

PATERNAL EFFECTS ON OFFSPRING QUALITY  
IN *CAMPSIS RADICANS*

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**Abstract.**—We investigated paternal effects on seedling performance in relation to patterns of fruit abortion in *Campsis radicans* using a series of 14 experiments with various combinations of pollen donors and recipients. In eight experiments significant paternal effects on three or four dependent performance variables were detected by multivariate ANCOVA. These effects were independent of seed weight, which was controlled in the experimental design and in the statistical analysis. In six of the eight experiments with significant results the favored pollen recipient sired the more vigorous offspring. In general, therefore, patterns of fruit abortion with respect to outcross donor enhance progeny fitness. Maternal discrimination is reduced, however, when pollen from several outcross donors is deposited on the same stigma, a likely occurrence in nature. Discrimination among pollen from different outcross donors is also less important than the ability to discriminate between self- and cross-pollen because the latter distinction has much larger effects on offspring performance. This is one of the first studies to show a relationship between patterns of maternal choice among outcross pollen donors and quality of resultant offspring.

Female and hermaphroditic plants and animals are commonly exposed to multiple mates and/or pollen or sperm from multiple donors. If potential mates or their gametes differ in ways that affect offspring fitness, then selective mating, differential use of pollen or sperm, or preferential maturation of certain zygotes will be adaptive. Maternal selectivity at one or more of these levels occurs in both animals (Downhower and Brown 1980; Thornhill 1983) and plants (Bookman 1984; Bertin 1985; Marshall and Ellstrand 1986). For females to derive any fitness benefits from such selectivity, the progeny sired by the favored mate, sperm, or pollen must be superior to those sired by others. Paternity can affect offspring performance in animals (Howard 1978; Woodward 1986) and plants (Marshall and Ellstrand 1986; Schmitt and Antonovics 1986; Marshall and Whittaker 1989). A critical need is to determine whether maternal choice favors mates that sire the best offspring.

Low fruit-to-flower ratios and abortion of healthy fruits are common among angiosperms, especially outcrossing species in which fruit and seed production is limited by nutrients rather than by the availability of pollen (Stephenson 1981; Sutherland and Delph 1984; Lee 1988). Plants often abort fruits selectively on the basis of seed number or size of the pollen load (Jennings and Topham 1971; Stephenson 1981; Lee and Bazzaz 1982; McDade and Davidar 1984; Lee and

Hartgerink 1986; Lee 1988 and references therein). Many species also abort fruits preferentially from flowers receiving self- rather than cross-pollen (Waller 1979; Aker and Udovic 1981; Lee 1988 and references therein). In a few cases, different non-self-donors, or the number of pollen donors whose pollen is represented on a stigma, have been shown to provide a basis for differential fruit abortion (Murneek 1933; Bertin 1982b; Bookman 1984; Schemske and Pautler 1984; Vander Kloet and Tosh 1984; Marshall and Ellstrand 1986).

Whenever a plant aborts some fraction of its fruit crop, it will be to that plant's advantage to abort fruits selectively to enhance the quality of remaining fruits and seeds. Selective abortion of fruits with few seeds is well-known (Akamine and Girolami 1959; Bertin 1982a; Snow 1982; McDade and Davidar 1984). Such a pattern of abortion can be beneficial to the maternal parent simply because the ratio of pericarp to seed may decline in many-seeded fruits (Mitchell 1977; Lee and Bazzaz 1982; Herrera 1984). Abortion of few-seeded fruits could also enhance offspring quality if many-seeded fruits tended to result from heavy pollinations, which would cause intense gametophytic competition and improve offspring vigor (Lee 1984; Winsor et al. 1987).

Enhanced maternal fitness could also result from differential abortion with respect to paternity if offspring sired by different pollen donors differed in average fitness. Several studies have demonstrated paternal effects on offspring attributes such as seed size and offspring performance (Bertin 1982b; Marshall and Ellstrand 1986; Mazer et al. 1986; Schmitt and Antonovics 1986; Marshall and Whittaker 1989; Nakamura and Stanton 1989). Where present, such paternal effects are typically much weaker than maternal effects on the same variables (Schemske and Pautler 1984; Mazer et al. 1986; Mazer 1987; Marshall 1988).

