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Sexual selection: Another Darwinian process

Sélection sexuelle : un autre processus darwinien

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ABSTRACT

Why was sexual selection so important to Darwin? And why was it de-emphasized by almost all of Darwin's followers until the second half of the 20th century? These two questions shed light on the complexity of the scientific tradition named "Darwinism". Darwin's interest in sexual selection was almost as old as his discovery of the principle of natural selection. From the beginning, sexual selection was just another "natural means of selection", although different from standard "natural selection" in its mechanism. But it took Darwin 30 years to fully develop his theory, from the early notebooks to the 1871 book *The Descent of Man, and Selection in Relation to Sex*. Although there is a remarkable continuity in his basic ideas about sexual selection, he emphasized increasingly the idea that sexual selection could oppose the action of natural selection and be non adaptive. In time, he also gave more weight to mate choice (especially female choice), giving explicit arguments in favor of psychological notions such as "choice" and "aesthetic sense". But he also argued that there was no strict demarcation line between natural and sexual selection, a major difficulty of the theory from the beginning. Female choice was the main reason why Alfred Russel Wallace, the co-discoverer of the principle of natural selection, engaged in a major controversy with Darwin about sexual selection. Wallace was suspicious about sexual selection in general, trying to minimize it by all sorts of arguments. And he denied entirely the existence of female choice, because he thought that it was both unnecessary and an anthropomorphic notion. This had something to do with his spiritualist convictions, but also with his conception of natural selection as a sufficient principle for the evolutionary explanation of all biological phenomena (except for the origin of mind). This is why Wallace proposed to redefine Darwinism in a way that excluded Darwin's principle of sexual selection. The main result of the Darwin–Wallace controversy was that most Darwinian biologists avoided the subject of sexual selection until at least the 1950s, Ronald Fisher being a major exception. This controversy still deserves attention from modern evolutionary biologists, because the modern approach inherits from both Darwin and Wallace. The modern approach tends to present sexual selection as a special aspect of the theory of natural selection, although it also recognizes the big difficulties resulting from the inevitable interaction between these two natural processes of selection. And *contra* Wallace, it considers mate choice as a major process that deserves a proper evolutionary treatment. The paper's conclusion explains why sexual selection can be taken as a test case for a proper assessment of "Darwinism" as a scientific tradition. Darwin's and Wallace's attitudes towards sexual selection reveal two different interpretations of the principle of natural selection: Wallace's had an environmentalist conception of natural selection, whereas Darwin was primarily sensitive to the element of competition involved in the

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intimate mechanism of any natural process of selection. Sexual selection, which can lack adaptive significance, reveals this exemplarily.

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R É S U M É

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Pourquoi la sélection naturelle était-elle si importante pour Darwin ? Pourquoi a-t-elle été massivement ignorée par les évolutionnistes darwiniens jusque dans la seconde moitié du xx^e siècle, à de très rares exceptions près ? Ces deux questions révèlent la complexité de la tradition scientifique nommée « darwinisme ». L'intérêt de Darwin pour la sélection sexuelle est presque aussi ancien que sa découverte du principe de sélection naturelle. Dès le début, la sélection sexuelle a été présentée par lui comme un autre « moyen naturel de sélection », bien que différent de la sélection naturelle proprement dite dans son mécanisme. Il fallut néanmoins 30 ans à Darwin pour pleinement développer sa théorie, depuis les cahiers de notes manuscrites de la fin des années 1830 jusqu'au livre de 1871 *La descendance de l'homme et la sélection sexuelle*. Bien qu'il y ait une remarquable continuité dans les idées fondamentales de Darwin au sujet de la sélection sexuelle, on décèle des changements subtils mais significatifs. Il a pris conscience que l'action de la sélection sexuelle pouvait s'opposer à celle de la sélection naturelle. Il a aussi accordé une importance croissante au choix par les femelles et justifié son emploi aussi croissant de notions psychologiques telles que le « choix » et « le sens esthétique ». Mais il a aussi soutenu qu'il n'y avait pas de frontière bien définie entre sélection naturelle et sélection sexuelle. La compatibilité de ces différentes thèses était problématique dès le départ, et les problèmes qui en résultaient ont, en grande partie, déterminé le sort de la notion après Darwin. La notion de choix par les femelles fut le principal objet des attaques de Wallace – co-découvreur du principe de sélection naturelle – contre la sélection sexuelle. Wallace cherchait à minimiser la sélection sexuelle par toutes sortes d'arguments, mais il a surtout totalement dénié l'existence même de l'un de ses modes, le choix par les femelles, car cette hypothèse lui semblait à la fois superflue et anthropomorphique. La critique de Wallace ne s'explique pas seulement par son adhésion au spiritualisme ; elle est aussi liée à sa conception du principe de sélection naturelle, qu'il considérait comme un principe suffisant pour l'explication évolutionniste de tous les phénomènes biologiques (exception faite de la genèse de l'esprit). L'effet le plus visible de la controverse entre Darwin et Wallace au sujet de la sélection sexuelle fut que ce sujet fut massivement négligé par les évolutionnistes darwiniens jusque dans les années 1950 au moins, avec la notable exception de Ronald Fisher. Cette controverse mérite cependant encore l'attention des biologistes, car les difficultés qu'elle révélait éclairent la structure des débats et recherches contemporaines sur le sujet. L'approche moderne tend à présenter la sélection sexuelle comme un aspect spécial de la théorie de la sélection naturelle, tout en reconnaissant les difficultés soulevées par les interactions entre ces deux processus naturels de sélection ; mais (contre Wallace), elle voit aussi dans le choix du partenaire sexuel un processus majeur, qui exige un traitement évolutionniste particulier. La conclusion explique pourquoi la sélection sexuelle constitue un cas-test pour comprendre ce qu'a été et ce qu'est le « Darwinisme » en tant que tradition scientifique. Wallace avait une conception environmentaliste de la sélection naturelle, qui le conduisait à ce qu'on appellerait aujourd'hui un panadaptacionisme. Darwin était sensible à l'élément de compétition qu'implique tout processus naturel de sélection dans son mécanisme même, et que la sélection sexuelle révèle indépendamment de toute signification adaptative.

