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Darwin's sexual selection: Understanding his ideas in context



Sélection sexuelle selon Darwin : comprendre ses idées dans leur contexte

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ABSTRACT

Darwin's writings need to be seen in their fullness, as opposed to quote-mining individual sentences without the context of his passages. Sometimes Darwin wrote at length, apparently favorably, about ideas that he subsequently undermined, replacing them with a more integrative view that reflected his own broad compass. Darwin understood that nature is not simple, that not all members of a group may have evolved under the same selective regime, and that variation of all kinds is fundamental to selection in its several forms. Sexual selection requires sexual dimorphism; it is not centred on variation within sexes but on selection for the ability to acquire mates. "Mutual sexual selection" was rejected by Darwin for every species except humans. Mating success is not a matter of mere numbers but of the transmission of the most attractive features to the opposite sex. The term "sexual selection" should only be used when one sex uses a feature not present in the other sex to attract mates or repel rivals for mates.

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RÉSUMÉ

Les écrits de Darwin nécessitent d'être vus dans leur ensemble et non à partir de phrases retirées de leur contexte. Quelquefois, il arrive que Darwin écrive longuement et apparemment favorablement sur des idées qu'il abandonne ensuite en les replaçant dans une perspective plus intégrative qui reflète sa vaste propre vue d'ensemble. Darwin a compris que la nature n'était pas simple, que tous les membres d'un groupe pouvaient ne pas avoir évolué sous le même régime sélectif et que la variation sous tous ses aspects était fondamentale pour la sélection sous ses différentes formes. La sélection sexuelle requiert un dimorphisme sexuel : il n'est pas centré sur la variation au sein des sexes, mais sur la capacité de sélection, au sein d'un sexe, d'acquérir des partenaires. La « sélection sexuelle mutuelle (ou réciproque) » a été rejetée par Darwin pour toutes les espèces, exception faite de l'espèce humaine. Le succès de l'appariement n'est pas une question de simple nombre, mais de transmission des traits les plus attractifs vers le sexe opposé. Le terme « sélection sexuelle » ne devrait être utilisé que lorsqu'un sexe utilise une caractéristique non présente dans l'autre sexe pour attirer des partenaires ou repousser des rivaux.

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1. Introduction

Borkovic and Russell (2014) mount an interesting case, based on quotations from Darwin's work, to disagree with our understanding of what sexual selection is, what its criteria are, why Darwin invented the concept, and how it is to be used in assessing bizarre structures in living and extinct animals (Padian, 2013; Padian and Horner, 2011a,b, 2013, 2014; for alternative views see Dodson, 2011, Hone and Naish, 2013, Hone et al., 2012, Knell and Sampson, 2011, and Knell et al., 2013a,b). We appreciate their point of view because it is only by understanding the historical roots of concepts that confusion can be corrected, and the issue needs healthy discussion. We maintain that a relatively recent side-tracking of Darwin's original concept, probably beginning quite unintentionally with West-Eberhard (1983) and Arnold (1994), has misled biologists into thinking that sexual selection is simply about leaving many offspring, and therefore, it does not require sexual dimorphism and it does not really differ from natural selection, which is also mistakenly thought by many to be all about leaving many offspring.

Borkovic and Russell take a different approach, which purports to hew to what Darwin actually said in his published works. However, we object to their attempt at the outset of their paper to claim the historical high ground by labelling our description of Darwin's concept "what they consider to be Darwin's definition of sexual selection", and labelling their own as "less a matter of interpretation, and more a matter of reference", as if we constructed our description out of whole cloth. We will show here that accuracy of reference requires readers to place isolated sentences in the contexts of Darwin's full arguments. One should also recognize when he was discussing a point of view that he wanted to acknowledge but did not accept himself. A third point, that should hardly bear mention, is that the use and meanings of words have changed between Darwin's days and ours, and that 19th-century authors were not always like us in how they laid out concepts and definitions: they expected readers to absorb the whole argument, not merely a sentence or two.

