UNIVERSITY OF MINNESOTA

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GRADUATE SCHOOL

WHO WANTS A PRETTY BIRD? -

THE FATE OF SEXUAL SELECTION AND MATE CHOICE FROM DARWIN TO T.H. MORGAN (1871-1919)

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On a Peacock's Feather:

In Nature's workshop but a shaving,
Of her poem but a word,
But a tint brushed from her palette,
This feather of a bird!
Yet set it in the sun glance,
Display it in the shine,
Take graver's lens, explore it,
Note filament and line,
Mark amethyst to sapphire,
And sapphire to gold,
And gold to emerald changing
The archetype unfold!
Tone, tint, thread, tissue, texture,
Through every atom scan,
Conforming still, developing,
Obedient to plan.
This but to form a pattern
On the garment of a bird!
What then must be the poem
This but is lightest word!
Sit before it; ponder o'ver it,
'Twill thy mind advantage more,
Than a treatise, than a sermon,
Than a library of lore.

From Alfred Russel Wallace's
Darwinism: An Exposition of the Theory of Natural Selection

INTRODUCTION

In a letter to his friend and fellow naturalist, Charles Darwin wrote: "My dear Wallace, – I am hard at work on sexual selection and am driven half mad by the number of collateral points which require investigation...." Later in the letter, he went on: "The more I work, the more important sexual selection apparently comes out."[1] The letter is presumed to have been written in February of 1868, three years before the publication of *The Descent of Man, and Selection in Relation to Sex.* Darwin would come to view sexual selection as so important that he dedicated almost two thirds of the *Descent* to the topic. While he had briefly introduced the theory in his 1859 *On the Origin of Species*, it was here that Darwin treated it in depth and offered countless examples of its action in nature. For Darwin, sexual selection was an attempt to explain the seemingly useless (and often maladaptive) traits that do not meet the strict, utilitarian demands of natural selection, such as the peacock's elaborate tail. These traits are generally confined to the male sex and include conspicuous coloration and structures, special weapons used in pre-mating battles and courtship behavior. According to Darwin, these traits evolved because they confer breeding advantages to animals, leading to their increased breeding success relative to those animals that lack them. While it is easy to imagine that the spur of the cock wins him advantages over his rivals in pre-mating battles over females, it is less clear why some male birds are decked out in colorful feathers and indulge their potential mates with beguiling song. To explain such traits, Darwin invoked mate choice. He

[1] Alfred Russel Wallace and James Marchant, *Alfred Russel Wallace* (New York: Harper and Brothers, 1916).

argued that potential mates discriminate in favor of those suitors whose song and feathers they find most appealing. Over time, female preferences accumulate the most pleasing variations to yield conspicuous secondary sexual characteristics.

In spite of Darwin's efforts and conviction of sexual selection, the theory had only a few supporters and fell largely out of favor by the late 1880's.[2] Most accepted male combat and the special weapons associated with it as a form of natural selection, but mate choice was rejected almost universally. While individuals, such as Alfred R. Wallace, Conwy Lloyd Morgan, St. George Mivart, and Thomas Hunt Morgan, agreed that female choice could not drive evolution, their reasons for doing so were diverse. In *The triumph of the Darwinian method*, evolutionary biologist Michael Ghiselin has written the following about the reception of female choice: "The reason why female choice is accepted or not reflects to some degree the difficulty of the problem and the ambiguity of the evidence, but there also exist basic disagreements about theoretical premises, methodology, and metaphysics."[3] Ghiselin is certainly correct in his assessment. Yet he goes on to state that "it may help at this point to refute the charge that Darwin attributed a sense of beauty, in an anthropomorphic sense, to fowl. He simply maintained that animals may, in some instances, be differentially attracted or repelled by various patterns or colors."[4] Ghiselin then quotes a passage from the *Descent* in which Darwin had

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[2] Helena Cronin, *The Ant and the Peacock : Altruism and Sexual Selection from Darwin to Today* (New York: Cambridge University Press, 1991). Cronin goes on to write the following about the theory's controversial history: "Not until a century after the publication of *Descent of Man* did it start to be fully appreciated. Now, at last, it has been assimilated to mainstream Darwinian thinking. Indeed, it is undergoing a spectacular revival, having become a growing, lively, even fashionable area of research. A happy ending, then - so far, at least - to a chequered career." 118.

[3] Michael Ghiselin, The Triumph of the Darwinian Method (Berekely: University of California Press, 1969), 217-218.

[4] Ibid.

emphasized that the aesthetic sense of animals is more akin to savages "who admire and deck themselves with any brilliant, glittering, or curious object," rather than like that of "a cultivated man, with his multiform and complex associated ideas."[5] Ghiselin also argues that "[w]hether one wishes to identify such phenomena with human tastes, and how closely the analogy holds, was utterly irrelevant to Darwin's argument." But there is much evidence that Darwin himself cared very much about the nature of choice and its manifestation in animals, as did his critics. Indeed, the rejection of female choice emerges as one of the most consistent reasons for the overall rejection of sexual selection. The question of how choice was viewed and what allowed Darwin to accept it when it was so objectionable to most of his followers becomes central to an understanding of Darwin's sexual selection and its reception by other scientists.

In order to gain an understanding what choice meant to Darwin, it is important to consider to what extent he considered animal choices to be akin to those of humans. The primary argument in the *Descent* is that animals and humans share common descent. Darwin sought to prove this not just by pointing out physical similarities between animals and humans but also by emphasizing their mental and emotional likenesses. Thus, the continuity between animals and humans was a central argument of the *Descent* and, as we shall see, key to the establishment of sexual selection. I would like to suggest (*pace* Ghiselin) that Darwin did, in fact, ascribe a very human-like appreciation of beauty to animals, especially birds. Indeed, as I will argue in my paper, Darwin believed that it was this sophisticated appreciation of beauty that allowed animals to select their potential mates. While Eileen Crist does not explicitly link Darwin's anthropomorphism to sexual

[5] Ibid.

selection, her *Images of Animals: Anthropomorphism and Animal Mind* offers a useful discussion of Darwin's use of anthropomorphic language and concepts. Crist rejects Ghiselin's claim that Darwin's use of anthropomorphic language was merely metaphorical. Instead, she argues that it was intentional and a natural consequence of his deep conviction that animals and humans share an evolutionary history. Crist also argues that implicit in this approach was Darwin's belief that animals act with purpose and that humans, if they are patient and careful, can discern the motivations that underlie animal actions. My work on sexual selection supports Crist's views of Darwin's intentional anthropomorphism. In addition, I argue that the acceptance of Darwin's evolutionary continuity was a necessary premise to his and his successors' acceptance of sexual selection. Supporters of sexual selection, such as George J. Romanes and George and Elizabeth Peckham, shared Darwin's view that animals differ from humans in degree rather than in kind. Because they believed in this close kinship, they accepted Darwin's claim that animals could make the aesthetically sophisticated mate choices. In contrast, critics of sexual selection, while diverse in many respects, generally agreed that humans differed from animals fundamentally. With their rejection of the *Descent's* proposed continuity also came a reluctance to accept the human perspective of emotions and mental faculties as a point of reference for evaluating animals.[6]

[6] Eileen Crist, *Images of Animals: Anthropomorphism and Animal Mind, Animals, Culture, and Society* (Philadelphia: Temple University Press, 1999). Crist has shown that an anti-anthropomorphic stance was prevalent with the early ethologists, such as Conrad Lorenz, in the 1950's and 60's. My research shows that resistance to Darwin's methodology could be felt much earlier and was already quite well established in the first decades of the twentieth century.

This paper examines the history of sexual selection from 1871 through roughly the first two decades of the twentieth century. It is largely an account of the decline of the theory's status in the scientific communities. Sexual selection was not abandoned merely because it lacked experimental support nor was it defeated by Wallace's famous attacks, as some have argued.[7] Rather, I would like to suggest that the notion of animals changed around the turn of the century in such a way that it no longer seemed possible for animals to make deliberate and aesthetically based mate choices. In the third chapter, then, I examine this change and how it affected the reception of sexual selection. With the re-discovery of Mendelian genetics in 1900 and the startling breakthroughs in artificial fertilization of Jacques Loeb the previous year, scientists were less inclined to explore the inner lives of animals, as Darwin and his contemporaries had. Loeb's work on the responses of animals to various stimuli sought to reduce animal behaviors to physico-chemical processes. As historian of science, Philip Pauly has argued, Loeb's ultimate goal was to gain experimental control over the organisms he studied. For most, including Mayer and Soule and T. H. Morgan, this method was preferable to the speculative evolutionary explanations of the previous century.

George Mayer and Caroline Soule applied Loeb's techniques to the study of the mating instincts of moths. Although their experimental data indicated that animals do, indeed, exercise some choice in the selection of their mates based on appearance, Mayer and Soule were unwilling to grant animals this agency. Instead, they explained mating

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[7] For a statement about its lack of experimental support, see Vernon L. Kellogg, *Darwinism To-day; a Discussion of Present-day Scientific Criticism of the Darwinian Selection Theories, Together with a Brief Account of the Principal Other Proposed Auxiliary and Alternative Theories of Species-forming* (New York: H. Holt, 1907).
Undue emphasis is placed on Alfred R. Wallace's attacks on the theory by Cronin in *Ant and the Peacock.*

behavior largely in terms of determined responses to stimuli, much like Loeb would have. Their account lacks any explanation or description of behavior, as their interests lay with accumulating data and reducing behavior to physico-chemical terms. In this context, then, mate choice no longer seemed like a viable proposition for animals; animals were no longer viewed as thinking beings that acted deliberately.

Mendelian genetics similarly offered a tool to study organisms without having to speculate about organisms' evolutionary pasts. It offered a means of experimentally investigating the transmission of genes. Animals were selected for their specific traits and bred at will and their offspring were investigated to determine the inheritance of traits. T. H. Morgan studied fruitflies, which were well suited to the laboratory. Modest in their needs, fruit flies bred readily, offered rapid life cycles and a useful array of visible mutations.[8] In the time before Morgan accepted Mendelian genetics (prior to 1911), his critique of sexual selection focused largely on the structure and coherence of Darwin's arguments. In his later Mendelian piece, *The Genetic and the Operative Evidence Relating to Secondary Sexual Characters*, Morgan experimentally examined the cause of the secondary sexual character in roosters known as cock feathering. He determined that sexual selection and mate choice were unnecessary to the explanation of this phenomenon, as he felt that his genetic and hormonal explanation could adequately accounted for its appearance. Thus, Morgan, like Loeb and Mayer and Soule, was eager to replace adaptationist accounts with more immediate, experimentally verifiable methods. And Morgan never directly addressed mate choice (since hens' preferences

[8] Robert E. Kohler, *Lords of the Fly, Drosophila Genetics and the Experimental Life* (Chicago: The University of Chicago Press).

hardly factored into the complex Mendelian mating schemes Morgan devised for his hens and roosters). Organisms that were only viewed as embodiments of their genes were no longer capable of wooing, charming and much less choosing potential mates. Thus, while the scientists of the late nineteenth century were divided as to the proximity of animals to humans, their early twentieth-century counterparts viewed them mostly as reactive to the successful manipulations of humans. As animals were pushed further and further away from humans, the possibility that they might pass aesthetic mate choices, like Darwin had proposed for them in the *Descent*, appeared equally remote.

CHAPTER ONE

Charles Darwin and Alfred R. Wallace - Setting the Stage

Charles Darwin dedicated the second part of his 1871 *Descent of Man and Selection in Relation to Sex* to an in-depth discussion of sexual selection. Darwin argued that males consciously display their finery before females and that females select their mates according to their liking. Mate choice, according to Darwin, relied on the female's ability to discriminate amongst subtle variations and choose in favor of the most attractive males. Thus, the claim that female choice was based on the animal's aesthetic sense met with objections from Wallace and subsequent critics. But for Darwin, the establishment of an aesthetic sense in animals was in keeping with his larger project of pointing out seemingly human traits in animals. Darwin also believed that because animals and humans were so closely related, humans can gain an intimate knowledge of animals' inner lives. This is seen both in the *Descent* and in the *Expression of the Emotions*, where Darwin showed how human expressions find their equivalents in animals.

The debate over sexual selection between Charles Darwin and Alfred R. Wallace was largely a result of their growing disagreement over mechanisms of evolution and their differing views on the evolutionary relation between humans and animals. In his 1871 review of Darwin's *Descent*, Wallace agreed that mate choice could drive evolution for secondary sexual characteristics in the higher animals. Nonetheless, Wallace was already uncomfortable with the large role Darwin had accorded the theory in evolution. The fact that some of the adaptations that Darwin had sought to explain by means of sexual selection, such as the peacock's tail, seemed maladaptive, became increasingly

unacceptable to Wallace. By the time he wrote *Darwinism* in 1889, he had rendered sexual selection and mate choice virtually ineffectual and had largely replaced them with natural selection. Wallace insisted on the all-powerful version of natural selection that Darwin had presented in the *Origin*, while Darwin had already introduced a milder version in the *Descent*.

But the difference between Darwin and Wallace, I will argue, also had to do with the ways in which they viewed animals and humans. While Darwin argued that humans had evolved from animals by natural selection and still bore essential resemblances as a result of their common descent, Wallace believed that natural selection was not sufficient in explaining human intellect and morals. Instead, he urged that the intervention of a higher, intelligent power must have been involved in the creation of humans. Thus, Wallace rejected the continuity between animals and humans which Darwin had proposed in his *Descent*. It is perhaps not surprising, then, that Wallace ultimately decided that animals were not capable of passing the sorts of human-like judgments Darwin's sexual selection required of them in their choices of potential mates.

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It has been argued by both supporters and critics of sexual selection – as well as by historians – that there was a close relationship between natural and sexual selection in Darwin's writings. While this association has been characterized in different ways, an understanding of sexual selection certainly necessitates a discussion of natural selection. To this end, I shall outline the essentials of natural selection as they pertain to the subsequent discussion of sexual selection and mate choice.

In the *Origin*, Darwin presented his theory of evolution by natural selection, whereby heritable variations are preserved or eliminated depending on whether they are advantageous or disadvantageous to the animal. The theory was based on three main premises. First, Darwin observed that organisms in nature exhibit variations that they may pass on to their offspring. Second, following Thomas Malthus's *Essay on Population*, he argued that an ever increasing population leads to competition for limited resources and the consequent and inevitable destruction of a large portion of that population. This competition is especially fierce for organisms that are closely related by species, location, or habit, because they are most likely to depend on the same resources. Third, in this struggle for existence any variation which proves advantageous to an organism in its survival over another will allow that individual to survive and pass on the trait to its offspring. Darwin succinctly summarized his theory in the following passage:

> Owing to this struggle for life, any variation, however slight and from whatever cause proceeding, if it be in any degree profitable to an individual of any species, in its infinitely complex relations to other organic beings and to external nature, will tend to the preservation of that individual, and will generally be inherited by its offspring. The offspring, also, will thus have a better chance of surviving, for, of the many individuals of any species which are periodically born, but a small number can survive.[9]

Darwin went on to expand this account by defining the "struggle for existence" more broadly to include the "dependence of one being on another and including (which is more important) not only the life of the individual, but success in leaving progeny."[10] It is this

[9] Charles Darwin, *On the Origin of Species by Means of Natural Selection, or The Preservation of Favoured Races in the Struggle for Life.* Ernst Mayr (Introduction), A Facsimile of the First Edition (Cambridge: Harvard University Press, 1975), 61.
[10] Ibid., 62.

expanded notion of evolutionary success that includes procreation, which informs Darwin's sexual selection.

But Darwin was also explicit in the *Origin* about the vigilance with which nature destroys injurious adaptations:

> On the other hand, we may feel sure that any variation in the least degree injurious would be rigidly destroyed. This preservation of favourable variations and the rejection of injurious variations, I call Natural Selection.[11]

In addition to this severe form of natural selection, Darwin also accepted Jean Baptiste de Lamarck's (1744-1829) mechanism of evolution. In (perhaps overly) simple terms, Lamarck's theory held that traits acquired during an animal's life could be passed on to offspring. Lamarck also believed that the body parts on which an animal depended a great deal, would become augmented during the animal's life, while others would wither from disuse. Such augmentations or diminutions would also be inherited by future generations. Thus, Darwin proposed that the gradual accumulation of beneficial traits and the concomitant elimination of injurious ones by natural selection, coupled with Lamarck's theory of the inheritance of acquired characters, lead to gradual changes in species until they either go extinct or give rise to new ones. This, in essence, was Darwin's causo-mechanical explanation of how evolution occurred. Natural selection offered an alternative to other theories of evolution and Natural Theology that was as compelling as it was controversial.

However, Darwin's explanatory framework was challenged by characteristics in nature that seemed purposeless and often injurious in the struggle for existence. Such

[11]Ibid., 81.

traits included the bright coloration, seemingly useless ornamentation, and the mating behavior exhibited by some species. Because these characteristics did not appear to confer any advantages to their possessors – as is stipulated by natural selection – Darwin invoked sexual selection to explain them. But Darwin gave only a short account of the theory in the *Origin*, devoting scarcely three pages (out of a total of 490) to the topic without referencing it in the index.

It was not until the second part of the *Descent* that Darwin addressed sexual selection in depth. He enumerated the traits for which sexual selection accounted and explicitly excluded those involved directly in procreation. Sexually selected traits, then, are:

> ...other sexual differences quite disconnected with the primary organs with which we are more especially concerned – such as the greater size, strength, and pugnacity of the male, his weapons of offence or means of defence against rivals, his gaudy colouring and various ornaments, his power of song, and other such characters.[12]

As the above quote suggests, these traits are generally specific to one sex (usually the male). Species in which the male and the female differ will be referred to as sexually dimorphic.[13] But not all sexually selected traits are dimorphic. Some traits, while generally more pronounced in one of the sexes, are present in both (such as the rudiments of spurs in some hens). Here Darwin proposed that these traits, though sexually selected by only one sex, are inherited by both. But not all sexually dimorphic traits can be ascribed to sexual selection. According to Darwin, certain traits (such as the mammae in

[12] Charles Darwin, *The Descent of Man, and Selection in Relation to Sex*, John Tyler Bonner (Introduction), Robert M. May (Introduction), (Princeton: Princeton University Press, 1981), i, 254.

female mammals) that are inherited by one sex only, fall under natural selection because they aid the members of one sex to nourish or protect the young. In other words, only those traits are sexually selected that serve to attract mates (but are not used directly in procreation).

Within sexual selection, we may distinguish between two main components: battle for mates and the courtship rituals (which include display and mate choice).[14] The pre-mating battles over mates (or the "law of battle," as Darwin called it)[15] explain the special weapons exhibited by some males. These aid them in their battles with other males over the possession of females. This part of Darwin's theory was accepted almost universally by all who accepted natural selection. Indeed, the connection to natural selection is quite strong. Only those that survive the battles or are successful candidates for procreation. Therefore, the traits which aided them in their battles against their rivals are passed to future generations. Courtship rituals, on the other hand, have less violent implications. These describe the showy antics and display that the male performs before the female and the choosing the female does from among her prospective show-offs. Thus, Darwin was well aware that even if pre-mating battles lead to clear victors and losers, the variations which helped the victors in their battles would not be preserved or augmented if, in the end, the losers get to breed in equal numbers as the winners. If each male ends up with a female and each pair has roughly the same number of off-spring, weapons would be of little use and the very act of fighting a senseless endeavor.

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[13] Darwin's use of the term dimorphic seems to be limited to species in which there are tow distinct types within a sex. An example of this is Darwin's mention of the two distinct types of males within the Curstacean species of *Tanais*. Darwin, *Descent of Man*, i, 328.

[14] This division is roughly present in most commentaries of sexual selection, though most emphasize mate choice in the latter category.

However, if it could be shown that the victors in battle somehow out-produce their less combative counterparts, then certainly the traits, which led to their victory would be present in more offspring. Darwin offered more than one way this might be achieved, making use of differential breeding ratios and female choice.[16] If males were to considerably outnumber females, the struggle between rivaling males would become significant. In this model, males fight with each other and only those successful in battle are able to procreate with the few available females. The losers are either killed or not allowed to breed. In this scenario, the claws and spikes seen in some males are well accounted for because they serve the males in their contests and allow them to be passed to their offspring.

In the *Descent*, Darwin goes to considerable length to investigate the ratios between the sexes to determine whether this is the case. He offers detailed tables of ratios in horses, dogs, sheep, cattle insects, fishes and, of course, birds.[17] Similar effects are attained in polygamous species, where successful males get to breed with more females than their less fortunate counterparts. While the actual numbers of males to females may be equal, the number of available females is effectively reduced if victorious males claim more than one mate.

Another, more elaborate possibility Darwin offered, has to do with timing. In this scenario, the victorious males are able to breed first. Darwin reasoned that because males are generally ready for breeding before the females, their rivalries might be resolved by

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[15] Darwin, *Descent of Man*, ii, 40.
[16] While the law of battle was widely accepted, female choice met with immediate resistance and continues to be a point of contention in sexual selection debates.
[17]Darwin, *Descent of Man*, i, 303-15.

the time the first females reach breeding readiness. Darwin believed that the first females to reach breeding readiness would also be the most fit and vigorous. Because only a few are ready early, the ratio of males to females would again exceed one. The early females, then, would be allowed to choose from the victorious males. Presumably they would choose those males which were most to their liking. Here attractiveness seems to correlate loosely with vigor and health in the males. Thus, two vigorous and healthy parents would mate and be able to rear more offspring than the late-blooming female and her less vigorous and dowdy mate. The traits that help the male in battle are passed on to the offspring.