Few studies have sought possible relationships between fruit abortion and paternal effects on offspring quality. It has been shown (Bertin 1982b) that selective fruit abortion with respect to paternity in *Campsis radicans* favored pollen donors siring seeds that were heavier and more likely to germinate than those sired by the nonfavored donors. In *Raphanus sativus*, fruits sired by one pollen donor produced heavier seedlings than those sired by two other donors, and fruits and seeds sired by the favored donor had a lower likelihood of abortion than fruits and seeds sired by one of the two less favored donors (Marshall 1988; Marshall and Whittaker 1989). Overall, however, the evidence that selective fruit abortion according to pollen donor acts to increase progeny vigor is weak.

Our purpose in this study was to determine the effect of male parentage on offspring growth in *C. radicans*, using combinations of pollen donors and recipients with known patterns of fruit abortion. Our intent was to determine whether fruit abortion can enhance the genetic quality of offspring.

## METHODS AND MATERIAL

*Campsis radicans* (L.) Seem. (Bignoniaceae) is a perennial woody climber with large orange flowers visited by hummingbirds and bees. Fruits matured from 1% to 9% of flowers at four sites in Illinois and Missouri, and most aborted ovaries and fruits showed no evidence of damage (Bertin 1982a). Fruit production is

Each data set was analyzed in a multivariate ANCOVA with repeated measures. The dependent variables were shoot height, number of leaf pairs, shoot weight, and (where measured) root weight. Seed weight was a covariate for each pot, and the germination day of each seed was used as a covariate for that seed. In total there were six single-donor experiments, each representing a different combination of donor and recipient, and seven analyses, since growth data in one experiment were recorded at two times. While an experimental design that permitted a single analysis of all data may have been preferable, we did not attempt this because of limited glasshouse space, variability among benches in the glasshouse, and the difficulty of adhering to a uniform schedule of harvesting. We arbitrarily chose eight fruits from the mixed pollination treatments for analysis. At least 120 seeds from each fruit were weighed to the nearest 0.1 mg. They were planted individually in 8-cm square pots filled with 260 mL Metromix 350 under 150 mL of vermiculite. The pots were placed in a glasshouse and watered as needed. We inspected the pots daily and moved those in which germination occurred to a growth chamber to provide uniform growing conditions. The growth chambers were maintained on a 14L:10D cycle, with day and night temperatures of 25°C and 20°C and a light intensity of 43,000 lx during the day. In three of the eight experiments we planted four oat seeds in each pot to provide a more competitive environment. The oats were thinned to two individuals after 1 wk. For a given experiment, all *Candus* seedlings were harvested the same number of days from emergence (35–56 d for different experiments). At harvest, we measured shoot length and number of leaf pairs greater than 1 cm in length. We removed a small piece of root tissue for electrophoretic determination of paternity and dated and weighed both shoot and root. (Electrophoretic work followed procedures described in Bertin and Sullivan 1988.)

The data from each fruit constituted one experiment, and each experiment was analyzed by a multivariate ANCOVA for the four dependent variables: shoot height, number of leaf pairs, shoot weight, and root weight. The treatment was pollen donor, and seed weight was the covariate.

## RESULTS

Good donors sired more seeds in single-donor pollinations than did poor donors (table 1). Likewise, good donors in mixed pollinations sired more than 50% of seeds in all fruits but one. In neither set of pollinations was there a consistent effect of donor quality on seed weight. Among single-donor pollinations sired by the good donor were significantly heavier than those sired by the poor donor in two cases, the reverse was true in two cases, and there was no significant difference in two cases. In the mixed-donor experiments, donor had no significant effect on seed weight in any of the eight fruits.

For the paired plantings, sire accounted for significant variation in the dependent variables in six of seven analyses (table 2). In four of the analyses progeny sired by the favored donor significantly outperformed those sired by the less favored donor, but in two experiments the reverse was true. In the one experi-

highly nonrandom with respect to paternity (Bertin 1982b, 1985). Individuals are self-sterile following pure self-pollinations, but appreciable selfed seed is produced when self- and cross-pollen are mixed (Bertin and Sullivan 1988). The mechanism of self-sterility appears to involve either late-acting self-incompatibility or inbreeding depression (Bertin et al. 1989).

All fieldwork occurred at Trelease Prairie, 8 km northeast of Urbana, Illinois. All studied plants grew along a fence separating a cultivated field from a managed prairie.