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1. Introduction

Sexual selection represented a major investment for Darwin. Compare the size of *On the Origin of Species* (OS) (1859) [1] – the book devoted to natural selection – with the size of the second part of *The Descent of Man, and Selection in Relation to Sex* (DM) (1871) [2], entirely devoted to sexual selection. Both shared the same publisher and format, but the book on natural selection has 491 pages of text, whereas the piece on sexual selection in DM extends over 575 pages. There is no doubt

that sexual selection was tremendously important to Darwin.

However, the two sides of Darwin's theory of selection have had quite different fates. Although sexual selection generated a considerable interest in the years 1870–1880, it was massively neglected among Darwinians, thereafter. Indeed, very few among the Darwinian biologists manifested any interest in it before the 1950s. Ronald Fisher and Julian Huxley were noticeable exceptions. The subject was rediscovered by others around 1950, first as a way of restoring the spirit of genuine “Darwinism” in the context

of the rise of the Modern Synthesis [3]. Since the 1970s, the subject has been extensively discussed as a consequence of sociobiology and the disciplines that took over from it (especially behavioral ecology). Almost all modern authors highlight the ambiguity of Darwin's concept of sexual selection. Some of them deny that it exists, at least in the form of female choice as Darwin, or standard Darwinians, understood it [4,5]. It is a fascinating issue, indeed, to evaluate what contemporary authors mean when they speak of sexual selection, and what they mean precisely when they say that Darwin's hypothesis is either well established or obsolete. Michel Veuille's article in this volume [6] is devoted to this question. The present paper aims at complementing Veuille's scientific examination of sexual selection with an enquiry into the origins and early fate of Darwin's hypothesis.

We will examine two questions: why was sexual selection so important to Darwin?; and why was it de-emphasized by Darwin's followers? Taken simultaneously, these two questions tell us something about "Darwinism" as a scientific tradition. Darwinism may be taken in two senses. In the first sense, it is neither more nor less than Darwin's thinking and writing taken as a whole. In the second sense, Darwinism is the name of a school of thought that developed upon the basis of a limited number of concepts and methods taken from Darwin. Ordinarily, the two fundamental tenets of this scientific tradition are descent with modification, and natural selection. Whether this scientific tradition itself has been theoretically homogeneous or is a convenient word for a variegated historical entity is a question that will be left aside here (on this subject, see Gould's fascinating thoughts [7] and our own proposals [8,9]). We will here take sexual selection as a key case for evaluating the distance between Darwin's Darwinism and historical Darwinism.

Darwin was convinced that sexual selection was necessary to account for a major class of phenomena that were not explainable through natural selection, the secondary sexual characters (or most of them). He also thought that along with standard "natural selection," sexual selection was a special mode of what he called the "natural means of selection" or "natural processes of selection". For Darwin's followers, this raised immediately the following questions. If Darwin's selection referred to two different processes in nature, what was the relationship between these two processes? Were they really distinct processes? If so, what were their relations, both in terms of definition, and in terms of their interaction in nature? A lot of Darwinians were also concerned with one of the two forms of sexual selection that Darwin recognized, female choice. This notion looked like an anthropomorphic notion: was it really a "natural means of selection"? Last and not least, Darwin's followers were haunted by whether sexual selection challenged what Darwin himself called the "paramount power of natural selection" [1: 84]. Alfred Russel Wallace repeatedly criticized the hypothesis of sexual selection for all these reasons, especially after Darwin's death. His criticisms of sexual selection were closely dependent on his own view of the principle of natural selection, which he viewed as a universal principle of utility that sufficed

for making everything intelligible in evolution, except for mind. During approximately a century, most Darwinians avoided the subject of sexual selection because they adopted Wallace's view that sexual selection was an ambiguous and unnecessary hypothesis. The consequence of this is that, with a few exceptions, sexual selection remained neglected until the second half of the 20th century.

In the subsequent sections of this paper, I first examine the role of sexual selection in Darwin's thought. Then I summarize the controversy between Wallace and Darwin about sexual selection. Finally, I conclude on the issue whether sexual selection was genuinely Darwinian or not.

2. The rise of sexual selection in Darwin's thought

Darwin's interest in sexual selection is almost as old as his discovery of natural selection. The expression "sexual selection" does not appear in the 1836–1844 notebooks edited by Paul Barrett et al. [10], but there are several passages indicating that Darwin, just as his grandfather Erasmus, was aware of the role of sexual preferences in the modification of species. Two kinds of sentences illustrate this concern in the rare fragments that anticipated the hypothesis of sexual selection. Some sentences show that the young Darwin was puzzled by the mechanisms through which a female could recognize the most beautiful males. "How does Hen determine most beautiful, which best singer?" ("Old and useless notes" 1838–1840, [10: 600]). This sentence and others show that the young Darwin was prepared for what was to become much later the most problematic mode of sexual selection, the choice of the males by the females, a behaviour that presupposes significant cognitive and aesthetic abilities in animals. Darwin's notebooks also show that he understood very early that if animals could choose their sexual partners in a systematic way, such behaviour would be a natural case of selection that resembled artificial selection.

