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MEASUREMENTS OF NATURAL SELECTION ON FLORAL TRAITS IN WILD RADISH (*RAPHANUS RAPHANISTRUM*). II. SELECTION THROUGH LIFETIME MALE AND TOTAL FITNESS

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Abstract.—It has often been suggested that selection on floral traits in hermaphroditic plants should occur primarily through differences in male fitness. However, measurements of selection on floral traits through differences in lifetime male fitness have been lacking. We measured selection on a variety of wild radish floral traits using lifetime male fitness measures derived from genetic paternity analysis. These male fitness estimates were then combined with estimates of lifetime female fitness of the same plants to produce measurements of selection based on lifetime total fitness. Contrary to the prediction above, there was no strong evidence for selection on floral morphology through male fitness differences in any of the three years of the study, but there was strong selection for increased flower size through female fitness differences in one year. The main determinant of both male and female fitness in all years was flower number; this lead to moderately positive correlations between male and female fitness in all three years.

Key words.—Floral traits, lifetime male fitness, natural selection gradients, paternity analysis, *Raphanus raphanistrum*, wild radish.

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Biologists have long been fascinated by the diversity of flowers found in nature, and Darwin (1859) argued that this diversity was caused by natural selection. Recently a number of authors have argued that most selection on floral traits is caused by differences in male fitness (seeds sired; Charnov 1979; Queller 1983; Sutherland and Delph 1984; Bell 1985; Stanton et al. 1986), because male reproduction should be determined primarily or exclusively by pollination (mating) success. Female fitness (seed production), on the other hand, should be limited primarily by the resources needed to produce costly offspring rather than by mating success, particularly in species in which seed production is not pollen-limited (Snow and Lewis 1993). A related prediction, supported by animal data, is that variance in male fitness should be greater than variance in female fitness (Bateman 1948; Trivers 1972; Clutton-Brock 1988). These predictions, along with methodological advances, have spurred a number of recent studies of male fitness in plants (reviewed in Snow and Lewis 1993).

Most of these studies have measured components of male fitness, such as pollen removal and/or delivery of pollen or pollen analogs to stigmas (e.g., Campbell 1989; Stanton et al. 1992; Conner et al. 1995; see Table 1 in Snow and Lewis 1993 for a review). However, components may not always be closely related to total male fitness, that is, the number of seeds sired (Stanton et al. 1992; Snow and Lewis 1993). Others have used genetic markers to measure male success in siring seeds. Many of these studies have focused on patterns of gene flow without relating male fitness to specific plant traits (e.g., Schaal 1980; Handel 1983; Smyth and Hamrick 1987; Campbell 1991). A few studies have examined the effect of the number of flowers produced by a plant on the number of seeds sired; these studies have generally found a positive relationship (Schoen and Stewart 1986; Broyles and Wyatt 1990; Devlin and Ellstrand 1990; Devlin et al. 1992; but see Meagher 1991). A few other studies have found differences in the number of seeds sired among morphs in species with discrete polymorphisms for flower color (Schoen and Clegg 1985; Stanton et al. 1986) and style length (Kohn and Barrett 1992). Thus, the effect of floral traits on seed-siring ability has been determined for only a small subset of floral traits.

There are a wide variety of other floral traits that are important determinants of components of male fitness, such as floral size, shape, and relationships among floral parts (Waser 1983; Bell 1985; Campbell 1989). Increased corolla size has been shown to increase pollinator visitation in several species (Clements and Long 1923; Bell 1985; Galen and Newport 1987; Stanton and Preston 1988; Galen 1989; Young and Stanton 1990; Campbell et al. 1991; Eckhart 1991), which could result in directional selection for increased size. However, corolla size was not related to success in siring seeds in the one study to measure this (Stanton et al. 1991). Alternatively, Berg (1960) predicted that flower size would be under stabilizing selection to match pollinator size. This prediction was based on the absence of correlation between floral and vegetative traits in some animal-pollinated species (see also Primack 1987; Kang and Primack 1991; Conner and Sterling 1995).

Anther position relative to the corolla tube opening affects pollen removal (Wolfe and Barrett 1989; Murcia 1990; Harder and Barrett 1993; Conner et al. 1995). These studies all reported maximum pollen removal with maximum anther exsertion, defined as the height of the anther above the opening of the corolla tube. Alternatively, we have previously predicted that anther and stigma exsertion might be under stabilizing selection based on floral correlation patterns (Conner and Via 1993; Conner and Sterling 1995).

