

Introduction

Opening Pandora's Boxes in Sexual Selection Research

Today, about one hundred and fifty years after the publication of Darwin's *Origin of Species*, how do biologists, historians, and philosophers reassess the strengths and weaknesses of sexual selection? Answering this is the overall aim of this book.

At least two major concepts of contemporary biology originate in the works of Charles Darwin: natural selection and sexual selection. Originally, sexual selection dealt with the competition for mates, while natural selection was more concerned with individual survival. As Darwin says in the first edition of his *Origin of Species* (1859, p. 88): "This depends, not on a struggle for existence, but on a struggle between the males for possession of the females; the result is not death to the unsuccessful competitor, but few or no offspring. Sexual selection is, therefore, less rigorous than natural selection."

The concept of sexual selection was amply developed and refined in Darwin's *Descent of Man, and Selection in Relation to Sex*, along with several other issues like the "proportions of the sexes" (Darwin 1871; see Veuille, this volume). For Darwin, sexual selection "has led to the development of secondary sexual characters." (1871, vol. 1, p. 271) This is fully consistent with Darwin's commitment to an individualistic stance (Ruse, this volume).

More specifically, sexual selection consists of two different processes, "the power to charm the female" and "the power to conquer other males in battle." (1871, vol. 1, p. 279) Thus, there are two selecting forces within the process of sexual selection. They are usually termed "female choice" and "male-male competition." The first leads to ornaments, the second to armaments. On first inspection, sexual selection is just one kind of selection, with a different kind of selector: just as artificial selection is operated by breeders, so sexual selection (at least, its intrasexual component, female choice) is operated by mates, so natural selection is operated by a metaphorically personified agent called "nature". While Darwin's contemporaries readily accepted male-male competition, several issues were raised on the question of female choice. How could female animals develop the ability to discriminate between males or to consciously weigh up their differences? And, more importantly, was there not a contradiction between natural and sexual selection? As one

of Darwin's fiercest critics put it: "A crest of topaz is no better in the struggle for existence than a crest of sapphire. A frill ending in spangles of the emerald is no better in the battle of life than a frill ending in the spangles of the ruby. A tail is not affected for the purposes of flight, whether its marginal or its central feathers are decorated with white." (Argyll 1867, pp. 247–248)

Sexual selection claims to account for beauty in animal features: however, it raises the question of whether it can be consistent with the action of natural selection. While natural selection focuses on useful features, sexual selection opens up the possibility of an aesthetic sensibility and suggests that beauty somewhat determines animal anatomy and behaviour. How can evolutionary theory take into account what is obviously beautiful as well as the preference animal individuals seem to show towards beauty?

This question puzzled several naturalists who expressed doubts on sexual selection, faulting it for its anthropomorphical overtones. The most prominent of them is probably Alfred Russel Wallace, who scornfully asserted:

A young man, when courting, brushes or curls his hair, and has his moustache, beard or whiskers in perfect order and no doubt his sweetheart admires them; but this does not prove that she marries him on account of these ornaments, still less that hair, beard, whiskers and moustache were developed by the continued preferences of the female sex. So, a girl likes to see her lover well and fashionably dressed, and he always dresses as well as he can when he visits her; but we cannot conclude from this that the whole series of male costumes, from the brilliantly coloured, puffed, and slashed doublet and hose of the Elizabethan period, through the gorgeous coats, long waistcoats, and pigtails of the early Georgian era, down to the funereal dress-suit of the present day, are the direct result of female preference. In like manner, female birds may be charmed or excited by the fine display of plumage by the males; but there is no proof whatever that slight differences in that display have any effect in determining their choice of a partner. (Wallace 1889, pp. 286–7)

Wallace readily accepted male-male competition but rejected female choice. His name now stands for utility while Darwin's stands for beauty (Prum 2012, and Hoquet & Levandowsky, this volume). Following Wallace's criticisms, sexual selection became the laughing point of Darwinian theory. Biologists like Thomas Hunt Morgan considered it useless and dedicated several books to showing its irrelevance (1903, 1919). In his *The Scientific Basis of Evolution*, Morgan refers to secondary sexual characters and states that "Darwin attempted to explain their origin historically in his theory of sexual selection, while the modern attitude is to accept their presence as given, and to devote attention to the physiology of their development in the individual." (1932, p. 152) Here we understand an underlying opposition between ultimate and proximate causes. Are evolutionary or ultimate factors the most fundamental causes that account for animal traits—like courtship and display, what Darwin called "strange antics"—or should proximate factors (like hormones or immediate rewards) also be taken into account (see the contributions of Watanabe and Kreutzer & Aebischer in this volume)?

