



Review

Darwin's forgotten idea: The social essence of sexual selection



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ABSTRACT

Darwinian sexual selection can now be seen in the broader context of social selection, or social competition for resources (under sexual selection, mates or fertilization success). The social-interaction aspects of sexually selected traits give them special evolutionary properties of interest for neurobiological studies of stimulus–response systems because they can account for highly complex systems with little information content other than stimulatory effectiveness *per se*. But these special properties have a long history of being forgotten when other factors dominate the analysis of male–female interactions, such as the mistaken belief that differential responsiveness to signals produced by competing rivals (“female choice”) requires an esthetic sense; that species recognition explains all species-specific sexual signals; and, more recently, that successful signals must reflect good survival genes; or that male–female conflict involves female resistance rather than stimulus evaluation. A “conflict paradox” results when male–female conflict is seen as driven by natural selection, whose costs should often move the hypothesized “sexually antagonistic co-evolution” of sensory-response systems toward the powerful domain of *sexually synergistic co-evolution* under sexual selection. Special properties of sexual selection apply to other forms of social competition as well, showing the wisdom of Darwin's setting it apart from natural selection as an explanation of many otherwise puzzling and extreme traits.

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1. Introduction

Darwin (1859 [1872]) wrote two major books on evolution by selection. The first, *On the Origin of Species by means of Natural Selection*, is devoted primarily to evolution by natural selection, and the second, *The Descent of Man and Selection in relation to Sex* (1871) treats evolution under sexual selection. In 1860, while beginning work on the second book, Darwin wrote a letter to Asa Gray that refers in uncharacteristic dramatic language to traits that defy explanation in terms of natural selection, or the struggle for existence: “I remember well the time when the thought of the eye made me cold all over. . . now small trifling particulars of structure often make me very uncomfortable. The sight of a feather in a peacock’s tail, whenever I gaze at it, makes me sick!” (from Darwin, 1892 [1958], p. 244).

The peacock’s tail is part of a sexually selected communication system whose exaggerated complexity, like that of the human brain (see Flinn et al., 2005), is expected to characterize traits that are under strong social selection. The complexity of sexually selected communication is well illustrated in this issue. Social competition exploits a multitude of sensory-response capacities, often more than one simultaneously, as in the multimodal signals of golden-collared manakins (Barske et al, this issue) and spiders (Herberstein et al, this issue). Phonological and syntactical complexity is illustrated by Bengalese finches (see Suzuki et al., this issue); and Zuk and Beani (this issue) discuss contributions that explore striking sex-related differences in brain and behavior. Here I briefly review the special properties of social selection and show why it can produce complexity and exaggeration that exceeds that usually expected under natural selection. Understanding this distinction is important for any neurobiologist or animal behaviorist interested in the functions of signal-response systems, for the properties of such systems depend on the context in which they have evolved. The neural development of human infants, for example, shows a mosaic pattern of slowness in aspects that reflect a prolonged physical dependence on others, while being precocious in aspects under social selection for effective monitoring and manipulation of the caretakers on whom they depend (Hrdy, 2014).

This issue of Neuroscience & Biobehavioral Reviews offers a fresh look at sexual selection and beyond. Clearly, there is more to the evolution of the sexes than just sex as the production of offspring. But the evolutionary neurobiology of male–female interactions requires clarity about what Darwin meant by sexual selection. And the meaning of sexual selection is elusive when the distinction between natural and sexual selection is lost. So I briefly discuss some prominent examples of sexual-selection amnesia here. The point is not to defend sexual selection theory as the best possible explanation for sexually dimorphic traits, or to regard Darwin’s writings as sacred text. The point is to show how easily the special, social essence of sexual selection can disappear from view, and to argue for its importance in understanding the neurobiology and behavior of sexual interactions.

2. Darwin’s distinction between natural selection and sexual selection

Darwin insisted repeatedly on the distinction between sexual selection and natural selection, with sexual selection favoring traits that benefit their bearers “not from being better fitted to survive in the struggle for existence, but from having gained an advantage over other males, and from having transmitted this advantage to their male offspring alone. It was the importance of this distinction which led me to designate this form of selection as Sexual Selection” (1871 [1877], p. 210). “This form of selection depends, not on a struggle for existence in relation to other organic

beings or to external conditions, but on a struggle between the individuals of one sex, generally the males, for the possession of the other sex” (Darwin, 1859 [1872], p. 76). Darwin emphasized the importance of the distinction repeatedly. He sometimes used “ordinary selection” to refer to natural selection (e.g. 1871 [1877], p. 209) as distinct from sexual selection.

