Chapter 18
Mating Is a Give-and-Take of Influence and Communication Between the Sexes

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Abstract Reproductive interactions between males and females often involve exchanges of signals or stimulation between the sexes, as for example when male–female duetting is used in pair formation. Such exchanges may also be common during copulation. For instance, while males court the female during copulation, females often also touch the male or otherwise move in ways that seem easily perceived by the male. Such movements may offer feedback to males about how the female is reacting or going to react to his efforts. This may have important effects on the dynamics of mate choice and on its consequences for sexual selection and divergence; e.g., the feedback contained in female sexual response may allow males to adjust their behavior in adaptive ways. The presence of male displays and female preferences plus female feedback and male attentiveness may have important consequences for the patterns of assortative mating and fertilization that become established in a population. Here I highlight selected examples of various contexts in which male–female exchanges may occur, before and during copulation. My goal is to initiate a discussion about the sources of selection that may influence the evolution of female feedback to males and of male attentiveness to such feedback and to sketch out some potential consequences for the course of sexual selection.

18.1 Introduction

The logic of the theory of sexual selection is based on the recognition of two distinct evolutionarily stable strategies for sexual reproduction: the male strategy, which specializes in competing for access to the gametes of many females, and the female strategy, which specializes in securing from a limited number of

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males the genetic and non-genetic resources that increase progeny numbers and fitness (Andersson 1994; Kokko et al. 2006). From the nature of these strategies, it follows that males are selected to seek and attract females and induce in them favorable behavioral and physiological responses, whereas females are selected to respond differentially to potential mates, accepting and cooperating with some and rejecting others (Andersson 1994; Cordero and Eberhard 2003; Andersson and Simmons 2006). The resulting competition and discrimination within and between the sexes give rise to sexual selection, a powerful engine of evolution responsible for the most dramatic cases of rapid divergence and trait elaboration that are found in nature (Darwin 1871; West-Eberhard 1983, 2014; Andersson 1994; Safran et al. 2012; Rodríguez et al. 2013a; Seddon et al. 2013).

Although the logic of sexual selection is well understood, biologists are only beginning to fathom how the behavior of each sex exerts selection on the other sex. Recent work has started to reveal that the "traditional" view of the sex roles presented above may hide two-way flows of influence and communication between the sexes. As many chapters in this volume show, biologists have generally abandoned the view of females as passive observers of male displays for a better understanding of their active role in effecting their reproductive decisions. But we are still just beginning to realize how active females are during the reproductive process and also the extent to which males pick up on this for their own advantage. I think that a picture is emerging in which—in addition to selection on males to induce females to accept them and selection on females to respond selectively to males—there is also selection on females to influence male behavior and selection on males to attend to female responses and adjust their behavior accordingly (West-Eberhard 1983; Rodríguez and Barbosa 2014).

In this chapter, I present selected vignettes that illustrate a variety of forms that two-way avenues of influence and communication between males and females may take. These go beyond the realization that females as well as males may be under sexual and social selection (West-Eberhard 1983, 2014; Clutton-Brock 2007, 2009; Rubenstein and Lovette 2009) and may occur with or without sex role reversal (Gwynne 1991; Andersson 1994). The point is that even mating systems with "traditional" sex roles often feature reciprocal interactions that occur as males court and females make decisions about mating and fertilization. I begin with examples of interactions leading to copulation before examining interactions that take place during copulation. Some of the examples represent cases where males pick up on incidental cues provided by female responses, while others represent cases where males attend to specialized signals produced by females. I try to be clear in making this cue–signal distinction, but part of the message is that it may be too early to do so—many female signals may appear to us as by-products of female responses simply because we are only beginning to examine the possibility of male–female reciprocal interactions during the reproductive process.

This is not at all an exhaustive review. Instead, my goal is to highlight a sample of suggestive case studies that help refine our understanding of the behavioral, physiological, and evolutionary dynamics involved in traditional mating systems. I then initiate a discussion about the potential impact of these dynamics on sexual selection and its role in speciation.