Due to these puzzles and misconceptions, it is often claimed that sexual selection underwent a long century of absence, from its original wording in Darwin's *Descent* (1871) to its "rediscovery" by Trivers (1972) in the wake of sexual liberation. Examples of what I would call the "century of neglect" narrative—allegedly lasting

from 1871–1972—can be found in Cronin (1991) or Zuk (2002). However, it requires several important caveats. In this narrative, Ronald A. Fisher (1915, 1930) is singled out as having played an important role and is often quoted as a notable and singular exception among his peers for his idea of a “runaway process”. In fact, the story is much more complex, especially regarding female choice (Milam 2011, Gayon, this volume). Indeed, throughout the 20th century one can list many names and projects that contributed to the development of sexual selection as both a theory and a field for experimental studies: in the 1910s, the entomologist Frank E. Lutz (1879–1943), at the Cold Spring Harbor Biological Laboratory, was doing experimental work on sexual selection with drosophila strains (Lutz 1909); from the 1910s to the 1930s, Julian Huxley made field studies of great crested grebes (1914, 1938), while Theodosius Dobzhansky (1944), Ernst Mayr (1946) and their colleagues were actively researching the question of mate choice using drosophila as a model organism and making several observations in the field.

Their work prompted a British plant geneticist, A.J. Bateman, to study intra-sexual selection in drosophila. His paper, published in *Heredity* in 1948, was, at first, rather overlooked until, in 1972, it was quoted by Robert Trivers, triggering an exponential rise in citations as well as the exceptional fortune Bateman’s paper has enjoyed in the last quarter of a century. From Darwin to Bateman to Trivers, a common thread is the depiction of two stereotypical sex roles: coy females versus eager males. This view became a motto for many sociobiologists and, conversely, it was targeted by many critics of sexual selection, including feminist scholars. Trivers’ concept of “parental investment” explains how natural selection may be reconciled with sexual selection. If parental investment increases the progeny’s chances of surviving, then each individual offspring can be considered as an investment. This, in turn, reduces the parent’s ability to produce further offspring. The basic principles of the theory are that females are limited by the number of offspring they can successfully rear and that males are limited by the number of eggs they can fertilize. But its implications are subtler than that. Due to unequal parental investment, one sex (often, but not necessarily, the female) plays the role of “limiting resource” while the other (often, but not necessarily, the male) is mainly a contributor of genes to the making of the offspring, with little or no further contribution to parenting beyond this, and it is he who is competing for access to mates. Sex cells are, of course, an element of parental investment, though certainly not its only component. In this framework, due to their limited stock of costly eggs, females are the sex-limiting factor, with males, on the contrary, having a large number of small sperm. Gestation and lactation, in mammals for instance, are also important components of female investment, while in other orders, like sea-horses, females simply deliver the eggs whereas pregnant males provide the more taxing investment of developing the embryos.

Severed from the idea of stereotyped sex roles, sexual selection becomes a “logical imperative” (as is suggested by Parker and Pizzari, this volume). In the summary of the fourth chapter of his *Origin of Species*, Darwin gave what has been called the “recipe” approach to natural selection: if ingredients x, y and z are given, then evolutionary change will necessarily follow. The recipe is applicable, in principle,

to any entity capable of some form of reproduction (Godfrey-Smith 2009). Similarly, the recipe version of sexual selection starts with gamete competition and anisogamy, thus emphasizing pre-copulatory factors rather than post-copulatory ones. In this version, anisogamy is the primary sexual difference, playing a crucial but not exclusive role in sexual selection. Other factors may also be included in sexual selection in order to construct it as a testable hypothesis (Gowaty, this volume).

