



This work is licensed under the Creative Commons Attribution-Noncommercial-Share Alike 3.0 United States License. To view a copy of this license, visit <http://creativecommons.org/licenses/by-nc-sa/3.0/us/> or send a letter to Creative Commons, 171 Second Street, Suite 300, San Francisco, California, 94105, USA.

THEORIES OF SEXUAL DIFFERENCE: THE SEXUAL SELECTION HYPOTHESIS
AND ITS ANTECEDENTS, 1786 - 1919

R.B. Aiken¹

Department of Zoology, Erindale College
University of Toronto, Mississauga, Ontario, L5L 1C6
CANADA

Quaestiones Entomologicae
18: 1-14 1982

“ There is one great difficulty with a good hypothesis. When it is complete and rounded and the corners smooth and the content cohesive and coherent, it is likely to become a thing in itself, a work of art. It is then like a finished sonnet or a painting completed. One hates to disturb it. Even if subsequent information should shoot a hole in it, one hates to tear it down because it was once beautiful and whole.”

John Steinbeck, 1951 (p. 180)

ABSTRACT

Since Hunter's recognition of primary and secondary sexual characters, biologists have offered explanations for the question of why males and females of many taxa exhibit striking structural differences. Natural theologians of the early nineteenth century considered such differences to represent the intricacy of some creative power. Darwin's early writing about sexual selection emphasized intrasexual selection and later incorporated the key ideas of imbalanced sex ratio (especially in polygamous animals) and female choice. Darwin's chief opponent, A.R. Wallace, grew away from the sexual selection argument and proposed the vitalistic notion of greater male vigour and that secondary sexual differences were a result of females needing protective colouration. Critics also attacked female choice as a selective agent because it implied some aesthetic sense of females and because it was not seen as providing a sufficiently consistent selective force to act in any direction. The ideas of three such critics, the Duke of Argyll, St. George Mivart and J. Stolzmann, are examined.

RÉSUMÉ

Depuis l'époque où Hunter reconnut les caractères sexuels primaires et secondaires, les biologistes ont tenté d'expliquer de plusieurs façons le pourquoi des différences structurales souvent frappantes entre mâles et femelles. Au début du XIX^{ème} siècle, les théologiens de la nature considéraient que de telles différences reflétaient la complexité d'un certain pouvoir créateur. Les premiers écrits de Darwin sur la sélection sexuelle insistèrent sur la sélection intrasexuelle, et subséquemment incorporèrent les idées capitales de proportions inégales des sexes (particulièrement chez les animaux polygames) et de choix des mâles par les femelles. Le principal adversaire de Darwin, A.R. Wallace, se détacha du débat entourant la sélection sexuelle; il émit l'hypothèse que les différences sexuelles secondaires résultent de la nécessité pour les femelles d'avoir une coloration protectrice, et proposa la notion vitaliste de vigueur plus grande chez les mâles. Les critiques attaquèrent également l'idée que le choix des femelles constitue un agent sélecteur parce qu'elle implique une certaine notion d'esthétique de la part des femelles, et parce que ce choix n'était pas perçu comme pouvant exercer une force sélective suffisamment constante pour agir d'une façon directionnelle. Les idées de trois de ces critiques, le duc d'Argyll, Saint-George Mivart, et J. Stolzmann, sont examinées.

¹Present address: Department of Entomology, University of Alberta, Edmonton, Alberta, Canada T6G 2E3

THE THEORY OF SEXUAL SELECTION

By 1871, Charles Darwin could have, quite easily, retired gracefully, his scientific reputation established beyond any doubt. He could have abandoned his work of theorizing about grand schemes of nature and devoted himself to his more restricted studies of earthworms, orchids and moving plants. He had successfully weathered the storm (in terms of scientific acceptance) over his theories of descent with modification, having been the focus of more criticism and debate in a decade than most other scientists would encounter in several lifetimes. Yet, in 1871, he published 'The Descent of Man and Selection in Relation to Sex', probably not without some inkling of the debates his work would rekindle.

In the Descent, Darwin tried to tie off one of the more annoying loose ends of the Origin of Species – a theory about the evolution of secondary sexual characters. In retrospect, the title of the book has proven to have laid the wrong emphasis. By far the greatest amount of controversy and scientific discussion has revolved not around the schema for the evolution of man but rather the process by which he envisioned the races of man to have differentiated – sexual selection. Sexual selection was Darwin's attempt to explain one of the thorniest problems of animal morphology – the varied and often bizarre structures, colours and actions that distinguish the sexes. The theory of sexual selection as it appeared in 1871 (earlier versions of it will be discussed below) goes somewhat as follows.

In sexually reproducing species, there are often striking differences in what are termed secondary sexual characters. These differences can be placed (although not absolutely) in two categories. The first encompasses all those structures (horns, antlers and the like) with which males fight among themselves. Darwin hypothesized that the strongest, most vigorous males would, most often, win such encounters and gain more matings than those who were not victorious. These victorious males would then produce offspring more disposed to developing such structures and the strength and vigour necessary to use them successfully in fighting.

