Trait selection in flowering plants: how does sexual selection contribute?

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Synopsis By highlighting and merging the frameworks of sexual selection envisioned by Arnold (1994) and Murphy (1998), we discuss how sexual selection can occur in plants even though individuals do not directly interact. We review studies on traits that influence pollen export and receipt in a variety of hermaphroditic and gynodioecious plants with the underlying premise that pollination dynamics influences mate acquisition. Most of the studies reviewed found that phenotypes that enhance pollen export are in harmony with those that enhance pollen receipt suggesting that in many cases pollinator visitation rates limit both male and female function. In contrast, fewer traits were under opposing selection; but when they were, the traits most often were associated with enhancing the specific aspects of a given sex function. Our review helps clarify and illustrate why sexual selection can be a component of trait evolution in hermaphrodite plants.

Introduction

In his influential book *The Descent of Man and Selection in Relation to Sex* (Darwin 1871), Darwin spends a chapter discussing secondary sexual characters in "lower classes of animals," particularly hermaphroditic ones. However, he is fairly dismissive of applying sexual selection to these hermaphrodites because they "have too imperfect senses and too low mental powers" to appreciate each other's beauty and general characteristics. It is therefore not surprising that he did not include a chapter on plants. We have progressed considerably in our thinking on sexual selection, and we now readily include aspects of sexual selection in studies of trait evolution of hermaphroditic animals. However, applying and embracing such thinking with plants, especially hermaphroditic ones, has taken somewhat more time to achieve. For example, just over a decade ago, Stanton (1994), in a symposium issue focused specifically on comparisons of sexual selection in plants and animals, stated that "some colleagues and reviewers continue to view the application of sexual selection thinking to plant reproduction with deep suspicion." And following that symposium, Grant (1995) stated that because in his view (1) secondary sexual characters "are the defining feature of sexual selection" and (2) plants lack these characters, he called into question the notion of sexual selection operating in plants.

Here, we discuss a framework of trait selection championed by Arnold (1994) that differs very little fundamentally from how Darwin viewed it, but that, nevertheless, is easily applicable to hermaphroditic flowering plants. It involves thinking about the various pathways to fitness and takes a selection-gradient approach. We combine this with a novel dichotomy of how to view different mechanisms of sexual selection developed by Murphy (1998). Using this 2-part framework, we then review a series of studies on traits that influence pollinator visitation in a variety of plants, including both hermaphroditic and gynodioecious species. In doing so we hope to elucidate the types of traits that may be under sexual selection. We would also like point out how male and female function, when tied together in hermaphrodites, may sometimes select for similar trait values or be influenced by different traits that do not interfere with each other, and hence are in harmony, while at other times they are constrained by opposing selection on the same traits via the 2 sexual functions. Furthermore, we review some of the studies that illustrate how sexual selection on traits may be in opposition to selection via other aspects of fitness.

Framework for trait selection

When sexual selection is opposed by another selective force, a name is especially useful. (Arnold, 1994)

[C]ompetition among plants to pollinate other plants does not involve struggles, or even contact, between
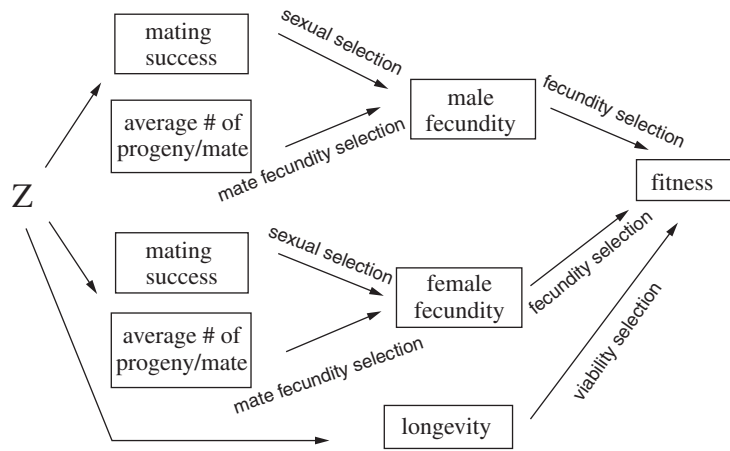
Fig. 1 A framework proposed by Arnold (1994) for the various pathways to fitness in hermaphrodites. Z represents a trait, with arrows indicating various opportunities for variation in this trait to affect fitness, including sexual selection, fecundity selection, the fecundity of one's mates, and viability selection.

