



International Association for Ecology

The Efficiency of Pollen Transfer and Rates of Embryo Initiation in *Cryptantha* (Boraginaceae)

Author(s): Brenda B. Casper

Source: *Oecologia*, Vol. 59, No. 2/3 (1983), pp. 262-268

Published by: [Springer](#) in cooperation with [International Association for Ecology](#)

Stable URL: <http://www.jstor.org/stable/4217095>

Accessed: 19/09/2011 13:34

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Springer and International Association for Ecology are collaborating with JSTOR to digitize, preserve and extend access to *Oecologia*.

<http://www.jstor.org>

The efficiency of pollen transfer and rates of embryo initiation in *Cryptantha* (Boraginaceae)

Brenda B. Casper

Department of Biology, University of Utah, Salt Lake City, UT 84112, USA

Summary. The efficiency of pollination and rates of embryo initiation were compared in two species of *Cryptantha* (Boraginaceae) which differ greatly in their patterns of seed (nutlet) production. *Cryptantha flava* normally matures only one of the four ovules per ovary while *C. flavoculata* often matures all four. The general floral morphology and composition of insect floral visitors were found to be nearly identical in the two species, but *C. flavoculata* produces twice as much pollen per flower as *C. flava*. Despite this difference, the amount of pollen deposited on stigmas by pollinators is similar. This may be due to the larger stigmatic surface area in *C. flava*. In both species, the abortion of fertilized ovules, rather than insufficient amounts of pollen, appears to be the primary factor regulating the number of seeds per flower. The pollination ecology of these species is discussed in relation to current theories regarding the allocation of resources to the production of pollen and seeds.

Introduction

The question of how plants divide resources between the production of pollen and seeds has been approached in two very different ways. Sexual selection (sex allocation) theory assumes that seed production is generally limited by the availability of resources and that reproduction through pollen is limited by the ability of pollen grains to gain access to unfertilized ovules (Bateman 1948; Charnov 1979; Willson 1979). If this is true, then pollen grains are produced in excess, and they essentially compete for ovules to fertilize. Cruden (1977), in contrast, has proposed that the ratio of the number of pollen grains to the number of ovules reflects the efficiency of the pollination system and that this ratio is determined by the minimum amount of pollen necessary to achieve maximum seed production.

The determination of whether seed production is limited by resources or the availability of pollen is an active area of research in plant reproductive ecology (Stephenson 1979; Willson and Price 1980; Bierzychudek 1981; Udovic 1981; Udovic and Aker 1981; Bertin 1982a; Lee and Bazzaz 1982a). Nevertheless, little is known about the actual efficiency of natural pollination systems at the flower level. How much pollen is normally deposited on the stigma?

Present address: Department of Biology, University of Pennsylvania, Philadelphia, PA 19104, USA

How many of the ovules are fertilized? What proportion of the fertilized ovules develops into seeds? This study compares the pollination ecology of *Cryptantha flava* (A. Nels.) Payson and *Cryptantha flavoculata* (A. Nels.) Payson (Boraginaceae) with the specific objective of examining the efficiency of the pollen donor function of flowers. These species were selected because they have similar floral morphologies, which suggest similar pollination systems, but differ greatly in their patterns of seed production.

While I do not attempt to determine the reproductive success of particular individuals through pollen, I examine for both species the amount of pollen produced, the composition of insect floral visitors, and stigmatic pollen loads. I also compare the number of embryos initiated per ovary in the two species. The usual maturation of only a single seed (nutlet) in *C. flava* is known to result from embryo abortion in the remaining fertilized ovules (Casper and Wiens 1981), but embryo initiation rates have not been obtained for *C. flavoculata* which matures a variable number of the four ovules per flower. If large numbers of embryos abort, seed production cannot be used as a measure of pollination success or of the number of ovules fertilized. Hand pollination experiments in both species test whether or not the amount of genetic diversity in the pollen applied to a stigma affects the number of ovules that mature. Finally, seed number per flower and mean seed weight were determined in order to estimate the relative amounts of resources allocated to male and female functions in the two species.

