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The Evolution of Gender-Biased Nectar Production in Hermaphroditic Plants

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Abstract

The evolution of secondary sexual floral traits may be driven by selection through male or female reproductive success. Even so, the gender-biased function of a floral trait is often unapparent because secondary sexual traits and primary sexual organs of both genders co-occur within most bisexual flowers. Within dichogamous plants, however, secondary sexual traits may be unambiguously expressed in association with the primary sexual organs of one gender, making these species uniquely suited to studies of natural and sexual selection on floral traits. The objectives of this article are to summarize patterns of gender-biased nectar production and to critically explore theories relevant to its evolution. We list 41 species with gender-biased nectar production and provide two sets of adaptive hypotheses for the trait: sexual selection hypotheses and inbreeding avoidance hypotheses. We formulate these hypotheses using sexual selection theory in plants and the literature that relates pollinator foraging to plant inbreeding. We also consider explanations based on resource trade-offs, enemies, and genetic correlations. Support for the sexual selection and inbreeding avoidance hypotheses is provided by only a few well-studied species. We outline a series of experiments that should facilitate sorting among hypotheses. Plants with gender-biased nectar production are likely to provide unique insights into the roles of natural and sexual selection in the evolution of floral traits.

Introduction

Gender-specific traits in plants with simultaneously bisexual flowers may appear to be confined to the primary sexual structures of the flower. For example, traits of the pollen grain are generally unambiguously male-specific in function, whereas the nectar production rate or the corolla color, both secondary sexual traits, cannot be immediately associated with either male or female floral function. Secondary sexual traits of flowers can, nonetheless, contribute disproportionately to male or female reproductive output. Corolla phenotype and nectar volume, for example, have been shown to serve gender-biased functions in a few well-studied species (e.g., Bell, 1985; Stanton et al., 1986; Campbell, 1989; Galen & Stanton, 1989; Melendez-Ackerman & Campbell, 1998). Nonetheless, the co-occurrence of both primary and secondary sexual structures within the simultaneously bisexual flower introduces some ambiguity into studies of the gender-biased function of secondary traits, because most secondary traits are physically associated with both floral genders.

Dichogamous plant species—those that temporally separate male function and female function within flowers—may provide a unique means of reducing this ambiguity. In dichogamous species, the expression of a secondary sexual trait may vary with sexual phase. Floral nectar production rates, for example, can be higher during one of the sexual phases, and the result is gender-biased nectar production (GBNP). The unequal distribution of nectar between male and female phases immediately associates a different nectar production schedule with each gender and may reflect a true functional bias towards male or female fitness. Gender-biased nectar production is therefore likely to be particularly informative about the nature of sexual or natural selection on secondary traits, yet it has been studied in only a few isolated cases.

In this paper, we show that a diverse group of hermaphroditic plants exhibits gender-biased nectar production, and we critically evaluate hypotheses that may explain the nectar production patterns in these species. First, we summarize published examples of dichogamous species that exhibit nectar production biases, and we describe trends apparent among these species. Then, we explore theories relevant to the trait's evolution, which correspond to five main categories: sexual selection, natural selection against inbreeding, resource trade-offs, floral enemy effects, and evolution by correlated traits (pleiotropy). We focus our discussion on sexual selection and inbreeding avoidance theories, and from these, we extract four main hypotheses that may explain gender-biased nectar production. We then discuss the remaining three topics and finish with an experimental framework designed to help researchers discriminate among the main hypotheses.

Gender-Biased Nectar Production (GBNP) in Dichogamous Plants

Dichogamy is remarkably widespread within the angiosperms (Bertin & Newman, 1993; Barrett, 2003). Within dichogamous species, the number that bias nectar production toward the male or female phase is currently unknown. Species that exhibit gender-biased nectar production have in fact received little attention, although they are likely to provide a unique perspective to studies of the evolution of secondary sexual floral traits. For these reasons, we attempted to compile an exhaustive list of hermaphroditic species with gender-biased nectar production from the literature. Topics of searched literature included, but were not limited to, the physiology and biology of nectar production, pollinator behavior at inflorescences, and sexual selection in hermaphroditic plants. Plant species were included if dichogamy was clearly established, if nectar production rates in male-phase and female-phase flowers were consistently different (i.e., one phase was almost always more rewarding), and if all plants in the study populations produced only bisexual flowers (i.e., studies of monoecious, dioecious, and gynodioecious plants were excluded).

RESULTS FROM THE LITERATURE SEARCH

Commonalities among Dichogamous Plants with GBNP

Our literature search revealed 41 dichogamous species with male- or female-biased nectar production, representing 18 families and 22 genera (Table I). Despite wide taxonomic diversity among species, nearly all share a few key characteristics. Most genera (20 of 22) are protandrous (male phase precedes female phase in time); the only two protogynous (female phase precedes male phase) taxa are *Ribes speciosum* and *Scrophularia* spp. All listed species may have more than one flower open at the same time, although flower counts range from fewer than five (*Campanula rotundifolia*; Cresswell

Table I.

Dichogamous species with gender-biased nectar production.

Family and species	Nectar collection technique[a]	Gender bias	Volume of nectar produced (μL)		Mass of sugar produced (mg)		M:F ratio[b]	Pollinator type[c]	Vertical nectar gradient[d]	Visit bias[e]	References[f]
			Male	Female	Male	Female					
Protandrous species:											
Campanulaceae											
Campanula rotundifolia	Standing	F	0	0.01	0	8.25×10^{-2}	0:0.01	B	no	Y[p]	Cresswell & Robertson, 1994
Lamiaceae											
Lavandula stoechas	12 hour	F[g]	0.047	0.093	2.4×10^{-3}	2.6×10^{-3}	1:2.0*	B	no	Y	Gonzalez et al., 1995
Brassicaceae											
Streptanthus culteri	Unknown	F	0	>0	0	>0	0:>0	I	?	?	Rollins, 1963
Streptanthus carinatus	Unknown	F	0	>0	0	>0	0:>0	I	?	?	Rollins, 1963
Plantaginaceae											
Digitalis purpurea	24 hour	F	less	more	less	more		B	yes ↑	Y	Best & Bierzychudek, 1982
Onagraceae											
Epilobium angustifolium	12 hour	F	—	—	6.3×10^{-4}	11.7×10^{-4}	1:1.9*	B	yes ↑	Y	Pyke, 1978b; Galen & Plowright, 1985a, 1985b†
Ranunculaceae											
Aconitum columbianum	24 hour	F[h]	1.95	2.62	—	—	1:1.3*	B	yes ↑	Y	Pyke, 1978b
Delphinium virescens	Standing	F[h]	0.3	0.45	—	—	1:1.5	B	yes ↑	Y	Waddington, 1981
Delphinium barbeyi	24 hour	F[h]	2.4	4.42	—	—	1:1.8*	B	yes ↑	Y	Pyke, 1978b
Delphinium nelsonii	Standing	F	—	—	0.21	0.43	1:2.0*	B/H	yes ↑	Y	Pyke, 1978b; Cruden et al., 1983†
Rubiaceae											
Pentagonia macrophylla	24 hour[i]	F	70.7	122.6	—	—	1:1.7	H	no	N	McDade, 1986
Ericaceae											
Macleania bullata	Lifetime	M[h]	50	25	—	—	2.0:1*	H	no	?	Navarro, 2001
Gesneriaceae											
Chrysothemis friedrichsthaliana	12 hour	M	9.28	6.36	3.05	1.80	1.5:1*	H	no	Y	J. Carlson, unpubl.
Moussonia deppeans	24 hour	M	1.76	1.18	—	—	1.5:1*	H	no	N[q]	Lara & Ornelas, 2001