18.2 Examples of Back-and-Forth Interactions Leading to Pair Formation

18.2.1 Females Advise Males on How to Court Them

Female behavior may often offer feedback to males about the effect that their courtship is having, allowing for real-time adjustments. A dramatic example has been documented in bowerbirds (Borgia and Presgraves 1995; Patricelli et al. 2002, 2006). Female bowerbirds prefer high-intensity male displays, but such displays may also startle the females and hinder pair formation. The best courtship display is therefore not necessarily the most intense, but the most intense that a given female can stand. Males would thus benefit from gaging the tolerance for high-intensity displays of the female they are courting and tailoring their behavior to her. In satin bowerbirds, as a female watches a male display, her behavior and posture indicate her reactions: She may crouch, and the more that she crouches, the less threatened and more receptive that she is (Fig. 18.1a). Experiments using robotic females to manipulate female behavior (Fig. 18.1b) show that males attend to female crouching and modulate their behavior accordingly: They increase display intensity when the female crouches more and reduce it when the female is startled, so that the more attentive males increase the success of their courtship efforts (Patricelli et al. 2002, 2006).

18.2.2 Male–Female Signal Exchanges Lead to Pair Formation

In some cases, female behavior does not only provide cues that males may attend to or not. Instead, female responses to male behavior are an integral part of the
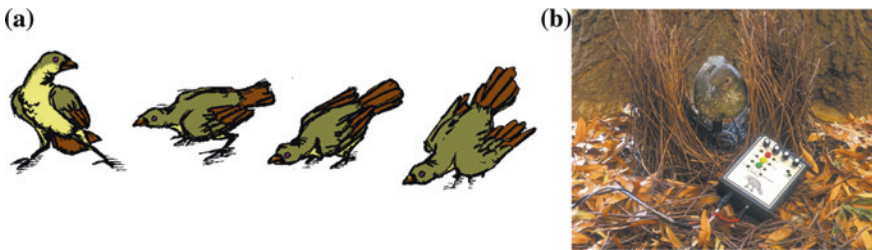

Fig. 18.1 Female behavior in satin bowerbirds provides feedback to males about their courtship efforts. **a** Variation in female posture indicates receptivity to high-intensity displays. The image on the *left* is of a female in the upright position upon arrival at the bower. The images to the *right* show stages of crouching, with the rightmost image showing the solicitation posture. Artwork by J. Albert Uy, reproduced with kind permission by J. Albert Uy and Gail Patricelli. **b** Experimental bower and robotic female (showing remote controller) used in tests of male attentiveness to female feedback. Photograph and permission by Gail Patricelli

pair formation process. In many insects and spiders, for instance, pair formation involves signal exchanges between males and females, or duets (Kraft 1982; Bailey 2003; Cocroft and Rodríguez 2005) (Fig. 18.2). In most insects that communicate with airborne sound, female signals are very short and mainly seem to convey their presence to the male (Bailey 2003). But in insects that communicate with substrate-borne vibrations, female response signals often resemble male signals in length and variability (Rodríguez and Barbosa 2014) (Fig. 18.2). This opens up the possibility that female duetting signals may contain feedback cues that males may attend to.

An example of information in female duetting signals occurs in *Enchenopa* treehoppers, phloem-feeding insects that communicate with plant-borne vibrational signals (Rodríguez and Cocroft 2006; Cocroft et al. 2008) (Fig. 18.2). *Enchenopa* females have strong mate preferences for male advertisement signals, and they express their preferences with their duetting behavior, being more likely to signal back to males that produce attractive signals (Rodríguez et al. 2004, 2006).
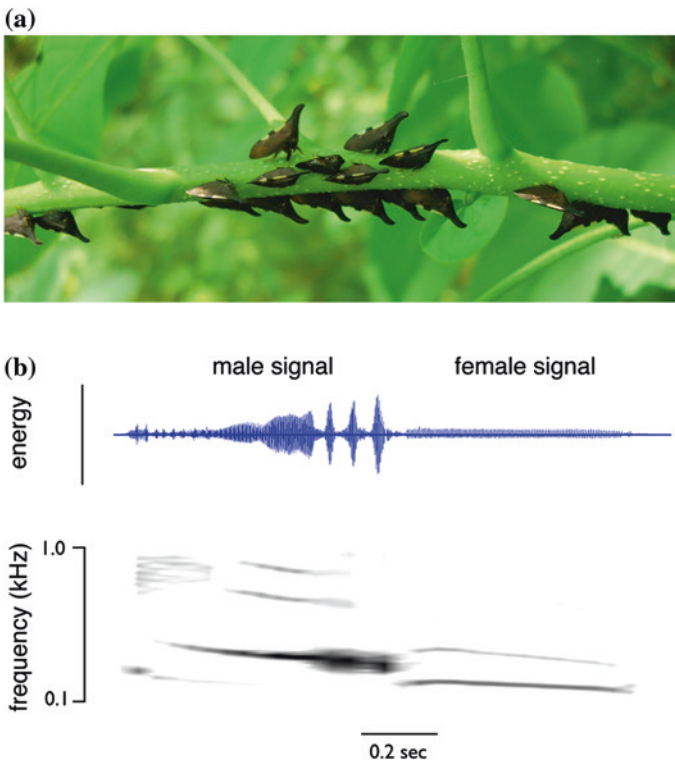

