Perspectives

The sight of the peacock's tail makes me sick: The early arguments on sexual selection

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Why does a peacock have a beautiful train, while a peahen is sober without such flamboyance? Darwin proposed the theory of sexual selection to explain the differences between the sexes of the same species. Recently the study of sexual selection has been one of the most flourishing areas in evolutionary biology. However, the theory met with great resistance from biologists since the publication of the idea and the history of the theory included a lot of misunderstanding and confusion. There are several reasons for this. First, classical Darwinism failed to recognize social competition as an important selective force. Second, the good-for-the-species argument, which persisted in the days after Darwin, made the sexual selection argument more difficult to understand. Compared to the discussions on animals, Darwin's argument on human sex differences is not satisfactory. The reason probably lies in the debate over human racial differences which prevailed in the 19th century.

1. Introduction

The last 20 years or so have witnessed an impressive outburst of studies on sexual selection. Indeed, hardly a week passes by without a paper on sexual selection published in journals of evolution, behaviour and ecology. Sexual selection has been recognized as a force powerful enough to shape almost any aspect of male and female morphology and behaviour (Andersson 1994).

It was Darwin, who first proposed the theory of sexual selection. After the publication of *The Origin of Species* in 1859, he was aware that he had not given full consideration to sex differences in this book. He thought that differences between sexes which belong to the same species should be explained scientifically, and he felt that his theory of natural selection was not enough. He needed another theory, which he proposed in his second big book, *The Descent of Man and Selection in Relation to Sex* in 1871.

However, the idea of sexual selection met with a great deal of scepticism, and the history of the theory has been filled with confusions, objections, hostile rejections and numerous misunderstandings. Now at the end of the 20th century, no evolutionary biologist casts a serious doubt on sexual selection. To know the reasons for this confusion will give us some insights into the strengths and weaknesses of Darwin's argument and how far we have come about after him.

2. The peacock's feather

In earlier days, when Darwin was constructing the theory of evolution by natural selection, the structure of the eye often made him sick. The eye seemed too perfect to be developed through natural selection. But this problem was solved to his satisfaction.

Then, the peacock's feather posed a more formidable threat to his mind. It is beautiful, eye-catching, but extravagant, flamboyant, absurd, and absolutely non-utilitarian. Obviously females can do without them. So why on earth do males have those apparently superfluous feathers?

On the 3rd of April in 1860, Darwin wrote a letter to Asa Gray at Harvard, mainly to thank him for his favourable review of *The Origin of Species*, which was published in the previous year, and included the following lines:

> It is curious that I remember well the time when the

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> thought of the eye made me cold all over, but I have got over this stage of the complaint, and now small trifling particulars of structure often make me very uncomfortable. The sight of a feather in a peacock's tail, whenever I gaze at it, it makes me sick! . . .
>
> (Burkhardt *et al* 1993; p 140)

In *The Origin of Species*, he had already made a rough sketch of the idea of sexual selection as opposed to natural selection. But that was a brief description of about three pages. He hadn't fully developed his idea on this subject at that time.

Then, in 1868, one of the Victorian gentleman naturalists, the Duke of Argyll, who was also the Lord Privy Seal of the Parmerstone cabinet, published a book entitled *The Reign of Law*. This was a book written to attack the theory of natural selection, fuelled by the famous anti-Darwinian anatomist, Richard Owen. But as Adrian Desmond and Jim Moore's biography of Darwin vividly describes,

> . . . the real sting in the book came with Argyll's discussions of hummingbirds. He asked the crunch question, the one that made Darwin flinch. Why should a topaz crest
> be selected in shimmering hummingbirds in preference to sapphire? Or a frill end in emerald spangles rather than ruby? This was beauty for God's sake – there was no earthly reason for it, no struggle could explain it.
>
> (Desmond and Moore 1991; p 546)

By that time, Darwin had collected numerous data on sex differences and mating behaviour of animals from all major taxa, and had given full consideration to the workings of sexual selection. He had a lot to say about not only the colours of hummingbirds, but also the colours of butterflies, crustaceans, about the chirpings of male crickets, the songs of many male birds, and antlers and tusks and big body sizes of male mammals. This finally resulted in the publication of *The Descent of Man and Selection in Relation to Sex* in 1871.

