

Communication under sexual selection hypotheses: challenging prospects for future studies under extreme sexual conflict

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Abstract Animal communication has been the target of multiple and controversial theoretical and experimental studies. Inter-sexual communication has been considered essential for specific identification and as a mechanism for mate choice. Communication has been re-interpreted as a way for exploitation, taking advantage of pre-existent sensory biases. Both female choice and sensory exploitation hypotheses have assumed the clear existence of inter-sexual communication prior to mating. On the contrary, extreme sexual conflict hypotheses would not recognize the existence of communication among the sexes. We surveyed the percentage of studies involving communication under female choice, sensory exploitation and extreme sexual conflict contexts. We discuss the traditional idea that forced copulations are considered synonymous of the absence of communication among the sexes. We provide suggestions for future studies on communication under extreme sexual conflict.

Keywords Female choice · Sensory exploitation · Extreme sexual conflict · Coercion · Biases

Introduction

The great diversity of biological definitions of communication as well as controversies on the role of information in studies of animal communication are a result of many different approaches (Carazo and Font 2010; Rendall et al. 2009; Seyfarth et al. 2010). Reproductive biology and in particular sexual behaviour is one of the fields in which the main characteristics of the components of communication (e.g. signals, information, signaller and receiver) have been evaluated (Searcy and Nowicki 2005). Many examples of intra- and inter-sexual communication have been described in the classic works of Darwin (1871), Thorpe (1961) and Bastock (1967), as well as in reviews on sexual selection (Andersson 1994; Eberhard 1996; Arnqvist and Rowe 2005; Andersson and Simmons 2006). Communication has been interpreted and discussed in different ways depending on the perspectives of each theoretical sexual selection paradigm.

In general, informational approaches (involving a cooperative perspective) are directly or indirectly used to describe communication during an inter-sexual interaction in studies on female choice and extreme sexual conflict (i.e. sexual coercion and/or sexually antagonistic coevolution) (Eberhard 1985; Andersson 1994; Eberhard 1996; Arnqvist and Rowe 2005). In contrast, adaptive approaches are mainly considered in studies on inter-sexual sensory exploitation (Christy 1988, 1995; Endler and Basolo 1998; Vahed 2007). But, as we will review in the following sections, these approaches have changed during the last years and new theoretical discussions are needed.

Brief background to current thinking

Traditionally, inter-sexual communication has been considered essential for specific identification and as a mechanism

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for mate choice. Mating systems characterized by males with exaggerated secondary sexual characters emitting conspicuous signals during sexual interactions can be considered widespread in the Animal Kingdom and have captured biologists' attention since Darwin (1871). Signal exchange between the sexes during courtship and copulation should permit not only the evaluation of potential sexual partners but also species recognition. The origin and maintenance of sexual signals and processes modelling their evolution have been widely discussed during the last decades (Guilford and Dawkins 1991; Zuk 1991; Ryan 1998; Zuk and Tinghitella 2008; Rendall et al. 2009).

Sexual selection by female choice gives a possible explanation for the evolution of sexual signals. In general, males are the courting and competitive sex while females are choosy regarding to mating acceptance and paternity (Andersson 1994). As a consequence, male signals in sexual contexts will follow female preferences. Whether the female responds positively to male signals during courtship will depend on variables such as success in the emission of the signals, adequate transmission through the environment, correct reception by the female and, after decodifying the signal, female decision to respond to the signal (Guilford and Dawkins 1991; Endler 1992).

Though most studies related with female choice are focused in sexual communication during courtship and until the acceptance of copulation, the evaluation of the mating partner can continue during and after copulation, what has been called cryptic female choice (Thornhill 1983; Eberhard 1996). The term "cryptic" emphasizes our limitations as human observers to detect processes that take place inside the female body. This fact may well be extended to the detection of subtle animal signals imperceptible to us as observers, but essential for females when taking mating decisions (see below about the same limitation in research on extreme sexual conflict).