These three examples of differential breeding (male-to-female ratios greater than one, polygamy/polyandry, and timing) do not conflict with natural selection. Indeed, subsequent commentators on sexual selection (including Alfred R. Wallace) saw this as a relatively unproblematic extension of natural selection. According to this view, females may be viewed as a limited resource. During the mating season the pressure for this resource increases and leads to struggles between males. Those males that have any slight variation that proves useful to them in battle will be at an advantage that allows them to leave more offspring. Those lacking such adaptations will either be killed or prevented from breeding. This is in keeping with Darwin's expanded definition of natural selection, which includes success in leaving progeny. Indeed, Wallace retained this aspect of Darwin's theory in the face of his increasing unease and eventual rejection of sexual selection.[18]

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[18]Malcolm J. Kottler, "Darwin, Wallace, and the Origin of Sexual Dimorphism," *Proceedings of the American Philosophical Society* 124(1980): 203-26.

However, those characteristics that do not aid in battle and seemed purely ornamental, continued to pose problems for Darwin's theory. But feather-ruffing and prancing are hardly fit to eliminate rivals in pre-mating battles. It is here that Darwin invoked mate choice. He observed that many species perform extended mating rituals in which they engage in elaborate courtship displays and song. He also noted that many birds assume brighter coloration after their molt which coincides with the mating season.[19] Darwin concluded that once the battles are decided, females must choose according to their tastes. Indeed, display was to Darwin's mind the most compelling argument for sexual selection and mate choice. This conviction rested on an argument of utility. That males display their plumage and engage in special behaviors during the mating season was incontestable. Further, it was generally accepted that this behavior was for the benefit of potential mates. To Darwin, then, the only reasonable explanation was that the display was intended to excite the female. To reject this proposition amounted to denying that the behavior has a purpose, which was unacceptable to Darwin:

> He who thinks that he can safely gauge the discrimination and taste of the lower animals, may deny that the female Argus pheasant can appreciate such refined beauty; but he will then be compelled to admit that the extraordinary attitudes assumed by the male during the act of courtship, by which the wonderful beauty of his plumage is fully displayed, are purposeless; and this is a conclusion which I for one will never admit.[20]

Thus, Darwin insisted on the utility of male's courtship antics. The elaborate pre-mating behaviors of males that are aimed at impressing potential mates are useful only if these, indeed, impress the females.

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[19]Darwin, *Descent of Man,* ii, 85.

But while male behavior might be purposive, female choices certainly are not. That female choice is based on ornamentation rather than practicality may seem commensurate with Victorian conceptions of female decision-making proclivities. In humans, however, Darwin reversed the roles of choice and ornamentation. The most influential men choose the prettiest women. This, Darwin believed, was evidenced by women's penchant for ornamentation and, of course, their natural prettiness. In fact, Darwin noted that women even tend to adorn themselves with the very feathers that served their former male owners in their struggles for sexual favor.[21] Darwin's switch in gender of the agent of choice from animals to humans is interesting for many reasons, especially because it undermines to some extent the continuity that Darwin was trying to establish between humans and animals. A full understanding of how gender influenced Darwin's version of sexual selection, however, would necessitate a deeper look at human sexual selection and Darwin's attitudes toward choice and women, in general. While undoubtedly interesting, such a discussion is beyond the scope of this paper and will have to await a later project.

But regardless of whose choice it is, the fact that sexually selected traits range from the useless to the down-right injurious seems to contradict the utilitarian and competitive Malthusian world view that Darwin championed. Why would females choose so poorly? Surely those males chosen merely for their good looks would not fare well and neither would their offspring. Thus, some traits which might be favored by sexual selection (that is, by choosing females) might make the animal less adapted to its

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[20]Ibid., 93.
[21]Ibid., i, 63.

day to day life. Indeed, many of the sexually selected traits that Darwin discussed are subject to this problem and Darwin was explicit on several occasions in the *Descent* that extreme, sexually selected adaptations might prove injurious to the organism:

> As birds always breed when food is abundant, the males probably do not suffer much inconvenience in searching for food from their impeded powers of movement; but there can hardly be doubt that they must be much more liable to be struck down by birds of prey. Nor can we doubt that the long train of the peacock and the long tail and wing-feathers of the Argus pheasant must render them more easy prey to any prowling tiger-cat than could otherwise be the case. Even the bright colours of many male birds cannot fail to make them conspicuous to their enemies of all kinds.[22]

Thus, the most desirable mate, may also be the most vulnerable to elimination by natural selection.

But Michael Ghiselin does not see natural and sexual selection in conflict with one another. He believes that sexual selection was "Darwin's most brilliant argument in favor of natural selection, of which it is a corollary."[23] He emphasizes that in terms of selection, in general, what truly matters is that differential breeding is achieved: "Selection, whether artificial, natural, or sexual depends upon differential reproductive success and not on adaptive advantage to the individual or group."[24] In other words, an animal may be highly adapted to its environment and live to be ancient, but unless that animal also leaves offspring, the traits which make it well adapted die with the animal. Reproductive success is, therefore, a necessary component to evolutionary success. Only if an animal can pass its beneficial traits to offspring, will these traits accumulate over

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[22]Ibid., ii, 97.
[23]Ghiselin, *Triumph of the Darwinian Method*, 215.

time. To this extent, then, Ghiselin is correct in emphasizing the importance of reproductive success in selection. But the ultimate reproductive success surely has a great deal to do with how adaptive an animal is to its surroundings. That is, if an animal is maladapted to its surroundings, it may not reach breeding maturity or may not survive from one breeding season to the next. Thus, by privileging reproductive success at the expense of adaptiveness, Ghiselin conflates natural and sexual selection.

Darwin was aware of the potential conflict between natural and sexual selection – in his correspondence with Wallace, this arose as one of the greatest sticking points between the two naturalists. But Darwin believed that in nature, natural and sexual selection could act alongside one another. However, in order to make room for sexual selection, it seems that Darwin had to mitigate the power and scope of natural selection somewhat. In the *Origin*, Darwin was explicit that Nature eliminates *any* trait that is in *the least degree injurious*. By the time he wrote the *Descent* he was less resolute on this point and allowed for an interplay between natural and sexual selection. Sexually selected adaptations are preserved, provided they are not grossly mal-adaptive:

> … natural selection will determine that characters of this kind shall not be acquired by the victorious males, which would be injurious to them in any high degree, either by expending too much of their vital powers, or by exposing them to any great danger. The development, however, of certain structures – of the horns, for instance, in certain stags – has been carried to a wonderful extreme; and in some instances to an extreme which, as far as the general conditions of life are concerned, must be slightly injurious to the male.[25]

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[24]Ibid.
[25]Darwin, *Deescent of Man*, i, 278-79.

Thus, slightly injurious adaptations might be tolerated and natural selection and sexual selection emerge as two counter-valing forces. Darwin concluded that success in leaving offspring must, at times, outweigh the risk of decreased fitness.[26]

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While Darwin believed that the mechanisms of natural and sexual selection could co-exist, he recognized that female choice posed significant challenges. Indeed, female choice emerged as the single most consistent issue brought up against sexual selection. But in order to understand these attacks (which will be examined in the following two chapters), it is important to examine what female choice meant to Darwin and how he viewed the aesthetic and cognitive abilities of animals. Darwin's animals were able to perform choices that were previously thought to be uniquely human. As Eileen Crist suggests in her *Images of Animals*, the continuity between animals and humans was predicated on the common descent of animals and humans for which Darwin argued in the *Descent.*[27] I believe that it was this continuity that served as the foundation to his claims about display and mate choice. Moreover, because animals and humans, according to Darwin, share basic mental and emotional configurations, humans can

[26]Ibid., 279.

[27]Eileen Crist writes:

> ...Darwin intended his anthropomorphic portraiture of animals as a realistic, veridical appraisal. Rather than assessing his anthropomorphism as either, error, metaphor, or undeserving of serious attention, I argue that his understanding of animal life reflects his view of evolutionary continuity. ... Darwin's language embodies a coherent and powerful understanding of animal life, one that is at odds with mechanomorphic and skeptical views widespread in behavioral thought during the twentieth century. P 12.

Crist, *Images of Animals*, 12.

understand and know the minds of animals in much the same way that they can understand and know those of their fellow humans.

There is a strong connection between sexual selection and cognitive development in Darwin's work. Darwin believed that sexual selection involves complex behavior and higher mental faculties to exert the requisite "will, choice, and rivalry of the individuals of either sex."[28] For Darwin, this was true both for the males, who engage in the complex behavior intended to woo potential mates and for females, who exert their choice, often with apparent sophistication. The following passage from the *Descent* shows Darwin's view of the intent of courting and the mental capacities it involves:

> When we behold two males fighting for the possession of the female, or several male birds displaying their gorgeous plumage, and performing the strangest antics before an assembled body of females, we cannot doubt that, though led by instinct, they know what they are about, and consciously exert their mental and bodily powers.[29]

Darwin's characterization of courting as both instinctive and conscious seems conflicted. As we shall see, the inclusion of both concepts is typical of his discussions of display and choice. However, the dominant tone here points to conscious and intelligent display and choice. That Darwin's sexual selection relied on higher mental development is further evidenced by the reasoning he offered for rejecting the possibility of sexual selection in certain animals. He denied their participation in sexual selection because of their low mental development:

> In the lower divisions of the animal kingdom, sexual selection seems to have done nothing: such animals are often affixed for life to the same spot, or have the two sexes

[28]Darwin, *Deescent of Man*, i, 258.
[29]Ibid.

> combined in the same individual, or what is still more important, their perceptive and intellectual faculties are not sufficiently advanced to allow of the feelings of love and jealousy, or of the exertion of choice.[30]

Conversely, Darwin argued that the "mental powers of the Crustacea are probably higher than might have been expected," on the grounds that they engage in sexual selection.[31]

The question of whether sexual selections are made intelligently, consciously or instinctively was an issue for Darwin. In his version of sexual selection, there are elements of both instinct and intelligence. For Darwin, instinct is an action that is exercised unconsciously. In the *Origin*, Darwin confined himself largely to a discussion of instincts, avoiding the slippery slope to humans that a discussion of higher intelligence undoubtedly would have presented. In his chapter on instinct, Darwin first declined to give an exact definition since he held that "every one understands what is meant, when it is said that instinct impels the cuckoo to migrate and to lay her eggs in other birds' nests."[32] In the sentence that followed, Darwin was less obtuse and explained that instinct is any action that is performed without previous experience.[33] While instincts may impel an organism to act without conscious or learned knowledge, Darwin never clearly demarcated instinct from intelligence. Intelligence may modify instinct. Quoting a Pierre Huber, Darwin declared that a "little dose ... of judgment or reason, often comes into play, even in animals very low in the scale of nature."[34] Instincts vary, are heritable and may be of varying service to an organism. Consequently, they are subject to the

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[30]Ibid., ii, 396.
[31]Ibid., ii, 334.
[32]Darwin, *Origin of Species*, 207.
[33]Ibid.
[34]Ibid..,208.

same laws as physical structures.[35] Instincts, like physical structures, are subject to modification by continuous habit over long time periods and habits, in turn, are subject to natural selection.[36] It is in this way that intelligence offers more than occasional cognizance of instinctive action: it can intervene and, if done often enough, cause changes in instinct. Thus, instinct leads to behavior and may, in turn, be modified by it.

Both instinct and habit are present throughout the animal kingdom. Howard E. Gruber in his *Darwin on Man*[37] makes a strong argument that the establishment of continuity between animals and humans was one of Darwin's primary motivations behind writing the *M* and *N Notebooks*. Darwin argues publicly for the continuity of behavior in the *Descent* and the *Expression of the Emotions in Man and Animals*. In response to those opposed to evolution who insisted that certain traits are strictly human and, in fact, make us such, Darwin pointed to their inchoate form in animals. In the *Expression of the Emotions*, Darwin pronounced that "[e]ven insects express anger, terror, and love by their stridulation."[38] Thus, animals can be seen using primitive tools and rudimentary language and they possess a sense of beauty and (the most flagrant of all claims!) a rudimentary basis for the belief in God.[39] Yet, as Darwin chiseled away at the anti-evolutionists' separation between man and animals, he was quite clear about the mental superiority of

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[35]Ibid., 209.

[36]Under habit Darwin understood the general, day to day activities an animal engaged in. He did not distinguish between habit and instinct or deliberate action. (See *Origin*, 134, 183, 204) Following Lamarck, Darwin believed that habit could influence structure and vice versa.

[37] Gruber, Howard E. *Darwin on man : a psychological study of scientific creativity*. 2d ed. Chicago: University of Chicago Press, 1981.Howard E. Gruber. *Darwin on Man: A psychological Study of Scientific Creativity*,

[38]Darwin, Charles. *The Expression of the Emotions in Man and Animals*, Paul Ekman (ed.), 3rd Edition (Oxford: Oxford University Press, 1998).
New York: Julian Friedmann ;
St. Martin's Press, 1979.y 347

humans. Self-consciousness, individuality, the power of abstraction and general ideas depend on developed language and are, therefore, unique to humans.[40] Further, only human animals are capable of reflection, which allows for morality.[41] Nonetheless, the message that humans only differed from animals in degree rather than in kind was clearly pronounced in the *Descent*. This continuity between animals and humans allowed Darwin's animals to exercise sexual selection.

But this close kinship between animals and humans was also reflected in Darwin's view of how humans can come to know about the inner lives of animals. Indeed, as Crist has also argued, the similarity between humans and animals served as the premise to Darwin's epistemology. That is, Darwin believed that humans can know the content of animal minds by observation much in the way that humans can, to a certain extent, judge the content of other humans' minds from observing their behavior.[42] In the following passage from the *Descent*, Darwin argued that the way to understand display and female choice in animals was analogous to the way an alien could judge the behavior of rustics courting a country girl at a fair:

> With respect to female birds feeling a preference for particular males, we must bear in mind that we can judge of

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[39]Darwin, Charles. *The descent of man, and selection in relation to sex*. First edition, first issue. ed. London,: J. Murray, 1871., I, 51-69

[40] Ibid., i, 62.

[41]Ibid., ii, 391-92.

[42]Eileen Crist, in her discussion of George and Elizabeth Peckham's work, follows the phenomenologist Alfred Schutz in calling this *Verstehen*, (to understand or as the noun, understanding). *Verstehen*, according to Crist, refers to "[t]he intelligibility of action from another's perspective," which "can range from being directly perceivable to tenuously inferred on the basis of knowledge that ranges from thoroughly commonsensical or universal to particular and private." Here Crist is arguing that, in the case of humans, we have an ability to draw correct conclusions about the actions and behaviors of other humans because we share a common basis of understanding and rely on others' actions to be meaningful. She extends the idea of *Verstehen* to the Peckhams' approach to animals. They believed that the actions of animals are both meaningful and deliberate. (The Peckhams' work will be considered in Chapter 2). Crist, *Images of Animals*, 51-55.

> choice being exerted, only by placing ourselves in imagination in the same position. If an inhabitant of another planet were to behold a number of young rustics at a fair, courting and quarreling over a pretty girl, like birds at one of their places of assemblage, he would be able to infer that she had the power of choice only by observing the eagerness of the wooers to please her; and to display their finery.[43]

The analogy was perhaps not as well chosen as it could have been. The notion that an alien would in fact judge the rustics' behavior correctly is as interesting as it is beyond the reach of proof. Moreover, the analogy also undermined his efforts to establish continuity between humans and animals. Surely an alien is different in kind as well as degree. Nonetheless, Darwin's point is clear. Humans can judge the mental motivations that underlie animals' actions just as an empathetic alien might correctly gauge the intentions of wooing country folk.

Taking a closer look at Darwin's use of animal observations in his *Expression of the Emotions in Man and Animals* sheds further light on his approach to animal thought and expression. Darwin considered animal observations a powerful tool and used them to test his theoretical generalizations. The following passage gives a good sense of his methodological approach to animal observations, since it shows both the limits and the possibilities he saw in their use:

> ... I have attended as closely as I could, to the expression of the several passions in some of the commoner animals; and this I believe to be of paramount importance, not of course for deciding how far in man certain expressions are characteristic of certain states of mind, but as affording the safest basis for generalization on the causes, or origin, of the various movements of expression. In observing animals, we are not likely to be biased by our imagination;

[43] Darwin, *Descent of Man,* ii, 122-23.

> and we may feel safe that their expressions are not conventional.[44]

Darwin was explicit here that the observation of animal expressions should not be used to decipher the emotional basis of human expression. Nonetheless, he found that there were several methodological advantages to studying animals rather than observing humans.

Darwin believed that animals (aw well as children and the mentally ill) are easier to study because their expressions are purer than those of adult humans.[45] Animals, he argued, are unfettered by the self-conscious censorship and affectation that plague adult expressions. Darwin also believed that by studying animals, he would be able to maintain the necessary critical distance to reach unbiased conclusions.[46] In observing humans, Darwin believed that the observer could easily empathize to the extent that the "imagination" would get in the way.[47] By observing animals the boundary between the subject and object could better be maintained.

But animals also offer insight into the evolution of human expressions. Because they are less evolved, their expressions are more proximal to their original causes and uses. Because humans evolved from lower animals, animals can offer insight into the earlier forms of human emotional expressions. This phylogenic argument is the type Darwin used in discussing the erection of hair in humans and animals.[48] He wrote that birds will erect their feathers when confronted with an enemy. Darwin claimed that birds and other animals erect their feathers and fur to appear larger and more intimidating.

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[44] Charles Darwin, *The Expression of Emotions in Man and Animals*. London
New York: Julian Friedmann ;
St. Martin's Press, 1979., 24.
[45] Ibid., 20.
[46] Ibid., 24, 33.
[47] Ibid., 19.

This, Darwin reasoned, is related to the appearance of goose bumps in humans when afraid. Yet, the appearance of goose bumps is no longer a voluntary action in humans nor does it make us look any larger or more intimidating. But from observing the phenomenon in animals, Darwin concluded that its original purpose must have been just that.

This example shows that the assumption that animals and humans share a common emotional history underlies Darwin's method. He takes it for granted that basic emotions span across the higher animal classes. But perhaps more important is the insight the example gives us into Darwin's belief in the accessibility of animal minds and emotions. Throughout the discussion (and, indeed, the entire *Expression*), Darwin took it for granted that he could know the animals' emotional states. He confidently described what animals looked like when they were feeling savage, affectionate, cheerful, dejected or disappointed. Crist remarks that Darwin viewed animals as having rich subjective lives of their own in which their actions are meaningful and exercised with agency.[49]

This knowledge of animals' inner lives was based on experience and common sense. Darwin believed that by interacting with an animal, humans can gain an understanding of the animal's basic emotions. Hence, Darwin *knew* the emotional content of his dog's actions, because he *knew* dogs in general and his own dogs in particular. I believe it was this basic, common sense access to animals that allowed Darwin's animals to perform mate choice and sexual selection.

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[48] Ibid., 99-105.

[49] Darwin called a group of birds that were congregating on a tree for a "dance-party, as it is called by the natives... so absorbed, that a skillful archer may shoot nearly the whole party." Darwin, *Expression*, 34.

But in spite of the access to animal minds Darwin and some of his contributors enjoyed, the exact nature of these choices still remains somewhat unclear. The role of aesthetics plays in mate choice was certainly a matter of concern for Darwin as well as his critics. In response to Wallace's review of the *Descent*, Darwin wrote to him:

> I have recognized for some short time that I have made a great omission in not having discussed, as far as I could, the acquisition of taste [in animals], its inherited nature, and its permanence within pretty close limits for long periods.[50]

Darwin's view of aesthetics was complex. He came to accept the role of beauty in sexual selection only gradually and with reservation. In one of his earliest notebook entries, he denied that animals possess any "notions of beauty."[51] Here Darwin also juxtaposed sensibilities about beauty *with* instinct and declared that the two are incompatible with one another. In another entry, Darwin seemed unwilling to accept that selection for utility can co-exist with one of beauty. A brief entry in his *C Notebook* sometime between February and July of 1838 shows that the choice exerted after male competition was ascribed to utility alone; aesthetic choice was excluded for this reason.[52] But in his later *M* and *N Notebooks*, Darwin's treatment of a sense of beauty became more nuanced. He explored the difference between instinct with respect to a sense of beauty and taste and reached the conclusion later expressed in the *Descent*. That is, while a sense and appreciation of beauty is instinctive, taste clearly is not. This Darwin concluded from the strange ornamentations some human tribes consider beautiful. Still, in the *Descent*, Darwin was clear that he believed a sense of beauty to be present in animals and he even

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[50] Wallace and Marchant, *Alfred Russel Wallace*, i, 261.
[51] Charles Darwin and Paul H. Barrett, *Charles Darwin's Notebooks, 1836-1844: Geology, Transmutation of Species, Metaphysical Enquiries* (Ithaca: Cornell University Press, 1987), *B Notebook*, 211.

went so far as to grant that the tastes of birds largely coincide with those of humans.[53] Yet, in keeping with his resolution that beauty can be instinctive, Darwin concluded the following about the female bird's mate choice: "It is not probable that she consciously deliberates; but she is most excited or attracted by the most beautiful, or melodious, or gallant males."[54] For Darwin, a sense of beauty evolved in animals as it did in humans. In keeping with his fuzzy separation between intelligence and instinct, Darwin continued to waffle between instinct and deliberate action in sexual selection. But the belief that animals were capable of deciding, at times consciously, was certainly present in much of Darwin's work. Further, his epistemology allowed him to draw such conclusions. Not only was it possible to gain knowledge of animals' emotions and capabilities, this knowledge also overtly drew from knowledge about humans. This does not bespeak methodological laxity. Rather, it was a consequence of Darwin's notion of common descent and evolution.

