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Sex Allocation and Reproductive Success in the Andromonoecious Perennial *Solanum carolinense* (Solanaceae). II. Paternity and Functional Gender

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ABSTRACT: According to Bateman's principle, male fitness in entomophilous plant species should be limited by mating opportunity, which is influenced by the size or number of flowers. We determined male-specific fitness consequences of floral phenotype in andromonoecious *Solanum carolinense*, examined the relationship between male and female reproductive success within plants, and evaluated the distribution of functional gender among plants. A maximum likelihood-based paternity analysis, based on multilocus allozyme phenotypes of parents and offspring from four experimental plots, was used to determine male reproductive success and its relationship to floral phenotype. Male success was enhanced by an increase in the proportion of male flowers produced but not by an increase in total flower number, even though all flowers contain male parts. Larger flower size increased male success in only one plot. Male and female reproductive success were negatively correlated, and plants varied in functional gender from completely female to completely male. This gender specialization may occur because hermaphroditic and male flowers differ in their ability to contribute to male and female success. Although sex allocation theory predicts a positive relationship between the size or number of plant parts and reproductive success, this study indicates that aspects of floral morphology that affect gender specialization should also be considered.

Keywords: andromonoecy, Bateman's principle, functional gender, paternity analysis, sex allocation, *Solanum carolinense*.

Bateman's principle (Bateman 1948; Wilson et al. 1994) asserts that fitness gain through male function is limited

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primarily by mating opportunity, while fitness gain through female function is limited primarily by resource availability for offspring production. This idea has been integrated with sex allocation theory (Charnov 1982). When applied to plants, sex allocation theory predicts that floral attractiveness (e.g., large petals, nectar availability) is more important to fitness gain through male function than female function because attracting pollinators will increase mating opportunities. Although male success should be correlated with mating opportunities, one or a few visits by pollinators may be adequate to fertilize all ovules; thus, female fitness should not be as strongly affected by floral attractiveness. Because male success relies on both pollinator response to floral attractiveness and another plant's resource base for seed production, male reproductive success is also predicted to be more variable than female reproductive success.

Empirical support for Bateman's principle in plant species is limited and has been equivocal (see reviews in Wilson et al. 1994; Campbell 2000). Fitness through male function has been shown to increase with increased pollen production (Devlin et al. 1992) or the number of flowers producing pollen (Queller 1983; Schoen and Stewart 1986). For entomophilous plants, flower size (Bell 1985; Young and Stanton 1990) and overall floral display (Broyles and Wyatt 1990, 1995; Fishbein and Venable 1996) are also considered to be important for male success. Some studies, however, have found that flower size can be as important for female success as it is for male success (Campbell 1989; Stanton et al. 1991; Wilson et al. 1994; Conner et al. 1996a, 1996b) and that display size is not always correlated with male success (Meagher 1991). In studies comparing variance in male and female performance, male success has been found to be more variable than female success (Müller-Starck and Ziehe 1984; Meagher 1986), less variable than female success (Devlin and Ellstrand 1990; Dudash 1991), and more variable or less variable in different years (Conner et al. 1996b).

In hermaphroditic species, male and female reproductive success are often positively correlated, although weakly

(Broyles and Wyatt 1990; Devlin and Ellstrand 1990; Conner et al. 1996*b*). It has been assumed that some traits, such as flower production or overall plant vigor, influence both sex functions. However, some characteristics of the floral display may disproportionately increase success through one or the other sex function, as predicted by sex allocation theory. Thus, individuals that differ in their floral phenotype may differ in their functional gender, the relative amount of reproductive success gained through female function (Lloyd 1980, 1984).

In order to address the relationship between floral phenotype and male success as well as the relationship between male and female success, it is necessary to measure male success using paternity analysis (e.g., Meagher 1986, 1991; Schoen and Stewart 1986; Broyles and Wyatt 1990; Devlin and Ellstrand 1990; Adams and Birkes 1991; Stanton et al. 1991; Karron et al. 1995*a*, 1995*b*; Conner et al. 1996*b*; Burczyk and Prat 1997; Kaufman et al. 1998; Morgan 1998). On the basis of multilocus genotype profiles for a set of offspring, their known mothers, and the array of potential fathers, one can determine maximum likelihood fertility estimates for all of the males in a population (Roeder et al. 1989; Smouse and Meagher 1994). Recently, the maximum likelihood approach has been extended to enable direct regression of male characters on fertility (Adams and Birkes 1991; Adams et al. 1992; Smouse et al. 1999), allowing us to address more effectively the assumptions of sex allocation theory.

This article is part of a series exploring the relationship between sex allocation and sex-specific success in the andromonoecious perennial plant *Solanum carolinense*. Prior work has shown that floral characters are heritable in this species (Elle 1998) and that increased flower number and a decreased proportion of male flowers enhance female success, which is unrelated to flower size or vegetative vigor (Elle 1999). In this article, we explore the relationship between allocation to reproductive characters and both realized male success and functional gender by addressing the following questions: What is the distribution of male success in experimental populations of *S. carolinense*? What is the relationship between male success and floral phenotype? What is the functional gender of individuals, and how is functional gender related to floral phenotype?

Methods

The Study System

Solanum carolinense (L.), Solanaceae (horse nettle), is a self-incompatible andromonoecious perennial and so produces both male and hermaphroditic flowers. Male flowers are smaller overall (Solomon 1986; Elle 1998), have greatly reduced nonfunctional pistils, and are incapable of setting

fruit (Solomon 1986). Hermaphroditic flowers are produced basally, the male flowers (when present) at the tips of inflorescences. Pollen viability does not differ between the two flower types (Solomon 1985). The showy anthers are attractive to pollinators, for whom pollen is the only reward (Solomon 1987). Flowers are buzz pollinated by large-bodied bees, which hang from the flowers and vibrate their flight muscles, causing pollen to be ejected from a terminal pore in the anther (Buchmann 1983; Solomon 1986). Fruit contain an average of 160 seeds (E. Elle, unpublished data).

Ripe fruit were collected from 12 source plants in each of three natural populations: a sheep pasture at Cook College, Rutgers University, New Jersey; Brookfield Landfill on Staten Island, New York; and an old field (~15 yr since abandonment) at Hutcheson Memorial Forest, Franklin Township, New Jersey. Three distinct populations were used as seed sources to increase the genetic and phenotypic variation among plants used in this experiment. Source populations were 20–70 km distant from one another. Source plants were chosen that were spatially separated so as to minimize the probability of choosing multiple ramets from single genets.