2. Sexual selection

Borkovic and Russell maintain that nothing in Darwin's original work requires sexual dimorphism for sexual selection. Specifically, their concerns are that "(1) Darwin never used the term sexual dimorphism to describe differences between the sexes; (2) Darwin describes allometric sexual differences as products of sexual selection, and presents sexual monomorphism as an acceptable outcome of sexual selection; (3) Darwin states that sexual selection depends on variation within a sex, and that this variation is independent of the action of selection; (4) Darwin identifies his own bias for discussing structures that would be recognized today as being sexually dimorphic". We will approach these concerns in turn.

(1) Darwin never used the term sexual dimorphism to describe differences between the sexes. Borkovic and Russell say that because Darwin never used the exact words "sexual dimorphism", it was not essential to his concept of

sexual selection. This is a historically naïve demand. How could a concept be originally framed with a phraseology that was only invented years later? Did "mass extinctions" not exist as a concept for paleontologists from Cuvier and Lyell onward, simply because the exact term was not used until the 20th century? Scholarship requires moving beyond elementary diction to consider central ideas in their fullness.

Let's see how Darwin originally defined sexual selection. Borkovic and Russell quote many passages from Darwin's books, usually a sentence or two removed from context; however, inexplicably they do not cite the passage in which Darwin (1859) established the concept of sexual selection, repeated almost verbatim in *The Descent of Man and Selection in Relation to Sex* (Darwin, 1871). Because he repeated the passage almost verbatim, it must have seemed sufficient to him to define his concept. Here, it is (Darwin, 1859, pp. 87–88):

Thus it is, I believe, that when the males and females of any animal have the same general habits of life, but differ in structure, colour, or ornament, such differences have been mainly caused by sexual selection; that is, individual males have had, in successive generations, some slight advantage over other males, in their weapons, means of defence, or charms; and have transmitted these advantages to their male offspring.

This seems unambiguous enough: Darwin begins by noting qualitatively different features between the sexes, then proposes that sexual selection is responsible, in that some males are better than others at attracting mates and (or) repelling rivals for mates, and that these differences are hereditary. It is clear that the dimorphic features in question are responsible for the differential mating success. So, he is beginning with differences between the sexes in defining sexual selection. This is certainly sexual dimorphism. (Also note that he is not centering his definition on variation within a sex, contrary to Borkovic and Russell's argument (3), to which we will return.)

But it is not enough to rely on a single sentence. Let's analyze the whole section in which Darwin introduces sexual selection (Darwin, 1859, pp. 87–90). Darwin begins by saying that "Inasmuch as peculiarities often appear under domestication in one sex and become hereditarily attached to that sex, the same fact probably occurs under nature. . . ." So, from the outset, he builds his concept on the contrasting morphology of the sexes, working as he often does from the familiar domesticated species to those in nature, noting that "selection will be able to modify one sex in its functional relations to the other sex". Beginning his discussion of sexual selection, he says that victory (in sexual competition) will depend "not on general vigour, but in many cases, special weapons, confined to the male sex". What is this if not dimorphism?

Darwin immediately follows this with examples of male animals that have weapons or defences that the females lack, and that are used in male-to-male competition for mates: i.e., dimorphism. He then lists the "more peaceful" characters of birds, including song, plumage, and behavioral displays (overlooked by Borkovic and Russell), that attract females; i.e., dimorphism. So, he establishes

straightaway weapons and attractants as the two purposes of the dimorphic features that he lays out. He then presents the definitional passage quoted above. He finishes by cautioning us that not all such peculiar characteristics found in the males (and Darwin understood that the cases featuring females in this context were very few) have evolved as a result of sexual selection. However, he notes in this passage that his space is limited, and his discussion of the details has to be postponed.

Therefore, Darwin's exact words (although he did not precisely use the later-invented term "sexual dimorphism"), and the logic and flow of his argument, falsify Borkovic and Russell's claim that sexual dimorphism was not essential to his definition of sexual selection. It was its very heart.