Into the second category, fall structures and behaviour patterns used directly in courting females. Those males with brighter colours, longer plumes or more melodious songs would be preferred and hence chosen by females for mating. The elaboration of such attributes would occur over several generations through the selective preference of the female. Darwin stipulated that the necessary pre-conditions for sexual selection were a greater variability of one sex, the greater proportion of one sex and competition among the members of the more numerous sex -- in most species, the males -- for mating. I shall elaborate further on these points below and let this statement of the theory stand for the present.

PRECEDENTS AND PREDECESSORS

Darwin was not operating in a vacuum. All theorizing must, to some extent, grow out of what has gone before. If it does not grow directly from previous theory, then it must make use of known fact. I will examine those that preceded Darwin to gain some understanding of the facts and theories extant at Darwin's time and a feeling for the perspective Darwin may have had.

The key in examining development of the sexual selection hypothesis is not to discuss it in terms of Darwin's final (1871) formulation. Rather, the problem is best studied from the

perspective Darwin himself most probably would have had. The question seems to be not specifically one of why a male is colourful, possesses horns or antlers or displays more readily but rather a more fundamental amalgam of these points -- why are the sexes so different in so many species?

A convenient benchmark for discussion of differences between sexes is the work of John Hunter (1786). Hunter was the first to distinguish primary (those sexual differences present at birth) from secondary sexual characters (sexual differences attendant with the onset of sexual maturity). These secondary sexual characters are the subject of all subsequent debate.

Most authors of the late eighteenth and early nineteenth centuries recognized the more mundane sexual differences (e.g. one sex larger than the other) as well as the more beautiful and bizarre. Many examples of differences in secondary sexual characters amount to little more than descriptions of oddities of animal structure that happened to catch the attention of a particular author. Kirby and Spence (1828) describe the mating pads on the forelegs of the male water beetle *Acilius sulcatus* (L.)

“Particular care seems to have been taken by the Creator that when all the above inhabitants are paired, the male should be able to fix himself firmly by means of his remarkable anterior tarsi... and these asperities &c, in the upper surface of his mate as not to be displaced by the fluctuations of that element, the reluctance of the coy female or any other slighter cause.”

Similarly, in describing sexual difference in antennae of moths, they note that those of males are often more complex and speculate:

“For what end the Creator has so distinguished them is not quite clear; but most probably this complex structure is for the purpose of receiving from the atmosphere information of the station of the female.”

Not all discussion of sexual differences consisted of such isolated examples: more general phenomena were discussed.

One class of structural features that attracted the notice of every writer on the subject was the horns and antlers that males use in combat with each other, particularly at the time of mating. For example, Hunter (1786) writes

“... as males of almost every class of animals are probably disposed to fight, they are, as I have observed, stronger than the females. In many, there are parts designed solely for that purpose.”

and Kirby (1835) writes

“... the head ... generally only in the male is ornamented...these are used by the males in their mutual combats.”

In all passages quoted so far, each author shows a clear idea of the immediate function of the structure being discussed. The forelegs of male *Acilius* are to grasp females, the complex antennae of male moths are for detecting females and male horns and antlers (which I will refer to collectively as armaments) are for winning fights. The purpose of winning such fights, however, was stated by fewer. A clear exposition was given by Kirby (1835):

“... at the time of pairing, males contend fiercely and sometimes fatally for the females.”

But for one author, the statements quoted so far seem to be reflective of the state of the art in dealing with the ‘why’ of such structures. That author was Erasmus Darwin. The portion of his *Zoonomia* (1794) relevant to sexual selection is worth quoting at length.

“As air and water are supplied to animals in sufficient profusion, the three great objects of desire, which have changed the forms of many animals by their exertions to gratify them, are those of lust, hunger, and security. A great want of one part of the animal world has consisted in the desire of the exclusive possession of the females; and these have acquired weapons to combat each other for this purpose, as the very thick, shield-like, horny skin of the shoulder of the boar is a defence only against animals of his own species, who strike obliquely upward, nor are his tusks for other purposes, except to defend himself, as he is not naturally a carnivorous animal. So the horns of the stag are sharp to offend his adversary, but are branched for the purpose of parrying or receiving the thrusts of horns similar to his own, and have therefore been formed for the purpose of combating other stags for the exclusive possession of the females; who are observed, like the ladies in the times of chivalry, to attend the car of the victor.

The birds which do not carry food to their young, and do not therefore marry, are armed with spurs for the purpose of fighting for the exclusive possession of the females, as cocks and quails. It is certain that these weapons are not provided for their defence against other adversaries, because the females of these species are with this armour. The final cause of this contest amongst the males seems to be, that the strongest and most active animal should propagate the species, which should thence become improved.”

