which finds its origin in anisogamy (see Table 1; Schärer et al. 2012). Due to differences in gamete size, the production of eggs is generally considered to be more costly than the production of sperm, and consequently, for females, reproductive success is limited by their capacity to produce eggs, whereas for males, reproductive success is more dependent on their access to females (e.g., see

Arnold (1994) for a review but see also Janicke et al. (2016) for a meta-analysis on the selection pressures suffered by males, which are stronger than those suffered by females, potentially equating the costs experienced by both sexes). This difference in the costs of gamete production entails a difference in the benefits obtained per unit of energy invested that does not allow males and females to reach their optimal reproductive fitness simultaneously (Parker 2006). As a result, any trait that increases males' fertilization success will be selected even if such a trait implies a cost for their female partners. The conflict then arises because the strategies that males employ to increase the investment of females are actually decreasing the reproductive fitness of females. Of course, the development of manipulative mating strategies is not exclusive to males, as females also contribute to this conflict by evolving their own mechanisms that lead to increases in male investment and a reduction of their own costs (e.g., Chapman et al. 2003). To give one classic example, a male's paternity success will be significantly increased if he manages to prevent the female he has mated with from remating with other males (e.g., via mate guarding). This will secure his paternity, but at the same time, it implies an important cost for the female in that she will lose future opportunities to mate with other males. Under that particular scenario, females are expected to develop other strategies that will allow them to somehow avoid the costs of such mate guarding. This adaptation of the females would not benefit the males and would again lead males to counter-adapt and so forth. Hence, the conflict between the individual interests initiates a process of adaptation and counter-adaptation to the strategies employed by one sex and the other that, over time, results in a continuous evolutionary arms race between the sexes (e.g., see Koene 2012). It is important to note that there are some authors who have criticized this view and instead suggest that mating should be seen as cooperative rather than as a conflict (e.g., Cordero and Eberhard 2003). These authors claim that, for example, females actually increase their fitness from mating with males that are able to manipulate them because they will sire sons

Sexual Conflict in Nonhumans, Table 1 Definitions of important psychological and biological concept that we use in the text but that may not be familiar to readers of either field of research

Definitions	
Circular reaction	Repeated display of a basic sensory-motor schema (that animals are born with). It allows animals to interact with the environment and to satisfy their needs, but, as a result of repetition, the schema is modified, resulting into a new one. The new schema will again affect the way an animal interacts with and alters its environment, as well as the schema itself
Anisogamy	Size difference between the types of gametes; generally, females produce large gametes that are usually non-motile (eggs or ovules), and males produce smaller gametes that are often motile (sperm or pollen)
Accessory gland substances/products/proteins	Products of (male) accessory reproductive glands, usually peptides or proteins. They can be transferred to the mating partner during sperm transfer (along with the sperm) or disassociated from sperm transfer (e.g., via injection using a specialized organ). These substances are also referred to as seminal fluid products/proteins (SFPs) when they are added to the sperm before transfer of the semen (i.e., sperm plus SFPs)
Allohormones	Substances, such as proteins and peptides, that are transferred between individuals of the same species and that induce a direct physiological response, bypassing sensory organs
Organic selection	Organic selection refers to the fact that each individual has the ability to accommodate to the new circumstances of the environment, contributing to its own selection. This is also referred to as the <i>Baldwin effect</i> (i.e., changes in behavior affect reproductive success and adaptation but it does not necessarily imply a change in the genome)

that will also be able to manipulate next-generation females (and the same would be true for males who mate with manipulative females). From this perspective, sexual reproduction can be viewed as a cooperative task where males and females have a common goal that is to obtain better-quality offspring. However, we will here stick to the term “sexual conflict” as it allows us to refer to manipulative traits that are initially harmful for the other sex although they may become beneficial in the long run (see also Brennan and Prum 2012).

Who Is Involved in the Conflict?

Although sexual conflict arises from the different interests of males and females, it can involve more participants than just a male and a female. Generally speaking, it could be argued that as long as there is polygamy, more individuals than just the mating couple will be affected by sexual conflict. In the case of polygamous males, multiple mating can have different costs for the female. For

example, males may be sperm-depleted, which could lead to a lower fertilization rate or they may reduce parental care (because they are busy somewhere else) compromising the survival of the offspring. Similarly, polyandry (i.e., a female mating with multiple males) is costly for males: the costs of producing sperm and other accessory gland substances will be high when considering that paternity will be shared with other males (see Parker and Birkhead 2013 for a review on polyandry). In this case sexual conflict is tightly related to intrasexual competition and mate choice, which does not only occur before mating but can also happen after mating (i.e., post-copulatory). For example, when a female mates with more than one male, sperm of different males will compete for the fertilization of the ova, and the female can exert a choosy role over the sperm received, reducing the benefits of some of the males she had mated with. This *cryptic female choice* can be inferred, for instance, by looking at paternity biases in her offspring or by looking at the differential reproductive investment that the female performs (see Chapman 2006 for a brief

comment on this). One example of such cryptic female choice that leads to sexual conflict can be observed in the female decorated cricket (*Gryllodes sigillatus*). In this species the male transfers a spermatophore (an ampulla that contains the sperm) that is covered by a gelatinous substance called spermatophylax. The female detaches the spermatophylax from the spermatophore and eats it right after copulation has taken place. Once she has eaten it, she removes the spermatophore and thus sperm transfer is terminated. This allows females to bias paternity: the longer she takes to remove the spermatophore, the more sperm she accepts from the male, which is directly related to the male's paternity success. In a study conducted by Ivy and Sakaluk (2007), females of this species were allowed to mate two times with two different males that were either attractive or unattractive. When the second male they mated with was attractive, females retained the spermatophore for longer (i.e., they accepted more sperm) regardless of whether the first male they had mated with was attractive or unattractive. Females thus reduced the first male fitness just by accepting the spermatophore of the second male. This could also be seen as a female mate choice strategy that results in costs for the first male. The female would accept more sperm from the high-quality male because it is beneficial for her, and as a side effect, the first male will lose fitness. This example illustrates why sometimes it is difficult to establish clear boundaries between mate choice and sexual conflict.