If doubt remains, we suggest a reading of the 500 pages of *The Descent of Man* that are devoted to the various groups of animals and whether their features have been shaped by sexual selection. We have personally enumerated some 300 examples, in every one of which dimorphism is required for consideration of the role of sexual selection (details upon request to the first author). Not a single example that we could find is based on another criterion. One needs look no farther than Darwin's discussion of "Vermetes" (Darwin, 1874, p. 407), where he states (emphasis ours):

In this class, although the sexes, when separate, sometimes differ from each other in characters of such importance that they have been placed under distinct genera or even families, yet the differences do not seem of the kind, which can be safely attributed to sexual selection. These animals are often beautifully coloured, but as the sexes do not differ in this respect, we are but little concerned with them.

He dismisses nearly all invertebrates except some arthropods and a very few mollusks, most amphibians, most reptiles (except some lizards), and some birds and mammals for the same reasons. It seems inconceivable that anyone could read Darwin and not comprehend the centrality of sexual dimorphism to his concept of sexual selection.

(2) Darwin describes allometric sexual differences as products of sexual selection, and presents sexual monomorphism as an acceptable outcome of sexual selection. Borkovic and Russell, like some other authors, use the term "allometry" in the context of sexual selection without defining it. (Darwin did not use the term: it was not invented until the early 20th century by Julian Huxley.) As we will show, their first clause quoted above is sometimes correct (but not for the reason they state), and the second is not.

First, males and females may differ in adult size for at least two reasons related to growth trajectory. There may be a single trajectory for males and females, and one sex may continue to grow after the other has ceased growth. Or the males and females may have different growth trajectories from early in ontogeny, resulting in differences not just in absolute sizes but in shapes, including structures unique to one sex. We know now, but Darwin and his contemporaries did not, of the role that hormones play

in these differentiating trajectories. The latter kind of trajectory produces the distinct dimorphisms that are at the heart of Darwin's concept of sexual selection. The former kind of trajectory is more problematic.

Contrary to Borkovic and Russell's discussion, we never said that size dimorphism between the sexes cannot result from sexual selection. However, size differences by themselves cannot by default constitute or be ascribed to sexual selection. We said (Padian and Horner, 2014, p. 101):

Dimorphism is not simply difference; size difference is not dimorphism in Darwin's sense because it does not describe a structure, function, or behavior that one sex has and the other does not. It is possible for larger males [e.g., in crocodiles] to use their size difference in repelling rivals and attracting mates, but if they also use it for greater success in trapping prey, then more information is needed to determine why it evolved or how it is maintained.

An example is the water flea *Daphnia*, in which females are substantially larger than males. This has nothing to do with competition for mates or repelling rivals for mates. The female's larger size allows more eggs to be incubated. This is actually a primary rather than a secondary sex characteristic, and Darwin's sexual selection concerns secondary sex characters only (Gayon, 2010).

The quotations that Borkovic and Russell provide from Darwin to support their argument is taken out of context. The first one is "If the males had been habitual fighters, the size of their bodies would probably have been increased through sexual selection, so as to have exceeded that of the female. . ." (Darwin, 1874: 297; emphasis theirs). But they miss the point of the passage, which begins by noting "A most remarkable distinction between the sexes of many beetles is presented by the great horns which rise from the head, thorax, and clypeus of the males. . ." Darwin is again, as he always does in the *Descent*, framing his argument about sexual selection in the context of sexual dimorphism. He notes much variation in the horns of both males and females (depending on species), and frankly admits that he cannot explain all taxa with a single hypothesis. The quotation above represents only one hypothesis that Darwin considered (including "ordinary work", defence against enemies, and competition for mates). Again, there is no problem with size dimorphism being involved in sexual selection, if the greater or smaller size can be shown to be differentially advantageous in attracting mates or repelling rivals for mates. But size difference alone cannot be assumed to have been shaped by sexual selection. Darwin concludes the passage with a paragraph that Borkovic and Russell overlook:

The conclusion that the horns have been acquired as ornaments is that which best agrees with the fact of their having been so immensely, yet not fixedly, developed—, as shown by their extreme variability in the same species, and by their extreme diversity in closely-allied species. This view will at first appear extremely improbable; but we shall hereafter find with many animals standing much higher in the scale, namely fishes, amphibians, reptiles and birds, that various kinds of

crests, knobs, horns and combs have been developed apparently for this sole purpose.