We determined the patterns of fruit abortion with respect to paternity in 1982 and 1983. We bagged inflorescences on several plants, hand-pollinated flowers using pollen from marked donor individuals, and scored percentage fruit production for each donor-recipient combination (see Bertin 1985 for methods). To produce the seeds for the current experiments we made further hand pollinations on seven of the same plants in 1984 and 1986, using pollen from both good and poor donors. (In this article good donors are defined as those siring at least three times as many fruits on a given recipient as a poor donor, from the same number of single-donor pollinations.) These pollinations were of two types. On five recipient plants we pollinated alternate flowers with pollen from good and poor donors. On two other plants we mixed pollen from equal numbers of sires from good and poor donors and applied these mixtures to stigmas. These mixed pollinations used only pairs of donors that were homozygous for different alleles at the 6-phosphogluconate dehydrogenase locus and only recipients that were also homozygous for one allele at this locus. The paternity of all progeny could thus be assigned electrophoretically.

We used different procedures for examining seedling growth, depending on whether paternity of seeds was known beforehand (different pollens on different stigmas) or not (mixed pollinations).

For the single-donor pollinations we assembled all sound fruits sired by poor donors and good donors. In total we used six combinations of donors and recipients. For each donor-recipient combination, we randomly selected equal numbers of seeds from each of the poor fruits so as to produce a total sample of 300–400 seeds. An equal number of seeds was counted from a similar number of randomly selected fruits sired by the good donor. Each seed was weighed to the nearest 0.1 mg, and half-sib seeds from the two treatments were paired by weight. Any that could not be so paired were discarded. Seeds were planted in opposite corners of 8-cm square pots containing 260 mL of Metromix 350 under 150 mL of vermiculite. We placed all plants in a glasshouse, watering and fertilizing them as needed. We recorded date of emergence of each seedling and harvested all plants 10–16 wk from planting date. All plants from a given donor-recipient combination were harvested on the same date, but different growth periods were used in different experiments to facilitate scheduling. At harvest we measured the shoot length, counted the number of leaf pairs greater than 1 cm in length, and dried and weighed the shoot. In four of the experiments the roots were also cleaned, dried, and weighed. In one experiment we recorded leaf number and shoot length at 10 wk in addition to recording data at harvest.

TABLE 3

AVERAGE HEIGHTS OF SEEDLINGS Sired BY GOOD AND POOR DONORS IN PAIRED-SEEDLING EXPERIMENTS

Recipient	Height (cm)		Difference (%)
	Good	Poor	
5	27.6	27.4	- .7
22	20.8	28.7	38.0*
41	15.5	13.6	14.0*
41	17.9	15.2	17.8*
41	7.3	17.9	17.8*
42	6.5	7.4	- 12.2*
43	37.5	27.5	36.4*

NOTE.—Sample sizes are as in table 2. Asterisks denote significant differences.

TABLE 4

EFFECTS OF SIRE ON SEEDLING PERFORMANCE IN SINGLE-SEEDLING EXPERIMENTS

Fruit Number	Good Donor	Poor Donor	Growth Period (d)	N	Competition	TSQ	P	Significant Effects
10	8	8	77, 18	56	+	2.77	.03	H, L
10	9	9	35	49	+	.29	.88	
10	9	9	85, 27	85	0	1.30	.28	
10	1	1	68, 24	49	0	2.28	.07	
10	1	1	32, 11	35	+	.52	.72	
10	1	1	14, 22	56	0	4.07	.01	H, L, R
3A	2	2	43, 13	43	0	1.90	.13	
10	1	1	54, 12	49	+	3.57	.01	H, L, S, R

NOTE.—Abbreviations are as in table 2. All fruits are from two recipients, 1 or 8, denoted by the first digit of the fruit number. N, Number of seeds sired by each donor, with the good donor listed first. "+", "0", "-" in competition column indicates presence of oat competitors. For each significant difference, seedlings sired by good donors outperformed those sired by poor donors.

the poor donor. One of the remaining fruits showed a difference approaching significance (8-1-1,  $P = .07$ ). For 15 of the 20 dependent variables among the fruits showing no significant effects (five fruits times four dependent variables), mean performance was greater among seedlings sired by good donors than those sired by poor donors (table 5). If the sequential Bonferroni technique is applied, none of the above differences exhibits tablewide significance.

The presence of competing oats produced no consistent effects, as significant (individual, not tablewide) effects of paternity occurred in one of three experiments with competition and in two of five experiments without competition. The duration of the growth period may have had some effect, as both of the experiments that ran for the longest time (56 d produced (individually) significant results, and the other significant result was in one of the experiments run for the next longest period (49 d). In separate ANCOVAs performed on each of the four

TABLE 1

RELATIVE NUMBERS OF SEEDS Sired BY GOOD AND POOR DONORS IN SINGLE-DONOR POLLINATIONS

Recipient (DONORS)	Nos. of Seeds Sired (N)		P
	Good Donor	Poor Donor	
5 (9, 8)	503.7 (6)	303.0 (5)	4.10 .015
22 (8, 3)	903.0 (5)	636.2 (4)	6.97 .002
41 (3, 9)	751.3 (3)	680.0 (1)	.91 NS
41 (3, 10)	751.3 (3)	632.3 (3)	2.51 NS
42 (3, 10)	833.0 (2)	600.0 (2)	19.35 .033
43 (3, 8)	616.3 (3)	491.8 (4)	4.46 .021

NOTE.—N denotes numbers of fruit examined. The values T and P are from *t*-tests comparing seed numbers in the two treatments.