Another situation in which more individuals are involved is that of *infanticide*. Infanticide usually takes place when a female is taking care of her offspring. In this situation the target of this harmful strategy is the offspring, sired by a different male, that the female is taking care of. By killing her offspring, the male increases its own reproductive success as it can shorten the interval to the next ovulation, and therefore he can induce mating responsiveness in the female (see Hrdy 1979 for a review on infanticide). An example of infanticide can be observed in a spider species, *Stegodyphus lineatus*. The female of *S. lineatus* guards her fertilized eggs in a sac for about 30 days, after which she opens the sac and the

young hatch. Once the eggs hatch, she feeds her offspring by regurgitation and then she gets eaten by the spiderlings. Given the suicidal maternal care and the fact that encounters between a male and a female are very rare (one or two in their lifetime), when a male encounters a female that is guarding an egg sac, he will attempt to mate with her. To do so, males need to remove the egg sac from the female so that she is induced to re-lay eggs and remate. This is very costly for the female because even if she remates, the egg cluster size will be significantly smaller, and hence, her reproductive fitness will be significantly reduced. For this reason, females defend their eggs when they encounter a male (Schneider 1999, and references therein).

Finally, although until now we have discussed sexual conflict between males and females, sexual conflict also occurs in hermaphrodites (reviewed by Schärer et al. 2014; Koene 2016). Since hermaphrodites are both male and female, in order to distinguish between the two sexual functions, we will use the term "sperm donor" to refer to the male function, whereas "sperm recipient" will refer to the female function. In the case of hermaphrodites that take turns when mating (i.e., they are functionally both male and female but at each mating encounter then can only perform one of the two roles), a conflict will ensue whenever the two mating hermaphrodites want to adopt the same, and thus incompatible, role. This can lead to a situation in which only one of them performs the desired role, reducing the fitness of its partner. Even if there is no conflict over the sexual role to be performed, sperm donors, as in separated-sex animals, will attempt to affect the female function of the sperm recipient. This can be done by means of accessory gland proteins that increase the sperm recipient's allocation to the female function (e.g., by inducing the sperm recipient to lay larger eggs). A clear example has been described in the great pond snail *Lymnaea stagnalis*, a simultaneous hermaphrodite that chooses roles when it mates. The snail that performs the male role transfers accessory gland proteins, among which LyAcp10 (called ovipostatin) that causes a delay in egg laying in the snail that performs the female role (Koene et al. 2010). This

delay is followed by a higher investment per egg in snails that repeatedly received inseminations (Hoffer et al. 2012), which increases hatchling success (Hoffer et al. 2017) and thus overall fitness of the sperm donor. A more traumatic manipulation can also be found in banana slugs (*Ariolimax dolichophallus*), which have been reported to bite off the penis of the partner after copulation. Such a strategy seems to force the partner to allocate all its resources to its female function, preventing it from mating in the male role (Reise and Hutchinson 2002).

In short, sexual conflict results in costs or harmful consequences for the partner, but sometimes those costs are suffered by someone else, as it happens in the case of infanticide. Cryptic female choice can also reduce the reproductive benefits a male would obtain when the female mates with more than one male. Finally, although for a long time it was widely accepted that hermaphrodites would not experience sexual conflict, recent empirical research has now revealed that it does occur.

When Is There a Conflict?

The conflict between males and females over reproductive investment can occur at different levels. Here, we will focus on only four of these, namely mate access, paternity, egg investment and parental care, but see Kokko and Jennions (2014) for more. In some species *mate access* is already an important source of conflict even in the absence of competitors. For example, the female alfalfa leaf-cutting bee (*Megachile rotundata*) actively resists mating with a male by kicking him with her legs and using abdominal thrusts to dislodge him. A female's success at avoiding mating represents a high reproductive cost for the male but is beneficial for the female as she avoids the costs of (superfluous) mating. On the contrary, a male's success at mating reduces a female's fecundity, longevity, and ability to forage (Rossi et al. 2010).

In species that mate more than once, another or a more attractive partner may be encountered. In such a situation, it would be interesting for both

males and females to be able to mate again, but this would reduce paternity success of both the former and current mating partners, prompting a conflict over *paternity*. One way of preventing such a paternity cost is by mate guarding, which can be done either pre- or postcopulatory. For example, after mating, males of the moth *Achroia grisella* start signaling to attract other females, increasing the likelihood of engaging in a second copulation. However, because males have just mated, they need to produce new sperm and this takes several hours. In order to increase their paternity success, males copulate for several hours, while the new second ejaculate is being produced. These long second copulations represent a precopulatory mate guarding strategy because it prevents the female from mating with a virgin male and increases the paternity success of the male that performs such guarding. Indeed, when males perceive a male competition situation (i.e., another male competitor's song), the latency to start a second copulation is significantly reduced: they engage quicker in precopulatory mate guarding (Jarrige et al. 2016). Mate guarding can also take place after mating and a typical example of such postmating guarding strategies are mating plugs, which can, for example, be found in male bumblebees (*Bombus terrestris*). They transfer a sticky substance into the female sperm-receiving organ that reduces her willingness to remate (Baer 2003 and references therein). Bumblebees also make use of a more simple strategy to increase their paternity success. They engage in long-lasting copulations so that half of the female's spermatheca (i.e., where the sperm are stored before fertilization takes place) is filled with their sperm (Baer 2003). Some other animals, like dragonflies, use sperm removal strategies to overcome conflicts over paternity. Their copulatory organs possess small spines that trap the sperm from previous mating encounters and that allow them to remove the other males' sperm from the females' sperm storage organ before transferring their own sperm (Córdoba-Aguilar et al. 2003). All the mentioned displays provide males with advantages since they reduce male-male competition and increase their paternity success; however, for females this is not necessarily

optimal (see Brennan and Prum 2012 for a discussion on this). This again illustrates that intrasexual mate competition is highly linked to sexual conflict, blurring the boundaries between the two concepts.