From Darwin's treatment of mental development in the *Descent*, it is clear that cognitive faculties play an important role in sexual selection. Darwin explicitly argued for this ability in animals and rejected the possibility of sexual selection in the lower animals on the grounds that they are not sufficiently mentally developed. Gruber shows that one of Darwin's goals in the *Descent* was to establish mental continuity between animals and humans. To this end, Darwin showed that the mental faculties that might be considered strictly human are also present in animals. This, for Darwin, was evidence

[52]Ibid., 261.
[53]Darwin, *Descent of Man*, ii, 39.

that humans are descended from lower animals. It attacked the very separation Natural Theologians clung to in defense of the divine creation of humans. Yet Darwin also used this evidence to show that animals are sufficiently developed mentally to exert the behavior necessary for sexual selection. Thus, Darwin argued that courtship rituals involve active cognition, while the sense of aesthetics of female birds is akin to that of humans. But it is not clear whether the exertion of choice is active or instinctive or both. Further, Darwin does not say exactly how a sense of aesthetics may benefit animals and, consequently, how it evolved. It is true, then, that Darwin never explicitly (or implicitly, as far as I can tell) addressed the mechanism whereby sexual selection and mate choice evolved. For Darwin it may have been sufficient to have come up with a strong explanatory model for a series of phenomena that were not readily explained by natural selection. Sexual selection offered a good alternative. Further, Darwin never intended for sexual selection to be a substitute for natural selection. Rather, the two evolutionary forces were seen to act alongside each other and other mechanisms not considered here.

Wallace on Sexual Selection

But to truly understand Darwin's theory of sexual selection and especially its reception, it is necessary to examine Alfred Russel Wallace's position on the theory. In many respects, Darwin's theory grew out of his intermittent but intense correspondence with Wallace. Much of the exchange over sexual selection took place before the

[54] Ibid., 123.

publication of the *Descent*.[55] Thus, while Wallace's views on the theory changed over time, Darwin was aware of his friend's concerns about the theory when he wrote the *Descent*. Indeed, Wallace was one of the earliest supporters of the theory and also one of its most enduring critics. Wallace offers us a glimpse of a critic who was very much Darwin's contemporary and who was also sympathetic both to Darwin and to natural selection. But his position on sexual selection is also instructive in terms of the theory's larger reception. In 1871, he wrote a prominent review of the *Descent* in the *Quarterly Review*. Though fairly positive, many of his objections would remain tremendously influential and cast shadows over subsequent discussions of the theory.

The debate between Darwin and Wallace has been ably documented by historians.[56] In his excellent article, "Darwin, Wallace and the Origins of Sexual Dimorphism," Malcolm Kottler has shown that a lengthy, in-depth debate between the two authors on the origins of sexual dimorphism preceded the publication of the *Descent*. But for the purpose of this chapter, I will focus on the public statements on sexual selection by Wallace and Darwin.[57] The works considered here represent the culmination of the private debates between Wallace and Darwin.[58]

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[55] According to Kottler, the debate was debated between 1867-68 and then briefly resumed in 1871 after the publication of the *Descent*.
Kottler, "Darwin, Wallace, and the Origin of Sexual Dimorphism," 203-26.

[56] For examples, see Kottler, "Darwin, Wallace, and the Origins of Sexual Dimorphism" and Cronin, *Ant and the Peacock*.

[57] See footnote 54 for dates.

[58] They are: the *Descent*, Wallace's Review of the Descent of Man," in *The Academy*, March 15, 1871, 177-83 and his 1889 work, *Darwinism, an Exposition of the Theory of Natural Selection with some of its Application*, London (New York: Macmillan, 1891). The relevant background that precedes them is based mostly on Malcolm J. Kottler's article, in which he documents the gradual divergence between the two authors' views on sexual selection.

In March of 1871, Alfred R. Wallace's review of the *Descent* was published in *The Academy*. Wallace praised Darwin's book as "one of the most remarkable works in the English language" and agreed that Darwin "has proved the vast importance of sexual influences in modifying the colours and the structure of the more highly organized animals."[59] And while Wallace deemed the evidence for sexual selection, and especially female choice, to be wanting in the lower animals,[60] he seemed quite satisfied with the case of birds:

> Among birds is found the first direct proof that the female notices and admires increased brilliancy or beauty of colour, or any novel ornament; and, what is more important, that she exercises choice, rejecting one suitor and choosing another.[61]

But Wallace's endorsement was not without reservations. While he conceded that sexual selection could "exert... a most powerful influence over the higher forms of life," he also believed that Darwin had gone too far in his reliance on it. Wallace regretted that in doing so, Darwin (of all people!) was not giving natural selection enough agency in the development of sexual dimorphism in birds. For Wallace, natural selection had acted in two separate but related ways that Darwin seemed unwilling to grant. Wallace argued that both male and female would become more brightly colored if females consistently chose the brightest mates. But brightly colored females are more vulnerable to predators when they incubate their eggs than more moderately colored females. Natural selection, then, would select against females with injurious colorations and would cause them to

[59]Wallace, "Review of the Descent of Man," 183.
[60]Ibid., 181.
[61]Ibid., 179.

become less conspicuous over time. But female tastes would continue to drive sexual selection to make brighter males. Over time, the mechanism of inheritance itself would change from equal to sex-limited inheritance. Thus, natural selection wold also act on the mechanism of inheritance. To Wallace, it seemed only logical that the mechanism of inheritance would itself be subject to natural selection – it varies, is heritable, and certainly some mechanisms of inheritance seem more useful than others under given circumstances. As evidence of the adaptiveness of hereditary transmission, Wallace pointed out that in species where both males and females are conspicuous, the female generally incubates her eggs in a covered nest hidden from predators. Conversely, sexually dimorphic species, "with very rare exceptions… build open nests."[62]

Wallace's concern with natural selection gradually eclipsed his tenuous support of sexual selection and mate choice. In *Darwinism*, published in 1889, seven years after Darwin's death, Wallace sought finally to bring secondary sexual characteristics in alignment with "the general laws of growth and development," that would "make it unnecessary to call to our aid so hypothetical a cause as the cumulative action of female preference."[63] While most of the debate between Darwin and Wallace that preceded the *Descent* "focused on the cause of coloration in the less conspicuous sex," as Malcolm Kottler has pointed out, *Darwinism*'s chapter on dimorphism was almost entirely concerned with the more colorful sex. By the time he wrote *Darwinism*, the adaptiveness of drab females was established to Wallace's mind. What remained to be proved was that the conspicuous colors and mating behaviors of males could also be reconciled with

[62]Ibid., 181.
[63]Wallace, *Darwinism*, 295.

natural selection. Unlike in his review of the *Descent*, Wallace no longer discussed the mechanism of inheritance, and he rejected female choice entirely. Instead, he proposed mechanisms for coloration and behavior that were explicable strictly in terms of natural selection. He continued to accept that battle amongst males for the possession of females could account for the special weapons in male animals, but he explicitly treated it as a form of natural selection.

Wallace granted that males displayed their sexual ornaments especially during the mating season. Indeed, he considered "[t]he extraordinary manner in which most birds display their plumage at the time of courtship, apparently with the full knowledge that it is beautiful, ... one of Mr. Darwin's strongest arguments."[64] He even conceded that this behavior might please the female. Yet to Wallace's mind, this was not legitimate evidence that the display of ornaments evolved for the *purpose* of exciting the female nor that female choice had driven their evolution. Wallace argued that the mate choices of animals are too irrational to meet the demands of sexual selection. In what seems like a tactical about-face, Wallace illustrated his point by comparing animal choices to those of humans:

> A young man, when courting, brushes or curls his hair, and has his moustache, beard, or whiskers in perfect order, and no doubt his sweetheart admires them; but this does not prove that she marries him on account of these ornaments, still less that hair, beard, whiskers, and moustache were developed by the continued preferences of the female sex. So, a girl likes to see her lover well and fashionably dressed, and he always dresses as well as he can when he visits her; but we cannot conclude from this that the whole series of male costumes, from the brilliantly coloured, puffed, and slashed doublet and hose of the Elizabethan

[64]Ibid., 287.

> period, through the gorgeous coats, long waistcoats, and pigtails of the early Georgian era, down to the funeral dress-suit of the present day, are the direct result of female preference. In like manner, female birds may be charmed or excited by the fine display of plumage by the males; but there is no proof whatever that slight differences in that display have any effect in determining their choice of a partner.[65]

In the 1871 review, Wallace's qualms about mate choice had focused on the lower animals and their lack of mental complexity and aesthetic sophistication. From the above quote it seems that mental sophistication was less at issue at this point than was the overall efficacy of mate choice. Here Wallace is saying that no matter how intelligent those who choose are, mate choice cannot drive evolution the way Darwin had argued. Further, Wallace once and for all rejected that colorful "fashions" were products of the powers and tastes of those who choose. Instead, Wallace sought to establish alternative means for explaining brilliant coloration and elaborate mating behavior.

Wallace, like Darwin, continued to believe that species started out in their most neutral coloration. But according to Wallace, variations in color arise as byproducts of "the complex chemical and structural changes ever going on in the organism."[66] Natural selection, then, acts upon these colors to achieve the myriad colorations and patterns in nature. Because they are due to natural selection, the colors are necessarily adaptive. These include colors of "warning, recognition, mimicry, or special protection."[67]

Wallace also offered a physiological explanation of coloration. Following the research in Alfred Tylor's 1886 *Coloration of Animals and Plants*, Wallace argued that

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[65]Ibid.
[66]Ibid., 288.

patterns of coloration correspond with the underlying structural or physiological features of the animal. Thus, "diversified coloration follows the chief lines of structure, and changes at points, such as the joints, where function changes."[68] The most pronounced markings, they argued, could be seen over areas of major nerves and muscles and in areas of high use, such as the pectoral muscles of birds.[69] Frank Beddard performed a dissection of a bird of paradise at Wallace's request and confirmed these findings. He agreed that "[t]he plumes arise, therefore, close to the most powerful muscle of the body, and near to where the activities of that muscle would be at a maximum."[70] Thus, the extra vital energy gives rise to "abnormal growths in those parts of the integument where muscles and nervous action are greatest."[71] Once these variations appear, they would continue to develop as natural selection would preserve the fittest animals (i.e., those with the most surplus energy). According to Wallace, then, secondary sexual characters are a consequence of overall fitness, both in their original appearance and their subsequent development.

This line of reasoning, which associated structure with function, also allowed Wallace to link display with vigor. He argued that because the physical structures are due to increased vital energy to those regions where they appear, "the skin-muscles which serve to elevate them would increase as well." From this he argued that "the nervous development as well as the supply of blood to these parts being at a maximum, the erection of the plumes would become a habit at all periods of nervous or sexual

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[67]Ibid.
[68]Ibid.
[69]Ibid., 289.
[70]Ibid., 292.
[71]Ibid.

excitement."[72] The fact that males sometimes display their plumes in the absence of females had already been noted by Darwin in the *Descent*. Thus, the display of these plumes would be an indication of the animal's vigor. Wallace, quoting Darwin, further reasoned that if females chose at all, it must be for "the most vigorous, defiant, and mettlesome males."[73] The most active animals would be "necessarily attractive to the female."[74] To Wallace's mind, the necessary association between ornamentation and vigor was sufficient evidence that female choice based on aesthetics alone was not only improbable but also unnecessary:

> We have, thus, no reason for imputing to her any of those aesthetic emotions which are excited in us, by the beauty of form, colour, and pattern of these plumes; or the still more improbable aesthetic tastes, which would cause her to choose her mate on account of minute differences in their forms, colours, or patterns.[75]

This and other passages might suggest that Wallace rejected female choice merely on the grounds that sexual ornament and display could be explained by other means. However, Wallace, believed sexual selection to be maladaptive and irreconcilable with natural selection and was, therefore, disposed to look for alternative explanations. His conception of natural selection was the version Darwin had presented in the *Origin*. Selection for frivolous ornaments simply did not agree with this view of natural selection according to which all aspects of nature are subject to constant and relentless scrutiny. It was important for Wallace to show that the brightly colored males were, in fact, adaptive. Even if females selected the most ornamented males, they would only prosper if the male

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[72]Ibid., 293.
[73]Ibid.
[74]Ibid., 294.

also happened to be the most fit. Because Wallace's physiological explanation linked fitness and ornament, it allowed for precisely this scenario. Thus, if female choice existed, it could only be in accordance with natural selection:

> If the most brightly coloured and fullest plumaged males are not the most healthy and vigorous, have not the best instincts for the proper construction and concealment of the nest, and for the care and protection of the young, they are certainly not the fittest, and will not survive, or be the parents of survivors. If, on the other hand, there is generally this correlation – if... ornament is the natural product and direct outcome of superabundant health and vigour, then no other mode of selection is needed to account for the present of such ornament. The action of natural selection does not indeed disprove the existence of female selection of ornament as ornament, but it renders it entirely ineffective.[76]

Of course, this watered down version of female choice rendered the mechanism virtually superfluous. But Wallace did not spend much time discussing female choice in *Darwinism*. It seems, that by this time, the issue was very much overtaken by his desire to establish natural selection as an all-sufficient mechanism.

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Malcolm Jay Kottler has shown in "Darwin, Wallace, and the Origin of Sexual Dimorphism," that Wallace's rejection of sexual selection began with his skepticism of female insects' ability to exert the requisite choice to drive selection.[77] Already in his 1867 "Mimicry, and other Protective Resemblances among Animals," Wallace made the connection between mental faculties and choice explicit:

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[75]Ibid.
[76]Ibid., 295.

> For it is evident that if colours which please us also attract them and if the various disguises which have been here enumerated are equally deceptive to them as to ourselves, then both the powers of vision and their faculties of perception and emotion must be essentially of the same nature as our own – a fact of high philosophical importance in the study of our own nature and our true relations to the lower animals.[78]

Four years later, in his review of Darwin's *Descent*, Wallace expanded on his doubts that the females of the lower species can exert choice in the way sexual selection would require.[79]

But Wallace's reluctance to grant animals the agency in mate choice that Darwin's theory of sexual selection demanded, may also have been due to his view of animals and humans. While Wallace originally believed that humans and their moral and mental faculties might be explained entirely by natural selection, he later came to reject this view.[80] In 1865, Wallace had an experience that would profoundly alter his outlook on life and his scientific position. Wallace attended a seance and subsequently converted to spiritualism.[81] Two years before Darwin's *Descent* was published, Wallace publicly denied that natural selection could account for "the moral and higher intellectual nature of man."[82] Wallace believed that in order for these distinctly human faculties to have

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[77]Kottler, "Darwin, Wallace, and the Origin of Sexual Dimorphism," 223.
[78]Alfred Russel Wallace, "Mimicry and other Protective Resemblances among Animals," in *Westminster Review* 32 (1867): 1-43, 42.
[79] Wallace, "*Review of the Descent of Man*," 182.
[80] In this section, I follow Robert J. Richards's discussion of Wallace on human evolution (pp. 162-169, 176-186.) Richards writes that in an essay of 1864, "On the Origin of Human Races," Wallace argued that natural selection was sufficient to explain reason and morality in humans.
Robert J. Richards, *Darwin and the Emergence of Evolutionary Theories of Mind and Behavior, Science and its Conceptual Foundations* (Chicago: University of Chicago Press, 1987), 163.
[81]Ibid., 178.
[82]Again, this quote is from Richards' chapter on Wallace. Wallace wrote in a review of Lyell's work: "Neither natural selection or the more general theory of evolution can give any account whatever of the origin of sensational or conscious life … But the moral and higher intellectual nature of man is as unique a

come about, Divine intervention was necessary. That is, although humans may have physically evolved from their lower forbearers, an intelligent power must have intervened on behalf of humans to ensure their mental and moral superiority. By thus severing the evolutionary continuum between humans and their ancestors, Wallace eliminated the sort of continuity Darwin had urged between humans and animals. And while Wallace discretely omitted any clues about his spiritualism in his review of the *Descent*, surely it must have seemed a stretch to have even birds exercise the sorts of choices that Darwin's theory demanded.

For Wallace, then, the debate over sexual selection was in large part about natural selection. While he accepted sexual selection and mate choice in his review, he believed that Darwin had over-emphasized its role in evolution at the expense of natural selection. He granted that birds had a sense of aesthetics and would choose their mates accordingly but objected to Darwin's claim that insects could do the same. And even then, Wallace was uncomfortable with female choice. He criticized Darwin for not showing enough evidence that female tastes would remain sufficiently constant over time and geographic areas to drive evolution. Moreover, Wallace already accorded natural selection a greater role than Darwin had. He argued that while sexual selection could account for the conspicuous coloration of male birds, natural selection had kept the incubating female

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phenomenon as was conscious life on its first appearance in the world, and the one is almost as difficult to conceive as originating by any law of evolution as the other."
Ibid., 178. (Original Source: Alfred Russel Wallce, "Review of Principles of Geology by Charles Lyell, 10th ed., 2 vols. (London, 1867, 1868); Elements of Geology by Charles Lyell, 6th ed. (London, 1865)," Quarterly Review 126 (1869): 359-94.)

from acquiring the same colorations as the male and had changed the mechanism of inheritance from equal to sex-limited. Thus, for Wallace, the adaptiveness of the female's inconspicuous coloration was a strong argument for natural selection. But even the limited role he had granted sexual selection in his review eventually became unacceptable to him. By the time he wrote *Darwinism* he had come up with what seemed like a more satisfying solution to the male's conspicuous coloration. He argued that conspicuous coloration was a byproduct in the integument of body parts that are subject to high physico-chemical use. Similarly, Wallace argued that behavior was linked to vigor. During the mating season, males were particularly energetic, leading to the curious courtship antics previously described as display. And clearly, the more vigorous an animal, the more brightly its coloration and spirited its behavior. Thus, Wallace provided a consistent explanation to coloration and courtship behavior that relied directly on vigor. Females would be excited by the colors and behaviors of the males and if they chose at all, would naturally choose the one who most excited them and therefore was the most fit. Thus, if female choice was a factor at all, it was in keeping with natural selection and certainly not due to the female's sense of aesthetics.

Darwin's theory of sexual selection required a great deal of animals, in general, but even more of female animals, in particular. While Darwin was not always consistent in his characterization of what mental faculties were involved in female choice, it clearly depended on aesthetics and an elevated mental state. This was evidenced by Darwin's treatment of choice and was recognized by his contemporaries and successors, as I will show in the following two chapters. Darwin restricted mate choice and sexual selection

to the higher animals. But even so, the fact that he believed animals could pass such judgments was controversial but very much in agreement with Darwin's larger argument for continuity between human and animals for which he argued in the *Descent* and the *Expression.* But this proximity of animals and humans did not just allow Darwin's animals to perform mate choices based on aesthetics; it also enabled Darwin's epistemology of animals. In this chapter, I have sought to show with reference to Eileen Crist's work that Darwin's access to animal minds, was much like he would have known the emotional and mental contents of other humans. But this was not just an anthropomorphic projection of human emotions on animals. Rather, Darwin sought to show how previously thought to be uniquely human traits were found in animals. Thus, to some extent, Darwin projected the animal onto humans to show their common evolutionary history. Because Wallace relied on a spiritual explanation of humans, he did not accept that animals and humans were separated merely by evolution. Conversely, Wallace believed that a higher, intelligent power had intervened to give humans superior intelligence and morality. This essential difference between animals and humans, upon which Wallace insisted, also sheds light on his rejection of sexual selection. While he at first accepted mate choice in the higher animals, he eventually came to reject its possibility altogether. Instead, Wallace focused on explaining secondary sexual characters by natural selection. In the subsequent chapter I will show how Darwin's conviction in the essential commonality between animals and humans was necessary to the acceptance of sexual selection. Animals had to be very similar to humans to perform the seemingly human-like choices that Darwin's version of sexual selection required of them. Moreover, this proximity had significant methodological and epistemological

consequences. Those who accepted the continuity were able to study animals by referencing the human psyche, while those who rejected it were largely denied access to animals' minds and rejected the interpretation of animals with reference to humans.

CHAPTER TWO

Turn-of-the-century Experts on Animal Minds -
George J. Romanes, George and Elizabeth Peckham, C. Lloyd Morgan,
and St. George Mivart on Sexual Selection

Questions about sexual selection continued to focus on female choice through the last decades of the nineteenth and the early twentieth centuries.[83] Many considered it the keystone to Darwin's theory and critics, including Wallace, Conwy Lloyd Morgan and St. George Mivart, doubted that the lower animals were capable of distinguishing amongst the subtle variations on which Darwin had insisted. And even if female animals were able to distinguish, they doubted that they would actually discriminate. Further, echoing one of Wallace's early concerns, it seemed improbable that tastes would be sufficiently uniform and constant amongst females to drive the evolution of such traits. The evidence Darwin had presented was scarce and critics did not tire of pointing this out. Yet, certainly (and perhaps because of this), views on female choice were largely influenced by general views on animal intelligence and aesthetic sensibilities. It is, therefore, particularly instructive to turn to the writers who were considered authorities on the minds of animals and to examine their views on sexual selection, in general, and female choice, in particular.

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[83] Mary Bartley in her dissertation, *A Century of Debate: The History of Sexual Selection Theory (1871-1071)*, Ph.D., 1994, Cornell University, has called the 1880's and 1890's "a period ... of "choosing sides" over natural selection and sexual selection," 49. Her analysis casts the debate over sexual selection largely in the context of neo-Larmarckism versus neo-Darwinism. She argues that supporters of natural selection (or neo-Darwinists) sought to divert attention away from sexual selection, as attacks on the latter were thought to reflect poorly on the former. In contrast, detractors of natural selection (neo-Lamarckians) dwelled on the links between natural and sexual selection and found sexual selection an easy target and an effective means of weakening the entire Darwinian position. Bartley's analysis is useful but also obscures some of the diversity amongst the detractors of sexual selection.