The statement I find most helpful to clarify the distinction between natural and sexual selection as social selection features an example – the prehensile organs (claspings antennae, and legs) of male crustaceans:

We may suspect that it is because these animals are washed about by the waves of the open sea, that they require these organs in order to propagate their kind, and if so, their development has been the result of ordinary or natural selection. . . if the chief service rendered to the male by his prehensile organs is to prevent the escape of the female before the arrival of other males, or when assaulted by them, these organs will have been perfected through sexual selection (Darwin 1871 [1877] p. 209).

Here Darwin distinguishes between the non-social and the social environments – a struggle with waves vs conspecific rivals in the effort to hang onto a mate. Both can affect “mating success” or “reproductive success,” and both can occur simultaneously, but only the social struggle falls under sexual selection (see also Murphy, 1998). This passage also illustrates the difficulty, and the ultimate futility, of trying to make an absolute distinction between natural and sexual selection in view of discoveries made in subsequent research. Sexual selection is now more broadly defined in terms of fertilization success, to include male–male sperm competition and “cryptic female choice,” or contests where a male competes to induce females to process the male’s sperm, discard the previous male’s sperm, oviposit more quickly, resist further males, etc. Such cryptic social contests among rivals were invisible to Darwin and his contemporaries, and so were unsuspected even when affected by visible morphology (such as elaborate male genitalia) or external behaviors, such as movements by the claspings organs of a male crab that might affect the internal responses of a female (see Birkhead and Møller, 1998; Eberhard, 1985, 1996, 2009). These more recently studied phenomena expand the scope of sexually selected interactions envisioned by Darwin’s example.

Notwithstanding the difficulties of a consistent distinction between natural and sexual selection, given the clear evidence of Darwin’s intended meaning the Darwinian concept of sexual selection can be reworded as *social competition for mates or fertilization success via courtship and male–male contests* (“Darwinian sexual selection”) as contrasted with non-interactional definitions (see Murphy, 1998).

Sexual selection often involves communication – courtship and threat signals – but the signals need not convey any information about the quality of the sender under natural selection. Darwin (1858, p.98) recognized that health and vigor could play a role in female choice, and that natural and sexual selection may act together to favor the same traits. But he consistently classified health and vigor signals as products of natural, not sexual selection. *Signals under sexual and other kinds of social selection (see below) are favored because of their effects on others, not their value as indicators of quality in other contexts.* It is for this reason that sexually selected signals are sometimes considered “abstract” or “symbolic.”

3. Darwinian sexual selection as social selection

Given the many examples discussed by Darwin, Darwinian sexual selection is a kind of social selection, or interactive intraspecific competition for resources, where the contested resource is mates (fertilization success). Darwin recognized two kinds of competitive social behavior under the heading of sexual selection:

courtship – contests of attractiveness, or ability to stimulate potential mates in ways favorable to mating; and battle – contests of strength, where the interactions involve weaponry and threats among rivals. Although sometimes courtship is called “inter-sexual” and combat “intra-sexual” sexual selection, this is potentially confusing: all sexual selection is *intra-sexual* competition for mates, whether via courtship or battle (see also Fisher 1930, p. 147).

Examples of non-sexual social competition include territorial and dominance (status) competition among females, worker choice of queens in social insects, and competition among offspring for parental attention (see Amundson, 2000; Benenson, 2013; Clutton-Brock and Huchard, 2013; Lyon and Mongomerie, 2012; Mas and Kölliker, 2008; Stockley and Bro-Jorgenson, 2011; West-Eberhard, 1983, 1984). Monogamous females may have displays that reinforce the pair bond and increase paternal investment, an additional kind of non-sexual social selection (e.g. see Servedio et al., 2013 on female adornments in the great crested grebe).

Darwin did not generalize beyond sexual selection to other kinds of social selection. He thought that most exaggerated or colorful traits of females in monomorphically bright species evolved under sexual selection on males and then were transferred to females as a pleiotropic effect with no evolved function. *Cross-sexual transfer* in the expression of sexually selected traits does occur during evolution and is an important source of evolutionary novelty (see West-Eberhard, 2003, chapter 15). Although Darwin did not focus on the competitive behavior of females (for possible reasons see Andersson, 1994; and Hrdy, 2013), he did suggest that there might be *mutual sexual selection* (“a double process of selection”), on males to choose females and on females to choose males (1871 [1877], p. 225). Darwin also noted sex-role reversals, where females are the sexually selected sex, and associated them with a reversal of sex roles in parental investment, an insight usually attributed to later authors like Bateman (1948) and Trivers (1972). For a review on male mate choice in insects, see Bonduriansky, 2001; Beani et al., this issue). But females engage in other kinds of social competition, e.g. territorial or dominance interactions, using or displaying male-like or female-limited bright or complex socially competitive traits (see West-Eberhard, 1978, 1983, 1984).