Experimental Plots

Experimental design has been described elsewhere (Elle 1999), with the most relevant information repeated here. Two plots were set up in opposite corners of a 30 × 70-m rectangle in each of two sites. Plots A and B were in an old field at Hutcheson Memorial Forest (HMF), Franklin Township, New Jersey, in a 10-yr-old experimental field. Plots C and D were established in an agricultural field at Rutgers Vegetable Research Farm 3 (VRF), New Brunswick, New Jersey, ~25 km away from HMF. Both sites were bordered by woods with no known population of *S. carolinense* within 500 m. All four plots were studied in 1994, and two plots (one in each site) were followed for a second year to assess between-year variation.

In order to facilitate paternity analyses, plants used to set up field plots were chosen to maximize genetic variability. Approximately 600 seedlings (15 from each source plant) were screened for allozyme variation by means of starch gel electrophoresis performed on leaf tissue, utilizing protocols modified from Soltis et al. (1983) and Pasteur et al. (1988). Assay/buffer combinations found to be polymorphic and subsequently used for this study were peroxidase (PER), 6-phosphogluconate dehydrogenase (6-PGD), and triose phosphate isomerase (TPI, two loci), on a histidine pH 5.7 buffer system and glutamate oxaloacetate transaminase (GOT) on a lithium borate pH 8.3 buffer system. Gels were run at 220 V and 50 mA in a cold room (5°C) for either 4 h (histidine) or 6 h (lithium

borate). Thus, 43 plants with 24 unique multilocus genotypes were identified. Expected exclusion probabilities (Chakraborty et al. 1988) based on allozyme data for the subset of these 43 plants that flowered in each plot-year (table 1), although on the low side, are typical of those obtained in previously applied analyses of paternity in plant populations (Meagher 1986; Chakraborty et al. 1988; Conner et al. 1996b). The purpose of generating expected exclusion probabilities is usually to determine the feasibility of proceeding with a paternity analysis. In this case, we are presenting expected exclusion probabilities to demonstrate that a paternity analysis using maximum likelihood methods can be informative even in the face of relatively low expected exclusion probabilities.

Each plot consisted of a hexagonal array (1-m spacing between plants) containing clonal replicates of each of the 43 individuals chosen for this experiment. Placement of the 43 plants was independently randomized for each plot. Size and spacing within these experimental plots are similar in overall scale to natural populations of *S. carolinense*. Hexagonal arrays were used to ensure uniform density and to maximize the number of nearest neighbors for all plants, thus minimizing possible impacts of variation in intermate distance on reproductive success (Schmitt 1983; Van Treuren et al. 1993; Karron et al. 1995a).

We treated each plot as genetically distinct in the paternity analyses. Although there may have been some gene flow between plots within a site in 1994, previous studies have indicated that pollen movement in entomophilous species is often restricted to a few meters (Levin 1981; Handel 1983; Meagher 1986; Galen 1992; Krauss 1994; Smouse et al. 1999), although there can be pollen movement over greater distances (Ellstrand and Marshall 1985; Campbell 1991; Kohn and Casper 1992; Godt and Hamrick 1993; Broyles et al. 1994). Furthermore, the distance between plots within sites (40 m) exceeded USDA Animal and Plant Health Inspection Service isolation standards for seed purity in Solanaceous crops (<http://www.aphis.usda.gov>). Thus, although we expected some gene flow between plots within a site in 1994, we assume that it is low enough to enable us to analyze each plot separately. This assumption was supported by the fact that obtained slightly different results for adjacent plots (see "Results"); the effect of gene flow would be to homogenize results among plots. In 1995, only one plot per site was left in place and the other destroyed so that there was no possibility of gene flow between plots within a site in the second year of the study.

Phenotypic Measurements

For each individual within each plot-year combination, we counted the total number of flowers (hermaphroditic plus male), from which we calculated the proportion of male

Table 1: Allele frequencies and paternity exclusion probabilities (P_{ex}) of potential male parents (plants in flower) for each plot-year included in the analysis

	Allele frequencies			P_{ex}
Plot A 1994:				
PER	.59	.4118
6-PGD	.91	.0908
TPI-1	.88	.1209
TPI-2	.88	.1209
GOT	.21	.69	.10	.14
Cumulative53
Plot B 1994:				
PER	.66	.3417
6-PGD	.86	.1411
TPI-1	.89	.1109
TPI-2	.86	.1411
GOT	.23	.66	.11	.26
Cumulative55
Plot C 1994:				
PER	.55	.4519
6-PGD	.91	.0908
TPI-1	.89	.1109
TPI-2	.89	.1109
GOT	.24	.67	.09	.25
Cumulative53
Plot D 1994:				
PER	.61	.3918
6PGD	.89	.1109
TPI-1	.89	.1109
TPI-2	.88	.1209
GOT	.25	.64	.11	.27
Cumulative55
Plot A 1995:				
PER	.63	.3718
6PGD	.92	.0807
TPI-1	.89	.1109
TPI-2	.92	.0807
GOT	.13	.76	.11	.21
Cumulative48
Plot D 1995:				
PER	.56	.4418
6PGD	.91	.0908
TPI-1	.90	.1008
TPI-2	.90	.1008
GOT	.21	.68	.11	.25
Cumulative52

Note: Abbreviations used in the table are as follows: PER = peroxidase; 6-PGD = 6-phosphogluconate dehydrogenase; TPI = triose phosphate isomerase (two loci); and GOT = glutamate oxaloacetate transaminase.

flowers. Total flower production is a measurement of allocation to male function because all flowers produce anthers with viable pollen, while the proportion of male flowers produced measures the frequency of flowers that are incapable of achieving reproductive success as females.

We determined flower size by measuring corolla width, pistil length, and anther length and width of four hermaphroditic flowers. Production of male flowers was sporadic; therefore, flower size measures used in the analysis are individual means calculated from hermaphroditic flowers only (table 2). One of the plots (plot C 1994) produced very few flowers because of herbivory and weed growth; flower size data for this plot-year are therefore not presented. In other instances where flower size could not be measured for a plant, mean flower size for that plot-year combination was used in the paternity analysis.

Because vegetative size of individuals indicates their potential resource status, which may affect sex allocation (Queller 1997), it was included in the analysis. For each individual in each plot, we measured height at the end of the growing season, the number of branches produced, and length and width of either two leaves per plant (1994) or one leaf per ramet (1995). These characters were summarized for each plot-year using principal components analysis. The first principal component accounted for 50%–76% of the variation in the data and is positively loaded on all vegetative characters measured (Elle 1999); thus, it was used as an estimate of overall vegetative vigor.

