

**Is there a Unifying Concept of Sexual Selection that Applies to Both Plants and Animals?**



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## IS THERE A UNIFYING CONCEPT OF SEXUAL SELECTION THAT APPLIES TO BOTH PLANTS AND ANIMALS?

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*Abstract.*—This article introduces a symposium on sexual selection in plants and animals and seeks a definition of sexual selection that applies to both kingdoms. Ten different criteria that could be used as a basis for defining sexual selection are reviewed. In particular, I argue that “mate choice” and “sexual competition” are problematic elements that should be avoided in a definition. In place of these elements, I argue for a mating success definition of sexual selection and propose that it constitutes a unifying concept that applies to both plants and animals.

This issue of *American Naturalist* is devoted to the proceedings of a vice-presidential symposium on sexual selection in plants and animals that was convened on June 19, 1993, in Snowbird, Utah, at the annual meeting of the American Society of Naturalists. The goal of the symposium was to make a bridge between the botanical and zoological literatures on sexual selection, and the symposium participants were charged with the task of discussing the concept of sexual selection as it might apply to both plants and animals. Botanists and zoologists have had an insouciant disregard for each others' literature on sexual selection. The participants agreed that a symposium was timely and might be beneficial to both camps.

I suggested the following question as a theme for the symposium: Is there a unifying concept of sexual selection that applies to both plants and animals? Despite the fact that over 100 yr have elapsed since Darwin (1859, 1871) proposed the concept of sexual selection, no agreement exists on how to apply a single version of the concept to both plants and animals. The application of the sexual selection concept to plants has been especially contentious. If indeed there is no useful concept of sexual selection for plants, our theme question has an important corollary. Does the absence of a useful concept of sexual selection in plants challenge accepted notions of sexual selection in animals? On the other hand, if there is a unifying concept of sexual selection, what is it?

A large volume of sexual selection studies has been published, especially in the last decade. Reviews of the empirical and theoretical literatures on animals are provided by West-Eberhard (1979), Bradbury and Andersson (1987), Kirkpatrick (1987), Pomiankowski (1988), Maynard Smith (1991), Wiley (1991), Ryan and Keddy-Hector (1992), and me (Arnold 1987). The concept of sexual selection as it applies to plants has been discussed recently by Charlesworth et al. (1987),

Queller (1987), Lyons et al. (1989), and Willson (1990). Despite much work in both kingdoms and many reviews, however, the common ground between plants and animals has been little discussed (Willson 1990, 1991).

In this issue, Mary Willson, Maureen Stanton, Allison Snow, David Queller, Martin Morgan, and I focus on connections between sexual selection concepts in plants and animals. Willson (1994) reviews the history of the sexual selection as it has been applied to animals and plants. She asks whether plants have the necessary conditions that make sexual selection possible and then reviews the evidence for sexual selection in plants. Stanton (1994) focuses on mechanisms of selection arising from male-male competition during pollination in plants. Snow (1994) reviews mechanisms of postpollination selection in plants and discusses their relationship to sexual selection. Queller (1994) also explores postpollination selection in plants but takes a different perspective by examining the parallels between parent-offspring conflict and conflicts between mating partners. Morgan (1994) presents a quantitative genetic model for evolutionary change in hermaphrodites. Using this model, he contrasts evolutionary responses to sexual selection in hermaphrodites and organisms with separate sexes. Finally, I (Arnold 1994) discuss the rationale and procedures for measuring sexual selection in animals and plants, using a mating success definition of sexual selection.

In the remainder of this article, I will consider why we need to bother with a definition of sexual selection, discuss criteria that can be used to arrive at a definition, and, finally, suggest a new definition. I have no illusions that mine will be the last word, nor should it be.

#### WHY A DEFINITION OF SEXUAL SELECTION MATTERS

Busy scientists often cannot be bothered with definitions, especially in two situations. When an attempt to find a consensus on a definition is premature, warring camps merely restate their positions. On the other hand, when everyone agrees on an unstated definition, the attempt to put it in writing can be tedious. Neither of these situations holds in the case of sexual selection. After 130 yr, the time seems right to seek a consensus, especially because divergent opinions are still expressed.