Specifically, I will discuss the work of Darwinian comparative psychologists Conwy Lloyd Morgan and George John Romanes and his use of the work of Dr. and Mrs. Peckham, an American couple that studied the mating behavior of spiders. Romanes was a strong supporter of Darwinism and sexual selection. Similarly, the Peckhams' observations of spiders were explicitly aimed at overthrowing some of Wallace's objections to sexual selection. Both Romanes and the Peckhams believed animals to be capable of discriminating, choosing, and displaying a wide range of emotions. Their anecdotes tell of human-like trials and tribulations of animals and the authors confidently describe what animals think and feel throughout these. Indeed, their studies were largely empathetic with an underlying assumption that animals' inner lives were similar in kind (if not in degree) to those of humans. This is essentially the emotional and mental continuity that Darwin had urged in the *Descent* and in the *Expression*. C. L. Morgan and Mivart, on the other hand, rejected this continuity. While their reasons for doing so were not the same, the separation between animals and humans resulted in both cases in a rejection of sexual selection. Further, because animals and humans were viewed as fundamentally different by Morgan and Mivart, these authors did not allow themselves the access to animals' minds that Darwin, Romanes and the Peckhams had enjoyed.

In this chapter, I will show how the views of animals and their mental and aesthetic abilities shaped late nineteenth and early twentieth century attitudes about sexual selection. I will argue that the acceptance of Darwin's continuity between animals and humans was necessary to the acceptance of sexual selection. Those that rejected it believed that animals were fundamentally different from humans and were unwilling to accept the complex mental and aesthetic decisions animals had to make in sexually

selecting their mates. While the question of female choice was certainly influenced by attitudes of gender, this will be addressed as a subtext. I believe that gender attitudes must have informed scientists' reception of sexual selection. But I believe this to have been a secondary factor to their views of the minds of animals.

George John Romanes

George J. Romanes (1848-1894) was a devoted friend and supporter of Charles Darwin. Not surprisingly, he spoke in favor of sexual selection in his 1901 *Darwin and After Darwin.* Unlike Vernon L. Kellogg six years later, Romanes considered "the evidence in favour of sexual selection ... both large in amount and massive in weight."[84] He considered sexual selection the indisputable corollary to natural selection. While natural selection could explain the importance of utility in nature, sexual selection explained the role of beauty. Sexual selection, like natural selection, provided a mechanical-causal explanation. Unlike Kellogg who (as we shall see) emphasized the connections between natural and sexual selection, Romanes was careful to keep the two apart: "[I]t is a theory wholly and completely distinct from the theory of natural selection; so that any truth or error in the one does not in the least affect the other."[85]

Romanes thought it obvious that the higher animals exercised some discrimination in their mate choices and to this extent considered sexual selection established fact. There were, however, two subsequent claims of Darwin's theory that he deemed inferential and, therefore, in need of proof. The first was the claim that animals

[84]George J. Romanes, D*arwin and after Darwin. An Exposition of the Darwinian Theory and a Discussion of post-Darwinian Questions*, (Chicago: The Open Court Publishing Company, 1892), i, 384-85.

choose their mates based on aesthetics. Second, he argued that if taste is accepted, then it must be shown that the mechanism provides a sufficient causal explanation to bring about the traits in question. The challenge was to establish that such aesthetic capabilities did, indeed, exist in animals.

Before moving on to a general discussion of Romanes's arguments in favor of sexual selection it should be noted that he recognized that the explanation of beauty, as it was offered by sexual selection, had significant strategic value against arguments of design and natural Theology. Romanes believed that Darwin's theory eliminated the need for divine explanations. Even the human eye, which William Paley had considered the most compelling evidence for God's design in nature, was brought under the purview of naturalistic explanation precisely because of its utility. They argued that like a beautifully engineered and crafted telescope, the eye must have been designed with its end in mind. To Romanes, sexual selection could do the same for beauty. Where natural selection had not been able to offer explanations for things that did not meet strict utilitarian criteria of natural selection, sexual selection could:

> Thus, whether we look to the fact of adaptation or to those of beauty, everywhere throughout organic nature we meet with abundant evidence of natural causation, while nowhere do we meet with any independent evidence of supernatural design."[86]

It is important to bear in mind that for Romanes, this position did not inevitably lead to atheism. But he did believe that nature could no longer be relied on to provide unequivocal proof of God's benevolence and wisdom the way it had for Natural

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[85]Ibid., i, 384.
[86]Ibid., 411.

Theologians, such as Paley, Bell, or Chambers. Thus, sexual selection provided the missing piece to an all encompassing "mechanical interpretation of nature."[87]

But Romanes recognized that for arguments based on animal behavior to legitimately overthrow those of Natural Theology, animals would have to be shown to have the mental capacity to make sexual selections. Specifically, Romanes had to show that animals have an aesthetic sense. The bower birds, which build "elaborate play-houses in the form of arched tunnels, built of twigs upon the ground," seemed ideal candidates for this task. Romanes described these birds' efforts to decorate their nests and bowers in *Darwin, and after Darwin.* Following an account by John Gould, Romanes described how bower birds decorate their bowers with various objects that appear to please them. The garden bower bird of Papua is especially striking, as he does not content himself with merely building a fancy house. Indeed, according to Gould's description, he also seems to be a fastidious landscaper who lavishes great care and attention on his grounds:

> The central pillar [of the bower] is banked up with moss at its base, and a gallery is built round the interior of the edifice. This gallery is decorated with flowers, fruits, fungy, &c. these are also spread over the garden, which covers about the same area as the play-house. The flowers are said to be removed when they fade, while fresh ones are gathered to supply their places. Thus the garden is always kept bright with flowers, as well as with the brilliant green of mosses, which are collected and distributed in patches, resembling tiny lawns.[88]

These gardens appeared to serve no purpose other than the enjoyment of their owners, which seemed to indicate that these birds have an appreciation of beauty. Both Darwin

[87]Ibid., 412.

and Romanes used Gould's account of the birds' habits and concluded that it was proof of their aesthetic sense.[89] Romanes considered it a given that the birds would use it to evaluate members of the opposite sex in male selection.[90]

Romanes also considered the mating behaviors of male animals. Like Darwin, Romanes believed that behavior was the strongest evidence in favor of sexual selection. Special structures, as well as colors, seemed to serve only the purpose of courtship. The mature male of the South American Bell-bird is a brilliant white with a peculiar tube-like structure over his beak. When deflated, the structure hangs slackly across the side of the bird's beak; when inflated it stands upright. Four species within this genus posses these types of structures which are only inflated during courtship. Again, Romanes sees no other means of explaining this than through sexual selection:

> And as no other function can be assigned to it than that of charming the female when it is erected in courtship, the peculiarity of form and mechanism which it presents - like the elaboration of patterns in cases where colour only is concerned - virtually compels us to recognise in sexual selection the only conceivable cause of its production.[91]

These structures are restricted to the male sex only, which to Romanes strongly suggested that they originated by sexual selection. But the real proof of the theory, to Romanes' mind, was that the birds only inflate these structures during the mating season and in the presence of females.

Romanes also addressed Wallace's claim that coloration naturally correlates with overall vigor and can be explained entirely by natural selection. Romanes agreed with

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[88]Ibid., 382-383.
[89]Ibid., 380.
[90]Ibid., 383.

Wallace that the "general brilliancy of color" might increase as an animal's overall vigor increases. But he did not consider natural selection an adequate explanation of the very elaborate and intricate ornaments, such as the peacock's tail.[92] These, Romanes argued, could only be explained by invoking the discerning eye of potential mates in courtship. Thus, Romanes dismissed Wallace's objection and argued that "by ... virtually ignoring the only facts which that theory [of sexual selection] endeavours to explain, Mr. Wallace is not really criticizing the theory at all."[93]

Similarly, Romanes denied that the colorations seen only in the male sex were attributable to surplus energy. Romanes reminded his reader that natural selection eliminates the useless and certainly would not have allowed such adaptations to evolve unchecked had they not served a purpose. He went on to enumerated the costly consequences of the peacock's tail: it costs the peacock a good deal of vital energy and makes him more conspicuous to predation. Clearly, if natural selection alone were at work, such adaptations would not come about in such extreme form. And ultimately, for Romanes these ornaments presented "a plain and obvious reference to the relationship of the sexes."[94]

However, despite Romanes's concern with sexual selection's compatibility with natural selection, he was more interested in the issue of animal intelligence. In his review of the *Descent*, Wallace had shared this concern: "at best the theory can only apply to the more intelligent animals, and so must necessarily fail to explain the phenomenon of

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[91]Ibid., 398.
[92]Ibid., 394-95.
[93]Ibid., I, 394.

beauty in the less intelligent, or in the non-intelligent, as well as in all species of plants."[95] It is worth noting that for Romanes, an aesthetic sense did not "necessarily imply ... any constant relation between such a sense and high levels of intelligence in other respects."[96] Indeed, birds displayed the most obvious examples of this behavior and were considered less intelligent than mammals. Nonetheless, Romanes agreed that Darwin's version of sexual selection required higher mental abilities than were normally attributed to animals:

> For it is obvious that the theory can only apply to living organisms which are sufficiently intelligent to admit of our reasonably accrediting them with aesthetic taste - namely, in effect, the higher animals. [97]

To reply to Wallace's charge that animals' tastes would not be sufficiently uniform or consistent to direct the evolution of secondary sexual characters, Romanes drew from his own experience as a comparative psychologist:

> Although we know very little about the psychology of the lower animals, we do observe in many cases that small details of mental organization are often wonderfully constant and uniform throughout all members of a species, even where it is impossible to suggest any utility as a cause.[98]

Yet Romanes knew that this posed a problem to which Wallace had alluded in his criticism of the theory. Many of the lower animals and plants exhibited great beauty to the human eye. Indeed, even inanimate objects often seemed beautiful. However, these phenomena would not be covered by sexual selection. Indeed, Romanes excluded "[t]he whole of the vegetable world, and the whole of the animal world at least as high up in the

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[94]Ibid.
[95]Ibid., 391.
[96]Ibid., 380.
[97]Ibid., 405.
[98]Ibid., 399.

scale as the insects," on the grounds that they were "incapable of aesthetic feeling."[99] Romanes explained the beauty of inanimate objects by referring to the subjective nature of beauty. Beauty, he suggested, is ultimately "in the eyes of the beholder." [100] But inanimate objects were not in need of an evolutionary or "mechanical" explanation and Romanes believed that Darwin had sufficiently established that the beauty of plants could be explained through natural selection. Their beauty is not an end in itself. Rather, plants advertise their nectar and pollen to potential pollinators by means of their brightly colored flowers.

The lower animals proved more vexing in this regard:

> ...here we are bound to confess that the beauty which so often meets us cannot reasonably be ascribed whether to natural or to sexual selection. Not to sexual selection for the reasons already given; the animals in question are neither sufficiently intelligent to possess any aesthetic taste, nor, as a matter, of fact, do we observe that they exercise any choice in pairing.[101]

Since beauty here seemed neither explicable in terms of natural selection (as in the case of the flowers of plants) nor in terms of sexual selection (to attract mates capable of appreciating their beauty), Romanes conceded that "[o]n the principles of naturalism, therefore, we are driven to conclude that the beauty here is purely adventitious, or accidental."[102] But unwilling to capitulate entirely, he declared that the beauty in the lower life forms generally amounted to either "the radiate form, or to the bright tints." The radiate form refers to the radial axis of symmetry seen in the lower animals as

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[99]Ibid., 405.
[100]Ibid., 404.
[101]Ibid., 408.
[102]Ibid.

opposed to the bilaterally symmetric body plan (which indicates symmetry about a single axis) that humans and many other animals have. Romanes postulated that the radial form, to which many of the lower organisms seemed to owe their beauty, was in fact due to some unknown utility. He concluded this from the body type's great abundance in nature. Because so many different animal species had a radial body type, Romanes reasoned that "if the attainment of beauty had here been the object, surely it might have been even more effectively accomplished by adopting a greater variety of typical forms - as, for instance, in the case of flowers."[103] In terms of the beauty due to bright colors of some of the lower animals, Romanes hazarded that it might be a byproduct of its chemical composition. As an example, he waxed enthusiastically that "there is nothing more magnificent than arterial blood."[104] Of course, under normal circumstances, the blood is not visible. Its color, therefore, can be neither ascribed directly to natural nor to sexual selection. Similarly, Romanes argued that in the lower animals, beauty could only be incidental.

While Romanes believed to have answered Wallace's objections the way Darwin would have,[105] he also marshaled evidence that had not been available to Darwin. His inclusion of the Peckhams work was just the sort of evidence needed to lend his efforts a more contemporary flavor. Dr. and Mrs. Peckham's observational work on spiders was an example of how structure coupled with behavior could constitute strong evidence for

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[103]Ibid.

[104]Ibid.

[105]Romanes wrote: "Unfortunately the work in which they are mainly presented was published several years after the second edition of the *Descent of Man*, so that Mr. Darwin never had a suitable opportunity of replying. But, if he had had such an opportunity, as far as I can judge it seems that his reply would have been more or less as follows."

sexual selection. The Peckhams were convinced Darwinians and their work was aimed explicitly at overthrowing some of Wallace's objections to sexual selection.

Spiders offered a particularly good example of sexual dimorphism, as the members of the sexes of many species differ dramatically from each other. The Peckhams performed a series of mating experiments where they placed different spiders in "mating boxes"[106] and observed their behavior. These boxes were aimed at overcoming some of the difficulties of watching the animals in the wild.[107] The Peckhams' findings supported what Darwin had considered some of the most compelling evidence for sexual selection and mate choice: that males displayed before the females, while the females carefully watched them. In the case of the male *Phidippus rufus*, the male has "beautiful white hairs on the lower part of the palpi [feelers]," while the female has green hairs. The Peckhams noted that the male waves these palpi before the female. In doing so, they expose the palpi's underside so that the white hairs are visible to the female.[108]

But the Peckhams also performed experiments where they expressly wished to show that female spiders choose their partners. In one experiment, they placed twelve

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[106]The Peckhams wrote:

> The larger ones were 15 inches long by 11 ½ wide and 3 deep; the smaller, 7 ¼ long by 5 ¾ wide and 2 ½ deep. The sides of each box were marked off into inches so that the distance of the spiders from each other could be easily noted. The floor was made of coarse cotton cloth, for the purpose of ventilation, while the top was of glass, so that the inmates of the cage could be kept fully in view at all times; this top could be opened and closed.

George Peckham and Elizabeth Peckham, "Observations on Sexual Selection in Spiders of the Family Attidae," in Carl J. Bajema, *Natural Selection in Human Populations; the Measurement of Ongoing Genetic Evolution in Contemporary Societies*, New York: Wiley, 1971), 299.

[107]While the Peckhams do not elaborate on the specific difficulties they faced, they report that previous attempts to observe their mating habits went "with little success."
Ibid., 298.

[108]Ibid., 306.

male and twelve female spiders together in the mating box. After two hours, three pairs had formed. According to their observations, "[t]he females seemed to have some difficulty in choosing from among the males, but after a decision had been reached and a male accepted, there appeared to be complete agreement, and the male, thereafter, commenced to build his house."[109] Yet the preceding discussion of the spiders' interactions, did not make it obvious that the females actually chose their mates: "Soon they were all moving about, the males making advances to the females, who seemed to endeavor to escape."[110] In another experiment six females and one male were placed in a mating box. The Peckhams "saw [the male] mate with all of [the females]; and each, after a time made a cocoon." While this experiment confirmed that this species of spiders might be polygamous (at least under these circumstances), it, like the previous experiment, did not show conclusively that females choose a particular male. In fact, none of the Peckhams' experiments offered definitive proof of female choice, as none of them tested whether a female when confronted with more than one male would prefer one over the other. But, as I mentioned above, a good deal of the Peckhams' efforts were directed at disproving Wallace's objections to sexual selection and it was in these detailed descriptions that the Peckhams were at their strongest. Specifically, they wished to dispute that the duller colors (usually seen in the female) are due to natural selection for her protection and that the brighter colors (usually in the male) are due the animal's "surplus in vital energy."[111] The Peckhams found that in contrast to Wallace's assertion,

[109]Ibid., 302.
[110]Ibid., 301.
[111]Ibid., 266.

"[m]any of these covered nests are occupied by dull-colored females."[112] Agreeing with Darwin, they believed it "highly probable that in spiders, as in birds, the color was developed prior to the formation of these [nesting] habits."[113] Based on their observations, they also concluded that there was no causal relationship between vigor and coloration, as Wallace had suggested in *Darwinism*. To test this claim, they observed pairs of female spiders of the species *Phidippus mositans* (where the male is more colorful than the female) interact in a glass jar. After the first two concluded their brief but deadly combat, they repeated the experiment and found that, in each case, one of the females killed the other. Subsequently, they placed a male into the jar with the following result:

> ...we put in a well-developed male, which, though smaller, was compactly built and apparently strong enough to bring the virago to terms; but, to our surprise, he seemed alarmed and retreated, trying to avoid her; she, however, followed him up, and finally killed him.[114]

The Peckhams concluded that "females are more powerful and pugnacious than males," in spite of the male's more colorful appearance.

In considering the Peckhams own strong support for sexual selection and Romanes' use of their work to that end, it is instructive to take a closer look at the characteristics of the Peckhams' spiders. As it turns out, the Peckhams' spiders run the gamut of personalities and emotions. Some are described as patient, sensitive, timid and cautious, while others are fierce or clever. The Peckhams described the males of a species with especially dangerous females, as "very prudent little fellows [that] ... were

[112]Ibid., 276.
[113]Ibid.

fully conscious that "he who fights and runs away will live to fight another day.""[115] Indeed, it seems that these spiders even showed a familiarity with the truisms of proverbs. Eileen Crist describes the Peckhams' method as one which assumes a *Verstehen* or understanding of the intentions that underlie the actions of animals.[116] She argues, correctly I believe, that the Peckhams' strongly anthropomorphic language and their inclusion of anecdotal evidence were in keeping with their belief that the actions of animals are meaningful.[117]

But Romanes' inclusion of the Peckhams' work was not anomalous in its strongly anthropomorphic flavor. In his earlier work, *Animal Intelligence*, Romanes recounted countless stories of birds that were loyal, clever, selfish or devoted; birds that grieved, governed and punished each other. Others supposedly exhibited acts of courage, friendship and, of course, love.[118]

This raises the question of how Romanes and the contributors to his work, came to know these animals so intimately. In the introduction to *Animal Intelligence*, Romanes described his methodology as one which allows experimenters to infer the minds of animals by analogy to their own minds. Romanes wrote: "The investigator's subjective mind aids as an analog to the objective mind under investigation."[119] But more important was Romanes' view of animals and their mental abilities in his attitude toward sexual selection. Romanes accepted the continuity between animals and humans that Darwin

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[114]Ibid., 272.
[115]Ibid.
[116]See footnote 45. Although her discussion focuses on the Peckhams' work on wasps, her observations apply here as well.
Crist, *Images of Animals*, 51-87.
[117]Ibid., 86.
[118]Peckham in Bajema, *Natural Selection in Human Populations*iley.

had proposed in the *Descent*. Indeed, Romanes's proposed method of studying animals by referencing human mental states, relied on this common cognitive basis and allowed observers to know animals empathetically. This methodology was very much exhibited by the Peckhams' work, who reported on the emotions and feelings of their spiders with confidence. Because of this shared cognitive basis, it was conceivable that animals were capable of sexual selection. But perhaps more importantly, it afforded observers access to animal minds allowing them to infer from the animal's behavior that it was, in fact, engaging in sexual selection. I believe that it was this methodological license that allowed Romanes and like-minded researchers to gain an intimate knowledge of animals' mental states. That said, Romanes did offer a rather interesting rejoinder to Wallace's objection that there was no evidence that female hens actually prefer the cock with the brightest feathers and the most showy personality. To this, Romanes replied:

> ...I do not see much weight in [Wallace's] merely negative difficulty as to there being an absence of evidence upon hen birds being charmed by the plumage, or the voice of their consorts. For, on the one hand, it is not very safe to infer what sentiments may be in the mind of a hen; and, on the other hand, it is impossible to conceive what motive can be in the mind of a cock, other than that of making himself attractive, when he performs his various antics, displays his ornamental plumes, or sings his melodious songs.[120]

Thus, for Romanes the male bird's intentions were quite clear. The hen, on the other hand, remained somewhat of a mystery about which he declined to speculate. But Romanes's uncertainty about the hen's motives hardly seems to have been due to a belief that humans were denied access to hens' minds. As is evidenced by Romanes's

[119]George J. Romanes, *Animal Intelligence* (New York: D. Appleton and Company, 1883), 2-3.

confidence in reading the cock's mind, the experimenter could know the animal to the extent that he could relate to the animal by means of his own frame of reference. I would argue that precisely because his understanding of animals was empathetic, Morgan felt that it was more prudent to avoid inferring what the hen's mental or emotional state was. While he deemed them capable of choice, he was unsure exactly of how this choice would play itself out. Thus, Romanes's reticence to speculate about the mind of the hen had perhaps more to do with Romanes's own puzzlement with the world of courting, rather than a genuine doubt about the possibility of sexual selection.

Thus, for Romanes, natural selection was able to explain utility while sexual selection provided a means to explain that which appeared useless. This was not just beneficial from a scientific perspective, but also had considerable philosophical value. Natural selection had been able to provide answers where opponents of evolution had insisted that the usefulness of animal adaptations was the direct result of an intelligent designer. Natural selection provided an answer that also took the utility of an adaptation into account. Indeed, its reliance on utility left aspects of nature that did not seem useful exposed to alternative explanations or, more dangerously, as damaging counter-evidence against natural selection. If natural selection could not account for seemingly harmful or just useless adaptations its explanatory powers seemed deficient and the theory was left vulnerable to claims that beauty may have been created for its own sake by the Creator. Romanes recognized the importance of Darwin's theory of sexual selection, precisely because it could explain what natural selection could not. But in spite of this complementarity, Romanes also wanted to keep the two theories distinct. He seems to

[120]Ibid., 398.

have been particularly intent on maintaining this separation when it came to critiques of either of the theories. It seems that Romanes felt a need for sexual selection to make the Darwinian explanatory system more complete, but was worried that the controversial theory would do harm to natural selection. This made it all the more important to defend sexual selection.