Campanulaceae											
Lobelia laxiflora	Lifetime	M	15.2	11.77	—	—	1.3:1*	H	?	?	Feinsinger, 1978; Lara & Ornelas, 2002†
Lobelia deckenii	Lifetime	M[j]	1715	1368	117	123	1.3:1*	S	no	?	Burd, unpubl.†, Burd, 1992†, Burd, 1995
Lobelia gregoriana	Lifetime	M	more	less	more	less		S	?	?	M. Burd, pers. comm.
Lobelia mildbraedii	Lifetime	M	more	less	more	less		S	?	?	M. Burd, pers. comm..
Lobelia telekii	Lifetime	M	—	—	2.4	1.3	1.8:1	S	yes ↓	Y	Evans, 1996†; M. Burd, pers. comm.
Lobelia cardinalis	12 hour	M[h,k]	—	—	1.07	0.44	2.4:1*	H	yes ↓	Y	Devlin & Stephenson, 1985
Lobelia cardinalis	Lifetime	M[k]	17.49	6.71	—	—	2.6:1*	H	yes ↓	?	Lara & Ornelas, 2002
Loranthaceae											
Ligaria cunefolia	Lifetime	M	more	less	more	less		H	no	?	Rivera et al., 1996
Lythraceae											
Cuphea llavea	Standing	M	14.53	7.24	4.25	2.19	2.0:1*	H	no	?	Cruden et al., 1983
Alstroemeriaceae											
Bomarea acutifolia	24 hour	M	8.8	1.7	—	—	5.2:1	H	no	?	Snow & Grove, 1995
Alstroemeria aurea	12 hour	M[l]	4.2	1.2	1.16	0.37	3.5:1*	B	no	Y	Aizen & Basilio, 1998
Agavaceae											
Agave mckelvyana	12 hour	M[m]	58%	42%	—	—	1.4:1	B	no	?	Sutherland, 1987
Boraginaceae											
Echium vulgare	Standing	M	0.65	0.45	—	—	1.4 1*	B	no	Y	Klinkhamer & de Jong, 1990
Lamiaceae											
Melittis melissophyllum	Lifetime	M[h,n]	12.1	8.8	2.8	1.2	1.4:1	B	no	?	Guitián et al., 1995
Balsaminaceae											
Impatiens capensis	Standing	M[h]	1.44	1.16	0.53	0.38	1.2:1*	B/H	no	Y	Bell et al., 1984
Protogynous species:											
Scrophulariaceae											
Scrophularia auriculata	12 hour	F[h]	5.7	8.1	1.8	3.0	1:1.4	W	yes ↓[o]	?	Olivencia & Alcaraz, 1993
Scrophularia balbisii	12 hour	F[h]	8.7	11.7	2.6	3.2	1:1.3	W	yes ↓[o]	?	Olivencia & Alcaraz, 1993
Scrophularia tanacetifolia	12 hour	F[h]	6.4	9.1	2.6	3.7	1:1.4	W	yes ↓[o]	?	Olivencia & Alcaraz, 1993
Scrophularia laxiflora	12 hour	F[h]	10.1	13.5	3.7	4.3	1:1.3	W	yes ↓[o]	?	Olivencia & Alcaraz, 1993
Scrophularia sambucifolia	12 hour	F[h]	22.2	38.2	7.8	11.5	1:1.7	W	yes ↓[o]	?	Olivencia & Alcaraz, 1993
Scrophularia viciosoi	12 hour	F[h]	6.1	9.1	2.6	4.3	1:1.5	W	yes ↓[o]	?	Olivencia & Alcaraz, 1993
Scrophularia reuteri	12 hour	F[h]	11.2	17.0	3.7	6.0	1:1.5	W	yes ↓[o]	?	Olivencia & Alcaraz, 1993
Scrophularia valdesii	12 hour	F[h]	19.6	21.9	6.1	7.6	1:1.1	W	yes ↓[o]	?	Olivencia & Alcaraz, 1993
Scrophularia aquatica	Standing	F	less	more	less	more		W	no[o]	?	Corbet et al., 1981
Scrophularia grandiflora	12 hour	M[h]	35.2	32	8.9	8.1	1.1:1	W	yes ↑[o]	?	Olivencia & Alcaraz, 1993
Scrophularia sublyrata	12 hour	M[h]	9.2	8.3	3.7	3.3	1.1:1	W	yes ↑[o]	?	Olivencia & Alcaraz, 1993
Scrophularia oxyrhyncha	12 hour	M[h]	5.9	5.2	2.1	2.0	1.1:1	W	yes ↑[o]	?	Olivencia & Alcaraz, 1993

Table I, *continued*

Family and species	Nectar collection technique[a]	Gender bias	Volume of nectar produced (μL)		Mass of sugar produced (mg)		M:F ratio[b]	Pollinator type[c]	Vertical nectar gradient[d]	Visit bias[e]	References[f]
			Male	Female	Male	Female					
Saxifragaceae											
Ribes speciosum	12 hour	M	more	less	more	less		H	no	Y	Stiles, 1976

[a] Nectar was collected from flowers using the following techniques: 12-hour nectar production rates of bagged flowers (12 hour); 24-hour nectar production rates of bagged flowers (24 hour); lifetime production for each phase, measured over the entire duration of the male or female phase (Lifetime); standing crop of unbagged flowers sampled once at a given time of day (Standing); and unknown measurement technique (Unknown).

[b] The male-to-female nectar production ratio (M:F) was calculated on volume of nectar (μL) unless only mass of sugar was available. When the difference between male- and female-phase nectar production was tested for statistical significance, the M:F ratio is flagged by an asterisk (*).

[c] Pollinator types are bee (B) insect (I), hummingbird (H), sunbird (S), and wasp (W).

[d] Arrows denote the direction within the inflorescence in which per-flower nectar production declines. For example, an upward arrow indicates that flowers near the bottom of the inflorescence produce the most nectar and those near the top of the inflorescence produce the least.

[e] A visit bias was observed when the pollinator more frequently visited flowers of the more-rewarding phase.

[f] When two or more references are listed, a dagger (†) denotes the sources of the reported nectar production data.

[g] Volume of nectar in male- and female-phase flowers was significantly different, but mass of sucrose in flower phases was not different. This was most likely because sample sizes were smaller for mass measurements ($n = 14$ for volume, $n = 7$ for mass; Gonzalez et al., 1995).

[h] Nectar measurements were extrapolated from published data. Any statistic performed on these species did not use the extrapolated data.

[i] Volume of nectar in male- and female-phase flowers was taken at roughly 22 rather than 24 hours after bagging, because female-phase flowers were wilted and difficult to measure by late afternoon (McDade, 1986).

[j] Volume of nectar produced was consistently male-biased; however, mass of sucrose produced was not significantly gender-biased, and concentration was consistently female-biased (Burd, 1992).

[k] Plants studied in New Mexico did not exhibit a significant gender bias (Cruden et al., 1983), but those in Pennsylvania and Mexico did (Devlin & Stephenson, 1985, Lara & Ornelas, 2002; see Langenberger & Davis, 2002).

[l] Lifetime nectar production was male-biased, but standing crop was not gender-biased, possibly because bees more frequently visited male-phase flowers (Aizen & Basilio, 1998).

[m] Percentage of daily total nectar volume produced per branch (Sutherland, 1987).

[n] Mass of sugar produced was consistently male-biased; however, volume was not gender-biased (Guitián et al., 1995).

