

## Sexual Selection and Male Sacrifice: From Darwin until Now

In order to elicit copulation from females, males will often offer mating gifts as an enticement. Mating gifts, such as a juicy fly, are ultimately given to lengthen the time for sperm transfer, increasing the chance for paternity (Thornhill 1976). Andrade has shown that in Australian Redback spiders (*Latrodectus hasselti*), the male gives the ultimate mating gift - his own body. There has been some resistance to the idea that being consumed during copulation could be an adaptive strategy for the male. This is not simply the case of a more dominant female overcoming the weaker male during copulation. A “somersault” behavior that has been observed in the field, in which the abdomen of the male is placed directly under the female’s mouthparts, has shown the male’s complicity in the cannibalism (Andrade 1996). This apparently suicidal behavior actually gives an adaptive advantage to the male and is favored by sexual selection for the paternal advantages gained (Andrade 1996). This review will show how the idea of sexual selection has been shaped throughout the past century and half since Darwin. It will follow Darwin’s idea through time, and show how it has allowed Andrade to come to the conclusion that male copulatory suicide is in fact an adaptive strategy, and further, will show how Andrade has come to influence the evolutionary community today.

Sexual Selection was originally proposed by Darwin in The Origin of Species by Means of Natural Selection in 1859. He stated that “[Sexual selection] depends, not on a struggle for existence, but on a struggle between the males for possession of the females: the result is not death to the unsuccessful competitor, but few or no offspring.” Sexual selection is an immediate competition for females in the ultimate battle to perpetuate one’s genes. In 1871 Darwin expanded on this idea. He reasoned that in the struggle for

mates, any characteristic that grants success will have a sexually-selective value. This sexually-selected trait will be perpetuated regardless of the natural-selective value of this same trait. Sexual selection could occur during female choice between rival males using male display-characters (otherwise known as inter-sexual selection) or could occur during combat between rival males (or intra-sexual selection) (Darwin 1871).

Darwin had indirectly shown the two different selective forces acting during reproduction: natural selection and sexual selection. Sexual selection, unlike natural selection, has the ability to select for characteristics that are no longer advantageous for survival, but that have a high sexually-selective value. Fisher, in 1930, expanded upon Darwin's ideas and predicted that when there is a display-based intra-sexual advantage among males, the reinforcement by female selection for this trait will initiate a "run-away" evolutionary process which will sometimes lead to characters deleterious in the general struggle for existence (Fisher 1930). According to Fisher's run-away model, then, deleterious genes are able to evolve when females preferentially select for specific display-based characteristics via sexual selection.

Huxley, in 1938, pointed out that the more intense the intra-sexual competition, the more likely it will be that characteristics that are deleterious to existence will evolve. This is because the "intensity of selective advantage is more sharply graded by intra-sexual competition than by any other type of selection" (Huxley 1938). This can be attributed to what he calls the fractional reproductive advantage, where the fitness of a trait is limited by the reproductive capacity of a single female or to the all-or-nothing mating advantage where some individuals fail to secure mates at all. The all-or-nothing model has two components. The successful males may only obtain one mate, as in

monogamous species, or they may be able to obtain more than one mate, exemplified by polygamous and promiscuous species. Only in the latter can characteristics that are deleterious to existence evolve (Huxley 1938).

Although it may seem that natural selection would be able to eliminate such deleterious characteristics, they do in fact occur in nature (exemplified by the Australian Redback spider). In these cases, the genetic benefit gained by this characteristic (an increase in one's fertility) outweighs the phenotypic cost incurred (the loss of one's life). According to Bateman (1948), because a male's fertility depends on the number of matings he gets, there would be selection for polygamous tendencies in males, producing an "indiscriminate eagerness" in mating. Females, on the other hand, would show a "discriminating passivity" (Bateman 1948). This can be seen in sexual selection. In a polygamous species there will be competition for these discriminate females. This can lead to characteristics that are sexually advantageous, but deleterious to existence, as previously hypothesized by Huxley.

As a result of considerable competition for females, male parental investment will decrease while mating effort increases. Trivers, in 1972, hypothesized that because parental investment will lower the number of copulations a male can obtain, intra-sexual selection will offset the selection for increased parental investment, therefore decreasing male parental investment (Trivers 1972). Females, on the other hand, make a greater initial investment in their offspring and will have a greater selective pressure for parental investment. Discord between selection for low paternal parental investment and female preference for increased male parental investment has resulted in nuptial feeding

(Thornhill 1976). The male can then occupy a female with the consumption of his mating gift, granting him an increased chance of a successful mating.

An extreme example of nuptial feeding would be the mating gift of one's own body, as in sexual cannibalism. Although at the time there were not much empirical data, Buskirk in 1984 predicted that sexual cannibalism would only be observed in species where males normally expect few matings and in which cannibalism would increase the number of offspring produced from a mating. This is exemplified by the male "copulatory suicides" of the Australian Redback spiders (*Latrodectus hasselti*). It was found by Andrade in 1996 that cannibalized males were able to copulate longer than those that were not eaten. When the female submits to copulation, the male performs a "somersault" behavior, in which the abdomen is placed directly under the female's mouthparts (Andrade 1996). The female then proceeds to consume the male while copulation continues. This act of copulatory suicide is simply an extension of a mating gift; females will permit longer copulations when they are occupied by eating the male, therefore giving the male a longer time for sperm transfer to occur. Further, females were less likely to mate with another male after consumption of their first. This apparently suicidal behavior gives an adaptive advantage to the male. Because males are unlikely to be able to mate more than once even if they do survive copulation, the cost of being eaten is low and sexual cannibalism has been favored by sexual selection for the paternal advantages gained (Andrade 1996).

Even though there is a direct benefit to the male, with a cost as great as one's life to mate, one would predict there to be selection for traits to allow them to escape cannibalism. Fromhage (2005) showed experimentally that opportunistic mating with

females who are already feeding greatly reduces the risk of cannibalism. As a further benefit, when it is mechanically possible to copulate with a female that has already mated, the chance of fertilization of that female's eggs is over 60 percent. This is an incredible success rate and one has to wonder why this strategy has not been selected for, and how there is such a high success rate given the shortened copulation duration.

Snow in 2004 tested the assumption made by Andrade that sperm transfer is limited by copulation duration. Snow surprisingly discovered that the majority of sperm was transferred in the first five minutes of copulation. Increased paternity due to copulation duration could therefore be due to the transfer of nongametic ejaculatory substances or cryptic female choice. According to Snow's research, cannibalism itself may even play a role in sperm transfer (Snow 2004).

From the first idea of sexual selection proposed by Darwin only 150 years ago, Andrade was able to come to the conclusion that an action that seemed to be male copulatory suicide was actually an adaptive strategy to perpetuate one's genes. This idea, as well as that of Darwin and his predecessors, has already had its hand in further research. Further studies will need to be done to determine why opportunistic mating does not occur more often in nature if it is coupled with such a high success rate and exactly why copulation duration coincides with increased paternity when sperm transfer is limited to the first five minutes. Through this paper one can see - much like many of the complex behaviors that we observe today - how dramatically a single idea can evolve throughout time.

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