The concept of sexual selection was more clearly formulated in the 1842 and 1844 unpublished essays, which were the very first drafts of the OS. The 1842 essay is no more than a personal sketch, which was not supposed to be read by anyone. Many sentences are telegraphic, or incomplete, or illegible. But it testifies to Darwin's very first attempt to put in order his seminal thoughts about evolution. Here are the few lines devoted to sexual selection, in their totality:

"Besides selection by death, in bisexual animals illegible the selection in time of fullest vigour, namely struggle of males; even in animals which pair there seems a surplus? and a battle, possibly as in man more males produced than females, struggle of war or charms. Hence, that male which at that time is in fullest vigour, or best armed with arms or ornaments of its species, will gain in hundreds of generations some small advantage and transmit such characters to its offspring. So in female rearing its young, the most vigorous and skilful and industrious, whose instincts are best developed, will rear more young, probably possessing her good qualities, and a greater number

will thus be prepared for the struggle of nature. Compared to man using a male alone of good breed.” [11: 10]

There are a number of obscurities in this text, but Darwin clearly introduces the concept of a “natural means of selection” [11: 4, 7] different from “selection by death”. This special mode of selection is presented as a struggle of the males for the possession of the females, founded either on “war” or “charms”, or in other terms, “arms” vs “ornaments”. Note also the parallel made by Darwin between this special kind of selection and the competition between females for rearing a maximum number of young. This does not seem to be sexual selection, but Darwin’s comparison shows that in both cases, what counts is the greater “vigor” of both males and females. This suggests that, by that time, Darwin viewed sexual selection as an auxiliary means of producing adaptations (whereas in the late writings, sexual selection will be able to produce non-adaptive traits). Finally, this text also compares this particular mode of selection with human artificial selection, but the significance of the comparison is unclear.

The 1844 essay is much clearer and more explicit:

“Besides this natural means of selection, by which those individuals are preserved, whether in their egg or seed or in their mature state, which are best adapted to the place they fill in nature, there is a second agency at work in most bisexual animals tending to produce the same effect, namely the struggle of the males for the females. These struggles are generally decided by the law of battle; but in the case of birds, apparently, by the charms of their song, by their beauty or their power of courtship, as in the dancing rock-thrush of Guiana. (...) The most vigorous males, implying perfect adaptation, must generally gain the victory in their several contests. This kind of selection, however, is less rigorous than the other; it does not require the death of the less successful, but gives to them fewer descendants. This struggle falls, moreover, at a time of year when food is generally abundant, and perhaps the effect chiefly produced would be the alteration of sexual characters, and the selection of individual forms, no way related to their power of obtaining food, or of defending themselves from their natural enemies, but of fighting one with another. This natural struggle amongst the males may be compared in effect, but in a less degree, to that produced by those agriculturalists who pay less attention to the careful selection of all the young animals which they breed and more to the occasional use of a choice male.” [11: 92, 93]

Here again, we do not find the term “sexual selection”. Darwin speaks of a “struggle of the males for the females”, an expression which he will use again and again as the definition of “sexual selection” in further work. This struggle has two possible modes: “battle” or “courtship”. In both cases, Darwin insists that this “kind of selection” relies exclusively on differential reproduction, not differential survival. As in the previous manuscript, this process is presented as a special means of producing vigor and adaptation. But he explains that the struggle between

males produces adaptations that are tailored with respect to the fight between males, not to the “struggle for existence”. Finally, the 1844 essay compares sexual selection with artificial selection. Nevertheless, at this stage, Darwin does not seem ready to think of sexual selection as an evolutionary mechanism that could act as a force opposed to natural selection.

A full section is devoted to sexual selection in OS [1: 87–89]. There, for the first time, Darwin used this term in a published text. The general definition resembles very much that of the 1842 and 1844 essays: “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” [1: 88]. Contrary to a common claim, Darwin does not propose two, but three modes of inter-male competition: general vigor, direct fighting based on special weapons, and a struggle “of a more peaceful character”, founded upon ornaments, songs, dances, etc., which make the females “choose the most attractive partner” [1: 89]. This classification is confirmed in the conclusion of the chapter, where Darwin opposes sexual selection based on vigor to sexual selection founded upon direct rivalry: “Amongst many animals, sexual selection will give its aid to ordinary selection, by assuring to the most vigorous and best adapted males the greatest number of offspring. Sexual selection will also give characters useful to the males alone, in their struggles with other males.” [1: 127]. This way of presenting sexual selection suggests some sort of continuity between natural selection and sexual selection. At one extreme, some males produce more offspring because they are just more vigorous, but this does not imply any sort of fight. At the other extreme, the last mode of sexual selection seems to be quite arbitrary with respect to any sort of environmental adaptation, because it relies on the females’ “individual preferences and dislikes” [1: 89]. In OS, Darwin does not yet use the expression “choice exerted by the female” (later relabeled “female choice” by Wallace); this expression appears only in DM (1871). But the corresponding terminology is clearly here, with all its famous implications: females “choose”, as a function of their “individual preferences”, and of their sense of “beauty”. Darwin was obviously aware of the objections that could be posed to the claim that evolution could result from a process that relied upon individual psychology: “It may appear childish to attribute any effect to such apparently weak means” [1: 89]. But he immediately added: “if man can in a short time give elegant carriage and beauty to his bantams, according to his standard of beauty, I can see no good reason to doubt that female birds, by selecting, during thousands of generations, the most melodious or beautiful males, according to their standard of beauty, might produce a marked effect” [1: 89].