[o] Gradient was present early in the flowering season, but it was likely to disappear later in the season (Olivencia & Alcaraz, 1993).

[p] Visit bias toward phase with more nectar occurred only after all pollen was removed from male-phase flowers (Cresswell & Robertson, 1994).

[q] Visit bias was toward female-phase flowers, the less-rewarding phase (Lara & Ornelas, 2001).

& Robertson, 1994) to greater than 100 (*Agave mckelvyana*; Sutherland, 1987). Further, flowers of all but four species develop asynchronously, such that individual plants may have both male- and female-phase flowers open simultaneously. As a result, if self-compatible, these 37 species are susceptible to inbreeding between flowers on the same plant (in addition to inbreeding within flowers). Those species unlikely to be self-pollinated by flowers on the same plant, because of synchronous flower development throughout whole plants, are *Agave mckelvyana, Alstroemeria aurea, Bomarea acutifolia,* and *Pentagonia macrophylla*. Almost three-fourths of the listed species produce flowers in racemes (flowers mature sequentially from the bottom to the top of a vertical inflorescence). This floral arrangement frequently results in a vertical gradient of nectar rewards within the inflorescence, the direction of which depends on the gender bias and the type of dichogamy (Table I). In summary, most listed plants are protandrous, have both male and female flowers open at the same time, and at least half have a nectar gradient within inflorescences.

GBNP is Male-Biased as Often as Female-Biased

The nectar production rate is greater in the male phase in 21 species and in the female phase in 20 species. At a broader taxonomic level, 14 genera include species with male biases and nine include species with female biases. Willson and Ågren (1989) noted a similar relative frequency of male- and female-biased nectar production in taxa with unisexual flowers as well. In their literature review, they found a total of 23 monoecious or dioecious species with differential rewards in male and female flowers; 11 species produced more nectar in male flowers, and 12 species produced more nectar in female flowers. Nectar production biases in monoecious, dioecious, and gynodioecious plants have been reviewed recently (Eckhart, 1999) and are being actively researched (Ashworth & Galleto, 2002; Gehring et al., 2004).

Nectar Production Biases Are Modest in Most Plants with GBNP

Species with gender-biased nectar production generally exhibited a less than twofold difference in nectar production between male- and female-phase flowers, although average nectar production per flower varies widely among species (Table I). The male/female ratio of nectar production ranges from 1.1 to 5.2 for species with male-biased nectar production (mean = 1.9, median = 1.5), whereas the female/male ratio ranges from 1.2 to 3.6 for species with female-biased nectar production (mean = 1.6, median = 1.5). These ratios exclude the three protandrous species that produce no nectar during the male phase. Although nectar production ratios may at first appear small, pollinators can often discriminate against less-rewarding flowers on plants with female/male nectar production ratios as low as 1.2 (Table I).

Trends within Male-Biased and Female-Biased Groups and within Taxa

Species that exhibit the same nectar production bias (male or female) tend to have similar pollinators and inflorescence structures, if the genus *Scrophularia* is considered separately. Species with female-biased nectar production are most often bee-pollinated (8 of 11) and produce the most-rewarding flowers (female) at the base of racemose inflorescences and the least-rewarding flowers (male) at the top (6 of 11). Species with male-biased nectar production, in contrast, are typically bird-pollinated (13 of 18) and lack spatial arrangements of nectar rewards or produce the least-rewarding flowers (female) at the top of racemose inflorescences. These comparisons are not phylogenetically independent, and, thus, some similarities may be due to common ancestry rather than convergent evolution.

The species in the genus *Scrophularia* generally lack commonalities observed in the larger group. For example, unlike other species with gender-biased nectar production, *Scrophularia* species are protogynous and wasp-pollinated (Olivencia & Alcaraz, 1993). The relatively small male:female nectar production ratios and the lack of individual statistical tests on the nectar production data of some *Scrophularia* species (e.g., the species with male biases) suggest that a few of the measured biases may be biologically insignificant.

Gender-biased nectar production may be a phylogenetically conserved trait in some taxa, as evidenced in part by its presence in 12 *Scrophularia* species, six *Lobelia* species, three *Delphinium* species, and two *Streptanthus* species. Despite frequent recurrence of gender biases among congeners, the direction of a nectar production bias is not necessarily fixed within lineages. *Scrophularia*, as already mentioned, includes at least nine species with female-biased nectar production and at least three species with male-biased nectar production (Olivencia & Alcaraz, 1993). The direction of bias may also differ among individuals in the same population (*Lobelia deckenii* on Mount Kilimanjaro, Burd, 1992) or among conspecific populations (*Lobelia cardinalis* in New Mexico, Cruden et al., 1983; compared to those in Pennsylvania, Devlin & Stephenson, 1985; or in Mexico, Lara & Ornelas, 2002; see Langenberger & Davis, 2002).

Is GBNP Heritable?

Discrepancies within species in the direction of nectar production bias may reflect the influence of the environment on a plastic trait (e.g., Southwick & Southwick, 1983; Campbell, 1996), or they may reflect genetic variation among individuals. Nectar volume has high genetic variation and is heritable in *Echium vulgare* and at least five other angiosperms (Zimmerman & Pyke, 1986; Hodges, 1993; Mitchell & Shaw, 1993; Boose, 1997; Klinkhamer & van der Veen-van Wijk, 1999; Leiss et al., 2004; reviewed in Mitchell, 2004). The heritabilities of traits causing a temporal change in nectar production rates, the purported targets of selection for this review, are not known for any dichogamous species (Mitchell, 2004). Most likely, nectar production biases, like nectar production rates, are influenced by both genes and the environment (Boose, 1997; Vogler et al., 1999; Leiss et al., 2004).

We assume that the temporal pattern of nectar production has some heritable basis for most species. In this light, we consider the listed species as valuable experimental units for evolutionary studies of secondary floral traits. Such studies may test basic predictions of the evolved or optimal direction of gender biases in dichogamous plants, based on sexual selection, inbreeding avoidance, and other theories. In the following sections, we critically review the theoretical background of these hypotheses, and then we consider their utility in light of currently available observations.

Evolutionary Hypotheses for GBNP

SEXUAL SELECTION HYPOTHESES

In both plants and animals, sexual selection results from competition for mates between individuals of the same sex and species. Sexual competition is unique in plants, however, because it can occur indirectly via pollinators (Charnov, 1979; Lloyd & Yates, 1982; Arnold, 1994). In effect, plants "court" the pollinators rather than the opposite sex itself, making pollinators the target audience for many secondary traits of hermaphroditic flowers. Despite clear parallels between animal and plant examples of sexual selection, the analogy of sexual selection across the two groups remains controversial, questioned by some (Broyles & Wyatt, 1990; Wilson et al., 1994; Broyles & Wyatt, 1995) and advocated by others (Stephenson & Bertin, 1983; Andersson, 1994; Arnold, 1994; Willson, 1994; Queller, 1997; Skogsmyr & Lankinen, 2002).

Selection that acts predominately through one floral gender is the subject of a growing body of theory within floral evolution, yet some recent contributors make little mention of sexual selection and, in some instances, use instead the term gender-specific selection (e.g., Burd & Callahan, 2000; Ashman & Morgan, 2004). Gender-specific selection is like sexual selection in that it involves different effects on male and female fitness, but unlike sexual selection, these differences need not be caused by intrasexual competition for mates (i.e., they may be caused by natural selection). Use of the term gender-specific selection circumvents the need to further classify floral traits as naturally or sexually selected, a task that may be both controversial and difficult (Lloyd and Yates 1982, Skogsmyr and Lankinen 2002). Nonetheless, sexual selection has almost certainly played a distinctive role in the evolution and maintenance of many floral traits (Willson, 1994; Skogsmyr & Lankien, 2002), and we advocate its explicit consideration in studies of floral evolution.

