Pollen Limitation of Female Reproduction in Lobelia Cardinalis and L. Siphilitica
Author(s): Mark O. Johnston
Source: *Ecology*, Vol. 72, No. 4 (Aug., 1991), pp. 1500-1503
Published by: Ecological Society of America
Stable URL: http://www.jstor.org/stable/1941123
Accessed: 27/08/2008 12:44

Ecology, 72(4), 1991, pp. 1500–1503

POLLEN LIMITATION OF FEMALE REPRODUCTION IN LOBELIA CARDINALIS *AND* L. SIPHILITICA

Mark O. Johnston[1]

It is common for hermaphroditic angiosperms to make more flowers and ovules than fruits and seeds (Willson 1979, Bawa and Webb 1984, Sutherland and Delph 1984, Sutherland 1986). Two kinds of hypotheses have been put forth to explain the existence of these nonfruiting flowers (reviewed by Sutherland 1987). One set proposes that the nonfruiting flowers serve to increase reproductive fitness through the female and/or male component. In such cases seed production is limited by resources other than pollen. An alternative hypothesis proposes that plants typically do not receive enough pollen for full fruit- or seed-set. These two kinds of limits on female reproductive success have different evolutionary implications. Whenever seed production is resource limited, for example, there will be competition among plants for male success, causing selection on traits influencing pollen dissemination. When seed production is pollen limited, on the other hand, there will be less competition among potential sires but stronger selection on characters influencing pollen receipt (Johnston 1991).

Theoretical examination of this issue suggests that pollen limitation of female reproductive success in hermaphroditic plants may not be evolutionarily stable: in a consistently pollen-limited population, individuals allocating more to pollen dispersal and less to ovules, which by definition will not receive sufficient pollen, should increase in frequency until the population is resource limited (cf. Haig and Westoby 1988).

Whether seed production is limited more by access to pollen or to other resources remains unknown for all but a few species. Though many studies have reported increased fruit- or seed-set with supplemental hand pollination, it is difficult to assess the prevalence of pollen limitation because most of these studies were not carried out on the whole plant (see Bawa and Webb 1984, Horvitz and Schemske 1988, Zimmerman and Pyke 1988). Supplemental pollination of a subset of flowers may boost their reproductive output at the expense of that of other flowers on the same plant. Therefore, comparisons based on a subset of flowers can conclusively demonstrate resource limitation (when no increase in seed production can be achieved) but not pollen limitation. The purpose of this study was to determine whether pollen availability limited female reproductive success at the whole-plant level in two hermaphroditic pollinator specialists: hummingbird-pollinated *Lobelia cardinalis* L. (two populations) and bumble bee-pollinated *L. siphilitica* L. (Lobeliaceae). Supplemental pollen was added to all flowers in the treatment group of each species, thereby providing an unambiguous test of the pollen-limitation hypothesis. In a Pennsylvania population of *L. cardinalis,* Devlin and Stephenson (1987) found no pollen limitation of seed production in an experiment similar to the present one. They concluded, however, that pollen limitation probably occurs in some years, because the naturally pollinated plants had lower seed-set in 1980 than 1982, while the supplementally pollinated plants did not. The experiments reported here therefore add information on spatial variation in pollen limitation within *L. cardinalis,* and suggest predictions of the relative strengths of selection acting in the two populations (Johnston 1991).

Study Species and Populations

Lobelia siphilitica and *L. cardinalis* are herbaceous, short-lived perennials that grow near lakes and streams primarily in eastern North America (McVaugh 1936, Bowden 1959, Devlin and Stephenson 1984, 1985). The blue flowers of *L. siphilitica* are visited primarily by bumble bees. East of the Mississippi River *L. cardinalis* is pollinated solely by *Archilochus colubris,* the Ruby-throated Hummingbird. The plants flower from late July to mid-September, fruit from August to October, and overwinter as rosettes. Both species are self-compatible and suffer no decrease in seed number with self-fertilization (Johnston 1990). However, as there is no overlap in the sexual phases of the protandrous flowers, autogamous self-fertilization is almost nonexistent.