competitors... traits can be subject to sexual selection even if they do not affect the outcome of intra- and intersexual interactions. (Murphy, 1998)

Arnold (1994) strove for a simple definition of sexual selection that would simultaneously be applicable to plants and animals, while being distinguishable from other forms of selection (see Fig. 1): "Sexual selection is selection that arises from differences in mating success (number of mates that bear or sire progeny over some standardized time interval)." The first part of this definition seems straightforward. However, the parenthetical part can be problematic for those who study organisms with external fertilization; for example, Levitan (1998), in a paper on aquatic animals with external fertilization, noted that Arnold's definition does not include selection that arises from differences in fertilization efficiency. In essence, the problem is similar for plants because there are often multiple flowers per plant and multiple ovules per flower. Each of these flowers would afford an opportunity for pollen to arrive on a stigma and each ovule would further subdivide opportunities. The equivalent in animals would be a female with more than one reproductive tract, each of which gave access to a separate set of ovaries. As a consequence of this equivalence to multiple reproductive tracts, the "number of mates" portion of the definition could be considered overly limiting if one were to consider number of mates on a whole-plant rather than a per-flower or per-ovule level. It would not, for example, necessarily allow selection for increased duration of flowering (the equivalent of endurance rivalry; Lloyd and Yates 1982; Murphy 1998) to be interpreted as having fitness consequences encompassed by sexual selection. We therefore adopt the first portion of Arnold's definition—"selection that

arises from differences in mating success"—for our discussions herein.

Darwin (1871) contrasted sexual selection with natural selection, whereas Arnold (1994) takes the approach of being clear about the various possible pathways to fitness and includes mate acquisition, fecundity, the fecundity of one's mates, and viability all as potentially having effects on an individual's fitness (Fig. 1). This concurs with Charlesworth and others (1987), who points out the need to determine whether traits affect mating probability, in contrast to fecundity and viability, as a way of defining sexual selection. We realize that although some may be more comfortable with the dichotomy of sexual and natural selection, others see sexual selection as a subset of natural selection, with natural selection generally having 3 components—survival, mating success, and fecundity—sexual selection being the second of these. In any case, taking the latter approach allows one to partition the various selection components, and may therefore provide insight into trait evolution. This could be especially true when selection via one of these components runs counter to selection via one of the others (see below).

Another dichotomy of Darwin's (1871) that had considerable influence on the study of sexual selection is that of intra- versus intersexual selection (that is, contests and mate choice). There are 2 problems with this emphasis, as pointed out by Murphy (1998). First, Murphy effectively argues that this dichotomy has a semantic fallacy, in that competition for mates between members of the same sex is universal to all types of sexual selection and hence all mechanisms have an intrasexual-competition component (see also Brown, 1983). Second, it adds to the difficulty of discussing traits in a sexual-selection framework that do not affect

the outcome of intra- or intersexual interactions. Stanton (1994) pointed out that part of the hesitation of applying sexual selection to plants "may reflect an unwillingness to apply terms that connote, to some, direct behavioral interactions to immobile plants." If 2 plants are not actively interacting, but are only interacting indirectly via pollinators, how can they be considered as exemplifying male–male contests or female choice?