Gender-biased expression of nectar in hermaphrodites likely indicates a history of sexual selection in many species. Here we consider two separate sexual selection hypotheses for the function of this trait. The first, known as the male function hypothesis, predicts pollinator limitation on male fitness as the cause of sexual selection for predominately male-functioning traits (Bateman, 1948; Charnov, 1979; Queller, 1983; Bell, 1985). The male function hypothesis has been defined similarly by others, although without explicit association with sexual selection (Burd & Callahan, 2000; Ashman & Morgan, 2004). This hypothesis has also been called the pollen donation hypothesis (Broyles & Wyatt, 1990), or the fleurs-du-mâle hypothesis (Queller, 1983). The second hypothesis predicts pollen limitation on female fitness as the cause of selection for predominately female-functioning traits (Delph & Lively, 1992; Burd, 1994; Wilson et al., 1994). We call this the female function hypothesis for consistency. Although other gender-specific and sexual selection hypotheses exist to explain secondary traits (e.g., Ashman & Morgan, 2004), we limit our discussion to these two basic hypotheses. We provide numerous examples that support each hypothesis; first, we limit our discussion to plants that do not exhibit gender-biased trait expression, and later we highlight the examples of gender-biased nectar production that are likely explained by one of the sexual selection hypotheses.

Bateman's Principles and the Male Function Hypothesis

Sexual selection for exaggerated male phenotypes requires that the relationship between fecundity and mating success be stronger for males than females. Bateman (1948) provided the first experimental evidence of this relationship in his study of competition for mates in *Drosophila*. He showed that males exhibit a greater variance in both number of offspring and mating success, and he demonstrated a stronger correlation between these fitness components in males than females (reviewed in Arnold, 1994). These observations formed the basis of Bateman's three principles of intrasexual selection. Trivers (1972) expanded on Bateman's principles and suggested that differential parental investment between males and females was the cause of mate limitation on male fecundity and resource limitation on female fecundity. Collectively, their work suggests that males should experience stronger sexual selection than females. When Bateman's principles are specifically applied to hermaphroditic plants (Charnov, 1979; Arnold, 1994; Willson, 1994), the prediction arises that sexual selection acts on floral traits predominately through male function, because male fecundity is limited by pollinator visits and female fecundity is limited by the resources needed to set seeds (Arnold, 1994). This is the framework of the male function hypothesis.

Experimental studies of a variety of secondary floral traits that lack gender-biased expression lend preliminary support to the male function hypothesis. For example, the amount of pollen removed or number of seeds sired is often limited by the number of pollinator visits to plants, whereas the number of seeds set is not (Queller, 1983; Bell, 1985; Queller, 1985; Sutherland, 1987). Further, at least one study has shown greater variance in mating success of male parents compared to female parents (Meagher, 1986). Thus, attractive floral traits of hermaphroditic flowers may serve a predominately male function in some species, as predicted by Bateman's principles. Nectar production, in particular, benefits male function through its positive correlation with both the number of pollinator visits (Mitchell & Waser, 1992; Mitchell, 1993; Melendez-Ackerman & Campbell, 1998) and the amount of time spent per flower (Thomson, 1986; Jones & Reithel, 2001). In the hermaphroditic *Asclepias quadrifolia* and *Ipomopsis aggregata*, plants with increased nectar production receive more pollinator visits and export more pollen, but do not set more seeds (Pleasants & Chaplin, 1983; Mitchell, 1993). Plant species with unisexual flowers have also been cited in support of the male function hypothesis; many monoecious and dioecious species produce larger male flowers and/or have males that produce more nectar than females (Willson & Ågren, 1989; Delph & Lively, 1992; Eckert, 1999; but see Delph et al., 1996). In conclusion, studies of secondary traits in both hermaphroditic and unisexual species are often consistent with the male function hypothesis.

Beyond Bateman: Pollen Limitation and the Female Function Hypothesis

Bateman (1948) demonstrated that sexual selection was caused by mate limitation on male reproductive success. He did not predict stronger mate limitation on female reproductive success because females tend to be more dependent on resources for reproduction than on access to mates. Nonetheless, resources do not always more strongly limit female function, as evidenced by the frequent occurrence of pollen limitation. Pollen limitation is the failure of a plant to achieve maximum female reproductive success because of insufficient pollen delivery—in terms of quantity and/or quality of pollen grains (Ashman et al., 2004). Burd (1994) reviewed studies of 258 plant species and found evidence of pollen limitation in 62% of cases examined. A reanalysis of these and other data using phylogenetically independent contrasts (Larson & Barrett, 2000) and a recent review (Ashman et al., 2004) further support these findings.

In species with pollen limitation, secondary traits may often be more female-biased than male-biased in function. Nevertheless, there are only a few experimental demonstrations of sexual selection to increase female mating success (female function hypothesis), in the absence of gender-biased expression. Devlin and Ellstrand (1990) found variance in mating success to be greater for female rather than male function in *Raphanus sativa*. Selection through female fecundity was also stronger in *Asclepias syriaca*, based on data that showed differences between male and female selection gradients on floral traits (Morgan & Schoen, 1997). Strong correlations between female mating success and certain secondary traits were found in a congener, *A. exaltata* (Broyles & Wyatt, 1995). In this study, however, male mating success was also strongly dependent on the same traits. In summary, the ubiquity of pollen limitation suggests that selection may indeed act strongly through female function, but evidence for this hypothesis is currently quite limited.

The Sexual Selection Hypotheses in Plants with GBNP

Sexual selection in dichogamous plants with gender-biased nectar production is somewhat distinct from examples highlighted in the preceding paragraphs. In plants with gender-biased nectar production, the sexual selection hypotheses not only require a gender-differential relationship between mating success and fecundity, but they also suggest that pollinators are responding to reward differences and are visiting preferentially the more-rewarding floral gender. Pollinator preferences for certain flowers on a plant are known for some species on Table I and are highly likely for many others, as we will explain in the next section. Thus, in theory, the male function and female function hypotheses are respectively equipped to explain male- and female-biased nectar production. Nevertheless, only the male function hypothesis is currently supported by empirical data.

Six species with male-biased nectar production have been considered within the context of sexual selection, and all are basically consistent with the major predictions of the male-function hypothesis. Of these species, *Impatiens capensis* (Balsaminaceae) provides a notable example. Flowers produce twice as much nectar and spend roughly twelve more hours in the male than female phase, which results in eight times as many visits to male-phase flowers (Bell et al., 1984). Although they did not explicitly test if male reproductive function was pollinator-limited in this plant species, Bell et al. (1984) stated that multiple pollinator visits were required to remove all of the pollen grains present on the anthers of male-phase flowers, whereas one or two visits to a female-phase flower were enough to deliver all the pollen necessary to fertilize all of its 3-5 ovules (see also Temeles & Pan, 2002). Thus, the nectar production pattern in *I. capensis* supports the male-function hypothesis. *Alstroemeria aurea* (Aizen & Basilio, 1998) and *Lobelia cardinalis* (Devlin & Stephenson, 1985), both with male-biased nectar production, also conform to predictions of this hypothesis. *Alstroemeria aurea* required 3.3 visits to male-stage flowers for every visit to female-stage flowers to maximize contributions of each sex, with 3.1 times as much nectar produced in the male stage (Aizen & Basilio, 1998). Studies of *Agave mckelvyana*, *Bomarea acutifolia*, *Chrysothemis* *friedrichsthaliana*, and *Echium vulgare* provide some support for the male-function hypothesis as well. The remaining species with male-biased nectar production have yet to be studied in this context.