This study was conducted at two sites in southwestern Michigan, Wintergreen Lake of the Kellogg Bird Sanctuary (Kalamazoo County) and Glass Creek (Barry County), a forest stream 40 km to the north. Both species grow along Glass Creek, while only *L. cardinalis* occurs at Wintergreen Lake. Compared to the population at Glass Creek, *L. cardinalis* at Win-

---

[1] Committee on Evolutionary Biology, The University of Chicago, 915 East 57th Street, Chicago, Illinois 60637 USA. Present address: Department of Biology, McGill University, 1205 Avenue Docteur Penfield, Montreal, Quebec, Canada H3A 1B1.

TABLE 1. Mean values for naturally and supplementally (hand-) pollinated plants in three populations of *Lobelia* in southwestern Michigan. Asterisks indicate significant effect of supplemental pollination (Wilcoxon's signed rank-sum test, two-tailed).

	Lobelia cardinalis				*Lobelia siphilitica*	
	Wintergreen Lake		Glass Creek		Glass Creek	
	Natural	Supplemental	Natural	Supplemental	Natural	Supplemental
Flower number	12.2	12.2	12.3	12.8	13.1	13.7
Fruit number	7.1	10.1*	6.2	10.2**	3.8	7.3*
Seed number	1550	4626**	3663	7935**	612	2318***
Total seed mass (μg)	76 210	187 778**	148 955	274 318**	19 094	59 216**
Mass per seed (μg)	49.3	41.3***	39.5	36.8	30.5	27.6
Fruits per flower	0.64	0.83†	0.38	0.78***	0.32	0.54*
Seeds per flower	139	329**	206	504***	62	176***
Seeds per fruit	223	450*	532	619	170	304**

* $P < .05$; ** $P < .01$; *** $P < .001$.
† $P < .06$.

tergreen Lake is much denser and has higher hummingbird activity.

Methods

Throughout each population's flowering period in 1988 I matched pairs of individual plants for flower number, date of first flower, and density of surrounding flowers. Close matching by flower number was possible because all buds are produced before flowering commences. I randomly chose one plant (experimental) from each pair to receive supplemental hand pollinations, while the other (control) received only natural pollinations. I used a plastic cocktail spear to cover all open stigmas on experimental plants with a mixture of outcross pollen from one to five individuals. This procedure was performed every 2 to 4 d so that every stigma on experimental plants was saturated with pollen at least once. All seed-producing capsules were collected. There were 15 pairs of *L. cardinalis* at Wintergreen Lake, 17 pairs of *L. cardinalis* at Glass Creek and 20 pairs of *L. siphilitica* at Glass Creek.

For each pair of plants I determined the difference between experimental and control values of flower number, fruit number, seed number, total seed mass, mass per seed, fruits per flower, seeds per flower, and seeds per fruit. Wilcoxon's signed rank-sum test for paired values (Sokal and Rohlf 1981) was used to ascertain whether experimental and control plants differed in each of these measures. Because of the large number of very small seeds in each species, seed number per plant was obtained by first determining the mass of 50 seeds to the nearest 10 μg. Total seed number was then estimated by the product 50 seeds × (mass of all collected seeds)/(mass of 50 seeds).

To determine the degree of pollen limitation in each population, I obtained the mean of the control plant-to-experimental plant ratio for each reproductive measure. One pair was omitted from *L. siphilitica* because the experimental plant made no seeds or fruits (denominator = 0). The Mann-Whitney *U* test (Sokal and Rohlf 1981) was used to determine whether the *L. cardinalis* populations differed in each measure of the degree of pollen limitation.