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To fully understand the evolution of floral traits through natural selection, several types of information are desirable. First, measurements of selection through both male and female fitness on a variety of floral traits are needed (Morgan 1992). This has rarely been done, particularly for male fitness (but see Campbell 1989; Campbell et al. 1991). Second, these selection measurements should be based on differences in the number of seeds sired and produced over the lifetime of the plant, since measurements based on only part of an organism's life can lead to erroneous results (Lande and Arnold 1983; Arnold and Wade 1984; Endler 1986; Travis and Heinrich 1986; Clutton-Brock 1991). Lifetime number of seeds sired has rarely been measured (but see Devlin and Ellstrand 1990; Devlin et al. 1992). Finally, selection estimates should be made in multiple years, because patterns of fitness and selection can vary widely across years (Schoen and Stewart 1987; Campbell 1989; Schemske and Horvitz 1989). Only a handful of studies have measured male fitness in multiple years (Meagher and Thompson 1987; Campbell 1989; Devlin et al. 1992). To our knowledge, no study to date has accomplished all of these goals; most importantly, no previous study has reported measurements of selection on floral traits based on total lifetime male and female fitness.

In this paper we report measurements of selection on floral traits based on estimates of total lifetime number of seeds sired in wild radish, *Raphanus raphanistrum.* Measurements of selection were conducted in three years, and included measurements of directional and stabilizing selection on anther exsertion and flower size, and directional selection on pollen production per flower and total lifetime flower production. Male fitness estimates were also combined with previous estimates of female fitness (Conner et al. 1996) to produce selection measurements based on total lifetime fitness through both sexual functions.

Materials and Methods

Field Methods

Raphanus raphanistrum (Brassicaceae) is a cosmopolitan annual weed of disturbed habitats. Wild radish is self-incompatible and therefore requires insect pollination for successful reproduction (Sampson 1964). Measurements of selection were made in three separate experimental populations, one in each of three years (1991–1993), at the Phillips Tract natural area located near Urbana, Illinois. Thus, independent measurements of selection were made in each of the three years. Wild radish typically exists only in extremely small, isolated populations in central Illinois (< 10 individuals; Conner, pers. obs.), probably because it is not a common weed of corn and soybeans, which cover most of the land. Therefore, seeds used were collected from a large population near Binghamton, New York for which genetic information on floral traits is available (Conner and Via 1993). The nearest known natural population of wild radish was located approximately 3 km from the study site.

Wild radish is pollinated by a variety of bees, butterflies, and flies (Kay 1976; Stanton et al. 1989). Species pollinating wild radish vary widely over short spatial and temporal scales, but most of the same species visit wild radish in central Illinois and central New York (Conner and Rush 1996; G. Eickwort, pers. comm.). Our study populations were visited mainly by bees and flies in the following percentages: 1991, 55% honey bees and 32% small native bees; 1992, 40% small bees, 40% syrphid flies, and 6% honey bees; and 1993, 55% small bees and 38% syrphid flies (Conner et al. 1996).

Field methods were described in detail in Conner et al. (1996); a brief summary follows. Two complementary methods were used. In 1991 and 1992, 57 and 60 plants respectively were planted in a grid with 1-m spacing. Planting in 1991 occurred in August, so that plants flowered in September and October, the end of the normal wild radish flowering season. In 1992 most of the flowering occurred in July and August, the normal peak flowering time. Possible edge effects were tested for by including a categorical variable denoting whether or not each plant was on the edge of the grid. This variable was not significant in either year, and its inclusion did not alter any results, so it was left out of final analyses.

Six morphological traits were measured on two to four flowers from each plant: petal length and width, corolla tube length, lengths of one short and one long filament, and pistil length (for details of traits and measurement methods see Conner and Via 1993). The number of ovules per flower were also counted, and in 1992 only, pollen production per flower was estimated as follows. Bridal-veil mesh bags were placed over groups of buds to prevent insect visitation, and pollen was collected from flowers that opened inside the bag. The number of pollen grains was then counted using a Coulter counter (for details see Rush et al. 1995). Finally, the total number of flowers produced by each plant was estimated in 1992 by counting the pedicels on the plant after senescence.

In 1993, seven groups of 16 potted plants each were grown in the greenhouse, for a total of 112. Each group was brought to the field site alone and exposed to natural pollination for three to ten hours. The above traits were measured in the field on one flower from each plant, and the total number of open flowers was counted. Pollen was collected from one flower on one to four dates spanning the experiment for measurements of pollen production. All seven groups were brought to the field on different days, and then the entire process was repeated six times in July and August. Thus, each plant group was exposed to natural pollination and had measurements taken on six days that spanned the natural peak flowering period of wild radish.

During all times that the experimental plants were not at the field site in 1993, similar "dummy" arrays of wild radish plants were left at the field site so that there were always wild radish plants available for pollinators. These arrays were removed from the site at least 15 min before setting out the experimental arrays, but some transfer of pollen from these plants to the experimental plants is possible from leftover pollen on the pollinators' bodies. If this occurred, it could increase random error in the male fitness estimates (if a dummy plant that had a genotype similar to an experimental plant sired a seed), or those offspring might be excluded from all potential fathers (see below). The latter would not affect the male fitness estimates.

Electrophoresis

Seeds from each field plant were randomly sampled for electrophoretic paternity determination. The number of off-

TABLE 1. Allele frequencies at isozyme loci in *Raphanus raphanistrum,* arranged from most to least common within each locus.