3. Early argument against sexual selection

Darwin posited that sexual selection is different from natural selection. He wrote,

> Sexual selection depends on the advantage which certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction.
>
> (Darwin 1871; vol. 1, p 256)

Further,

> It is certain that in almost all animals there is a struggle between the males for the possession of the female. This fact is so notorious that it would be superfluous to give
> instances. Hence, the female, supposing that their mental capacity sufficed for the exertion of a choice, could select one out of several males.
>
> (Darwin 1871; vol. 1, p 259)

Thus he described mate competition, usually male–male competition, and mate choice, usually female choice.

It is well known that his idea of female choice was rejected by many people and this situation continued until quite recently. But it was not just female choice. Many biologists wanted to get rid of the entire notion of sexual selection. Among the evolutionists of his day, the strongest opposition came from Alfred Russel Wallace. In order to grasp the line of arguments against sexual selection theory since its publication, let us consider what three eminent biologists said about the theory, namely, Wallace, Thomas Hunt Morgan, and Julian Huxley.

3.1 *Alfred Russel Wallace (1823–1913)*

Wallace was Darwin's contemporary natural historian and the co-author of the paper on evolution by natural selection which was presented at the Linnean Society in 1858. We sometimes have the impression that Darwin and Wallace discovered the same thing, proposed the identical idea, and agreed upon everything. In fact, there were differences in opinion between them in almost all aspects of selection, and the discrepancy was the largest on the subject of sexual selection (Kottler 1980, 1985; Cronin 1991).

Since Darwin first mentioned the idea of sexual selection in *The Origin of Species*, much correspondence had been exchanged between the two. Darwin summarized the nature of the argument between them in *The Descent of Man*, and he discussed why he did not adopt Wallace's idea on this subject.

Wallace didn't deny the existence of male–male competition, but he said it was natural selection. He wrote in his book, *Darwinism*, in 1889,

> it is a very general fact that the males fight together for the possession of the females. This leads . . . to the stronger
> or better-armed males becoming the parents of the next generation . . . . From this very general phenomenon there necessarily results a form of natural selection which
> increases the vigour and fighting power of the male animal . . . .
>
> (Wallace 1889; p 282)

When I first read this paragraph, I couldn't understand why he particularly stated that this should be a form of "natural selection". In fact this was the main point of the early argument. I will go back to this theme later to discuss it in more detail.

Wallace rejected the idea of female choice. He explained

the female's drabness in terms of protection, and the male's brightness in terms of general vigour. He said that many female birds didn't have bright colour because they had to be protected while incubating. He couldn't actually explain the brightness of male colour well enough, but he said that sometimes, contrary to common sense, the brightness had protective function. And he claimed that if animals had enough vigour, colours and ornaments naturally developed, and only because of the need for protection, females were prevented from having bright colours through natural selection.

Wallace was famous for his research on the protective colouration of animals. Probably because of this expertise of his own, his argument was mainly about colours. He said little about calls, stridulations, and odour. In his book, *Darwinism*, chapters are arranged according to the different usages of animal colour, but there is no extensive discussion on sex differences covering all aspects of morphology and behaviour.

There is some truth in his argument about the protective colour of females. But Darwin wasn't convinced and he refused such kind of adaptive explanations. Darwin emphasized the arbitrariness of female choice. And I think that he had his own reason for that, to which I will come back later.

3.2 *Thomas Hunt Morgan (1866–1945)*

Thomas Hunt Morgan was an American geneticist and a Nobel prize laureate of the early 20th century. He was one of the founders of modern genetics who established the material bases of inheritance. What was his opinion on Darwin's sexual selection?