Materials and methods

The species. Both *Cryptantha flava* and *C. flavoculata* are perennials and belong to the section *Oreocarya* which comprises the perennial and biennial members of the genus. The range of *C. flava* includes much of the Colorado Plateau of eastern Utah and parts of adjoining states. This species is usually confined to sandy soils. The range of *C. flavoculata* is a much larger geographical area, extending throughout most of Utah and Nevada, and portions of Wyoming, Colorado, and California. Unlike *C. flava*, *C. flavoculata* apparently is not restricted to any particular soil type. This study was conducted in 1979–1981 in populations located in and near Steinaker State Park in Uintah County, Utah where the two species co-occur.

The perennial species of *Cryptantha* have well developed caudices that produce rosettes and scapes in early spring.

The inflorescences of *C. flava* and *C. flavoculata* may be 35–40 cm tall. The flowers of both species are heterostyled; the flowers of some individuals (pins) have long styles and anthers positioned about halfway down the corolla while flowers of other individuals (thruns) have shorter styles and anthers located at the top of the corolla tube. The white flowers of *C. flavoculata* have yellow coronas that fade to white as the flowers age. The corollas of *C. flava* are similar in size (approximately 1 cm in diameter) but are entirely yellow. In the region where this study was conducted, *C. flavoculata* flowers from late April through the middle of May while the flowering period of *C. flava* is during late May and early June. Technically, the fruit consists of four nutlets, but I will often refer to these as seeds.

Floral morphometrics. In order to evaluate the relative effectiveness of particular insect floral visitors as pollinators in the two species, distances between various floral structures were determined for the pin and thrum morphs using a magnifying lens inset with a scale of 0.1 mm resolution. The floral characteristics measured are illustrated in Fig. 1. The stigmatic surface area was estimated from the diameters of the stigmas which were measured under a dissecting microscope at 12X using a stage scale of 0.05 mm resolution. The stigma was assumed to be a circle.

Insect visitors. Insect floral visitors were observed in two populations of each species during the three flowering seasons. Observations were made at different times during the day and during different parts of the flowering seasons. For each period of observation, several plants were selected at random, and the numbers and types of insects visiting the plants for at least a 30 min period were recorded. A total of 458 insects were observed on *C. flavoculata* during an observation time of 19 h. During a 17 h 40 min observation period for *C. flava*, 654 insects were observed. Specimens of the insect visitors are deposited in the University of Utah entomological collection.

Pollen production. A single undehisced anther from each of the 36 sampled flowers of *C. flava* and 24 flowers of *C. flavoculata* was crushed and the pollen suspended in 50 μ l of aniline blue in lactophenol. A hemocytometer was used to count the number of pollen grains in four 0.1 μ l quantities of the suspension. The mean number of pollen grains in the four replicates was multiplied by the dilution factor and by five, the number of anthers per flower. This value was divided by four to obtain the pollen/ovule (P/O) ratio. There is some question about how the P/O ratio for a species with consistently high rates of ovule abortion, such as *C. flava*, should be calculated. For *Geranium maculatum*, which exhibits similar fixed abortion, Cruden (1977) used the number of ovules that generally mature to calculate the P/O ratio. I have used total ovule number for *C. flava* since, as this study will show, the amount of pollen usually deposited on the stigma is not less for *C. flava* than for *C. flavoculata*.

Stigmatic pollen loads. Stigmatic pollen loads were determined for at least 40 flowers of each floral morph of both species. Flowers on which the corolla had begun to wither were collected during the peak of the flowering season. No more than two stigmas were collected from a single plant. The stigmas were mounted in a glycerin gel stained with

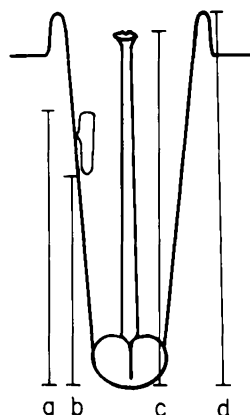


Fig. 1. Schematic diagram of floral structures measured: *a* top of anther to base of ovary, *b* bottom of anther to base of ovary, *c* stigma to base of ovary and *d* corolla tube length

basic fuchsin (Beattie 1971). The number of pollen grains on each stigma was counted at a magnification of 100 \times or 400 \times with the aid of an ocular grid. The number of foreign pollen grains on each stigma was also recorded. Stigmas were collected from two populations of each species in 1979 and from a single population in 1981.