Locus	Alleles 1	2	3	4	5	6
1991:						
FOR	0.55	0.45				
IDH	0.94	0.06				
LAP	0.43	0.25	0.18	0.09	0.04	0.01
PGI	0.53	0.28	0.14	0.05		
PGM-1	0.65	0.35				
PGM-2	0.57	0.17	0.14	0.12		
PGM-3	0.77	0.13	0.10			
TPI	0.77	0.21	0.02			
1992:						
FOR	0.64	0.36				
IDH	0.87	0.12	0.01			
LAP	0.42	0.20	0.17	0.15	0.05	0.01
PGI	0.61	0.27	0.09	0.03		
PGM-1	0.77	0.23				
PGM-2	0.39	0.32	0.17	0.12		
PGM-3	0.69	0.20	0.11			
TPI	0.72	0.26	0.02			
1993:						
FOR	0.73	0.27				
IDH	0.93	0.05	0.02			
LAP	0.50	0.22	0.17	0.05	0.04	0.02
PGI	0.65	0.22	0.11	0.02		
PGM-1	0.68	0.32				
PGM-2	0.47	0.21	0.17	0.15		
PGM-3	0.71	0.15	0.09	0.05		
TPI	0.72	0.28				

spring sampled from each plant was weighted by that plant's total seed production. Therefore, more offspring were sampled from field plants that produced more seeds. In 1991, 16 of the plants flowered late and were unable to complete seed development before the first frost. Therefore, paternity was based on the offspring of the other 41 plants only; these plants produced 97% of the total number of seeds in the population. The total numbers of offspring genotyped were 1866 from 1991, 2092 from 1992, and 2750 from 1993.

Standard starch-gel electrophoretic techniques were used (Murphy et al. 1990; for details, see Conner et al. in press). Eight polymorphic loci with a total of 27 alleles (Table 1) were scored: formate dehydrogenase (FDH, EC 1.2.1.2), isocitrate dehydrogenase (IDH, EC 1.1.1.42), leucine aminopeptidase (LAP, EC 3.4.11.1), phosphoglucose isomerase (PGI, EC 5.3.1.9), phosphoglucomutase (3 loci; PGM, EC 2.7.5.1), and triose phosphate isomerase (TPI, EC 5.3.1.1). These marker loci all exhibit Mendelian inheritance and are not tightly linked (Conner et al. in press). No parents shared the same multi-locus genotype within a year.

Analyses

Male fertility, defined as the proportion of offspring of each female that was fathered by each male, was estimated using maximum likelihood methods (Roeder et al. 1989). The empirical exclusion probabilities were 0.88 in 1991, 0.89 in 1992 and 0.85 in 1993. This means that the average number of nonexcluded males for each offspring was 6.8 in 1991, 6.6 in 1992, and 2.4 in 1993. All possible fathers were excluded for some of the offspring (120 or 6.4% in 1991; 116 or 5.5% in 1992; and 290 or 10.5% in 1993), so these offspring were not included in the fertility estimates. The higher percentage of excluded offspring in 1993 could be due to seeds fathered by the dummy array plants (see above), and/or to the smaller number of possible fathers in that year.

As an index of the variation in these male fertility estimates, the maximum-likelihood variance of each was divided by the fertility estimate itself (fertilities $< 1\%$ not included). This number was multiplied by 100 to give a percentage. The median of this percentage was 3.9% in 1991, 4.2% in 1992, and 5.3% in 1993. Therefore, the male fertility estimates appear to be accurate.

The estimates of each male's fertility on a particular female were multiplied by the number of seeds produced by that female (viable seeds only in 1991 and 1992, all seeds fertilized in 1993; see Conner et al. 1996) to estimate the number of offspring sired by each male on that female. These numbers were summed over all females to give an estimate of the total number of seeds sired by each male. To estimate the total

TABLE 2. Standardized selection gradients for the floral traits based on male fitness only. The results for each year represent a separate multiple regression of relative total male fitness on the variables listed below. The fitness estimate (dependent variable) was lifetime number of viable seeds sired in 1991 and 1992, and the total number of seeds sired in the six days of pollination in 1993. Significance levels and R^2 in 1991 and 1992 are from a regression using ln-transformed fitness values, but selection gradient values are from untransformed relative fitness. Per-flower pollen number was measured in 1992 and 1993 only. The flower production variable was number of days flowering in 1991, the total number of flowers produced over the plant's lifetime in 1992, and the total number of flowers open on the six days of pollination in 1993. The anther exsertion^2 and flower size^2 rows give the quadratic terms testing for stabilizing/disruptive selection on these traits.

	1992		1992		1993	
	β or γ	*P*	β or γ	*P*	β or γ	*P*
Flower size	0.10	0.49	−0.20	0.24	0.01	0.80
Flower size^2	0.09	0.38	−0.23	0.11	0.06	0.52
Anther exsertion	−0.11	0.13	0.04	0.78	0.09	0.05
Anther exsertion^2	−0.17	0.52	0.08	0.22	0.04	0.61
Pollen #/flower	—	—	0.16	0.22	0.07	0.14
Flower production	0.50	< 0.0001	0.56	0.0008	0.10	0.04
Total R^2	0.40	0.0001	0.34	0.006	0.19	0.05
N	57		49		112	

fitness of these hermaphroditic plants, this estimate of male fitness was added to the number of seeds produced (female fitness) by the same plant.