Not only is Darwin again hooking sexual selection to sexual dimorphism; he is hinging his entire concept of sexual selection on the need to explain unusual structures that have no apparent adaptive function.

Borkovic and Russell's second quote is: "As in many kinds of fishes the males habitually fight together, it is surprising that they have not generally become *larger and stronger than the females through the effects of sexual selection*. . . Increased size must be in some manner of more importance to the females, than strength and size are to the males for fighting with other males; and this perhaps is to allow of the production of a vast number of ova". (Darwin, 1874:335; emphasis theirs). Again they seem to miss the point of the passage. Darwin begins by noting that in fishes the males are almost always smaller than the females, and often much smaller; and he relates this to the need of the females to brood more eggs (as in the *Daphnia* example given above). So, it is not a matter of why the males are not larger, but why the females are so large. He concludes: "Increased size must be in some manner of more importance to the females, than strength and size are to the males for fighting with other males", but he does not relate this to sexual selection. In fact, he finds it irrelevant in this case.

The third example quoted by Borkovic and Russell, relating to certain birds, is simply a case of females being the larger and more dominant sex. Again, there is no objection to size dimorphism being related to sexual selection, as long as it is demonstrably linked to attracting mates or repelling rivals for mates. Therefore, the first of Borkovic and Russell's claims in this section – that sexual size difference should automatically be assumed as a result of sexual selection – is incorrect. It has to be tested, and Darwin understood this.

The final two quotes that these authors provide in this section relate to a different point: that both sexes can select similar characters in each other, and that these are shaped by sexual selection (Darwin, 1874: 226 and 614). Rather than deal with these isolated sentences, let's see what Darwin's context was in the paragraph immediately preceding the quotation that Borkovic and Russell cited from his page 226 (emphasis ours):

It may be suggested that in some cases a double process of selection has been carried on; that the males have selected the more attractive females, and the latter the more attractive males. This process, however, though it might lead to the modification of both sexes, would not make the one sex different from the other, unless indeed their tastes for the beautiful differed; *but this is a supposition too improbable to be worth considering in the case of any animal, excepting man*. There are, however, many animals in which the sexes resemble each other, both being furnished with the same ornaments, which analogy would lead us to attribute to the agency of sexual selection. In such cases, it may be suggested with more plausibility, that there has been a double or mutual process of sexual selection; the more vigorous and precocious females selecting the more attractive and vigorous males, the latter rejecting all

except the more attractive females. *But from what we know of the habits of animals, this view is hardly probable, for the male is generally eager to pair with any female. It is more probable that the ornaments common to both sexes were acquired by one sex, generally the male, and then transmitted to the offspring of both sexes*. If, indeed, during a lengthened period the males of any species were greatly to exceed the females in number, and then during another lengthened period, but under different conditions, the reverse were to occur, a double, but not simultaneous, process of sexual selection might easily be carried on, by which the two sexes might be rendered widely different.