The framework developed by Murphy (1998) negates this problem. He argues that a more applicable framework is one that divides sexual selection into 2 components based on the following question: Is the variance in mating success the result of trait-dependent outcomes of direct interactions between conspecifics? If the answer is no, then the variance is classified as contributing to *interaction-independent sexual selection*; if yes, then it is classified as *interaction-dependent sexual selection*. He is careful to classify interactions as including those in which only one or both of the individuals detects the other, and actual physical contact is not required (signals count as an interaction). He points out that any given trait can be under both interaction-independent and interaction-dependent sexual selection—one does not preclude the possibility of the other. Furthermore, a trait may confer an advantage to both mating success and other components of fitness—again, these are not mutually exclusive. This fits in well with the notion of multiple pathways to fitness exemplified by the path-like diagrams of Arnold (1994; Fig. 1).

Using Murphy's dichotomy, interaction-independent sexual selection is the form of sexual selection that occurs in plants. As an example of this, Murphy (1998) points out that in animal-pollinated plants, individuals with relatively elaborate floral displays (more and/or larger flowers) are likely to acquire more pollinator visits and hence disperse more pollen and have higher fitness through mating success than individuals with more meager displays. In other words, the enhanced male fitness is mediated via pollinators rather than direct interactions among the plants themselves. This could be equally true for fitness achieved via female function, especially when seed production is limited by pollinator abundance (Wilson and others 1994; Ashman and Morgan 2004) or female-biased sex ratio (Ashman and Diefenderfer 2001; see more on this below). Moreover, research has suggested that selection for elaborate floral displays is sometimes opposed by viability selection, because of decreased allocation to other life-history functions and genetic correlations among traits (Bond and Maze 1999; Delph and others 2002, 2004, 2005).

Murphy (1998) concludes that the 2 broad categories of mechanisms that he distinguished "can serve as a conceptual framework for understanding and investigating sexual selection, providing a guide to types of traits that should receive theoretical or empirical attention." Murphys and Arnold's clarity of distinctions allow one to consider trait evolution through a comprehensive prism that breaks down forms of selection.

Sexual selection through male and female function: empirical studies

Here, we review a handful of studies that have investigated how traits that affect pollinator visitation can be considered as being under sexual selection via either male or female function (see Table 1 for an overview). We chose these studies because they investigated male and female function using the same currency: the amount of pollen (or pollen analogs) being moved around by pollinators—either removed (male function) or received (female function). These measures assume that access to mates is a direct function of the amount of pollen exported or received. A positive relationship between siring success and pollen export has been confirmed in a few systems (Broyles and Wyatt 1990; Galen 1992; Nilsson and others 1992; Ashman 1998). And while it seems reasonable to assume that the number of potential sires increases with the amount of pollen received (either because pollen receipt increases with sequential visits or large loads are diverse due to pollen carryover), the relationship between pollen-load size and mate diversity (or multiple paternity) has not been determined for any system despite the fact that multiple paternity is common (for example, Campbell 1998).

One of the first studies to quantitatively investigate how morphological features of flowers impact both pollen export and pollen receipt was in *Polemonium viscosum*, a monocarpic, hermaphroditic alpine species that is principally pollinated by bumble bees (Galen and Stanton 1989). This species is self-incompatible, meaning that visits by pollinators are required to move pollen from plant to plant for fertilization, as pollen from a particular plant cannot fertilize ovules from that same plant. Galen and Stanton (1989) set up experimental arrays (in which they controlled for flower number per plant), released bumble bees into them, and subsequently measured the amount of pollen removed from and deposited onto flowers, as well as a host of morphological floral traits. Measuring pollen removal is a tricky business. They approached this task by collecting anthers that had their full complement of pollen (unvisited, newly

Table 1 Studies reviewed herein (in order of date of publication) that investigated how morphological traits of flowers and other reproductive traits affected both pollen removal (male function) and pollen receipt (female function) by pollinators