Standardized selection gradients (Lande and Arnold 1983) were calculated by regressing relative male fitness and relative total fitness on the floral traits after standardizing the floral traits to mean = zero and variance = one. The first principal component of all six floral morphological measurements was used as a measure of overall floral size (Conner et al. 1996). Linear and quadratic terms in the regressions were used to test for directional and stabilizing/disruptive selection respectively. In the male fitness analyses, both directional and stabilizing selection on floral size and anther exsertion were measured (see introduction), as well as directional selection on total flower production and pollen production per flower. Quadratic terms were not fit for these latter variables because of limited sample size and because there were no specific hypotheses of stabilizing or disruptive selection on these traits. In the total fitness regressions, these traits plus stigma exsertion and ovule number were included. There were no significant correlations among the floral traits (predictor variables), and all variance inflation factors (Neter et al. 1985) were less than two; therefore, there was little collinearity. See Conner et al. (1996) for further details of the analyses.

To determine whether mating opportunities affected male fitness (Nakamura et al. 1989), the initial 1991 and 1992 male fitness regressions included the number of seeds produced by the four closest neighbors of each plant as an additional variable. These were not significant, so were not included in final regressions. Neighbor effects were controlled in 1993 by rerandomizing positions on each field day.

A categorical variable for the seven plant groups was included in the 1993 analyses. None of the interactions between group and the other variables were significant and thus were not included in final regression models.

In 1992, pollen was collected from single flowers on only 49 of the 60 plants, so the selection analyses based on male fitness included only these 49 plants. Removing pollen number as a variable and therefore including all 60 individuals did not change the results for the remaining variables. Pollen production was not included in the total fitness regressions, because it was not significant in the male fitness regressions and the larger number of independent variables required the full sample of 60 plants.

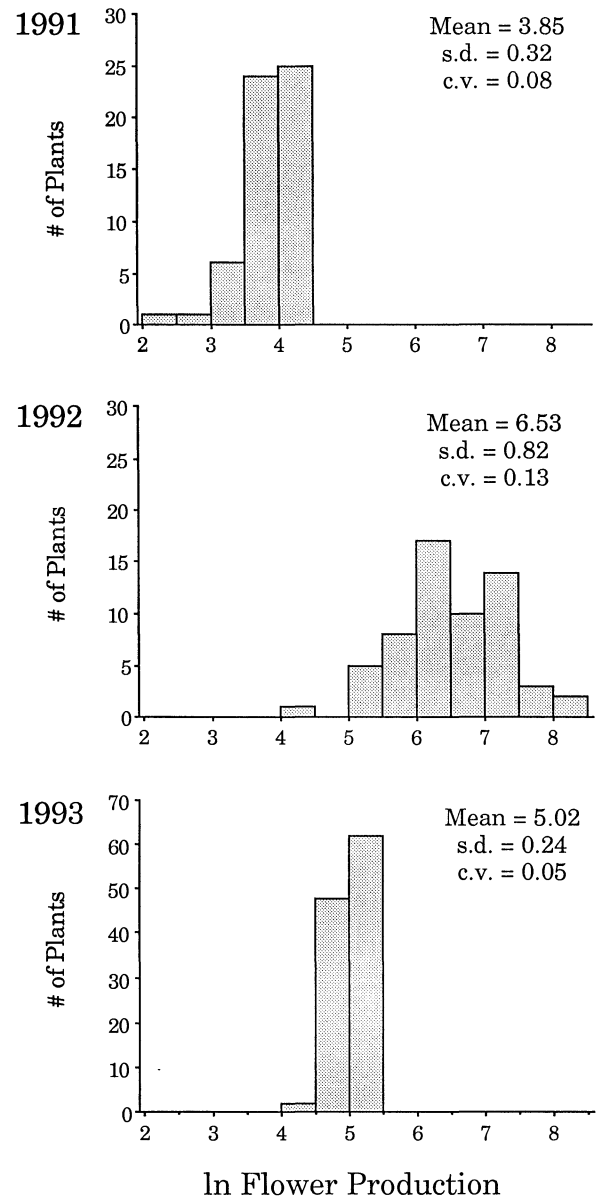

FIG. 1. Frequency distributions of flower production in the three years. Variables are ln-transformed to facilitate comparisons across years.

RESULTS

Male Fitness Selection Gradients

The selection gradients based on male fitness were consistent across the three years. This was particularly true for the first two years that were based on total lifetime fitness (Table 2), in spite of the fact that plants in these two years were planted at different times of the year and had different pollinators (see Methods). The traits together explained a significant proportion of variance in total male fitness in all years, but the R^2 values were greater in 1991 and 1992. This greater R^2 was due to the stronger selection on flower number in those two years as compared to 1993. There was significant selection for increased flower number in all years, but the standardized selection gradients were five times larger in the first two years than in 1993. It is possible that the lower slope in 1993 could be due to the lower variation in flower number in that year, but the variation was also low in 1991 (Fig. 1).