There is a book entitled *A Critique of the Theory of Evolution* written by him in 1916. The book is based on his lectures on evolutionary biology which he delivered at Princeton University in 1915 and 1916. There are only few paragraphs in this book which treated the theory of sexual selection. Here, after the explanation of eye colour mutants in *Drosophila*, he stated:

> Zoologists know that sexual dimorphism is not uncommon in wild species of animals, and Darwin proposed the theory of sexual selection to account for the differences between the sexes. He assumed that the male preferred certain kinds of females differing from himself in a particular character, and thus in time through sexual selection, the sexes came to differ from each other.
>
> (Morgan 1916; p 61)

This paragraph is mysterious enough to make us suspect that there were some serious misunderstandings about the sexual selection theory. Following this paragraph, he immediately continues:

> In the case of eosin eye color no such process as that postulated by Darwin to account for the differences between the sexes was involved; for the single mutation that brought about the change also brought in the dimorphism with it.
>
> (Morgan 1916; p 62)

Morgan wrote another book especially on sexual characters, entitled *The Genetic and the Operative Evidence Related to Secondary Sexual Characters*, in 1919. In this book he discussed sexual selection in more detail, devoting one whole chapter to this subject. He states that:

> Darwin appealed to three processes to account for the facts [presence of sex differences]: (1) to natural selection
> between the members of the same sex; (2) to choice on the part of the other sex; (3) to the "inheritance of use" . . . . Competition of the males with each other for the females would, Darwin said, lead to the survival of those males best endowed with organs of offense and defense.
>
> (Morgan 1919; p 43)

Here, again, contemporary readers may find his use of the word "natural selection" and "survival" in this context odd. And Morgan states that:

> Several objections of greater or less weight have been urged against Darwin's interpretation. It has been pointed out that the combats within the species are seldom fatal and that the defeated rival finds another mate.
>
> (Morgan 1919; p 43)

So, was he thinking not about differential reproduction among males but differential survival through male–male fighting? It sounds like that. However, in the next page, he states,

> If monogamy is not the rule, if the male captures or attracts several females and keeps a harem, . . . then the advantage of his more developed weapon might lead to more offspring, and that if it could be shown that such intraspecific weapons prevail more frequently within polygamous species, a fair argument for natural selection might be made.
>
> (Morgan 1919; p 44)

Isn't it exactly what Darwin proposed as sexual selection through male–male competition? So, what is the point of Morgan's discussion here? It is rather confusing, but my guess is that Morgan misunderstood that Darwin's argument was about the differential survival among males through fighting; he believed that Darwin proposed that males with better weapons survived better in their fight for females, thus leading to the sophistication of weapons through natural selection.

Probably this is why he thought that the fact that combats within the species were seldom fatal was a serious blow to Darwin's argument. The last citation from page 44 is not the explanation of Darwin's idea but Morgan's own

paraphrasing of the process which, he thought, was a permissible "line of defence" of the argument.

As for female choice, Morgan dismissed the idea as pure speculation on the ground that there was no direct evidence to show that females of any kind of animals choose their mate. He states that the male courtship display "may be an inborn reflex to visual or other sensory stimuli that is a part of his attack on the female" (Morgan 1919; p 51).

However, he correctly pointed out that the theory of female choice did not necessarily require consciousness or aesthetic sense on the part of the female. He states that if the female sense organ was made to be sensitive to particular stimuli so that "the female was more likely to mate with a more brilliantly coloured male than a less brilliantly coloured one, the theory may be made to apply regardless of whether she is 'conscious' or not of the difference to which she responds" (Morgan 1919; p 50).

Morgan concludes that we do not need the theory of sexual selection because now we know the genetic mechanisms underlying the sex differences. He states,

> There would be no need, then, to assume that the difference had been slowly built up by selection, but rather that the difference arose at some time by a single mutant step. The incorporation of the step in the species would then follow if the effect of the gene were useful in mating or if it had some other primary significance for the welfare of the species, the different effect produced on the male and female being only an unimportant by-product of its action.
>
> (Morgan 1919; p 54)

He did not distinguish proximate causes from ultimate causes, and, for him, the proximate causes would be enough to explain the phenomena. Nobody was aware of the distinction at that time. And probably the excitement of the discoveries of genetic mechanisms at that time overwhelmed the logical argument of the theory.

3.3 *Julian Sorell Huxley (1887–1975)*

Julian Huxley was the grandson of T H Huxley and one of the central figures at the time of the modern synthesis of evolution (Huxley 1942). During the time of the modern synthesis, not much was discussed about sexual selection, but Julian Huxley published many papers on this subject. However, I have to say that he brought more confusion than progress in the argument. He invented a plethora of technical terms like "epigamic selection", "combat selection", "distance threat" and "short range threat", which were not helpful at all.