Social (including sexual) selection and natural selection are both Darwinian selection – differential fitness, or reproductive success, and both may influence the evolution of a particular trait. So why insist on distinguishing between them? There are powerful reasons for the distinction in studies of sensory-response systems, whose peculiarities, exaggeration, and degree of complexity can be explained or even predicted by the selective context in which they evolved.

4. Special properties of social selection

The social essence of sexual selection gives rise to a number of special evolutionary properties seldom or never shown by traits under natural selection alone (see Wolf et al., 1999 for a model). Some of these properties enhance the *diversifying* effect of selection on different populations, promoting the evolution of phenotypes that are unusually distinctive or extreme and population or species specific (West-Eberhard, 1983); other aspects enhance the *strength* of sexual selection (Rodriquez et al., 2013 discuss this distinction). Special properties of social selection include the following (for more complete discussions see Lyon and Mongomerie, 2012; West-Eberhard, 1979, 1983, 1984).

4.1. The unending nature of change

Social selection promotes the evolution of extreme phenotypes in part because combat and contests of attractiveness represent

unending races among rivals: the social environment for social selection changes with every improvement in a sexually competitive trait, so that there are moving targets and an unending co-evolutionary race. Under natural selection, by contrast, the contest is with a relatively unchanging environment, or one that usually does not change in response to progress achieved, a notable exception being co-evolutionary races between species-specific parasites or pathogens and their hosts. As expressed by Darwin (1871 [1877], p. 226): “in regard to structures acquired through ordinary or natural selection, there is in most cases, as long as the conditions of life remain the same, a limit to the amount of advantageous modification in relation to certain special purposes; but in regard to structures adapted to make one male victorious over another, either in fighting or in charming the female, there is no definite limit to the amount of advantageous modification; so that as long as the proper variations arise the work of sexual selection will go on.”

4.2. The potential for runaway change under choice

Fisher (1930) extended Darwin’s interactional concept of sexual selection to incorporate original insights based on genetics. Fisher noted that the elaboration of traits involving combat or threat signals are constrained to reflect “genuine prowess” or true ability to fight (Fisher 1930 [1958], p. 156; see also West-Eberhard, 1979). Contests involving choice, by contrast, have the potential for a runaway process, with a genetic correlation between traits affecting preference and attractiveness producing mutual reinforcement of the evolution of those traits until eventually slowed or checked by some disadvantage under natural selection (Fisher, 1930). Note, that the runaway process of ever-accelerating geometric increase in trait exaggeration applies not only to the quantitative increase in each quantitatively variable stimulus and response, but also to the increase in numbers of traits added – the complexity of displays. So, combined with the relative lack of a ceiling for change, and the large number and diversity of stimuli that can simultaneously affect choice, the runaway process has a greater potential to have a long-term effect on sexual selection than argued by theoreticians who emphasize the limits to genetic variation under sexual selection on a single quantitatively variable trait (sometimes called the “lek paradox” [review in Andersson, 1994]).

The Fisherian runaway process begins with differential female responsiveness (“preference”) to signals originally established under natural selection, which is then exaggerated because any such preference is favored by selection on preference itself. Price (2008), following Fisher, emphasizes the “stimulatory value” of the ancestral naturally selected trait, and considers the Lande (1981) model of the process, which begins with spread due to drift, “unlikely to be of great importance” because there is so little evidence that drift has been responsible for the origin and spread of any new phenotypic trait (see also West-Eberhard, 2003, p. 144).

Under social selection theory Fisher’s ideas regarding female choice of mates can be extended to apply to choice in other contexts, such as parental choice of offspring competing for parental attention (e.g. see Lyon et al., 1994), and worker choice (acceptance or rejection) of competing queens in social insects (West-Eberhard, 1983, 1984).

4.3. The relentlessness of social selection within and across generations

Social competition within groups for access to resources – in the case of sexual selection, mates – affects every reproducing individual of every generation in sexually reproducing species, whereas natural selection is not always so consistent: not every individual

of a population may be affected by a particular kind of predator, for example, or be subjected to the same range of climatic conditions.