Results

Pollen quantity limited fruit number, seed number, total seed mass, fruit number per flower, and seed number per flower in all three populations (Table 1). For all whole-plant measures of reproductive success except total seed mass, *L. cardinalis* at Wintergreen Lake was less pollen-limited than *L. cardinalis* at Glass Creek (Table 2). *L. siphilitica* individuals receiving only natural pollinations produced 55% as many fruits, 34% as many seeds and 40% as much total seed mass as plants receiving supplemental pollinations. For *L. cardinalis* at Glass Creek these values were similar. In contrast, naturally pollinated *L. cardinalis* at Wintergreen Lake produced 86% as many fruits and 79% as many seeds as supplementally pollinated plants. How-

TABLE 2. Mean performance of naturally pollinated (control) plants, expressed as a proportion of the performance of supplementally pollinated (experimental) plants, in the three *Lobelia* populations. Values for the two populations of *Lobelia cardinalis* followed by different letters are significantly different (Mann-Whitney *U* test, one-tailed, $P < .05$).

	Lobelia cardinalis		*Lobelia siphilitica*
	Wintergreen Lake	Glass Creek	Glass Creek
Flower number	1.01 a	0.98 a	0.96
Fruit number	0.86 a	0.48 b	0.55
Seed number	0.79 a	0.35 b	0.34
Total seed mass	0.99 a*	0.39 a*	0.40
Mass per seed	1.22 a	1.11 a	1.13

* $P < .06$.

ever, they made 99% as much total seed mass, indicating that supplemental pollination created more but lighter seeds. This trend existed in all three populations, but was significant only in *L. cardinalis* at Wintergreen Lake (Table 1). The flower number of control and experimental plants did not differ in any population (Table 1).

Discussion

In *L. cardinalis* pollen availability limited female reproductive success more strongly at Glass Creek, where hummingbirds are rarely seen visiting *Lobelia* (M. O. Johnston, *personal observation*). At Wintergreen Lake total seed mass was significantly pollen limited (Table 1), even though control plants produced 99% as much as experimentals (Table 2). This value was greatly affected by one pair of plants, however, in which the control-to-experimental plant ratio was 6.27. Removal of this outlier decreases the average relative performance of controls in this population to 0.61. For *L. cardinalis* plants pooled from three populations in Pennsylvania and grown in a common garden, mean seed mass was negatively correlated with seed number per flower and nearly significantly negatively correlated with seed number per plant (Devlin 1989).

Temporal and spatial variation.—The degree of pollen limitation can vary temporally as well as spatially (e.g., Galen 1985, McCall and Primack 1985, Piper et al. 1986). Compared with pollinator generalists, plants with fewer pollinators may experience fluctuations in pollinator visits more commonly, especially if the pollinators visit other species. While temporal variation was not addressed in this study, data on natural fruit number per flower, seed number per flower and seed number per fruit are available for each population from a selection study conducted in 1987 (Johnston 1991). For naturally pollinated *L. cardinalis* at Wintergreen Lake in 1987, the average number of fruits per flower (0.79, $n = 133$), seeds per flower (414) and seeds per fruit (521) were all significantly greater than for naturally pollinated plants in 1988 (Mann-Whitney U test, one-tailed, $P < .01$), suggesting increased pollen limitation in 1988. Seed number per fruit (239, $n = 14$) in *L. siphilitica* was also greater in 1987 ($P < .05$). The number of fruits per flower and seeds per flower did not differ between years in *L. siphilitica,* and none of the three ratios differed between years in *L. cardinalis* at Glass Creek.