Females can also reduce a male's paternity success by preventing males' sperm from reaching the eggs. For example, red jungle fowl (*Gallus gallus*) females expel males' sperm. Such a strategy can be of great advantage for reducing the costs of mating with a lower-quality male, as it would happen in the case of inbreeding. As shown by Pizzari et al. (2004), when females of this species were inseminated by a brother, the number of sperm that reached the eggs or that was stored in the female's sperm storage organs was significantly lower (no differences were observed in the amount of sperm that males transferred to their sisters or to the unrelated females). An even simpler method of discarding sperm is that of sperm digestion. For example, in many hermaphrodites the sperm that is received can either be digested in a specialized organ or stored for fertilization. In the land snail *Cornu aspersum* (formerly *Helix aspersa*), most – about 99% – is digested (Rogers and Chase 2001).

Another source of conflict between males and females is the offspring, and the first stage at which this conflict can be observed is that of **egg investment**. As previously described, in *Lymnaea stagnalis* the individual that performs the female role receives an accessory gland protein (LyAcp10) that induces a delay in egg laying. Such a delay seems costly for the sperm recipient because its egg investment is increased and the number of offspring decreased (Hoffer et al. 2012), and, as a result, this may move the sperm recipient away from the optimal division of investment in current and future female reproduction (Hoffer et al. 2017).

In some species, both parents need to take care of their young as otherwise it would be difficult for the latter to survive. This particular situation leads to two different conflicts. One is over the amount of resources that each of the parents is going to invest in the current offspring, and the other is over the optimal moment they should stop investing in the current partner's offspring and

divert their resources to new offspring (that could be sired by a different partner or not). There are a number of experimental studies in which the sexual conflict over **parental care** is assessed, especially in birds. To study this, researchers have experimentally manipulated the amount of parental investment performed by either the male or the female. In some cases, one of the parents was removed (which allowed to see if a single parent could provide the same amount of care that is usually provided by two parents), and, in some others studies, the care provided by one of the parents was reduced (e.g., by handicapping one of them). In a recently published meta-analysis on how sexual conflict is resolved in different species of birds (Harrison et al. 2009), it was shown that when one of the parents reduced its caring behavior in terms of food provisioning, the other one compensated by increasing its parental effort although it did not compensate fully. Concerning the moment a parent should stop investing in the current offspring and try to reproduce again, one of the cues an animal can use is partner attractiveness. The attractiveness of the current partner is an indicator of the quality value of the current offspring: the more attractive the partner is, the higher the perceived value of the offspring when compared to future offspring (that may not be sired by an attractive mate), and thus investment in the current offspring is expected to increase (see, e.g., Limbourg et al. 2004). An example of how longer or shorter investment in the current offspring is dependent on the partner's attractiveness can be seen in blue tits (*Parus caeruleus*). The crown of blue tits presents a UV coloration that is different for males and females and that indicates sexual attractiveness in both sexes. In an experiment conducted by Limbourg et al. (2004), the coloration of the UV component was reduced by using UV-blocking chemicals during the nestling period (i.e., after mate choice had taken place). The results showed that females that had been paired with males of reduced UV coloration invested less in their offspring (they fed them at lower rates) than females that had been paired with non-manipulated males. Taken together, these studies on parental care show that when one of the parents reduces feeding or care-

providing rates, this immediately exerts a reduction in the gains that the other parent obtains from having mated with him or her.

In summary, we have reviewed four of the possible reasons why males and females are in conflict. The first one is the act of mating in itself, where animals may not be willing to mate or they may prefer others as partners. The second source of conflict is paternity. Mating with more than one partner will increase genetic variation among the offspring, which can provide great advantages. Because sperm are relatively cheap to produce, males will benefit from fertilizing all the eggs produced by different females, whereas for females it would be more profitable to have their eggs fertilized by different males. The allocation of resources to the eggs once they are fertilized is another source of conflict between males and females, as well as the resources that each of the parents invests in raising the offspring when they need parental care. All these situations suppose a conflict for both parents that will be dealt with differently, as described below, depending on the particular way each species mates.

How Does Sexual Conflict Vary Depending on the Species' Specific Mating Strategy?

There is only one mating system in which sexual conflict would be expected to be more limited: **monogamy**. In situations in which there is strict monogamy, meaning that mating takes solely place with a single partner, the traits that decrease the reproductive fitness of one sex will also cause a decrease in the reproductive fitness of the other sex (Hosken et al. 2001). Hence, males would be expected to be less harmful for females, and females would be expected to suffer more if they were to adopt a promiscuous strategy versus monogamy (Crudginton et al. 2005). However, the absence of sexual conflict in monogamous mating species can usually only be inferred, since absolute strict monogamy seems to be extremely rare, and even under strict monogamy, conflict can still arise over other mating aspects

such as when to reproduce, how often or how many offspring to produce.

In some species, mating occurs in a very traumatic fashion: males cause injuries to the female's genital or non-genital structures. These injuries increase males' fitness for several reasons. For example, **traumatic mating** can allow males to better anchor to the female, but it also represents a more effective way of transferring accessory gland proteins that boost females' investment in reproduction (reviewed by Lange et al. 2013). This reproductive strategy is, for example, observed in the land snail *Cornu aspersum*. During courtship, snails of this species force a calcareous dart through the partner's body wall. Once they have "shot" each other, they mate simultaneously as male and female, transferring a spermatophore to each other. The mucus that accompanies the dart contains substances (called all hormones; see Table 1) that shorten the distance to the spermatophore-receiving organ (so the distance the sperm need to travel is shorter; Lodi and Koene 2016a) and close off the tract that leads to the sperm digesting organ (so less sperm gets digested), thereby increasing paternity success (reviewed by Lodi and Koene 2016b). Between species, the female function of land snails with love darts has counter-adapted to the manipulation of the dart by increasing the length of the duct through which the sperm travel (Koene and Lodi 2016b).