Species	Opportunity for selection	Traits under selection via		Harmony or opposition?	Explicit framework	Citation
		Male function	Female function			
Polemonium viscosum	NA	Corolla flare (wide)		Harmony	Neither	Galen and Stanton (1989)
			Style exsertion (high)	Harmony		
Ipomopsis aggregata	M = F	Corolla width (wide)		Opposition	SS	Campbell (1989)
			Stigma exsertion (high)	Opposition	and	
			Pistillate phase (more time)	Opposition	BP	
		Flowering date (late)	Flowering date (late)	Harmony		
Impatiens P2 pallida	NA	Porch height (larger)		Harmony	Neither	Wilson (1995)
P5		Vestibule (larger)	Vestibule (smaller)	Opposition		
		Roof-floor diff. (larger)		Opposition		
P6		Vestibule (larger)		Harmony		
Impatiens C3 capensis	NA		Roof-floor diff. (smaller)	Harmony	Neither	Wilson (1995)
C6		Porch height (larger)	Porch height (smaller)	Opposition		
		Roof-floor diff. (smaller)		Opposition		
C7		Vestibule (larger)		Opposition		
Asclepias syriaca	F > M		Corolla pigment (more)	Opposition	SS	Morgan and Schoen (1997)
		Optical density (more)		Harmony	and	
			2-tone color (more diff)	Harmony	BP	
		Hood length (longer)	Hood length (longer)	Harmony		
			Hood width (wide)	Opposition		
			Horn length (longer)	Opposition		
			Slit length (longer)	Opposition		
			Insertion width (wider)	Harmony		
Cypripedium acaule HR	F > M	Stalk length (longer)	Stalk length (longer)	Harmony	BP	O'Connell and Johnston (1998)
		Flower height (higher)	Flower height (higher)	Harmony		
		Labellum length (shorter)		Harmony		
		Flowering date (earlier)	Flowering date (earlier)	Harmony		
LL		Flower height (higher)	Flower height (higher)	Harmony		
		Labellum length (longer)		Harmony		
		Labellum width (wider)		Harmony		
		Frontal area (more)		Harmony		
		Flowering date (earlier)	Flowering date (earlier)	Harmony		
Fragaria virginiana	NA					
Females abundant		Petal size (larger)	Petal size (larger)	Harmony	Neither	Ashman and Diefenderfer (2001)
Females rare		Petal size (larger)		Harmony		

We list 1) the name of the plant species (and population) studied, 2) whether or not the opportunity for selection (variance in mating success) was equivalent for male and female function (M = F), greater for male function as predicted by Bateman's principle (M > F), or greater for female function (F > M), 3) which traits were significantly under either direct and/or indirect selection for each of the sex functions (and direction of selection), 4) whether this selection was harmonious for the 2 sex functions or in opposition, and 5) whether the authors of the work mentioned sexual selection (SS) or Bateman's principle (BP) in their paper as part of the explicit framework for the research.

opened flowers) and counting pollen with a particle counter for each plant used in the arrays. They could then count pollen in anthers after the daily visitation sessions and estimate the amount of pollen removed by subtracting the amount remaining from the starting amount. Pollen deposition was relatively easy to estimate: stigmas were mounted, stained, and the number of adhering pollen grains counted under a microscope. They found that there were no trade-offs between pollen removal and receipt; they state "each was influenced by unique aspects of floral morphology." Pollen removal was influenced by corolla flare (the petals are fused into a tubular corolla): the wider the corolla, the more pollen was removed. In contrast, pollen receipt was greater in flowers that had relatively exserted styles (the degree to which the part of the flower that the pollen grows down to reach the ovaries sticks out from the opening of the flower). So in this species, the 2 sexual functions were in harmony because although different traits were under selection via each sex function, these traits did not interfere with or covary with each other.