Paternity Analyses and Male Reproductive Success

Male reproductive success was evaluated with a paternity analysis program (PatQuest, available from T.R.M. on request) based on maximum likelihood methodologies discussed in Meagher (1986), Smouse and Meagher (1994), and Smouse et al. (1999). Analyses were performed sep-

Table 3: Tests of significance for differences among males in their reproductive contributions for each plot in each year (male effects)

	N_p	N_f	df	LLR	P
1994:					
Plot A	185	29	21	68.2	.0000
Plot B	77	22	18	19.1	.3863
Plot C	103	32	21	22.2	.3881
Plot D	352	32	22	23.8	.3599
1995:					
Plot A	84	19	14	34.7	.0016
Plot D	1,202	40	23	223.7	.0000

Note: Abbreviations: N_p = number of progeny analyzed; N_f = number of flowering individuals in plot; df for male effects = number of genotypes - 1 (see "Methods"). The log-likelihood ratio (LLR) is asymptotically χ^2 distributed, from which distribution P values are calculated.

arately for each plot-year combination. At least 10 seeds per maternal parent were germinated, and their leaves were subjected to electrophoresis to determine multilocus allozyme genotypes. For individuals producing multiple inflorescences, five seeds per inflorescence were assayed. Thus, individuals with high seed production had more offspring included in the paternity analysis, reflecting the distribution of potential mating opportunities over time. Also, variation among plots in seed set resulted in variation in the overall number of progeny analyzed per plot (see table 3).

Maximum likelihood (ML) analysis of male fertility profiles (Smouse and Meagher 1994) is based on Mendelian

Table 2: Means \pm standard deviation for floral and vegetative phenotypes

	1994				1995	
	Plot A	Plot B	Plot C	Plot D	Plot A	Plot D
Floral phenotype:						
Flower number	21.6 \pm 32.9	11.2 \pm 6.6	9.3 \pm 9.7	18.8 \pm 15.7	11.5 \pm 9.6	60.6 \pm 55.3
Proportion male flowers	.34 \pm .33	.26 \pm .26	.40 \pm .31	.55 \pm .26	.41 \pm .37	.14 \pm .15
Corolla diameter (mm)	28.7 \pm 2.9	27.8 \pm 2.2	...	29.4 \pm 3.4	24.7 \pm 2.9	27.8 \pm 3.9
Pistil length (mm)	11.2 \pm 1.0	10.1 \pm 2.6	...	11.5 \pm 1.6	9.0 \pm 1.3	10.5 \pm 1.3
Anther length (mm)	7.0 \pm .5	6.8 \pm .8	...	7.1 \pm .5	5.9 \pm .7	7.1 \pm .7
Anther width (mm)	1.9 \pm .1	1.8 \pm .1	...	1.9 \pm .2	1.7 \pm .2	2.0 \pm .4
Vegetative phenotype:						
Final height (cm)	40.9 \pm 11.5	32.8 \pm 7.6	30.0 \pm 7.9	37.0 \pm 8.6	24.2 \pm 7.2	33.4 \pm 8.6
Branches	5.3 \pm 3.6	5.2 \pm 2.3	4.7 \pm 3.0	5.1 \pm 2.7	.3 \pm .5	3.2 \pm 2.1
Leaf length (cm)	9.7 \pm 1.1	9.2 \pm 1.2	7.2 \pm 2.0	9.6 \pm 1.6	6.7 \pm .7	8.2 \pm 2.0
Leaf width (cm)	3.3 \pm .5	3.1 \pm .49	2.3 \pm .7	3.1 \pm .6	2.2 \pm .4	2.7 \pm .8
Ramets (spring 1995)	3.1 \pm 1.9	2.6 \pm 1.8	4.4 \pm 2.1	3.4 \pm 2.1
Female success (total seeds)	398.9 \pm 682.7	288.7 \pm 238.3	79.8 \pm 75.6	733.7 \pm 756.0	52.0 \pm 56.3	2,766.3 \pm 3,062.3

Note: Flower number, proportion male, and total seed set were measured on flowering individuals only: plot A 1994, 29; plot B 1994, 22; plot C 1994, 32; plot D 1994, 32; plot A 1995, 16; plot D 1995, 37. Flower size measurements were based on the following number of individuals: plot A 1994, 13; plot B 1994, 15; plot D 1994, 11; plot A 1995, 12; plot D 1995, 35. Vegetative characters were measured on all 43 individuals; ramet production was counted in spring of 1995.

segregation probabilities $\{x_{ik}\}$ for the i th mother-offspring genotype pair on the k th male genotype. Maximum likelihood estimates of male fertility, $\Lambda = [\lambda_1, \lambda_2, \dots, \lambda_k]'$, where λ_k is the relative fertility of the k th male, are obtained by maximizing the likelihood function:

$$L(\Lambda | \text{genetic data}) \propto \prod_{i=1}^N (\lambda_1 x_{i1} + \lambda_2 x_{i2} + \dots + \lambda_k x_{ik}). \quad (1)$$

Tests for significant heterogeneity among ML fertility estimates $\{\lambda_k\}$ are based on a log-likelihood ratio (LLR) criterion, which is twice the difference between the log-likelihood for the ML estimates and the one for a null model in which all males are assumed to have equal contributions. The resulting LLR is asymptotically χ^2 distributed with degrees of freedom equal to one less than the number of distinct male genotypes (Smouse and Meagher 1994). Nonflowering plants were not included in the analysis because they could not have contributed pollen. As noted below, LLR statistics, though asymptotically χ^2 , are not particularly amenable to testing using χ^2 test criteria. We apply χ^2 test criteria in our analysis of heterogeneity in male success because we are primarily using this test as guidance as to whether to proceed with more detailed analysis of factors contributing to male reproductive success rather than as a finishing point for the analysis.

If plants vary in paternal contributions, the next step is to evaluate the relationship between male success and phenotype. We used an extension of the likelihood model above (Smouse et al. 1999) to assess the effects on male success of seven phenotypic features: flower number, the proportion of flowers that are male, flower size (corolla diameter, pistil length, anther length, and anther width), and vegetative vigor. Thus, male fertilities are estimated according to the following model:

$$\log(\lambda_k) = \beta_1 z_{1k} + \beta_2 z_{2k} + \dots + \beta_j z_{jk}, \quad (2)$$

where the $\{z_{jk}\}$ are measurements of the j th feature in the k th male and $\{\beta_j\}$ are regression coefficients that relate the j th feature to male fertility. Estimates of $\{\lambda_k\}$ can then be assessed according to likelihood criteria (eq. [2]) to obtain ML estimates of $\{\beta_j\}$. To test for significance of the model incorporating all traits, we generate LLR test statistics where the null model includes no male features ($\{\beta_j\} = 0$) and the alternative includes all seven features. Statistical significance indicates that at least one phenotypic feature is contributing to variance in male fertility. To test individual features, we contrast a model including the six other features with the full (seven feature) model. In each of these tests,

degrees of freedom equal the difference in the number of features included in the contrasted models.