4.4. The very large number of factors and cues that can initiate change in new directions (see [West-Eberhard, 1983](#))

The very large number of factors and cues that can initiate change in new directions include (1) *environmental factors* that modify the effectiveness of signals and fighting tactics (e.g. see [Trillo et al., 2012](#) on the effect of bat predation in reducing signal complexity; [Price \(1998, 2008\)](#) extensively discusses the relationship between social selection and ecological factors for diversification in birds); (2) multiple *pre-existing sensory capacities* of rivals and courted individuals. Every sensory modality, under selection in numerous evolutionary contexts, can produce stimulus–response systems that can secondarily serve as attention-getting or attractive devices under social selection (see [Ryan, 1990](#) on sensory exploitation); (3) *variations in the responsiveness of receivers*, due to such variables as age, condition, and experience; (4) *imitation* of successful individuals in species capable of learning; (5) *indicators of superior fitness* favored under natural selection (“good survival genes”), and subsequently modified under social selection for attractiveness *per se*; and (6) the advantage of *novelty* in combat and display, where a new trait can arrest the attention of others and thereby affect their preferences, or subvert the tactics of unprepared rivals ([Darwin, 1871a](#); [West-Eberhard, 1983](#)).

4.5. The potential for very large differences in reproductive success

Traits that influence sexual/social contests are under extraordinarily strong selection (large fitness differences can be associated with winning vs losing under social selection), especially in populations where individuals are obliged to compete within groups where one or a few group members can monopolize access to some resource (e.g. leks, shared territories, or within shared nests).

In general, selection on males and females is *synergistic* in terms of its effects on sexually selected traits (i.e., the socially competitive traits of males), and this helps account for the often striking nature of traits under sexual selection. Even when female choice is based on male victory in contests among males, with no direct interaction or Fisherian genetic correlation between the sexes involved, there is mutually reinforcing synergism rather than antagonism, in the traits favored by selection on males and females. This synergism applies even when the interests of the two sexes are not identical, due to underlying differences in parental investment.

5. When to suspect that sexual/social selection may be important

I have very often seen publications and lectures by otherwise competent and even eminent biologists, where sexual selection or social competition ought to be considered but is not, even while the author(s) labor mightily to give a thorough account for the evolution of a trait. Innocent ignorance about sexual selection is sometimes betrayed by misuse of its concepts, like assuming “male choice” in a species whose polygamous mating system justifies attention to female choice instead. And the term “sexual selection” appears in titles of papers dedicated to subjects like good-genes female choice and sexually antagonistic co-evolution, that in fact view those phenomena as dominated by natural, not sexual, selection (see below).

Sexual-selection *amnesia* and the related problem of neglect of social aspects of sexual selection are easily remedied problems once

the symptoms and signs of sexual/social selection are recognized. A role for sexual or some other form of social selection should be investigated, though it is not proved, whenever a trait shows one or more of the following symptoms:

- Extreme development or striking complexity (as in peacock’s tails, the horns of beetles, animal genitalia, the human brain, the colorful mouths of nestling birds), sometimes leading to sexual dimorphism or rank-dependent polymorphism in the expression of such traits. When a striking or complex trait is sexually monomorphic, female-limited, or observed in immatures it may be under non-sexual social selection.
- Marked geographic variation, phylogenetic diversification, or species- and population-specificity of a trait, suggesting rapid divergence of genetically isolated populations, or culturally isolated populations capable of learning (plumage of birds; horns of beetles; human languages and dialects).
- Use in contests or socially competitive displays as revealed by observations of behavior, as in observations of combat or courtship where colorful plumes or extreme morphologies come obviously into play.

6. Sexual-selection amnesia and the interplay between natural and sexual selection

The Darwinian concept of sexual selection as social selection has been repeatedly forgotten within evolutionary biology, beginning soon after publication of Darwin’s treatise on the subject (for a concise history of reasons see [Andersson, 1994](#)). Sexual selection amnesia also characterizes many modern discussions of sexual selection, which often emphasize the importance of natural selection for the evolution of sexual signals and female choice. When that happens rich possibilities for insights regarding the evolution of male and female neurobiology, behavior, and morphology are inadvertently lost from view.

During the mid-twentieth century synthesis in evolutionary biology [Fisher \(1930\)](#) importantly extended Darwin’s approach to sexual selection (see above), but there was a nearly complete blackout of the theory among organismal biologists (with some exceptions, e.g. [Huxley, 1938](#)). This affected students like me who were steeped in the organismic evolutionary biology of the time, especially as applied to speciation and animal behavior. Divergence between populations was seen as a result of selection for adaptation to ecological differences, and when it concerned sexual behavior and associated morphology the divergent phenotypes were seen primarily or even exclusively as products of selection for pre-mating reproductive isolation or species recognition – traits evolved under selection to prevent costly interbreeding between incompatible gene pools that had diverged under natural selection (see especially [Dobzhansky, 1937](#); [Mayr, 1963](#)). Despite the weakness of this argument as an explanation of elaborate secondary sexual traits (see [West-Eberhard, 1983](#); [Eberhard, 1985, 1996](#)) it persists in the minds of many biologists today. So any casual mention of species recognition as the explanation for such traits should be regarded as a blinking red arrow pointing toward a need for careful consideration of the possibility that sexual selection could have played a role.