But while Romanes found it expedient to accept sexual selection and was in a position to do so, the usefulness and elegance of the theory should not be underestimated as a factor in his acceptance of it. Like Darwin, Romanes was compelled by sexual selection, because it seemed the very best explanation to all the common phenomena in nature that could not be explained by natural selection. Romanes wrote that "it is difficult to imagine that all the large classes of facts which an admission of this common cause serves to explain, can ever admit of being rendered intelligible by any other theory."[121]

Conwy Lloyd Morgan

C. Lloyd Morgan (1852-1900), also a comparative psychologist, considered Romanes his friend and colleague. When Romanes died in 1894, Morgan saw his works through the press and added some finishing touches for publication.[122] Yet Morgan's methodology for studying animals and his conclusions about sexual selection were decidedly more conservative than those of his late mentor. He accepted sexual selection, in general, while rejecting female choice.

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[121]Ibid., 390.
[122]Richards, *Darwin and the Emergence.*

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[121]Ibid., 390.
[122]Richards, *Darwin and the Emergence.*

Morgan agreed with Darwin that males engage in conscious behavior to "influence" females and to ultimately gain their favors. In his 1900 *Animal Behaviour*, he quoted examples where male animals' ornamentation was only displayed in the presence of females. Morgan believed that behavior and ornamentation were intimately connected and concluded that this sort of behavior was intended for the benefit of the female:

> From the case of the Argus pheasant, which is only a sample of the large class of cases in which the male has special adornments, we see that the behaviour has often direct relation to the display of such plumage, or, in some apes, of coloured surfaces, so that behaviour and ornamentation must be taken together.[123]

Morgan also considered it likely that the outcomes of these courting efforts resulted in varying degrees of success for the males.[124]

Yet Morgan ascribed the female a rather more modest role in courtship than Darwin and his more ardent supporters had. Following the Swiss comparative psychologist, Karl Groos, Morgan believed females to be instinctively coy. They argued that the male seeks to overcome the female's reluctance to pairing in his courtship efforts. In addition, courting serves to generate "the requisite amount of pairing-hunger"[125] in the male. Morgan deemed it the physiological "craving" that is necessary for mating to occur. In dramatic language, Morgan draws the following parallel:

> Courtship is thus the strong and steady bending of the bow that the arrow may find its mark in a biological end of the utmost importance in the survival of a healthy and vigorous race.

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[123]C. Lloyd Morgan, *Animal Behaviour* (London: E. Arnold, 1900), 263.
[124]Ibid., 261.
[125]Ibid.

> The coyness and reluctance of the female afford the conditions under which the bow is bent to the full. But they also afford the conditions of the apparent act of choice.[126]

Notably, Morgan referred to the "*apparent* act of choice," (my italics) and it is here that Morgan parted company with other supporters of sexual selection. Indeed, Morgan considered the insistence on an aesthetic mate choice "unnecessary surplusage" and rightfully noted that Darwin himself was not always consistent in his language about female choice:

> Darwin occasionally expressed himself unguardedly in the matter; he says, for example, that the female appreciates the display of the male, and places to her credit a taste for the beautiful. But he also distinctly states that "it is not probable that she consciously deliberates; she is most excited or attracted by the most beautiful, or melodious, or gallant males." This is all that is really necessary for the theory of sexual selection.[127]

To Morgan, the choice the female makes is not based on deliberation. Rather, it is based on her perception of the male. If he elicits positive feelings in her, she, in turn, associates these feelings with him. Morgan believed that she projects her inner subjective state on him "because he is the centre of a conscious situation."[128] But while Romanes had declined to speculate about the inner life of the hen, Morgan offered the following insight:

> Take now the case of a coy hen bird, to whom several males pay court. The sight of this one, behaving after his kind, excites in small degree the sexual impulse and emotions. Her heart beats but little the faster for all his antics, her respiratory rhythm is scarcely affected, her

[126]Ibid., 266.
[127]Ibid., 263.
[128]Ibid., 268.

> feathers, like her feelings, remain comparatively unruffled. He has acquired meaning from the reaction to his presence; it is not, however, a very attractive meaning. But that other, perhaps from mere persistency, perhaps because he is more "vigorous, defiant, and mettlesome: (she, at any rate, certainly knows not why), deeply stirs her organic being, sets her all aglow, and breaks down the barriers of her coyness. And this he does because he is the centre of a conscious situation which has acquired, through her experience of his presence, a meaning and an interest that are at last irresistibly attractive. It is a choice from impulse, not the result of deliberation....[129]

This, according to Morgan, placed female choice safely in the perceptual rather than the ideational domain of cognition. The perceptual, according to Morgan, is driven by impulse, while the ideational involves reflection and volition; the sorts of rational behaviors of which animals are most likely incapable. While Morgan granted that both animals and humans are exposed to the sorts of experiences that can be pleasurable (such as the sight of the pheasant's tail), he did not believe that this would lead to an aesthetic ideal in animals. According to Morgan, such an appreciation would necessitate "comparison, abstraction, and generalization," rational processes of the ideational sort that he placed beyond the grasp of animal minds. The "appreciation of the beautiful," then, is a "reflective superstructure" that derives from the pleasurable feeling derived from certain perceptions. Through the course of evolutionary history, humans gradually gained the mental capability to form an abstract concept of these sorts of perceptions. Subsequent encounters with beauty would allow the rational being to compare them against this aesthetic standard. Similarly, Morgan held that ethics required the abstraction of an ideal of conduct against which subsequent actions could be compared.

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[129]Ibid., 268-69.

Morgan believed that the pleasure derived from certain situations served as the "perceptual germs" that had, in the case of humans, evolved into moral and aesthetic values. Thus like Darwin, Morgan proposed an evolutionary development of aesthetic and ethical sensibilities. But the similarity between Darwin and Morgan must not be overemphasized here. Darwin wished to show that the same aesthetic and ethical sensibilities were present in animals, albeit in a quite rudimentary form. In contrast, Morgan's "perceptual germs" were not to be interpreted as less developed moral and aesthetic faculties. Rather, they were remote precursors which cannot develop without the concomitant evolution of reason - a faculty he largely denied animals.

Morgan espoused minimalist explanations that did "not interpret behaviour as the outcome of higher mental processes, if it can be fairly explained as due to the operation of those which stand lower in the psychological scale of development." Impulse certainly was a more comfortable fit with this "canon of interpretation" than deliberation would have been. But Morgan's rejection of female choice based on an aesthetic ideal was not just a function of his desire to explain animal behavior conservatively; rather, it seems to have been a natural consequence of his larger conceptual and epistemological framework. In general, Morgan's conservatism in interpreting the mental processes of animals was much more far-reaching than that of some of his contemporaries, particularly supporters of sexual selection. Morgan stressed that his canon "by no means excludes the interpretation of a particular act as the outcome of the higher mental processes, if we already have independent evidence of their occurrence in the agent."[130] Yet the

[130]Ibid.

acquisition of such corroborating evidence seemed nearly impossible to obtain, given Morgan's stringent methodological constraints.

In his discussion of the methodological problems associated with studying the minds of animals, Morgan quoted two specific difficulties from G. F. Stout's *Manual of Psychology*. The first referred to the limitations of language in describing mental processes in animals. Stout argued that because language is distinctly human and "is especially constructed to describe the mental states of human beings," it would "mislead us when we attempt to describe the workings of minds that differ in any great degree from the human."[131] The second of Stout's concerns addressed the inherently subjective nature of interpretations of behavior. Stout argued that because the psychologist is denied access to the mind of those he is studying, he suffers the temptation of ascribing his own mental states to those under his investigation. In Stout's own words, "the besetting snare of the psychologist is the tendency to assume that an act or attitude which in himself would be the natural manifestation of a certain mental process must, therefore, have the same meaning in the case of another."[132] Stout considered this inclination particularly "seductive when the animal mind is the subject of inquiry."[133] Both Stout and Morgan stressed the need to meticulously scrutinize the circumstances under which an animal might behave a given way and to avoid "taking this or that isolated action apart from the totality of conditions under which it appears."[134]

[131]Ibid.
[132]Ibid., 270.
[133]Ibid.
[134]Ibid.

To summarize briefly, Morgan believed that sexual selection occurred only insofar as some animals are more successful breeders than others. While males are conscious in their wooing efforts, females form perceptual images and associations of their wooers. Moreover, females, according to Morgan, are instinctively passive. In Morgan's version of sexual selection females are mostly reactive. This, of course, does not lend itself to the decision-making role that Darwin had ascribed to female animals. But aside from these gendered predispositions, Morgan's view of animals' cognitive make-up, irrespective of sex, also made it impossible for them to form aesthetic ideals and consequently to make sexual selections. According to Morgan, both humans and animals possess the perceptual domain of cognition, which allows them to sense stimuli impinging on the animal from the outside world. Yet to form abstractions of these perceptions against which further abstractions can be consciously evaluated, a further mental capacity is necessary. This Morgan called the ideational domain of cognition and he reserved it strictly for humans. He argued that the ideational capacity was required for the evolution of an aesthetic ideal. Because animals lack the ideational capacity, they lack aesthetic ideals, and therefore, cannot make their decisions based on them. Thus, where Darwin's and Romanes's animals had been similar enough to humans to pass aesthetic judgments, Morgan's animals were incapable of making sexual selections both because female animals did not possess the requisite character and because animals, in general, did not have a sufficiently complex neuro-physiological make-up. To Morgan's mind, then, female animals were the farthest from being capable of making the sorts of choices Darwin had reserved for them. First, is the fact that they are female, which indicates their inherently passive and receptive nature. Second, animals, regardless of

sex, are mentally incapable of making aesthetic judgments. But, aside from deeming animals incapable of passing aesthetic judgments, Morgan also barred himself access to their inner lives. He viewed the separation between animals and humans as fundamental and impenetrable.

St. George Mivart

In July of 1871, an anonymous review of the *Descent* appeared in the *Quarterly Review*. While the author called Darwin a "powerful and acute intellect," he also deemed his "power of reasoning ... to be in an inverse ratio to his power of observations."[135] And while the work contained "most varied, interesting, and important biological data," the reviewer found that Mr. Darwin's work was plagued by a "singular dogmatism" and was based on a "radically false metaphysical system."[136] Letters to friends show that Darwin was deeply troubled by the review and it did not take him long to suspect St. George Mivart (1827-1900) of the damaging piece's authorship.[137]

Mivart, who was originally trained as a lawyer, received his scientific training under Huxley and Owen.[138] Mivart was well versed in the science of the day and seemed to bring his acute, lawyerly scrutiny to scientific critiques. But Mivart was also a devout

[135][Mivart, St. George], "Darwin's Descent of Man," in *Quarterly Review* 131 (1871): 47-90, 87.
[136]Ibid., 25, 45, 46, 48.
[137]Robert J. Richards describes Darwin's reaction to the review and a letter to Huxley where he expressed his suspicion about the identity of the reviewer.
Richards, *Darwin and the Emergence*,226. Mary Bartley also quotes a letter to J. D. Hooker of September 16, 1871 where he expresses his distress about the way the review made him look and blames Mivart's attack on his "accursed religious bigotry."
Bartley, *A Century of Debate*, 52.
[138]Richards, *Darwin and the Emergence*, 353-54.

Catholic intent on reconciling natural science with Divine creation.[139] Mivart believed that science could not contradict religion. As a consequence of his religious convictions, Mivart rejected Darwin's proposed link between animals and humans. He insisted that morality, religion and reason were exclusively human and it is in this context that Mivart rejected sexual selection. Thus, while Mivart accepted that natural selection played a role in nature – albeit a role much diminished from what Darwin had ascribed it in the *Origin* – he could not accept sexual selection, even on these terms.

In his review, Mivart devoted considerable space to a discussion of sexual selection, as he considered it "the corner-stone of Mr. Darwin's theory."[140] He went on to say that "unless he [Darwin] has clearly established this point, the whole fabric falls to the ground."[141] It seems that Mivart was aiming to bring about precisely this consequence with his systematic attacks on the work. Most of his criticisms found their ammunition from the very pages of the *Descent*. Throughout the review, he highlighted the passages in which Darwin had mentioned exceptions or expressed doubt about sexual selection's action. What had appeared in Darwin's work as cautious qualifications to sexual selection, Mivart turned into a veritable parade of counter-evidence. Mivart argued that if

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[139]In his review of the *Descent*, Mivart was reserved about his desire to reconcile religious orthodoxy with science. He made no overt mention of his religious convictions, save in the final sentence of the piece. Here he expressed his hope that Darwin "may yet live to furnish us with another work, which, while enriching physical science, shall not, with needless opposition, set at naught the first principles of both philosophy and religion."
[Mivart], "Darwin's Descent of Man," 48.
However, in his later work *Lessons from Nature*, Mivart's religious convictions are explicit. For a further discussion of Mivart's religious views and how they influence his science, see
Richards, *Darwin and the Emergence,* 353-55, 361-63. Richards also discusses how despite Darwin's silence in the Origin on man and ethics, Mivart correctly anticipated his arguments on these issues and criticized them in his Genesis of Species, 139.

[140][Mivart] "Darwin's Descent of Man," 29.
Most of the criticism of sexual selection voiced here are repeated – often verbatim – in a chapter devoted to the topic in Mivart's later work *Lessons from Nature.*

by Darwin's own admission sexual selection had not acted in the cases he considered exceptions, the adaptations in question might just as well be accounted for by the alternative causes. Indeed, Mivart considered this more probable and judged Darwin's invocations of sexual selection gratuitous.

In his discussion, Mivart also differentiated between "two very distinct processes" of sexual selection.[142] The first described the male pre-mating rivalries. This aspect of sexual selection Mivart accepted, though he (like Wallace) viewed it as "one kind of 'natural selection' [rather] than as a branch of 'sexual selection.'"[143] It was the second part of Darwin's theory – female choice – which, according to Mivart, ought alone be called sexual selection. Mivart focused on this aspect of sexual selection, as he considered it problematic and in dire need of proof.[144]

Mivart's assessment of the evidence in the *Descent* was disparaging, at best. The real difficulty for him lay in the issue of choice. According to Mivart, Darwin's theory of sexual selection comprised the "alleged preference or choice, exercised freely by the female in favour of particular males on account of some attractiveness or beauty of form, colour, odour, or voice, which such males may possess."[145] He did not doubt that the male displays might excite the female, but could not agree with Darwin (and Morgan) that this necessarily meant that the male performed to that end or that the female would necessarily exercise discrimination based on it:

> No doubt the plumage, song, &c., all play their parts in aiding the various processes of life; but to stimulate the

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[141]Ibid.
[142]Ibid., 29.
[143]Ibid.
[144]Ibid.
[145]Ibid

> sexual instinct, even supposing this to be the object, is one thing—to supply the occasion for the exercise of a power of choice is quite another.[146]

While Mivart granted that "the sexual instinct always seeks its gratification," he questioned whether "the female *ever* select[s] a particular plumage."[147] Here he quoted from the *Descent*, where Darwin recounted Sir Heron's observations of peafowl. Heron observed that hens did, in fact, show preference for a "particular peacock":

> They were all so fond of an old pied cock, that one year, when he was confined though still in view, they were constantly assembled close to the trellice walls of his prison, and would not suffer a japanned peacock to touch them. On his being let out in the autumn, the oldest of the hens instantly courted him, and was successful in her courtship. The next year he was shut up in a stable, and then the hens all courted his rival. This rival was a japanned or black-winged peacock, which to our eyes is a more beautiful bird than the common kind.[148]

Mivart conceded here that the birds had exhibited a preference. But he considered it unlikely that it was based on the male bird's plumage. Seizing on the author's statement that the japanned peacock might be considered more beautiful by humans than the birds' favorite choice, Mivart argued that female choice could not yield the sorts of results found in nature. Even if the birds might base their decisions on the male's plumage,

> … it would seem (from Mr. Darwin's concluding remark) to prove either that the peahen's taste is so different from ours, that the peacock's plumage could never have been developed by it, or (if the taste of these peahens was different from that of most peahens) that such is the

[146]Ibid., 32.
[147]Ibid.
[148]Ibid., 31-32.

> instability of a vicious feminine caprice that no constancy of coloration could be produced by its selective action."[149]

Wallace had similarly argued that birds' tastes must be different from human aesthetic sensibilities and that even if birds exercised such preference, their preferences would not be consistent across species nor constant over time to yield the sorts of sexually dimorphic colorations that Darwin's theory sought to explain. But Mivart had recast Wallace's concern in noticeably strong language to convey the inconstancy of female tastes. He referred to the female's tastes as subject to "vicious feminine caprice" and elsewhere he calls it "feminine caprice." To Mivart, female choice was not just impossible for animals because of their lower mental organization, but as his language reveals, it clearly was also a distasteful notion,.

Desiring to illustrate the "uncertainty which besets these speculations of Mr. Darwin … at every turn," Mivart also recalled Darwin's discussion of the glowworm. "What at first could be thought a better instance of sexual selection than the light of the glowworm used to attract her mate," Mivart asked. And indeed, the luminescence is only found in the female and might reasonably be thought to guide the male to her at night. Yet in Darwin's discussion of the glow worm, he had to concede that their luminescence probably did not come about by sexual selection. He reported that the immature larvae already possessed the luminescent quality. Because they are sexually immature, Darwin reasoned that selection for them was unlikely to be sexual.[150] Mivart also recounted

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[149]Ibid., 32.

[150]While it is conceivable that the trait might be useful in sexual selection in the adult, Darwin's view of heredity claimed that traits which appear only in one sex usually occur later in life. For a discussion of Darwin and Wallace's views of heredity, see Kottler, "Darwin, Wallace, and the Origin of Sexual Dimorphism."

Darwin's own doubts about the choosiness of female butterflies. Darwin dutifully reported (and Mivart quoted) that "in certain cases beauty does not charm the female" and some female butterflies "may frequently be seen paired with battered, faded, or dingy males.'"[151] In the case of the reptiles and amphibians, Mivart also found "the facts hostile to his [Darwin's] views."

In addition to making extensive use of Wallace's objections to sexual selection and mate choice, Mivart also entertained his suggestion that sexually dimorphic colors were naturally selected for the sake of protection. But while he deemed Wallace's objections to Darwin's theory cogent, he found Darwin's rejoinders equally damaging to Wallace's views. Finally, with both Darwin's and Wallace's arguments effectively put in their proper places, Mivart saw the path for his own theory cleared:

> Now as Mr. Wallace disposes of Mr. Darwin's views by his objections, so Mr. Darwin's remarks tend to refute Mr. Wallace's positions, and the result seems to point to the existence of some unknown innate and internal law which determines at the same time both coloration and its transmission to either or to both sexes.[152]

The introduction of an "unknown innate and internal law" may have given Darwin just the leg-up he needed to figure out the authorship of this review, as Mivart had alredy introduced it in the *Genesis of Species*, his book-length criticism of Darwinism published earlier that year.[153] More importantly, however, it also hinted at the philosophical differences between the two men.

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[151][Mivart], "Darwin's Descent of Man," 47-90.
[152]Ibid., 32.
[153]St George J. Mivart, *On the Genesis of Species* (New York: D. Appleton and Company, 1871).

To highlight these differences, Mivart's attack on sexual selection must be considered in light of his attitudes toward natural selection and Darwinism, in general. Mary Bartley examines the debate over sexual selection in the last two decades of the nineteenth century in the context of a larger debate between neo-Darwinians and neo-Lamarckians. She argues that opponents of neo-Darwinism (or neo-Lamarckians) used critiques of sexual selection to weaken natural selection.[154] While Mivart does not fall neatly into the neo-Lamarckian camp, his discussions of Darwinism certainly reveal his intentions of weakening natural selection (with the intention of making room for explanations that relied on Divine intervention). To Mivart, extreme Darwinism was anathema and his review of the *Descent* was used to some extent as an opportunity to attack Darwinism and natural selection in general. Mivart presented Darwin's theory of sexual selection as evidence of the weakness and insufficiency of natural selection. Since Darwin had to invoke sexual selection to explain traits, Mivart reasoned that natural selection could not adequately account for them. Mivart emphasized that Darwin had retreated from his earlier insistence on natural selection as the all-sufficient mechanism to bring about evolutionary change. Of course, Mivart's criticism unjustly cast Darwin as a neo-Darwinian, which he certainly was not. By dwelling on the ways in which Darwin had departed from his earlier position, Mivart sought to call Darwin's credibility into question. He commended Darwin on his candor but claimed that "it would be idle to dissemble, and disingenuous not to declare, the amount of distrust with which such repeated over-hasty conclusions and erroneous calculations inspire us."[155] Mivart

[154]See footnote 89.
[155][Mivart], "Darwin's Descent of Man," 47-90.

suggested that if the author could change his mind with such facility about issues on which he formerly stood with certainty, prudent readers might do well to take the arguments in the *Descent* with a grain of salt. In his conclusion, he declared that: "[o]n the whole, we are convinced that by the present work the cause of 'natural selection' has been rather injured than promoted...."[156]

However, we must be careful not to treat Mivart's rejection of sexual selection as equivalent to his treatment of natural selection. Mivart accepted natural selection, albeit in a much diminished form. Sexual selection, on the other hand, stood in conflict with his religious and philosophical views. While Mivart faulted Darwin for basing his science on a "radically false metaphysical system," his own philosophical and religious convictions strongly influenced his science and, indeed, precluded him from accepting sexual selection. But religion did not bar Mivart from accepting natural selection. Mivart believed that natural laws could act externally upon an organism and that natural selection could eliminate maladaptive forms.[157] He rejected Darwin's claim, however, that natural selection alone could bring about the origin of species. Nonetheless, natural selection was acceptable to Mivart. This raises the question of how his philosophy allowed him to accept natural selection but not sexual selection.

