

TOWARDS A DEFINITION OF SEXUAL SELECTION

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ABSTRACT: Darwin did not define sexual selection and others have interpreted it variously. Defining sexual selection in terms of differential acquisition of mates appears to be inconsistent with Darwin's use of the term. We suggest that sexual selection must be defined in terms of differential offspring production or siring. We propose two specific definitions and discuss the consistency of each with Darwin's writings and their ease of quantification.

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Sexual selection was unfortunately not explicitly defined at the time of its first usage (Darwin, 1859), and several different definitions have subsequently been given (Huxley, 1938; Ehrman, 1972; Wade and Arnold, 1980). Recently, Wade and Arnold (1980) have attempted to clarify the definition of sexual selection and to formulate a method for measuring its intensity. We applaud such efforts and believe they will be useful in linking natural history with quantitative genetics. We feel, however, that their definition of sexual selection has some shortcomings.

Wade and Arnold (1980) define sexual selection as the "variance in numbers of mates that bear a male's progeny." We suggest that 1) sexual selection is a process, not a variance per se, 2) an effective definition must include the possibility of sexual selection among females, and 3) this definition neglects some factors that can influence relative reproductive output of different males. These are 1) differences in numbers of offspring produced by different females, and 2) selective fertilization and/or zygote maturation following multiple insemination. Our first two suggestions can be incorporated into the definition with minor changes in wording, and these changes seem to be implied in Arnold and Wade (1983). The third requires more substantive changes for reasons given below.

If females do differ in fecundity or if selective fertilization does occur, male 'A' might sire a few offspring from many females, while male 'B' sires more total offspring but from fewer females. Given Wade and Arnold's (1980) definition, sexual selection would favor male A over B, but clearly male B would hold the reproductive advantage. Darwin (1871, p. 256) states that sexual selection depends "on the advantage which certain individuals have over other individuals of the same sex and species in exclusive relation to reproduction." It seems, then, that Darwin would have considered male B to have been favored by sexual selection. Thus, the number of offspring sired (males) or produced (females) seems to be a better measure of an individual's advantage or disadvantage in the process of sexual selection. This is supported by Darwin's (1871) contention that sexual selection could act in monogamous species, albeit with less intensity than in polygamous or promiscuous species. He suggested that males would compete with each other to breed with the earliest-breeding females, which would rear the most offspring. Whatever the truth of this notion, it illustrates that the measure of success in terms of sexual selection is not number of mates, but rather the number of offspring resulting from the matings.

In some species this distinction may not be very important because females may not differ greatly in production of offspring and each female may have only one mate. However, females of most animal species, but especially those with indeterminate growth, vary greatly in their production of offspring. The same is true of plants, which are also subject to sexual selection (Bateman 1948, Charnov 1979, Willson 1979).

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Multiple insemination or pollination occurs in animals (Hanken and Sherman 1980, Page and Metcalf 1982) and plants (Gutierrez and Sprague 1959), and selective fertilization following gamete exchange exists and may be common (Pfahler 1965, Martin et al. 1974, Bertin 1982).

How, then, should we define sexual selection? One possible definition (definition A) is "the differential production (females) or siring (males) of offspring by individuals of the same species and sex that are capable of reproducing." The appropriate measure of the intensity of sexual selection is the variance in number of offspring sired or produced by reproductively-capable individuals of the same species and sex. This definition applies to both males and females. The qualifiers "capable of reproducing" and "production of offspring" rather than "production of surviving offspring" eliminate selection based on differential survival (e.g. "affecting ability to survive in the struggle for existence" p. 257) and any factors that affect an individual's ability to reproduce at all (e.g. organs required "in order to propagate their kind" p. 256) which Darwin (1871) clearly excluded from sexual selection. According to this definition, sexual selection is a subset of natural selection, with factors related to survival constituting the remainder of natural selection. Our points remain valid, however, if sexual and natural selection are considered distinct phenomena.

Definition A has the advantage that the intensity of sexual selection is, theoretically at least, easy to measure. It has at least two potential disadvantages. First, adaptations related to survival and reproduction can never be entirely separated. Among reproductively-capable individuals, for example, traits promoting survival between reproductive episodes clearly can affect the production of offspring. Darwin (1871, p. 257) himself recognized that the distinction between traits attributed to natural selection and sexual selection was frequently unclear: ("in most cases it is scarcely possible to distinguish between the effects of natural and sexual selection"). A second objection is that this definition is broader than that envisioned by Darwin, who dealt especially with adaptations relating to the obtaining of mates. The intensity of sexual selection, since it involves number of offspring, would be influenced, for example, by the ability of different females in a population to assimilate food and convert it into gametes or zygotes.

This objection could be overcome by defining sexual selection (Definition B) as "the differential production (by females) or siring (by males) of offspring by individuals of the same sex and species as a result of mate selection." Mate selection would include the processes of male and female competition and male and female choice. We believe that this definition is more consistent with Darwin's writing than definition A and may be closer to most biologists' views of sexual selection than definition A. Definition B has the disadvantage that a quantitative measure of the intensity of sexual selection would be difficult to achieve. This is because of the problems in partitioning out the variance in offspring production among the myriad factors, including mate selection, that might influence fecundity, although papers by Wade (1979) and Arnold and Wade (1983) represent an important advance here.

Thus, our definitions are more appropriate than Wade and Arnold's (1980) definition for describing sexual selection, as the term was used by Darwin. They are not necessarily, however, more amenable to quantification. Definition A allows easier measurement of the intensity of sexual selection than definition B, but it may be less satisfying conceptually. In fact, no single definition may satisfy all purposes and then it becomes imperative that users of the term make their usage explicit.

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