Another mating strategy is called **sexual parasitism**. An example of sexual parasitism is that of deep-sea anglerfishes, in which the males attach to the females either temporarily or permanently. In Krøyer's deep-sea angler fish, *Ceratias holboelli*, the tissues of the male fuse with those of the female, and even their circulatory systems become shared. The male is then dependent on the female, and he fertilizes her via the circulatory system (Pietsch 2005). Sexual maturity of both sexes is only reached when the male attaches himself to the female. Interestingly, more than one male can be attached to a single female, a situation that would cause high male-male competition over the siring of the offspring. However, to date no studies have addressed how this sexual conflict is dealt with (which is not surprising given

that the natural habitats of these animals makes such studies very difficult).

In some species, females display *sexual cannibalism*. Clearly, the male will not achieve any reproductive fitness when the female cannibalizes the male before sperm transfer. On the contrary, sexual cannibalism after copulation presents a (somewhat) more beneficial situation for the male in terms of reproductive success. But in either case, the female's reproductive strategy leads to a very high cost for the male since he loses any future reproductive opportunities. As a result, males can develop different strategies to avoid being eaten by the female. For example, in the web spider *Pisaurina mira*, males have evolved to wrap the female's legs with silk before mating with her, thus increasing his own mating success and survival (Anderson and Hebets 2016).

In many insects and spiders, males provide females with *nuptial gifts* in order to entice females to mate. A particular effect of edible nuptial gifts is that they also serve to prolong ejaculate transfer (e.g., Vahed 2007). For example, in the cricket *Gryllobates sigillatus*, successful copulation occurs after the spermatophore has been transferred to the female. As already reported, this spermatophore is attached to a gelatinous substance called spermatophylax that the female detaches from the spermatophore and eats right after copulation has taken place. Females will take a considerable time to eat the spermatophylax (about 40 min) after which they will remove and eat the spermatophore. When the spermatophylax quantity is small, females will take less time to eat it and will remove the spermatophore sooner, diminishing the amount of sperm transferred and thus resulting in a lower rate of male fertilization success (Sakaluk et al. 2006). Contrarily, larger spermatophylax result in increased quantities of sperm transferred, leading to a higher proportion of eggs fertilized by that male (i.e., reduced sperm competition). Moreover, prolonged ejaculate transfer will also result in a higher transfer of (allo)hormonal substances (i.e., accessory gland secretions) that are known to reduce female mating receptivity (again reducing sperm competition) or to increase the rate of

oviposition (increasing paternity success). Thus, accepting such nuptial gifts from the males implies several costs for the females, such as longer sexual refractory periods that prevent females from mating with other males, thus reducing the benefits that the female can obtain from polyandry (reviewed in Vahed 2007).

All the examples given in this section illustrate that sexual conflict is a constant but that the particular mechanisms that animals use to influence the mating partner vary from species to species. Together with the examples of the previous sections, this overview shows that males of different species try to increase their reproductive success via different strategies that are all aimed at increasing the likelihood of siring the female's offspring. These strategies range from preventing the female from mating with another mate, reducing her willingness to mate again, to increasing her investment in egg production. Sometimes they can even evolve to such extremes that result in physically injure to the partner, as illustrated by the case of traumatic mating. Likewise, in an attempt to maximize their own fitness and at the same time reduce the costs of mating, females have also evolved different behavioral (e.g., cannibalism) and physiological (e.g., sperm digestion) strategies to avoid mating or to bias paternity.

Causes of the Conflicts

In this section, we will look at the causes of sexual conflict following the scheme suggested by Nico Tinbergen (1963) for the study of animal behavior. According to him, a particular behavior can be explained in terms of its causation (physiology), survival value (function), ontogeny (development), and evolution (phylogeny). We will provide examples of how sexual conflict can be addressed at each of the four levels, but since one of the main aims of this review is to emphasize how sexual conflict can be affected by experience, we will specifically focus on the ontogenetic aspects that underlie mating behavior and sexual conflict.

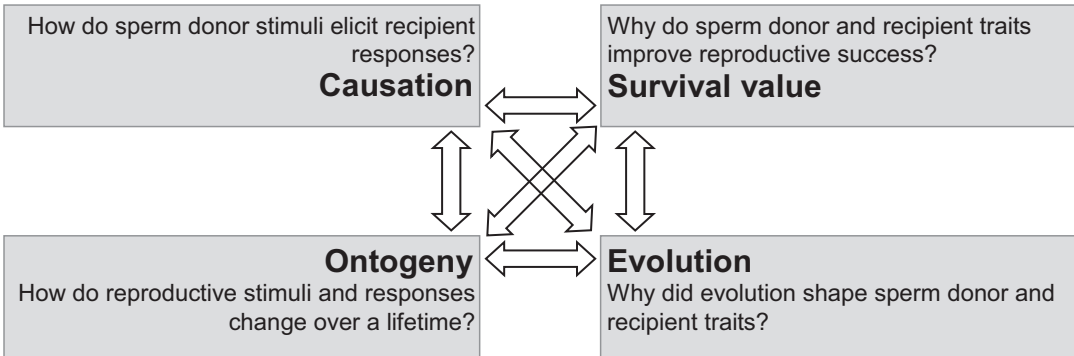
The main reason why we will focus at the ontogenetic level is that when considering the different aspects that affect evolution, behavior has long been recognized as one of the main driving forces (e.g., Baldwin 1896). Indeed, behavior and cognition are present in all daily aspects of an animal's life, from foraging to predator-avoidance and sexual decisions, and they can be a source of new and fast adaptations. Surprisingly, the role that they play in some of these domains has been widely overlooked, or even denied, and only very recently have researches started to pay attention to them (West-Eberhard 2003). Concerning sexual selection, some authors have begun to acknowledge that learning has significant implications for mate choice (Witte and Nöbel 2006) or for speciation through sexual selection (Verzijden et al. 2012). Sexual conflict is tightly linked to sexual selection and forms a very important factor that affects the evolution of male and female traits (e.g., Panhuis et al. 2001), but is exclusively explained in terms of genetic mechanisms (i.e., intra-locus and inter-locus sexual conflict; see Koene 2012 for these concepts). Neither in a comprehensive book (Arnqvist and Rowe 2005) nor in a recent edited volume (Rice and Gavrilets 2014) on sexual conflict was any special attention paid to the role played by the psychological aspects of behavior and cognition, while a recent chapter (Chapman 2015) barely skimmed the surface of this important topic within evolutionary psychology. For this reason, we would like to highlight the fact that psychological processes (attention, perception, motivation, learning, memory, and decision-making) are also at play in the context of sexual conflict and that their study is of great relevance for shedding light on this field of research. Tinbergen used the term "ontogeny of behavior" to refer to the way in which an animal acquires knowledge or a skill (Tinbergen 1963, p. 423). Animals are born with simple and innate sensory-motor coordinations that guide their first experiences, but the outcomes of those experiences will affect the way in which the animal behaves in a circular reaction (see Table 1) that is in constant development (Piaget 1976; see Sánchez and Loredó (2007) for a more detailed definition of this Baldwinian effect). As a