This sentence was the origin of the big controversy that developed in the 1870s about sexual selection, with Alfred Russel Wallace as the major protagonist. Two major issues were at stake. The first controversial issue arose from the claim that many animals, from fishes to primates, have perceptive, emotional and cognitive abilities that make them able to discriminate and choose their sexual partners. This claim raised no more or less than the problem of the

gradual evolution of the mind. The second controversial issue arose from the explanation of major features of organisms (a number of secondary sexual characters, morphological or behavioral) through a hypothetical aesthetic sense in animals. As highlighted by Elena Cronin, this meant that the beauty of nature was no longer an affair between only God and humans [12]. It also meant that not everything in nature could be interpreted in terms of design and harmony, whether this design was attributed to God or to natural selection [13]. None of these issues were trivial, either from a scientific, or metaphysical, or theological point of view.

OS had just three pages on sexual selection. These pages suggest that sexual selection might well explain a vast array of sexual differences. However, this book does not try to demonstrate that the hypothesis of sexual selection does accounts for a large number of secondary sexual characters in many groups of animals. This was the object of the second part of the 1871 book entitled *The Descent of Man, and Selection in Relation to Sex*.

I will not comment in detail this book, which has been incredibly neglected by the majority of biologists, historians and philosophers who have written about Darwin (including myself), with the exception of Cronin. I will just point out a few striking features of the 1871 book (designated DM in the rest of this paper):

- (a) In comparison with OS, DM (especially, the 575 pages devoted to sexual selection) is quite a difficult book. True, it appeals to common intuitions about sexual differences, but it also relies on a huge amount of documentation of secondary sexual characters. The second part of the book devoted to sexual selection begins with a long chapter entitled “Principles of sexual selection” [2: 253–320]. Following this theoretical chapter, twelve chapters examine the problem of the origin of sexual secondary characters in a number of animal classes, from worms and mollusks to primates and humans. Most of the book is devoted to insects, fishes, amphibians, reptiles, and mammals.
- (b) Darwin’s method in DM is the same as in OS. This method consists in defending a given hypothesis by showing that it can account for a vast range of previously uncorrelated phenomena. Since William Whewell, this traditionally has been called the method of the “consilience of induction” [14,15]. According to this doctrine, whose effect upon Darwin has been remarkably analyzed by Michael Ruse [15], the more an hypothesis can explain independent classes of facts, the more acceptable it is, because it is less likely that such an hypothesis will be ad hoc. In OS, the spectrum of phenomena explained by the hypothesis of natural selection is extremely wide: it encompasses morphological and behavioral adaptations, divergence of character, stratigraphic distribution of the fossil record, geographical distribution of species, extinction, embryological evolution, and classification, among other things. The scope of sexual selection is much narrower: it consists only of the secondary sexual characters (although not all of them), in a limited number of groups of animals – mainly “higher animals” with

significant perceptive and cognitive capacities. Nevertheless, the method is the same as in OS. DM aims at explaining a huge number of previously uncorrelated phenomena such as conspicuous coloration, asymmetrical sex ratios, and all sorts of anatomical structures and behaviors, with the help of a single unifying hypothesis, sexual selection. In spite of the huge amount of observation gathered by Darwin (mainly from books and journals), the argument is theoretical. Darwin’s hypothesis had several major consequences that he listed carefully, and that furnished potential tests for the hypothesis. For instance, if there is sexual selection of any sort, the struggle should be more severe as the sex ratio diverges from 1:1. The intensity of sexual selection should also increase as a function of the degree of polygamy (polygyny or polyandry, because in DM Darwin admits that sexual selection, especially mate choice, can exist in both males and females). Another prediction relates to mate choice, so important in DM. According to Darwin, mate choice presupposes the existence of elaborate perceptual and behavioral abilities. Therefore, sexual selection through mate choice should be more efficient in species that have more complex perceptual and behavioral capacities. Darwin mentions other general predictions from his hypothesis. I will not list them here. What I want to insist upon is that Darwin’s entire 1871 enquiry into sexual selection consists in confronting his predictions with a number of particular cases, and looking at particular classes of animals, one after the other. Quite often, Darwin felt uncertain (especially about the problem of sex ratio). But DM relied upon a highly elaborate theoretical structure, which still orients and constrains modern researches about sexual selection. Quite often modern specialists say that this or that prediction made by Darwin has been refuted. Be they right or not, they should be aware that the basic theoretical framework for this kind of discussion, with its fascinating hesitations, was first set in place by DM.

- (c) An interesting question is why Darwin decided to combine in a single book a part on the origin of human abilities (*Descent of Man...*), and another part on sexual selection (*... and Selection in Relation to Sex*). Darwin has not been perfectly clear about this. Contingent factors may have affected the decision to write a huge book tackling these two subjects, which had been of interest to him since the 1830s. But the book (1st edition, 1871) begins with six chapters on the origin of Man, and ends with two chapters on the question of secondary sexual characters in the human species. Darwin’s principal conclusions about the human species result from both series of chapters. They can be summarized in the following way:
 - (1) External differences between males and females are important in the human species, but are not great in comparison with species with highly asymmetrical sex ratios, or with highly polygamous species.
 - (2) External differences between races (color, morphology), are the result of sexual selection (mate choice), which was not a surprise for Darwin, because humans are such a clever species. External racial differences

between humans are thus mainly the result of the infinitely varying and capricious aesthetic preferences of various peoples. Although this hypothesis has been sometimes discussed up to today in certain cases (for instance, in the case of the external differences between the Tutsis and the Hutus), this is one of the strangest ideas ever developed by Darwin, at least with respect to the generality that he gave to it.