In contrast to the predictions of the two hypotheses outlined in the introduction and the expectations of a large body of theory, there was little evidence for selection on floral morphology or per-flower pollen production through differences in male fitness. There was evidence for weak directional selection for increased anther exsertion in 1993, but the significance level was marginal and there was no corroborating evidence for this selection from the other two years. Most of the other selection gradients were not close to significance (Table 2).

TABLE 3. Standardized selection gradients for the floral traits based on total lifetime fitness. The results for each year represent a separate multiple regression of relative total fitness (seeds sired + seeds produced) on the variables listed below. Pollen number per flower was excluded from the 1992 analysis so that all 60 individuals would be included (see Methods). See Table 2 for further details.

	1991		1992		1993	
	β or γ	*P*	β or γ	*P*	β or γ	*P*
Flower size	0.07	0.66	0.04	0.002	0.01	0.83
Flower size^2	0.15	0.03	0.08	0.87	0.05	0.31
Anther exsertion	−0.10	0.15	0.06	0.46	0.04	0.20
Anther exsertion^2	0.08	0.60	0.00	0.44	0.02	0.61
Stigma exsertion	0.00	0.80	−0.06	0.85	−0.04	0.14
Stigma exsertion^2	0.26	0.06	−0.06	0.44	−0.02	0.54
Pollen #/flower	—	—	—	—	0.03	0.28
Ovule #/flower	0.14	0.007	0.04	0.69	0.03	0.26
Flower production	0.60	< 0.0001	0.62	< 0.0001	0.14	< 0.0001
Total R^2	0.82	< 0.0001	0.80	< 0.0001	0.37	< 0.0001
N	57		60		112	

Total Fitness Selection Gradients

The selection gradients based on total fitness (Table 3) show the patterns expected from the separate male and female selection gradients (Table 2; Conner et al. 1996). All the traits together explained about 80% of the variance in total fitness in 1991 and 1992, and 37% of the variance in 1993. There was strong selection for increased flower production in all three years, which was expected because selection for increased flower production was found in all years through both male and female fitness. Selection for increased flower size occurred in 1992, but contrary to theoretical expectations, this was due to selection through female fitness differences (Conner et al. 1996) rather than male fitness differences (Table 2). There was little evidence for other selection on floral morphology with the exception of possible weak disruptive selection on flower size in 1991, which was due to selection through female fitness differences (Conner et al. 1996), again contrary to theoretical expectations. Finally, selection for increased ovules per flower occurred in 1991 through female fitness differences.

Male and Female Fitness Variance and Covariance

One consequence of the strong relationship between flower production and both male and female fitness in 1991 and 1992 is that male and female fitness are moderately positively correlated in those years (Fig. 2). This correlation was much weaker in 1993, the year in which male fitness was only weakly determined by flower number. As further evidence that the correlation between male and female fitness is due at least in part to flower number, when flower number is corrected for by performing a partial correlation analysis, all of the resulting partial correlations between male and female fitness are reduced relative to the uncorrected correlations and only one is significant (1991: $r = 0.49$, $P < 0.001$; 1992: $r = 0.06$, $P > 0.5$; 1993: $r = 0.16$, $P > 0.05$).

Patterns of variance in total male and female fitness also differed between years and differed from theoretical expectations. Female variance was greater than male variance in both 1991 and 1992, contrary to expectations, while male variance was greater than female variance in 1993 (Fig. 3). The 1992 and 1993 differences are significant by Levene's tests (1991: $F = 2.65$, $P = 0.11$; 1992: $F = 4.66$, $P = 0.03$; 1993: $F = 9.55$, $P = 0.002$).

Functional gender (Lloyd 1980) was calculated by dividing total seed production by total fitness (seed produced + seeds sired; Fig. 4). The variation in functional gender was greatest in 1991, in which three plants set no viable seeds (functional gender = 0) and one plant fathered no seeds but did set viable seeds (functional gender = 1). Functional gender was less variable in 1992 and especially 1993, but even in the latter year functional gender ranged from 0.18 to 0.89.

DISCUSSION

Selection on Floral Morphology

Contrary to theoretical expectations, no strong evidence for selection on floral morphology through differences in lifetime male fitness was found in any of the three years of this study, but there was strong evidence for selection on flower size through female fitness in 1992. Floral size traits are highly heritable (Conner and Via 1993), so populations should respond to this selection. Contrary to predictions based on correlation patterns (see Berg 1960; Conner and Via 1993; Conner and Sterling 1995; Conner and Sterling 1996), there was also no evidence for stabilizing selection on anther exsertion or floral size. More studies that measure selection on floral traits through lifetime male and female fitness are needed to determine the generality of these results.

