

## Review

# Sexual selection in plants: Pros and cons

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Contributed by Verne Grant, October 11, 1994

**ABSTRACT** Sexual selection has long been regarded as a special mode of selection in animals. Various authors have argued in a growing number of publications since 1979 that sexual selection is also operative in plants, and consequently, two divergent concepts of sexual selection are now being stated in the literature, the original Darwinian concept and the new plant-centered concept. An essential feature of the Darwinian concept is the distinction between primary and secondary sexual characters. Sexual selection is a process producing secondary sexual characters in males; such characters are well known in animals but are unknown in plants. Proponents of sexual selection in plants do not mention the subject of primary and secondary sexual characters, and they make no effort to establish the existence of secondary sexual characters in plants. The evidence they do present for sexual selection in plants consists of primary sexual characters and other reproductive traits that are products of selection modes other than sexual selection.

Sexual selection has traditionally been regarded as a process confined to dioecious animals (1, 2). The view that this process is also operative in dioecious or hermaphroditic plants has grown in strength in recent years. Influential early statements of the alternative view were put forward in 1979–1983 by Willson, Burley, Stephenson, and Bertin (3–6), and the theme was subsequently developed in 1987–1991 by Queller and Willson (7–9). Recently, a symposium was devoted to the question (refs. 10 and 11, p. S1), “Is there a unifying concept of sexual selection that applies to both plants and animals?” All the symposium participants (11–16) take an affirmative position on this question.

Meanwhile some other students have greeted the claim of sexual selection in plants with considerable skepticism (17–19). Their negative views are largely ignored in the recent symposium (10). A division of opinion now exists, and the time has come for a critical review of the arguments and evidence for and against sexual selection in plants.

Crucial to the discussion is the definition of sexual selection. Everyone can

probably agree with Arnold (11) that it is desirable to state a modern definition of sexual selection that is generally applicable yet consistent with Darwin’s original usage and subsequent historical usage.

Arnold (11) considered 10 possible defining criteria of sexual selection and concluded that mating success is the best. He proposed (ref. 11, p. S9) the following definition: “Sexual selection is selection that arises from differences in mating success (number of mates that bear or sire progeny over some standardized time interval).” A variant form of the same definition is offered by Stanton (13).

When adherents of the sexual-selection-in-plants viewpoint apply the criterion of mating success to plants, they succeed in finding traces of sexual selection in both dioecious and hermaphroditic plants. The problem is that the definition of Arnold (11) and Stanton (13) does not fully meet Arnold’s other criterion, namely, consistency with Darwinian usage. It departs from the original and historical concept of sexual selection in subtle but fundamental respects, as I will indicate later.

Willson (ref. 12, p. S16) states a much broader concept of sexual selection as the following quotation shows: “For purposes of this survey, Darwin’s original concept of sexual selection is expanded to encompass all events related to sexual competition and mate choice whenever they occur in the reproductive sequence, from pre-courtship to postnatal phases [9]. For example, sperm competition and gametophyte competition become part of sexual selection, as I use the term, because conceptually they are forms of intermale competition.” Willson’s statement is far removed from the long accepted concept of sexual selection. It establishes sexual selection in plants, to be sure, but does so by drastically redefining the term.

The recent literature on sexual selection in plants reveals the need for a discussion of the basic question, What is sexual selection? The term had one meaning for Darwin, which is followed by mainstream evolutionists, and has a different and much broader meaning for some modern authors.

### Darwinian Sexual Selection

Darwin’s detailed treatment of sexual selection was presented in Part II of *The*

*Descent of Man* (1, 2) after a previous brief introduction in *The Origin of Species* (20). At the very start of his main treatment (ref. 1, vol. 1, pp. 253–254), he drew a distinction between primary and secondary sexual characters in dioecious animals, which followed an earlier naturalist, John Hunter, in the use of these terms (21).

Primary sexual characters are traits directly concerned with sexual reproduction *per se*, e.g., structure of the gametes, morphology of the sex organs, “reproductive glands,” etc. In dioecious animals, the males generally produce a superabundance of sperms compared with the number of eggs, have strong sex drive (“eagerness of the male”), seek out and pursue the females, and effect fertilization or insemination; whereas the females tend to be specialized for nourishment and protection of the embryo or young. Darwin attributed the complementary specializations of the sexes in primary sexual characters to “natural selection” or “ordinary selection” as opposed to sexual selection (ref. 1, vol. 1, pp. 256–258).

Secondary sexual characters are accessory characters, found usually in males, that are not necessary for reproduction *per se* but that contribute to the success of males in securing mates. This class of characters includes superior size, strength, weapons, ornamentation, songs, scents, display behavior, etc., of male animals. Such characters are widespread and conspicuous in the animal kingdom, and Darwin (1, 2) devoted 12 chapters to a systematic description of them.

The theory of sexual selection was proposed to account for them. “These characters are the result of sexual and not of ordinary selection . . .” (ref. 1, vol. 1, p. 258). The divergence between the sexes mentioned earlier is such as to foster competition among males for females. In this competition, individual males with better weapons or plumage, etc., than their rivals will have an advantage in mating and will leave more progeny than the less favored males (refs. 1 and 2, ch. 8).