Despite the absence of empirical studies on most species, there are two lines of indirect evidence that sexual selection is a probable explanation for at least some species with gender-biased nectar production. For example, gender-biased expression of nectar is often accompanied by a similarly biased expression of other floral characteristics. Flowers of *Impatiens capensis* show increased longevity of the more-rewarding male phase (Bell et al., 1984). Petals of other species begin to wilt notably during the less-rewarding female phase (McDade, 1986; J. Carlson unpubl.), or they change color as they pass into the less-rewarding female phase (Klinkhamer & de Jong, 1990). The concurrent biasing of multiple traits provides some indirect support to the sexual selection hypotheses.

An additional line of indirect evidence relies on specific behaviors of the pollinators. If sexual selection is currently maintaining gender-biased nectar production, pollinators must be able to distinguish between male- and female-phase flowers. They also must visit preferentially flowers of the more-rewarding phase. Based on current information on the species of our lists, pollinators appear to prefer flowers in the more-rewarding phase for seven species with male-biased nectar production (five of these are without nectar gradients) and eight with female-biased nectar production (two of these are without nectar gradients; Table I). For species that have discriminating pollinators, increased rewards can result in increased mating success, which would allow nectar to be a sexually selected trait. When pollinators do not discriminate or intrasexual competition seems unlikely, the evolution of gender-biased nectar production may more closely correspond to an alternative possibility, based on natural selection against inbreeding.

INBREEDING AVOIDANCE HYPOTHESES

Floral traits that reduce maladaptive inbreeding are favored by natural, rather than sexual, selection. This is because such traits increase offspring quality per mate, but generally not mating success. Inbreeding occurs whenever pollen fertilizes the ovules of its own flower (autogamy) or ovules of other flowers on the same plant (geitonogamy). In either case, both male and female components of fitness may be drastically reduced by the production of fewer or inferior offspring by inbred flowers (Charlesworth & Charlesworth, 1987). Inbreeding further reduces male reproductive success owing to pollen discounting, which is the loss of pollen that could have sired outcrossed seeds (de Jong et al., 1993; Fishman, 2000). Both Rathcke (1992) and Harder et al. (2001) suggest that reproductive losses to geitonogamy are more severe for male than for female fitness, providing an opportunity for gender-specific selection in the absence of sexual selection. Mating among flowers on the same plant is thought to be a very common mode of self fertilization (Lloyd, 1992), making it an important, although frequently ignored, force in floral evolution (de Jong et al., 1993).

According to the inbreeding avoidance hypotheses, gender-biased nectar production is an adaptation to decrease geitonogamous inbreeding through its effects on pollinator behavior. Maximal pollen export (i.e., minimal inbreeding) is predicted when many individual pollinators each visit only a small fraction of the available flowers on a plant (Iwasa et al., 1995; Ohashi & Yahara, 2001), and when each pollinator visits flowers in a particular order, if flowers are dichogamous. Pyke (1978b), Feinsinger (1978), and

Rathcke (1992) proposed that these behaviors could be triggered by within-plant variation in nectar rewards, as occurs in plants with gender-biased nectar production. Given that pollinators respond as expected, gender-biased rewards should reduce geitonogamous self-pollination.

The predictions of the inbreeding avoidance hypotheses for gender-biased nectar production are as follows: there are sufficient costs of inbreeding through within-plant pollen movement, and there is a particular response from the pollinators. Of these predictions, the effects of inbreeding provide the primary dichotomy between the inbreeding avoidance and the sexual selection hypotheses. We nevertheless focus the following discussion on the second requirement of the inbreeding avoidance hypotheses, that of pollinator foraging behavior and, specifically, the behavior of pollinators foraging for nectar rather than pollen. A distinct set of pollinator foraging behaviors provides the means by which gender-biased nectar production may be favored.

Predictions Derived from Foraging Theory

Foraging theory predicts that pollinators use information and experience to make decisions that optimize energy intake and maintain a positive energy balance; that is, they choose optimal foraging strategies (Best & Bierzychudek, 1982; Hodges, 1985). Two strategies are particularly relevant for pollinators foraging on plants with variable rewards: absolute or probabilistic threshold departure rules (based on the marginal value theorem; Charnov, 1976; Pyke et al., 1977; Stephens & Krebs, 1986; Dreisig, 1989; Pappers et al., 1999) and risk-sensitive behavior, perhaps better described as avoidance of unpredictable rewards (Stephens & Krebs, 1986; Kacelnik & Bateson, 1996). Each of the above strategies corresponds to one of our two inbreeding avoidance hypotheses. The first, called the declining rewards hypothesis, predicts that a pollinator often visits flowers in order of declining reward quality, and it stops inspecting flowers on a plant if it encounters flowers below a threshold value of nectar. The second, the unpredictable rewards hypothesis, states that a pollinator does not visit flowers in any particular order because rewards are unpredictable, and it departs a plant once it detects a variable nectar supply among flowers on that plant. Using either strategy, pollinator responses to variability may reduce geitonogamy, but the actual cues used differ depending on the strategy. In the following two subsections, we describe these two inbreeding avoidance hypotheses, and we evaluate how well they apply to gender-biased nectar production.

The Declining Rewards Hypothesis

A pollinator may use rules to visit and depart from a plant with or without previous knowledge of rewards. Nevertheless, optimal foraging theory assumes that a nectar-feeding animal knows which plants and flowers within its diet are most rewarding and exploits these options accordingly (Stephens & Krebs, 1986). The assumption of a well-informed pollinator is supported by observational and experimental data (Gass & Sutherland, 1985; Hurly, 1996; Garrison & Gass, 1999; Healy & Hurly, 2001). We therefore begin our discussion of the declining rewards hypothesis under the assumption that pollinators have some preconception of reward quality before visiting the flower.

The declining rewards hypothesis predicts that pollinators foraging on variable inflorescences behave in two particular ways to maximize the rate of energy gain. First, pollinators direct movements within inflorescences from more- to less-rewarding flowers.

This prediction is well supported by foraging studies, particularly those using bees foraging on racemes with nectar gradients (Pyke, 1978a, 1978b; Best & Bierzychudek, 1982; Galen & Plowright, 1985b; Hurly, 1996; Evans, 1996). Second, pollinators should depart before visiting relatively poor options on the inflorescences. This behavior, known as complete or partial preferences, is commonly observed across pollinator taxa (Best & Bierzychudek, 1982; Bell et al., 1984; Devlin & Stephenson, 1985; Galen & Plowright, 1985a, 1985b; Klinkhamer & de Jong, 1990; Kadmon et al., 1991; Cresswell & Robertson, 1994; Gonzales et al., 1995; Aizen & Basilio, 1998). Thus, empirical evidence shows that pollinators often—but not always—leave the inflorescence before visiting less-rewarding flowers.

The above rate-maximizing behaviors are likely to reduce inbreeding only when gender-biased nectar rewards are distributed appropriately among flowers. That is, if female-phase flowers are more rewarding, then pollinators should move from female to male within plants and visit fewer males overall, causing little geitonogamy. If male-phase flowers are more rewarding, however, rates of geitonogamy may be relatively high. If flowers are equally rewarding, an intermediate degree of inbreeding is expected. Thus, female-biased rewards may best reduce inbreeding when rewards are predictable, relative to constant or male-biased rewards.