Direct selection on characteristics of female sensory system in a context different to mating might favour the existence and exaggeration of particular male traits. By using female responses strongly selected under other contexts, male signals can turn into sensory traps that manipulate the receiver response in the emitter's own profit (West-Eberhard 1979, 1984; Proctor 1991, Proctor 1992). According to Ryan (1998), sensory exploitation implies that males evolve traits to exploit pre-existing receiver biases, rather than preferences and traits coevolving via genetic correlations. Christy (1995) highlighted that although sensory traps and sensory exploitation seem to refer to the same processes, they do not. Sensory traps arise in the context of signal evolution with an origin in sensory exploitation but driven by relations between mimics, models and responses to both of them, with the prediction that female choice will favour mimetic courtship signals (Christy 1995).

We would expect that in systems where conflict between the sexes over mating decisions occurs, pre-existing biases in one sex will provide a promising setting for exploitation and manipulation by the other sex (West-Eberhard 1984; Arak and Enquist 1993, 1995; Holland and Rice 1998; Arnqvist and Rowe 2005). Females in general have a higher reproductive investment and as a consequence the roles of "exploited" and "exploiter" will be assigned to females and males, respectively (Arnqvist and Rowe 2005). By taking advantage of the potential mate sensory biases, the emitter can generate high costs to the receiver by making females accept unnecessary copulations, inducing sexual reluctance or preventing female choice on honest characters. As a consequence, females can generate resistance and induce further exaggerations of male traits, driving an antagonistic coevolution among the sexes (Holland and Rice 1998; Parker 2006; Rowe et al. 2005; Vahed 2007). However, the concept that one sex exploits a sensory bias in the other sex does not necessarily imply that the other sex is exploited and consequently suffers a reduction in fitness. Unfortunately, anthropomorphic view of animals imposed by researchers has imposed terms biased by a sex-stereotyped perspective (Karlsson Green and Madjidian 2011). Indeed, in some cases, even though selection for increased effectiveness of the male's signal may have involved tuning the signal to the female's sensory biases, this does not in itself imply conflict. The female could still benefit from the interaction if male capacities of exploitation are inheritable and provide sons with their consequent benefits (Cordero and Eberhard 2003, 2005). Therefore, communication is the heart of the matter under sensory exploitation and sensory trap hypotheses.

Communication under extreme sexual conflict

Strategies that enhance the reproductive success of one sex may conflict and impose a naturally selected cost on the other sex. Both the level of cost and the threshold of acceptance of such a cost can differ between the sexes and this difference defines the degree of sexual conflict (Parker 1979). Sexual coercion and sexually antagonistic coevolution (SAC) hypotheses (Chapman et al. 2003; Arnqvist and Rowe 2005) originate in the core of extreme expressions of sexual conflict. Sexual coercion, especially in the form of male harassment and forced copulation (Rowe et al. 1994; Clutton-Brock and Parker 1995), occurs when a sex—in general males—overcomes physical resistance of the other sex—in general females—with force or threats of force (Smuts and Smuts 1993). In sexually antagonistic coevolution, one sex (usually males) evolves a manipulative trait which is countered by a resistance trait in the other sex. Although sexual coercion is associated with SAC, its mere

presence does not imply that this type of evolution occurs (Pizzari and Snook 2003).

In contrast to what was stated for the previous sexual selection hypotheses of female choice and sensory exploitation, communication has been traditionally excluded from studies testing extreme sexual conflict, considering that sexual coercion implies a communication breakdown between sexual partners (Fig. 1). Indeed, some studies have contrasted communication and sexual coercion hypotheses as mutually exclusive from one another (Baena and Eberhard 2007). In addition, sex-stereotyped perspectives (i.e. active males vs. reactive females) of theoretical models in sexual conflict research (Karlsson Green and Madjidian 2011) did not help us for a better understanding of the complexity of inter-sexual coevolutionary dynamics.