It has been shown that LLR test statistics can have a considerable departure from a χ^2 distribution in paternity analyses, typically in terms of greatly inflated values, even though they are asymptotically χ^2 (Smouse et al. 1999), so we applied a bootstrap analysis to our results, where feasible, to generate an additional test criterion. For overall analyses of ML fertility estimates $\{\lambda_k\}$, it was not feasible to apply bootstrap tests simply because the underlying parameter space (one per male included) was too large. For the tests of significance of $\{\beta_j\}$, we conducted bootstrap tests of significance based on random permutation among males of their feature profiles. We conducted two series of bootstrap tests. In the first bootstrap, we performed 1,000 random permutations of the male feature profiles among the males, and then generated univariate analyses for each of the $\{\beta_j\}$. The results from this bootstrap, in which a model including a single β parameter is contrasted to the null where all $\{\beta_j\}$ are set to 0, is analogous to a Type I ANOVA (SAS Institute 1988). The reasoning behind this analogy is that, because the character is being tested in isolation, its effects will also encompass nonorthogonal effects of the other phenotypic features included in the analysis because of the covariance structure of the data. The phenotypic measures used here are all correlated to some degree, both genetically and phenotypically (Elle 1998, 1999). In the second bootstrap, we randomized male feature profiles as before, but to test for a specific β parameter, we contrasted the log likelihood of the model including all $\{\beta_j\}$ to one that excluded only the parameter being tested, resulting in a test that is analogous to a Type III ANOVA. Because the full model and null model include all of the other phenotypic characters, the covariance structure involving the other characters is, to some degree, being accounted for in this analysis. Because of the increased complexity of this analysis, 400 random permutations were performed.

Distance between potential mates can also be an important determinant of male fertility and can be evaluated by use of an extension of the above likelihood model that incorporates a distance effect parameter γ (Adams and Birkes 1991; Smouse et al. 1999) as follows:

$$\log(\lambda_{jk}) = \gamma \delta_{jk}, \quad (3)$$

where $\{\lambda_{jk}\}$ represent the fertility of the k th male on the j th female, and $\{\delta_{jk}\}$ represent \ln distance between the k th male and j th female. Because the consequence of departures from χ^2 in paternity analyses is typically an inflated test statistic, application of bootstrap test criteria is particularly important when χ^2 test criteria indicate a statistically significant result where there may not be one. There was no

need to conduct bootstrap analyses on distance effects results because they showed no statistical significance (see “Results”).

Comparison of Male and Female Reproductive Success

Because *S. carolinense* is a cosexual species, male and female reproductive success can be enumerated and compared within plants. However, it is important to note that male reproductive success and female reproductive success are measured in different ways, such that comparisons between them should be treated as approximate. Maximum likelihood estimates of male fertility result from a statistical model and, thus, are not equivalent to estimates of seed set, which are based on direct measurement. Furthermore, ML estimates of male fertility are known to be biased downward in terms of variance because the performance of less successful males is overestimated and the performance of more successful males is underestimated (Roeder et al. 1989; Smouse and Meagher 1994; Morgan 1998). Because our hypothesis is that male success should have a higher variance than female success, this bias will make our analysis relatively conservative. Nevertheless, the results of this portion of our study, although of inherent biological interest, should be viewed in the context of these statistical caveats.

For each plot-year combination, variances in male and female success were calculated and compared using *F* ratios. For individuals with at least some reproductive success through one or the other sex, we calculated correlations between male and female success. Plants with no reproductive success through either male or female function were excluded from the correlation estimates because their inclusion would lead to artifactually inflated positive correlations.

Functional gender was calculated for those individuals with nonzero reproductive success and so with a definable gender. Using protocols developed by Lloyd (1980, 1984), we calculated functional gender (G_i) as $f_i/(f_i + m_i)$, where f_i is the relative number of seeds produced by the *i*th individual and m_i is the relative number of seeds sired by that same individual. Functional gender ranges from 0 (fully male) to 1 (fully female), with equisexual plants having a gender of 0.5.

The effect of flower number and proportion male on functional gender was evaluated through multiple regression. Because flower size and vegetative size were found to be unimportant for female success (Elle 1999), inconsistently related to male success (see “Results”), and unimportant to functional gender in preliminary analyses, these variables were not included in the analysis presented. To conform to the assumptions of the regression analysis, flower production was log transformed and proportion male

was arcsine square root transformed. Both of these variables were standardized to mean = 0 and variance = 1 before the analysis.

Results

Male Reproductive Success

In three of the plot-year combinations, plants had significantly heterogeneous male success (table 3; fig. 1). In the other three plot-year combinations (all in the first year), plants did not vary significantly in male success. Spatial and temporal environmental variation was obviously of some importance to male success.

Relationship of Phenotype to Male Success

For the three plots in which plants exhibited differences in their male reproductive success, we tested the model relating floral characters to male success. In all cases, the full model including flower number, proportion male, the four flower size variables, and vegetative vigor accounted for a significant proportion of the variation among plants in male success (table 4), indicating that differences among males in their relative success are influenced by phenotype.

For purposes of comparison, we present statistical test evaluation using both χ^2 and bootstrap criteria for Type I univariate and Type III multivariate tests (table 4). Bootstrap test results confirmed that, overall, the LLR test statistics were substantially inflated relative to χ^2 distribution test criteria, so we used the bootstrap test criteria to interpret phenotypic effects on male reproductive success. In general, Type I univariate bootstraps showed several parameters to be statistically significant, and Type III multivariate bootstraps showed the same parameters to lack significance (table 4). Thus, χ^2 test criteria were excessively lax, Type I bootstrap criteria were relatively conservative, and Type III criteria were very conservative. To provide guidance on the interpretation of these bootstrap results, we examined the distribution of bootstrap results for each male feature. For presentation, we have chosen bootstrap results for proportion of male flowers (fig. 2) because that character appears to be an important factor in determining male reproductive success (see table 4). The Type I analyses appear to have a greater discriminatory potential in that, as the parameter value departs from 0, the resulting test statistics also increase in approximate proportion, whereas for the Type III analyses, as the magnitude of the parameter increases so does the variation in LLR scores. Although precise power calculations are not feasible for these analyses, the tendency for LLR variation to increase with the magnitude of the parameter estimate suggests that the Type I analyses have a higher statistical power than the Type III