- (3) Intellectual and moral differences between human races are not the result of sexual selection, but of natural selection at the level of “tribes”. Darwin believed that intellectual features were selected both for the benefit of the tribe and of the individuals. He claimed that moral features resulted from a kind of natural selection acting on characters detrimental to the individuals but beneficial to the community. These theses are extensively discussed in the first part of the book. Taken together, the three series of theses that I have just summarized testify for the overall unity of the book. My contention is that, at a certain point of his life, Darwin felt the necessity to better articulate the various “natural means of selection” that he had distinguished in the course of his work: natural selection (individual selection and “tribe” or group selection – as we call it today), and the various kinds of sexual selection that he recognized.
- (4) Let us finally consider the content of the hypothesis of sexual selection in the 1871 book. Darwin devotes 70 pages to it in the chapter “Principles of selection” (instead of fewer than three pages in OS). Darwin defines it in the following terms: “[it] depends on the advantage which certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction” [2: I, 256]. This definition is close to the former definitions given by Darwin. However, it is more precise. Note that Darwin does not restrict the process to the struggle of males for the possession of the females as he did before [2: I, 263], although most cases discussed in the book refer to inter-male competition. Darwin explains the reason why he has introduced the expression “sexual selection”. The adjective “sexual” applies not only to the kind of competition involved (competition between members of the same sex), but also to the outcome of the process (selection of secondary sexual characters belonging to only one the sexes), which implies that some hereditary characters are exclusively transmitted within a given sex: “the males have acquired their present structure, 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” [2: I, 257]. In DM, the opposition between “struggle for existence” and struggle for a mate becomes extremely important. This led Darwin to underscore the potentially non-adaptive outcome of sexual selection, even though he also insisted that “in most cases it is scarcely possible to distinguish between the effects of natural and sexual selection” [2: I, 257].

In 1871, Darwin devotes a rather long discussion to the “manner of action” of sexual selection [2: I, 259–263]. He acknowledges that “the precise manner in which sexual selection acts is to a certain extent uncertain” [2: I, 259]. It is worth spending some time on Darwin’s hesitation on this subject. Modern accounts of Darwin’s concept of sexual selection state that Darwin distinguished two modes of it: direct fighting between males and female choice. In a sense, this is legitimate, because, in practice, this dichotomy prevails in most of the particular cases of sexual selection examined in the book. But Darwin is more cautious and more hesitant in his introductory chapter on sexual selection. As in OS, he distinguishes not two, but three modes of sexual selection. One is a kind of intra-sexual competition based on “vigor” (quicker development, better health, bigger strength, etc.). The second kind consists of direct fighting between males with the help of special weapons and behavioral capacities. The third kind is differential attractiveness for the other sex. Darwin tends to fuse together the first two categories; this attitude corresponds to the standard distinction that modern authors draw between intra-sexual selection (“any form of competition between individuals of the same sex based upon their own attributes”), and inter-sexual (or epigamic) selection (“based upon a choice exerted by the individuals of the other sex”) [16]. But Darwin’s general analysis of the concept of sexual selection shows that he was haunted by the question of how far “vigor” interferes with direct male rivalry and female choice. This was obviously a serious source of embarrassment for Darwin. In the same text, he oscillated indeed between two opposed claims: sometimes, he says that there is no clear-cut demarcation line between natural selection and sexual selection; sometimes, he argues that there is definitely a difference between the “struggle for existence” and the “struggle for the possession of females”. Let us examine these two conflicting claims.

On the one hand, Darwin holds that natural selection controls sexual selection. No characteristic that would be detrimental to the species as a whole can succeed in the long run: “Sexual selection will also be dominated by natural selection for the general welfare of the species” [2: I, 296]. Thus, we cannot be surprised that Darwin emphasizes “vigor” in all the modes of sexual selection that he recognizes. The best-armed and strongest males are also likely to be the healthiest. Similarly, in the case of female choice, Darwin says that females will tend to choose not only the “most attractive” (e.g. more ornamented or best songsters), but also the more vigorous. The following quotation shows Darwin’s hesitation:

“The courtship of animals is by no means so simple and short an affair as might be thought. The females are most excited by, or prefer pairing with, the more ornamented males, or those which are the best songsters, or play the best antics; but it is obviously probable, as has been actually observed in some cases, that they would at the same time prefer the more vigorous and lively males. Thus, the more vigorous females, which are the first to breed, will have the choice of many males; and though they may not always

select the strongest or best armed, they will select those which are vigorous and well armed, and in other respects the most attractive.” [2: I, 262].

On the other hand, Darwin insists that, contrary to what he had first believed, in most species the sex ratio is 1:1. This is a serious difficulty: “. . . sexual selection would be a simple affair if the males considerably exceeded in number the females” [2: I, 263]. But this does not seem not be the case. Therefore, Darwin could hardly argue that sexual selection relied on an analog of the Malthusian principle that he had used for his statement of the principle of struggle for existence:

“If the males were to the females as two to one, or as three to two, or even in a somewhat lower ration, the whole affair would be simple; for the better-armed or more attractive males would leave the largest number of offspring. But after investigating, as far as possible, the numerical proportions of the sexes, I do not believe that any great inequality in number commonly exists” [2: I, 261].