Implications, and results from other species.—It is often proposed that male reproductive success is limited by access to eggs or ovules, while female reproductive success is limited by resources ("Bateman's [1948] principle"). While it is clear that seed production in many plant species is limited by resources other than pollen (Zimmerman and Pyke 1988, and references therein), we still do not know whether pollen limitation is a common feature of plant populations. Only a handful of studies has compared fruit or seed production at the whole-plant level where all (or nearly all) flowers on experimental plants received supplemental pollen. These studies cover a range of breeding systems and life histories, and the results have been mixed. There was no evidence of pollen limitation in the hermaphroditic perennials *Thalictrum thalictroides* (Lubbers and Christensen 1986), *Calathea ovandensis* (Horvitz and Schemske 1988) and *Polemonium foliosissimum* (Zimmerman and Pyke 1988); in the monocarpic, hermaphroditic perennials *Agave mckelveyana* (Sutherland 1987) and *Cynoglossum officinale* (de Jong and Klinkhamer 1989); or in the andromonoecious *Lomatium salmoniflorum* (Thompson and Pellmyr 1989). In contrast, pollen limitation has been demonstrated in natural populations of the hermaphroditic perennial orchids *Encyclia cordigera* (Janzen et al. 1980), *Platanthera blephariglottis* (Cole and Firmage 1984), and *Tipularia discolor* (Snow and Whigham 1989); in the seasonally unisexual perennial *Arisaema triphyllum* (Bierzychudek 1981); in the hermaphroditic perennials *Polemonium viscosum* (Galen 1985) and *Ipomopsis aggregata* (Hainsworth et al. 1985); and in the Australian perennial *Telopea speciosissima* (Whelan and Goldingay 1989). Future studies conducted at the whole-plant level will allow us to discover whether the degree of pollen limitation varies with mating system, pollinator type, habitat marginality, and time.

Acknowledgments: I thank D. W. Schemske for advice and encouragement in all aspects of my doctoral research, of which this study forms a part. For discussion and/or comments on the manuscript, I thank D. Charlesworth, L. Delph, B. Devlin, C. Galen, S. Kalisz, K. M. Karoly, M. T. Morgan, D. J. Schoen, S. J. Tonsor, M. J. Wade, J. H. Willis, and an anonymous reviewer. I am also very grateful to Joe Johnson for aiding my research at the Kellogg Bird Sanctuary and to Kathryn Griffeths for permission to work on her land.

Literature Cited

Bateman, A. J. 1948. Intra-sexual selection in *Drosophila.* Heredity **2**:349–368.

Bawa, K. S., and C. J. Webb. 1984. Flower, fruit and seed abortion in tropical forest trees: implications for the evolution of paternal and maternal reproductive patterns. American Journal of Botany **71**:736–751.

Bierzychudek, P. 1981. Pollinator limitation of plant reproductive effort. American Naturalist **117**:838–840.

Bowden, W. M. 1959. Phylogenetic relationships of twenty-one species of *Lobelia* L. section Lobelia. Bulletin of the Torrey Botanical Club **86**:94–108.

Cole, F. R., and D. H. Firmage. 1984. The floral ecology of *Platanthera blephariglottis.* American Journal of Botany **71**: 700–710.

Devlin, B. 1989. Components of seed and pollen yield of *Lobelia cardinalis*: variation and correlations. American Journal of Botany **76**:204–214.

Devlin, B., and A. G. Stephenson. 1984. Factors that influence the duration of the staminate and pistillate phases of *Lobelia cardinalis* flowers. Botanical Gazette **145**:323–328.

Devlin, B., and A. G. Stephenson. 1985. Sex differential floral longevity, nectar secretion, and pollinator foraging in a protandrous species. American Journal of Botany **72**:303–310.

Devlin, B., and A. G. Stephenson. 1987. Sexual variations among plants of a perfect-flowered species. American Naturalist **130**:199–218.

Galen, C. 1985. Regulation of seed-set in *Polemonium viscosum*: floral scents, pollination, and resources. Ecology **66**: 792–797.

Haig, D., and M. Westoby. 1988. On limits to seed production. American Naturalist **131**:757–759.

Hainsworth, F. R., L. L. Wolf, and T. Mercier. 1985. Pollen limitation in a monocarpic species, *Ipomopsis aggregata*. Journal of Ecology **73**:263–270.

Horvitz, C. C., and D. W. Schemske. 1988. A test of the pollinator limitation hypothesis for a neotropical herb. Ecology **69**:200–206.

Janzen, D. H., P. DeVries, D. E. Gladstone, M. L. Higgins, and T. M. Lewinsohn. 1980. Self and cross pollination of *Encyclia cordigera* (Orchidaceae) in Santa Rosa National Park, Costa Rica. Biotropica **12**:72–74.