Since a large portion of each style was mounted with the stigmas collected in 1979, only the pollen grains actually on the stigma or adjacent to it were counted. The counts of pollen grains for these stigmas may, therefore, be conservative. In 1981, care was taken to include as little of the style as possible, and the stigma was squashed to spread the pollen.

Embryo initiation and seed production. Young ovaries (6–8 days after anthesis) were fixed in FAA, embedded in paraffin, and sectioned longitudinally at 12 μ m. Only enlarging ovaries were examined. The number of ovules that contained embryos was determined for each ovary. Flowers used in this analysis were collected in 1980 from two populations of *C. flava* ($n=48$) and from two populations of *C. flavoculata* ($n=37$). The distribution of the number of embryos per flower was compared with the distribution of the number of mature seeds per flower for each species in 1979 and 1980. These seed production data were obtained from flowers selected at random from at least 12 plants collected from one population of each species from which the embryo initiation data were obtained. Seed production patterns of pins and thrums were also compared in both species.

Hand pollinations. Eighteen plants were selected in one population of each species for pollination experiments. Two flowering stalks on each plant were covered with fine mesh nylon cloth just prior to flowering. Four to nine flowers on each stalk were hand-pollinated using a camel hair brush. The flowers on one stalk were pollinated with pollen obtained from one other individual. The flowers on the second stalk were pollinated with a mixture of pollen from five different individuals. All pollinations were legitimate (pin \times thrum or thrum \times pin) crosses. Before pollination, the thrum morphs were emasculated by severing the corolla tube just below the point of anther attachment. Anthers were not removed from pin morphs because the stigma protrudes above the anthers. Pollen was mixed by placing the anthers from one flower of each pollen donor in a small Petri dish and then mixing pollen from the anthers using the brush. An attempt was also made to vary the quantity of the pollen applied to the stigmas. Within each treatment,

Table 1. Comparison of floral morphometrics. Letters in parentheses correspond to those in Fig. 1. Plus or minus (\pm) values are standard errors. Sample sizes are in parentheses

Measurement ^a	Pin Morph		Thrum Morph	
	<i>C. flava</i>	<i>C. flavoculata</i>	<i>C. flava</i>	<i>C. flavoculata</i>
Top of anther to base of ovary, mm ^(a)	6.20 \pm 0.08 (11)	7.21 \pm 0.10 (34)	9.70 \pm 0.19 (17)	9.49 \pm 0.10 (34)
Bottom of anther to base of ovary, mm ^(b)	5.10 \pm 0.11 (11)	5.48 \pm 0.09 (34)	8.50 \pm 0.18 (17)	7.79 \pm 0.11 (34)
Stigma to base of ovary, mm ^(c)	9.20 \pm 0.18 (11)	9.96 \pm 0.12 (34)	5.40 \pm 0.07 (17)	5.57 \pm 0.09 (34)
Corolla tube length, mm ^(d)	11.20 \pm 0.08 (11)	10.10 \pm 0.11 (34)	10.60 \pm 0.24 (17)	11.08 \pm 0.09 (34)
Stigmatic surface area, mm ²	0.18 \pm 0.002 (10)	0.10 \pm 0.002 (10)	0.16 \pm 0.002 (10)	0.11 \pm 0.002 (10)

^a Letters in parentheses correspond to those in Fig. 1

flowers received either a "light", "medium", or "heavy" application of pollen. The brush was washed in 100% ethanol after each cross.

Nutlet weights. A total of 50 nutlets were collected from several different plants of each species and individually weighed to the nearest 0.01 mg. Because mature nutlets of *C. flava* are not deciduous, it was necessary to break the nutlets away from the styles. If a nutlet was damaged in the process of removing it from the flower, it was not included in this analysis.

Results

Floral morphometrics. The floral measurements for both *C. flava* and *C. flavoculata* are presented in Table 1. Only small differences are apparent in the spatial arrangement of the floral structures between the two species. In *C. flavoculata* the corolla tube of the thrum morph is approximately 1 mm longer than that of the pin, while in *C. flava* the corolla tube of the pin morph is longer. Differences in measurements a and b (Fig. 1) between the species are attributable to the fact that the anthers of *C. flavoculata* are larger than the anthers of *C. flava*. The stigmatic surface area is more than 50% larger in *C. flava* than in *C. flavoculata*.