There are several possible explanations for our failure to detect selection through male fitness differences. First, since wild radish is pollinated by a large number of different insect species, perhaps selection on floral morphology does occur in populations pollinated by species other than those represented in our study. However, the pollinator composition was quite different in 1991 than in the other two years, but no selection through male fitness occurred in any year.

Second, our study may not have had adequate statistical power to detect weak selection, particularly if this selection was swamped by overwhelming effects of flower number (Snow and Lewis 1993). However, most of the *P*-values were not even close to significance, indicating that much larger sample sizes would be needed given the selection

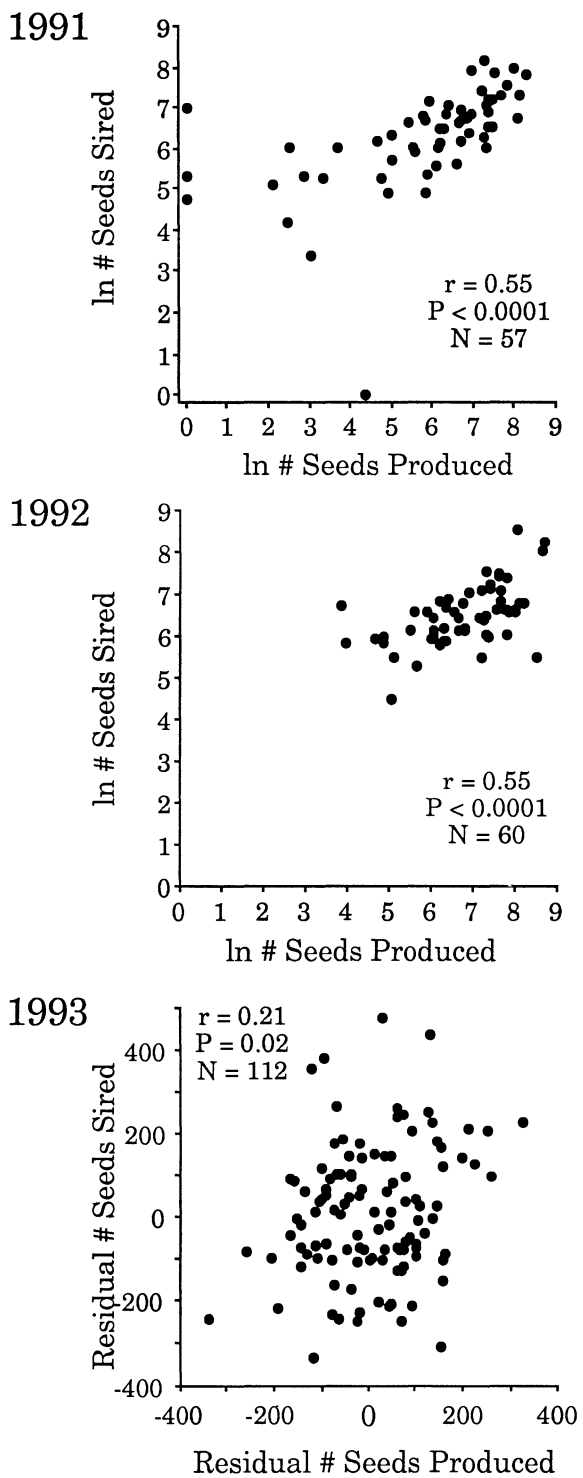

FIG. 2. Scatterplots depicting the relationships between total male and female fitness for each of the three years of the study. Pearson product-moment correlation coefficients with significance levels are presented. Data for 1991 and 1992 were ln-transformed, and data for 1993 were the residuals after removing the effects of group (see Methods). Removal of the 1991 outlier with zero seeds sired increases the correlation coefficient to 0.65.

gradients estimated. Also, in 1993 we had large sample sizes for a study estimating male fitness and had weak flower number effects, but still found little evidence for selection on morphology. It is possible that chance incompatibilities between plants in our small arrays in 1993 increased the random error in the regressions, but in several thousand random crosses of plants from the same population the frequency of incompatible matings was less than 10% (Conner, unpubl. data).

Finally, there may have been selection in the past but the population may now be at equilibrium. For example, the high correlation between filament and tube lengths means that variance in anther exsertion is relatively low. Studies that use populations with experimentally increased variation in phenotypic traits could be used to test for this possibility (Schluter 1988).

Selection on Flower Number

We found strong selection for increased flower number through both male and female fitness in all years except male fitness in 1993, when this selection was weak (Conner et al. 1996; Table 2). Studies on a variety of species have also shown that flower number is the major determinant of female fitness in plants (see discussion in Conner et al. 1996). While there are much fewer studies of total male fitness, and almost none that have examined the relative importance of flower number and other floral traits together, the pattern thus far is the same as for female fitness: increased flower number leads to increases in male fitness (Schoen and Stewart 1986; Broyles and Wyatt 1990; Devlin and Ellstrand 1990; Devlin et al. 1992; but see Meagher 1991). In contrast, there was no evidence that per-flower pollen production affects male fitness. Therefore, while more studies of total lifetime male and female fitness are certainly needed, it seems likely based on studies to date that flower number in many or perhaps most species will be the principal determinant of total hermaphroditic fitness. Likely exceptions to this pattern include species that produce few flowers; in these species floral morphology and per-flower pollen and ovule production may be more important determinants of fitness than total flower number.