Huxley, too, like Wallace, put much emphasis on conspicuous colours and traits. Indeed, what he tried to explain seemed not to be the evolution of sex differences but the evolution of conspicuous traits. In one of his papers on sexual selection, he wrote:

> Many conspicuous characters (bright colors, songs, special structures or modes of behavior), to which Darwin assigned display function, have now been shown to have other functions (see Huxley 1937, for examples). These include: (a) deflection of predator attack, notably inter-individual
> deflection, from more to less biologically valuable individuals (see Heinroth 1938: Bulwer's Pheasant); (b) warnings (to enemies of other species) of noxious or dangerous qualities; (c) false warning (Batesian mimicry) and bluff; (d) recognition characters (not only between adults, irrespective of sex, but between the sexes and between juveniles and adults (see Molony 1937); (e) threat (to rivals of the same species and usually the same sex) of combative impulse and prowess: see Hingston 1933.
>
> (Huxley 1938a; p 418)

He claimed that traits which Darwin thought to be used for courtship display have since been identified to have many other functions as those mentioned above and that this seriously weakened Darwin's argument. Then he introduces the distinction between "(A) recognitional threat, which advertises the presence of a potential combatant to rivals at a distance", and "(B) short range threat", which is divided again into two categories: "(i) by the revelation of striking patterns, etc., advertising their possessor as a potential combatant," and "(ii) by the revelation of actual weapons or combative prowess, as in baring the canines by snarling, enhancement of apparent size by bristling of hair, etc."

He also claimed the continuity of sexual characters. In another paper, he wrote:

> Even in some species if weapons exist which are exclusively used for combat with rivals, this condition grades
> insensibly into that where the weapons are of use in the general struggle for existence by being employed against enemies of other species, and then passes over into that where the weapons are developed in varying degrees of completeness in the female also.
>
> (Huxley 1938b; p 32)

Distance threat is fine, short range threat is fine, and the gradations are fine. However, all these things did not explain at all why those characters usually develop only in males and "in varying degree" among females. Wallace and Morgan at least tried to deal with sex differences, but Huxley, in the maze of the newly-invented classifications and terms, seemed to have lost track of the argument of sex differences.

4. Nature of natural selection

As mentioned above, Wallace and others strongly insisted

that this was the matter of natural selection, not sexual selection. In our modern understanding of selection theory, there is no essential reason to distinguish sexual selection sharply from natural selection: sexual selection is part of natural selection. But the reason for Wallace and others to insist that this was a form of natural selection was different. Cronin (1991) pointed out that the main reason was that classical Darwinism failed to recognize social competition as an important agent of selection.

Indeed, having read the arguments by Wallace, Morgan and Huxley, it is rather surprising that very little was discussed about the differential reproduction among the members of the same species. For classical Darwinism, the struggle for existence was fought mainly against the abiotic environment, like cold climate or lack of water in an arid desert, and mainly between species, not within them, and in consequence, asocial. And above all it was about an individual's survival, not reproduction, as Herbert Spencer's popular phrase, "survival of the fittest", symbolises.

The title of Chapter 2 of Wallace's *Darwinism* is "The struggle for existence". Here he listed many examples to illustrate the struggle for existence in nature, all of which were between species against the abiotic environment. Indeed he talks about the potential rapid increase of organisms and the competition between them. However, the competition is thought to be fought against some absolute criteria, not a relative one. For example, if the climate becomes cold, some absolute criterion for cold-resistance will be set, and only those individuals above this limit can survive: the individuals that perish are the ones which couldn't make that absolute criterion.

But sexual selection is solely about social conflict within the species. It is caused by competition for mates among conspecific individuals, and that competition at times is caused by the preferences of the opposite sex. There is nothing intrinsically "wrong" about the defeated individuals. Darwin recognized the relative nature of this competition. He stated that,

> . . . but in the majority of cases, they serve only to give one male an advantage over another, for the less well-endowed males, if time were allowed them, would succeed in pairing with the females . . . .
>
> (Darwin 1871; vol. 1, p 207)

However, I think that people for a long time failed to recognize the importance of differential reproduction caused by the relative ranking of individuals.