result, any behavior performed by an organism is affected by experience, and not solely determined by instincts. The responses that every individual constructs based on its sensory-motor coordinations and experience constitute new learned adaptations, skills, or behavioral responses that have a positive effect on the survival of organisms, as they allow animals to better adapt to the changing demands of the environment or even to certain genetic variations that constrain their survival. This has clear implications in evolutionary terms, and for this reason, the analysis of psychological processes that are involved in the construction of new adaptive habits is of great importance despite the fact that they are not themselves directly determined by the genes (reviewed by Sánchez and Loredó 2007). Although Tinbergen explicitly referred to learning when talking about ontogeny, it must be taken into consideration that learning is intrinsically linked to other cognitive processes (such as attention, perception, or decision making) in such a way that experience affects them and they affect experience. Because of this, when examining the ontogeny of behavior, we will not only address the importance of learning but also of other cognitive aspects that are relevant for sexual conflict.

Importantly, as will become apparent, these four categories are not mutually exclusive, and none of them, when analyzed in isolation, provide a definite answer to sexual conflict (or any other question), but, when taken together in an integrative perspective (see Fig. 1), they can serve to reach a comprehensive understanding of sexual conflict.

Causation

Causation essentially refers to the physiological mechanisms that underlie a given response, and one example of how physiological responses affect sexual conflict can be seen in the already mentioned case of the land snail (*Cornu aspersum*). In this species, dart shooting enhances sperm storage as it prevents sperm from being digested. However, the female function of the snail that receives the dart and the mucus that covers the dart can counteract this attempt of manipulation by means of sperm digestion,



Sexual Conflict in Nonhumans, Fig. 1 Schematic illustration of the four questions of Tinbergen applied to the field of sexual conflict. Sperm donors (males) are endowed with physiological mechanisms (causation) that affect sperm recipients' (females') reproductive resource allocation and vice versa. However, physiological responses to reproductive stimuli can be affected by animal's experiences over their lifetime (ontogeny). The way in which sperm donors and recipients deal with sexual conflict situations has an important effect on their reproductive success (survival value) that affects the way in which reproductive

traits evolve (evolution). Importantly, as depicted in the figure, all four questions are interlinked, and thus, an integrative study of the four of them is important in order to comprehensively understand sexual conflict. It is also useful to note that causation and ontogeny topics are generally addressed with "how?" questions, while survival value and evolution with "why?" questions. Moreover, it is useful to realize that causation and survival value focus on the here and now, while ontogeny and evolution look at changes over time

which drastically reduces paternity success of the sperm donor (Rogers and Chase 2001, reviewed in Lodi and Koene 2016a). As a result, these two physiological responses create a constant arms race, which is also commonly seen in separate sexed species.

Survival Value

When studying the function of specific traits of males and females that affect reproductive fitness, one essentially addresses the question of why this has evolved (what is the survival value?). From the neo-Darwinian or modern synthesis perspective, survival value or fitness is often inferred by looking at genetics: if a trait contributes to an animal's survival and reproduction, it will be selected and passed on to the next generation. Although this parallelism between survival value and genetics is oversimplified, for our purpose it suffices here as it allows us to illustrate how survival value can be measured.

Drosophila melanogaster provides a great model for the genetic measurement of survival value. In this species, different accessory gland proteins affect sperm competition among males. One of them is Acp36DE, a protein that binds to

sperm and that enters into the spermathecae of the females, facilitating sperm storage. Genetically modified males that cannot produce Acp36DE transfer normal amounts of sperm to the female when copulating, but their sperm are not accumulated in the sperm storage organs of the female. Because of this, no displacement of previous males' sperm takes place and a lower fertility rate is achieved (Chapman et al. 2000), thus revealing the adaptive (survival) value. Likewise, mutations in a different protein (Acp26Aa, called ovulin) impair the capability of inducing females to lay eggs. This protein has been shown to be responsible for the stimulation of the ovary to release oocytes. Females that were mated to mutated males that were not able to produce this protein laid significantly fewer eggs than females that were mated to wildtype males (Heifetz et al. 2000). These two studies show how sexual conflict strategies can be addressed at a genetic level and how sexual conflict is of great importance for animals' survival or fitness.

Ontogeny

Throughout this review we have been talking about mating as if it was a simple behavioral

response or action that all animals can display automatically or innately (i.e., determined by physiological or genetic aspects). Nevertheless, cognitive processes are also involved. For copulation to happen, “animals must be able to respond to hormonal and neurochemical changes that signal their own sexual desire and arousal, to identify external stimuli that predict where potential sex partners can be found, to actively seek out or work to obtain sex partners, to distinguish external chemosensory cues or behavioral patterns of potential sex partners from those that are not sexually receptive, and to pursue desired sex partners once sexual contact has been solicited. At each step, animals depend not only on the perception of their own internal state, but on the accurate prediction of external events. Such predictions are based on experience, both with the relation between external and internal stimuli and the relation of these stimuli to their sexual consequences” (Pfaus et al. 2001, p. 291). In this description of mating, many psychological processes are involved (e.g., motivation, perception, identification or even prediction). Such processes and the responses that animals display, as claimed by these authors, are mediated by their previous experience, in which learning and memory play a crucial role.