This harmony was absent in the results of a study published in the same year by Campbell (1989) on *Ipomopsis aggregata*, which found sex-specific patterns of selection. This species is also monocarpic (flowers once and dies) and self-incompatible; hummingbirds pollinate the red, tubular flowers. Campbell (1989) did a phenotypic-selection analysis of floral traits in the field over a 3-year period and placed the work explicitly in a sexual-selection framework. She took a different approach to measuring pollen removal and deposition, using fluorescent powdered dyes (which she applied to anthers) as a pollen analog. In order for selection to occur there must be variation in the traits under study and variation among individuals in their relative fitness. So one of the first things that Campbell did was quantify the opportunity for selection. She found that the variance in relative fitness was similar for male and female function, regardless of whether this was estimated on a per-flower or per-plant basis. She noted that this ran counter to the expectation based on Bateman's principle (Bateman 1948) of greater variation in male mating success. Selection-gradient analyses also showed that direct and indirect selection on traits through male function were sometimes in opposition to selection through female function. For example, fitness through male function (pollen donation) was enhanced in flowers that had wide corollas, had stigmas that were not very exserted, and that stayed in the male phase for a relatively long time. Selection was in the opposite direction for these same traits through female function (pollen receipt). Campbell noted that this opposing selection could be responsible for the high

variation found in some floral traits. Moreover, it would lead to substantial differences among individuals in their functional gender, even though all were morphologically hermaphroditic.

Just as in Campbell (1989), Wilson (1995) and Morgan and Schoen (1997) separately quantified opportunities for selection via the 2 sexual functions in hermaphrodites. Their results are phrased in terms of phenotypic selection, although their measures of performance have to do with pollen movement rather than fitness per se.

Wilson (1995) conducted selection studies in several populations of 2 annual herbaceous jewelweeds, *Impatiens pallida* and *I. capensis* pollinated by bumble bees. Both species have complex flowers with yellow or orange perianths. Floral dimensions measured included the vestibule (chamber) height, porch-petal size, and roof-floor symmetry. Although in many populations none of the traits was under significant selection, when selection was significant the sex functions were often in opposition (Table 1). For instance, in one *I. pallida* population (P5), vestibule height was under selection to decrease via pollen export but to increase via pollen receipt. Wilson's results also demonstrate the high degree of spatial variability in selection via male and female function.

Morgan and Schoen (1997) worked with *Asclepias syriaca* (milkweed), a self-incompatible, bee-pollinated species with elaborate flowers that contain "hoods" and "horns" and whose pollen is packaged into pollinia (which are somewhat analogous to spermatophores; Delph and Havens 1998). These pollinia make estimating pollen removal and pollen receipt relatively easy to quantify in the field; one may simply count the number of pollinia out of 10 remaining in a flower to estimate removal and the number of pollinia inserted into the 5 stigmatic slits to estimate receipt. They found greater opportunity for selection through female function, suggesting that selection on floral traits is stronger via pollen receipt than pollen donation—a result that contradicts Bateman's principle. However, consistent with Bateman's principle, they found antagonism between male and female functions in these hermaphrodites for 4 out of 8 floral traits that were under selection (either univariate and/or multivariate selection analyses): corolla pigment, hood width, horn length, and stigmatic-slit length.

Phenotypic-selection analysis of floral traits via pollinator visitation was carried out in *Cypripedium acaule* (pink lady's slipper orchid) by O'Connell and Johnson (1998). Perhaps revealing some ambivalence, the authors list "Bateman's rule" as a key word, but they do not mention it or sexual selection anywhere in the text of the paper (O'Connell and Johnston 1998).

This orchid is different from the species discussed above, in that it offers no reward to the queen bumble bees that pollinate it and most individuals produce only one flower each year. However, like milkweed, its pollen is contained in pollen packets, making estimates of reproductive success fairly straightforward. While they found that variances were higher for female function than for male function, selection coefficients and gradients did not differ significantly for pollen-packet removal versus receipt. This led them to ask why selection was operating similarly through the 2 sex functions, and they concluded that it was related to the packaging of pollen. Male fitness could be saturated with 2 visits (there are 2 pollen packets per flower) and female fitness could be saturated with one visit. Hence, a plant receiving *any* pollinator visits would obtain high success through both sex functions.