Here is a clear attempt to go beyond a discussion of immediate function for a structure and seek a more fundamental reason for its existence. This very passage led modern analysts of the relationship of between the work of Erasmus and Charles Darwin to conclude that the theory of sexual selection was not original (Irvine, 1955; King-Hele, 1963). This is only partially true. The above passage shows that E. Darwin did elucidate the function of male combat before Charles Darwin, but the female choice part of the theory was original.

Juxtaposed with the analysis of male armament given by E. Darwin (1794), the efforts of Kirby and Spence (1828) at theorizing pale. The contrast in what we might consider the ‘scientific’ or ‘modern’ approach of Erasmus Darwin and that of Kirby and Spence stems from the direction in which each author approached the problem. Kirby (1835) had neither the inclination nor desire to upset the applecart of natural theology. His *Bridgewater Treatise* was designed expressly to show “the power, wisdom and goodness of God” through an examination of biological phenomena. If the thrust of one’s writing is to show that the animate world is a divine machination then all other explanation becomes superfluous. Just as today, the adaptation of an animal to its circumstances is assumed *a priori* to be illustrative of natural selection, Kirby assumed such adaptation illustrated the magnificent intricacy of God’s workings. Paley (1822) must be given the last word for the natural theologians. His concise and single reference to differences between the sexes is,

“ Nor do the works of the Deity want this clearest species of relation. The sexes are manifestly made for each other. They are for the grand relation of animated nature; universal, organic mechanical; subsisting, like the clearest relations of art, in different individuals: unequivocal, inexplicable without design.”

There was one other great facet of animal appearance that was somewhat more problematic -- animal colouration. Since colour could not be seen as having a decisive role in the outcome of any biological interaction, discussions of its function soon came to musings on aesthetics and standards of beauty. The *raison d’etre* for colour came under the same nostrum as male armament – being illustrative of the wisdom of God. Lesser (1791) combined the theological and aesthetic approaches to animal colour. According to Lesser, brightly coloured insects are beautiful to charm the eye and butterflies possessing bright underwings flash them so “their

beauty can be admired". His final conclusion is that since colourful insects are generally of no use "we should be grateful to the Creator for giving them to us". Interestingly, it was this very question of the function of animal colour and beauty that was to cause Darwin much theoretical trouble.

The final point is one that is somewhat less concrete than the previous arguments and must, to some extent, be read into the writings of various authors. It is the nearly universal practice of anthropomorphizing the behavioural roles of the sexes in mating. Males (human or otherwise) were viewed as aggressors, vying lustily for the attentions of the coy, demure females. Kirby and Spence (1828) best show this approach in their description of insect song noting that "female insects are too intent upon their business, too coy and reserved to tell their love even to the winds". Even Erasmus Darwin speaks of males fighting for "exclusive possession of the females". Apparently social outlook and norms transcended even the theoretical differences these men might have wrestled with.

Here, too, was a crucial gap in reasoning about sexual interactions that Darwin's sexual selection was to fill. All previous authors failed to clarify the logical sequence between winning a fight and mating with a given female (or females). The assumption seems to have been that it was absolutely obligatory that a female mate with the victorious male. This is curious in view of the reference Kirby and Spence (1828) made to the coyness of *Acilius* females.

DARWIN'S EARLY WRITING ABOUT SEXUAL SELECTION

Darwin's writings about sexual selection prior to publication of the *Descent of Man* (1871) are in five sources: his notebooks of 1838 (de Beer, 1960); his sketch of 1842; his *Essay* of 1844; in a joint paper with Wallace (1858); and in *Origin of Species* (1859).¹

Darwin's notebooks of 1838 (de Beer, 1960) show marked differences from previous authors. Three tendencies appear in these notebooks that set the intellectual stage for development of sexual selection theory.

First, to use Kuhn's (1970) terms, Darwin appears not to have tried to fit the facts into the paradigm of such people as Kirby, Lesser and Spence. One of the first references to sexual differences to appear in Darwin's notebooks is,

"Gould seems to think that (the) widow bird replaced Birds of Paradise -- if such fantastic sexual ornaments have so intimate a relation in two continents as to be called into existence on two continents, our ignorance is profound and such it appears."

Clearly, he is not satisfied with the old natural theology or aesthetic arguments.

Secondly, Darwin's continual search for a utilitarian reason for the existence of a particular structure is evident. He writes that secondary sexual characters are developed

"... only when they first become of use"

Finally, Darwin can be seen as attempting to relate diverse types of secondary sexual characters to a common cause,

¹The works of 1858 (with Wallace), 1844 and 1842 are reprinted in Darwin and Wallace (1958).

Quaest. Ent., 1982, 18 (1-4)

“Daines Barrington says cock birds attract females by song, do they by beauty -- if not war (sic) not.”