A definition of sexual selection matters because it affects the conduct of science. The necessity of a definition of sexual selection is particularly clear in the enterprise of measurement. If you cannot define it, you cannot measure it. Until 15 yr ago, no one attempted to quantify sexual selection, and the definition of sexual selection was not so pressing. Today, however, measurement is an active enterprise, and a definition is crucial (Wade and Arnold 1980; Arnold and Wade 1984a, 1984b; Koenig and Albano 1986; Koenig et al. 1991). (Grafen [1987] provides an antidote to obsession with measurement.) But if the notion of sexual selection is so troublesome, why not just abandon the name? Abandonment carries the cost of disengaging us from history. If we can attain a consensus on what sexual selection means, the prize is continuity with Darwin and 130 yr of usage. Even if we were to abandon the name, we would need to find another to put in its place. When sexual selection is opposed by another selective force, a name

is especially useful. Finally, the search for a definition that straddles the plant and animal kingdoms might challenge accepted wisdom in both fields and lead us in new directions.

#### THE SEARCH FOR A UNIFYING CONCEPT OF SEXUAL SELECTION

A surprising variety of opinions about the meaning of sexual selection have been put forth (Appendix). Furthermore, some of these opinions are in conflict or at least difficult to reconcile. To understand the conflicts, let us turn to the various criteria that have been used to define sexual selection.

#### *Criteria Underlying Concepts of Sexual Selection*

Concepts of sexual selection are based on a variety of criteria: concordance with Darwin, agents of selection, sexual dimorphism, sexual differences in selection, fitness currency, gender consistency, taxonomic consistency, consistency between empirical and theoretical usage, and, finally, simplicity. Each of these criteria could have some influence on the concept of sexual selection that eventually prevails. To find a concept that satisfies all criteria, however, is not an easy task. Some concepts do satisfy most if not all criteria, whereas others are in glaring conflict with particular criteria.

*Concordance with Darwin.*—Darwin's (1871) extensive discussion of sexual versus natural selection suggests that he did not draw the distinction lightly. Indeed, his concept of sexual selection was surprisingly subtle. Darwin (1871, pp. 256–258) attributed to natural selection, rather than sexual selection, the elaboration of the following kinds of traits: sexually dimorphic traits not involved with reproduction, primary sexual structures, structures used to feed and protect offspring, and male amplexic organs that are required for mating even in the absence of rivals. To simply say that sexual selection involves reproduction or that it concerns all aspects of sexuality is to ignore Darwin's sense of the concept. Many authors have done just that. Several articles are available for more discussion of misinterpretations of Darwinian sexual selection (see, e.g., Bateman 1948; Ghiselin 1974; O'Donald 1980; Wade and Arnold 1980; Arnold 1983).

While it is relatively easy to say what Darwin did not mean by sexual selection (because he was explicit on the point), it is more difficult to pinpoint the common denominator in the phenomena that he subsumed under sexual selection. Key phrases such as "the advantage which certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction" (Darwin 1871, p. 256) are open to a variety of interpretations. These phrases must also be reconciled with the list of excluded phenomena. My own bias is to view mating success as the fitness currency that defines Darwin's common denominator in an elegantly simple way (see below). But Darwin never used the term "fitness currency," and he did not speak of selection in modern statistical terms, so this view will not satisfy all students of history.

Even if we succeed in pinpointing the common denominator in Darwinian sexual selection, a concept based solely on Darwinian usage is not sufficient. Darwin had little to say about sexual selection in plants, for example. Other contemporary

discussions also range beyond Darwin's writings: ways to measure sexual selection, elimination of gender bias, and consistency between empirical and theoretical usage. Darwin alone cannot rescue us from debates about definitions.

*Agents of selection.*—Nearly every textbook or classroom introduction of sexual selection resorts to an “agents of selection” definition. Sexual selection is selection exerted by mate choice or intrasexual (e.g., male-male) contest. Darwin himself repeatedly referred to these two categories of sexual selection (Darwin 1859, 1871).

At various times the idea of selection via mate choice has been controversial in the zoological literature (Wallace 1889; Huxley 1938). It is currently a point of contention in the botanical literature (Willson and Burley 1983; Charlesworth et al. 1987; Queller 1987). To tie a definition of sexual selection to the concept of mate choice is to sow the seeds of dissension.