Intriguingly, one of the traits that was undergoing selection in the lady's slipper orchids was the date of flower opening, in part because of the likelihood of pollinators learning to avoid the nonrewarding flowers later in the season (O'Connell and Johnson 1998). Selection through total fitness (male plus female) was highest in individuals who opened their flower relatively early in the flowering season. The authors concluded that selection through mate acquisition (for early flowering) was in opposition to other forms of selection (early frosts destroy buds and flowers), although they did not use this framework in their discussion.

When there are 2 sex morphs in a population, as there are in gynodioecious (females and hermaphrodites) or dioecious (females and males) species, the opportunity for sexual selection is expected to vary with the relative frequencies of the pollen and ovule donors (that is, sex ratio). For instance when females are rare, and thus the pool of ovules is small, there will be stronger competition among pollen donors for access to ovules. When access to female mates is limiting male reproductive success, then selection is expected to be stronger for traits that enhance early and rapid pollen export, such as flower size. In contrast, when females (and ovules) are abundant, but pollen donors are rare, there will be stronger competition among pollen recipients for access to pollen, hence selection on attractive traits of females will be stronger than when pollen is abundant. This has strong analogies to selection in free-spawning sea urchins, in which egg traits that enhance fertilizations are under sexual selection when sperm is limiting (Levitan 1996).

To test these ideas in the gynodioecious wild strawberry *Fragaria virginiana*, in which hermaphrodites produce very few fruits (that is, could be viewed as functional males), Ashman and Diefenderfer (2001) constructed artificial arrays that differed in their sex ratios. The small, white, bowl-shaped flowers of this species are visited by a diverse array of generalist bee and fly pollinators that increase visitation with increasing number of open flowers and increasing petal size (Ashman 2000; A. L. Case and T.-L. Ashman unpublished data). To focus their study on flower size alone, Ashman and Diefenderfer (2001) trimmed all experimental plants to a single open flower per plant. Plants were arranged in either "high" sex ratio (75% hermaphrodite pollen donors) or "low" sex ratio (16% pollen donors) arrays. Replicate arrays were exposed to pollinators for a day, the majority of the flower's lifetime. Male fitness was determined by pollinator visitation rate and pollen export for each hermaphrodite plant, and female fitness was determined from visitation rate, pollen receipt, and seed set for each female plant. Phenotypic-selection analyses showed that selection via all components of female fitness was stronger in the low sex-ratio arrays than the high sex-ratio arrays, although in the latter petal size was not under significant selection. In contrast, petal size was always under selection to be bigger, regardless of sex ratio, via male components of fitness. Thus, the sex functions are in harmony but the degree varied with sex ratio (more harmonious under low sex ratio, less harmonious under high sex ratio).

Discussion

Thinking about and quantifying the selective forces acting on traits is enhanced by a framework laying out the various pathways to fitness. We explained a framework in which variation in a trait that affects an individual's ability to acquire mates is one of the pathways and is considered as comprising sexual selection (Arnold 1994). Combining this with the idea of interaction-independent sexual selection (Murphy 1998), one can envisage how a particular phenotype of a trait can be selected over another phenotype via sexual selection (mating success) even when conspecifics do not interact directly. We have argued that within this 2-part context, traits that cannot be placed easily within the dichotomy of contests or mate choice can be seen as having a sexual-selection component.

Importantly to us, it is a persuasive framework for thinking about how sexual selection operates to influence the evolution of traits that affect pollen donation and receipt. Our review of empirical studies that investigated how variation in traits impacts the movement of pollen from and to plants focused on hermaphroditic flowering plants that are visited by animal pollinators, but we note that this framework can apply to wind-pollinated plants as well. In the case of free-spawning

invertebrates in the ocean, traits such as egg size have been appropriately viewed as being under sexual selection, when in such cases the bearer of the sperm is water (Levitan 1996, 1998). Likewise, the bearer of the pollen can be wind, and variable traits that impact an individual's ability to have its pollen more or less effectively dispersed to other plants or to have more or less pollen captured on stigmas, can be thought of as having a sexual-selection gradient in exactly the same way.