Insect visitors. The distributions of major classes of insect visitors to the two species (Fig. 2) are not different (K-S two sample test; $D = 0.078$; NS). The most common visitors to both *C. flava* and *C. flavoculata* are in the Anthophoridae. These are large bees (approximately 1.5 cm long) with mouthparts that may extend for 6 mm in some species. The structure of the mouthparts and the long tongue apparently facilitate foraging for nectar in the narrow tubular flowers. These bees also collect pollen. The frequency of visits by the different species was not determined, but commonly represented genera are *Anthophora*, *Emphoropsis*, and *Synhalonia* (F. Parker, personal communication).

The second most frequent class of insect visitors is lepidopterans (mostly butterflies) especially the fritillary butterfly *Closyne acaustis*. Butterflies constitute a higher percentage of total visitors to *C. flava* than to *C. flavoculata*, and if only the numbers of butterflies and Anthophorid bees are compared in the two species, *C. flava* receives proportionally more butterfly visits $\chi^2 = 15.14$; $df = 1$; $P < 0.001$.

Beeflies (Bombyliidae) are less frequent visitors to both species. They represent a slightly greater proportion of the visitors to *C. flavoculata* than to *C. flava*.

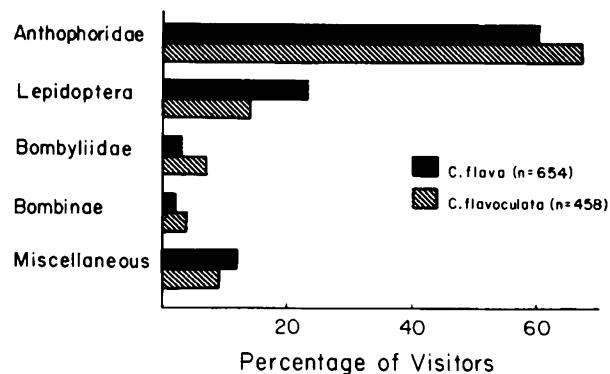


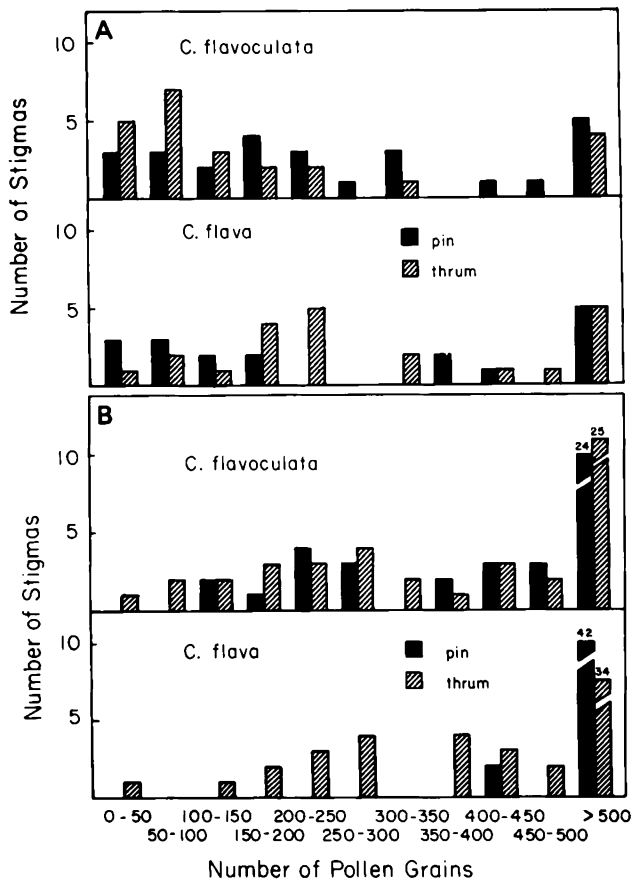
Fig. 2. Composition of insect floral visitors to *C. flava* and *C. flavoculata*

Table 2. The pollen/ovule ratios. Plus or minus values (\pm) are standard errors. Sample sizes are in parentheses

Species	Morph	
	Pin	Thrum
<i>C. flava</i>	109,938 \pm 4,369 (20)	102,581 \pm 4,419 (16)
<i>C. flavoculata</i>	219,731 \pm 7,669 (14)	230,313 \pm 11,350 (10)

Pollen production. The P/O ratios for the two morphs of both species are presented in Table 2. The pollen production per flower is twice as great in *C. flavoculata* than in *C. flava*. Pollen production does not differ appreciably between pins and thrums in either species.