Sexual selection theory seemed to undergo a revival in the early 1970s, with interest in its relationship to parental investment and the nature of mating systems ([Emlen and Oring, 1977](#); [Trivers, 1972](#), and other authors, including [Mayr, 1972](#), in [Campbell, 1972](#)). But then important components of Darwin’s idea were forgotten again when vast areas of research on sexual behavior focused on approaches that propose alternative explanations (next section).

6.1. Natural and sexual selection in signal evolution

One remedy for sexual selection amnesia is to see the evolution of sexual signals as interplay between natural and sexual selection. Males exploit a great variety of neuro-hormonal channels during competitive and manipulative sexual interactions. Those channels probably usually, perhaps always, originate under natural selection, and then come under sexual selection during interactive competition for fertilization success. Then sensory-response systems can reach unusual levels of elaboration, plasticity, and diversification that would not occur under natural selection alone (see West-Eberhard, 2003; Price, 2006). Natural selection may ultimately curb the effects of sexual selection, and good condition under natural selection can help bear the costs of exaggerated socially selected traits (Price, 2006). But social interactions can take precedence over or complement survival selection when they determine access to critical resources like mates and other resources; and the special properties of socially mediated selection can drive neuro-hormonal systems to levels of elaboration beyond those achieved under natural selection alone. These features of the interplay between natural and social/sexual selection are often forgotten.

6.2. “Good-genes” indicators and the corruption of honest signals by socially-selected noise

“Good genes” interpretations of sexual signals argue that signals are indicators of genetic quality under natural (survival) selection. It is easy to forget that once a phenotypic trait is favored under female choice as an indicator of genetic quality it is inevitably subject, in addition, to sexual selection for enhanced signal quality, and its elaboration as an effective signal comes under sexual selection, not just natural selection (indicator function) (Fisher 1930), which favors good attractiveness genes alongside good survival genes. Then choosy females produce “sexy sons” as well as healthy sons. Under sexual/social selection “good genes” means good social-interaction genes, e.g. genes that contribute to being a good stimulator, or a good competitive fighter or manipulator of conspecifics.

Sexually selected elaborations, then, enhance signal effectiveness *per se* – they are tools of success in sexual/social competition. Thus, the health-indicating red color of a feather may be made more effective as a signal – and less effective as an indicator – by features other than red color that enable an individual to improve its social status, and thereby its access to resources. A feather may be enlarged relative to normal feathers, adorned by added details that make it more conspicuous, or waved before a female or a rival. These embellishments and exaggerations have nothing to do with the ability to produce the color itself – the indicator value of red. While energetic waving behavior may indicate further traits of value under natural selection, the attention-getting value of the embellishments are due to effects on success in social interactions, which in turn affect access to resources (in this case, mates).

Numerous traits preferred during mate choice correlate with resistance to parasites and disease, or demonstrate physical strength and prowess (for many examples see Hamilton and Zuk, 1982; Hamilton, 2001). Thus, a signal like the diet-dependent red facial patches of some male jumping spiders (see Herberstein in this Issue) or the red color of a feather may have originated as an incidental (unselected) byproduct of constitutional resistance to disease or ability to sequester essential nutrients, and been selected, in addition, under sexual selection for attractiveness to females. Indeed, some ornaments can be produced only by those males that carry the genes for resistance against pathogens and parasites (see Milinsky, this issue).

Extreme advocacy of the good-genes approach, however, takes the evolution of signals completely out of the realm of Darwinian sexual selection (e.g. see Hamilton, 2001, where sexual displays and

morphology are described as “sanimetric” (p. 794) with males usually the “sanimeter” or “health index” sex (p. 798)). Although this “eugenic” (Hamilton and Zuk, 1982) approach to sexual selection has produced exciting discoveries linking sexual display to signs of health (e.g. Hamilton and Zuk, 1982 and others; partial review in Hamilton, 2001), it has also led to amnesia regarding social selection *per se*.

Female choice based on strength and vigor (good survival genes) is a second-order consequence of sexual selection via courtship competition among males, which originates due to the investment asymmetry between the sexes (beginning with gametes, eggs and sperm): (1) contests of male attractiveness (courtship) and female choice (differential female responsiveness based on courtship differences) sets the stage for (2) the evolution of female choice based on indicators of male quality – genes beneficial to offspring under natural selection; or, in species with male parental care, offspring benefits (again, under natural selection) provided by good fathers.