Fig. 18.2 Plant-borne vibrational communication in *Enchenopa binotata* treehoppers (Hemiptera: Membracidae). **a** Adult aggregation on the host plant *Ptelea trifoliata* (Rutaceae). **b** The basic unit of adult communication in *E. binotata*: a male-female signal duet. The male signal consists of a whine (a near-pure tone that slightly drops in frequency from beginning to end) followed by a series of pulses. The female signal consists of a single component

Females also produce more and longer signals when duetting with males that they find attractive, and males pick up on such variation in female behavior, being more likely to signal when they perceive longer female signals—i.e., those produced by females interacting with males they found attractive (Rodríguez et al. 2004, 2012; Rodríguez and Barbosa 2014).

18.2.3 Females Reassure Males About Their Receptivity

The above example shows that female duetting signals may convey information to the male not only about the female's presence but also about her receptivity. Such indications may be especially important in species in which the female's "intentions" toward the male may vary drastically. When females are larger than males, for instance, they may present a threat of injury or cannibalism, as in many spiders. In such cases, males approach females with extreme care, ready to flee at the slightest hint that she may attack (Kraft 1982; Uhl and Elias 2011). Male caution may reach such levels that males require encouragement from a particular female behavior before they will approach and attempt to copulate. A potential example of such reassurance by females occurs in *Schizocosa* wolf spiders (Stratton and Uetz 1981; Sullivan-Beckers and Hebets 2011, 2014). In these spiders, males court the female with vibrational–visual displays, and receptive females respond to male displays by turning in semicircles. These turns provide males with an indication about the females' receptivity: Courting males approach the female gradually, even when they have already located her, advancing slightly after each turn (Sullivan-Beckers and Hebets 2011).

Encouragement for the male to approach the female may also come from slight changes in her behavior, rather than from any one given behavior. In *Kukulcania hibernalis* crevice weaver spiders, for instance, females are initially aggressive toward courting males, moving swiftly within their web retreat or lunging out. But as males continue to court, females begin to move more slowly within their retreat, and this change seems to be what prompts the male to approach (Barrantes and Ramírez 2013).

18.2.4 When Males Succeeded in Attracting a Mate but Did not Realize It

Even in species with mating systems that lack clear male–female duetting, some form of communiqué from the female may be required to complete pair formation. I am only aware of anecdotal evidence for this, but the observations are intriguing. Consider a male frog signaling at a frog chorus. When a female finally arrives at the male's side, he often appears not to notice her, and she has to prod him before he realizes she is there and stops signaling to proceed to amplexus (Fig. 18.3).
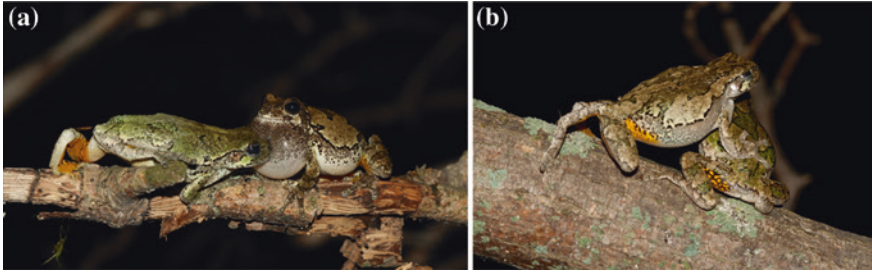
Fig. 18.3 Two occasions in which a female gray tree frog *Hyla versicolor* (Anura: Hylidae) arrived at the site of a signaling male and the male did not realize it. **a** The female (*left*) is prodding the male in an apparent attempt to proceed to amplexus, while he continues to signal (note his expanded vocal sac). **b** The female (*left*) climbing on the male as he continues to signal