Sexual selection is thus a second stage process that comes into play where there is a divergence between males and females with respect to primary sexual characters and where the individuals of one sex, usually the males, compete for mates.

The distinction between primary and secondary sexual characters is essential for understanding sexual selection. To be sure, the distinction between the two types of characters is not clear cut in all cases. Some reproductive characters may fall in a gray area and require special study. However, there is little doubt about the classification of the numerous accessory characters of male animals that are used in rutting, courtship, and mating and are emphasized in Darwin's books (1, 2).

Darwin expected secondary sexual characters to develop in animals which are dioecious, motile, and have well developed sensory organs and "mental powers," and the valid examples of such characters were found as expected in arthropods and vertebrates. In contrast, secondary sexual characters are not expected and not found in lower animal groups, which are sedentary or hermaphroditic and have poorly developed nervous systems and sensory organs (ref. 1, ch. 9). Plants are "analogous" to lower animals in the characteristics just mentioned (ref. 1, vol. 1, p. 274).

Evolutionists in the post-Darwin era—Wallace, Poulton, Romanes, and Weismann (22–25)—clearly understood the connection between sexual selection and secondary sexual characters. So did Fisher, Haldane, and Huxley (26–28) in the period 1930–1942. Authors of evolution books in the postsynthesis period have maintained the original concept (29–34), as have authors of countless papers in the journal literature. Controversies abound in the older and the modern literature, but they are conducted within the framework of the original concept of sexual selection.

### Definitions

Although Darwin (1, 2) did not give a formal definition of sexual selection, he did characterize the process very clearly. Later students have provided definitions true to the original concept (e.g., ref. 35). A set of definitions consistent with the traditional usage is presented here.

(i) Sexual selection is a process in dioecious animals that involves competition between individuals of one sex, usually males, for the acquisition of mates of the same species, and differential success of genetically different individuals in this competition, resulting in the development of secondary sexual characters.

The two main forms of sexual selection differ enough to make it useful to have separate definitions. (ii) Intermale sexual selection is differential success among male animals in direct or interference competition for female mates, resulting in the development of secondary sexual characters of male dominance or combat ability. (iii) Sexual selection by female choice is differential success of males in

securing female mates of the same species, based on female discrimination during courtship and mating, resulting in secondary sexual characters of male attractiveness and display. The two forms, *ii* and *iii*, may be combined in actual cases.

A rare case involves animals with sex role reversal, such as the phalarope, and may warrant a provisional definition of its own. (iv) Interfemale sexual selection is sexual selection based on competition among females for males in animal species with sex role reversal, resulting in secondary sexual characters in the female sex.

Definition *i* is a definition in the strict Darwinian sense. It and definitions *ii–iv* refer to forms of sexual selection that are known or postulated in dioecious higher animals. I agree with Arnold (11) that it is desirable to have a general definition that does not rule out beforehand the possible existence of sexual selection in other groups, including plants. The following generalized definition is proposed. It is more restrictive than Arnold's (11) definition to conform to the long established concept of sexual selection.

(v) Sexual selection is a process involving competition among individuals of one sex class for securing mates of the same species, and differential success of genetically different individuals in this competition, resulting in the development of secondary sexual characters.

Logical necessity requires the recognition of a selection mode complementary to sexual selection. (vi) Selection for efficiency of sexual reproduction is selection promoting differentiation and efficient division of labor between the sexes and functional efficiency of primary sexual characters. Selection mode *vi* grades into two other known modes: fecundity selection and selection for paternal care.

The process described in *vi* was recognized by Darwin as a mode of "natural selection" distinct from sexual selection, as noted earlier. Some modern authors have also given explicit recognition to it, though as a special mode of natural selection *sensu lato*: for instance, as selection for intrinsic differences in the reproductive roles of males and females (48) or as selection for a division of labor between eggs and sperms and between their bearers (19, 30).

### The Situation in Plants: Theory

The definitions of Arnold (11) and Stanton (13) are on the right track, insofar as they put the focus on mating success, but are not quite restrictive enough. Mating success in sexual organisms generally can produce either primary or secondary sexual characters. Mating success on the female side has produced egg cells with stored nutrients; mating success on the male side has led to a high ratio of motile sperms to eggs; and these are primary

sexual characters, the results of selection for reproductive efficiency.

Arnold (11) considered 10 criteria for defining sexual selection, but secondary sexual characters were not one of the 10. He did list and correctly reject sex dimorphism, which includes various sorts of gender-related characters.

The papers in the recent symposium (10) do not reject the concept of primary vs. secondary sexual characters on the basis of any reasoned argument; they just don't mention it anywhere. The same omission occurs in the earlier studies advocating sexual selection in plants (3–9). Yet secondary sexual characters are the defining feature of sexual selection. Consequently, much of the evidence advanced for sexual selection in plants is irrelevant.