Stigmatic pollen loads. The distributions of the numbers of pollen grains per stigma are presented for the pin and thrum morphs of both species in Fig. 3A for 1979 and Fig. 3B for 1981. Because of the difficulty in counting the actual number of pollen grains on a stigma, these numbers are approximate. The stigmatic pollen loads were slightly less in *C. flavoculata* than in *C. flava*. The pin stigmas of *C. flava* sampled in 1981 captured more pollen grains than thrums, but otherwise there was little difference between morphs. All of the stigmas of *C. flava* had more than 20 pollen grains, and stigmas with an excess of 100 grains were common. Three of the 50 stigmas of *C. flavoculata* sampled in 1979 had fewer than 20 grains. Foreign pollen was present on 38% of the stigmas of *C. flava* and 39% of the stigmas of *C. flavoculata*, but the number of foreign



grains was never greater than 25. Usually only one or two foreign grains were present.

Embryo initiation and seed production. In both *C. flava* and *C. flavoculata* more embryos initiated than actually matured. The distribution of the number of embryos per flower in *C. flava* for 1980 is graphed in Fig. 4 along with similar data obtained from the same populations in 1979. The 1979 data were previously reported in Casper and Wiens (1981). The distributions of the numbers of seeds per flower for 1979 and 1980 are also graphically represented. The rate of embryo initiation and the pattern of seed production in *C. flavoculata* are similarly compared in Fig. 5. The embryos were generally in the globular stage of development.

These results show that a slightly greater percentage of the ovules in *C. flavoculata* (73%) initiated embryos than in *C. flava* (63% for 1979, 58% for 1980). This difference between the species is significant when the 1979 data are compared ($\chi^2 = 7.73$; $df = 1$, $P < 0.01$). Size differences among the embryos within an ovary were often apparent. In some older ovaries of *C. flava* the endosperm had disintegrated in a portion of the ovules, making it possible to determine which of the embryos would have matured.

Pins and thrums did not differ appreciably in the number of embryos initiated per flower in either species. For *C. flavoculata*, the number of embryos per flower averaged 2.96 ($n = 23$) and 2.86 ($n = 14$) for pins and thrums respectively. In *C. flava*, the numbers were 2.72 for pins ($n = 22$) and 2.55 for thrums ($n = 22$).

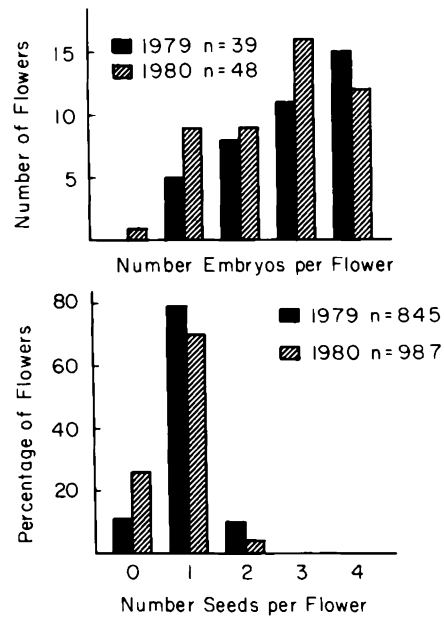


Fig. 4. Frequency distribution of the number of embryos per flower compared with the number of mature seeds per flower for *C. flava*.

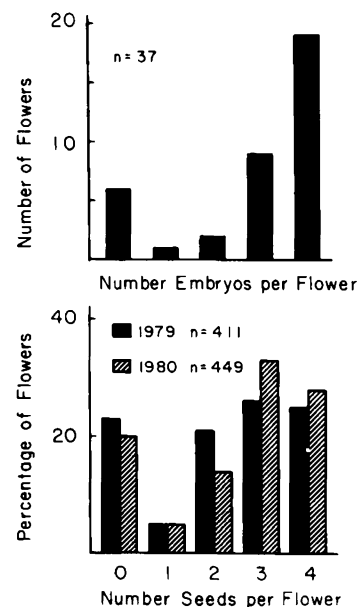


Fig. 5. Frequency distribution of the number of embryos per flower compared with the number of mature seeds per flower for *C. flavoculata*.