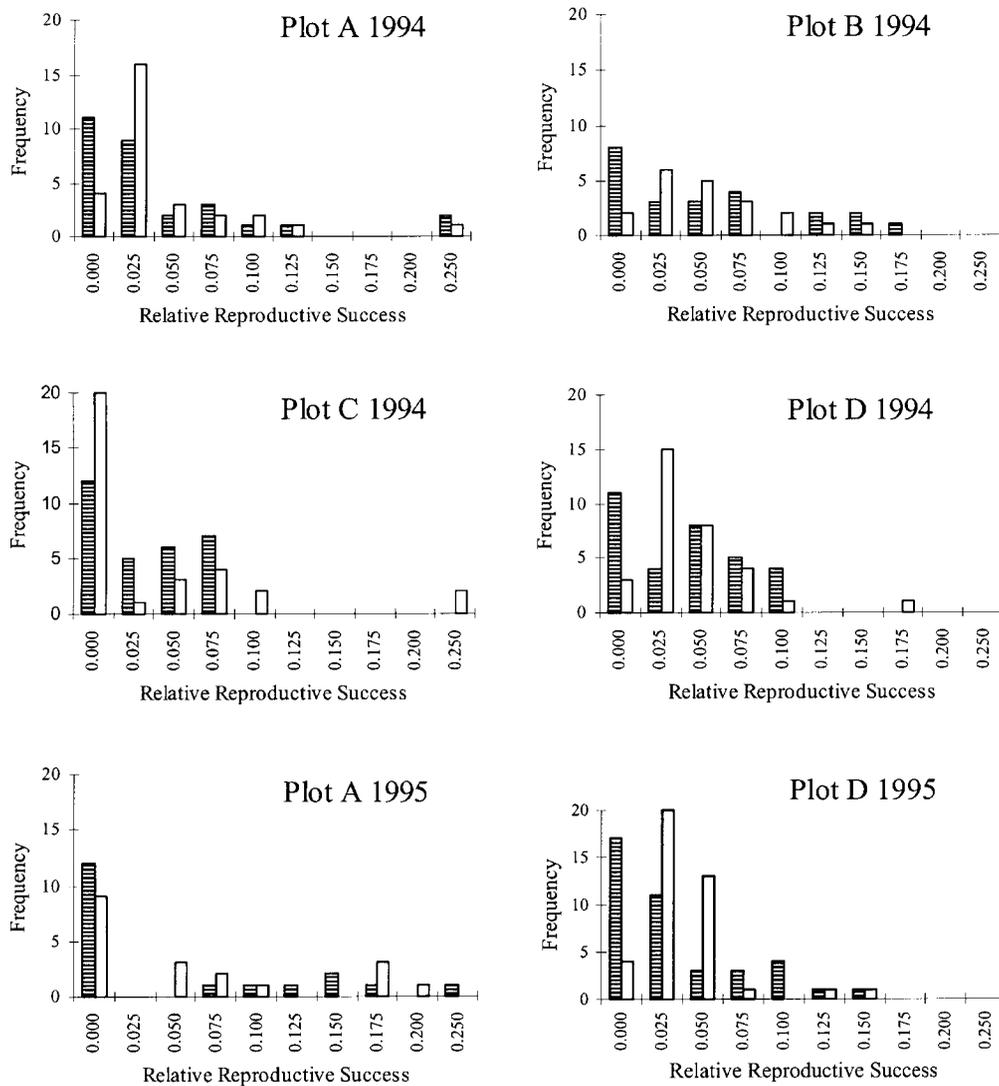


Figure 1: Frequency distributions of male (*hatched bars*) and female (*open bars*) reproductive success in each plot and year. Distributions include only individuals that flowered.

results (fig. 2). Thus, in the following paragraph, we based our interpretations primarily of the Type I test results, tempering our interpretations in light of the Type III test results.

The most consistent predictor of male reproductive success was the proportion of male flowers produced (table 4). The positive relationship between male success and proportion male flowers was highly significant in all three plots when χ^2 test criteria were utilized; when we utilized the Type I bootstrap criteria, the relationship was significant for only two of the three plots, with the third showing a nonsignificant trend. However, increased total flower production was only marginally related to male success in

one plot when the Type I bootstrap criteria was employed. This is especially interesting because all flowers produce pollen, and so an increase in total flower production was expected to have a strong positive relationship with male success. There was a tendency for plants with larger flowers to have greater male success, especially evident when the χ^2 test criteria were employed. When Type I bootstraps were used to determine significance, flower size was important only in plot D 1995. Although χ^2 test criteria indicated a relationship between vegetative size and male success in some analyses, there was no significant relationship when the more conservative Type I bootstraps were employed. As noted above, Type I and Type III anal-

Table 4: Paternity analysis results for the relationship between male reproductive success and floral phenotype

	Univariate (Type I)				Multivariate (Type III)			
	β	LLR	$P(\text{boot})$	$P(\chi^2)$	β	LLR	$P(\text{boot})$	$P(\chi^2)$
Plot A 1994: ^a								
Flower number:								
Total flower number	.02	32.7	.0600	.0000	.01	1.9	.5450	.1681
Proportion male	2.41	18.7	.1000	.0000	2.22	8.3	.2050	.0039
Flower size:								
Corolla diameter	-.07	.4	.8200	.5271	.03	.0	.9050	.9203
Pistil length	-.06	.1	.9100	.7518	-.49	.3	.7725	.5716
Anther length	-2.46	13.1	.8600	.0003	-1.73	.6	.7375	.4348
Anther width	-3.85	.9	.7400	.3428	-2.43	.1	.8300	.7290
Vegetative size – PC1	.41	5.8	.4500	.0160	.45	1.7	.5375	.1963
Plot A 1995: ^b								
Flower number:								
Total flower number	.02	.3	.8070	.5839	-.08	1.9	.4900	.1715
Proportion male	2.94	13.9	.0510	.0002	3.70	9.6	.1775	.0020
Flower size:								
Corolla diameter	-.19	2.3	.5100	.1294	-.46	.7	.5975	.3897
Pistil length	-.53	5.0	.2870	.0253	-1.39	2.4	.4025	.1190
Anther length	-1.01	2.7	.4290	.1003	2.46	5.0	.2650	.0259
Anther width	4.88	8.8	.1400	.0030	-.38	.0	.8850	.8875
Vegetative size – PC1	.33	3.5	.3630	.0614	.85	3.4	.3650	.0640
Plot D 1995: ^c								
Flower number:								
Total flower number	.01	27.9	.2400	.0000	-.01	10.8	.4050	.0010
Proportion male	3.98	68.2	.0500	.0000	5.70	8.8	.5000	.0030
Flower size:								
Corolla diameter	.13	64.9	.0500	.0000	.19	6.9	.4900	.0084
Pistil length	.42	70.3	.0300	.0000	-.84	26.1	.1900	.0000
Anther length	.65	40.7	.1300	.0000	1.14	21.8	.2525	.0000
Anther width	1.08	64.2	.0400	.0000	1.87	8.3	.4925	.0040
Vegetative size – PC1	-.11	1.1	.8500	.2943	-1.19	15.3	.3300	.0001

Note: The β values indicate the direction of the relationship, positive or negative. Log-likelihood ratios (LLR) for each model fitted, as well as χ^2 and bootstrap tests of significance, are also presented. Results of two different analyses are shown; the univariate case, analogous to a Type I ANOVA, and the multivariate case, analogous to a Type III ANOVA (see text for details). PC = principal component.

^a Overall LLR = 46.2, $P(\chi^2) < .0000$.

^b Overall LLR = 29.4, $P(\chi^2) < .0001$.