Darwin's theory first appeared in his Sketch of 1842, with reference to conditions necessary for sexual selection to occur. There is a surplus of males at breeding time and thus males with the “fullest vigour” will mate. It was a “struggle of war or charms”. Interestingly, at this point there was no explicit statement of female choice. Darwin seems to assume, as did many of predecessors, that females became the obligatory possession of victorious males. There was as yet no role for choice by females in his writings.

His Essay of 1844 expanded some points mentioned in 1842. He reiterated the “struggle by war or charms” notion and added two important points. The first was his recognition of what may be a functional as opposed to a strictly statistical sex ratio when he noted that the struggle would be severest in polygamous animals. Secondly, he noted that sexual selection was not as rigorous as natural selection since the penalty for failure was not death but fewer offspring.

In the first edition of *Origin of Species* (1859), Darwin gives essentially the same treatment to sexual selection as in *Darwin and Wallace* (1859 - see *Darwin and Wallace* (1958)). The argument is developed as follows. Darwin noted that variations often arise in one sex and are transmitted to that sex alone. Hence, one sex is modifiable “in its functional relations to the other sex”. He repeats the contention that sexual selection is less rigorous than natural selection and that the struggle is severest in polygamous animals.

The most significant new point in the *Origin* is that Darwin makes his first explicit reference to female choice as a selective agent:

“ ... if a man can in a short time give elegant carriage and beauty to his bantams according to his standard of beauty, then 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.”

Two points in this passage, one explicit and one implied, caused Darwin considerable trouble. He explicitly states that choice by the female could produce evolutionary change. Later authors did not believe that mere capricious choice could effect evolution in any one direction. Second, Darwin was seen as implying (by his standard of beauty statement) that females possessed some highly refined aesthetic sense not unlike our own.

Darwin ends his statement of sexual selection with an affirmation of his own belief in the extent of the process,

“ Thus it is, as 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.”

OPPONENTS AND CONTROVERSIES

Darwin's chief opponent on sexual selection was, oddly enough, one of his closest colleagues -- Alfred Russel Wallace. Their controversy both reveals a clash between two close friends and illustrates the danger of an hypothesis “becoming a thing in itself, a work of art.” (Steinbeck, 1951)

Wallace began with, as Vorzimmer (1970) puts it, “disinclination that led to complete disavowal” toward Darwin's hypothesis. In their joint publication, Darwin was concerned with sexual selection while Wallace concentrated on natural selection. Correspondence between

them reveals Wallace's growing "disinclination" quite clearly. In a letter to Darwin (29 May 1864 (Marchant, 1916)), Wallace questions some of Darwin's ideas about sexual selection stating that it would give "uncertain results" in the relation to man and that he (Wallace) has found "little polygamy in the lowest tribes". By 1868, Wallace questions some of Darwin's basic precepts. He does not understand how minute variations could be sexually selected. Wallace writes that sexual selection requires a "series of bold and abrupt variations". He asks Darwin "how would an inch in a peacock's tail or one-quarter inch in a Bird of Paradise be noticed or preferred". Darwin replied (29 March 1868 (F. Darwin, 1903)) that females would be assessing the whole appearance of the male and not just comparing relative plume lengths. Marchant (1916) claims that at this time (1867-1868), Wallace accepted the influence of sexual selection much more than he did later. Darwin himself (30 April 1868 (F. Darwin, 1903)) complains that Wallace does not allow for the role of colour independent of protection in print but does so in his letters.

Wallace's first clear break with Darwin on this question came in his letter of 18 September 1868 (Marchant, 1916). In this letter, he clearly spells out his general and specific arguments of animal colouration.

General Case

1. Females are exposed to more danger and often live longer.
2. Females thus need more protection.
3. If males and females were separate species, we would think that natural selection had operated on each.
4. Variation in one sex can often be transmitted to that sex alone. Thus, natural selection can operate as if the sexes were separate species.
5. Natural selection can't improve an animal beyond its needs.
6. In protected species, the sexes are similar.

Special Case

1. In weak flying moths, both sexes are mimics.
2. In strong flying moths, only the female mimicks.
3. Females can acquire bright colours.
4. There is no case of strong flying male alone mimicking.
5. Colour is more frequent in the male.
6. A male can't get more protection than he needs.

After this exchange of letters, the differences between the two men became sharper until 1877 when Wallace wrote Darwin that he was "opposed to voluntary sexual selection". Darwin replied that to think a peacock's tail and its movement during display were due to vitality and vigour (see below) was "incredible".