An informed guess places the frequency of such occurrences at about half of observed pair formation interactions in tree frogs (Höbel, personal communication). Similar "attention-getting" behavior by females has also been noted occasionally in the above *Enchenopa* treehoppers (Sullivan-Beckers, personal communication).

18.3 Examples of Back-and-Forth Interactions that Take Place During Copulation

The above cases illustrate varied contexts and ways in which female behavior can provide feedback to males during pair formation, and in some cases, males attend to such feedback and adjust their behavior. Such reciprocal interactions also occur during copulation; indeed, they are much more likely during copulation than at earlier stages and present a far greater diversity of contexts and opportunities. The reason is simple physical opportunity: During copulation, males are in direct contact with the female and are thus more likely to be able to detect movements and responses made by the females, perhaps even slight changes in behavior or physiology (Fig. 18.4). Moreover, female behavior during copulation sometimes fits the criteria that would class male behavior as copulatory courtship: Female movements are repeated and stereotyped; likely to be sensed by the male; mechanically unnecessary for the female to retain her position (or to dislodge the male from his position); and not performed in contexts other than copulation (Eberhard 1994, 2005). Female copulatory behavior fits these criteria in about 10 % of a sample of 131 species of insects and spiders that were scrutinized for behavior during copulation (Eberhard 1994), which probably represents an underestimate. Such female behavior may influence male–female interactions in a large variety of ways, which we

Fig. 18.4 Comparison of the opportunity for males to obtain feedback about female reproductive decisions between pair formation (**a**) and copulation (**b**). In these gray tree frogs, *Hyla versicolor* (Anura: Hylidae), the greater contact during copulation clearly affords greater opportunity for feedback. Of course, this depends on the number of reproductive decisions that remain to be made by the female once copulation begins. In the case of species with cryptic female choice, the list may be considerable. But even without cryptic female choice, female feedback, male attentiveness, and male–female coordination may yet be favored (Sect. 18.3.5)

are just beginning to explore. Thus, behavioral and physiological feedback from females to males seems much more likely during copulation than at earlier stages in the reproductive process.

18.3.1 Females Advise Males on How to Court Them: Copulatory Dialogues

A spectacular example of male–female give-and-take during copulation was documented in *Physocyclus globusus* pholcid spiders (Huber and Eberhard 1997; Peretti et al. 2006; Peretti and Eberhard 2010; Calbacho-Rosa and Peretti 2015). In this species, males court females during copulation by using their pedipalps to squeeze the female abdomen. Squeezes are probably quite hard, as they are performed with the thickest muscles on the male body. Females favor males that squeeze more, but they also appear to attempt to induce males to loosen their squeezes: Females stridulate during copulation, and they are more likely to stridulate while males are squeezing them, especially during long squeezes or if the male had recently not responded to stridulation. Thus, the best courtship squeezes are not necessarily the most intense, but the most intense that a female will tolerate. Indeed, the more attentive males (those that loosen squeezes more often when females stridulate) gain greater fertilization success (Peretti et al. 2006; Peretti and Eberhard 2010).

This example makes a striking parallel with the satin bowerbird case study mentioned above (Sect. 18.2.1), and I suspect that this kind of back-and-forth between the sexes may be widespread. Another potential example occurs in *Glossina pallidipes* tsetse flies (Briceño and Eberhard in preparation). In these flies, males

use their cerci to squeeze the tip of the female abdomen during copulation. Females may vibrate their wings during squeezes, and males seem to respond to the females' wing vibration by shortening their squeezes (Briceño and Eberhard in preparation).