EFFECTS OF SIRE ON SEEDLING PERFORMANCE IN PAIRED-SEEDLING EXPERIMENTS

Recipient	Period (d)	Good Donor	Poor Donor	N	Dependent Variables	TSQ	df	P	Best	Significant Effects
5	114	9	8	17	H, L, S, R	.83	4,12	.53		
22	98	8	3	100	H, L, S, R	10.19	4,95	0*	G	H, L, S, R
41	70	3	9	83	H, L	6.64	2,80	0*	G	H
41	41	3	9	83	H, L, S	5.88	3,79	0*	G	H
41	75	3	10	46	H, L, S, R	11.20	4,41	0*	P	S
41	75	3	10	46	H, L, S, R	4.41	0*			
42	79	3	10	11	H, L, S	4.83	3,7	.04	P	H, L, S
43	80	3	8	89	H, L, S, R	12.30	4,84	0*	G	H, L

NOTE.—H, Stem height; L, number of leaf pairs; S, shoot weight; R, root weight; TSQ, Hotelling's  $T^2$  from multivariate ANCOVAs with repeated measures. Asterisks denote results showing tablewise significance according to the sequential Bonferroni technique. Column headed "Best" denotes the donor (G, good; P, poor) that sired the more vigorous offspring. Parameters listed beneath "Significant Effects" column are those for which donor treatment is significant in univariate ANCOVAs.

ment with data recorded at two times, the same pattern was evident at both times. Typical of the relative performance of seedlings sired by good and poor donors, mean height of progeny sired by good donors ranged from 13% less than the height of those sired by poor donors to 38% greater (table 3).

To eliminate the bias that accompanies multiple significance tests we employed the sequential Bonferroni technique (Holm 1979; Rice 1989). For a table of  $k$  probabilities and a .05 significance level,  $P$  values are ranked from smallest to largest and compared with  $.05/k$ ,  $.05/(k - 1)$ ,  $.05/(k - 2)$ , and so forth. Under this procedure only the interpretation of results for plant 42 changes, with the difference becoming nonsignificant.

Among the eight fruits arising from mixed pollinations, significant effects of donor identity on seedling performance were detected in three cases (table 4). In each case the seedlings sired by the good donor outperformed those sired by

and that might tend to conceal the paternal effects demonstrated here. Furthermore, as noted by Mazer et al. (1986), the presence of strong maternal effects and/or male-by-female interactions would tend to reduce the intensity of selection on paternal traits. It should also be noted, however, that differences among individuals that are minor or nonexistent in a glasshouse may be more important under conditions of greater stress (Marshall 1988; Marshall and Whittaker 1989), competition (Stanton 1984b), or herbivory. Furthermore, some of our seedling growth experiments ran for only 5-7 wk, and paternal effects may be more detectable after longer periods of growth. This is suggested by the greater number of significant effects that were detected in the longer experiments reported in table 1 than those in table 3 and by the occurrence of the most pronounced differences in table 3 in those experiments with the longest growth periods.

#### Selective Abortion and Paternity

Among the eight experiments with significant donor effects on offspring performance, the performance of progeny sired by the good donor was better in six cases (three of four after the Bonferroni correction). Among the nonsignificant differences the trend was also toward better performance of the good donor's progeny (tables 3, 5). These results and those of Marshall and Whittaker (1989) are apparently the first reported cases of fruit abortion with respect to pollen donor that increases the average vigor of progeny independently of seed weight. Effects of seed weight were eliminated in the experimental design by pairing seeds according to weight or eliminated statistically by treating weight as a covariate. The results would probably have been changed little if donor effects on weight had been included in the analysis, because donor had a significant effect on weight in only 4 of the 14 experiments. A more powerful analysis in previous work showed a significant positive correlation between paternal success and weight of seeds sired in single-donor pollinations (Bertin 1982b). Because the covariate seed weight invariably had positive effects on seedling performance in the present study, any weight advantages of seeds sired by good donors would tend to increase seedling growth.