Wallace's Darwinism (1901) was his grand summary of his evidence against Darwinian sexual selection. This is a rather more readable and coherent account of his ideas than the general and specific cases mentioned above. Wallace submitted that, because of their greater vigour and vitality, males had a natural tendency to develop bright colours. In many species, these colours developed in association with underlying organs and areas of intense nervous

activity (e.g., the head). These colours were then passed on to both sexes. Females, however, did not acquire such colour because of their need for protection and the development of such was countered by natural selection. In his *Theory of Bird's Nests*, Wallace pointed out that females of many species that incubated in concealed nests were as colourful as their respective males. He then extended the argument to other groups, especially the Lepidoptera. He pointed out that in species which need protection (slow, weak fliers), both sexes mimicked other species. In species which were stronger, faster fliers, only females were the mimics. Both concepts were joined in what Wallace called his *Theory of Protective Resemblance*.

Armed with this notion and supported by Bates' (1863) mimicry hypothesis, Wallace was able to further generalize about protective function of colour and ornament in a wide variety of organisms that ran the gamut from birds to caterpillars. A number of papers (Butler, 1869; D'Orville, 1869; Alex. Wallace, 1869; Weir, 1869) were available noting the value of various bumps, spines, bristles and colours in various creatures.

The main problem with all this criticism and counter-theorizing was one of misplaced attack. Darwin tried to explain only the evolution of colours that were secondary sexual characters. He at no time meant to give a comprehensive theory of animal colouration. As George (1964) pointed out, Darwin and Wallace began by emphasizing different parts of the colour question and continued, each in his own track, for several years.

Careful consideration of both theories shows quite readily their differences in emphasis. Darwin was theorizing as to why males were brightly coloured. All Wallace (1891) could offer that pertained directly to this point was the vitalistic argument that male colour was due to "greater vigour and health and generally higher vitality". Wallace, in his *Theory of Bird's Nests*, had a perfectly reasonable hypothesis as to why females are dull -- not the same question Darwin was trying to answer.

Wallace cannot take full blame for extending the argument into areas in which it did not belong. An anonymous reviewer in the *Edinburgh Review* (1871) used presence of colour in asexual forms (animals on which sexual selection, by definition, cannot operate) and colour in inanimate objects as refutation of Darwin. The reviewer writes that identity of colour throughout the realms of animate and inanimate nature (i.e., red is red whether found in a bird or a rock) indicates similar cause. Perhaps this reviewer was St. George Mivart for in his *Lessons from Nature* (1876), he states:

"It is reasonable to suppose that whatever cause has produced brilliant colour in either fishes or caterpillars may have produced them in both."

But let us return to Wallace for a moment. The argument that Darwin and Wallace were examining different parts of the question of animal colour does not explain why the debate continued for so long. It does not explain why Wallace (who cannot be said to have suffered from lack of biological insight) put so much effort into what was apparently a "straw man" controversy. I think responsibility for any disagreement must rest squarely with Wallace. Darwin did not try to attack Wallace's ideas but was quite impressed with them. In a letter to Wallace (5 May 1867 (F. Darwin, 1903)), he wrote that Wallace's insight into female colour was "so much clearer and deeper than my own". All of Darwin's arguments were in favour of sexual selection and not against Wallace's protective resemblance theory.

Deeper reasons for Wallace's disagreement lie in the realm of speculation. It is possible that Wallace, having first been forced to share elucidation of the natural selection theory with

Darwin and then considered as the lesser light in the discovery, was trying to establish a major theoretical advance that was purely his own. The advance he tried to make was that of a comprehensive theory of animal colouration, a subject that had received little critical analysis before 1871.

Darwin (1871) admitted that female choice was the weakest part of the sexual selection hypothesis. Darwin had said that the females of a species could be the selective agent in the elaboration of male adornment by choosing males with the longest plumes, brightest colours, etc. To Darwin's critics, this hypothesis had two rather unpalatable implications.

The first was possession of some aesthetic sense by any non-human female animal. It must be pointed out that this notion of an aesthetic sense was not explicitly stated by Darwin. He wrote that females would choose males on the basis of their adornment but, at first, gave little concrete in the way of mechanism. Headley (1900), in a review of the whole question, wrote that Darwin needed to show both that females need adequate perception to choose and that they used that perception in choosing. This did not involve use of some subtle aesthetic sense but simply elaboration of some sense of colour and hearing. Such development, according to Headley, did not constitute an aesthetic sense. Similarly, in defence of Darwin, Romanes (1896) argued that the taste of the female animal was not the same as that in humans and did not necessarily imply intelligence.

On the other side of the coin, detractors were adamant -- female choice did imply aesthetic sense. Several (e.g., Edin. Rev. (1871)) thought Darwin was unfair in erecting what seemed to be untestable hypotheses. After all, how could one empirically decide what was going on in an animal's mind? There seemed to be one consistent characteristic in most of Darwin's detractors: they all had counter-explanations of their own. Three authors illustrate this point -- Stolzmann, the Duke of Argyll and Mivart.

In his *Reign of Law* (1884), Argyll errs by using the result of a process as an explanation for its mechanism. He argued that to account for beauty as attractiveness to females was beside the question, since females never mate with the wrong species anyway. His conclusion was,

" Mere ornament and variety of form for their own sake is the only principle or rule with reference to which the creative power seems to have worked."