There is another, more philosophical issue. As Darwin clearly stated, sexual selection is caused by the competition for mates between conspecific individuals of one sex, and it will lead to many types of secondary sex differences. He did not say that all the secondary sexual characters were the products of sexual selection. He proposed that if there was a sex difference in the intensity of competition for mates, it should bring about sex differences in characters for fighting and courtship display. So, they should have argued about this intensity of competition for mates among males and among females. However, nobody discussed this point. Perhaps English empiricism did not much embrace this kind of hypothetico-deductive argument (Ghiselin 1984)?

5. The good-for-the-species argument

On top of this, there was confusion caused by the group selection fallacy. For a long time, the argument on selection was muddled by the good-for-the-species argument. Group selection inevitably blurs the importance of social competition within species, so it made sexual selection theory more difficult to understand.

Darwin was sometimes not clear enough about what level of selection he had in mind, but this much is obvious that he didn't fall for the naive good-for-the species argument. Back in 1839, a naturalist called McLleland claimed that the bright colour of male fish was to make them conspicuous for the predator like a kingfisher, and to keep the number of superfluous males in check. Darwin didn't buy this idea, and said no naturalists of his age would believe such an explanation (Darwin 1871; vol. 2, p 17).

However, in 1885, a French naturalist, Jean Stolzmann, claimed exactly the same thing for plumes of the birds of paradise and dancing and singing and display antics of male birds. And Thomas Hunt Morgan (1919) said that Stolzmann's account of the origin of the plumes of the birds of paradise should be immortalized in the literature of the subject!

6. Problems with anthropomorphism

Many people scorned at the idea of female choice and rejected it. It has been often said that one of the main reasons for the objections to this idea was the anthropomorphism of Darwin's argument. He was blamed for having assumed the same kind of aesthetic sense and other mental powers as humans in other female animals. But I don't think this anthropomorphism was THE main reason. I think that the main reason was that, in the first place, with or without aesthetic sense, people couldn't imagine the possibility of the female exerting any choice over whom to mate with. And next (only next), if the theory assumed human-like aesthetic sense, then it was out of serious consideration.

He stated,

> Judging from various facts, the female, though comparatively passive, generally exerts some choice and accepts one male in preference to others. Or, she may accept, not the male which is the most attractive to her, but the one which is the least distasteful.
>
> (Darwin 1871; vol. 1, p 273)

The female was regarded to be shy, coy, passive, and always needed to be excited. With or without aesthetic sense, it was quite beyond the imagination of the people (or men) in those days that females might be capable of exerting any choice for their mates. People could never think of the possibility of decision-making on the part of the female. For a long time, Darwin was the only one to admit this possibility.

And he didn't reach this conclusion from the empirical evidence of any female animal exerting choice, but from the logical consequence of the relative intensity of competition for mates between the two sexes. If the male has to compete for the possession of the female, the female has to have the opportunity to exert some choice. If the male displays his gorgeous ornament to the female and she does not make any choice, all these displays and ornaments have no meaning at all, and this is impossible. Again, this was the hypothetico-deductive argument, which was not popular in British science of that time. Actually he had difficulty finding any direct supportive evidence for female choice.

The reason that I don't think that the main problem with his argument for female choice was his anthropomorphism is that Darwin used exactly the same kind of anthropomorphic argument for male–male competition as well, but people accepted this process of selection without any fuss about anthropomorphism.

He explained male–male competition like this,

> it is the male, which, with rare exceptions, has been chiefly modified. The cause of this is to lie in the males of almost all animals having stronger passions than the females. Hence it is the males that fight together and sedulously display their charms before the females.
>
> (Darwin 1871; vol. 1, p 272)

So, it is male passion. And such a mental capacity is limited to the higher order animals. Again, in *The Descent of Man*, he writes,

> Hence in these classes or sub-kingdoms, such as the Protozoa, Coelenterata, Echinodermata, Scolecida, true secondary sexual characters do not occur; and this fact agrees with the belief that such characters in the higher classes have been acquired through sexual selection, which
> depends on the will, desire, and the choice of either sex.
>
> (Darwin 1871; vol. 1, p 321)

The idea of male–male competition has been accepted from the start, and I have not come across anybody who rejected the idea of male–male competition because this argument was based on an anthropomorphic mental capacity on the part of the male. There was no evidence of female choice, but there was no empirical evidence, too, to show differential reproduction among males. But anyway people believed in male–male competition.