The potential for social selection is always present as the background for good-genes indicator selection and it can be expected to corrupt honest signals with socially selected “noise,” increasing the complexity of signals while undermining their value as indicators. This is a topic of importance for neurobiologists interested in the evolution of complexity: *Indicators of health seem unlikely to account for the great complexity of sexual communication.* The indicators that have been proposed (particular colors, brightness, strength or vigor, etc.) are quantitatively variable traits whose *health-correlated variability*, not complexity, makes them useful indicators. Their indicator value depends on the strength of the correlation between the indicator trait and the genes that affect health. *But sexual selection systematically undermines that correlation, introducing “noise” into the health-correlated signal* as it builds, instead, a correlation between the trait and its attractiveness to females. The same sort of noise is inflicted by sexual selection on the value of combat strength as an indicator of health and vigor, for successful male combat is affected not only by health and vigor but also by the efficacy of weapon form, fighting behavior, and aggressive display, all features affected in turn by social sexual selection. “In many cases, victory will depend not on general vigor, but on having special weapons. . . . A hornless stag or spurless cock would have a poor chance of leaving numerous offspring” (Origin, p. 69). And “. . . the shield may be as important for victory, as the sword or spear” (Origin, p. 69). Success in battle depends not on health alone, but on the tactics of opponents – whether they use weapons to push, pry, strike, pinch, or overturn rivals (e.g. see Eberhard, 1980) – variables not known to be related to health.

To call the good-survival-genes hypothesis “sexual selection,” as in “good-genes sexual selection” (a search term that recovers hundreds of publications on Google Scholar) is an ironic twist seen in a historical context because Darwin so strongly emphasized that sexual selection covers phenomena *not* explainable in terms of natural selection.

6.3. Conflict theory, and sexually antagonistic co-evolution

Another productive area of research views courtship interactions as conflict between the sexes – a battle of the sexes – in which females strive to resist persistent male sexual interactions that are costly to them in terms of natural selection (Parker, 1979; Arnqvist and Rowe, 2005). This results in “antagonistic co-evolution” as males increase forcefulness to overcome increased female resistance to costly interactions. Female responses to males are seen as evolving due to natural selection which favors self-protective female negativity, not the positive female choice of Darwinian sexual selection, where seemingly resistant female structures and behaviors can in fact screen for the mating acumen of males and thereby synergistically select for its improvement during evolution.

Sexual selection with female choice also predicts male–female conflict – a point sometimes forgotten in discussions of sexual conflict based on naturally selected conflict theory, therefore termed “narrow sense” conflict by Brennan and Prum (2012). The difference between the two kinds of conflict is not always clear. But the difference is important especially for neurobiologists: narrow-sense conflict theory sees the male–female co-evolution of sensory-response systems as mutually *antagonistic*, whereas under sexually selected conflict male–female co-evolution is *synergistic*, giving rise to the special mutually reinforcing properties of social selection already described (above). Some authors have unfortunately proposed that *attraction-preference* and *persistence-resistance* conflict should be synonymized, but this is profoundly mistaken for evolutionary neurobiology, as shown by Brennan and Prum (2012). The two kinds of conflict are expected to have very different evolutionary dynamics, with narrow sense conflict lacking the synergistic impetus that is a special property of interactions under sexual selection. So it is important, in a neurobiological context, to distinguish between these two interpretations of conflict, and not assume that because there is an appearance of conflict, as in the “marathoner” males of *Polistes* leks (see Beani, this issue), narrow-sense antagonistic conflict theory (force and resistance, rather than synergistic attractiveness and choice) applies.

Unfortunately the key references on narrow-sense conflict theory offer little guidance on how to distinguish between conflict based on natural vs sexual selection. Parker (1979, p. 130), in a seminal paper on sexual conflict theory states: “I have looked in some detail at the possible benefits which accrue to females via sons which inherit the sexual selection advantages of their fathers. In the models which will follow, *this effect will be omitted to keep the analyses simple*” (emphasis not in the original). With that, Parker sowed the seeds for sexual-selection amnesia within conflict theory (but see Parker, 2006, where the topic is taken up more extensively). The major book on conflict theory (Arnqvist and Rowe, 2005) first mischaracterizes Darwin’s view of female choice (p. 3) as akin to good-genes sexual selection, based on strength and vigor, and as most common under monogamy, a conclusion based on misreading a passage from Darwin with the opposite intent (in the cited passage Darwin was explaining why sexual selection cannot be as effective under monogamy). Under their description of conflict theory (p. 35) “male traits that decrease female fitness spread and are exaggerated because females ‘prefer’ them (i.e., bias mating or fertilization success toward males with exaggerated or more manipulative traits).” But there is little or no consideration here of the sexually selected alternative, where *positive* female choice involves sensitive screening for males that are attractive and successful manipulators of female responses. Positive choice is seen as overcome by female negativity (“resistance”) with a clear negative result for the evolution of sensory abilities: “The fact that these traits are costly to females leads to selection for resistance or the evolution of *insensitivity* to them” (ibid, p. 35, italics mine; see also Krakauer and Johnstone, 1995, which also ignores the possibility of signal value as stimulation not requiring “honesty”).