If we follow classical definitions such as those given by Wilson (1975) (see Table 1) and Maynard-Smith and Harper (2003), communication can also take place when both emitter and receptor interests are in conflict (Wilson 1975; Maynard-Smith and Harper 2003). Indeed, following Dawkins (1993), situations of conflict can lead either to the transmission of costly and conspicuous signals or, on the other hand, to the evolution of cryptic signals (i.e. undetected by our ordinary perception) transmitted from emitter to receiver. A first idea emerges: has communication been underestimated in cases of sexual conflict? As far as we know and in spite of the increasing number of studies testing extreme sexual conflict, the latter possibility remain relatively unexplored and deserve more exhaustive analyses. The aim of the present work was to evaluate the relevance that has been given to communication topics during the last years under female choice, sensory exploitation and extreme sexual conflict hypotheses. We discuss limitations and biases that could be explaining the results and propose areas for future research.

The survey

To visualize how the percentages of studies involving communication and sexual selection have changed over the last years, we surveyed the number of articles published under female choice, sexual exploitation and extreme sexual conflict (i.e. sexual coercion and/or sexually antagonistic coevolution) hypotheses. For that purpose we used the database of research literature SCOPUS and considered the articles published in *Acta Ethologica*, *Animal Behaviour*, *Behavioral Ecology*, *Behavioral Ecology and Sociobiology*, and *Ethology* as journals specialized in animal behaviour, and *American Naturalist*, *Evolution*, *Journal of Evolutionary Biology* and *Proceedings of the Royal Society of London (Ser. B)* as journals focused in the evolution of animal systems. We counted the number of articles published between 1982 and 2010 that according to their titles, keywords and abstracts dealt with each sexual selection hypothesis and recorded the number of articles focused on communication. We also recorded the communicatory channels that were implied on each published article. When we had any doubts, we proceeded to read the whole text of the article.

Results

The principal data of the survey are summarized in Fig. 2 and Table 2. Female choice hypotheses have been widely the most studied in the period considered. However, articles about sensory exploitation and extreme sexual conflict are gradually increasing in numbers during the last decades. Most articles based in communication correspond to studies under the female choice perspective due to, among other factors, a higher number of articles on female choice contexts. We expected most studies of sensory exploitation

Fig. 1 Traditional view of communication during sexual interactions. Selective cooperation contexts such as female choice, in which luring is a typical male strategy, implies presence of communication since a feedback of information between male and females is evident. In contrast, non-cooperative contexts such as sexual coercion apparently do not include sexual communication since a flow of information between sexual partners seems to be absent. We discuss this biased view in the present commentary

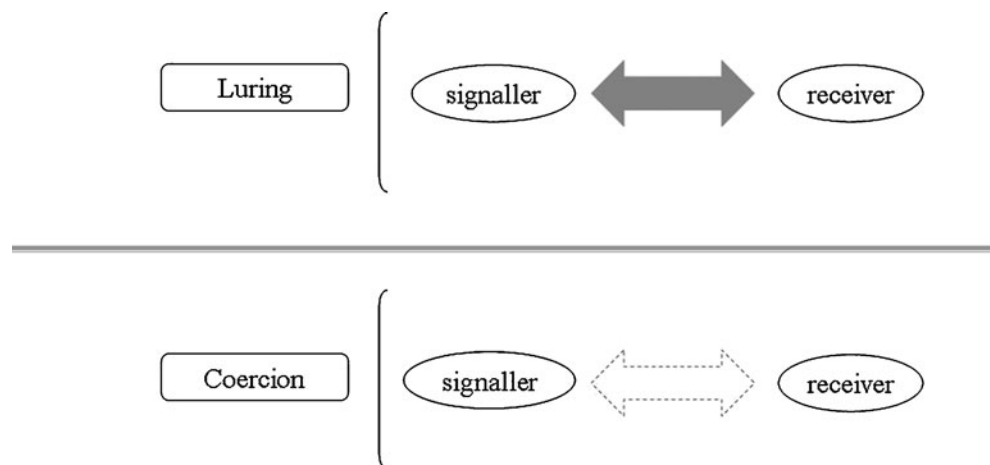


Table 1 Among the great diversity of papers, reviews and textbooks on animal behaviour we can find different definitions of communication, a fact that illustrates the difficulties to summarize these biological phenomena in a concise sentence; we summarize some historical examples