When pollinators cannot or do not discriminate, they may still use threshold departure rules, which should reduce geitonogamy if rewards are female-biased. Departure from a plant with an unknown reward distribution still follows a visit to a relatively unrewarding flower (Hodges, 1985; Dreisig, 1989) or short series of flowers (Cresswell, 1990; Pappers et al., 1999), but the pollinator does not target the most rewarding flowers at any point during the bout. Pollinators may choose not to discriminate if the rewarding gender is in the majority for the population (Schemske et al., 1996; Castillo et al., 2002) or if discrimination is useless (e.g., Pappers et al., 1999) or costly (Bell, 1986; Gilbert et al., 1991; Smithson & Gigord, 2003). In any case, the declining rewards hypothesis is still a viable explanation of gender-biased rewards.

The Unpredictable Rewards Hypothesis

The unpredictable rewards hypothesis states that pollinators foraging on variable inflorescences are risk-aversive, which should result in reduced plant inbreeding. Risk-aversive behavior is a foraging strategy in which a pollinator attempts to maximize nectar intake by avoiding variable or "risky" alternatives while foraging (Real, 1981; Kacelnik & Bateson, 1996). This body of theory assumes that the reward value of individual flowers on variable plants (or patches of plants) cannot be predicted by pollinators, which is a particularly unattractive possibility for pollinators seeking a positive energy budget (Caraco et al., 1980; Kacelnik & Bateson, 1996). For these foragers, the relationship between energy intake rate and fitness gains is often concave-down, which means that the energetic value of a food item decreases as satiation is approached (Stephens & Krebs, 1986; Kacelnik & Bateson, 1996). Given this relationship, the best foraging strategy is to avoid variable plants altogether (i.e., risk aversion), because the fitness benefit of choosing a more-rewarding flower on a variable plant is outweighed by the cost of choosing a less-rewarding flower (known as Jensen's inequality; Stephens & Krebs, 1986).

There is strong evidence that both vertebrate and invertebrate pollinators employ risk-aversive foraging strategies (reviewed in Kacelnik & Bateson, 1996). Most experiments demonstrate that pollinators avoid variable inflorescences, which are distinguishable based on color cues (Waser & McRobert, 1998; Hurly & Oseen, 1999). In other words, pollinators are often found to be risk-averse *between* inflorescences. Nevertheless, Biernaskie et al. (2002) showed that cryptic variability also can elicit risk-aversive behavior *within* inflorescences, such that departure is earlier from variable inflorescences. For risk-aversive behavior to pertain to within-inflorescence movements, however, we stress that pollinators must detect variability per se and depart from inflorescences following rewarding and unrewarding individual flowers with equal frequencies. If departure from variable inflorescences more often follows an unrewarding visit, then these behaviors are more congruent with threshold departure rules than risk-aversive behaviors.

Under the unpredictable rewards hypothesis, risk-aversive pollinators decrease inbreeding in plants with variable rewards, because they visit only a fraction of available flowers before departure. Here, variable rewards may be achieved by many nectar production patterns, including both male-biased and female-biased nectar production, as long as the reward status of flowers remains unpredictable to pollinators. If variable rewards are to be favored by selection, pollinator responses to variance must decrease inbreeding to the extent that plant reproductive success is increased relative to constant rewards. Indirect evidence that risk-aversive behavior reduces plant inbreeding is limited to a single study using artificial inflorescences. Biernaskie et al. (2002) found that both bees and hummingbirds visited fewer flowers on artificial inflorescences with variable as opposed to constant rewards. They concluded that similar responses to variability would reduce geitonogamy on real plants, but this has yet to be demonstrated.

The Inbreeding Avoidance Hypotheses in Plants with GBNP

The inbreeding avoidance hypotheses are equipped to explain both male- and female-biased nectar production, but these hypotheses are currently supported by only female-biased examples. Female-biased nectar production has been hypothesized to reduce inbreeding via the declining rewards hypothesis in six different bee-pollinated species. Four herbs with female-biased nectar production and vertical inflorescences (*Aconitum columbianum, Delphinium barbeyi, D. nelsonii, Epilobium angustifolium*) provided the data used to formulate this hypothesis (Pyke, 1978b). Pyke predicted that the upward direction of foraging and quick departure following a male-phase visit would cause little geitonogamy and was an adaptive plant trait. Waddington (1981) came to similar conclusions using *Delphinium virescens.* The best evidence for this hypothesis comes from a study by Best and Bierzychudek (1982) using *Digitalis purpurea*. Bee movements were shown to match almost perfectly the predictions of the declining rewards hypothesis: pollinators visited first female-phase flowers and moved on to visit relatively fewer male-phase flowers. They concluded that "the existing pattern of nectar presentation is evidence that natural selection has favored careful regulation of the amount of reward in individual *Digitalis* flowers" (Best & Bierzychudek, 1982, p. 78).

The inbreeding avoidance hypotheses are unlikely to apply to some species with gender-biased nectar production. For example, *Agave, Alstroemeria, Bomarea,* and *Pentagonia* are protandrous at the whole-inflorescence level, such that all flowers are male, then female, with no overlap. Thus, geitonogamy is probably rare or impossible in these species, such that selection on nectar production patterns would not be associated with inbreeding avoidance. Male-biased nectar production in general cannot be well explained by the declining rewards hypothesis, although it may be explained by the unpredictable rewards hypothesis. The unpredictable rewards hypothesis must be disregarded, however, if pollinators are able to discriminate and preferentially visit the more-rewarding flowers.

Variable rewards resulting from gender-biased nectar production theoretically need not be associated with cues or induce departure following a relatively unrewarding visit. Nevertheless, the only existing evidence for inbreeding avoidance comes from plants that do both. This suggests that the declining rewards hypothesis may be more relevant than the unpredictable rewards hypotheses to plants with gender-biased nectar production. If true, male-biased nectar production in most species is probably not an adaptation to reduce inbreeding depression. Based on current evidence, inbreeding avoidance hypotheses should most directly apply to species with female-biased nectar production, upward-decreasing nectar gradients, and, most importantly, a high cost of inbreeding via geitonogamy.

Plants with female-biased nectar production do appear to receive fewer male-to-female visits within the plant, but thus far, reduced inbreeding is inferred only from directionality. Fortunately, evidence that nectar (or lack thereof) can directly decrease geitonogamy does, however, exist in another plant group: the nectarless orchids. The production of rewardless flowers, like the production of variable rewards, is considered an adaptation to reduce consecutive within-plant visits, to ultimately reduce inbreeding (Dressler, 1981). This hypothesis has been explicitly tested in a few nectarless orchids (e.g., *Orchis mascula*, Johnson & Nilsson, 1999; *Disa pulchra*, Johnson, 2000), and is currently best supported by a recent study of *Anacamptis morio* (Johnson et al., 2004). *Anacamptis morio* inflorescences with rewardless flowers received fewer within-plant visits and thereby experienced less geitonogamy, relative to inflorescences with artificially induced rewards in flowers. Thus, natural selection can favor alternative nectar production patterns to result in reduced inbreeding, but evidence for such an effect in plants with gender-biased nectar production is currently lacking.

Other Factors Influencing the Evolution of GBNP

Sexual selection and natural selection against inbreeding are the best-supported explanations for gender-biased nectar production, and they consequently form the two central themes of our review. Nevertheless, three additional factors may also be highly relevant to the evolution of gender-biased nectar production on a case-by-case basis. These factors are resource allocation trade-offs, the effects of floral enemies, and pleiotropy. In the following subsections, we briefly describe each factor and its expected significance to the evolution of gender-biased nectar production. We have found no studies that explicitly link resource allocation trade-offs, floral-enemy effects, or pleiotropy to the evolution of gender-biased nectar production, and thus, empirical support for these possibilities is quite limited.