18.3.2 Females Warn Males of Likely Failure

Females sometimes appear to intimate when copulations are likely to fail. An example occurs in *Ozophora baranowskii* seed bugs (Rodríguez 1998, 1999). In these bugs, some copulations fail to result in sperm transfer, presumably because the female did not allow spermatophore transfer. During copulation, females tap males with their legs. The taps are not forceful. Instead, early in copulation, females tapped the male at higher rates in copulations in which no sperm transfer occurred and at lower rates in copulations that resulted in sperm transfer (Rodríguez 1998). These females thus appear to give males an early indication of their forthcoming decision. An analogous notice has been observed for female stridulation in some pholcid spiders, including the above *P. globosus*, in which females stridulate when an encounter is less likely to lead to copulation (Peretti et al. 2006; Dutto et al. 2011). I suspect that this type of feedback, before and during copulation, may turn out to be widespread (see e.g., Baena and Eberhard 2007).

18.3.3 Females Help the Males to Achieve Intromission

Females sometimes appear to help males in surprisingly active ways. Consider mating behavior in *Leiobunum vittatum* harvestmen (Fowler-Finn et al. 2014). Mating in this species begins when the male pounces on the female, wraps his legs around hers, and hooks his pedipalps on the base of her legs as she struggles and bobs. The female continues to struggle on and off during copulation. Nevertheless, she also lightly taps the male with her pedipalps in a way that would appear to be copulatory courtship (see above). Not only that, she also appears to help him achieve intromission, and he seems to be incapable of doing this by himself: When the male everts his penis to attempt intromission, the female places her pedipalps behind protrusions on the male's penis and appears to guide and pull him toward her. No intromission was observed without this behavior by the female (Fowler-Finn et al. 2014). Thus, it appears that in this species, males require the mechanical assistance from the females to achieve intromission.

There is a potential alternative interpretation of this female help. In the clade to which this harvestman belongs, males of some species provide nuptial gifts for females through their penis, and females acquire the nuptial gift by bringing the penis to their mouthparts (Macías-Ordóñez et al. 2010; Machado et al. 2015). In such cases, female tapping could be interpreted as solicitation of the nuptial gift

and guiding the penis toward her as securing the nuptial gift. Also, because the females' mouthparts and genital opening are close by, it is difficult to distinguish oral from genital insertion (Fowler-Finn et al. 2014). But even if a nuptial gift is involved, no intromission (whether oral or genital) ever occurred without the females' apparent help (Fowler-Finn et al. 2014). Thus, even if females were soliciting a direct benefit from the males, they also helped them achieve intromission in every observed instance. This is all the more remarkable if we recall that before and during copulation, there occur male–female struggles that would make one expect little assistance from the female for the male.

18.3.4 Females Stimulate the Male's Genitalia

A major advance in sexual selection has been the discovery of stimulatory functions for male genitalia in the context of cryptic female choice (Eberhard 2009). It thus seems fitting that a new development involves females that deliver stimulation directly to the male genitalia during copulation. In *Cyanopterus sphinx* fruit bats, for example, females often lick the base of the male penis during intromission, and there is a positive relationship between this licking and the duration of copulation (Tan et al. 2009). Licking may have antibiotic effects or other advantages, but there may also be some benefit in extending the duration of copulation, such as increased sperm transfer (Tan et al. 2009). Such potential benefits are suggested by yet another twist in the tale: In *Pteropus giganteus* flying foxes, males lick the female genitalia before and after copulation, and there is a positive relationship between the duration of precopulatory licking and the duration of copulation (Maruthupandian and Marimuthu 2013).

18.3.5 Females Let the Male Know When They Are Ready to Lay Eggs

As the stages of the reproductive process advance from pair formation to fertilization, one could expect that the need for a jostle of persuasion and influence would diminish, because the higher the number of decisions that a female has already made in favor of a given male, the better aligned that their evolutionary interests should become (Alexander et al. 1997). Nevertheless, even when nothing remains but to proceed to fertilization, there still remain opportunities for male–female reciprocal interactions. An example of this has been noted anecdotally in *Hyla versicolor* tree frogs (Höbel, personal communication). In these frogs, females do not lay all of their eggs at once. Instead, they lay a few eggs at a time, in bouts separated by a few minutes, and it may take a few hours until a female has laid all of her eggs. Immediately before each bout of egg laying, females shiver their body and arch their back. It is not known if these movements are required

for laying eggs or if they might constitute a specialized signal. Even in the former case, however, they could potentially alert the male (who all the while is in amplexus with the female; Fig. 18.4b) that egg laying is imminent, and this could help him time the release of his sperm appropriately. It is easy to imagine that the precision of this timing, and hence his fertilization success, could be severely hurt if such cues from the female were lacking.