Johnston, M. O. 1990. Natural selection, inbreeding depression and self-fertilization in two species of *Lobelia* with different pollinators. Dissertation. The University of Chicago, Chicago, Illinois, USA.

———. 1991. Natural selection on floral traits in two species of *Lobelia* with different pollinators. Evolution, *in press*.

Jong, T. J. de, and P. G. L. Klinkhamer. 1989. Limiting factors for seed production in *Cynoglossum officinale*. Oecologia (Berlin) **80**:167–172.

Lubbers, A. E., and N. L. Christensen. 1986. Intrasexual variation in seed production among flowers and plants of *Thalictrum thalictroides* (Ranunculaceae). American Journal of Botany **73**:190–203.

McCall, C., and R. B. Primack. 1985. Effects of pollen and nitrogen availability on reproduction in a woodland herb, *Lysimachia quadrifolia*. Oecologia (Berlin) **67**:403–410.

McVaugh, R. 1936. Studies in the taxonomy and distribution of the eastern North American species of *Lobelia*. Rhodora **38**:241–263, 276–298, 305–329, 346–362.

Piper, J. G., B. Charlesworth, and D. Charlesworth. 1986. Breeding system evolution in *Primula vulgaris* and the role of reproductive assurance. Heredity **56**:207–217.

Snow, A. A., and D. F. Whigham. 1989. Costs of flower and fruit production in *Tipularia discolor* (Orchidaceae). Ecology **70**:1286–1293.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. Second edition. W. H. Freeman, San Francisco, California, USA.

Sutherland, S. 1986. Patterns of fruit-set: what controls fruit–flower ratio in plants? Evolution **40**:117–128.

———. 1987. Why hermaphroditic plants produce many more flowers than fruits: experimental tests with *Agave mckelveyana*. Evolution **41**:750–759.

Sutherland, S., and L. F. Delph. 1984. On the importance of male fitness in plants: patterns of fruit-set. Ecology **65**: 1093–1104.

Thompson, J. N., and O. Pellmyr. 1989. Origins of variance in seed number and mass: interaction of sex expression and herbivory in *Lomatium salmoniflorum*. Oecologia (Berlin) **79**:395–402.

Whelan, R. J., and R. L. Goldingay. 1989. Factors affecting fruit-set in *Telopea speciosissima* (Proteaceae): the importance of pollen limitation. Journal of Ecology **77**:1123–1134.

Willson, M. F. 1979. Sexual selection in plants. American Naturalist **113**:777–790.

Zimmerman, M., and G. H. Pyke. 1988. Reproduction in *Polemonium*: assessing the factors limiting seed set. American Naturalist **131**:723–738.

Manuscript received 12 March 1990;
revised 30 October 1990; accepted 20 November 1990.

Ecology, 72(4), 1991, pp. 1503–1507

HETEROGENEITY AMONG FLORAL VISITORS LEADS TO DISCORDANCE BETWEEN REMOVAL AND DEPOSITION OF POLLEN

Paul Wilson[1] and James D. Thomson[1]

Flowers are often visited by many species of animals. These sometimes differ in size, behavior, and other characteristics that translate into differences in their effectiveness as pollinators (e.g., Schemske and Horvitz 1984, 1988, Herrera 1987, Young 1988). The differences may be manifest in their effect on reproductive success either through female or through male function (Lloyd and Yates 1982, Bell 1985, Campbell 1989, Snow 1989). A number of recent studies have measured pollen removal as a component of male function (Snow and Roubik 1987, Cruzan et al. 1988, Galen and Stanton 1989, Harder and Thomson 1989, Thomson and Thomson 1989, Wolfe and Barrett 1989, Harder 1990, Murcia 1990, Young and Stanton 1990); however, high pollen removal need not result in high subsequent deposition of the removed pollen or in high success at siring seeds. Here we provide an example in which pollen-collecting bees remove more pollen but deposit less of it than nectar-collecting bees. The pollen collectors are antagonists with regard to the male re-

---

[1] Department of Ecology and Evolution, State University of New York, Stony Brook, New York 11794 USA.