Mivart (1876) thought that Darwin conceded the point in question when he stated that variation in structure could occur spontaneously. To Mivart, it was only a matter of degree as to whether this variation gives a slightly different colour or a fully plumed Bird of Paradise. All the evidence, Mivart says, points to,

"The existence of some unknown, innate and internal law which determines at the same time colouration and its transmission to either or to both sexes."

Mivart clearly doesn't believe in female choice but the best he can offer as an alternate explanation is a restatement of the problem.

Stolzmann (1885) was the most rigorous of the three in criticising Darwin and came up with one of the more imaginative counter-theories. He argued that if one considered the question from a larger geographical and phylogenetic perspective, the notion of female choice was thrown into doubt. The fact that European birds were generally less colourful than tropical birds indicated that they (European birds) had less taste. Similarly, the fact that mammals

were less colourful than birds indicated that that they too had less taste. The first fact, Stolzmann argued, was illogical and the second was inconsistent with phylogenetic standing. Stolzmann's theory used many of the same precepts as Darwin's. He said that males were numerically superior, put less nourishment into eggs and offspring and were less important than females in perpetuation of the species. They were, in a sense, parasitic on females after mating was completed. Males were a drain on resources necessary to females and could even disrupt incubation. All colour and ornamentation, then, performed three functions: it allowed females to easily see males and avoid them; it allowed males to be easily seen by birds of prey; and it reduced the chances of a male's escaping a predator (females already being slower). Behaviour associated with such structures served to attract attention of celibate males and keep them from interfering with incubating females. It is unfortunate that Darwin died three years before the publication of Stolzmann's views. His response would have been interesting.

But what of Wallace? He was not as involved in the question of aesthetic taste of females as he was in the question of animal colouration. Interestingly enough, criticisms from Wallace focussed one ambiguity in the argument about female aesthetic sense. The process by which female choice was effected was not made clear. Most discussion revolved around the issue of whether females were exercising some conscious choice or were being excited by and yielding to a male. Was it selecting or succumbing? Darwin (1871) originally thought it was selection. He states:

“ No doubt this implies powers of discrimination and taste on the part of the female ... ”

Wallace (1891, 1901) objected to this notion of conscious choice, returning again and again to the admonition that female choice could not be shown in nature. Wallace stated that while female birds may be excited by a display of decorative plumage, there was no reason to suppose that this conferred a mating advantage.

It is difficult to understand Wallace's reasoning in the light of his own ideas. He stated that colour and ornament are concomitant with vigour and general health and that it is the most healthy, persistent males that will mate. Differences between Darwin and Wallace seem to be a matter of mechanism rather than than basic principles. Indeed, in view of a paper by Darwin (1876), it seems that Wallace is beating something of a dead horse. In that paper, there is a rather abrupt change of attitude by Darwin. He wrote, in discussing sexual selection in monkeys,

“ ... I presume that no supporter of the principle of sexual selection believes that the females select particular points of beauty in males; they are merely excited or attracted in a greater degree by one male than by another ... ”

In a preface to a paper by Van Dyck (1882), Darwin again stated that it was more correct to speak of females being excited by males rather than deliberately selecting.

Yet several authors persisted in making this argument for and against conscious female choice. Romanes (1896) and Montgomery (1910) still referred to the bases of aesthetic discrimination by females. Montgomery (1910) even took the argument a step further, entertaining the question of whether a male was conscious of his own beauty and its effect on the female. After a review of the subject, T.H. Morgan (1919) concluded that the evidence supported the notion that the female did succumb rather than select. The controversy did have one extremely beneficial effect: it stimulated great deal of research and careful observation

(e.g., Huxley, 1914; Montgomery 1910; Peckham and Peckham, 1899) and this research provided a great fund of factual knowledge for Morgan to draw upon. He concluded that more adorned males aroused females sooner. An aesthetic sense was not at issue for Morgan. He drew on Montgomery's (1910) work which showed by experiment that an aroused female shows little preference for the male that aroused her. Morgan also concluded that the

"... purpose of the display may mean no more than a reaction that leads to a result propitious to the species."

Morgan's essay was significant in that it collected the observed facts and drew a conclusion that took the argument out of the realm of the untestable and provided direction for further research.

There was another aspect of female choice that Darwin's critics refused to accept. It was that choice by females could provide a consistent enough selective force to produce modification of a structure and behaviour pattern in a given direction. One's point of view on this question would seem to depend largely on whether one accepted a more mechanistic view of a female being excited by and succumbing to a male. If this view was accepted, then to imagine all the females of a species possessing similar nervous, sensory and hormonal systems being excited by similar displays and structures is not a large step. Add to this that animals deviating too far from the norm had a greater chance of being culled out by natural selection. This was essentially Darwin's position (1876). He concluded,

"It should however be observed in the first place that although the range of variation of a species may be very large, it is by no means indefinite. I have elsewhere given good instance of this fact in the pigeon of which there are at least a hundred varieties differing widely in their colours and at least a score of varieties of the fowl differing in the same manner; but the range of colour in these two species is extremely distinct. Therefore, the females of natural species cannot have an unlimited scope for their taste."