Mate choice and intrasexual contest are especially difficult to recognize in plants. Active mate choice and physical combat between sexual rivals simply do not occur in plants. Darwin (1871) argued that sexual selection was unimportant in the lower phyla of animals because they were incapable of mate choice. Darwin probably viewed plants in the same way (Arnold 1994). Willson and Burley (1983) argued that more subtle forms of mate choice are prevalent in plants, but some investigators are more impressed with the differences between mate choice in plants and animals and question whether “mate choice” in plants is really deserving of the name (Charlesworth et al. 1987). An agents of selection concept of sexual selection has at best provided an ambiguous basis for recognizing sexual selection in plants.

Fisher (1958) observed that investigators are more interested in the distinction between the two agents of sexual selection than in their communality. His observation is still true today. The common element in mate choice and intrasexual contest is, however, essential to give depth to a definition of sexual selection. To find that common element, we will need to consider other criteria.

*Sexual competition.*—Competition between sexual rivals is an outstanding candidate for the common element in Darwin's two agents of sexual selection (Fisher 1958; Harvey and Bradbury 1991; Stanton 1994). The problem with competition is purely an operational one. The history of competition studies in ecology suggests that manipulative experiments are required to obtain unambiguous evidence of competition (Connell 1983; Schoener 1983, 1985). Thus, the cost of giving competition central place in a definition of sexual selection is an edict that manipulative experiments be conducted. This cost might not be insufferable, but it can be avoided.

*Sexual dimorphism.*—Sexual selection could be defined by its evolutionary consequences. Sexual dimorphism is such a candidate-defining principle. Sexual differences can, however, be produced by natural selection (Darwin 1871; Selander 1972; Slatkin 1984; Shine 1989). Furthermore, the epigamic structures and displays of many birds are sexually monomorphic, yet they seem to have been elaborated by a process of mutual sexual selection (Darwin 1871; Huxley 1914; Kirkpatrick et al. 1990). On close inspection, sexual dimorphism is an untrustworthy indicator of sexual selection. There is the additional problem that if we make

the production of sexual dimorphism a requirement for recognizing sexual selection, then we rule out the possibility of sexual selection in the many hermaphroditic plants and animals that cannot display sexual dimorphism.

*Sexual difference in selection.*—Some authors (Queller 1987) have used a sexual difference in selection to diagnose sexual selection. A problem with this diagnostic is that it defines some categories of sexual selection out of existence. Should sexual selection act the same in males and females, we would not recognize it as sexual selection.

*Fitness currency.*—We could define sexual selection by the fitness units that we would employ to measure it. This backward-sounding definition is suggested by the formal structure of evolutionary theory. In population and quantitative genetics, selection is often described as a covariance between trait values and some component of fitness (Price 1970, 1972; Lande and Arnold 1983; Wade 1985). To recognize different categories of selection, when selection is described as a covariance, we can ask how the selection categories differ in fitness currency.

Some varieties of selection are defined by their fitness currency. Fecundity and viability selection are two prominent examples and deal, respectively, with selection mediated through fecundity and viability differences. We can say that all selection within a generation is either fecundity or viability selection because fecundity and viability are the primary components of fitness. By components, we mean that fitness is a function of fecundity and viability and nothing more. The relationship of fecundity and viability to fitness can be captured by simple equations (Lotka 1956; Charlesworth 1980; Lande 1982) and represented as a path diagram (Arnold 1994; Arnold and Duvall 1994). Thus, a potentially powerful way to define sexual selection is to identify its fitness currency as a component of fecundity. Indeed, two kinds of currency have been proposed as the defining aspect of sexual selection: mating success and fecundity.

Using mating success as a currency yields a concept of sexual selection that is consistent with most of Darwin's writings. The immediate fitness consequences of mate choice and intrasexual contest are a change in mating success. The view that sexual selection involves differences in mating success has been expressed in many post-Darwinian discussions (see, e.g., Bateman 1948), including one (Wade and Arnold 1980) that went one step further by arguing that mating success is the defining principle of sexual selection.