Any trait that is variable and affects mating success can potentially be under sexual selection. As described here, for hermaphroditic flowering plants this includes (but is not limited to) morphological traits associated with the placement of flowers within plants (height above ground, tips of branches, etc.), numbers of flowers displayed, morphological traits of inflorescences and individual flowers, floral scent and nectar production, the timing and duration of flowering, the lifespan of each flower, how this lifespan is divided into male versus female phase, and the timing and pattern of anther dehiscence (see Castellanos and others 2006), or stigma receptivity.

This way of thinking about sexual selection clearly allows for selection to sometimes be stronger for male function as predicted by Bateman (1948) and sometimes stronger for female function (see also Ashman and Morgan 2004). Furthermore, sexual selection can shape the 2 reproductive strategies differently even if they are both under sexual selection. For example, a flower might be selected to frequently replace small amounts of nectar during a prolonged male phase and to produce just one large nectar serving during a briefer female phase. Of the 3 studies in Table 1 that explicitly looked at the opportunity for selection, 0 had more variability in male success, 1 had equal variability for the 2 sex functions, and 2 had more variability for female success. Moreover, pooling over all the species investigated, 23 traits were under selection via male function and 20 via female function. These results are corroborated by a survey of studies that manipulated floral traits and recorded whether male or female fitness was affected (Ashman and Morgan 2004): it was most common for both sex functions to respond similarly to the manipulation. Clearly, sexual selection in these species occurs fairly evenly through the 2 sex functions of hermaphrodites, although the reasons for this vary depending on the study species.

In terms of whether trait selection is usually harmonious (that is, either in the same direction or significantly affecting only one function) or in opposition via male and female function, this too appears to be species specific and highly variable. Harmony occurred for 21 traits, whereas opposition occurred for only 12 traits.

Harmony may be more common than opposition in some species because traits that attract pollinators under conditions of pollinator limitation benefit both sex functions (see also Ashman and Diefenderfer 2001). This appears to be the case for the pink lady's slipper orchid, a deceptive flower that does not offer rewards and which the pollinators learn to avoid. If pollen limitation is an indicator of pollinator limitation, then scenarios such as this may be common in hermaphrodite plants as pollen limitation is common (Ashman and others 2004). Of those traits that were in opposition, male function tended to select for larger petal parts in most instances (although exceptions occurred), a pattern that has also been seen in many gynodioecious and dioecious species (Bell 1985; Delph 1996; Delph and others 1996). This may apply when the number of pollinator visits needed to saturate male function is considerably greater than the number of visits needed to saturate female function (in other words, in those cases where being more attractive to pollinators leads to higher marginal fitness gains via pollen dispersal) (Wilson and others 1994). In contrast, selection via female function was for more exserted or larger parts associated with pollen capture (styles, stigmas, stigmatic slits) or greater time spent in the female phase—all traits clearly associated with enhancing pollen receipt. More work of the type shown in Table 1 will reveal whether these patterns hold generally for hermaphrodites or are a consequence of idiosyncratic aspects of these particular species. Moreover, we need direct demonstrations that these traits lead to increased mating success (number of mates) via both male and female function.

Not all of the authors whose studies we reviewed placed their work explicitly in a sexual-selection context. We can think of 2 reasons for this. One, that this context would not have offered them any additional insight into trait evolution in their study species, because they took a pathways-to-fitness approach or focused exclusively on mating success in any case. Two, because they felt that explicit mention of sexual selection would compromise the credibility of the study in the eyes of some readers. If it is the former, then all is well; if the latter, then we hope that this article helps to clarify and illustrate why thinking about sexual selection in hermaphroditic plants can be considered a valid component of trait selection.

Acknowledgments

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