18.4 Examples of Male–Female Interactions that I Have not Considered to Be Reciprocal

The examples in Sects. 18.2 and 18.3 go beyond documenting an active role for females in mate choice; they feature behavior that may convey feedback to the male, which he may use to his own advantage. To clarify the distinction between these two types of active participation by the female in the reproductive process, here I present examples of interactions that, although illuminating about the role of female behavior in mate choice in "traditional" mating systems, do not seem to involve potential female feedback and male attentiveness.

18.4.1 Females Signal to Attract More Potential Mates and Broaden Their Prospects for Choice

When males display to attract females, females do not simply watch the males, while they evaluate them and make their reproductive decisions. Instead, females move about from male to male or from site to site, seeking out and comparing the most attractive individuals and then making decisions (e.g., Uy et al. 2001; Murphy and Gerhardt 2002; Murphy 2012). Females may also seek to foster competition between males to facilitate their own comparisons and broaden the scope of their sampling. An excellent example of this occurs in *Gallinago media* great snipes (Sæther 2002). In these birds, males form leks where they gather to display and attract females. When females visit the leks, they produce loud signals, which attract males that then proceed to engage in fights. Males also lengthen their own signals in response to the females' signals, which makes them more attractive (Sæther 2002).

Another example of females seeking to increase the males they sample and to make them compete with each other occurs in the *Enchenopa* treehoppers mentioned in Sect. 18.2.2. Sometimes, when a male and a female are engaged in a duet and he is searching for her, he decreases the amplitude of his signals, but she increases the amplitude of hers (Rodríguez and Barbosa 2014). This would seem to increase the potential for detection by other males that may then approach the female and increase her prospects for choice. Similarly, female copulation

calls—produced by females during copulation—seem to function to attract other males that may supplant the one currently copulating with the female (e.g., Løvlie et al. 2014).

18.4.2 Females Push or Kick the Male, Rather Than Gently Tap Him

Some of the female behaviors involved in the above interactions are subtle. But female tactics are not always restricted to gentle persuasion. In a close relative of the seed bug mentioned in Sect. 18.3.2, females push the male forcefully rather than tap him lightly and do so mostly toward the end of copulation (Rodríguez 1999). This behavior thus appears to be a forceful way to end copulation, rather than a signal seeking to induce a change in the male behavior. Such attempts by females to shake off or dislodge males during copulation are not uncommon (Eberhard 1994). A dramatic example occurs in *Callosobruchus maculatus* bean weevils (Crudgington and Siva-Jothy 2000; Edvardsson and Tregenza 2005; Hotzy and Arnqvist 2009). In these beetles, males have spiny genitalia that puncture the lining of the female genital tract (Crudgington and Siva-Jothy 2000), and spine length is positively correlated with fertilization success across populations (Hotzy and Arnqvist 2009). But puncturing damages the females' genitalia and lowers their longevity and fecundity, and females kick the males toward the end of copulation (Crudgington and Siva-Jothy 2000; Edvardsson and Tregenza 2005). Preventing the females from kicking results in longer and more damaging copulations (Crudgington and Siva-Jothy 2000), although there is evidence that female kicking itself may worsen the damage caused by male genitalia (Wilson and Tomkins 2014).

18.4.3 Females Cooperate with the Male to Form a Copulatory Plug

Female choice hinges on selective cooperation with some males and rejection of others, and such cooperation may involve many potential types of behavioral or physiological interactions with males (Eberhard 1996; Cordero and Eberhard 2003). But cooperative interactions may occur without exchanges of stimulation and influence or feedback from females that modifies male behavior. An example occurs in *Leucauge mariana* orb web spiders (Eberhard and Huber 1998; Aisenberg and Eberhard 2009; Aisenberg et al. 2015). In these spiders, males begin to form a plug on the female's genital plate by depositing a paste. But this alone is not sufficient to form an effective plug. The latter requires that the females add to the male's paste a liquid that she secretes, and females may be swayed to

cooperate with the male in this manner by his copulatory courtship (Aisenberg and Eberhard 2009; Aisenberg et al. 2015). Similarly, in *Argiope keyserlingi* orb web spiders, all the female has to do is allow the male sufficient time to break off and lodge a fragment of his genitalia in her genital opening in a position that will make an effective plug; if she ends the copulation earlier, fragments of the male's genitalia are not lodged well and do not make an effective plug (Herbertstein et al. 2012; Schneider et al. 2015).