Another important set of questions relates to the well-worn issue of genetic determinism (Waage and Gowaty 1997): what difference exists between the “decisions” of the animal individuals (humans included) and their evolutionary roots or causes? If selection operates only on genes, then what relation is there between genetic sequences and behaviour? Questions bearing on the nature of homosexuality, of maternal instinct, and of altruism have been particularly debated, raising again and again the classical opposition between nature and nurture, but also between ultimate and proximate causes. The issue here is twofold. First, as several authors emphasize (especially Ah-King and Gowaty, this volume), new understandings of the mechanisms of gene expression and epigenetics lead to a revised account of individual development and of the way genes are said to determine phenotypes. Another question is whether the depiction of standard sex-roles (coy vs eager, choosy vs promiscuous, passive vs active) is flawed: does this mean that sexual selection is condemned to doom and oblivion (Roughgarden, this volume)?

The question of sex roles tightly links sexual selection to social issues such as women’s liberation. In a foreword to Cronin (1991, p. ix), John Maynard-Smith contrasted current enthusiasm for sexual selection with its previous and long-lasting disrepute, accounting for how “neglect of sexual selection turned to enthusiasm during the 1970s and 1980s.” Maynard-Smith supported the hypothesis that “this change of attitude” should be ascribed “to the influence of the women’s movement,” and affirmed that, “It is certainly not the case that the new research, theoretical and empirical, has been carried out by ardent feminists, but I think it may have been influenced, even if unconsciously, by attitudes towards female choice in our own species.” The role that feminism played in the history of sexual selection is a contested area, one that is broached in several chapters of this volume (e.g., Ah-King and Gowaty). One of the earliest and probably most important contributions to the feminist critique of Darwin’s ideas is the work published in 1875 by a Unitarian minister, Antoinette Blackwell. Blackwell criticized Darwin for failing to see how females actually developed new features. After all, both Darwinian mechanisms, male-male competition and female choice, account for evolution of male traits: “With great wealth of detail, he [Darwin] has illustrated his theory of how the male has probably acquired additional masculine characters; but he seems never to have thought of looking to see whether or not the females had developed equivalent feminine characters.” (1875, p. 16) Primatologist Sarah Blaffer Hrdy has brought out the role played by Blackwell: “Blackwell’s informed dissent was drowned out in the wake of popular acceptance of social Darwinism. Her contribution to evolutionary biology can be summed up with one phrase: the road not taken.” (1981, p. 13)

The notion of stereotyped sex-roles has been highly criticized. Women scientists like S.B. Hrdy (1981), Linda Fedigan (1982) and Barbara Smuts (1985) have shown how female primates in particular are far from being passive participants in the reproductive process. They challenge the assumption that females only mate for fertilization and show that copulation can occur under a variety of circumstances: primate females engage in non-cyclical and non-reproductive sexual activity with various males. Patricia Gowaty (1992) has argued that many points in evolutionary theory could be used by feminist thinkers, especially those regarding variation of female behaviour or female resistance to male control of female sexuality. She also argued that evolutionary biologists might learn from feminists as well.

Both Gowaty and Zuk warned their colleagues about possible male chauvinism blinding evolutionary biology to important insights and preventing it from making further progress. Zuk, for instance, stressed the fact that “an awareness of such bias can help us recognize the need to listen to a variety of voices, which will ultimately result in less biased and more productive science. [...] I address biologists as a feminist, to explore ways that feminism can affect and hopefully improve the study of the evolution of behavior.” (1993, p. 774) Referring to new insights in evolutionary biology, Zuk suggested, following Trivers, that the first creature was actually Eve and that she had not been fashioned out of one of Adam’s ribs as the traditional account would have it. As Trivers put it in an exam question quoted by Zuk: “And God made the first creature and called her “Eve,” and spoke to her, saying, “You and you alone are capable of nourishing an offspring out of your own body. In my own image I have made you. Out of your body all life here on earth shall flow. Go and reproduce and populate the earth. Natural selection will take care of the rest. For thou art Eve.”” As to Adam, he is just an additional creation, in order to allow Eve to fight efficiently against parasites: “And God caused a deep sleep to fall over Eve and She took one of Eve’s ribs and fashioned a male out of it.

To him She said, “You I will call Adam or man, for you are not fully woman, but were made from her to help her fight parasites, and, if possible, give her a little pleasure along the way.” (1993, p. 775) Such change of perspective, Zuk commented, “illustrates how use of feminist principles can expand conceptual possibilities for biology students.” (1993, p. 775) However, Robert Trivers abruptly replied that he “would rather derive [his] feminist principles from evolutionary biology than [his] evolutionary biology from feminist principles.”