Sometimes a long quotation is essential to understanding what Darwin was really talking about and how his concepts fit together. (Remember that Darwin and his colleagues did not understand the genetics of sex-linked traits.) For those who believe that Darwin endorsed "mutual sexual selection", this paragraph and the reasoning behind it (see below) should weaken those convictions. Note that he begins by saying that if both sexes select for the *same* attractive characters in the opposite sex it would not make them different; and so he dismisses the phenomenon, because for him it is not sexual selection (because there is no dimorphism, again). Note also that he then immediately qualifies his generalization by saying "in the case of any animal, excepting man". This statement is central to the other half of his book (how humans evolved), a topic that cannot be fully discussed here (but see [Desmond and Moore, 2009](#); [Millstein, 2012](#)). Darwin knew exactly what he was talking about: he understood that humans were different from all other animals, and that part of their superiority depended on the separation of roles of the sexes, or dimorphism (morphological and behavioral; see below), which had been selected by the opposite sexes. Human males are larger and stronger (though less different than in other apes), better protectors and providers; the females nurture the young, perform the domestic tasks, and hold the social group together. (His view may be repulsive to many today, but recall that Darwin was not only a product of his pre-Victorian upbringing and class, but also that he had both personally witnessed and read in many accounts the characterizations of societies all over the world where these patterns were viewed as virtually invariable.) *That is what, in the end, The Descent of Man is largely about: the importance of the unique differentiation of both human sexes through sexual selection as a major explanation of human evolution. And that is why in the Descent Darwin sets up the concept of "mutual sexual selection", only to knock it down for all animals except humans.*

In summary, Borkovic and Russell's second claim in this section, that sexual monomorphism was an acceptable outcome of sexual selection for Darwin, is incorrect.

We also find it surprising that Borkovic and Russell would not deem important the paragraph immediately following the passage they partly quote from page 614 of the *Descent* (Darwin, 1874). This subsequent paragraph reads as follows (emphasis ours):

The belief in the power of sexual selection *rests chiefly* on the following considerations. *Certain characters are*

confined to one sex; and this alone renders it probable that in most cases they are connected with the act of reproduction. In innumerable instances, these characters are fully developed only at maturity, and often during only a part of the year, which is always the breeding-season. *The males (passing over a few exceptional cases) are the more active in courtship; they are the better armed, and are rendered the more attractive in various ways. It is to be especially observed that the males display their attractions with elaborate care in the presence of the females; and that they rarely or never display them excepting during the season of love. It is incredible that all this should be purposeless.*

The fact that these statements reflect exactly Darwin's original introduction of the concept of sexual selection (1859), quoted above, and his later elaboration of it (Darwin, 1871, 1874) should be proof to any scholar of the centrality of sexual dimorphism to attracting mates and repelling rivals for mates in his formulation of the concept of sexual selection.

To conclude, size differences, including allometric ones between sexes, can play into sexual selection, but only if they can be shown to provide an advantage in mating. They are not, contrary to Borkovic and Russell, "an essential component of the theory"; they merely comprise a class of examples, albeit good ones.

(3) Darwin states that sexual selection depends on variation within a sex, and that this variation is independent of the action of selection. This claim by Borkovic and Russell is technically true in part, but irrelevant: it has nothing to do with the argument to the evolution of sexual selection, and it omits its most important part (that female choice utterly depends on this variation).

There are at least three major problems with their view. First, they are conflating the question of how a trait evolved with the very different question of the role of that trait. Darwin certainly stressed that there is variation in a trait within a sex; otherwise there would be nothing for selection to act upon. Variation is essential to all evolution; the passages that Borkovic and Russell quote are valid but beside the point. But variation itself is independent of the direction of selection, as Darwin frequently said. Second, it is not a matter of the fact that there is variation; rather it is a matter of the object of selection upon it. There can be natural selection, which is adaptive, or sexual selection, which favours access to mates. But their objects and mechanisms are different. This is why Darwin invented the concept of sexual selection: he needed to explain features, often bizarre, possessed by one sex and not the other that were not adaptive *per se* to the individual. Third, Darwin certainly emphasized a struggle in the process; otherwise selection would not be in play and the distribution of phenotypes would be random. There would be no distinction between males and females in these respects.