Most of Darwin's antagonists, however, took his earlier statement of female choice. Mivart (1876) stated that while he did not dispute that birds showed preferences, he could not accept that "instability of feminine caprice" could produce secondary sexual characters. Similar sentiments were echoed by Stolzmann (1885). Wallace (1901) seemed to address this question only in passing. This may seem strange except for one factor. Wallace, in his own theory of animal colouration, refused to accept that slight differences in males ability to excite females could lead to a female preference, seemed to have disposed of the question almost before it was raised.

I began by stating that Darwin realized his female choice hypothesis would not be accepted readily. He admitted in a letter to Wallace that it was an "awful stretcher". When all is said and done, however, I think most of the objection to the idea (especially in its original formulation) revolves around its lack of demonstrability. A statement appearing again and again (in various forms) concerns the absence of proof of female choice in nature. It was only near the end of Darwin's life that empirical evidence began to emerge (e.g., Van Dyck (1882)). It is unfortunate that Darwin did not live to see his ideas vindicated, at least in part, by later workers (Morgan, 1919).

I conclude with a few remarks about a question that I have avoided thus far. Is sexual selection a valid theory in its own right or merely a form of natural selection? Is Darwin, as the reviewer in the *Edinburgh Review* (1871) complained, being unfair in raising new categories? I think the answer lies both how widely one chooses to examine the question and what time frame

is used.

If one examines all animate nature, then sexual selection is a special process that applies only (by definition) to sexually reproducing animals. Natural selection can apply to all forms, sexual and asexual. But this observation is trivial since Darwin stipulated that it only applied to sexually reproducing forms. The question of time frame now emerges. If one takes the more modern view of such authors as Fisher (1930), Williams (1966, 1975) and Dawkins (1976) that the object of the evolutionary game is to have one's genes represented in the next generation, then negative results of natural selection (death of the individual) and sexual selection (failure to breed) are one and the same. Consequently, the line of demarcation between the two ideas is now recognized as being conceptually artificial. Historically, however, this is not fair to either Darwin or his critics. Although ideas that reproductive products from the sexes were somehow mixed in producing offspring were present (e.g. pangenes (Darwin, 1868), germ plasm (Weismann, 1904) and idioplasm (Nägeli, 1884)), such were viewed as mechanisms for ensuring species (as opposed to individual) survival. To them, individual death and failure to reproduce were distinct and thus sexual selection remained distinct from, although subordinate to, natural selection. The idea that selection operates at the level of the individual received much of its impetus from the work of Fisher (1930). The final statement of the problem goes to E.B. Poulton (1890) who best summarizes the thoughts of those who accepted sexual selection.

“Natural selection is a qualifying examination which must be passed by all candidates for honours: sexual selection is an honours examination in which many who have passed the previous examination will be rejected.”

ACKNOWLEDGEMENTS

I wish to thank Dr. M.P. Winsor, Institute for the History and Philosophy of Science and Technology, University of Toronto for many fruitful discussions and much constructive criticism. G.C. Williams reviewed the paper and provided some new and interesting insight. This paper was written while I was supported by NSERC (Canada) Operating 4946 to G.K. Morris (University of Toronto). The final stages of manuscript preparation were generously funded by the Department of Entomology, University of Alberta.

REFERENCES CITED

- Anonymous. 1871. Article VIII. *Edinburgh Review* 134: 99 - 120.
- Argyll, Duke of. 1884. *The works of the Duke of Argyll containing the Reign of Law, the Unity of Nature and Primeval Man*. John B. Alder. N.Y.
- Bates, H.W. 1863. *A naturalist on the river Amazons: A record of adventures, habits of animals, sketches of Brazilian and Indian life and aspects of nature under the equator during eleven years of travel*. J.M. Dent and Sons. London (reprint of the first edition with preface by E. Clodd (1892)).
- Butler, A.G. 1869. Remarks upon certain caterpillars etc. which are unpalatable to their enemies. *Trans. ent. Soc. Lond.* 1869: 27 - 29.
- Darwin, C. 1859. *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. John Murray. London. (facsimile of the first edition, Harvard Univ. Press (1964)).
- Darwin, C. 1868. *Variation of plants and animals under domestication*. John Murray. London.