Evolutionary biology teaches us that females are primary in evolution, males being secondarily derived to serve female needs; that once both sexes are present, female interests carry at least as much evolutionary weight as male interests; that mating systems with a strong component of female choice naturally evolve to give greater weight to female than male interests; and so on. (Trivers 1994)

Trivers also claims that “too-close adherence to political principles as a guide to reality tempts us to merely replace the self-deceptions of the past with a brand new set”—suggesting that, only if we forget about politics, may we achieve an objective, value-free science, emancipated from the dialectical trap of the feminist Scylla and

the masculinist Charybdis. However, he does not explain how he controls his own bias, nor does he make the effort to offer any suggestions on how to do so.

No doubt that, partly due to these entanglements with highly debated topics like gender roles and stereotypes, partly due to its status as sound and testable evolutionary hypothesis, sexual selection today is probably “one of the most dynamic areas” of evolutionary research (Parker and Pizzari, this volume). However, it still has an incredible ability to trigger wild controversies. While some acknowledged the Darwinian mechanism as almost self-evident, others criticized it as fatally flawed. In 2006, Joan Roughgarden and her colleagues vigorously challenged the validity of sexual selection as a central component of modern evolutionary theory (Roughgarden et al. 2006). Their paper boldly stated that sexual selection was ‘wrong’. This prompted an abundance of responses from evolutionary biologists (Kavanagh 2006), and it was, no doubt, an instigating factor in my own resolution to clarify the epistemological status of sexual selection through two conferences I organized in 2011 (see below).

From an epistemological point of view, the situation of sexual selection debates is much more complex and interesting than just an opposition between supporters and critics. Gowaty, for instance, actively defends Darwinian sexual selection against Roughgarden’s claims, although she has repeated Bateman’s experiments and concluded that his results were fatally flawed (Gowaty et al. 2012). Conversely, Cézilly (this volume) acknowledges the overall validity of the “Darwin-Bateman Paradigm”, but he agrees with Roughgarden that sexual selection theory has now moved far beyond coy females and eager males, and he takes issue with standardized sex preferences and stereotyped sex roles.

To the epistemologist’s eye, sexual selection is a somewhat fuzzy concept and new evidence coming from the field of science in action is a regular occurrence. I had the privilege of being invited to participate at a recent NESCent Catalyst Meeting that was held in Durham (NC) from July 15–17 2013 and organized by Joan Roughgarden. The meeting gathered 34 participants who actively reviewed the state of what Roughgarden calls “sexual selection studies”. One of our main goals was to come up with a consensus definition of sexual selection. David Shuker (2010) suggested starting out with the following: “Sexual selection describes the selection of traits associated with competition for mates.” Continuing, “More formally, sexual selection is the relationship between a trait and its effect on fitness through sexual competition.” (2010, p. e12) Several aspects of this definition were shared by many other participants: that sexual selection is not dependent on traditional sex roles like eager males and coy females; that sexual selection is not dependent on cheap sperm and costly eggs; that sexual selection differs from sexual conflict; and, that sexual selection is different from female choice. However, other aspects were also hotly debated; these are treated in later chapters of this volume. The NESCent meeting showed that Shuker’s tentative consensus statement is a sort of Pandora’s box, or rather a complex of intricate Pandora’s boxes that the participants meticulously and methodically opened, one after the other. I draw extensively on the final report of the conference in the following (Roughgarden et al. 2013).

The main Pandora's box is probably contained in wording like "competition for mates", which spawned several issues: is sexual selection about access to *mates*, or about access to *fertilizable gametes*? Maybe the whole question of "access to mates" or numbers of matings is secondary to number of actual fertilizations. What does "competition for mates" encompass? Not only the Darwinian mechanisms of male-male competition and female choice of males, but also competition to attract better mates. Several participants suggested that behavioural aspects should be precluded from the definition and that evolutionary biologists should only be concerned with an operational protocol for *measuring* sexual selection with a concept like "opportunity for selection" (a claim supported by Shuster and Wade 2003). Post-copulatory versions of these different themes were also suggested. Potentially, even if no consensus definition could actually be achieved, some major components could certainly be kept in mind: one of the major aspects of sexual selection is differential fertilization success, or the variance in the number of fertilizations, owing to the variance within one sex in, for example, the number of mates and/or the number of fertilizations per mating.