The answer to this question has to do, I believe, with Mivart's insistence on a separation between animals and humans. Mivart, like Wallace, invoked the invention of God into the process of the evolution of humans. While Darwin had argued that the courtship of animals might be understood empathetically by analogy to human behavior

[156]Ibid., 90.
[157]Mivart, *On the Genesis of Species*, 257.

(as the example in the first chapter that tells of the denizens observing the courting of the rustics at a fair demonstrated). Mivart argued that the alien would be justified in concluding that the country girl was exercising "an internal, mental faculty of choice ... only if he had reason to attribute to the rustics an intellectual and moral nature similar in kind to that which he possessed himself."[158] And it is precisely this point which led Mivart to reject not only sexual selection, but the entire argument of the *Descent*. To Mivart's mind such analogous inferences would only be valid if the intellectual and moral dispositions were commensurate. Insistence on separation between humans and animals precludes us knowing the animals as the alien cannot know the minds of the rustics if their modes of thinking diverge significantly.

While Mivart agreed with Darwin that animal and human minds have much in common insofar as they share common physical structures, Mivart insisted that humans here mental and moral qualities uniquely their own. He faulted Darwin for "assum[ing] that when two things have certain characters in common there can be no fundamental difference between them." To Mivart's mind, only humans possess the capacity for self-consciousness and reason. In the *Expression,* Darwin similarly reserved self-consciousness for humans, when he characterized blushing as a uniquely human trait caused by heightened self-awareness. However, Darwin clearly did not deny animals the capacity to reason.

Mivart argued that the difference between the animals and humans was not merely one of degree, but rather one of kind, from the fact that the two qualities which marked

[158][Mivart], "Darwin's Descent of Man," 33.

them (instinct and reason, respectively) were inversely proportional.[159] In other words, humans, whose mental abilities were the highest of the animals, consequently possessed the lowest instinctual development. Conversely, Mivart argued that ants have the highest level of instinctual development but do not possess reason. While Darwin may have roughly agreed with the ants and bees showing the highest level of instinct and that they are less intelligent than mammals, he did not place instinct and reason as two inversely proportional quantities. Intelligent actions over time could become instinctual but this need not be to the detriment of intelligence in Darwin's mind. And many of the behaviors that were previously thought to be strictly human were found in the higher animals as well.

Finally, Mivart reminded his readers that orthodoxy was on his side and that his position was "commended to us by our intuitions, by ethical considerations, and by religious teaching universally"[160] and that the burden of truth, consequently, rested on Darwin. Mivart believed that Darwin had wrongly equated reason with sensation. For Mivart this conflation essentially did away with "mental power whatever except sensation."[161] While Mivart did not wholly reject natural selection, he did not believe that it could accomplish what Darwin had argued without the intervention of God: the genesis of species and a system of morals and ethics. These distinctly human traits were not to be derived naturalistically the way Darwin argued in the *Descent*. Neither did Mivart accept that humans and animals formed a mental and emotional continuum. While Mivart granted that humans and animals had much in common in their physical and to a lesser

[159]Ibid., 37.
[160]Ibid.

extent mental make-ups, he also insisted that there were essentially differences between them. Humans, he argued, possess the ability to reflect and reason, they have self-consciousness and the ability to act morally. Animals lack these ideational capacities and dwell largely in the realm of perception and sensation. According to Mivart, animals also lack the most critical feature of Darwin's theory of sexual selection - aesthetic sensibilities. Mivart, of all the people considered so far, was perhaps the least willing to grant truth to any aspect of the theory. He believed that neither male nor female animals are capable of performing the necessary display and choice, respectively. Thus, by insisting on a separation between animals and humans, Mivart also rejected the possibility of sexual selection. Yet, while Mivart rejects the theory in its entirety, his references to "feminine caprice and even "vicious feminine caprice" suggest that he found the suggestion of female animals performing these tasks especially troublesome.

Mivart, like C.L. Morgan, objected to the intimate knowledge Darwin claimed to have of animal minds. Because animals were essentially different from humans, it was not possible to make inferences about the mental states that accompany their actions by assuming that they are like those of humans. Mivart cautioned that Darwin's example of the alien who observes rustics courting a girl at a country fair relies on the assumption that the alien has the same system of thought and behavior as the humans. To Mivart, the alien's inferences about human behavior would only be valid if this was, indeed, the case. Because Mivart believed animals to be fundamentally different from humans, clearly he rejected the sort of inferential reasoning that both Darwin and Romanes endorsed.

[161]Ibid.

Animals, according to Mivart, could not be legitimately known by reference to human mental, emotional, and behavioral states.

Bartley is surely right in ascribing Mivart's desire to diminish the power of natural selection. But it is important to appreciate the difference between Mivart's treatment of natural and sexual selection. The power of natural selection had to be diminished to make room for internal law. Sexual selection, on the other hand, had to be rejected entirely to maintain a separation between humans and animals. For Mivart, the separation of the animal and human mind was not so much a methodological concern as it was a religious imperative, as only humans were created in the image of God.

Conclusion

The reception of sexual selection in the late nineteenth-century had much to do with how individual scientists viewed animals and their mental features. This was particularly true for their reactions to female choice, which continued to be the main focus of sexual selection debates. The scientists discussed in this section (Romanes, the Peckhams, Morgan, and Mivart) all agreed that a high level of mental sophistication in animals is necessary for them to choose their mates, according to the way Darwin's theory of sexual selection had suggested. But in spite of this agreement, they differed considerably in their acceptance or rejection of Darwin's theory. Romanes supported Darwin's theory ardently, while C.L. Morgan accepted sexual selection but not female choice and Mivart rejected the theory altogether. Their reception of the theory was a product of the extent to which they concurred with Darwin's view of animals and their mental and aesthetic abilities. Specifically, the extent to which they agreed with

Darwin's argument in the *Descent* that animals and humans differ in degree rather than kind, strongly correlates with the extent to which they accepted sexual selection. Romanes accepted Darwin's argument for the continuity between animals and, consequently, believed that animals could perform mate choice based on aesthetic ideals. Moreover, Romanes believed that this continuity between animals made the human mind an appropriate frame of reference for studies of animals. To Romanes certainly the acceptance of sexual selection was useful, because it promised to expand naturalistic explanations to all domains of nature. While natural selection could account for utility, sexual selection could explain the beautiful, frivolous and seemingly useless. Thus, sexual selection provided a powerful compliment to natural selection. On the other hand, he was anxious to keep the two mechanisms separate when it came to the evaluation of their merits and faults. He knew that sexual selection, as much as it was useful, was also controversial and, in this respect, could damage natural selection. These fears were not unfounded, for those critical of natural selection, such as Mivart, were eager to point to the common flaws of the theories or even use sexual selection against natural selection. C.L. Morgan's and to a greater extent, Mivart's criticisms of sexual selection were also very much due to their conceptions of animal minds. To a large degree, both Morgan and Mivart severed the continuity between animals and humans that Darwin had insisted on. Because they believed animals to be essentially different, they did not believe that animals would be capable of making the human-like choices for which Darwin had argued. Morgan was explicit about the methodological implications for this as well. He rejected the extrapolation from humans to animals that Romanes had endorsed. Consequently, the knowledge he could gain of animals was far more limited. But aside

from deeming the overall mental development of animals too low to perform natural selection, Morgan viewed the female animal as largely passive and reactive to the male's advances. Thus, for Morgan, even if animals had the requisite mental development to perform sexual selection, it is unlikely that he would have ascribed the act of choice to the female.

Mivart, on the other hand, gave both male and female animals even less agency in pre-mating. While he conceded that the male's pre-mating antics might excite the female, he believed that he did so unwittingly. Similarly, the female was incapable of discriminating and choosing mates. But for Mivart, the separation between animals and humans was not just a methodological consideration but also a religious imperative. While sexual selection, in a toned-down form, was compatible with Mivart's religious views, sexual selection, exactly because it insisted on animal and human continuity, threatened the moral and religious superiority of humans. For this reason, Mivart was intent on demolishing Darwin's arguments of the *Descent*. Unlike Morgan, Mivart was not so much concerned with the inaccuracy that psychologically-informed observations on animals would yield. Rather, he seems to have been concerned with the implications for humans and religion that the suggestion of continuity bore.

CHAPTER THREE

Sexual Selection in the Face of a Changing Science –
Vernon L. Kellogg and Thomas Hunt Morgan

As the nineteenth century drew to a close, a younger generation of scientists became increasingly dissatisfied with the uncertainties that beset the methods and findings of evolutionary science.[162] Darwinism seemed beleaguered with problems and scientists were tired of its speculative nature. Vernon L. Kellogg's 1907 *Darwinism Today* reflects this feeling of discontent. Kellogg wrote: "The fair truth is that the Darwinian selection theories considered with regard to their claimed capacity to be an independently sufficient mechanical explanation of descent, stand to-day seriously discredited in the biological world."[163] The same young scientists educated in the 1880's and 1890's turned toward a new, experimental science that looked to physiology for its tools. Against this backdrop, two events further marked it a time of remarkable changes and discoveries in the life sciences.

In 1899, German-American University of Chicago professor, Jacques Loeb (1859-1924), made the startling announcement that he had caused a sea urchin egg to undergo development without the action of sperm. Artificial parthenogenesis, as Loeb called it, captured the public imagination and seemed to usher in an age where anything – even the

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[162]In this discussion I largely follow Garland Allen's argument about the "revolt against morphology," where he argues that scientists trained in the 1880s and 1890's turned toward the new experimental science.
Garland E. Allen, *Life Science in the Twentieth Century*, *History of Science* (New York: Wiley, 1975), 1-19.
[163]Kellogg, *Darwinism To-day*.

creation of life – appeared possible. But Loeb's discovery also caused stirs in the professional community of biologists; it represented a victory for a new science that espoused experimental control over living things.[164] In his 1912 *The Mechanistic Conception of Life*, Loeb described his parthenogenesis experiments and his earlier work on animal tropisms (plant responses to external stimuli), which were influenced by the Würzburg botanist, Julius Sachs. Sachs was mainly interested in determining how plants would react to different types and strengths of stimuli to gain an understanding of how their motions might be controlled. Ultimately, Sachs hoped to establish the principles of physiology that would be applicable to all living things.[165] Loeb adopted Sachs's approach and found that certain lower animals (hydroids and worms) moved in the direction of light (positive phototaxis) in much the same way as plants do. Among the other tropisms Loeb examined were "geotropisms (where gravity is responsible for the direction of motion), chemotropisms, [and] galvanotropisms...."[166] Thus, Loeb, like Sachs, blurred the distinction between animals and plants in an attempt to reduce their behaviors to predictable, physio-chemical responses. In this vein, he argued that light alters photo-sensitive chemicals in the eyes of animals.[167] If one eye faces the light source more than the other, more directly of the light-sensitive chemical is altered in that eye. As a result of this difference between the two eyes' chemical reactivity, the animal "automatically" rights itself such that both eyes face the light equally and the animal can approach the light head-on. Historian of science Philip Pauly has argued that by

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[164]Pauly, Philip J. *Controlling Life: Jacques Loeb and the Engineering Ideal in Biology, Monographs on the History and Philosophy of Biology* (New York: Oxford University Press, 1987

[165]Ibid., 36.

[166]Gerd Gigerenzer, ed. *The Empire of Chance: How Probability Changed Science and Everyday Life, Ideas in Context; 12*, (New York: Cambridge University Press, 1989), 127.

explaining nature in such reductionist terms, Loeb avoided the messy concepts of consciousness or will.[168] In the *Mechanistic Conception of Life*, Loeb wrote:

> ...we may already safely state that the apparent will or instinct of these animals resolves itself into a modification of the action of the muscles through the influence of light; and for the metaphysical term "will" we may in these instances safely substitute the chemical term "photochemical action of light."[169]

But in addition to ridding animals of concepts that imply their agency, Loeb's method also eliminated the need to explain animal features in terms of selective mechanisms. By offering immediate, physico-chemical explanations of animal behaviors, such explanations were no longer necessary. The authors of *The Empire of Chance: How Probability Changed Science and Everyday Life* comment on this feature of Loeb's experimental program:

> Loeb acknowledged that these tropistic movements were often "adaptive." For instance, a newly emerged caterpillar moves up the closest plant stalk toward the light, and thus to the top of the plant, where it can then feed upon young tender leaves. But for Loeb, the adaptiveness of such motions was entirely coincidental to their occurrence; their adaptiveness did not in the least increase the probability of their occurrence....[170]

The sorts of explanations Loeb was after were immediately testable, unlike the evolutionary accounts which made claims about remote selective forces that could not be verified experimentally. Loeb's experimental approach was aimed at gaining control over the organisms he was studying. Pauly has characterized this as the "engineering

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[167]Pauly, *Controlling Life*.
[168]Ibid., 40.
[169]Jacques Loeb, *The Mechanistic Conception of Life; Biological Essays* (Chicago, The University of Chicago Press, 1912), 30.
[170]Gigerenzer, *Empire of Chance*, 128.

standpoint" and has suggested that through its realization, "nature was fading away."[171] The aggressively experimental approach that aimed at controlling natural phenomena stripped nature of its idiosyncrasies; plants and animals were viewed as law-governed, physico-chemical response systems. Certainly, this approach to animals was a far cry from Darwin's accounts of birds that chose their mates for their beautiful plumes and song.

In 1900 another important event changed the face of science. Three scientists working on problems of heredity independently re-discovered the genetic work of Austrian monk, Gregor Mendel.[172] Originally published in 1866, in the *Proceedings of the Brünn Natural History Society*, the paper went largely unnoticed for nearly forty years.[173] But the re-discovery of Mendelism promised to solve the problems of inheritance. By simple mathematical ratios, the inheritance of traits could be predicted. Thus, Loeb had reduced organisms to predictable sets of physico-chemically induced responses, while the legacy of Mendel abstracted them to ratios and probabilities.

In this chapter, I will discuss Vernon Kellogg's (1867-1937) assessment of the theory's status in 1907 and his discussion of George Mayer and Caroline Soule's experiments on caterpillars. Mayer and Soule's work seems to have been directly

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[171]Philip J. Pauly's full quote reads as follows:

> The core of the Loebian standpoint was the belief that biology could be formulated, not as a natural science, but as an engineering science. More broadly, it meant that nature was fading away. As biologists' power over organisms increased, their experience with them as "natural" objects declined. And as the extent of possible manipulation and construction expanded, the original organization and normal processes of organisms no longer seemed scientifically privileged; nature was merely one state among an indefinite number of possibilities, and a state that could be scientifically boring.

Pauly, *Controlling Life*, 199.
[172]Allen, *Life Science,* 48.

influenced by the methods of Loeb. Their experiments resemble Loeb's on animal tropisms closely and Loeb is cited as a reference to their work. I will also show how Kellogg and Mayer and Soule were unwilling to entertain the possibility of mate choice, in spite of experimental results that seemed to suggest its action. This, I argue, was due to the fact that the Loebian organism was incapable of exercising the sorts of choices Darwin's theory required. With its focus on stimuli and predictive responses, aesthetics had no place in the engineering ideal.

The second part of this chapter examines the work of Thomas Hunt Morgan (1866-1945). Morgan was a professor at Bryn Mawr at the same time that Loeb held a teaching position there. One of Morgan's biographers, Garland E. Allen, has characterized Loeb's influence as "direct and unmistakable"[174] and Morgan's experimentalism is largely accredited to his contact with Loeb. But Morgan's career underwent another dramatic shift in 1910 when, through the fortuitous discovery of a mutant fruitfly with white eyes, Morgan became a convinced Mendelian. Based on further work on the fruitfly, Morgan and his students at Columbia formed one of the most successful and productive genetics laboratories in the world.[175]

Morgan's 1903 *Evolution and Adaptation* and his 1919 *The Genetic and the Operative Evidence Relating to Secondary Sexual Characters* were written before and after his conversion to Mendelian genetics, respectively. While Morgan rejected sexual selection and mate choice in both pieces, his approach and concerns shifted markedly in

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[173]Ibid., 47.
[174]Garland E. Allen, *Thomas Hunt Morgan: the Man and his Science* (Princeton: Princeton University Press, 1978, 325.

their interim. *Evolution and Adaptation* was largely a theoretical critique of Darwin's method and style of argument, whereas the 1919 piece was an attempt to investigate the secondary characteristics of feathering in roosters through surgical interventions and breeding experiments on cocks and hens. In *the Genetic and Operative Evidence*, Morgan concluded that cock-feathering in roosters - which had previously been ascribed to sexual selection - was, in fact, due to recessive traits and hormone action. By offering genetic and physiological explanations that could be shown to be directly causal through breeding and surgical experiments, the appeal to distance evolutionary accounts that did not lend themselves to experimental verification was rendered superfluous. Morgan believed to have disproved Darwin's theory of sexual selection without ever having addressed female choice in any depth. But it is clear that female choice no longer presented a viable option in Morgan's Mendelian research. Because Mendelian analysis focuses on the physical manifestations of largely invisible and certainly abstract "factors," behavior no longer was a consideration. Furthermore, the very nature of Mendelian crosses precludes animals from choosing their own mates. Thus, with the growing impatience toward Darwinian method and mechanisms and a new emphasis on highly controlled experimental manipulation of organisms, the scientific climate of the early twentieth century was less than hospitable to the notion of animal aesthetics and choice in driving evolution.

[175]For a discussion that focuses on the fly as an organism that shaped and enabled the fly groups work at Columbia and later, Caltech, see Robert Kohler, *Lords of the Fly, Drosophila Genetics and the Experimental Life* (Chicago: University of Chicago Press, 1994).

Vernon L. Kellogg

Vernon Kellogg's 1907 *Darwinism Today* was an attempt to give a rational rejoinder to some of the vociferous criticisms Darwin's theory of evolution by natural selection faced at the turn-of the century.[176] Kellogg was not just concerned with the polemical criticisms of German biologists, but also those voiced in other European countries, Russia and the United States.[177] He sought to give a measured account of the nature of the criticisms and some of the answers offered by proponents of Darwinism. Kellogg recognized that many of his contemporaries failed to distinguish between the theory of evolution and the proposed mechanisms by which it occurred. The two were often lumped together under the catch-all of Darwinism. But Kellogg wanted to dissociate the theory of evolution, which he considered to be accepted by almost all "naturalists of position and recognised attainment," from the more controversial causo-mechanical explanations of descent (such as natural and sexual selection). Thus, by explicitly diverting the discussion away from the theory of evolution itself, Kellogg sought to stave off the "relentless hands" that wanted to "clutch away …[the] foundations" that he and others had so painstakingly erected.[178] As it turns out, sexual selection did not fare well in these attempts.

In *Darwinism Today*, Kellogg likened the status of sexual selection to pangenesis, Darwin's ill-fated theory of inheritance. This, of course, was no minor brush-off. The

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[176] For an account of the importance of Kellogg's work, see Mark A. Largent. *"These Are Times of Scientific Ideals:" Vernon Lyman Kellogg and Scientific Activism, 1890-1930* (Dissertation: University of Minnesota, 2000).
[177]Kellogg, *Darwinism To-day*, 4.
[178]Ibid.

theory of pangenesis was largely discredited and Kellogg himself believed it wanting in empirical evidence. In a chapter entitled "Darwinism Attacked (Continued): The Theory of Sexual Selection," Kellogg discussed sexual selection at some length. He was unequivocal about the theory's lack of success and considered it "a fact that all the evidence (though it be little as yet) based on actual experiment is strongly opposed to the validity of the assumption that the females make a choice among males based on the presence in the males of ornament or attractive colours, pattern, or special structures."[179]

Kellogg's assessment of sexual selection was largely a recapitulation of the criticisms voiced by others. He agreed that the battle among males and the resulting weapons were sufficiently proven and that "a special sexual selection theory is hardly necessary to explain the development of the fighting equipment, antlers, spurs, claws, etc."[180] Like other commentators on sexual selection, he treated the theory in two parts - battle among males and female choice. Not surprisingly, Kellogg deemed the former established and in need of little discussion, while dedicating considerable space to female choice.

Kellogg's discussion of female choice was also fairly representative of his fellow scientists' opinions and attitudes (and does not differ markedly from the previous discussion). Kellogg doubted that females would bring the necessary aesthetic sense to mate choices. Even if they did, he doubted that they would be able to make out the subtle differences for which Darwin had argued. Further, Kellogg believed Darwin had not provided enough evidence of females actually making deliberate mate choices based on

[179]Ibid., 120.
[180]Ibid., 114.

aesthetics and Kellogg reported that "since Darwin not more than half a dozen other cases, all doubtful, have been recorded."[181]

But Kellogg's discussion also reflected new concerns with female choice. It was not just a question of aesthetic sophistication. Kellogg (and some of the researchers he discussed) started to doubt that the female temperament was conducive to making the sorts of choices for which Darwin had given them credit:

> Observation shows that in most species the female is wholly passive in the matter of pairing, accepting the first male that offers. Note the cock and hens in the barnyard.[182]

Although Kellogg did not provide any further discussion of the female's passivity here, the terminology was also present in Mayer and Soule's work, as we shall see.

Kellogg's work also demonstrated a general impatience with the science of Darwin's time. He criticized previous observations of traits that were purportedly sexually selected for being based on preserved museum specimens. He offered examples where real life observations clashed embarrassingly with the older form of natural history:

> ... the brilliant colours and the curious horns of the males of the dung beetles are, in life, always so obscured by dirt and filth that there can be no question of display to the female eyes about them. The dancing swarms of many kinds of insects are found to be composed of males alone with no females near enough to see...[183]

Kellogg went on to recount other examples where new findings overthrew poor observations or exposed previous ignorance.