Definition	Source
Communication occurs when the action or cue given by one organism is perceived by and thus alters the probability pattern of behaviour in another organism in a fashion adaptive to either one or both of the participants.	Wilson 1975
Communication is said to occur when one animal responds to the signals sent out by another animal.	Manning and Dawkins 1998
Communication is the transmission of a signal from one individual to another such that the sender benefits, on average, from the response of the receiver.	Slater 1999
Communication is the provision of information (by a sender) that can be utilized by a receiver to make a decision... is then an exchange of a signal between a sender and a receiver to the benefit of both parties.	Bradbury and Vehrencamp 1998
Communication is the completion of corresponding signals and responses.	Scott-Phillips 2008

to involve communication because of the nature of the subject. Indeed, if we examine the total percentages, communication was the core of 87% of studies of sensory exploitation, the 36% of studies on female choice and only

the 6% of studies about extreme sexual conflict. In spite of the great increase of studies on extreme sexual conflict during the last 3 years this did not traduce in an increasing number of studies on communication under this context.

Fig. 2 Number of articles published in the journals considered in the present study, under female choice, sensory exploitation and extreme sexual conflict hypotheses (above) and number of articles focused in communication under each hypothesis (below) between 1982 until 2010

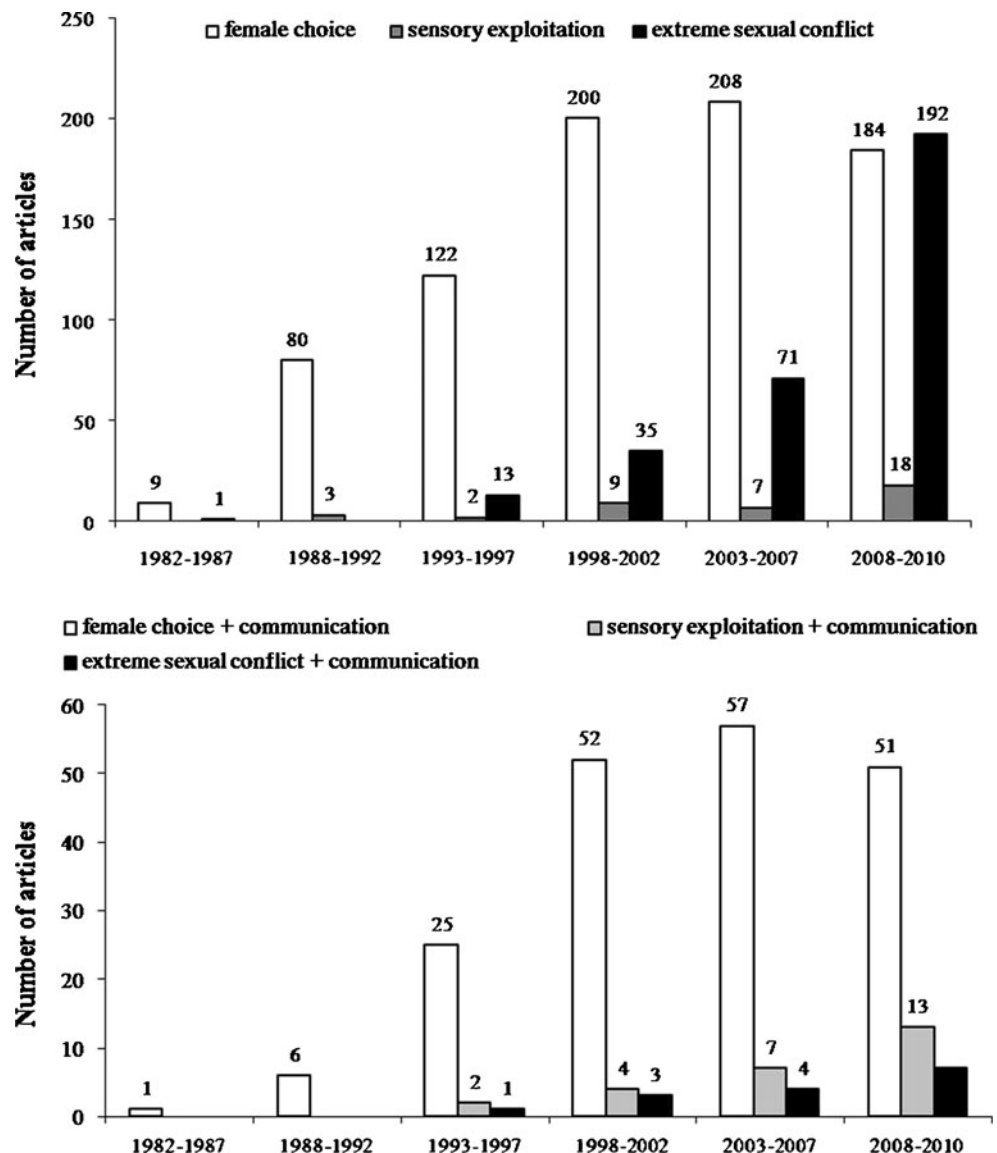


Table 2 Number of studies of communication under female choice, sensory exploitation and extreme sexual conflict hypotheses published between the years 1982 and 2010 in the selected journals, with percentages of the communicatory channels involved

	No. of studies involving communication	Channels of communication (%)
Female choice	192	Acoustic 40%; visual 33%; tactile 4%; chemical 6%; seismic 2% ^a
Sensory exploitation	26	Visual 65%; chemical 12%; acoustic 15%; tactile 4%; seismic 4%
Extreme sexual conflict	15	Chemical 40%; visual 20%; acoustic 33% ^b

Note the lack of tactile and seismic channels in extreme sexual conflict