Whether female resistance is better explained by narrow-sense conflict theory (female negativity due to signal detriments to fitness under natural selection) or sexual selection theory (female selectivity due to benefits to offspring of superior signaling genes) depends on whether the sexually selected benefits overcome the naturally selected costs of the male trait to females. This can only be evaluated on a case-by-case basis using data that compare the expectations of both interpretations (as in Arnqvist and Rowe, 2005, pp. 40–43; Brennan and Prum, 2012; Eberhard, 2004a,b; Holland and Rice, 1999; Parker, 2006). Demonstrating only a cost to females of mating activity, or a benefit for male signal behavior and morphology, is not enough.

6.4. A conflict-theory paradox and the emergence of sexually synergistic co-evolution

The reasoning behind narrow sense female-negative conflict theory suggests a “conflict paradox” where antagonistic conflict leads to its own decline. Suppose that a male signal fails to pass the benefit-cost threshold in the female required for spread under sexual selection – the trait is so detrimental to females that its negative value under natural selection determines its evolutionary fate more importantly than its value (to offspring) as a signal, and it falls solidly within the framework of narrow-sense female-resistance conflict theory. This is the case for aspects of forced copulation in some species of waterfowl during the breeding season (Brennan and Adkins-Regan, this issue). Still, there is a tradeoff under natural selection on females between effective resistance and the need to mate in order to reproduce: a perfectly resistant female in a sexually reproducing species would not mate at all (see Parker, 1979 for alternatives to sexual reproduction that might result). If selection favors mating, how could selection not favor selective mating?

As recognized by Arnqvist and Rowe (2005) mating with the most persistent male is selective mating. But the most persistent males are also the most female-damaging males and they should not, under natural selection on females, be the winners: females should prefer (be selected to mate with) the least damaging males among the persistent ones, or they should evolve resistance to the damage inflicted by those males. In either case, the damaging effects of persistence should be diminished over evolutionary time. Natural selection, then, should constantly work to reduce the importance of the condition – damage or cost females – required for the relevance of conflict theory to the evolution of that trait, raising the relative importance of sexual selection (low-cost *stimulation* of females). Paradoxically, then, conflict due to natural selection on females should promote conditions that favor its own reduced importance over time: under the assumptions of conflict theory natural selection should continuously move traits toward the realm of sexual selection. Under sexual selection the co-evolution of males and females is *synergistic rather than antagonistic*, driving sexual interactions in the same mutually reinforced direction – toward increasingly effective weapons or threats, and attractive male traits, and away from harmful sexual interactions where females “choose” persistent males only because their resistance to them is imperfect.

What does this mean for analyses of the stimulus–response courtship systems observed by students of neurobiology and behavior? With or without conflict, stimulatory courtship devices that are at the same time attractive and low in cost to females should accumulate during evolution more than do traits that promote maintenance of costly conflict. The paradoxical self-limitation of antagonistic conflict means that courtship devices observed in nature are likely to evolve toward increasing influence of sexual selection (differential attractiveness) as selection lowers the costs of male signals. When synergistic sexual selection predominates over antagonistic interactions (e.g. see Huber, 1995) the choosy behavior of females is better described as selective cooperation than as imperfect resistance to male persistence.

The predicted occurrence of positive selective mating despite marked narrow-sense conflict may be exemplified in some lineages of waterfowl, where both narrow-sense conflict and courtship occur, but are in temporally separate compartments. Persistence-resistance conflict marked by frequent forced copulation predominates during Spring breeding, whereas courtship affording opportunities for female choice takes place during Winter pair formation and has the greater effect on male fitness (Davis 2002, cited by Brennan and Adkins-Regan, this issue). This compartmentalization protects choice from interference by forced copulations. Brennan and Prum (2012) discuss vaginal pouches and other

features of the female reproductive tract that may have evolved as cryptic anatomical mechanism of choice in response to forced extra-pair copulations, for these mechanisms “force unwanted males to deposit their sperm further from the sites of sperm storage” (Brennan and Adkins-Regan, this issue) and “allow females. . . to reassert their choice” (Brennan and Prum, 2012, p. 2335).