Darwin had no clear answer to this difficulty. However, he insisted that the sexual struggle could not be reduced to the ordinary struggle for existence. Weapons and ornaments are the result of sexual and not ordinary selection because “unarmed, unornamented, or unattractive males would succeed equally well in the battle for life and in leaving a numerous progeny, if better endowed males were not present” [2: I, 258]. Hence, these strange declarations in which Darwin simultaneously holds that sexual selection relies on a combination of “vigor” and something that has no justification in terms of adaptation to the environment – either purely competitive weapons or attractiveness. In the context of such an hesitation, Darwin’s emphasis upon the psychological qualities that underlie the genesis of most secondary sexual characters is remarkable: “When we behold two males fighting for the possession of the female, or several male birds displaying their gorgeous plumage, and performing the strangest antics before an assembled body of females, we cannot doubt that, though led by instinct, they know what they are about, and consciously exert their mental and bodily powers.” [2: I, 258]. This is exactly what a number of readers could hardly admit, as shown in the next section.

3. The Darwin–Wallace controversy

The interaction between Wallace and Darwin was extremely complex. After 1858, they remained close friends, and they battled together in order to win people over to the idea of evolution through natural selection. However, they disagreed on a number of important issues (for a classification of these disagreements, see [17]). They disagreed on several aspects of the theory of selection. For example, in contrast with Darwin’s mainly individualistic concept of natural selection, Wallace admitted that natural selection could happen at several levels (individuals, groups, species) [18,19]. But the main disagreement was about sexual selection. After 1871, Wallace increasingly criticized this concept, and finally denied that there was

another “means of natural selection” beside standard natural selection. Wallace and Darwin also disagreed about the role of natural selection in the explanation of major classes of phenomena, such as the origin of hybrid sterility, the origin of sexual dimorphism, and the origin of Man and Human races (on these three controversies, see the admirable study by Kottler et al. [20]). Finally, the two scientists also had different views about the scope of the principle of natural selection in evolution as a whole. Whereas Wallace thought that natural selection was the only principle that ultimately accounts for all biological phenomena, Darwin thought that natural selection was the main evolutionary agent, but not the only one. Wallace was also extremely important in the original moulding of Darwinism as a scientific tradition, because it was he who abundantly used the term and defined it, not hesitating to eliminate elements that were crucial to Darwin. Sexual selection was a key issue in that respect. This is why I have decided to contribute to the present volume *Non-Darwinian Darwin* with an enquiry into sexual selection.

Sexual selection was certainly the major disagreement between Wallace and Darwin. It took quite a long time for the disagreement to emerge. In the famous 1858 communication by Darwin and Wallace delivered at the Linnean Society [21], Darwin had a full paragraph on sexual selection (in fact, an excerpt of the 1844 Essay commented on above), but Wallace did not have a similar idea. This is a major difference between the two papers, which has been pointed out by all commentators. During the 12 years that followed the publication of OS, Wallace did not object to sexual selection, and even approved it. Discrete reservations can be found here and there [13,22], but Wallace made no frontal attack. He completely changed his mind after the publication in 1871 of DM, which he reviewed. There, still discretely, he overtly disagreed both about the origin of the intellectual and moral faculties of humans and about sexual selection. After this date, he developed an increasingly radical criticism of Darwin’s hypothesis of sexual selection. I will here mainly rely upon Elena Cronin’s *The Ant and the Peacock* for the description of this criticism, one of the very rare studies on this subject [12].

Wallace attacked sexual selection on two fronts, corresponding to the two main modes of sexual selection that Darwin had distinguished, direct fights among males for the possession of the females, and “choice exerted by the female” (an expression that Wallace contracted into “female choice”). His criticisms of these two alleged processes were quite different.

Concerning the first kind of sexual selection, or direct struggle between males (or, in rare cases, females), Wallace argued that it resulted in characters that natural selection would favour anyway: strength, vigour, and weapons or other traits that Darwin interpreted as the result of inter-male competition. For instance, Wallace claimed that male weapons would be useful for defending the family (or a wider group) against predators. And, because these traits were useful for both sexes, Wallace said that they had been selected for the benefit of the species as such. Although Wallace admitted that individual sexual selection could not be totally dismissed in such cases, he considered that in all cases natural selection was

enough to account for the phenomena. Thus, at best, sexual selection was an auxiliary hypothesis.

Wallace's criticisms of female choice were different. He merely denied that such a process existed at all. Over 30 years, Wallace developed increasingly refined arguments against female choice. He elaborated two kinds of arguments. First, he tried to attribute to natural selection that which Darwin attributed to female choice, just as he had done to explain weapons. For instance, he explained the generally dull appearance of female birds by the necessity for them and their progeny to be protected against predators, whereas the conspicuous appearance of males allowed them to attract the predators, and to divert them from the nest. He also proposed that sexual dimorphism was in a number of cases a means of recognition for the members of a given species. Another explanation, still, was that the males' conspicuous features (colour, shape, dance, etc.) might result from the fact that variation among males was less constrained by natural selection than it was among females – not a very convincing kind of argument.

However, the main line of attack was more philosophical. Wallace merely denied that animals, or at least the majority of them, were able to “choose”. For Wallace, Darwin's application to animals of terms such as “choice”, “will”, “consciousness”, “aesthetic sense”, and “standard of beauty” was unacceptable because it was wholly anthropocentric. Such notions could be applied exclusively to humans and had no room in biology.