Mating success is commonly referred to and measured in the zoological literature but seldom in botanical studies. In an exemplary study of selection, Campbell (1989) used pollen removal and arrival as an index of mating success. In a more direct approach, Meagher (1986) was able to estimate the number of mates for males and females in a dioecious population of lilies by using allozyme markers. Later in this issue, I explore how such a direct index of mating success in plants could be used to measure important aspects of sexual selection (Arnold 1994).

In what units should mating success be measured? Number of matings, mates, or mates that bear or sire offspring? Should we take account of mate quality as well as number? This decision about units is equivalent to deciding where sexual selection leaves off and other forms of selection begin.

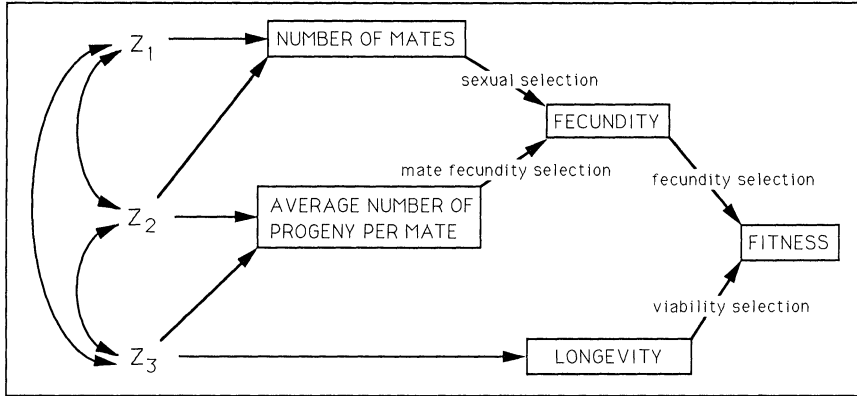


FIG. 1.—A hierarchy of fitness components that defines various types of selection. Three hypothetical phenotypic traits are denoted  $z_1$ ,  $z_2$ , and  $z_3$ . *Single-headed arrows* denote selection; *double-headed arrows* represent correlation between phenotypic traits.

The problem with number of matings (rather than number of mates) as a currency is that it fails to account for mate acquisition, the common feature of Darwin's two sexual selective agents. A male that mates with one female 10 times receives the same score as a male that mates once with each of 10 females. Furthermore, the mathematical function that relates number of matings to number of offspring is far more tortuous than the function that relates number of mates to number of offspring. In other words, units that involve mates rather than matings are both historically grounded and more efficient.

A natural way to decide on the units for mating success is to ask how mating success can be made a component of fecundity. One solution is as follows (putting units in parentheses): mating success (mates that bear or sire offspring) times average fecundity per mate (offspring per mate) equals total fecundity (offspring). Thus, with "mates that bear or sire offspring" the units for mating success, this measure becomes a primary component of fecundity (Arnold and Wade 1984a, 1984b). If, on the other hand, we choose simple mate number (i.e., count mates regardless of whether they bear or sire progeny) as units, then mating success is no longer a component of fecundity. In this case, mating success (simple mate count) puts a limit on total fecundity, but total fecundity is not a straightforward function of mating success. Components of fitness and the selection that they define are shown as a path diagram in figure 1 (see Arnold 1994 and Morgan 1994 for more discussion).

Although there are sound theoretical grounds for making mates that bear or sire progeny the currency for mating success (rather than a count of mates), the use of this currency means that some primary sexual features come under the rubric of sexual selection. The "production of progeny" clause puts us in conflict with Darwin's usage, but the conflict may not be severe. The conflict arises because traits such as ejaculate or pollinium size not only influence mate fecun-

dity but also can affect whether a mating event results in progeny and so influence mating success. Consequently, when we use mates that bear or sire progeny as the currency for mating success and sexual selection, pollinium size and pollen physiology (likewise, ejaculate size and sperm morphology) may have some slight effect on mating success as well as having a primary impact on mate fecundity. Some authors see no problem with such conflicts with Darwinian usage (see below). Furthermore, with modern molecular methods we are increasingly able to diagnose unambiguously maternity and paternity. With those methods we can detect matings that result in progeny, but we cannot detect matings that do not produce progeny. Partly for this reason, some have advocated using mates that bear or sire progeny as the fitness currency for sexual selection (Arnold and Duvall 1994).