^a Twenty-five combined cases: five seismic + acoustic; four visual + acoustic; four visual + seismic; one tactile + seismic; one tactile + chemical; one tactile + visual; five visual + acoustic + seismic; four visual + acoustic + tactile + seismic + chemical

^b One combined case: one chemical + tactile

The acoustic and visual channels of communication were the most represented in female choice studies, visual, acoustic and chemical under sensory exploitation hypotheses, and chemical and visual in extreme sexual conflict studies (see Table 2). In contrast, the tactile sense was the least represented channel in female choice and sensory exploitation hypotheses, while it was not represented under extreme sexual conflict.

Discussion

Studies on sexual selection have examined inter-sexual communication depending on the theoretical frameworks of the hypotheses involved. The survey indicates that female choice and sensory exploitation contexts imply a communicatory feedback between males and females while extreme sexual conflict is apparently associated with poor flow of information during inter-sexual interactions. However, this traditional perspective is supported on a traditional emphasis on information instead of focusing on basic evolutionary principles that ascribe signallers and receptors distinct roles and assume their potentially divergent interests in communication processes (Rendall et al. 2009). In addition, our perception about communication between the sexes is influenced by other factors such as the approach we use to examine and interpret the principal components of signalling (Coleman 2009). Therefore, if our evaluation is based only on conspicuous signals transferred in cooperative inter-sexual interactions, we will probably conclude that there is lack of communication when sexual coercion prevails during mating. As an example, fine-scaled observations were used in recent studies in arthropods (e.g. Vahed 2002; Peretti and Willemart 2007; Hrušková-Martišová et al. 2010) to detect the coexistence of sexual coercion (in the form of forced copulation) and luring behaviour (in the form of copulatory courtship) during copulation. Co-occurrences of these apparently opposing strategies during mating have not been explored in depth and may suggest the possible occurrence of mixed