While the causal connection between flower number and both male and female fitness should be strong, the possibility that at least some of the strong selection on flower number could be due to correlations with unmeasured traits cannot be ruled out. In particular, environmental correlations between flower number and fitness need to be considered (Price et al. 1988; Rausher 1992; for a discussion of the possible effects of environmental correlations on selection through female fitness, see Conner et al. 1996). In 1993, when plants were raised in pots in the greenhouse, these environmental correlations should have been small, because pot position in the greenhouse and field was changed frequently. The reduction or elimination of environmental correlations might explain why the selection on flower number was weaker in 1993, but it is not obvious what environmental variable would affect both flower number and male fitness in the same direction.

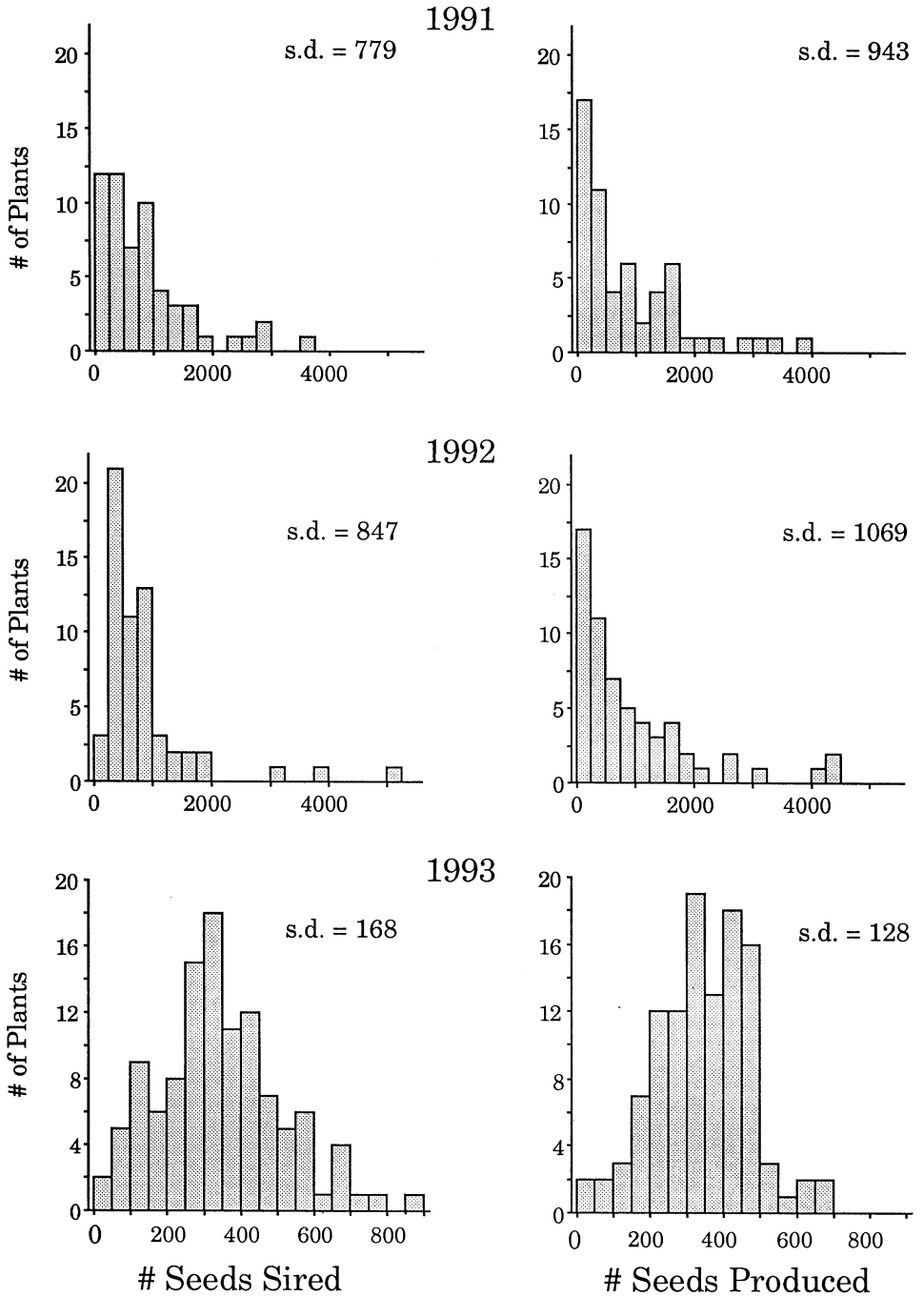

FIG. 3. Frequency distributions of total male and female fitness in the three years.