Overall, then, the beneficial effects of selective fruit abortion with respect to paternity in *Campsis* are at least threefold. Such abortion patterns result in fruits with more seeds and a lower ratio of pericarp to total seed weight, a tendency toward heavier seeds—a weight advantage that translates into better seedling growth—and seeds that are often genetically superior, as indicated by their enhanced growth independent of effects of seed weight.

These results are consistent with those of other studies showing that selective abortion of fruit or seeds improves offspring quality following mixed or natural pollinations. Stephenson and Winsor (1986) showed, for example, that naturally pollinated *Lotus corniculatus* produced more vigorous seedlings when fruit abortion was allowed to occur naturally rather than being randomly imposed. Similarly, in *Cucurbita pepo* patterns of fruit abortion favored retention of ovaries that received larger pollen loads and whose seeds grew more vigorously than those receiving smaller pollen loads (Winsor et al. 1987). In *Phaseolus coccineus* seeds from fruits allowed to undergo natural patterns of seed abortion produced

TABLE 5  
AVERAGE HEIGHTS OF SEEDLINGS SIBED BY GOOD AND POOR DONORS IN SINGLE-SEEDLING EXPERIMENTS

Fruit Number	Height (cm)		Difference (%)
	Good	Poor	
1-3-2	13.1	11.1	18.0*
1-5-3	6.5	6.2	4.8
1-6-2	7.5	7.7	-2.6
8-1-1	7.0	7.2	12.9
8-1-5	7.5	6.5	15.4
8-2-5	21.7	17.4	24.7*
8-3-8	36.6	33.2	10.2
8-5-3	7.9	5.1	54.9*

NOTE.—Sample sizes are as in table 4. Asterisks denote significant differences.

independent variables for each of the eight fruits, all but one of the 32 seed weight covariates were positive, 12 significantly so, which indicates a positive effect of seed weight on seedling performance.

#### DISCUSSION

#### Effects of Paternity

Maternal effects on offspring characteristics such as seed size and seedling performance are often considerable (Stanton 1984a; Schlichting and Devlin 1989). Paternal effects on the same variables sometimes appear to be absent (Bookman 1984; Schlichting and Devlin 1989) and where they occur are usually weaker than maternal effects (Schemske and Paulter 1984; Mazer et al. 1986; Mazer 1987; Marshall 1988; Richardson and Stephenson 1991). In *Raphanus raphanistrum*, for example, the maternal plant accounted for 38%–39% of variability in mean seed weight per fruit, while the pollen donor accounted for only 0%–3% (Mazer et al. 1986). Nevertheless, the growing literature describing paternal effects on offspring attributes (Kieesselsbach 1926; Bertin 1982b; Hellman and Moore 1983; Schemske and Paulter 1984; Marshall and Ellstrand 1986; Mazer et al. 1986; Marshall 1988; Marshall and Whittaker 1990; Andersson 1990; Richardson and Stephenson 1991) suggests that differences among seeds and seedlings based on pollen donor are often of sufficient magnitude to affect offspring performance and therefore maternal fitness. Such fitness differentials could in turn cause selection to favor mechanisms such as selective abortion of seeds or fruits that would enhance the average quality of a plant's remaining seed crop.

Under the conditions used in this study, paternal effects on seedling performance were detected in 8 of 14 experiments (4 of 14 with the Bonferroni correction). By using controlled environmental conditions during seedling growth we eliminated a source of variation that would be present under natural conditions

Several hypotheses have been proposed to account for low fruit-to-flower ratios in plants whose reproduction is not limited by pollen availability. These include (1) pollinator attraction, (2) bet hedging, or the provision of sufficient ovaries to allow maximal fruit production if resources are plentiful, (3) pollen donation, or a primary male function for the nonfruiting flowers, and (4) selective fruit abortion to enhance offspring quality (Willison and Rathcke 1974; Stephenson 1980; Queller 1983; Sutherland and Delph 1984). While a demonstration that selective fruit abortion enhances offspring quality is a necessary condition for hypotheses 4, it is not a sufficient condition. The advantages of selective fruit abortion might not by themselves be sufficient to overcome the costs of producing "extra" flowers. Any such advantage might either act in concert with selective pressures from hypotheses 1-3 or act subsequent to the evolution of low fruit-to-flower ratios that have appeared for other reasons.