RESOURCE ALLOCATION TRADE-OFFS

Costs associated with floral nectar production may impede directional selection on nectar production rates. Plant energetic resources may be insufficient to simultaneously increase nectar production, develop all fertilized ovules, and carry out all other essential biological functions. As a result, additional resources allocated toward nectar production must thereby be siphoned from other resource sinks, potentially negating the reproductive benefits of increased pollinator attraction. Evidence for a resource allocation tradeoff involving nectar has been found in *Asclepias syriaca* (Southwick, 1984) and *Blandfordia nobilis* (Pyke, 1991), but not in *Echium vulgare* (Klinkhamer & van der Veen-van Wijk, 1999; Leiss et al., 2004).

Haig and Westoby (1988) examined the resource allocation trade-off between reproduction and attraction from an evolutionary perspective. They predicted that plants should be selected to distribute resources such that reproductive output is limited simultaneously by both pollinators and resources. Resource allocation toward nectar production is therefore maintained at an optimal level: one that balances sufficient pollinator attraction with maximal ovule development. Thus, nectar production should stay constant, unless selection for augmentation is coupled with new, more efficient resource allocation strategies that increase resource provisioning to both plant functions.

Resource allocation trade-offs may limit the production of additional nectar during one floral phase, which may impede selection for gender-biased nectar production in some plants. Nevertheless, a net increase in nectar production is not a necessary requirement of gender-biased nectar production. For example, increased allocation to nectar production during one phase may be countered by decreased allocation to nectar production during the other, resulting in no net change in nectar production rates. Because the ancestral nectar production patterns of plants currently with gender-biased nectar production are unknown, the role of resource allocation trade-offs in their evolution is difficult to reconstruct. We conclude that resource allocation trade-offs alone are unlikely to promote or impede selection for gender-biased nectar production, yet they likely interact with other selection pressures to influence nectar production rates. Their combined result may be gender-biased nectar production with no net change in lifetime nectar production of flowers, relative to original conditions.

EFFECTS OF FLORAL ENEMIES

Floral enemies, such as nectar robbers, pathogens, and herbivores, have occasionally been implicated in the evolution and maintenance of floral traits (Linhart, 1991; Brody, 1997; Shykoff et al., 1997; Strauss, 1997; Galen, 1999). Here, we consider the possibility that nectar robbers and pathogens, in addition to pollinators, have been important selection agents favoring gender-biased nectar production.

Nectar robbers and pathogens may alter the outcome of selection on floral traits by rendering disadvantageous the traits that are initially most attractive to pollinators. Nectar robbers—birds or arthropods that steal nectar without pollinating the plant—may visit preferentially flowers with higher nectar rewards (Galen, 1999). Consequently, the most attractive flowers are those most likely to experience any reproductive costs of robbery, either due to nectar robber damage to developing seeds (Traveset et al., 1998; Galen, 1999) or, more commonly, through pollinator avoidance of robbed flowers (Roubik, 1982; Irwin & Brody, 1998; Irwin et al., 2001). Floral pathogens that use pollinators as vectors may affect floral trait evolution in a similar way (Shykoff & Bucheli, 1995; Shykoff et al., 1997). An increased risk of infection and sterilization of attractive plants is likely to counter possible benefits of increased pollinator visits when floral pathogens are involved.

If nectar robbery or floral pathogens are particularly damaging to the plant (through either male or female function), it may be beneficial to make flowers less attractive. This may be achieved by providing a smaller or less appealing nectar reward (Willson & Ågren, 1989; Adler, 2000). In species with gender-biased nectar production, a smaller reward may equate to reduced nectar production in one of the two sexual phases. The sexual phase whose fecundity is decreased more by robbery (or fungal infection) is predicted to have relatively smaller rewards, based on expectations that selection is gender-specific (Willson & Ågren, 1989; Irwin & Brody, 2000). Even in the absence of gender-specific selection, nectar may be biased away from the first phase (regardless of gender) if robbery is prolonged or signs of robbery are carried over to the next phase. In summary, gender-biased nectar production may be selected for by enemies if reduced nectar production during one sexual phase decreases damaging visits to flowers of that phase and thereby increases total plant fitness.

Selection imposed by floral enemies may explain gender-biased nectar production, but only in a limited spectrum of plants. First, plants must suffer a high cost of nectar robbery or disease to male function, female function, or both. Costs of robbery have been demonstrated for only a few plant species, and their relative importance to total reproductive success is a matter of debate (Maloof & Inouye, 2000; Irwin et al., 2001; Irwin & Maloof, 2002). The costs of a sterilizing fungal disease are less contentious (Shykoff et al., 1997). Second, the effects of floral enemies on a plant must decrease with decreasing nectar rewards during the male or female phase, which in turn must increase total reproductive output relative to plants with unbiased rewards. In *Impatiens capensis*, female-phase flowers produce less nectar than male-phase flowers, and these flowers also experience decreased nectar robbery (Temeles & Pan, 2002). For *I. capensis*, however, male-biased nectar production is probably not a result of selection for increased female output through decreased nectar robbery during the female phase. This is because the gender-specific costs of robbery to *I. capensis* are likely countered and overwhelmed by gender-specific selection for increased pollen removal by pollinators (Bell et al.. 1984; Temeles & Pan, 2002). In *I. capensis* and similar examples, selection by enemies is unlikely to override selection by pollinators. This may account for the paucity of evidence in favor of an enemy-associated effect on nectar production. Nonetheless, floral enemies may conceivably contribute to the overall strength of selection on nectar production patterns.

PLEIOTROPIC EFFECTS

Floral traits may evolve by selection acting on other, unrelated traits. These pleiotropic relations may explain gender-biased nectar production, particularly when this nectar production pattern does not appear to benefit the plant (i.e., unbiased rewards confer higher total fitness). Although genetic correlations due to pleiotropic effects are difficult to identify, phenotypic correlations between nectar production and other plant traits have been measured in many cases. Nectar volume is phenotypically correlated with many plant and flower traits, including corolla dimensions (positive correlation; Ashman & Stanton, 1991; Galen, 1999), root weight (positive correlation; Pleasants & Chaplin, 1983), and umbel size (negative correlation; Pleasants & Chaplin, 1983). Nectar volume is genetically correlated with a more limited subset of traits, including nectar sugar concentration (Klinkhamer & van der Veen-van Wijk, 1999) and flowering date (Mitchell & Shaw, 1993). Very few data are available on genetic correlations among floral traits, but those that exist suggest selection for correlated traits has the potential to influence floral evolution (Mitchell, 2004).

Phenotypic correlations may occur between the same trait in male and female individuals, in individuals in different environments (Roff, 1997), or in the male and female phases of the same flower. In species with gender-biased nectar production, nectar production rate and maturation of male and female parts necessarily vary together. In the protandrous plants *Streptanthus carinatus* and *S. culteri*, flowers do not open completely until they enter the female phase (Rollins, 1963). In this case, maturation of the nectaries likely matches that of the gynoecia, which results in female-biased nectar production. If the above phenotypic correlation between nectary and gynoecial development reflects a true pleiotropism, selection for traits causing protandry may thereby be the driving force behind female-biased nectar production in this species, rather than selection on the nectar production pattern itself. Secondary traits with gender-biased expression, such as color, corolla morphology, and pollen rewards, may also be pleiotropically linked to nectar production during a floral phase, and they are often subject to strong selection independent of nectar rewards (Waser & Price, 1981; Campbell et al., 1996; Melendez-Ackerman et al., 1997; Cresswell, 1999). When the true target of selection is developmentally linked through pleiotropy to nectar, gender-biased nectar production may arise and be maintained as a nonadaptive trait.