(4) Darwin identifies his own bias for discussing structures that would be recognized today as being sexually dimorphic. The passage that Borkovic and Russell cite here (Darwin, 1874:210) merely relates to a concept that he discussed over and over in the *Descent*: that sometimes it is difficult to understand whether a structure is used for

both adaptive and mating purposes, and therefore whether it was shaped by natural or sexual selection, or both. It is difficult to understand why Borkovic and Russell think that the passage they cite is somehow fatal to any of our arguments; in fact, we have raised it several times previously. But again, more revealing is that they seem to have overlooked the importance of the words immediately preceding the passage they cite, which read as follows (our emphasis):

When the two sexes follow exactly the same habits of life, and *the male has the sensory or locomotive organs more highly developed than those of the female*, it may be that the perfection of these is indispensable to the male for finding the female; but in the vast majority of cases, they serve only to give one male an advantage over another, for *with sufficient time, the less well-endowed males would succeed in pairing with the females*; and judging from the structure of the female, they would be in all other respects equally well adapted for their ordinary habits of life. Since in such cases, 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, sexual selection must here have come into action. *It was the importance of this distinction, which led me to designate this form of selection as Sexual Selection.*

3. Defining dimorphism

Borkovic and Russell quote our differentiation between "dimorphism" and "difference", saying it is inaccurate. We stated: "Dimorphism is not simply difference; size difference is not dimorphism in Darwin's sense because it does not describe a structure, function, or behavior that one sex has and the other does not" (Padian and Horner, 2014:10). They claim this is wrong, first, because Darwin did not use the term "sexual dimorphism", which although technically true in diction is certainly not true in concept, and we falsify this claim above. They further claim that "Darwin (1874) never once used the term 'dimorphic' to explain the differences that he was describing between the sexes, only within them". It is difficult to think that one could read Darwin's passages that we cite above, as well as hundreds of other examples in his book, and not recognize that Darwin constantly enumerated examples of dimorphism between sexes at least as strong as any that occurs within a single sex. Does anyone really believe that this question hinges on how often Darwin used the word "dimorphic"?

4. Sexual selection

Borkovic and Russell criticize our characterization of the essential components of Darwin's concept of sexual selection, namely: "(i) it explains why sexual dimorphism exists, and its central role in sexual selection; (ii) the dimorphic structures or behaviors are used by one gender to attract mates or repel rivals for mates; and (iii) these structures and behaviors help the bearer gain access to mates (not necessarily to leave more offspring, but to leave offspring that are more competitive in mating)" (Padian and Horner, 2013:1).

As to the first of our components (i), Borkovic and Russell niggle that some sexual dimorphism is not related to sexual selection. Yes, of course: Darwin noted this and so have we, for example in our discussion of *Daphnia* above. Remember that the whole question is in *how dimorphic features are used to attract mates and repel rivals*. We are perfectly content with the absence of sexual dimorphism in structure if there are behavioral differences that attract rivals and repel mates, but specific behaviors must be involved (i.e., it is not simply a matter of male bunnies fighting to the near-death if they are not using structures or behaviors lacked by the females, which in this case can fight as viciously with the same structures in different contexts). Male deer are graced with antlers (for part of the year), which one might think would be used to repel predators; but in fact they largely use their hooves to do so, as the females do.

As to our second component (ii), Borkovic and Russell overlook the difference between competition *among* and competition *for*. They seem to believe that everything about sexual selection centers on competition *among* the members of one sex; but they forget the whole object of sexual selection, which is to gain access to mates. What would the variation among males matter to sexual selection if it did not gain them better access to females? We believe that we have supplied enough extended passages above and in our other works to establish the centrality of sexually dimorphic structures to attracting mates and repelling rivals, which was instrumental to Darwin's own definition (not quoted by Borkovic and Russell) and other passages that mirror it exactly.

The third of our components (iii) appears to upset Borkovic and Russell because we emphasized the importance of leaving offspring that bear traits that are more competitive in mating, rather than simply leaving more offspring. We find it strange that any evolutionary biologist would not recognize that leaving boatloads of maladaptive or indifferently fit (naturally or sexually) offspring is no guarantee of success when the selective regime is at all competitive. We previously explained this apparent conundrum (Padian and Horner, 2011b: 24, left column). Let us start with a simple model. Morphotype A in a population produces twice as many offspring as Morphotype B, but in times of limited availability of food it is only 25% as good as Morphotype B at avoiding starvation. In times of plenty, A will outnumber B; but when resources are scarce the survivorship is reckoned by fertility times survivability, which in the case of A is 50% of B's success.