Anthropomorphic mental capacity or not, male–male competition seemed plausible, and people occasionally observed males fighting against each other. The final reason for which Wallace, T H Morgan and others rejected the idea of female choice was that there was no evidence for it. Female choice seemed not plausible at all, and they needed definite evidence to show that it existed.

People often accuse Darwin of unashamed anthropomorphism. But sometimes I see this among the critiques of female choice, too. This is St George Mivart on the review of the *Descent of Man*, "such is the instability of the vicious feminine caprice, that no constancy of colouration could be produced by its selective action" (Mivart 1871). And Geddes and Thomson (1889), in their book, *Evolution of Sex*, "permanence of female taste was scarcely verifiable in human experience". Is this a scientific argument? I have to wonder if their own bad experience with capricious women had great influence on their belief in female choice among animals!

We had to wait until the 1970s for the sexual selection theory to be resurrected. By that time, the good-for-the-species fallacy was mended, the importance of differential reproduction was fully appreciated, and it became textbook knowledge to separate the proximate questions from the ultimate ones.

7. Human sex differences?

Sexual selection is about sex differences. In *The Descent of Man*, from Chapter 8 to Chapter 18, Darwin described the details of sex differences in colours, ornaments, bodily appendages, songs, stridulations, and behaviour among insects, birds, fish, amphibians, reptiles, birds and mammals, and explained them by sexual selection. Therefore, when it comes to the chapters on humans, we naturally expect him to explain human sex differences.

However, what we are presented here is not actually about human sex differences, but racial differences. In *The Descent of Man*, Darwin wanted to establish two things. One was, of course, the descent of man, the evolution of humans from primate ancestors. The other was the origin of races. For the explanation of human origins, he used the principles of natural selection, but he used sexual selection to explain the origin of races. In fact, it was to explain human racial differences that he constructed the entire theory of sexual selection.

Indeed, in Chapter 19, he summarizes the sex differences in man. He says that men are taller and stronger, more hairy than women, and men have more powerful voices than women. The woman's body is rounder, women mature earlier, and have fairer skin than men. And he goes on to the sex differences in behaviour and mental capacity.

He saw that,

> Man is more courageous, pugnacious, and energetic than woman, and has more inventive genius.

(Darwin 1871; vol. 2, p 316)

Well? And,

> Man is the rival of other men; he delights in competition, and this leads to ambition which passes too easily into selfishness.
>
> (Darwin 1871; vol. 2, p 326)

That's a good observation. And he thought that women are more tender and less selfish than men, and overall, men are smarter than women. All right, here are lots of Victorian prejudices and stereotypic descriptions of men and women. But the problem is, he didn't fully analyse how mate competitions and mate choice worked among humans, either male–male or female–female competition, and either male choice or female choice. He says that among humans, too, men fight over women. If so, there must be female choice. But in Chapter 20, he discusses "On the effects of the continued selection of women according to a different standard of beauty in each race". He didn't give enough evidence for his argument, and compared to his discussion on animals, his line of thinking is less clear. You cannot often say such a thing about Darwin.

So why is this? I think that the answer lies in the debate over the origin of races which prevailed in the 19th century.

8. Monogenism vs polygenism

In Darwin's days, it was seriously debated whether all the different races of man belong to one species or not. There were two major schools, both non-evolutionary, monogenism and polygenism. Monogenism claimed that all races were descended from a single original pair, Adam and Eve. They recognized the great plasticity of the human physical structure, and contended that climate, environment, and local conditions modified the original form, resulting in separate races.

On the other hand, polygenism claimed that all the races were not the descendants of one pair. They emphasized the differences among races not only in physical characters but also in mental and moral attitudes. And they rejected the monogenist's notion of human plasticity. Their conclusion was that the differences were wide enough to regard them as different species.