One way of experimentally measuring the effect of learning in a sexual conflict situation is by means of *associative learning*, which is one of the most thoroughly studied forms of learning. As described by Pavlov (1927/2003), this type of learning takes place when an initially neutral stimulus (e.g., an acoustic stimulus) is presented together with a biologically relevant stimulus (e.g., food). When the neutral or conditioned stimulus (CS) is repeatedly paired with the meaningful or unconditioned stimulus (US), animals start displaying a conditioned response (CR) in the presence of the CS alone. In Pavlov’s classical experiment, the sound produced by a metronome (CS) was paired with food powder (US) that was fed to the dogs. After several learning trials, dogs started to salivate (CR) when exposed to the metronome alone, without needing the food to be present.

This type of learning has been shown to be adaptive for animal reproduction as well as it can increase their reproductive fitness at different levels, and one of the first experiments to show this adaptive value was that of Karen Hollis. In her most influential work, she exposed male blue gouramis (*Trichogaster trichopterus*) to a light (CS) followed by either the presence of a male or a female (US). After training, animals were allowed to interact in a test that was signaled by the CS. Animals of the Pavlovian group were able to predict their encounter with a female and responded less aggressively to the females. They delivered significantly less bites compared to the males that were not able to rely on the CS to predict the presence of the female, and they also spent more time in the courtship appeasement posture than the control males (Hollis 1999). This training did not only result in less aggressive behavior toward the female, but it also increased male blue gouramis paternity success: Pavlovian males took less time to induce spawning in the female, and they also produced significantly more offspring than control males. On the contrary, when the lightning of the red light was used to signal the presence of another male, the experimental males increased the number of aggressive responses (frontal displays, bites, and tail beatings) toward the intruder (Hollis 1999). This work demonstrates how Pavlovian conditioning in the blue gourami can help in the identification of a conspecific (male or female) as well as in the selection of the right behavioral repertoire to be displayed at a given encounter (courtship or aggressive behavior). Furthermore, these results show that associative learning had a great impact in terms of sexual conflict: it reduced the level of male-female sexual conflict (i.e., it induced a faster and higher spawning response in the female). This in turn increased the reproductive and paternity success of the learning males as exhibited by the large amount of offspring sired by the males who were able to use the red light as a predictor of the female.

Comparable results have been observed in the Japanese quail *Coturnix japonica*. In a study conducted by Domjan et al. (1998), a context was used as the CS to signal a mating encounter

(US) for the males in the learning group, whereas males of the control group were exposed to the same stimulation but in such a way that they were not able to associate both events. Males in the learning group produced larger ejaculates and a larger number of spermatozoa compared to the control group. These results show how being able to predict a mating encounter can increase sperm competition-related physiological responses in the male Japanese quail while increasing the male's chances of siring a higher proportion of the female's eggs. More notably, the effect of Pavlovian conditioning over paternity success can go even beyond the production of sperm. As Adkins-Regan and MacKillop (2003) reported, the number of fertilized eggs significantly increased when either the male or the female had been subjected to Pavlovian conditioning, which also shows that physiological resistance responses of females can be modified depending upon the females' ability to predict a mating encounter. This type of training can also provide advantages in those situations in which there is male-male competition. This was experimentally tested in a study in which two different males had the opportunity to copulate with the same female, but only one of them received classical conditioning training. In the test, both males copulated with the female and whether the learning or the control male copulated first or second with the female was counterbalanced. The male who had been subjected to classical conditioning training was not only quicker at mating but also sired significantly more offspring (78% vs. 28% instead of the usual 50–50% rate that is found in this species) regardless of who mated first with the female (Matthews et al. 2007). Notwithstanding, how such male-driven paternity bias can affect female fitness remains unexplored (i.e., the learning male is not necessarily the best one in terms of genetic quality).

Taken together, these studies demonstrate that Pavlovian conditioning can facilitate several stages of the mating sequence by somehow reducing the different sexual conflicts that may be present. The reduction of sexual conflict can be

achieved by a change in the behavioral response, as in the case of the blue gourami: increased or decreased aggressive or courtship responses. Importantly, such behavioral changes had an effect of significance on the spawning response of the female. Likewise, learning mediates the physiological responses of the Japanese quail as manifested by the increase of sperm production, fertilization rate, or even paternity rate.

However, not all the experience that affects sexual conflict is acquired through associative learning and experience does not necessarily lead to a reduction of the sexual conflict. Experiments with guppies (*Poecilia reticulata*) have shown that when females are allowed to choose between two different males, they consistently prefer the same given male but that this preference can be reversed if they are allowed to observe a second female near the non-preferred male (Dugatkin and Godin 1992). In this scenario, females are conducting two different perceptual assessments: they are evaluating the quality of the two males but also the quality of the model female. Indeed, it has been observed that guppy females will choose the same male an older female has chosen, but not the one chosen by a younger female (Godin et al. 2005). In this case, age-dependent *imitation* would actually increase sexual conflict in terms of female-female competition. In a situation in which there are several females that select the same male, the male might experience sperm depletion, thus reducing the benefits the female would obtain.

In some of the examples already mentioned in the previous sections (e.g., the males of the moth *Achroia grisella* who reduced the latency to their second mating when they heard another male's song; the female of the red jungle fowl that was able to get rid of sperm coming from a brother, or the birds who reduced their investment in their offspring as a consequence of a reduction of their partners' attractiveness), it is clear that animals assess the quality of their partners and invest accordingly. In all these examples, animals perceive a situation, assess the information they have processed, and make a decision on the quality of

the mate. However, in none of these examples was the role of experience examined, and one could feel tempted to attribute the responses observed in each case to instincts or physiological mechanisms. In turn, studies in which learning has been shown to be relevant (see below) invite us to be cautious about such attributions.