It seems unlikely that the ability to discriminate seeds sired by pollen from different cross-pollen donors has been the major impetus for the evolution of selective fruit abortion in *Campsis*. First, patterns of abortion for two maternal plants (41, 42) sometimes favored pollen donors that gave rise to less vigorous seedlings. In several other cases pollen donors for whom maternal preferences differed greatly sired seedlings of apparently equal quality. Second, most naturally pollinated fruits undoubtedly contain a mixture of seeds sired by different donors. Patterns of selective seed abortion with respect to outcross donor in *Campsis* are generally much less pronounced than patterns of selective fruit abortion when all seeds in a fruit are sired by the same donor (Bertin 1990). However, the discrimination of seeds sired by self-pollen from those sired by outcross pollen does produce substantial fitness benefits following both mixed- and single-donor pollinations (Bertin and Sullivan 1988; Bertin et al. 1989). It seems likely that selection has acted primarily to effect this discrimination, and it is possible that the patterns of selection with respect to outcross donors are an incidental result of the mechanism for discrimination between self- and cross-pollen.

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#### LITERATURE CITED

- Akamine, E. K., and G. Giroiani. 1959. Pollination and fruit set in the yellow passion fruit. Technical Bulletin of the Hawaii Experiment Station 39.
- Aker, C. K., and D. Udovic. 1981. Oviposition and pollination behavior of the yucca moth, *Tegeticula maculata* (Lepidoptera: Prodoxidae), and its relationship to the reproductive biology of *Yucca whipplei* (Agavaceae). *Oecologia* (Berlin) 49:96-101.

more vigorous seedlings than seeds from fruits wherein seeds were aborted by hand (Rocha and Stephenson 1991), and the same may be true in *Cryptantha flava* (Casper 1988).

#### A Potential Mechanism

The results of this study and previous work (Bertin 1982b, 1985, 1990) are consistent with the idea that progeny heterozygosity plays a major role in determining progeny vigor both before seed maturation and during seedling growth. In this scenario the crossing of distantly related individuals would result in high levels of fruit production, many-seeded fruits, large seeds (because the large number of vigorous embryos would provide a strong hormonally mediated sink for maternal resources), and vigorous seedlings. This explanation is consistent with a proposed mechanism of self-sterility in *Campsis*, namely, inbreeding depression (Bertin et al. 1989), and is consistent with the fact that donor quality is specific to recipient (Bertin 1982b; note also that the status of donors 3 and 8 differs among recipients in table 1). Significant effects of genetic relatedness between pollen donor and recipient on fruit weight and seedling vigor have been found in several cultivars of *Vaccinium* spp. (Hellman and Moore 1983) and in *Raphanus sativus* (Karron and Marshall 1990). Similarly, differences in fitness of progeny sired by pollen donors at different distances from the maternal plant have been attributed to differences in genetic similarity between donors and recipients (Schemske and Pautler 1984; Waser et al. 1987; Waser and Price 1989). Additional mechanisms may be at work in other species. In *R. sativus*, for example, donor effects sometimes occur across maternal plants (Marshall and Ellstrand 1986), which indicates the operation of factors that, unlike heterosis, are not dependent on particular donor-recipient combinations.

#### Maternal Choice and Low Fruit-to-Flower Ratios

Several articles have suggested that fruit abortion or other mechanisms of maternal choice may lead to sexual selection (Stephenson and Bertin 1983; Willison and Burley 1983). Although our results are consistent with this possibility, a demonstration of two additional factors is required. First, we have not ruled out environmental variability among males as a cause for the observed differences. Conceivably, environmental influences during pollen development could affect the nutrient-garnering ability of seeds that they sire without affecting seed weight, although this seems unlikely. Second, for maternal choice to cause sexual selection, it would have to be fairly consistent among pollen recipients. A major part of selectivity in *Campsis* is dependent on the particular donor-recipient combination, although we have not yet performed the kind of analysis that would permit a clear discrimination of paternal and interaction effects (Lyons et al. 1989).

Plants that exhibit patterns of selective fruit abortion that enhance average fitness of progeny clearly are at an advantage compared to those that abort fruit randomly. However, this does not automatically mean that low fruit-to-flower ratios have evolved to promote selective fruit abortion or that the ability to discriminate among outcross pollen donors has been the driving force in the evolution of the capability for selective fruit abortion.