Should the currency of sexual selection take into account the fecundity of mates as well as their number? In the Darwin-Fisher theory of sexual selection in monogamous birds, for example, early-breeding females are more fecund and so exert selection via mate choice (Darwin 1871; Fisher 1958; Price et al. 1988; Kirkpatrick et al. 1990). This form of selection has been viewed as sexual. Even though all successful males have a single mate, sexual selection among them can be said to occur because the model supposes differences in the rate of mating. (The use of mate number as a currency for sexual selection always implies some standardized time interval, so the currency is implicitly a rate; see below.) The Darwin-Fisher model also involves differences in mate fecundity, and these differences are correlated with mating rate. Thus, when early-breeding (fecund) females choose males on the basis of some plumage character, males experience both mate fecundity selection and sexual selection, even though there may be no differences in mate number. Eberhard (1985, 1991) has argued that genitalia, as well as courtship behavior that occurs after insemination, also should be viewed as sexually selected traits, primarily on the grounds that a form of mate choice plays a role. Such traits could determine whether the mate bears a male's progeny (and so qualify as sexually selected in a narrow sense), but their primary effect would be on the number of progeny produced by the mate. Thus, if we make mating success (mates that bear or sire progeny) the acid test for sexual selection, some of the selection on genitalia and postinsemination courtship is sexual selection, but most of it is mate fecundity selection. In many circumstances, it may be possible and useful to make a distinction between sexual and mate fecundity selection rather than suppose that sexual selection involves differences in mate quality.

Most authors appreciate that differences in mating success should not include differences in survival rate or life span. Confusion arises especially when lifetime mating success is discussed (Koenig and Albano 1986; Hubbell and Johnson 1987; Clutton-Brock 1988). If one simply counts the number of mates over a lifetime and calls that mating success, the count is likely to reflect differences in life span. To use mating success as a currency to evaluate sexual selection, one needs to correct for differences in life span or in the time intervals over which mating success is assessed (e.g., by using life spans or interval lengths as covariates in



ANOVA or regression analysis). If such corrections are not made, sexual selection can be confounded with viability selection, and other spurious results can arise (Koenig and Albano 1986).

Some authors have proposed that sexual selection should be measured in offspring units (Selander 1972; Bertin and Stephenson 1983). Bertin and Stephenson (1983, p. 293) objected to the mating success definition of sexual selection offered in an earlier article (Wade and Arnold 1980) on the grounds that it excluded selection arising from differences in mate fertility as well as "selective fertilization and/or zygote maturation following multiple insemination." I (Arnold 1994) show how sexual selection can be measured in either mating success or offspring units (depending on the component that is wanted) and stress that sexual selection is only a part of fecundity selection. Although Bertin and Stephenson (1983) do not distinguish between sexual and fecundity selection, they do make the valid points that sexual selection is a process, not a variance, and that an effective definition should not exclude the possibility of sexual selection in females.

Another objection to the use of mating success as the currency of sexual selection is that such a concept fails to account for all the consequences of mate choice. In species with parental care, mates might be chosen on the basis of parenting ability. The fitness units for evaluating such mate choice would seem to be offspring survival rate rather than mating success. The crucial points in this example are that parenting ability experiences two types of selection, and both types can be accounted for using either zygotic offspring or surviving offspring as a currency for total fitness. Parenting ability affects mating success; some would call the effect sexual selection. Parenting ability also affects offspring survival rate; Kirkpatrick and Lande (1989) call the effect "parental selection." Whether we use zygotic offspring or surviving offspring as the currency for total fitness, there are still two paths from parenting ability to total fitness. The fact that one path involves mate choice does not seem a good argument for also labeling the other path sexual selection, especially when the label is expressly excluded by Darwin's writings.