But even a very old and somewhat basic question such as "Is sexual selection a component of natural selection?" (Mayr 1972) can receive no clear answer; many biologists happily agree that it is, but some claim that sexual and natural selections are actually quite distinct processes. Is this question merely pedantic? For the historian of science, it is clear that many of Darwin's readers thought at first that sexual and natural selections might contradict each other, that, for instance, ornaments like the cumbersome peacock's tail could be detrimental to individual survival. But, strikingly enough, this important question is still raised today, as it is related to central theoretical concerns: what features of the individual organism can be said to be, in Darwin's terms, "advantageous" or "useful", or, in more recent parlance, "functional" or increasing of "fitness"? What is selected; viability of the individual, or transmission of genes?

Moreover, the concept of sexual selection has been profoundly updated since Darwin. The sharp discrepancy between Darwin's (1871) original insights and the contemporary notion of sexual selection throws some doubts on the unity of the concept (see Roughgarden, this volume). If one takes the historical dimension of sexual selection seriously, then one sees how changing definitions make it somewhat an umbrella-term. While biologists constantly refer to Darwin's views and depict themselves as the true heirs of Darwin's mantle, there is little consistency in these claims of legacy. Darwin had no idea of mathematization of sexual selection; he strongly suggested that sexual selection was linked to typical sex roles. One aspect of sexual selection that Darwin was completely unaware of is the role of selfish genetic elements (SGEs): genes, organelles or micro-organisms might manipulate patterns of inheritance in order to increase their representation in the next generation (Weddell & Price, this volume). The impact of SGEs on sexual selection and especially on male and female reproduction is difficult to measure. Another issue at stake is whether SGEs may play a role in shaping mating systems.

Another Pandora's box in Shuker's initial definition is that it requires genetic covariance between variation in a sexually-selected trait and variation in fitness. This raises the question of whether sexual selection is for "good genes" or, if not, then at least for signals of genetic quality. This even led to the paradoxical hypothesis of the "handicap principle". According to Zahavi, odd or costly traits such as the peacock's tail are in fact *adaptive*: they signal the ability of the individual to survive and function while encumbered with the cost (Zahavi 1975). The perspective that selection is ultimately for quality is called "Wallacean", because of Wallace's emphasis on vigour of males, while the opposite view, purporting that selection is for truly aesthetic, and possibly detrimental, features is called "Fisherian". Fisher's runaway-process (1915) develops a case wherein a female preference for a male trait leads to an increase in the male trait which in turn leads to an increase in the female preference for that trait, and so on—with no necessary positive impact on fitness. One could say that the viability impact of natural selection (how a trait increases individual fitness) may be in opposition to the sexual preference aspect: this hypothesis of indirect benefit of sexually attractive offspring is called the "sexy son" hypothesis.

A recent review suggested that, through sexual selection, females get "sexy sons" rather than "good genes" (Prokop et al. 2012). However, Joan Roughgarden (2009) suggested that an ornament might be "sexy" in a given generation, and the same ornament might also be heritable, but this does not necessarily entail that it will be "sexy" in the next generation. Female preferences may not be heritable, even if male traits are. Lack of cross-generational conservation of preferences is clearly evinced by studies on the collared flycatcher case, which show that the female preference for ornament was not heritable (Qvarnström et al. 2006).

Based on 24 years of study with 8500 birds on the Swedish island of Gotland, heritabilities were measured for several factors: heritability of the white badge (a male ornament, considered a sexually selected character), heritability of fitness, heritability of female preference for the badge, genetic correlation between preference and badge. Results of this study showed that ornament is moderately heritable but that male fitness is weakly heritable. This seems to suggest that the badge does not function in sexual selection, the low correlation of the badge size and male fitness showing that the badge size is not an indicator of good genes. Furthermore, daughters do not inherit the preference of their mother—which also disparages the sexy sons hypothesis. The question here is: does this one species study really carry enough weight to make us cast doubt on the validity of the sexual selection model? Or should it be discarded as irrelevant, dealing only with one species, or with the work of only one group of scientists? Cézilly (this volume) highlights several methodological issues in female choice experiments: repeatability of experiments, bias due to the fact that one team publishing on one topic would work always with the same animal population, etc.