behavioural evolutionary patterns in some groups (Peretti and Córdoba-Aguilar 2007). For instance, in some groups (e.g. winged insects, ducks) coercive behaviours capture our attention because they generally involve typical clasping organs in males and notable behaviours in females, such as shaking, kicking or stroking (Eberhard 1996). However, non-coercive patterns like brief and slight male tapping on the female body or vibrations may be overlooked if videos are played at high speed. As a consequence, the presence of communicatory channels between the sexes can remain unnoticed.

Under extreme sexual conflict the information contained in the signal (e.g. strong pressure on female body) could be “I will hurt you if you do not cooperate with me (i.e. to accept copulation)”. On the other hand, the female by resisting could be sending the message “I will not surrender that easily” as a way to inhibit the male from his sexual attempt or conversely as a way of displaying her fighting ability and body condition. This perspective fits better with a “functional” notion of information (Carazo and Font 2010) that defines the informative content of a signal as precisely what makes the response to a signal adaptive for receivers.

Therefore, taking previous concepts into account, it seems evident that we underestimate communication when extreme sexual conflict occurs. Our sensorial universes undoubtedly limit our perceptions of animal communication. As various authors have stressed (Dawkins 1993; Huber 2005), much of animal communication takes place via signals that are difficult for us to perceive. Male coercion could include signals emitted with the aim of intimidating the other sex or displaying physical resistance. Conversely, female physical resistance could be associated with resistance signals emitted to inform the male her willingness to accept the fight. Moreover, the action of coercing or resisting intrinsically could be transmitting a message to the potential sexual partner. The message could be a threat, a signal emitted with the message “I disagree with your attempt and will fight back”. For example in spiders, aggressiveness is considered highly adaptive as it is

possibly related with hunting abilities and could be used for mutual mate assessment. Courtship and copulation in spiders can include pushes and forcing between the sexes, facts that could help the estimation between sexual partners and be positively related to mating success (Costa 1975; Eberhard and Huber 1998; Peretti et al. 2006). This context is something similar to a contest scenario where individuals compete aggressively and directly against one another and, additionally, can assess information about their own and their opponent's fighting ability (Briffa and Elwood 2009).

In addition, one possibility to examine communication between males and females, particularly under extreme sexual conflict, would be to use models of females, which cannot react to male behaviour, and see how this changes male response. In the near future one would expect researchers to be able to use female robots to mimic particular behaviours and test male response, but for the moment probably the most promising research would be using dead females as lures (A. Cordero Rivera, personal communication). In this scenario, males could be very persistent when females do not produce rejection signals, even those we are unaware of. One practical example is an anecdotal observation of a male damselfly trying to mate with a female that died after minutes of being captured in tandem: the male persisted for over 24 h in mating attempts, when usually males give up after a few minutes, presumably because females give them rejection signals (Cordero et al. 1992).

Undoubtedly, sexual coercion scenarios (e.g. harassment, forced copulations) require at least communication at basal levels, allowing species-specific recognition during courtship and/or copulation. Life histories, ecological and evolutionary pressures will be determining the characteristics of the signals displayed in sexual encounters.