- Andersson, S. 1990. Paternal effects on seed size in a population of *Crepis tectorum* (Asteraceae). *Oikos* 59:3-8.
- Bertin, R. I. 1982a. Floral biology, hummingbird pollination and fruit production of trumpet creeper (*Campsis radicans*, Bignoniaceae). *American Journal of Botany* 69:122-134.
- . 1982b. Paternity and fruit production in trumpet creeper (*Campsis radicans*). *American Naturalist* 119:694-709.
- . 1985. Nonrandom fruit production in *Campsis radicans*: between-year consistency and effects of prior pollination. *American Naturalist* 126:750-759.
- . 1990. Paternal success following mixed pollinations of *Campsis radicans*. *American Midland Naturalist* 124:153-163.
- Bertin, R. I., and M. Sullivan. 1988. Pollen interference and cryptic self-fertility in *Campsis radicans*. *American Journal of Botany* 75:1140-1147.
- Bertin, R. I., C. Barnes, and S. L. Guttman. 1989. Self-sterility and cryptic self-fertility in *Campsis radicans* (Bignoniaceae). *Botanical Gazette* 150:397-403.
- Bookman, S. S. 1984. Evidence for selective fruit production in *Asclepias*. *Evolution* 38:72-86.
- Casper, B. B. 1988. Evidence for selective embryo abortion in *Cryptantha flava*. *American Naturalist* 132:318-326.
- Downhower, J. F., and L. Brown. 1980. Male preferences of female mottled sculpins, *Cottus bairdi*. *Animal Behaviour* 28:728-734.
- Hellman, E. W., and J. N. Moore. 1983. Effect of genetic relationship to pollinizer on fruit, seed, and seedling parameters in highbush and rabbyleaf blueberries. *Journal of the American Society for Horticultural Science* 108:401-405.
- Herrera, C. M. 1984. Selective pressures on fruit seediness: differential predation of fly larvae on the fruits of *Berberis hispanica*. *Oikos* 42:166-170.
- Holm, S. 1979. A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics* 6:65-70.
- Howard, R. D. 1978. The influence of male-defended oviposition sites on early embryo mortality in *Raphanus sativus*. *Evolution* 44:260-268.
- Kieselschick, T. A. 1976. The immediate effect of gametic relationship and of parental type upon the kernel weight of corn. *Nebraska Agricultural Experiment Station Research Bulletin* 33:1-69.
- Lee, T. D. 1984. Patterns of fruit maturation: a gametophyte competition hypothesis. *American Naturalist* 123:427-432.
- . 1988. Patterns of fruit and seed production. Pages 179-202 in J. Lovett Doust and L. Lovett Doust, eds. *Plant reproductive ecology*. Oxford University Press, New York.
- Lee, T. D., and F. A. Bazzaz. 1982. Regulation of fruit maturation pattern in an annual legume, *Cassia fasciculata*. *Ecology* 63:1374-1388.
- Lee, T. D., and A. P. Hartgerink. 1986. Pollination intensity, fruit maturation pattern, and offspring quality in *Cassia fasciculata* (Leguminosae). Pages 417-422 in D. L. Mulcahy, G. B. Mulcahy, and R. L. Whitaker, eds. *Biotechnology and ecology of pollen*. Springer, New York.
- Lyons, E. E., N. M. Waser, M. V. Price, J. Antonovics, and A. Moten. 1989. Sources of variation in plant reproductive success and implications for concepts of sexual selection. *American Naturalist* 134:409-433.
- Marshall, D. L. 1988. Postpollination effects on seed paternity: mechanisms in addition to microgametophyte competition operate in wild radish. *Evolution* 42:1256-1266.
- Marshall, D. L., and N. C. Ellstrand. 1986. Sexual selection in *Raphanus sativus*: experimental data on nonrandom fertilization, maternal choice, and consequences of multiple paternity. *American Naturalist* 127:415-445.
- Marshall, D. L., and K. L. Whitaker. 1989. Effects of pollen donor identity on offspring quality in wild radish, *Raphanus sativus*. *American Journal of Botany* 76:1081-1088.
- Mazer, S. J. 1987. Paternal effects on seed development and seed yield in *Raphanus raphanistrum*: implications for natural and sexual selection. *Evolution* 41:355-371.
- Mazer, S. J., A. V. Snow, and M. L. Stanton. 1986. Fertilization dynamics and parental effects upon fruit development in *Raphanus raphanistrum*: consequences for seed size variation. *American Journal of Botany* 73:500-511.
- McDade, L. A., and P. Davidar. 1984. Determinants of fruit and seed set in *Favonia dasypleta* (Malvaceae). *Oecologia* (Berlin) 64:61-67.