The result of these various arguments against sexual selection finally led Wallace to reproach Darwin for having weakened the spirit of “Darwinism”. This reproach was formulated in the first pages of the book *Darwinism*, published six years after Darwin's death:

“Although I maintain, and even enforce, my differences from some of Darwin's views, my whole work tends forcibly to illustrate the overwhelming importance of natural selection over all agencies. I thus take up Darwin's earlier position, from which he somewhat receded in the later editions of his works... Even in rejecting that phase of sexual selection depending on female choice, I insist on the greater efficacy of natural selection. This is pre-eminently the Darwinian doctrine, and I therefore claim for my book the position of being the advocate of pure Darwinism” [23: ix–xii]

4. Striking the balance between Wallace and Darwin

As emphasized by Elena Cronin, Wallace's arguments brought much to the explanation of sexual dimorphism. He showed that a number of aspects of sexual dimorphism were under the control of natural selection. But his arguments did not account for the most spectacular aspects of sexual dimorphism: extravagant colours, ornaments and courtship behaviours. Conversely, as long as Darwin could participate in the debate, he repeatedly emphasized his belief that female choice (or, more generally, mate choice) was driven by a search for beauty itself. As he said in the last edition of the OS (1872) “a great number of male animals, as all our most gorgeous birds,

some fishes, reptiles and mammals, and a host of magnificently colored butterflies have been rendered beautiful for beauty's sake” [24: 162]. For Darwin, because mate choice was correlated so closely with the development of “mind” and higher cognitive abilities in animals, it was the only way of accounting for the irreducible contingency and extravagance of a lot of secondary sexual characters. The two scientists never came to an agreement on the subject of sexual selection.

If we retrospectively contemplate the Darwin–Wallace controversy over sexual selection, we can understand better what was at stake. In a sense, both authors were right and wrong.

Wallace was right to emphasize the adaptive importance of a number of phenomena that Darwin attributed to sexual selection. The modern theory of honest signaling [25] suggests that extravagant characters, such as the peacock's tail and courtship, signals to the female that the male is really healthy because he has such costly feathers and behavior. Recent work has indeed shown that the number of displays performed by a male peacock is correlated with important physiological qualities, especially its capacity to produce appropriate antibodies against infectious diseases [26]. On the other hand, Darwin was right to emphasize the proper evolutionary dynamics based upon on female choice, but he had no clear argument about the efficacy of such a process. His repeated claim that higher animals are endowed with some sort of will and aesthetic sense was not enough. In 1915, the young Ronald Fisher was probably the first to propose an evolutionary speculation able to describe the “runaway” process that sexual preference is able to induce [27]. This model was further developed and made more widely known in his 1930 *Genetical Theory of Natural Selection* [28: 147–156]. This reasoning is sometimes presented in a rather schematic way. It is worth looking at Fisher's real words because they were obviously motivated by the quarrel between Wallace and Darwin, which played such a major role in the Darwinians' reluctance to work on sexual selection until the second half of the 20th century. Fisher was indeed one of the very rare authors who took the subject seriously and was aware of the difficult problems, methodological and conceptual, raised by female choice.

In his 1915 paper, Fisher begins his discussion of sexual selection by quoting and discussing Wallace's attack against Darwin's use of the notion of female choice: “The objection raised by Wallace (Darwinism, chapter X) that animals do not show any preference for their mates on account of their beauty, and in particular that female birds do not choose the males with the finest plumage, always seemed to the writer a weak one” [27: 115]. A similar concern about Wallace's book pervades the section on sexual selection in the 1939 book [28: 147]. In both texts, Fisher reexamines Darwin's notion of mate choice with no particular reference to the animals' sense of “beauty”. He focuses on the notion of “sexual preference”, and argues that it can be a major cause of change even though the character preferred by the females no longer has any adaptive value: “Even if, in the course of time, it [a given feature] ceases to be an index of vitality whatever, the taste for it would continue to increase in strength if it has

already become strong, because although the offspring show no general superiority in the ordinary course of life, they retain their ascendancy in sexual selection, and have, therefore, a better chance of surviving" [27: 118]. Fisher insists that, after a certain point, such a process "owes nothing to natural selection, which may even have turned against it" [27: 118]. As shown by these two quotations from the 1915 paper, Fisher subtly displaces the object of the debate over mate choice. Instead of taking sexual preference in one sex as a starting point for the explanation of the evolution of secondary sexual characters in the other sex, he considers the evolution of the sexual preference itself as part of the *explanandum*. Darwin also had a general schema for explaining the evolution of sexual preference: he referred to the development of perceptual, intellectual and emotional qualities in higher animals (making them able to "choose" and have an "aesthetic sense"), but he did not take the increase of a given ornamental character and the increase of a particular taste in a given species to be correlated. This is indeed what Fisher did. In *The Genetical Theory of Natural Selection*, he writes:

"If instead of regarding the existence of sexual preference as a basic fact to be established only by direct observation, we consider that the tastes of organisms, like their organs and faculties, must be regarded as the products of evolutionary change, governed by the relative advantage which such tastes may confer, it appears, as has been shown in a previous section, that occasions may be not infrequent when a sexual preference of a particular kind may confer a selective advantage, and therefore become established in the species" [28: 151]

Then, Fisher analyzes the dynamics of a process of sexual selection in the following way. One must first postulate that in one sex, for instance the males, a heritable character (e.g., some particular feature of the plumage of a cock) gives a small advantage to the individuals that have it (so that the character is expressed). Let us also admit that the members of the other sex have a small heritable preference for that character. Then let us consider the consequences for these two traits in terms of reproductive advantage. First, the female preference will confer an additional advantage to the cocks who have the desired trait, this advantage being proportional to the intensity of this preference. Secondly, "the intensity of preference will itself be increased by selection so long as the sons of hens exercising the preference most decidedly have any advantage over the sons of other hens" [28: 152]. The consequence of this is that the development of the plumage character will still proceed even after it has passed the point at which its advantage in natural selection has ceased. Hence, the conclusion:

"The two characteristics affected by such a process, namely plumage development in the male, and sexual preference for such development in the female, must then advance together, and so long as the process is unchecked by severe counterselection, will advance with ever-increasing speed. In the total absence of such checks, it is to see that the speed of development will be

proportional to the development already attained, which will therefore increase with time exponentially, or in geometric progression." [28: 151]

Fisher called this a "runaway process" [28: 153], which (addition of the 1958 second edition of *GTNS*), "...however small the beginnings from which it arose, must, unless checked, produce great affects, and in the later stages with great rapidity" [28: 152]. He also insisted that the actual speed and outcome of the process should in practice depend on a balance between sexual selection and natural selection. Fisher was also aware that this was just a theoretical approach, for which he did not even provide mathematical treatment. Others did it for him much later (especially [29]). Fisher also mentioned that his model would be extremely difficult to test in practice, because it involved a high number of parameters and assumptions to check empirically. In their review of the numerous works that have been done on the subject since the 1980s, Danchin and Cézilly specify the contribution Fisher's runaway selection made to the history of sexual selection studies: "The genetic models mentioned earlier do not prove that all extravagant sexual traits found in nature are the result of a Fisherian runaway process. They only show that, under some conditions, such an evolution is theoretically possible." [30: 393].

I will not comment further here on the fate of sexual selection in the history of evolutionary biology ([6,16]). The objective of this section was just to show how much the Darwin–Wallace controversy, with its weaknesses on both sides, helps us to understand why the subject of sexual selection has been so much neglected some seventy years after Darwin's DM. The three main issues were: the complexity of the notion (with its various modes and its controversial definition); the relationship between natural selection and sexual selection (both in terms of definition and objective interaction); and the special problem of mate choice, which has been disputed ever since Darwin.

5. Conclusion

To conclude, I would like to highlight the relation between the Darwin–Wallace controversy over sexual selection and the different conceptions of natural selection of these two authors.

Wallace had an environmentalist conception of natural selection [20]. What counted for him was the capacity of natural selection to adjust organisms to their own environment. This conception pervades the entirety of his work. It is why he emphasized that under unchanged conditions, "[natural selection's] primary effect will, clearly, be to keep each species in the most perfect health and vigor, with every part of its organization in full harmony with the conditions of its existence." It is only under changed conditions that natural selection results in evolutionary change: "...the very same process which, so long as conditions remain substantially the same, secures the continuance of each species of animal or plant in its full perfection, will usually, under changed conditions, bring about whatever change of structure or habits may be necessitated by them" [23: chapter V]. This fits well with

Wallace's reluctance to accept sexual selection, a natural mode of selection, which is a natural mode of selection that refers not only to the environment, but rather to a purely competitive process among the members of one sex within the species.

Darwin's understanding of natural selection was different. For him, natural selection was not only a process that adjusts organisms to their environment, but also a competitive process within the species, which can change the species even under unchanged conditions. Provided that there is heritable variation affecting the chances of survival or reproduction, natural selection will act upon the species and potentially change its structure and habits. For Darwin, then, utility was relative both to the environment and to the state of competition between the species. This is why sexual selection seemed was so appealing to Darwin. As it was based exclusively upon differential reproductive success among individuals of one sex, sexual selection did not rely upon an adaptive advantage. In his book *The Triumph of the Darwinian Method*, Michael Ghiselin has clearly stated this point: "Sexual selection is Darwin's most brilliant argument in favor of natural selection, of which it is a corollary. Selection, whether artificial, natural, or sexual, depends upon differential success, and not on adaptive advantage to the individual or group. If, owing to some historical accident, it happened that an organism had some characteristic that was otherwise useless or even deleterious, but which did enable him to leave more progeny than other members of his sex, then perhaps that character would be become more abundant in the population." [13: 215]. Ghiselin's formulae are perhaps a little excessive, because Darwin also held that, ultimately, natural selection counterchecks any character that would threaten the chances of an organism to survive in a given environment. But Ghiselin is right that net differential reproductive success is the immediate *modus operandi* of natural selection. The important point here is that sexual selection was a major piece in his overall strategy for denying any role to the hypothesis of design in the explanation of evolution. Sexual selection, especially in the form of mate choice, revealed the purely competitive aspect of selection in nature.

We see, therefore, that the Darwin–Wallace controversy over sexual selection tells us something important about "Darwinism" as a scientific tradition. For Wallace, sexual selection was outside Darwinism because it lessened the power of natural selection as a process that produces harmony in nature at all levels. For Darwin, sexual selection, because of its primarily competitive and individualistic nature, revealed something important about how selection in general works in nature. These two "Darwinian" styles are still alive today, and sexual selection is more than ever a test case for them. As noted by Joan Roughgarden in her recent book *The Genial Gene: Deconstructing Darwinian Selfishness*, sexual selection can be regarded today in two ways. On the one hand, it is a well-established research discipline, that "need not be based upon Darwin's picture" [4: 18]. On the other hand, it is the epitome of a particular way of thinking about evolution, in terms of competition, selfishness, and

conflict [4: 236]. In her book, Roughgarden takes sides against this view of evolution; she obviously finds it repugnant. However, she also adds that "regardless of what we would like the truth to be, the issue before us is whether such metaphors correctly characterize biological nature" [4: 236]. Beyond Darwin's own philosophical preferences, it is no doubt his merit to have opened the field of sexual selection, which decidedly provides test case for anyone who would claim that "Darwinism" as a scientific tradition is something simple and trivial.

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