Sexual signalling in systems under sexual coercion can be expected to vary in characteristics and/or intensity along the reproductive period, as a consequence of variance in mating opportunities, operational sex ratios and level of disagreement of sexual interests. Therefore, more empirical studies in natural conditions are needed in order to include life history and ecological contexts in our analysis—e.g. Christy and Salmon (1984) in crabs; Rowe et al. (1994) in water striders; Cordero Rivera and Andrés (2002) in damselflies; Bailey and Zuk (2008) in crickets. Currently, it is well-known that individual reproductive histories of both sexes influence the frequency of occurrence of their behavioural patterns (Savalli and Fox 1999; Danielson-François and Bukowski 2005), in particular, in modulating contexts of extreme sexual conflict. For example, history-dependent effect must be evaluated when cooperative and coercive strategies occur simultaneously in different mating phases of a single species (e.g. in coho salmon—Watters 2005; in bush crickets—Vahed and Carron 2008). Combin-

ing these approaches with fine-scaled analyses of behaviour could help answer some of the main questions about sexual communication such as what are the signals involved during the interaction, what is the form in which information is transferred between the sexes and what is the degree of behavioural plasticity in signalling according to life history and ecological constraints. In this scenario, future research should focus on the interaction between different modes of communication under changing environmental conditions (Van der Sluijs et al. 2011).

The survey of the present study also shows that during the last years the chemical channel has been increasingly studied, probably because of technological advances that allow the detection and identification of substances used in chemical communication. This anthropogenic bias was also detected by Coleman (2009) who, based on a search of the literature on mate choice, found that across sensory modalities, studies of visual and acoustic signals were the most common (46% and 30%, respectively), with relatively few studies investigating chemical, tactile and electrical signals in mate choice (3%, 3% and less than 1%, respectively). Therefore, this novel scenario opens a wide avenue for future research on sexual communication through chemical signals, in particular for studies on sexual conflict where the bias for the other channels seems to be higher. In addition, the low number of studies focused on the tactile channel under sexual selection hypotheses may be the result of underestimation due to observers' limitations in detecting subtle mechanic-sensory signals and individual responses during sexual interactions. This is a paradox of behavioural sciences since the tactile channel could be easily explored experimentally (e.g. by modifying appendages and/or covering receptors) in some groups used as model organisms for sexual selection studies such as insects and spiders (Andersson 1994; Eberhard 1996; Choe and Crespi 1997; Arnqvist and Rowe 2005).

Concluding remarks

Perhaps the most important conclusion from the analysed survey is that future work should test the fact that communication could also be occurring under extreme sexual conflict. For this research scenario, firstly, it is important to point out that the “arms race” between the sexes (Parker 1979) does not necessarily exclude the occurrence of either female choice or sensory exploitation. Indeed, the antagonistic seduction hypothesis (Holland and Rice 1998) suggests that males are selected to evolve a more extreme display trait to overcome the increased receiver threshold in a cyclic antagonistic coevolution. As a result, a chase-away process between male signals and female receivers develops, leading to exaggerated male

display traits and discriminating females. Furthermore, as Cordero and Eberhard (2003) stated, females under extreme conflict with males could nevertheless benefit in obtaining sons with superior manipulative abilities. Detailed studies of female and male behaviour during courtship and copulation, testing for the possibility of cryptic communication among the sexes seem promising for elucidating the degree of sexual conflict and its consequences on the communication systems and mating strategies of each species.

Secondly, though many species show sexual coercion in the form of forced copulation, a first phase of communication between the sexes—involving signals emitted by the female to the male—should be necessary to guarantee species-specific recognition and mate detection. Furthermore, we should be careful when interpreting sexual behaviour in coercive mating. From a functional information approach (Font and Carazo 2010) both forcing and resistance movements could be acting as signals that expect to generate a response on the other sex. If so, in these cases the degree of conflict among the sexes would be lower than expected and coercion as defined would need a detailed re-interpretation. Indeed, a promissory field for comparative and experimental studies would be to investigate the consequences of communication between sexes for the evolution of sexual strategies. In particular, how sexual conflict might be decreased as a result of communication (threats, bluffs, etc.), just as fights decrease in many animal contests as a result of signalling (Searcy and Nowicki 2005). However, to answer appropriately this question under an evolutionary context it is necessary to include fine-scaled observations in our studies on sexual communication. Paradoxically, this behavioural tool still waits for a better exploitation.

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