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[181] Ibid., 115.
[182] Ibid., 114.
[183] Ibid., 115.

In addition to these theoretical and methodological objections, Kellogg turned his attention to experimental evidence which he considered "the most serious obstacle in the way of the sexual selection theory...."[184] Kellogg is unambiguous about the theory's lack of success. He considers it "a fact [that] all the evidence (though it be little as yet) based on actual experiment is strongly opposed to the validity of the assumption that the females make a choice among males based on the presence in the males of ornament or attractive colours, patterns, or special structures."[185]

Kellogg went on to report the experiments of Alfred G. Mayer, published in the entomological journal *Psyche* in 1900 and those of Mayer and Caroline Soule in a 1906 *Journal of Experimental Zoology*. In these experiments, Mayer and Soule altered the wings of sexually dimorphic butterflies to see whether the females displayed a preference for wing types. According to Kellogg, Mayer and Soule found no difference in mating preference for males that had wings of various colors. He also dutifully, albeit discretely, reported "that males with wings cut off were more apt to meet with resistance from the females than perfect males were." Following this admission, he immediately went on to state that based on these experiments, "Mayer and Soule conclude that the mating instinct in the males of C. promethea and P. dispar is a phenomenon of chemotaxis. Sexual selection on the ground of colour alone does not affect it, and there is no associative memory connected with it."[186] Certainly this conclusion contradicted the preceding statement that short-winged males are less desirable than their long-winged counterparts. This raises the question of why Kellogg so blatantly disregarded the experimental

[184] Ibid., 120.
[185] Ibid.

evidence in favor of sexual selection. The answer may be found in Mayer and Soule's original paper where the paradox is similarly reflected.

In the first part of Mayer and Soule's "Some Reactions to Caterpillars and Moths," the authors performed a series of experiments that closely resemble those performed by the experimental biologist Jacques Loeb to investigate the D. plexipuus caterpillar's propensity to feed solely upon milkweed plants. Not only does this little creature exhibit a seeming preference for the milkweed, but the authors reported that "individual larva commonly spends its entire life upon a single plant."[187] Generally, the caterpillar contents itself with crawling about near the top of the plant where it feeds on the young, tender leaves. Based on a series of experiments, the authors drew the following conclusions about the caterpillar:

> It appears that positive phototaxis and negative geotaxis are all that are required to maintain the larva of D. plexippus upon the young leaves of its food plant, and to practically prevent its wandering away from the plant itself. The larva certainly displays no "judgment" in finding its most nutritious food, and probably its reactions are almost if not quite unconscious, for they are displayed with almost machine-like regularity at every recurrence of the stimulus, however as Jennings ('04) has shown, animals are not machines for their method of behavior is often that of trial and error and internal as well as external factors modify behavior.

The final statement is interesting as a qualification to what it means to be a machine or an animal.

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[186] Ibid., 123.
[187] Ibid., 417.

Later in the paper, Mayer and Soule turned their attention to the adult of the C. promethea – a species of butterflies in which the males have black wings, while the females' wings are light brown. Here the authors addressed the question of sexual selection with reference to Darwin's claim that sexual selection can account for the conspicuous coloration of male Lepidoptera. In particular, the authors wished to address "whether the females exercised any selection in the choice of their mates." They referred to previous experiments by Mayer which showed that "the female exercised no choice." Here the authors do not seem to have changed any particulars of the experimental set-up, other than an increase in the number of butterflies tested.

Mayer and Soule compared the mating success of three-hundred moths whose wings were painted with scarlet and green ink to three-hundred unaltered male butterflies.[188] The authors neglected to record the number of females in the experiment which would certainly have been appropriate, considering Darwin's concern for sex ratios. Again, Mayer and Soule found no difference between the mating success of the artificially colored males and their unaltered counterparts. From this they concluded that "the peculiar black coloration of the male appears not to have been caused by sexual selection on the part of the female, or at any rate the female promethea moths of the present day show no dislike for abnormal coloration in the male."[189]

In the subsequent series of experiments, the authors tested the mating preferences of the Porthetria dispar (P. dispar), a species in which the male's wings are brown and the

[188] It is interesting that the authors chose to paint the males' wings red and green. Surely this does not constitute the slight variations Darwin had in mind. A more subtle investigation might have tested female preference when confronted with various shades of gray, brown and black since these resemble the sexual dimorphism of the species.

female's white. In one experiment, the authors cut the wings of male and female moths and mating results were recorded in a table. Of "one hundred attempts to mate" the authors found that "the success achieved by the wingless males in their attempts to mate was much less than that of the perfect males."[190] In the following experiments, the authors painted the eyes of the female in order to test whether the selection really occurred by sight. The authors found that "when the female is blinded the wingless males succeed fully as well as do those which are normal. Selection on the part of the female is therefore conditional upon the possession of sight."[191] The results of both experiments were presented in a table. Finally, the authors reported an experiment performed on P. dispar in which wings were again colored scarlet or bright green. As with the C. promethea, no difference was observed in the mating success of the colored versus the normally colored animals.

While the authors found no color preference in the female P. dispar, the higher breeding success of the male with unaltered wings certainly could have been considered significant experimental evidence in favor of visual wing selection by the female. Yet the authors seem to have been curiously unwilling to accord these findings much importance. In the end, they dismissed sexual selection on the part of the female in favor of correlation: "In a word the actual basis of elimination is correlation, not sexual selection exercised by the female in respect to color."[192] While it is true that the color test alone did not yield evidence in favor of such selection, the authors appear to have been unfazed by

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[189] Alfred G Mayer and Caroline G. Soule, "Some reaction of caterpillars and moths," in *Journal of Experimental Zoology* 3 (1906): 415-433., 428.
[190] Ibid., 128.
[191] Ibid., 429.
[192] Ibid., 430.

the evidence of choice based on wing size. Instead, they chose to emphasize the role of chemotaxis in mating. Males whose antennae were covered with flower paste did not mate as long as the scent organs remained covered but did again upon removal of the paste. Thus, Mayer and Soule concluded that "the mating instinct can only be called forth through the sense of smell, and not through associative memory."[193] An appeal to associative memory would have implied that animals have a conscious cognitive part in their mating. This form of memory would require the animal to associate a sensation with a previous memory or abstract idea. Mayer and Soule rejected this possibility in favor of reducing the animals' actions to physico-chemical responses, much like Loeb would have.

From these experiments and the conclusions Mayer and Soule derive from them, it seems that the authors associated "mating instinct" only with male insects. A closer examination of the language used by Mayer and Soule proves interesting. Throughout the article, Mayer and Soule did not discuss sexual selection in terms of an active preference by the female. Rather, the experiment is considered only in terms of female resistance to male advances. The results of the experiments in which C. promethea's wings were colored red and green are given solely in terms of resistance:

> Seventy per cent were successful and thirty per cent gave rise to no visible resistance on the part of the female although no mating occurred. In one instance only was a normal male resisted successfully by the female, while in another case the male succeeded in mating although the female made some show of resistance. Two of the green colored males were successfully resisted by two females, although even a slight showing of resistance on the part of

[193] Ibid.

> the female was too rare and exceptional to be of any moment in selection.[194]

In two tables that show the results of these experiments, the authors similarly give the categories only in terms of resistance. But Mayer and Soule offered no description of what exactly was meant by "female resistance." One of the parameters in the table also records the number of "Female[s] Attacked by Male without Resistance on Her Part but without Mating."[195] Surely, this category would have benefited from some clarification.

By looking at individual scientists and their work, I have hoped to show how their views of animal minds shaped their views of and approaches to the study of sexual selection. Romanes believed that the hen was a rather elusive creature and he declined to speculate about the exact nature of her thoughts. But he did not preclude her from making the sorts of deliberate, subtle and aesthetic choices that Darwin had proposed for her. And Romanes had little doubt about the cock's intentions; his antics were obviously aimed at impressing the hen. Romanes' methodology allowed him to infer such knowledge about animals by analogy to his own mind (i.e. human minds, in general). C. Lloyd Morgan, on the other hand, had more stringent methodological constraints and a higher standard of what it means to make a choice. He rejected the analogical reasoning between human and animal minds (upon which Romanes had relied). For Morgan, animals were fundamentally different from humans and the cognitive and linguistic

[194] Ibid., 428.
[195] Ibid., 429.

structures were not transferable. Because of this, Morgan's animals were not capable of exercising aesthetically-informed choices.

Mayer and Soule expressly wished to test sex selection when they performed the moth experiments. They are the only ones discussed here who have the sort of experimental evidence Kellogg seemed to have been looking for. Yet, neither Kellogg, nor the two authors seem willing to accord this much importance. Darwin believed insects could perform sexual selection (although Wallace, as I mentioned, had his doubts already by the time he reviewed the *Descent*). But for Mayer and Soule and Kellogg it was not so much a matter of butterflies, in particular, not being intelligent enough to perform sexual selections, as it was that animals, in general, were no longer viewed as independent thinking beings. Their organisms had ceased to be the sorts of animals that could make deliberate, aesthetic or even idiosyncratic choices the way Darwin's sexual selection demanded. The rejection of sexual selection, therefore, was not just due to a lack of experimental evidence, as Kellogg and others have suggested. Rather, I believe that it was due to the scientific construction of animals as deterministic response systems. The early twentieth century scientists no longer delighted in pointing to the elevated status of animals alongside humans that the study of evolution in the previous century had emphasized. On the contrary, successful experimentation in the vein of Sachs and Loeb, sought to control animals and to reduce the phenomena they exhibit to a level with plants and even non-living matter. Therefore, the laboratory culture of the early twentieth century – in contrast to Darwin's method and scientific climate – no longer was conducive to granting animals the ability to exercise agency in their mate choices the way Darwin's theory of sexual selection required. Selectionist explanations were rejected in

favor of physiological explanations that allowed for immediate verification and manipulation.

T.H. Morgan

While perhaps not the primary object of the work, Gar Allen's biography of T.H. Morgan documents his long-standing interest in issues related to sex. Morgan first came to investigate what determined the sex of an embryo – heredity or environment – through his early work in experimental embryology.[196] In 1903, he published a work discussing the various theories of hereditary sex determination. This interest, according to Allen, introduced Morgan to both the chromosomal and the Mendelian theories (which would eventually be the object of his Nobel-winning work).[197] Morgan's final conversion to Mendelism in 1910 was also linked to sex and came in 1910 via the discovery of a "sex-limited" mutation that led to white eyes in male fruit flies. In light of this, it is perhaps no surprise that Morgan expressed his opinions on sexual selection explicitly and at some length.

What makes Morgan's statements on sexual selection especially interesting is that he offers us a glimpse of both sides of the Mendelian divide. Morgan wrote *Evolution and Adaptation* in 1903, seven years prior to his conversion to Mendelism. *The Genetic and the Operative Evidence relating to Secondary Sexual Characters*, on the other hand, was based on experiments begun in 1911, shortly after he came to accept Mendelian genetics. Both pieces bear the stamp of Morgan's intellectual development. While

[196] Allen, *Thomas Hunt Morgan*, 126.
[197] Ibid., 125.

Morgan remained unconvinced of sexual selection (and to some extent, natural selection), his arguments and focus changed significantly in the time that elapsed between the two pieces. The earlier work focused largely on the structure of Darwin's arguments, whereas in the latter piece, Morgan applied his Mendelian-informed experimentalism to the study of secondary sexual characters.

Morgan's 1903 *Evolution and Adaptation* reflected the general malaise that Darwinism faced at the turn of the century. The work's "Preface" foreshadowed that Darwin's science would not fare well under Morgan's scrutiny:

> The advance of science in the last hundred years has shown that the kind of speculation that has real worth is that which leads the way to further research and possible discovery. Speculation that leads to this end must be recognized as legitimate. It becomes useless when it deals with problems that cannot be put to the actual test of observation or experiment. It is in this spirit that I have approached the topics discussed in the following pages.[198]

Like many of his contemporaries, Morgan believed that followers of Darwin placed too much weight on natural selection and conflated the utility of a variation with its cause. Morgan believed that selection could and would eliminate unfit species. Similarly, a species with a useful variation might be spared this fate. But to say that the variation originated because of its utility was dangerously teleological.

In *Evolution and Adaptation*, Morgan declined to speculate on the causes of variations, but supported William Bateson's and Hugo DeVries's theories of discontinuous variations, rather than the continuous distribution urged by Darwin. Discontinuous variations had several advantages over Darwin's theory. Because the

[198] Thomas H. Morgan, *Evolution and Adaptation*, viii.

variations were large and discrete, offspring would inherit them fully or not at all. DeVries had argued that a sub-species could form within a single generation if enough individuals exhibited the variation. This successfully accommodated the problem of swamping that was raised by Darwin's Scottish critic, Fleeming Jenkin. Jenkin had argued that if offspring inherit characters that are intermediate between their parents' traits, any new variation would become progressively more diluted and be lost altogether over the course of a few generations. Mutationism successfully side-stepped this problem. Morgan also believed that mutationism held to more realistic limits about the amount of change a species could undergo. Artificial selection had, according to Morgan, demonstrated that selection for specific traits could not aspire and attain limitless goals. A rabbit's ears might be bred to be very long but would not yield endlessly to the breeder's whims.

In his 1903 *Evolution and Adaptation*, Morgan characterized sexual selection as an "extension of the selection principle into a new field."[199] Both domesticated species and wild species were explained by artificial and natural selection, respectively. Morgan argued that "there remained only to account for the secondary sexual differences between the sexes by the principle of sexual selection."[200] This narrow parsing of domains to the three forms of selection was somewhat misleading. Morgan was certainly correct in ascribing secondary sexual characters to Darwin's sexual selection. But Morgan's singular emphasis on this aspect obscures that Darwin had a much broader range of phenomena in mind when he spoke of sexual selection. For Darwin, the theory also

[199] Ibid., 167.
[200] Ibid.

accounted for characters that could not be classified as secondary sexual characters, such as racial differences in humans and other traits passed on to both sexes. But more importantly, Morgan's definition makes no mention of beauty and aesthetics in nature. While Morgan includes it in his later discussion, the omission here is telling. Morgan clearly believed that sexual selection was more important as a test of the selection principle, in general. This is not surprising. Morgan remained deeply suspicious of selection for the rest of his life.[201] Much of his reticence in accepting natural selection he transferred to sexual selection. Similarly, he viewed objections to sexual selection as part of the arsenal against selection. Indeed, because Darwin's theory depended on the selection of minute variations in individuals but often led to non- or maladaptive traits, Morgan saw sexual selection as an important illustration of why selection could not drive adaptations to the point of speciation.

Like others, Morgan divided sexual selection into the law of battle and the "*selective power* of the female."[202] And again, like most other commentators on sexual selection, Morgan emphasized the latter – female choice: "It is this part that adds a distinctly new element to Darwin's other two theories of selection [natural and artificial], and it is this part that we naturally think of as the theory of sexual selection *par excellence*."[203]

But most of Morgan's objections were methodological. He criticized Darwin for not substantiating his claims or for holding to them in the face of contrary evidence. He also believed that Darwin had applied explanations inconsistently. Like Mivart, he

[201] Allen, *Thomas Hunt Morgan*.
[202] Morgan, *Evolution and Adaptation*, 168.

quoted Darwin's own doubts and urged that what Darwin considered to be exceptions were more plausible than the proposed rule.

Morgan was especially chaffed by Darwin's explanations of heredity, which he deemed inconsistent and loose. Generally, Darwin argued that sexually selected traits would be inherited in one sex only at the outset. Yet, on occasion, Darwin had the irksome propensity to claim that traits that were sexually selected in one sex would be passed on to members of both sexes. Sometimes Darwin would even concede that certain traits that were limited to one sex only, were probably not due to sexual selection. Even more egregious to Morgan, however, were Darwin's lapses into Lamarckian explanations in cases where others were less forthcoming:

> ...once more we find that Darwin makes use, as a sort of last resort, of the principle of the inheritance of acquired characters. As long as the theory of selection, in any of its forms, appears to offer a satisfactory solution, we find the facts used in support of this theory, but as soon as a difficulty arises the Lamarckian theory is brought to the front. It is this shifting as we have already more than once pointed out, that shows how little real basis there is for the theory of sexual selection.[204]

As the quote indicates, Morgan did not believe Darwin's inconsistent reasoning to be limited to inheritance. He found it to be pervasive and did not seem to tire of pointing it out. In the case of the size difference between male and female animals, Morgan disgustedly counted "no less than four distinct conjectures."[205]

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[203] Ibid.
[204] Ibid., 205.
[205] Ibid., 180.

Morgan also repeated Darwin's discussion of bird species in which one sex varies across geographic location while the other remains constant. Darwin proposed that the sexes were unequally affected by their geographic locations. To Morgan, the admission that there was something inherently different in the way the two sexes responded to the same environment seemed a grave admission in the face of sexual selection:

> ...if it is admitted that, on account of the difference in the constitution of the two sexes, the influence of the surrounding conditions would produce a different effect on them, it would seem that there is no need whatsoever for the theory of sexual selection. What Darwin is probably attempting to show is that the material for the further action of sexual selection is already given; but the question may well be asked, if the external conditions have done so much, why may they not have gone farther and produced the entire result?[206]

Morgan believed that such inconsistencies were very damaging to Darwin's case. He would return to the search for inherent difference between the sexes in his experiments on secondary sexual characters in his later work.[207]

Morgan also rejected Darwin's interpretation of male display. In doing so, he rejected one of Darwin's most compelling arguments – purpose. Darwin considered male display one of the most powerful pieces of evidence in favor of sexual selection. Males behaved in a certain way during the mating season. Often the behavior only took place before the female and seemed aimed at displaying structures that were unique to the male sex. Darwin took it for granted that the behavior was purposive. Instinct like other

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[206] Ibid., 173-74.

[207] This is the line of investigation he later pursues in the *Genetic and Operative Evidence.* Thomas H. Morgan, *The Genetic and the Operative Evidence Relating to Secondary Sexual Characters, Carnegie Institution of Washington Publication, no. 185* (Washington: Carnegie Institution of Washington, 1919).

characteristics would be passed to subsequent generations only if they were beneficial. For Darwin, the task was to figure out what its purpose was. Display to attract the female certainly seemed like a reasonable explanation. Morgan could accept that the male's behavior might excite the female. Yet he did not consider it a legitimate inference that it arose for that reason.

However, even when it came to the higher animals, Morgan was skeptical of female choice and believed it had not been sufficiently proven. While he granted that females might be excited as a result of the males' display, he did not believe that there was any evidence that females actually chose and rejected mates based on the quality of the ornaments or display. And Morgan rightfully questioned the origins of an animals' aesthetic sense. None of the forms of selection for which Darwin had argued could comfortably accommodate the female's sophisticated aesthetic sensibilities:

> The development, or the presence, of the aesthetic feeling in the selecting sex is not accounted for on the theory. There is just as much need to explain why the females are gifted with an appreciation of the beautiful, as that the beautiful colors develop in the males. Shall we assume that still another process of selection is going on, as a result of which those females are selected by the males that appreciate their unusual beauty, or that those females whose taste has soared a little higher than that of the average (a variation of this sort having appeared) select males to correspond, and thus the two continue heaping up the ornaments on one side and the appreciation of these ornaments on the other? No doubt an interesting fiction could be built up along these lines, but would any one believe it, and, if he did, could he prove it?[208]

[208] Morgan, *Evolution and Adaptation*, 216.

Thus, Morgan rejected sexual selection on much the same grounds as natural selection. Although he mentioned aesthetic sensibilities and conscious choice, they certainly were not his main emphasis. Morgan was clearly uncomfortable with the suggestion of female choice, but it is not entirely clear why this was the case. Most of Morgan's discussion was so deeply steeped in methodological objections that there is little explicit indicaton of how he viewed animals and their abilities. However, there is some evidence that Morgan disapproved of Darwin's strongly emotion-oriented assessments of animals. On one such occasion, Morgan criticized Darwin's characterization of ant encounters. Darwin had interpreted events where ants touch their fellow ants with their feelers when they meet as a sign that the two felt affection for each other. Morgan protested this interpretation. Instead, he argued that this act of "fondling" serves to identify fellow ants by their smell.[209]

But for Morgan sexual selection was both a strike against selectionist explanations and an example of the unreasonable degree to which utilitarian explanations would be taken by Darwin and his followers. Morgan's attacks on sexual selection formed only part of his attempts to weaken the extent to which Darwinists insisted on selection as an explanatory device. Sexual selection offered an example of how small adaptations, if they were indeed accumulating, had resulted in preposterous adaptations. The fact that Darwinians insisted on turning the useless into something useful was a powerful example of how blinded the Darwinian insistence on utility could be.

[209] Ibid., 184.

Morgan concluded his 1903 discussion of sexual selection by declaring that "the theory is incompetent to account for the facts that it claims to explain."[210] He went on to propose a more promising approach to the study of secondary sexual characters:

> It is certain in this case that we are dealing with a phenomenon that must be studied quite apart from any selective value that the secondary sexual organs may have. If this is granted, it will be seen that there is here a wide field for experimental investigation that is practically untouched.[211]

It was precisely such an investigation that Morgan undertook in 1911, shortly after his acceptance of Mendelism. The results were published in 1919 as *The Genetic and the Operative Evidence relating to secondary Sexual Characters*.[212] It is a short treatise on secondary sexual characters based on a series of breeding experiments with surgically altered roosters and hens (Sebright and Black-Breasted Game Bantams) with a chapter dedicated to sexual selection. Littered with typographical errors, the work seems to have been hastily written (and certainly poorly edited). But its findings are the culmination of nearly a decade of intermittent work, involving several people who helped Morgan with aspects of the dissections as well as analysis and hundreds of birds. The discussion of sexual selection offers an interesting contrast to his 1903 statements on the subject. Most notably, it seems that Mendelism gave Morgan a means of attacking the problem of secondary sexual characters with an experimental program. *The Genetic and the Operative Evidence* is not a simple genetic analysis. The "operative" in the title refers to the surgical removal of the sex organs. Anatomical and histological examinations,

[210] Ibid., 457.
[211] Ibid.

dissections, comparisons of overall feathering and individual feathers and an awareness of hormone function all informed Morgan's study. But, more importantly, Morgan, like Loeb, was proposing an experimentally verifiable, physiological explanation of sexual dimorphisms instead of a speculative evolutionary account.