^c Overall LLR = 137.8, $P(\chi^2) < .0000$.

yses were generally in agreement, although significance was greatly reduced in the Type III analyses. However, in two cases the analyses indicated differences in sign for the β coefficient of particular plant traits. Considering only those traits for which the χ^2 tests indicated significance for both the Type I and Type III tests, the two traits for which this occurred are both from plot D 1995 (table 4). Both flower number and pistil length had positive β coefficients with the Type I (univariate) test and negative β coefficients with the Type III (multivariate) test. However, significance utilizing the bootstrap criteria was attained only for pistil length (Type I test only), so we will ignore the lack of agreement indicated with the χ^2 test, noting only that this

pattern of significance likely results from the way the different analyses account for the covariance structure of the data.

Distance from male plants to potential mates showed no significant effects within plots and only marginally significant effects between plots (fig. 3). Analyses of distance effects between plots within each site were compromised by the fact that each plot contained the same clonal replicates and hence the same genotypic arrays. However, the estimated effects of distance incorporating both plots within a site indicate an exponential decay of gene flow with increasing distance in 1994, giving some support to our assumption that the plots were genetically isolated

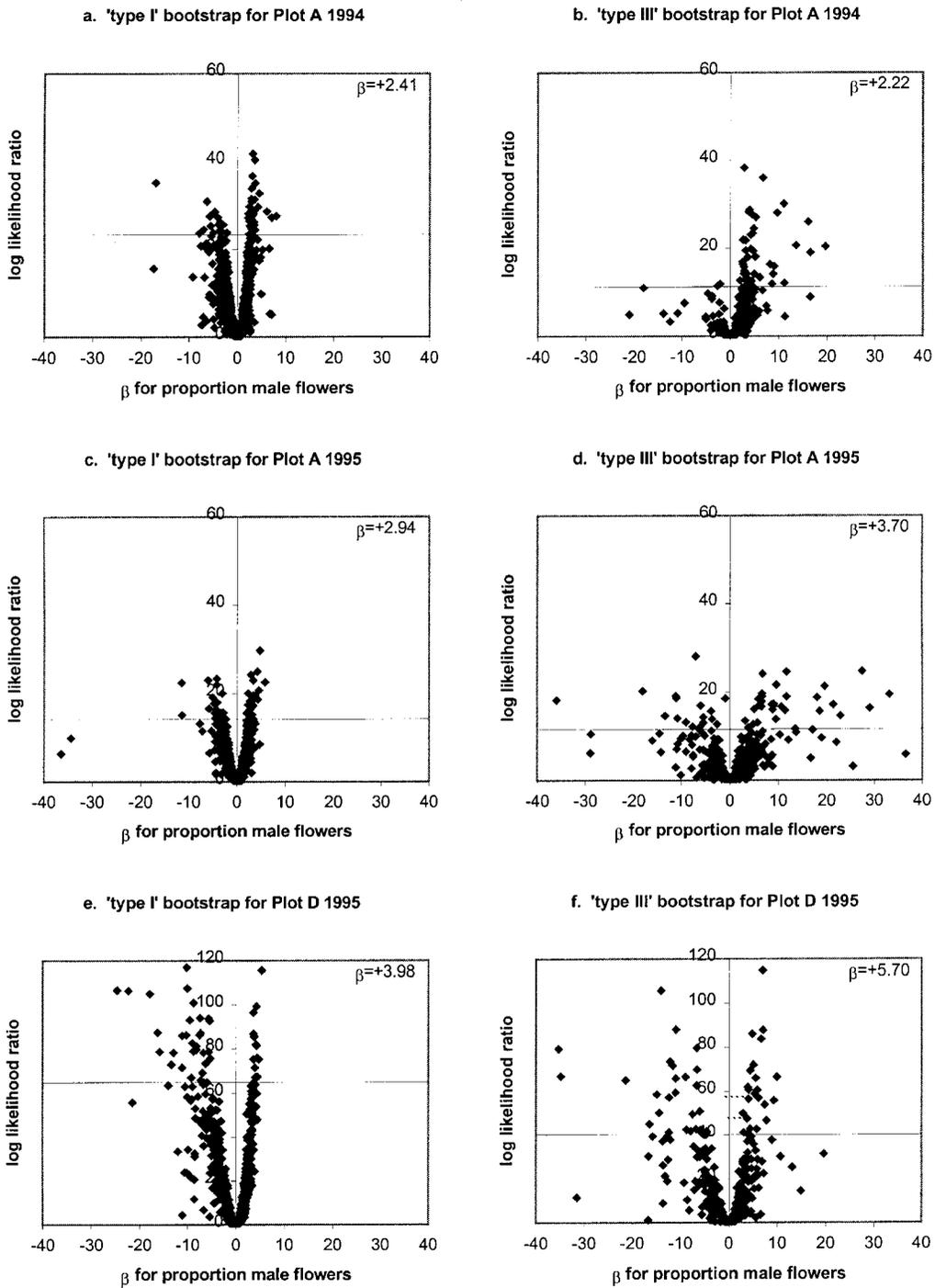


Figure 2: Bootstrap test results for the relationship between proportion of male flowers and male reproductive success. Horizontal lines in each panel represent the 5% critical value in tests of significance; the parameter value (β) is indicated. Variation in the magnitude of LLR scores among plots was not meaningful because these statistics are plot specific, so we used plot-specific Y-axis scale for plot A 1994 (a, b), plot A 1995 (c, d), and plot D 1995 (e, f).

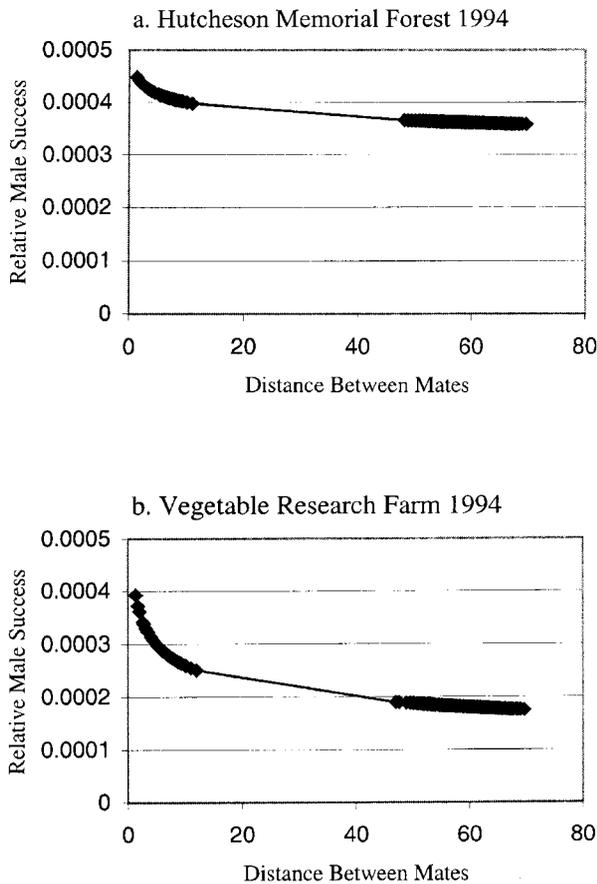


Figure 3: Relationship between interplant distance and male reproductive success. Pollen dispersal shows a nonsignificant trend toward exponential decay in site 1 (a, Hutcheson Memorial Forest, plots A and B, $\gamma = -0.05625$, $P = .5740$) and site 2 (b, Vegetable Research Farm, plots C and D, $\gamma = -0.20313$, $P = .2130$).

from one another, although gene flow between plots may have contributed to the lack of significantly heterogeneous male success in three of the plots in the first year.