*Gender consistency.*—A definition of sexual selection should not be gender biased (Bertin and Stephenson 1983; Hrdy 1986). A definition should be applicable to both sexes and hermaphrodites. It is tempting to use the term "male-male contest" instead of the neutral but awkward "intrasexual contest." Today, after many generations of this substitution, our minds have become closed to the possibility of sexual competition between females. Sexual selection on females is viewed as rare, found only in jacanas, phalaropes, and a few other "role-reversed" taxa. Hrdy (1986) has argued persuasively that our concepts of sexual competition have been stereotyped and gender biased from Darwin's time until our own. At least the jacana enjoys a footnote, but routine sexual selection in females or in hermaphrodites is virtually never discussed in either the botanical or zoological literatures.

*Taxonomic consistency.*—An ideal definition of sexual selection should be applicable to both plants and animals. A definition should not rule out the possibility of sexual selection in plants. Animals with external fertilization and some kinds

of spermatophores also are vulnerable to exclusion if "insemination" or allusions to intromittent structures creep into our definition.

*Empirical-theoretical consistency.*—Empirical and theoretical studies of sexual selection should try to use the same definition. Most theoretical articles dealing with sexual selection characterize sexual selection by using a mating success fitness currency (see, e.g., Lande 1980, 1981). Empiricists, of course, are not obliged to toe the same line as theoreticians. Nevertheless, the greater variation in usage among empiricists is cause for concern, particularly if this variability presages a divergence in usage between the theoretical and empirical literatures.

*Simplicity.*—The simpler a definition, the better.

#### A DEFINITION OF SEXUAL SELECTION

In light of the foregoing discussion, I propose the following definition of sexual selection. *Sexual selection is selection that arises from differences in mating success (number of mates that bear or sire progeny over some standardized time interval).* This definition gains some simplicity by not attempting to define selection itself. It also avoids the difficulties of applying mate choice to plants and operationally defining competition. Nevertheless, this definition is consistent with most of Darwin's writings. Because this definition is cast in terms of a fitness currency, its connections to formal evolutionary theory are straightforward. This definition is not gender or taxon biased and so should be applicable to plants and animals, as well as to hermaphrodites.

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#### APPENDIX

##### OPINIONS ABOUT THE MEANING OF SEXUAL SELECTION

"[T]he advantage which certain individuals have over others of the same sex and species in exclusive relation to reproduction" (Darwin 1871, p. 256).

"The term 'sexual selection' must . . . be restricted to the direct results of male struggle and combat" (Wallace 1889, p. 296).

"[S]exual selection as used by Darwin should be replaced by two terms": epigamic selection "will include selection involving display-characters common to both sexes" and intrasexual selection "will apply to all selection involving competition between individuals of one sex in the struggle for reproduction" (Huxley 1938, p. 431).

“The intensity of intra-masculine selection is due to the greater dependence of the fertility of males on frequency of insemination” (Bateman 1948, p. 367).

“At present it seems best to simply define sexual selection as all mechanisms which cause deviations from panmixia” (Ehrman 1972, p. 106).

“We define ‘sexual selection’ on males as variance in numbers of mates that bear the male’s progeny” (Wade and Arnold 1980, p. 456).

“[T]he differential production (females) or siring (males) of offspring by individuals of the same species and sex that are capable of reproducing” (Bertin and Stephenson 1983, p. 294, definition A).

“[T]he differential production (by females) or siring (by males) of offspring by individuals of the same sex and species as a result of mate selection” (Bertin and Stephenson 1983, p. 294, definition B).

“(1) One or both of Darwin’s agents of sexual selection . . . must be occurring. (2) As a consequence of these agents, there must be a variance in fitness. . . . (3) Selection must act on a character conferring some advantage ‘over other individuals of the same sex and species, in exclusive relation to reproduction’ (Darwin 1871)” (Koenig and Albano 1986, pp. 403–404).

“[C]ompetition between individuals for mates caused by traits which yield unequal fitness gains through male and female function, where the selective value of a trait is not due to its effect on survivorship of the sporophyte itself. . . . To distinguish between sexual and natural selection on such traits, one must determine whether the trait affects the mating probability (sexual selection) or the viability or fecundity of the offspring (natural selection)” (Charlesworth et al. 1987, p. 318).

“[S]election that arises from differences in mating success (number of mates that bear or sire progeny over some standardized time interval)” (Arnold, this article, p. S9).

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