Within the mating sequence, psychological processes have been shown to especially affect mate access, which is the first level at which sexual conflict is observed. As just illustrated, mate choice can be affected by learning from other conspecifics, but it can also be modified upon individual experience. For example, mate choice preference can be determined by simple exposure to a given phenotype (i.e., *familiarity*). Female wolf spiders (*Schizocosa uetzi*) do not display any innate preference for two extreme male phenotypes (brown or black pigmentation of a portion of the tibia of the forelegs) when they had not been exposed to either phenotype as subadults. However, they did show learned preferences after having been exposed to one or the other phenotype before reaching maturity: they were more likely to mate with the male of the familiar phenotype and also more likely to cannibalize the male that had the unfamiliar phenotype (Hebets 2003). This demonstrates the impact that learning can have on a sexual conflict situation, with extreme consequences for the males. In naturalistic situations, this conflict is reduced because males mature earlier than females and court them while they are still in their last stage before reaching maturity. This allows females to learn about the different male phenotypes so that the likelihood of mating with a particular phenotype increases and the chances of cannibalizing the male of that familiar phenotype are reduced.

For other species, familiarity is not enough and successful mating provides animals with *cumulative experience* that shapes the way sexual conflict is dealt with, as it occurs in the Pacific field cricket (*Teleogryllus oceanicus*). In this species males produce two songs, a short-range one and a long-range one, the long-range ones being the

most preferred by females. Nonetheless, it was experimentally shown that if females mated with an unattractive male (short-range song producer) and on the following day they encountered another unattractive male, in this second mating, females took less time to mount males (which signals female's willingness to mate), and they also retained this second male's spermatophore for longer (Rebar et al. 2011). The longer retention of the spermatophore correlates with the amount of sperm that is transferred and therefore paternity (see above), so, in this situation, females' previous experience would reduce sexual conflict with the second mating male.

All the examples mentioned above show that mate choice is not innate but a cognitive process that starts with the detection and perception of the mate (or of a model) and that it also implies an evaluation of the processed information as well as a decision-making process that is influenced by different sorts of past experience (Ryan et al. 2009). The outcome of this complex series of processes is going to affect one of the most important decisions that animals make in terms of reproduction, and it will also have important consequences in terms of sexual conflict. Based on the experiments reported, learning and cognition affect sexual conflict at the level of mate choice and paternity success (as shown in the case of the female crickets that retained the spermatophore for longer), but it can also have major implications for the offspring. In several studies it has been observed that parents' investment in their offspring varies according to their mate preferences. For example, in a study conducted with house mice, male preferences between two females were assessed before pairing half of the males with their preferred females and the other half with their non-preferred females. The litter size and the number of offspring that survived to the reproductive age (among other variables) were greater when males were allowed to mate with their preferred female than when they had to mate with their non-preferred female (Gowaty et al. 2003). Similarly, female canaries of the species *Serinus canaria* allocate different

amounts of testosterone to the eggs they laid depending on the attractiveness of the males' song to which they had been exposed. They allotted more testosterone to the eggs they laid when they were exposed to attractive male songs than when they were exposed to unattractive songs. This difference in the allocation of testosterone leads to hatching asynchrony that in turn affects the survival of the offspring, so the male whose offspring has received less testosterone will see his parental success significantly reduced (Gil et al. 2004). These results certainly show that there is an ongoing assessment of the quality of the partner and that such evaluation has important consequences on the total fitness of both males and females. In both examples given, males and females were investing less in the offspring they had sired, thus increasing the partners' costs. Interestingly, so far there are no studies that test the possible changes in offspring number or viability after preference for a given mate has been altered as a result of learning.

In short, learning and other cognitive processes are involved in sexual conflict situations. They can affect sexual conflict at, at least, two of the four levels: mate access and paternity. Concerning egg investment and parental care, it is certain that animals do assess their partner's quality to invest accordingly; however, the role of learning still needs to be more convincingly explored and integrated into our thinking. Thus, although ontogeny exerts an important effect, it must be acknowledged that a systematic evaluation of how animal psychology affects sexual conflict is still needed in order to fully appreciate the role that ontogeny plays in this domain.

Evolution

Phylogenetic analyses can shed light on the evolution of genetic, physiological, or behavioral responses that we observe in the field of sexual conflict. This type of analyses would allow us to identify the preceding events that have contributed to the occurrence of such adaptations. For example, regarding physiological traits that are involved in sexual conflict, phylogenetic

comparisons have revealed how males and females have developed adaptations and counter-adaptations to overcome sexual conflict. An example of this can be observed in male seed beetles (Coleoptera: Bruchidae), who possess spiny genitalia that injure the wall of the female copulatory duct. This trait is thought to provide benefits to the males as it allows them to better anchor themselves to the female during copulation and seems to also transfer accessory gland proteins (Hotzy et al. 2012). However, the presence of spines on males' genitalia imposes a cost for the females, and a comparative study of the male and the female genitalia of three different species of seed beetles has shown that, as males developed more harmful genitalia, females counter-adapted by evolving a more resistant copulatory tract, protected with thicker connective tissue (Rönn et al. 2007).

Regarding the phylogenetic analyses of behavioral responses, studies are not very abundant, but one example can be found in the diving beetles (Coleoptera: Dytiscidae). In this family, females of two different species (*Rhantus binotatus* and *Dytiscus alaskanus*) have been observed to exhibit behavioral mating resistance (rapid and erratic swimming and attempts to dislodge the male by driving him into the substrate or against objects). In contrast, females of two other species (*Ilybius gagates* and *Neoporus undulatus*) do not show any resistance behavior when males attempt to mate with them. The behavioral resistance response seems to have coevolved as a counter-adaptation to long-lasting matings: the two species that do not resist male mating attempts take shorter to mate than the other two (Miller 2003 and references therein). However, no intermediate stages have been described so far, so this analysis remains inconclusive.

Finally, species' general mate preferences have been reported to also have an evolutionary origin as it has been observed in the platyfish preference for long-sword males. Swordless platyfish are thought to be more ancestral than swordtails, and female preference for the morphological trait has been suggested as a pre-existing bias that shaped the evolution of the genus *Xiphophorus*. Swordtail females of two species that do not

possess swords (*X. maculatus* and *X. variatus*) display clear preference for males that have artificially longer swords than normal males. Moreover, the exact same pattern of results was observed in females of a sister genus (*Priapella*) that do not possess swords at all. These results indicate that female preference for a sword-bearing male had to arise in an ancestor of the two genera (Basolo 1995).