The confusion that producing lots of offspring is the measure of evolutionary success was generated unintentionally by the early modelers of the Modern Synthesis, who understood that in the long run the most adaptive individuals would be likely to leave more offspring *with their adaptive features* to populate the next generation. However, they had no way to quantify “adaptiveness” and so for the sake of simplicity they elided their logic to comprise simply those who left more offspring (Padian and Horner, 2011b: 24). (This is why the historical term “fitness” seems strange to our ears as a measure of fecundity, but makes perfect sense in its original description of adaptedness.) Many later evolutionary biologists have not understood the

historical elision of this reasoning (and this is reflected in virtually all textbooks), but it is fundamental to separate fecundity and adaptiveness to avoid tautology in evolutionary theory. As Waddington (1967) said, in the midst of a prestigious conference on mathematical challenges to the Neodarwinian synthesis, “You ask who are the most fit; and the answer is, those who leave the most offspring. And you ask, why do they leave the most offspring? And the answer is, because they are the most fit”. However, if empirical evidence shows that those who produce more offspring have adaptive traits that others lack (or have less of), and that these traits improve their survival, then natural selection is not a tautology.

5. Mutual sexual selection

We believe that we have shown above the lack of evidence for this concern of Borkovic and Russell above by treating at length Darwin's full writings on the subject. Darwin did not use the term “mutual sexual selection”, and when he talked about the possibility that sexes could select for the same features in each other that were related to mating success, he dismissed it (Darwin, 1874: 226). His sole exception was humans, in the sense that both sexes selected features in the other; *but the features were different*, and this is what produced the secondary sexual characteristics, plus other features, in men and women.

6. The hierarchy of concepts in sexual selection

Borkovic and Russell object to our construction of a hierarchy of concepts related to social interactions in animals (Padian and Horner, 2013, 2014). In their view, “mate competition and mate choice are fundamental components of Darwin's conceptualization of sexual selection: the action of either, when enforced through differing reproductive success, forms the selection component of sexual selection”. So, for them, the only component of selection in sexual selection is among males. Here and elsewhere in their paper, they make no mention of the importance of female choice, which was so important to Darwin (Gayon, 2010; Veuille, 2010). As we said above, what would be the conceivable purpose of all this male competition if it were not to gain access to female mates? Darwin understood the role and importance of female choice. Why is this absent from their considerations?

We stand by our proposed hierarchy of these concepts. Readers are referred to our full discussions of why certain kinds of actions such as species recognition must precede the more intimate ones of mate choice and sexual selection (Padian and Horner, 2013, 2014).

7. Conclusion

Borkovic and Russell are incorrect about the fundamental aspects of Darwin's original concept of sexual selection, regardless of how later authors have misinterpreted him. Variation within a sex was obviously important to Darwin's concept of sexual selection, as it was to natural selection. However, at least as important was female choice on this variation as it applied to mating success, which Borkovic

and Russell ignore. Sexual dimorphism and female choice are two aspects that separate sexual and natural selection, but variation within a sex does not. Sexual dimorphism was absolutely essential to Darwin's concept of sexual selection, and without it sexual selection simply reduces to leaving more offspring, which makes it indistinguishable from the bowdlerized concept of natural selection popular in some textbooks that omit the central importance of differential adaptive advantage to natural selection. "Mutual sexual selection" was rejected by Darwin for all species except humans, expressly because it would not lead to the differences between the sexes that comprised the heart of his concept of sexual selection. It is critical to understand Darwin's full arguments in context, rather than relying on isolated sentences and whether a specific word or term – sometimes not invented in his time – was expressly used.

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