- Mitchell, R. 1977. Bruchid beetles and seed packaging by palo verde. *Ecology* 58:644-651.
- Murreek, A. E. 1933. The nature of shedding of immature apples. *Missouri Agricultural Experiment Station Research Bulletin* 201.
- Nakamura, R. R., and M. L. Stanton. 1989. Embryo growth and seed size in *Raphanus sativus*: maternal and paternal effects in vivo and in vitro. *Evolution* 43:1435-1443.
- Queller, D. C. 1983. Sexual selection in a hermaphroditic plant. *Nature* (London) 305:706-707.
- Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43:223-225.
- Richardson, T. E., and A. G. Stephenson. 1991. Effects of parentage, prior fruit set and pollen load on fruit and seed production in *Campanula americana* L. *Oecologia* (Berlin) 87:80-85.
- Roeha, O. J., and A. G. Stephenson. 1991. Effects of nonrandom seed abortion on progeny performance in *Phaseolus cochineus* L. *Evolution* 45:1198-1208.
- Schemske, D. W., and L. P. Paurler. 1984. The effects of pollen composition on fitness components in a Neotropical herb. *Oecologia* (Berlin) 62:31-36.
- Schlichting, C. D., and B. Davlin. 1989. Male and female reproductive success in the hermaphroditic plant *Phlox drummondii*. *American Naturalist* 133:212-227.
- Schmitt, J., and J. Antonovics. 1986. Experimental studies of the evolutionary significance of sexual reproduction. III. Maternal and paternal effects during seedling establishment. *Evolution* 40:817-829.
- Snow, A. A. 1982. Pollination intensity and potential seed set in *Passiflora vitifolia*. *Oecologia* (Berlin) 55:231-237.
- Stanton, M. L. 1984a. Developmental and genetic sources of seed weight variation in *Raphanus raphanistrum* L. (Brassicaceae). *American Journal of Botany* 71:1090-1098.
- . 1984b. Seed variation in wild radish: effect of seed size on components of seedling and adult fitness. *Ecology* 65:1105-1112.
- Stephenson, A. G. 1980. Fruit set, herbivory, fruit reduction, and the fruiting strategy of *Catalpa speciosa* (Bignoniaceae). *Ecology* 61:57-64.
- . 1981. Flower and fruit abortion: proximate causes and ultimate functions. *Annual Review of Ecology and Systematics* 12:253-279.
- Stephenson, A. G., and R. I. Bertin. 1983. Male competition, female choice, and sexual selection in plants. Pages 109-149 in L. Real, ed. *Pollination biology*. Academic Press, New York.
- Stephenson, A. G., and J. A. Winsor. 1986. *Lotus corniculatus* regulates offspring quality through selective fruit abortion. *Evolution* 40:453-458.
- Sutherland, S., and L. Delph. 1984. On the importance of male fitness in plants: patterns of fruit set. *Ecology* 65:1093-1104.
- Thornhill, R. 1983. Cryptic female choice in the scorpionfly *Harpobittacus nigriceps*. *American Naturalist* 122:765-788.
- Vander Kloet, S. P., and D. Tosh. 1984. Effects of pollen donors on seed production, seed weight, germination, and seedling vigor in *Vaccinium corymbosum* L. *American Midland Naturalist* 112:392-396.
- Waller, D. 1979. The relative costs of self- and cross-fertilized seeds in *Impatiens capensis* (Balsaminaceae). *American Journal of Botany* 66:313-320.
- Waser, N. M., and M. V. Price. 1989. Optimal outcrossing in *Ipomopsis aggregata*: seed set and offspring fitness. *Evolution* 43:1097-1109.
- Waser, N. M., M. V. Price, A. M. Montalvo, and R. N. Gray. 1987. Female mate choice in a perennial herbaceous wildflower, *Delphinium nelsonii*. *Evolutionary Trends in Plants* 1:29-33.
- Willson, M. F., and N. Burtley. 1983. Mate choice in plants. Princeton University Press, Princeton, N.J.
- Willson, M. F., and B. J. Ritcheke. 1974. Adaptive design of floral display in *Asclepias syriaca* L. *American Midland Naturalist* 92:47-57.

- Winsor, J. A., L. E. Davis, and A. G. Stephenson. 1987. The relationship between pollen load and fruit maturation and the effect of pollen load on offspring vigor in *Cucurbita pepo*. American Naturalist 129:643-656.
- Woodward, B. 1982. Sexual selection and nonrandom mating patterns in desert anurans (*Bufo woodhousei*, *Scaphiopus couchi*, *S. multiplicatus* and *S. bombifrons*). Copeia 1982:351-355.
- . 1986. Paternal effects on juvenile growth in *Scaphiopus multiplicatus* (the New Mexico spadefoot toad). American Naturalist 128:58-65.

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