Comparison of Male and Female Success

Male fertility variance does not significantly exceed female fertility variance as determined by *F*-tests (plot A 1994, $F = 1.20$, $P = .32$; plot B 1994, $F = 1.98$, $P = .063$; plot C 1994, $F = 3.10$, $P = .001$; plot D 1994, $F = 1.10$, $P = .3962$; plot A 1995, $F = 1.67$, $P = .14$; plot D 1995, $F = 1.48$, $P = .11$; see fig. 1). In the one plot where the difference is significant, plot C 1994, female variance is greater than male variance. However, there is an apparent trade-off between male and female success in this species. Although only two of the correlations between male and female reproductive success are statistically significant, five

out of six estimates are negative (table 5). Functional gender ranges from completely male to completely female in all plots (fig. 4). Functional gender (femaleness) is only weakly related to phenotype but tends to increase with increased flower production and decrease with an increased proportion of male flowers (table 6).

Discussion

In *Solanum carolinense*, paternal contributions to the offspring pool are highest in plants that produce the highest proportion of male flowers. Total flower production, although a truer estimate of total allocation to male function through the production of pollen-containing anthers, is not a strong predictor of paternity, and large flower size, assumed to be important in attracting pollinators, is not a reliable predictor of male success. In addition, the variance in male success is not significantly greater than the variance in female success. Thus, the predictions of sex allocation theory, as a reinterpretation of Bateman's principle, are not strongly supported in this system.

Several researchers have used genetic markers to examine the relationship between floral characters and male success, but the results have been equivocal. Pollen production and/or the number of pollen-producing structures (flower number) have been shown to be important predictors of paternity (Broyles and Wyatt 1990, 1995; Devlin et al. 1992; Conner 1996b), especially in wind-pollinated species, where selection may act directly on the number of polleniferous units rather than on aspects of the floral display (Schoen and Stewart 1986; Burczyk and Prat 1997). More rare is the case where total flower number is not related to paternity, as in Meagher (1991) and this study.

One possible explanation for the results of this study is that geitonogamy is occurring in plants with the greatest number of flowers. Geitonogamy, the movement of pollen within individuals, cannot result in seed set in this self-

Table 5: Pearson correlation coefficients between male and female reproductive success for individuals with at least some fertility through one or the other sex

	<i>N</i>	<i>R</i>	<i>P</i>
1994:			
Plot A	27	-.19	.3473
Plot B	22	.20	.3636
Plot C	27	-.61	.0008
Plot D	31	-.22	.2394
1995:			
Plot A	12	-.31	.3192
Plot D	39	-.34	.0363

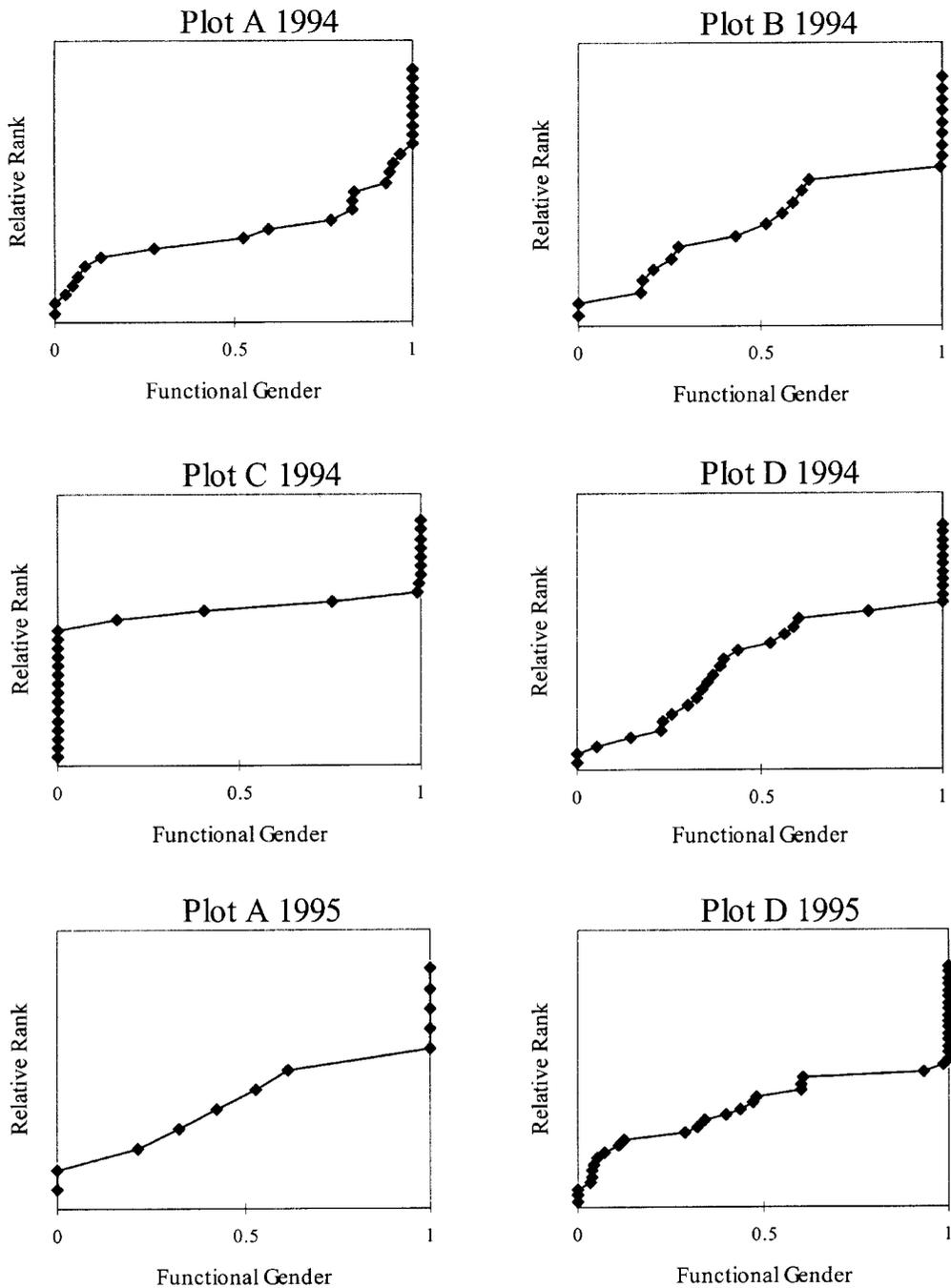


Figure 4: Rank order plots of functional gender (relative femaleness) of plants within each plot-year