Future Directions

In this paper, we highlight plants with gender-biased nectar production for their potential to advance various lines of research within floral biology and evolution. To date, few of these species have been subject to intensive study, and for many, none of the hypotheses recognized by this paper have been tested. Below, we outline a series of experiments and predictions that, when performed together, should indicate the hypothesis (or hypotheses) that best explains gender-biased nectar production in a particular species. We assume here that gender-biased nectar production is a heritable trait, but suggest that this assumption be explicitly tested for each species studied. The experiments we propose pertain to two categories: first, the study of plant reproductive biology, and second, the study of pollinator behavior. The former category may be further divided into tests for intrasexual selection and for fitness costs due to inbreeding.

TESTS OF HYPOTHESES FOR GBNP USING PLANTS

Detecting Intrasexual Selection in Plants

To assess intrasexual competition for pollinators, the relationships between mating success and male versus female reproductive output must be measured, and the strengths of these relationships may then be compared to nectar production rates during each sexual phase. In addition, it must be shown that nectar production and pollinator visits are directly related. The experimental manipulation of nectar may be used in direct tests of sexual selection hypotheses. If the augmentation of nectar in a floral phase increases pollinator visits to that phase, and increased visits differentially affect male and female reproductive output (i.e., there is an interaction between sexual phase and nectar addition), then there may be intrasexual competition for pollinators. If nectar production is male-biased and male reproductive output is more strongly limited by nectar production (and pollinator visits) than is female reproductive output, then the male function hypothesis is supported. If nectar production is female-biased and female reproductive output is more strongly nectar-limited, then the female function hypothesis is supported.

Assessing the Costs of Inbreeding in Plants

To explore the inbreeding avoidance hypotheses from the plant perspective, the potential for inbreeding via geitonogamy and inbreeding depression must be measured. Because inbreeding may have gender-biased effects, its consequences must be measured separately for male and female reproductive output, in terms of both pollen discounting and inbreeding depression. If a plant population is self-compatible, has male- and female-phase flowers open simultaneously, and produces fewer offspring or offspring of poorer quality when inbred as opposed to outcrossed, this is preliminary support for both of the inbreeding avoidance hypotheses. Decreased inbreeding, as caused by gender-biased nectar production, must also be linked with increased plant reproductive success. Nectar manipulations again may serve to tease apart the relationships among gender-biased rewards, reproductive losses to inbreeding, and reproductive gains through outcrossing. In this case, however, pollen tracking or paternity analysis is needed to determine the number of inbred versus outcrossed offspring produced by plants receiving different nectar treatments.

TESTS OF HYPOTHESES FOR GBNP USING POLLINATORS

Reproduction in animal-pollinated plants cannot be fully understood without consideration of the pollinator. Similarly, most of our hypotheses cannot be fully tested without some measurement of pollinator responses. We therefore suggest that researchers quantitatively assess pollinator foraging behavior on plants with gender-biased rewards to test specific assumptions of the sexual selection and inbreeding avoidance hypotheses. Below, we explain how the present-day responses of pollinators should reflect the relative likelihood of the different evolutionary hypotheses for gender-biased nectar production. If the selection environment has changed drastically, these observations should at least reflect the role of pollinators in the maintenance of the trait today.

Distinguishing between Alternatives Using Pollinator Foraging Behavior

Both the sexual selection and inbreeding avoidance hypotheses are based on the assumption that a pollinator is unlikely to visit all flowers on a multiflowered plant (both male and female flowers present) during every visit to the plant. If true, then knowledge of partial preferences and directionality should facilitate discrimination among most evolutionary hypotheses. For example, under the sexual selection hypotheses, pollinators must exhibit partial preferences for the more-rewarding flower, which in this case implies that they are able to distinguish male- and female-phase flowers (based on spatial location or visual cues). Under the declining rewards hypothesis, an informed and discriminating pollinator is not an essential requirement, although it is anticipated, based on optimal foraging theory. Under the unpredictable rewards hypothesis, in contrast, a pollinator cannot be informed or discriminating, and all flower types may be visited at roughly equal frequencies.

Sexual selection and inbreeding avoidance hypotheses also differ in the required directionality of within-plant movements made by pollinators. Under the sexual selection hypotheses and the unpredictable rewards hypothesis, there is no required order of visits, such that male-to-female moves may be as frequent as female-to-male moves, regardless of gender-biased direction. Under the declining rewards hypothesis, however, pollinators are required to move from higher rewards to lower rewards within the plant. Nevertheless, these criteria are unlikely to allow investigators to completely discriminate between sexual selection and inbreeding avoidance hypotheses. This is because both directionality and frequency may be similar under either set of hypotheses. Pollinators often (but not always) visit more-rewarding flowers first, and depart before visiting less-rewarding flowers (required by declining rewards and permitted by sexual selection), which results in a higher frequency of visits to more-rewarding flowers (required by both sexual selection and declining rewards). These comparisons, in combination with results from the plant reproductive biology experiments, should, nevertheless, allow elimination of hypotheses that are unlikely to have contributed to gender-biased nectar production in individual species.

Concluding Remarks

In many influential articles and reviews, Willson (1979, 1990, 1994) has argued that sexual selection is an important yet generally underappreciated force in the evolution of floral traits. We concur and endorse sexual selection as a potential explanation for gender-biased nectar production in many hermaphroditic plants. Nonetheless, we find sexual selection hypotheses insufficient to completely explain all examples of gender-biased nectar production, and we contend that hypotheses based on selection against inbreeding are important alternative or complementary explanations for many species. We cite available data on plants with female-biased nectar production and nectar gradients along vertical racemes to support these claims. We also stress that both sets of hypotheses are not mutually exclusive, and more than one hypothesis may apply to a single species. Finally, we propose that other factors, such as pleiotropy or floral enemy effects, may also be of importance in the evolution and maintenance of gender-biased nectar production, particularly if the primary hypotheses are not supported.

We acknowledge that no single test discriminates between the different hypotheses, and more than one hypothesis may apply simultaneously. Nonetheless, we have proposed sets of tests that together address in detail the leading evolutionary hypotheses for gender-biased nectar production in hermaphroditic plants. We stress that all possibilities warrant consideration in future studies and that the few well-established examples should perhaps be reexamined to definitively rule out alternative hypotheses. Completing the causal links among nectar production patterns, pollinator behavior and male and female components of plant fitness promises to be a complex task, but it is also an important and timely one. In addition to providing unique insights into gender-biased expression and function of floral traits, such research has the potential to unify diverse fields. Multiple disciplines, including pollinator cognitive biology, plant reproductive biology, and floral evolution, must all be brought to bear if we are to fully understand the underlying causes of gender-biased nectar production as a functional, evolved trait.

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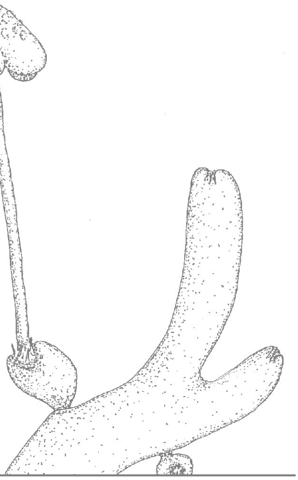

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