Another theoretical issue at stake here is whether heritability is an important aspect of sexual selection or not. If sexual selection is a behavioural process, then what matters is whether, within one given generation, the bearers of a defined trait

leave more progeny than their same-sex conspecifics; it does not necessarily lead to evolutionary consequences, meaning that, although there are several heritable features (badge size, female preference, etc.), heritability may well not be a necessary component of sexual selection. However, many biologists tend to accept that sexual selection (be it intra-sexual competition or inter-sexual preferences or choice) involves heritability since it leads to evolutionary consequences.

On the long debated issue of the evolutionary causes and consequences of female choice, some (like Cézilly, this volume) suggest that we should focus more on female choice *per se* and on female preferences. Are these arbitrary? Rational? Useful? What is the meaning of rationality? Comparison and deliberation may be good criteria, but transitivity may well be the fundamental axiom of rational choice. Others (like Prum, this volume) emphasize the importance of sexual autonomy, defined as the opposite of sexual coercion from the opposite sex.

The question of the null-models is also a cause of strong disagreement in the biological community (see Prum 2010, and this volume): under the search for a null-model, the basic question at stake is: “How can we understand whether sexual selection is, or is not, currently occurring in a given population?” This important issue (which hypotheses should define the “null”) is also a Pandora’s box about which it seems equally difficult to achieve a definite consensus.

As a philosopher of science, I was very much interested, both on the epistemological and historical levels, in seeing various biologists debate on these issues. I invited a large panel of biologists, historians and philosophers to gather in Paris to try to understand how each of them was variously reassessing the strengths and weaknesses of sexual selection. Two conferences were held in Paris in 2011: “*The aesthetic sense in animals (Le sens esthétique des animaux)*”, held at Université Paris-Ouest Nanterre on 13–14 January 2011; “*What’s left of sexual selection? (Que reste-t-il de la sélection sexuelle?)*”, held at the Musée National d’Histoire Naturelle and at Université Paris-Ouest Nanterre on 19–20 May 2011. Both meetings were funded by the French National Research Agency (Agence Nationale de la Recherche), the Biosex Research Project (ANR-07-JCJC-0073-01) and Université Paris-Ouest (Pôle 5 “L’humain en devenir”, EA 373, ED 139). The Institut Universitaire de France and the UMR 7205 OSEB (Origine structure et évolution de la biodiversité, MNHN-CNRS-EPHE) also made these meetings possible, through their logistic support. I thank Malek Bouyahia, Melanie Petremont and Eva Rodriguez at the ANR BIOSEX Project for their support in putting these two conferences together. The Biosex Project (<http://biosex.univ-paris1.fr/>) was a 4 year research group (2007–2011) under the direction of Elsa Dorlin (then at the university Paris 1 Panthéon-Sorbonne). Our aim at Biosex was to bring together scholars from the humanities and the biological sciences, as well as to build an interdisciplinary interface for reflecting on the ways in which biology has conceptualized sex, especially since Darwin. Assessing the question of sexual selection was a core issue in our project, given the theoretical and political intricacies of this topic and also the way feminism and sociobiology have interacted in order to bring out “a better science.”

The two conferences brought together specialists of behavioural ecology, historians of science, and philosophers. The participants were asked to reassess

the importance of the concept of sexual selection from historical, epistemological and theoretical perspectives. The title of the second conference in particular, “What’s left of sexual selection?”, could be understood in two different ways: (a) from a technical biological perspective: is the sexual selection concept still useful 151 years after Darwin introduced it in his *Origin of Species* and 140 years after the publication of his *Descent of Man*? (b) As a general social concern, playing with the “left/right” dichotomy: is “sexual selection” a progressive or a reactionary notion?

The present book is divided into three sections. Section 1 assesses the character of the “second” Darwinian revolution, the one dealing not with natural but with sexual selection. Section 2 studies how current sexual selection theory goes further than Darwin in many respects. Section 3 deals with animal aesthetics, as a developing area in sexual selection studies.

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Current Perspectives on Sexual Selection

What's left after Darwin?

Hoquet, T. (Ed.)

2015, XXIII, 307 p. 22 illus., 5 illus. in color., Hardcover

ISBN: 978-94-017-9584-5