6.5. Post-copulatory sexual selection: sperm competition or female choice?

The term, and the concept, of sperm competition has the potential to focus so strongly on male-male gamete interactions that socially selected female choice may be forgotten (see Simmons, 2001 on this and other aspects of sperm competition). Sperm competition emphasizes male-male combat at the gametic level. But sperm compete within females, on a female-defined playing field that permits what has been called *cryptic (internal) female choice* (see Eberhard, 1985, 1996). When the female-choice aspects of sexual selection are forgotten in this brand of partial amnesia about the nature of male-male competition, then the possibility of a sexually synergistic co-evolutionary race affecting sperm structure and the female-influencing traits associated with gametic competition is set aside, and assumed to be unimportant.

In keeping with the importance of cryptic female choice and sperm competition, male genitalia, like other kinds of male morphology subject to sexual selection, are often highly complex and species specific; and it is usually difficult to argue that they are primarily instruments of male-male combat, or primarily evolving under natural selection. Indeed, male genitalia may be the aspects of male morphology most likely to be pure products of sexual selection.

6.6. Sensory exploitation and sensory traps: natural-selection origins of social signals.

Courtship signals are a kind of communication. Ethologists long ago realized that communication systems in animals start with pre-existing responses that permit a particular movement or cue to become a “signal” – an input produced by one individual that evokes a particular response by another (review in Smith, 1977, chapter 11). Ryan (1990) has emphasized the role of sensory-exploitation of pre-existing female responses, beginning with his classic studies (Ryan, 1985) of sexual selection and communication in frogs (see also Enquist and Arak, 1993, 1998; Ghirlanda and Enquist, 1998 for neural network models; Endler, 1992 on complex evolutionary interactions between sensory systems, signals and environment that he calls “sensory drive”).

The assignment of a female response to sensory exploitation of naturally selected responses alone is eminently reasonable for the *origin* of a particular male signal, and for certain naturally selected effects on subsequent evolution (Endler, 1992). But any signal subject to choice is potentially subject to modification under sexual selection. Then a correspondence between male signal characteristics and female sensory capacities could be a product of co-evolution under sexual selection rather than sensory exploitation of pre-existing capacities due to natural selection. The built-in ability to evaluate stimulus intensity of naturally selected stimuli could jump-start the accelerated evolution of attractiveness and choice under sexual selection. So the nature of derived signals cannot with certainty be attributed to sensory exploitation except at their origin.

The importance of sensory exploitation independent of sexually selected modification is likely limited to the origin of new signals *except when the response is due to a sensory trap* – a situation where the female response is so strong and unhesitating in a wide variety of contexts that it is permanently subject to sensory exploitation by

males (West-Eberhard, 1979). Examples of sensory traps that are exploited by males are the urgent response of a mother monkey to an infant's cry of distress (Moynihan, 1970); and the emergency predator-escape response of female fiddler crabs (Christy et al., 2003), responses so crucial that they may be relatively immune to selection for modification in the context of sexual selection.

7. Conclusion: natural and sexual selection as causes of neurobiological evolution

Under sexual/social competition there is an unending race for success in *social* environments, where interaction with conspecific competitors screens off access to critical resources such as mates. This implies a new set of expectations for neural system evolution, with indicator-honesty not required and no limit to the elaboration of signal-response complexity as long as costs do not exceed resource-accrual benefits of social success. Competitive social interactions, especially those that involve choice (such as differential responsiveness to signal variants during courtship), can produce a self-accelerating process of sexually synergistic co-evolution leading to extreme complexity in the neural, behavioral, and morphological traits that affect social selection.

In sum, natural selection is a relatively conservative force in the evolution of sensory-response systems compared to social selection. So extreme elaboration of male traits used in courtship, threat or battle indicates that sexual selection is likely important, even when natural selection (good survival genes, persistence-resistance conflict, sexually antagonistic co-evolution, or sensory exploitation) is involved.

Mutually reinforcing synergism between natural and sexual selection results in some of the most extreme traits known (consider, for example, the powerful electric discharge of electric fishes used in both signaling and predation (Stoddard, 1999); high-frequency sound in bats (see Kingston et al., 2001); and the enormous size of dinosaurs – all traits with both trophic and socially competitive functions; see West-Eberhard, 2003 for a brief review). A spectacular product of natural-social selection synergy is the human brain, whose analysis has led researchers back and forth over the conceptual border between natural and social selection, between tool-making vs spear-throwing, foraging vs war, technical vs Machiavellian and empathetic skills. Both natural and social selection are likely involved in the evolution of neuro-behavioral complexity, and an either-or explanation is not justified. Still, it is important to distinguish between the two kinds of selection, especially in research on complex neuro-endocrine and behavioral systems involved in social interactions. It is one more tribute to Darwin's genius that he seemed to anticipate the kinds of controversies discussed here when he saw beyond natural selection to write about *The descent of man and selection in relation to sex*, a vision of human evolution that features social aspects of selection.

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