18.5 Discussion

Sexual selection research has achieved several major breakthroughs in the last few decades. These include the belated acceptance of Darwin's proposal that female mate choice is widespread in nature (Darwin 1871; West-Eberhard 1983; Andersson 1994; Andersson and Simmons 2006); the discovery that male–male competition, courtship, and mate choice continue after mating begins (Eberhard 1985, 1996, 2009; Birkhead and Møller 1998); and technical progress allowing the examination of genital behavior inside the body of the female (Briceño et al. 2010; Eberhard 2011; Briceño and Eberhard 2015). Another major breakthrough may lie in the realization that as females make mating and fertilization decisions, the changes in their behavior and physiology that effect those decisions provide males with indications about their motivation and attitude. Males may be able to use those cues to make inferences about likely female responses and adaptively modify their own behavior and tactics. Thus, male–female interactions that have historically been characterized as one-way avenues of communication between male signalers and female receivers may in fact involve two-way avenues of communication, stimulation, persuasion, and influence.

Here I have examined examples of such exchanges: four case studies dealing with precopulatory interactions and another six involving interactions during copulation. At both stages of the reproductive process, there seems to be ample opportunity for feedback from the female to the male. In some cases, such feedback has been shown to be used by males to modify their behavior and improve their mating or fertilization success. Of course, this short list of vignettes very likely underestimates the variety of contexts and circumstances in which reciprocal male–female interactions may be involved in pre- and postcopulatory mate choice.

18.5.1 The Evolution of Female Feedback and Male Attentiveness

Under what conditions does selection favor females that provide feedback to males? And under what conditions does selection favor males that attend to such feedback? There are varied potential benefits to this. It may increase the

efficiency of sexual interactions and reduce associated costs. For instance, if a female intimates early during copulation that she will not allow sperm transfer, and if the male attends to her indication and gives the mating up, both may save fruitless expenditure of time and energy and decrease the risk of being caught by a predator. The male might also save sperm, e.g., if females reject males by ejecting freshly transferred sperm, as in the seed bug and pholcid spider case studies discussed above (Sects. 18.3.1 and 18.3.2) (Rodríguez 1998, 1999; Peretti et al. 2006; Peretti and Eberhard 2010). Alternatively, feedback may represent a way to resolve a trade-off that arises when intense stimulation is attractive but potentially harmful, as in the pholcid spiders above (Sect. 18.3.1). It may also help synchronize male and female activities once their evolutionary interests are more aligned (e.g., Sect. 18.3.5).

When addressing the above questions, two considerations suggest that we may not always need to identify benefits to females from providing feedback to males in order to explain the evolution of such feedback. The first consideration is that female responses that offer feedback may range from incidental cues to specialized signals. Indeed, feedback may originate as incidental cues that come under selection to influence male behavior to the females' advantage, thereby giving rise to specialized signals—which is one of the main hypotheses about the evolution of signals in communication systems (Greenfield 2002). We should thus expect to find in nature cases where males attend to incidental cues and other cases where males attend to signals and only in the latter cases would it make sense to ask about the benefits that may have selected for such feedback signals. Further, we do see in nature the full spectrum between females that provide feedback and females that use force, even among closely related species, as in the two seed bugs discussed above (Sects. 18.3.2 and 18.4.2) (Rodríguez 1998, 1999). We also find the full spectrum between attentive and forceful males. Research should seek to identify the causes of such variation in the nature of male–female interactions.