In summary, phylogenetic analysis can help us to better comprehend the evolution of morphological, physiological, or behavioral traits that are involved in sexual conflict. However, as at the level of ontogeny, more studies that analyze the evolution of the aforesaid traits are needed for a complete understanding of sexual conflict.

Summary and Concluding Remarks

While the boundaries and definition of sexual conflict are still a matter of debate, in this review we have defined it as a consequence of the differential investment in reproduction of males and females (or the sperm donor and recipient in the case of hermaphrodites). This differential investment leads to more or less harmful mating strategies that can be displayed (at least) at four basic different levels: mate access, paternity, egg investment, and parental care. The participants involved in a sexual conflict scenario and the general strategy that allows overcoming the sexual conflict will vary depending on the level at which sexual conflict takes place and the species under study. When the sexual conflict is over mate access, animals can harass their mates or even cannibalize them. This immediately implies mate-avoidance responses or the development of different choice criteria by the individual that is competed for (usually the female). When the conflict is over paternity, strategies such as mate guarding, cryptic female choice, sperm digestion, sperm removal, or accessory gland proteins will be used to influence the partner's investment or to avoid being manipulated. Seminal fluid proteins are also important when there is a conflict over egg investment, just as some other resource allocation mechanisms that can be displayed by the females

(e.g., time of spermatophore acceptance). Finally, when the conflict is over parental care, a reduced investment in terms of feeding or protection can be observed among some animals, especially birds.

The particular way in which sexual conflict takes place and is dealt with at each level will strongly depend on the mating strategy of the species of focus (e.g., male spiders that wrap females to avoid being cannibalized and to increase paternity success). All the mentioned adaptations that animals have developed to increase the partner's investment lead to counter-adaptations on the other sex. It is for this reason that sexual conflict plays a fundamental role in evolution. Importantly, behavior is a ubiquitous component of animals' lives; however, the way in which psychological processes shape how sexual conflict is dealt with has been widely overlooked in the literature on sexual conflict. The studies reviewed in the preceding show how different psychological mechanisms, especially learning, affect the investment of males and females in reproduction, reducing or increasing it.

Analyzing sexual conflict in terms of Tinbergen's four questions, especially in terms of ontogeny, has allowed us to understand sexual conflict and its role in evolution in a more comprehensive way. Notwithstanding, caution should also be taken when doing this, for two main reasons. The first one is that although it might seem that the four questions about behavior are independent from one another, they are fully interlinked (sometimes overlap), and all contribute to a full explanation of a behavior (Tinbergen 1963; see also Fig. 1). The second one is that, due to the current focus of genetics as the causal factor of any aspect of an animal's life, it has been somehow implicitly accepted that Tinbergen's four questions are hierarchical; being changes in the genes that causes changes in the physiological response, what in turn allows animals to develop behavioral changes to finally cause phylogenetic changes that lead to evolution. As a consequence of this, ontogeny has not received the deserved attention from an evolutionary perspective, or, if it has, it has been reduced to genetics. Indeed, conventional thinking considers that evolution is

solely gene-mediated and behavior is very often also explained in terms of a genetic trait that can be selected upon (see, e.g., Gottlieb 2002). According to this perspective, all the possible behaviors an animal can display are encoded in that animal's genome, and if a given behavior leads to successful adaptation, it will be passed onto the offspring of that animal until it becomes a common trait (i.e., instinct) among a given population. Conversely, from the perspective of organic selection (see Table 1; Baldwin 1896) and EvoDevo, the *ability* to produce a behavior or a response in itself can become common due to a genetic change but not the adaptive evolutionary response per se (e.g., a behavioral innovation, such as the use of a tool, can become general within a group or population and be maintained along generations through social influence resulting in adaptation but not in evolution; West-Eberhard, 2003). Behavior and physiology are the two most flexible, faster, and reversible responses animals can display in a changing environment situation. They allow animals to express a novel phenotype, increasing the adaptation and the accommodation of the phenotypic change, but such adaptation and accommodation of the phenotype does not necessarily imply a genetic change. Like any other advantageous phenotypic variation (e.g., morphological variations), behavioral changes that increase adaptiveness will also be selected, but they will not be necessarily inherited (Sánchez and Loredo 2007; West-Eberhard 2003). Because of its high level of flexibility and its fundamental role on adaptation, behavior has long been recognized as a leading factor in evolution by some authors (Baldwin 1896), but its importance as such has only started to receive attention very recently. Experimental work like that of Karen Hollis in the blue gourami or that of Michael Domjan in the Japanese quail showed how associative learning (a change at the ontogenetic level) does actually have a major effect in the physiological responses involved in reproduction. There is also experimental evidence from the field of epigenetics that shows that changes at the ontogenetic level can have important effects not only at the physiological but also at the genetic level (it can affect gene expression).

This evidence questions the general assumption of a one-way genetic causation mechanism, and it contributes to the growing body of evidence on the connections between the different levels of causation (as depicted in Fig. 1) as well as to the acknowledgment of behavior as a crucial factor in evolution. Again, it must be emphasized that behavioral responses are not a genetically driven display. Behind any behavior that we observe, psychological processes such as perception, learning, memory, or decision-making are constantly present. They are the mechanisms that allow animals to interact with and to adapt to a changing environment. For this reason, whether our aim is to understand foraging, predator-avoidance, or sexual conflict, an integrative approach in which psychological processes and ontogeny are considered must be adopted. This does not deny the importance of genetics, but a complete picture of animal evolution will only be achieved if the different levels of analysis are fully integrated. In this work we have tried to provide a more integrative overview of sexual conflict by gathering examples of the four levels as a first step to a full and comprehensive understanding of sexual conflict and its evolution, although as noted in different parts of the manuscript, more work needs to be done to achieve this goal.

Cross References

- ▶ [Classical Conditioning](#)
- ▶ [Copulatory Plugs](#)
- ▶ [Copulatory Intrasexual Competition](#)
- ▶ [Counteradaptations/Female Counterstrategies](#)
- ▶ [Cryptic Female Choice](#)
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- ▶ [Sperm Competition- Evidence in Nonhumans](#)

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