Initially monogenism was attractive to many, for it did not conflict with the Genesis version of creation. In the early 19th century, most scientists were monogenists. But by 1850, polygenism was gaining favour. It emphasized the importance of cranial shape as a trait which was thought to be resistant to environmental change. In 1842 a Swedish anatomist, Anders Retzius, invented the cephalic index to describe the cranial shape quantitatively. This is calculated as the proportion of the breadth of the head to the length of the head. If it was less than 75%, the head was called a dolicocephalon, if it was more than 80% it was termed a brachycephalon, and in between it was called a mesocephalon. The Swedes (and Retzius was one), were dolichocephalic, but many Europeans like the French and southern Germans were brachycephalic. The invention of this index ignited fiery arguments on which race was the most advanced. However, the Europeans as a whole were more dolichocephalic than other races, so they could maintain the superiority of their race over others.

After the introduction of the cephalic index and the arguments on the rank order of races in the mid-19th century, monogenists were beginning to reject their somewhat egalitarian concept of race in favour of a more hierarchical view. They came to accept that races were ranked essentially on a scale based on skin colour and the shape of head. Polygenists claimed that the newly-discovered races which were not described in the bible were subhuman, which fact justified the slavery of these races. A physician and ethnologist of that time, James Prichard, who was a monogenist, summarized the polygenist argument as follows in his book, *The Natural History of Man* (1855), which Darwin often cited in *The Descent of Man*.

> The Sacred Scriptures, whose testimony is received by all men of unclouded minds with implicit and reverential assent, declare that it pleased the Almighty Creator to make of one blood all the nations of the earth, and that all mankind are the offspring of common parents. But there are writers in the present day who maintain that this assertion does not comprehend the uncivilised inhabitants of remote regions; and that Negroes, Hottentots, Esquimaux, and Australians, are not, in fact, men in the full sense of that term, or beings endowed with like mental faculties as ourselves. Some of these writers contend that the races above mentioned, and other rude and barbarous tribes, are inferior in their original endowments to the human family which supplied Europe and Asia with inhabitants – that they are organically different, and can never be raised to an equality, in moral and intellectual powers, with the offspring of that race which displays in the highest degree all the attributes of humanity. They maintain that the ultimate lot of the ruder tribes is a state of perpetual servitude; and that, if in some instances they should continue to repel the attempts of the civilised nations to subdue them, they will at length be rooted out and exterminated in every country on the shores of which Europeans shall have set their feet.
>
> (Prichard 1855; p 5)

It was in this scientific climate that Darwin published *The Descent of Man*. He wanted to prove that man descended from ape-like ancestors. But at the same time, he

had to explain the origin of racial differences. If he didn't do that, his theory of human origins would have been thought of as incomplete because the issue of race was so important at that time.

Darwin thought that racial differences in physical characters were trivial, unimportant, and of no essential value at all. He attributed this to the whim of sexual preferences. He thought that all human races belong to one species in a broad sense. So, his position was closer to monogenism, which explained racial differences in terms of local adaptation. However, monogenism was, along with polygenism, non-evolutionary. Therefore, I suspect that he didn't want to give any adaptive explanation for racial differences, in order to make it clear that his argument was different from the monogenist argument. Hence sexual selection by mate choice.

When Wallace explained the drabness of female birds as protection and the brightness of male birds as the by-product of their vigour, Darwin adamantly refused this explanation, without a particularly convincing reason. The "Darwinian" way of thinking is to suppose some utility in any of the unexplained traits, then to go on to investigate their function. So, as a "Darwinian", he should have given a bit more support to Wallace's explanation.

Isn't it that he didn't want any kind of adaptive value to sneak into his idea of mate choice, because, ultimately, what he had in his mind was this non-adaptive explanation for the human racial differences? And wasn't it because of this pressing issue of the origin of races in his time that he couldn't give a full account of sexual selection in humans? That is my guess.

If racial differences were not that important in the 19th century, Darwin's analyses on humans should have been directed more properly toward the analyses of sex differences, mate competition and mate choice among humans. Darwin suggested that songs, music, poems and art in general might have originated through sexual selection. He also suggested an interesting possibility that singing preceded the use of language. However, he did not give full consideration to all of these interesting points.

Indeed, it was before the dawn of the development of modern social sciences, as well as ecology, psychology, and the study of animal behaviour, when Darwin started to tackle the question of human nature. It is easy to pick up the weakness of his argument in *The Descent of Man,* but he definitely opened up a new field of human science. Now we have come to understand the vastness of this endeavour and have only started to make slow progress toward the solution.

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