Willson's (12) concept of sexual selection in plants, quoted earlier, equates sexual selection with selection in the reproductive phase of the life cycle, and as such it embraces a host of recognized selection modes.

### The Empirical Situation in Plants

A high ratio of pollen to ovules is the norm in seed plants. High pollen output is cited as an example of sexual selection by some students (4, 6, 12) but not by others (17, 27, 30). All authors agree that good pollen producers will increase in frequency at the expense of poor pollen producers in a plant population, other factors being equal (6, 12, 17, 27, 30, 36). High pollen output is a product of male competition but this does not necessarily mean that it is a product of sexual selection. Haldane (ref. 27, p. 121) presented pollen output in a discussion of competition and not, as Willson (12) says, in a discussion of sexual selection. I deliberately separated this case from sexual selection in my treatment (ref. 30, pp. 238–243). Charlesworth *et al.* (17) regarded it as an unclear case. High pollen output in plants, like high sperm number in animals, is best viewed as a product of selection for an efficient division of labor between the sexes and, hence, as a primary sexual character.

Sex dimorphism and species differences in the flowers of *Catasetum* and other orchids are presented as probable products of sexual selection (9, 12). Mechanical and ethological isolation is commonly associated with flower character differences in orchids (37–40). Mechanical and ethological isolating mechanisms in flowering plants are known to originate in two ways: as byproducts of primary divergence and as products of selection for reproductive isolation *per se* (40). The characteristics attributed to sexual selection in orchids are better explained by other known modes of selection.

Advocates of sexual selection in plants tend to view the attractive characters of flowers as comparable to the display char-

acters of male animals. Let us examine this viewpoint by asking how or whether attractive features of flowers fit into the dichotomy of primary and secondary sexual characters. They do not fit easily in either category. Sessile flowering plants cannot carry out cross-fertilization by themselves, but must use animals or other pollinating agents as a link in this process. Floral characters that attract animal pollinators would seem to be a step removed from true primary sexual characters, but they serve a different function than secondary sexual characters of display in animals.

Many reproductive phenomena in plants have a selective component but are not cases of sexual selection by any widely accepted meaning of the term. Examples are selective fertilization (41, 42), pollen tube competition, Renner effect (cf. ref. 43), selective ovule and seed abortion (44, 45), etc. Some of these and other phenomena are discussed in the recent symposium (10). In the search for analogues of sexual selection in plants, it would be beneficial to sort out and set aside the numerous phenomena that result from other selection modes. Narrow the search down to potentially promising cases that meet the requirements of a generalized definition of sexual selection (as in definition *v* above).

One possible case to reexamine from this standpoint is the large size of male flowers in some dioecious plants (*Fragaria*, etc.) (12, 46). Another is the differential attractiveness to pollinators and differential pollination success of different flower color morphs in hermaphroditic wild radishes (*Raphanus raphanistrum*) (47).

In a previous discussion (ref. 19, p. 137), I asked proponents of sexual selection in plants to cite valid examples of secondary sexual characters in plants. This challenge has not been picked up or met by participants of the recent symposium (10). Numerous reproductive characters and sex differences are mentioned but none are validated as secondary sexual characters. If such characters exist in plants, their existence still remains to be demonstrated.

### Conclusions

The theory of sexual selection was formulated to explain a class of characters that is prominent in animals, namely, secondary sexual characters related to dominance, combat, or attractiveness in males (1, 2). Intermale competition, which is widespread in eukaryotic organisms, is waged through active premating and mating behavior patterns in higher animals. These behavior patterns require motility, sensory organs, a well-developed nervous system, and mental faculties, features found only in higher animals. The selec-

tive component of male competition in animals possessing these features is capable of producing secondary sexual characters of male dominance or attractiveness (1, 2).

No prominent class of secondary sexual characters has been found in plants; if they existed they would have been discovered long ago, probably by Darwin. However, primary sexual characters are well developed in plants as they are in animals and other eukaryotic kingdoms. Recent advocates of sexual selection in plants ignore the distinction between primary and secondary sexual characters, and this has led them to cite the former as evidence of sexual selection. Products of other selection modes are also cited as examples of the operation of sexual selection.

We should not rule out the possibility that some process analogous to true sexual selection operates in plants and has left its stamp on plant characteristics. At present, we cannot say that such a process does not exist, and we cannot say that it does.

**Note Added in Proof.** Attention is called to the new book *Sexual Selection* by Andersson (49). The announcement of this book appeared while the present paper was in preparation, and my copy arrived after the manuscript had gone to press. Andersson adopts the new broad definition of sexual selection that equates this process with mate competition, and he accepts sexual selection in plants. I have to disagree with Andersson on both of these points, as I do with some other authors for the reasons given in this paper. At the same time, I recognize the value of Andersson's exhaustive treatise on sexual reproductive phenomena in animals.

I thank Billie L. Turner, Delbert Wiens, Ethan J. Temeles, Karen A. Grant, and an anonymous reviewer for reading the manuscript and making helpful suggestions.

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