- Darwin, C. 1871. *The descent of man and selection in relation to sex*. John Murray. London (second edition, 1880, Appleton and Co. N.Y.).
- Darwin, C. 1876. Sexual selection in relation to monkeys. *Nature* 15: 18 - 19
- Darwin, C. and A.R. Wallace. 1958. *Evolution by natural selection*. Cambridge Univ. Press. London.
- Darwin, E. 1794. *Zoonomia*. London.
- Darwin, F. 1903. *More letters of Charles Darwin*. John Murray. London.
- Dawkins, R. 1976. *The selfish gene*. Oxford Univ. Press. Oxford.
- de Beer, G. 1960. Darwin's notebooks on the transmutation of species. Part III. *Bull. Br. Mus. Nat. Hist. (Historical Series)* II: 119 -150.
- D'Orville, H. 1869. Do birds eat larvae of *Cucilla*? *Ent. Mon. Mag.* 6:16
- Fisher, R.A. 1930. *The genetical theory of natural selection*. Clarendon Press. Oxford.
- George, W.A. 1964. *Biologist philosopher. A study of the life and writing of Alfred Russel Wallace*. Abelard Schumann. London.
- Headley, F.W. 1900. *Problems of evolution*. Duckworth and Co. London.
- Hunter, J. 1786. *Observations on certain parts of the animal oeconomy*. London.
- Huxley, J.S. 1914. The courtship habits of the great crested grebe (*Podiceps cristatus*); with an addition to the theory of sexual selection. *Proc. Zool. Soc. Lond.* 35: 491 - 562.
- Irvine, W. 1955. *Apes, angels and Victorians. The story of Darwin, Huxley and Evolution*. McGraw-Hill. N.Y.
- King-Hele, D. 1963. *Erasmus Darwin*. Scribner's. N.Y.
- Kirby, W. 1835. *On the wisdom and goodness of God as manifested in the creation of animals and in their history, habits and instincts*. Wm. Pickering. London.
- Kirby, W. and W. Spence. 1828. *An introduction to entomology, or elements of the natural history of insects*. London. (fifth edition)
- Kuhn, T. 1970. *The structure of scientific revolutions*. Univ. Chicago Press. (second edition)
- Lesser, M. 1791. *Insecto-theology, or a demonstration of the being and perfections of God from a consideration of the structure and economy of insects*. Edinburgh.
- Marchant, J. 1916. *Alfred Russel Wallace. Letters and reminiscences*. Cassel and Co. London.
- Mivart, St. G. 1876. *Lessons from nature as manifested in mind and matter*. John Murray. London.
- Montgomery, T. 1910. The significance of the courtship and secondary sexual characters of Aranaeds. *Amer. Nat.* 44: 151 - 177.
- Morgan, T.H. 1919. The genetic and operative evidence relating to secondary sexual characteristics. *Publ. Carneg. Inst. Wash.* 285: 1 - 105.
- Nägeli, C. 1884. *Mechanisch-Physiologische Theorie der Abstammungslehre*. Munich.
- Paley, W. 1822. *Natural theology: or, evidences of the existence and attributes of the Diety, collected from the appearances of nature*. S. Andrus. Hartford.
- Poulton, E.B. 1890. *The colours of animals, their meaning and use especially in the case of insects*. Kegan, Paul, Trench, Trübner and Co. London. (second edition)
- Peckham, G.W. and E.G. Peckham. 1899. *Observations on sexual selection in spiders of the family Attidae*. *Occ. Pap. Nat. Hist. Soc. Wash.* 1.
- Romanes, J.G. 1896. *Darwin and after Darwin*. Open Court. Chicago.
- Steinbeck, J. 1951. *The log from the Sea of Cortez*. Viking Press. N.Y.
- Stolzmann, J. 1885. Quelques remarques sur le dimorphisme sexuel. *Proc. Zool. Soc. Lond.* 28: 421 - 433.

- Van Dyck, W. 1882. On the modification of a race of Syrian street dogs by sexual selection with a preliminary notice by Charles Darwin. *Proc. Zool. Soc. Lond.* 25: 367 - 370.
- Vorzimmer, P. 1970. Charles Darwin: The years of controversy. *The Origin of Species and its critics, 1859 - 1882.* Temple Univ. Press. Philadelphia.
- Wallace, Alex. 1869. *Zool. Rec. (Insecta)* 1869: 349.
- Wallace, A.R. 1891. Natural selection and tropical nature. *Essays on descriptive and theoretical biology.* MacMillan and Co. London.
- Wallace, A.R. 1901. Darwinism. An exposition of the theory of natural selection with some of its applications. MacMillan and Co. London.
- Weir, J. 1869. On insects and insectivorous birds and especially on the relations between colour and edibility of Lepidoptera and their larvae. *Trans. ent. Soc. Lond.* 1869: 21 - 26.
- Weismann, A. 1904. *The evolution theory.* (Translated by J.A. Thompson and M.R. Thompson.) Edward Arnold. London
- Williams, G.C. 1966. *Adaptation and natural selection: A critique of some current evolutionary thought.* Princeton Univ. Press. Princeton, N.J.
- Williams, G.C. 1975. *Sex and evolution.* Princeton Univ. Press. Princeton, N.J.