incompatible plant. Any pollen removal followed by deposition within the same genetic individual is thus wasted. Geitonogamy is expected to increase as flower number increases (Hessing 1988; Dudash 1991; De Jong et al. 1993; Klinkhamer and De Jong 1993; Harder and Barrett 1995). In addition, there may be interference between the sexual

parts within flowers. In buzz-pollinated plant species, the arrangement of the anthers in a cone and the presence of a protruding pistil are assumed to be adaptations for efficient removal and deposition of pollen (Buchmann 1983; Harder and Barclay 1994). It is possible that the protruding pistils of hermaphroditic flowers prevent bees from tightly

Table 6: Standardized selection gradient analysis for the effect of flower number and proportion of male flowers on functional gender

	1994								1995			
	Plot A		Plot B		Plot C		Plot D		Plot A		Plot D	
	β	<i>P</i>										
Flower number	.20	.0146	-.07	.3999	.05	.5596	.15	.0368	-.10	.5146	.37	.0001
Proportion male	-.08	.3145	-.16	.0572	.11	.2534	-.06	.3697	-.27	.0603	-.15	.0162
Total R^2	.23	.0427	.19	.1371	.09	.3299	.17	.0750	.34	.1535	.48	.0001
N_f	27	...	22	...	27	...	31	...	12	...	39	...

Note: The abbreviation N_f is the number of flowering plants in each plot and year combination that had some reproductive success through one or the other sex.

curling around the anther cone and thus from intercepting all of the pollen that is ejected; this hypothesis has not been tested explicitly, however. In male flowers, with their greatly reduced pistils, there is no interference with the proper positioning of the bee (Solomon 1985). Thus, male flowers, from which pollen can potentially be more efficiently removed than from hermaphroditic flowers, have the greatest impact on paternity, and total pollen production, as estimated by flower number, is less important in this species.

It has been postulated that flower size and shape should respond primarily through selection on male function (Bell 1985; Willson 1994). Alternatively, flower size may respond to selection through female function (Stanton and Galloway 1990; Stanton et al. 1991; Wilson et al. 1994) or may be determined by functions other than pollinator attraction (Delph et al. 1996). In *S. carolinense*, flower size is not an important determinant of female success (Elle 1999), and large flowers increased male success in only one plot-year combination. This may be because most plants flowered and data are most complete for this one plot-year (plot D 1995), increasing the power of our analyses. Overall, however, our results are similar to those of Conner et al. (1996a, 1996b), which indicate that flower size is unimportant for fitness gain through either sex function.

Vegetative size was included in the analysis to control for differences among individuals in vigor, which might affect sex-specific reproductive success (Queller 1997). Large plants should produce more seeds (have greater female success) than smaller plants (e.g., Mitchell 1994; Elle 1996; Klinkhamer et al. 1997). Male success should depend less on size. In dioecious species, male plants appear to require fewer resources for reproduction than female plants (Meagher and Antonovics 1982; Quinn 1991), and male function has been shown to be enhanced relative to female function under stressful conditions in cosexual plants (Solomon 1985; Devlin 1988; Costich 1995). Because larger plants often produce more flowers (e.g., Primack and Hall 1990; Mitchell 1994), male success could

conceivably be higher in larger plants. However, vegetative vigor did not enhance either female (Elle 1999) or male success in *S. carolinense*.

Bateman's principle predicts that male reproductive success will be highly variable among individuals, in part because males are competing for mates (Bateman 1948; Charnov 1982). In this study, only three of the six plots studied exhibited discernible variation among individuals in male reproductive success. Overall, the variance in male success was not large and was never significantly larger than the variance in female success. Meagher (1986), working with a dioecious perennial, found that male fitness variance was significantly greater than female fitness variance, as did Müller-Starck and Ziehe (1984), who studied a monoecious conifer. But, Devlin and Ellstrand (1990) and Conner et al. (1996b), both studying hermaphroditic wild radish, found that either male variance or female variance could be larger. These results indicate that variance in sex-specific fertility may be species specific, and determined primarily by environmental variation in the availability of resources and pollinators in a given time or place (Wilson et al. 1994).

Functional gender was highly variable in *S. carolinense*, ranging from completely male to completely female in all plot-year combinations. Gender, or femaleness, increased with an increased production of all flowers or a decreased proportion of male flowers. This is consistent with the relationship between female success and phenotype found for this species (Elle 1999), as well as the results of the paternity analysis presented here. Female success can only occur through pistil-bearing hermaphroditic flowers, while male success is primarily increased through the production of an increased proportion of male flowers, which may be more efficient at dispensing pollen as discussed above. Because the two sexes differ in the direction of the relationship between proportion male flowers and reproductive success, there was a trend for male and female success to be negatively correlated. This trend is especially interesting because other researchers have found a positive relationship between sex functions within individuals (Broyles and Wyatt 1990;

Devlin and Ellstrand 1990; Conner et al. 1996b). In each of these studies, both male and female reproductive success were found to increase with the total number of flowers produced, which is not the case in *S. carolinense*.

Because the proportion of male flowers produced is heritable in *S. carolinense* (Elle 1998), differences among individuals in male flower production can have important consequences, not only for sex-specific success and functional gender but also for mating-system evolution. Species in the genus *Solanum* exhibit a variety of mating systems, including true hermaphroditism, andromonoecy, and functional dioecy (Whalen and Costich 1986; Anderson and Symon 1989). The functionally dioecious *Solanum* species are morphologically androdioecious, with populations consisting of male and hermaphroditic individuals (Anderson and Symon 1989). Morphologically hermaphroditic plants, however, produce inviable pollen and so are functionally female. Functionally dioecious *Solanum* species could have evolved from andromonoecious ancestors similar to *S. carolinense* (Whalen and Costich 1986; Anderson and Symon 1989), where selection acts in different directions through male and female function on the proportion of male flowers produced, and plants with differing floral morphology differ in functional gender.

Our results suggest that floral evolution in this entomophilous species is not driven primarily by selection acting independently on allocation to male or female sex functions but rather that the trade-off between male and female success, as determined by the relationship between the two floral morphs and sex-specific fitness, is important. Although this research addressed sex allocation in a co-sexual species, these results have broader implications in terms of the role of allocation and resource limitation on gender specialization in plants.

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