The second consideration involves the potential for a process of male–female coevolution analogous to Fisherian selection (Fisher 1958; West-Eberhard 1983; Mead and Arnold 2004; Fowler-Finn and Rodríguez 2015). In terms of female feedback and male attentiveness, this process would follow from the following conditions: (i) genetic variation in the female response (behavioral or physiological) that provides feedback; (ii) genetic variation in male attentiveness to such feedback; and (iii) assortative mating or fertilization, such that more attentive males tend to mate or fertilize females that provide feedback—e.g., males and females that are better able to coordinate their interactions may be more likely to mate and achieve fertilization (cf. Derlink et al. 2014). Under these conditions, there would arise a genetic correlation between female feedback and male attentiveness. This genetic correlation would, in turn, have the following consequences: Male attentiveness would be favored by the presence of feedback; the resulting increase in attentiveness would bring an increase in feedback as a correlated response; the increase in feedback in turn would continue to favor attentiveness and so on in self-reinforcing loops halted only by loss of genetic variation or costs

to feedback or attentiveness (e.g., if providing feedback increased the risk of predation). Thus, the advantage to females may simply be the production of sons that are attentive to feedback and daughters that provide feedback.

18.5.2 Evolutionary Consequences of Female Feedback and Male Attentiveness

If "traditional" mating systems with competitive males and choosy females were to commonly feature feedback from females and attentiveness to that feedback by males, what would be the impact on our view of sexual selection and its consequences for divergence?

One potential consequence is for sexual conflict to be reduced. Consider males selected to deliver strong stimulation that improves their fertilization success but that may harm the female. In such cases, female feedback and male attentiveness may help resolve the stimulation–harm trade-off at an intermediate level of stimulation that proves effective but less damaging to the females (cf. West-Eberhard 2014).

Another consequence may be to increase the number of traits that may be involved in Fisherian selection. The standard theory for Fisherian selection features one trait in males (the display) and one trait in females (the preference) (Fisher 1958; Mead and Arnold 2004). Female feedback and male attentiveness may add traits to this mixture. For males, it seems straightforward to posit two traits: a display plus the ability to sense and react to feedback from the female. For females, it is similarly straightforward to posit two traits: a mate preference function (Ritchie 1996; Rodríguez et al. 2006, 2013b) and the behavior that expresses the mate preference and provides feedback to the male. Reality may be more complex than this, of course, but this scenario serves to highlight a series of potential outcomes. If a higher number of traits in each sex enter into the dynamics of Fisherian selection (if the required conditions are met; Sect. 18.5.1 above), there may be a greater likelihood of divergence in sexual traits and thus of reproductive isolation. For example, if feedback arises in one population and not in another, the pathways of male-female coevolution may diverge and lead to speciation.

It will be important to bear in mind that feedback and attentiveness may influence patterns of assortative mating and fertilization in a population. Male attentiveness to female feedback may reinforce the patterns of assortative mating that are established by female mate choice if males are more likely to pursue females that they know find them attractive (cf. Rodríguez et al. 2012; Rodríguez and Barbosa 2014). Alternatively, if males are able to tailor their courtship for different kinds of females, this may lead to patterns of mating that counter what would arise from female mate choice alone (cf. Kozak et al. 2009).

The above discussions have the implicit assumption that if selection were to favor male attentiveness and female feedback, it would favor high levels of attentiveness and feedback. But it is quite possible that intermediate levels would

be optimal—say, enough male attentiveness to fit the specific female they are interacting with, but not so much that stimulation weakens too much, or enough feedback to increase the likelihood of success for an attractive male, but not so much that any male could reach high attractiveness. If so, there may be multiple combinations of levels in feedback/attentiveness that reach optimal outcomes, such as high feedback paired with low attentiveness, or low feedback paired with high attentiveness. The resulting evolutionary dynamics in such cases might resemble the scenario of coadaptation theory developed for parent–offspring conflict (Agrawal et al. 2001; Kölliker et al. 2012). This might mean that some components of a mating system exhibit Fisherian-like dynamics of self-reinforcing coevolution driven by positive genetic correlations, while other components are stabilized by negative genetic correlations.

In conclusion, there is much insight to be gained from exploring the nature of male–female interactions throughout the reproductive process. This is challenging, because it requires observational, experimental, and comparative studies to ask whether and how the behavioral and physiological responses of each sex modify the responses of the other sex. At our current state of knowledge, perhaps the first step should be to explore the variety of forms feedback and attentiveness take in nature.

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