Future work will measure selection through lifetime female fitness on breeding values for the same traits to determine the effects of environmental correlations (Rausher 1992). Unfortunately, measuring selection on breeding values through male fitness is difficult or impossible with current molecular genetic technology, because the large sample sizes needed to estimate breeding values accurately would mean that there were far too many possible fathers for paternity analysis.

Male and Female Fitness Variance and Covariance

We found a moderately strong positive correlation between male and female fitness in 1991 and 1992, and a weakly significant positive correlation in 1993. To our knowledge, only two other studies have examined the correlation between total male and female fitness in a hermaphroditic plant, and both found significant correlations of about 0.4 (Broyles and Wyatt 1990; Devlin and Ellstrand 1990). Therefore, our re-

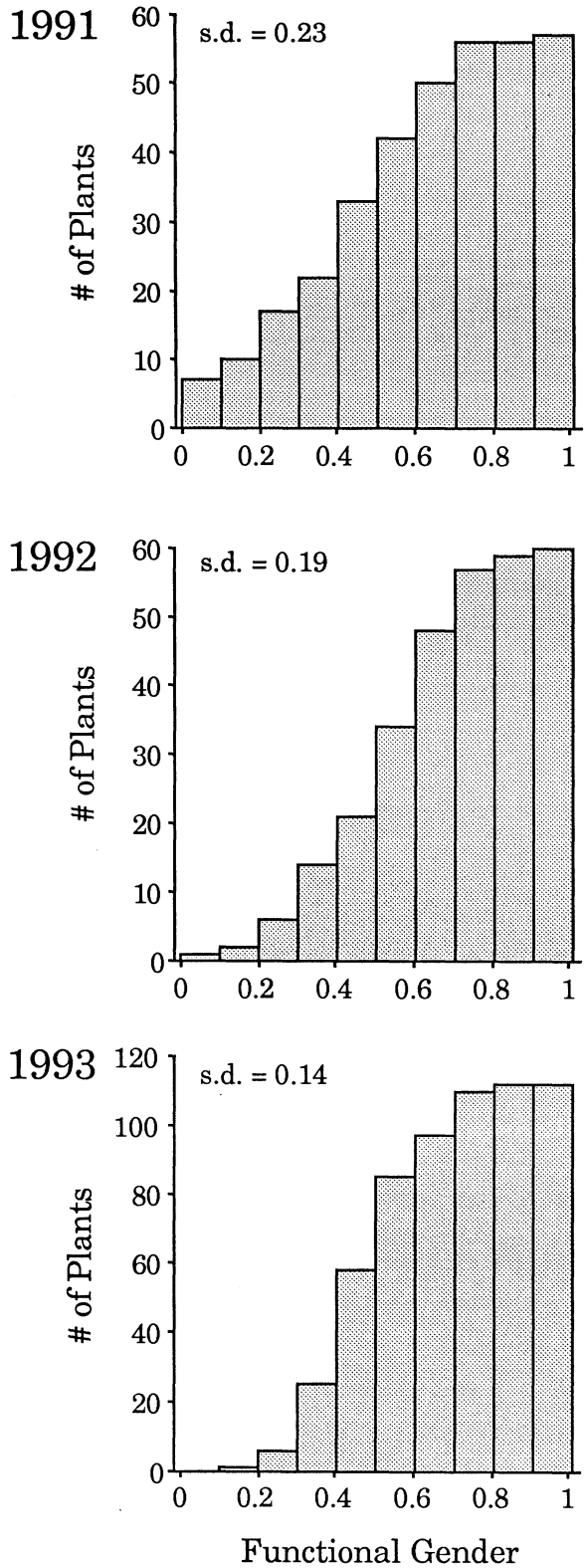

FIG. 4. Cumulative frequency distributions of functional gender for the three years, calculated as the number of seeds produced divided by total fitness (seeds produced + seeds sired).

sults show the strongest correlations found to date, but clearly more studies are necessary. Even in our case, accurate predictions of male fitness could not be made from female fitness estimates alone. In 1991 and 1992, the years with the strong correlations, the R^2 value was only 30%.

Male fitness variance was not greater than female fitness variance in the two years for which lifetime data were available, in contrast to theoretical predictions (Bateman 1948; Trivers 1972). Biologists have been interested in the relative amount of variance in fitness across the sexes as a way to determine the relative strength of selection on males and females, or male and female function in hermaphrodites. Relative fitness variance, however, may not be a good indicator of the strength of selection on any particular trait (Sutherland 1985a,b; Sutherland 1987; Conner 1988; Wilson et al. 1994), and therefore is not a very useful or interesting measure. This is particularly true when actual measurements of selection on traits are available, as in our study.

Conclusions

Our results contradict some widely held views in evolutionary biology. The only significant selection on floral morphology was caused by differences in female fitness, not male fitness. Furthermore, variance in lifetime female fitness was greater than male fitness in both years that lifetime fitness was measured. Further studies that measure selection on floral traits through differences in lifetime male and female fitness are necessary to determine how general these results are, and whether these widely held views are in need of modification.

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