Morgan's initial motivation for undertaking the experiments was to investigate the genetics of hen feathering. Hen-feathering describes the cock, whose plumage resembles that of the hen. A male with plumage that differs from the female's is referred to as cock-feathered. In some species, both types of males are present, while in others only one of the two varieties exists. Morgan chose to investigate the Sebrights because the males are always hen-feathered. He crossed these with Black-Breasted Game Bantams. The males of this race are exclusively cock feathered and the birds were thought to closely resemble their ancestral forbears. Morgan found that the male offspring of these crosses (F1) all exhibited hen-feathering. From this Morgan concluded that hen-feathering is a dominant trait. Upon examining the crosses that resulted when F1 birds were crossed, Morgan determined that the coloring must be due to more than one pair of factors.[213] Yet when Morgan surgically castrated the F1 and F2 hen-feathered males, their plumage was replaced with cock feathers, suggesting to Morgan that these birds had the capacity to cock feather all along.[214] Morgan also reported the discovery of abnormally shaped

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[212] Morgan, *The Genetic and the Operative Evidence.*

[213] Morgan wrote: "If one dominant suffices to produce hen-feathering, the F2 ratio would be 3 hen-feathered to 1 cock-feathered bird. The numbers would be 3 hen-feathered to 1 cock-feathered bird. The numbers found were 31 to 28. This realized ratio departs too far from a 3:1 ratio to make it probable that the results are due to a single factor. The F2 expectation for two dominants, both necessarily present to produce hen-feathering, is 9 hen-feathered to 7 cock-feathered birds.... The realized numbers, 31 to 28, are in close approximation to 9:7."
Ibid., 15.

[214] Ibid., 6.

testes, which he discovered during one the dissection of the birds. This "hint," as he called it, led him to take a closer look at the testes of the pure breeding Sebright. Histological examinations of the testicular tissue revealed that the hen-feathering Sebright's testes contain luteal cells "like those present only in the females of other breeds."[215] Here Morgan also recalled an example from Darwin's *Animals and Plants under Domestication,* where a Sebright hen took on cock-feathered in old age. Morgan remarked that the only other cases in which females became cock-feathered was when their ovaries were removed. Since it appeared that both the male and the female Sebright possess the capacity for cock-feathering when their reproductive organs were either removed or diseased (as in the case of Hewitt's old hen), Morgan concluded that the ovaries of the female and the luteal cells in the male's testes repress cock-feathering.

In the following chapter, Morgan again took up the discussion of sexual selection. Here it seems that Morgan had transcended the need to quibble over Darwin's style of argument. Armed with a modest but effective arsenal of experimental evidence and his new-found perspective on genotype and phenotype, Morgan conceded that to Darwin the problem of extravagant secondary characters must have seemed much greater:

> To-day we are not, I think, so oppressed with the difficulties of the situation, for we have become familiar with the fact that very slight genetic differences may cause very great differences in the end-product. In a word, the problem seems less formidable to us than it did to Darwin.[216]

[215] Ibid.
[216] Ibid., 43.

In general, Morgan was far less intent on exposing the theory's inconsistencies. Instead, he neatly divided sexual selection into three categories and spent the remainder of the chapter dismantling each in turn. Sexual selection, for Morgan, consisted of: "natural selection between the members of the same sex;" "choice on the part of the "other" sex;" and "the "inheritance of use."[217]

In his first category, Morgan addressed the pre-mating battles. While others before him had likened this process to natural selection, his terminology makes the connection very explicit. Darwin had offered several possibilities for how these battles might lead to increased breeding success for the victor but Morgan only accepted the model involving polygamy. Only if the victors were allowed to breed with more mates would the traits that had made them victorious be passed on with greater frequency than those of their less successful rivals:

> On the whole, I think that, for our present purpose, it will suffice to state it is consistent with the theory of natural selection to accept provisionally this part of Darwin's theory for those species in the higher groups in which polygamy holds, conceding, however, that even here it may have to be altered when fuller knowledge is gained.[218]

This insistence on a simple numeric version of the theory was not present in Morgan's earlier critique and is, I believe, consistent with (and possibly derived from) the heavy emphasis on numbers and ratios of Mendelian genetics.

But still more problematic was the issue of female choice. Morgan offered a brief survey of early twentieth-century research on mate choice, hormones and genetics. He

[217] Ibid.
[218] Ibid., 45.

deemed A. H. Sturtevant's fruit fly mating experiments a more trustworthy source of data than the more anecdotal accounts of sexual selection. According to Morgan, Sturtevant placed a female with a single mutation for gray wings with a wild type, a gray and a yellow male to see with which male the yellow-winged female would first mate. After each mating, "the male that first mated was noted and the trio discarded."[219] Morgan reported that "[t]he female "chose" the gray males 25 times and the yellow only 8 times."[220] In spite of the relatively strong numeric evidence, Morgan places the word chose in quotes.

Sturtevant also performed a control experiment in which a female was confronted with two males of the same wing color – either yellow or gray. In this case, Sturtevant found that the yellow-winged female mated with "the gray male 60 times and the yellow male 12 times."[221] Again, in spite of the numeric evidence, Morgan agreed that it "appears" as though the female chose the gray over the yellow male. But Morgan remarked somewhat cryptically that "the result would be the same in kind if the gray male were more active and mated quicker."[222] Thus, Morgan shifted the emphasis from the agency of the female to the male's behavior. When single males (of red and yellow wing color) were placed with a gray and a yellow female, Sturtevant found that both red and yellow males mated more frequently with the yellow females. Morgan draws the following conclusion:

> Both results are explicable on the view that the yellow female, being less active, is more easily captured by the

[219] Ibid., 51.
[220] Ibid.
[221] Ibid.
[222] Ibid., 52.

> yellow male than is the gray female. This view fits in also with the former experiment, where the yellow male is much less successful than the more active gray male. Such a conclusion gives a more consistent explanation of all the facts than does the theory of female choice, for on the latter we must suppose that the yellow females prefer the gray males and the yellow male prefers the yellow females, etc.[223]

Here Morgan seems to have forgotten to mention the set of experiments involving the red males. But his message is clear: Any interpretation is preferable to female choice.

In another set of experiments, Sturtevant tested white and red eye color. The red and then the white-eyed male mated more frequently with the white-eyed females and red and white females with the red males. Yet, here too Morgan offers an interpretation in terms of male activity and female passivity:

> The red male wins by virtue of his greater activity, while the white female is chosen more often, especially by the white male, because of her passivity (or weaker resistance). It may be claimed that these results do not show that the female does not choose, for such choice, if made, would be swamped by another condition of the experiment, viz, the greater aggressiveness of one kind of male and greater passivity of the other kind of female. This, of course, is true, but the experiment still shows that in these flies other influences are so much greater than "choice" by the female, if it exists, that the postulated effect of the latter practically disappears from the situation.[224]

This interpretation in terms of female "passivity" is reminiscent of Mayer and Soule's work, which Morgan discussed subsequently.

[223] Ibid.
[224] Ibid.

In response to Mayers and Soule's work, Morgan's reactions are predictable. Morgan remarked that Mayer's work is significant and recounted his findings that link the mating behavior of the male to the scent of the female. He also reported Mayer's experiment in which he cut and exchanged the typically male for the female wings on both male and female flies. Morgan noted that Mayer found no difference in mating behavior. These findings were reported free of any noticeable censorship by Morgan. Yet when he reported on Mayer and Soule's 1901 experiments that certainly could have lent themselves to interpretations favoring female choice, Morgan expressed concerns for the experiment's validity: "....the number of observations on which this statement is [sic] were far too few to be of any value, and there are several other observations that make any such conclusion from the evidence highly uncertain."[225]

In additon to his inclusion of contemporary experimental evidence, Morgan also displayed a new-found methodological and epistemological awareness in his discussion of sexual selection. Morgan was especially concerned with the distorting effects of applying the concepts and language of human psychology to the study of animals:

> Here we must employ perforce or for brevity's sake the terms used in human psychology, and run the risk at every turn of imputing to other animals the emotions to ours, there still remains always the danger, in the absence of real evidence, of imputing to them the particular emotion that we call "feeling for beauty"; and the greater danger of imputing an aesthetic sense so highly developed that the choice falls in the long run on the suitor better ornamented than his rivals.[226]

[225] Ibid., 53.
[226] Ibid., 45.

Morgan warned of "the very great danger of projecting "our human standards" into the world of animals...."[227]

Thus, Morgan's organisms were even further removed from Darwin's than Lloyd Morgan's or Mivart's had been. Indeed, Morgan's were Mendelian creatures. Fruitflies were creatures that could be manipulated at will. Chosen for the ease with which they could be bred and kept and for their short life cycles, Morgan was able to perform on an organism that without any tinges to conscience could be mated and then "discarded."[228] It is also in this piece that Morgan explicitly and derogatively characterizes Darwin's science as anthropomorphizing, which he identifies it as a threat to the scientific method:

> I doubt if anyone to-day would care to defend seriously the theory on the grounds of consciousness or aesthetic value of the exhibition, despite the fact that Darwin's language often takes this turn and the less-guarded statements of some of his disciples, such as Romanes, show little hesitation in anthropo-morphologizing the entire situation.[229]

Clearly, much more was at stake at this point than merely whether or not sexual (or any other form of) selection occurred. To Morgan, sexual selection and mate choice exemplified the sort of science he sought to distance himself from. Darwin's work was not just philosophically problematic and impractical. Its method was a threat to the "new science that was proving so productive and useful to Morgan:

> ...I can not but think that at present we have a good deal to lose in the way of scientific procedure and nothing to gain of scientific value in accepting Darwin's interpretation of sexual selection based on the display of the male as furnishing an opportunity to the female to make the "best"

[227] Ibid., 51.
[228] Ibid., 52.
[229] Ibid., 50.

> selection amongst her suitors on the basis of his adornment.[230]

Thus, Morgan's distaste for Darwin's methodology found its expression in his criticisms of sexual selection.

This analysis of Morgan's work has to some extent surrendered to the temptation of viewing Morgan's career in two discrete phases – before and after his acceptance of Mendelism. Yet, while this perspective might over-simplify aspects of Morgan's work, I also believe that it is useful in examining his treatment of sexual selection. Especially because his stance on sexual selection (and to some extent natural selection) remained unchanged, in spite of his dramatic conceptual shift, this approach reveals how Morgan's attitude and methodology changed with respect to sexual selection.

In 1903 sexual selection was mostly a theoretical problem for Morgan. While he called for experimentation on secondary sexual characters, he believed that it would have to be undertaken without reference to Darwin's theory of sexual selection. Morgan spent most of his discussion analyzing Darwin's method of argument and the merit of his logic and observations. Thus, his treatment of sexual selection did not differ much from his treatment of natural selection, as neither of these mechanisms lent themselves readily to experimental intervention. But with his adoption of Mendelism, Morgan did not just gain insight into hereditary transmission, he also discovered a new set of tools that proved extremely useful. In his *Operative and Genetic Evidence*, Morgan's methodology reflects this change and he attacks the problem of sexual dimorphism in much the same way that he would have treated any other problem of heredity – through breeding

[230] Ibid., 51.

experiments. But even in this piece, Morgan does not directly address the issue of sexual selection. That is, he never tests whether or not a hen rejects or favors a certain cock. Instead, Morgan shows that characters that were previously explained by sexual selection are actually due to hereditary transmission and hormonal repression.

While Morgan was not explicit on how he viewed animals, his genetic approach is telling. Morgan's best-known experiments were performed on fruit flies, which were chosen for their modest needs and rapid breeding cycles.[231] Morgan's fruit fly was, in essence, a disposable organism. Fruit flies were bred at will and subsequently discarded. In light of this, animal courtship must have seemed a rather remote proposition. Not surprisingly (and perhaps understandably), Morgan was reluctant to interpret Sturtevant's or Mayer and Soule's experiments in terms of choice. Yet even in his own experiments with cocks and hens, which exhibit greater mental complexity, experiments revolved around pre-determined crosses. Indeed, Mendelian breeding experiments, by definition, preclude free mate choices. It is reasonable to conclude, then, that Morgan's admonitions about anthropomorphizing in the study of sexual selection were geared more at the overall methodology rather than at sexual selection, in particular. Morgan also showed a new-found and somewhat puzzling concern with Darwin's approach to animal minds and choice in his 1919 work. On several occasions, Morgan warns of the dangers of ascribing human emotions to animals and criticizes Darwin of anthropomorphizing. Indeed, Morgan's remonstrance seems strangely emphatic. Clearly, for Morgan, more than sexual selection was at stake. By the time he wrote the *Operative and Genetic Evidence*, Morgan's own experimental approach was thriving and Darwin's examination of sexual

accounts of male wooing and female choice must have seemed especially archaic to Morgan's increasingly abstract and strongly experimental approach.

[231] Allen, *Thomas Hunt Morgan.*

CONCLUSION

In The *Descent of Man, and Selection in Relation to Sex,* Charles Darwin argued that humans and animals descended from common origins. In the book's closing lines he wrote:

> I have given the evidence to the best of my ability; and we must acknowledge, as it seems to me, that man with all his noble qualities, with sympathy which feels for the most debased, with benevolence which extends not only to other man but to the humblest living creature, with his god-like intellect which has penetrated into the movements and constitution of the solar system – with all these exalted powers – Man still bears in his bodily frame the indelible stamp of his lowly origin.[232]

But Darwin had not contented himself with merely pointing out the physical evidence that bespeaks "his lowly origin." Indeed, Darwin's claims were much more far-reaching and certainly more controversial. He had urged that those traits which humans had long cherished as uniquely their own, were not bestowed upon them by God, but had evolved in much the same way as their bodily structures. And just as man's stature betrayed his descent from animals, so Darwin pointed to noble and human-like features in animals that proved their kinship to humans. Animals showed the rudiments of ethics, aesthetics, and even the ability to worship. The development of these traits could be explained without recourse to God. It was this mental and emotional continuity between animals and humans that allowed Darwin to infer that animals are capable of exercising aesthetically informed mate choices to drive evolution by sexual selection.

[232] Darwin, *Descent of Man*, ii, 405.

Alfred Russel Wallace's objections to sexual selection and mate choice focused largely on the theory's (in)compatibility with natural selection and he insisted that the adaptiveness of the female bird's inconspicuous coloration be explained by natural selection. Already in his 1871 review of the *Descent,* Wallace had lamented that Darwin was unwilling to accord natural selection a role in the protective coloration of the female or in the modification of the mechanisms of inheritance. But the problem of the conspicuous coloration of the male sex remained and was not easily reconciled with an adaptive explanation. However, by 1889 when Wallace wrote *Darwinism*, he had come up with an explanation that seemed to satisfy his neo-Darwinian insistence on the omnipotence of natural selection in evolution. By linking conspicuous coloration and courtship behavior with vigor, Wallace had eliminated the need for female choice. In the unlikely event that females do choose their partners based on color or behavior, they would choose in keeping with natural selection. But should a female choose a less fit male, her propensity to choosy poorly would soon be eliminated as the unlucky couple would leave few offspring to inherit their mother's unfortunate tastes; thus, natural selection would effectively override it. In this way, Wallace elegantly combined Darwin's observations about display and coloration without compromising his desire to remain faithful to the version of natural selection that Darwin had presented in the *Origin*, where "any variation in the least degree injurious would be rigidly destroyed."[233]

But Wallace's rejection of sexual selection also had to do with his larger outlook on the world. After his conversion to spiritualism in the mid 1860's, Wallace no longer accepted Darwin's premise that humans evolved from animals entirely by naturalistic

[233] Darwin, *Origin of Species*, 81.

means. While he kept his views on the matter mostly under raps from all but the most discerning (or more likely, knowing) eyes in his review of the *Descent*, his position on matters of faith did not allow him to accept Darwin's continuity between humans and animals. Wallace believed that the intellect and moral sense of humans could not have evolved without divine intervention. Because he believed that the higher faculties were unique to humans, it comes as no surprise that he had trouble swallowing sexual selection, as it was presented by Darwin in the *Descent*. And indeed, Wallace would come to reject the theory altogether.

The subsequent generation of biologists (including George J. Romanes, Conwy Lloyd Morgan and St. George Mivart) similarly wrestled with the arguments Darwin had presented in the *Descent*. Their reception of sexual selection was tied not only to their larger attitudes towards Darwinian mechanisms of selection but also to their views of animals. Romanes agreed with Darwin pretty much on all matters, including sexual selection. Most importantly, he accepted that animals and humans differed only in degree rather than in kind. Romanes readily accepted the highly anthropomorphic evidence the Peckhams presented in favor of the sexual selection of spiders and presented similar anecdotal accounts in his *Animal Intelligence*. These animals were described in such human terms by Romanes and the Peckhams, that it would seem incongruous had they not also granted them the power of choice in the selection of their mates. While Romanes sought to avoid "anecdote mongering" in his descriptions of animals, he was explicit that the study of animals could profitably draw from human psychology. Romanes suggested that animals be studied sympathetically thereby granting humans the sort of access to animals' minds that Darwin had enjoyed. But Romanes's friend and disciple, C. Lloyd

Morgan was critical of this approach. Morgan argued that knowledge about animals' inner lives that relies on that of humans, is necessarily distorted and invalid. He believed that the projection of human emotions onto animals, while tempting, ought to be strictly guarded against, because of the essential differences between them. While he accepted sexual selection, in general, he did not believe that it was a product of conscious female choice. St. George Mivart similarly rejected both the continuity between animals and humans and mate choice in animals on the grounds that he deemed them incapable of making the human-like choices that Darwin's theory required. Unlike Romanes, Mivart (like Wallace) objected to Darwin's argument for continuity between animals and humans on religious grounds. But regardless of their motivations, late nineteenth-century opponents of sexual selection and especially mate choice converged on two key issue. Animals differ fundamentally from humans. Therefore, they cannot pass aesthetic judgments about their mates. For a sense of aesthetics, they agreed, is a human perogative.

But by the early twentieth century, the science of Darwin had come to look outdated and his assessment of animals unproductive and sentimental. In the third chapter, I have examined the final rift between Darwinian sexual selection and the scientific establishment. Darwinian mechanisms of evolution and his insistence on selection of continuous variations, came increasingly under attack around the turn of the century. While Darwin had stressed the importance of experiments in some of his own work and his examination of artificial selection, many of his accounts of animal behavior

relied on a distinctly anecdotal, natural history method.[234] In contrast, early twentieth century experimental science emphasized multiple trials and quantifiable parameters. Adaptiveness and utility no longer constituted satisfactory explanations for behaviors and structures as physiological and genetic explanations rendered the speculative nineteenth-century accounts of remote ancestry and evolutionary history superfluous. Vernon Kellogg's 1907 *Darwinism Today* reflects this impatience with the Darwinian approach. But in Kellogg's discussion of Mayer and Soule's experiments, even experimental evidence in favor of sexual selection went ignored. This is again the case in T. H. Morgan's analysis of Sturtevant's experiments on fruitflies' mating preferences (or lack thereof, as Morgan stressed). Influenced by Loeb's rigorously experimental approach to animals and the legacy of Mendel, organisms were viewed increasingly as predictable response systems. B.F. Skinner, inventor of the famous Skinner box, was a student of the Loeb disciple William J. Crozier. Skinner would come to apply the Loebian legacy of control and response measurements to human psychology with great renown.[235] The Loebian laboratory setting was designed to eliminate the idiosyncrasies of nature, while Mendelian analysis depended on pre-determined crosses between animals. Again, I wish to stress that animal breeding, with which Darwin had thoroughly acquainted himself, had long relied on pre-determined mating and the prevention of unfit unions. But for Darwin, the information he gained from breeders was only one part of an expansive research project that relied on many different methods and sources of information. In contrast, Morgan's Mendelian method was proving highly productive and rendering less

[234] Crist, *Images of Animals*.
[235] Pauly, *Controlling Life*, 194-98.

patient of alternative methods. This is evidenced by Morgan's criticisms of the Darwinian method in his 1919 *Operative and Genetic Evidence*. Morgan found Darwin's method of applying human psychology to animals distasteful and his own observations paid little attention to behavior, as animals were valuable only insofar as their physical structures bore traits. In Morgan's and Loeb's work, animals no longer resembled humans. Rather, the lowly fruitflies and light-bound caterpillars behaved remarkably like plants. Thus, while virtually all commentators on sexual selection recognized that a certain degree of cognitive and emotional complexity was required of animals to engage in purposive mating behavior and perform mate choice based on aesthetics, the favored organisms of the early twentieth century were either so low that Darwin himself would have doubted their ability to mate selectively and/or forced into an experimental set-up that precluded independent mate choices, regardless of their mental sophistication. The experimental culture of the early twentieth century no longer allowed for its animals to woo and select their mates. Moreover as the continuity between animals and humans was severed, the insight into animals' minds that Darwin, Romanes and the Peckhams had enjoyed was no longer desirable nor was it possible. This, then, brought on the end of sexual selection, not Wallace's powerful arguments.

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