The mean seed production in naturally pollinated flowers for the two morphs of each species is summarized in Table 3. In *C. flavoculata*, the thrum morphs produced slightly more seeds per flower than pins in both years. In 1979, the mean number of seeds per flower was higher for thrums than for pins of *C. flava*, but in 1980 the reverse was true.

Often a portion (sometimes 20%) of the flowers of *C. flavoculata* do not open. This is usually due to the presence of a dipteran larva inside the flower bud. In other cases, the flowers simply do not develop normally. These unopened flowers were not included in the seed production data.

Table 3. Seed production in naturally pollinated flowers by floral morph. All collections are from Steinaker State Park, Vernal, UT

Species	Year	Average no. seeds per flower (no. flowers, no. plants)	
		Pin	Thrum
<i>C. flava</i>	1979	0.94 (445, 9)	1.05 (400, 8)
	1980	0.83 (587, 11)	0.72 (400, 8)
<i>C. flavoculata</i>	1979	2.08 (242, 6)	2.47 (169, 6)
	1980	2.15 (199, 8)	2.66 (250, 8)

Table 4. Seed (nutlet) production following hand pollinations. Chi-square values are presented for intramorphic comparisons of seed production when pollen from only one donor plant is used and when pollen from five donor plants is used (K-S two sample test). Only flowers producing one or more seeds were included in the comparisons

Morph	No. pollen donors	No. flowers with <i>n</i> seeds per flower					χ^2 , df = 1
		<i>n</i> = 0	1	2	3	4	
<i>C. flavoculata</i>							
pin	1	32	7	3	5	5	0.48, ns
pin	5	33	5	2	6	5	
thrum	1	20	4	3	10	13	1.29, ns
thrum	5	35	7	3	5	11	
<i>C. flava</i>							
pin	1	30	21	2	–	–	0.36, ns
pin	5	30	25	–	–	–	
thrum	1	20	25	5	1	–	0.04, ns
thrum	5	14	29	7	1	–	

Hand pollinations. The results of the hand pollination experiments for *C. flavoculata* and *C. flava* are compared in Table 4. Virtually no differences were apparent among the results of the various hand-pollination treatments except the number of flowers that failed to mature seeds was somewhat greater for the category of flowers that received a "light" application of pollen. The data for the "light", "medium", and "heavy" applications of pollen, therefore, are combined. With the exception of large numbers of flowers that failed to produce seeds, the pattern of seed production in both species was nearly identical to that of naturally pollinated flowers. Most flowers of *C. flava* matured only a single seed while one, two, three, or four seeds occurred in *C. flavoculata* with approximately equal frequency. Only two of the 210 hand-pollinated flowers of *C. flava* produced three seeds. The number of pollen parents used in the cross apparently had no effect on the number of seeds that matured (Table 4).

Nutlet weights. The mean nutlet weight ($\bar{X} \pm S.D.$) was 2.43 ± 0.32 mg, $n = 50$ for *C. flava* and 3.22 ± 0.59 mg, $n = 50$ for *C. flavoculata*.

Discussion

Although *C. flava* and *C. flavoculata* differ in their patterns of seed production, the pollination systems, at least in the region in which these studies were conducted, are essentially

the same. In both species, the abortion of fertilized ovules, rather than insufficient amounts of pollen, appears to be the primary factor regulating the number of seeds produced per flower.

While this study examined the composition of insect visitors to the two species, no attempt was made to determine the relative effectiveness of the various insects as pollen vectors. Because the floral structures of the two species are similar, however, it is likely that insects effective in pollinating one species would be equally effective in pollinating the other. I also made no attempt to determine the intensity of insect visitation which might differ in the two species. Because weather conditions are generally more favorable when *C. flava* flowers, for example, it is possible that this species receives more total visits per flower.

Stigmatic pollen loads are evidence that the pollination systems are equally effective. The distributions of the number of pollen grains per stigma are nearly identical for the two species even though *C. flavoculata* produces twice as much pollen per flower as *C. flava*. That stigmatic pollen loads were found to be greater for both species in 1981 than in 1979 may be attributable to the different methods used in preparing the stigmas for observation.

Considerable data are available on the stigmatic pollen loads of heterostylous species (see Ganders 1979 for review). Usually morphological heterostyly is linked with an incompatibility system so that the only compatible crosses are those between individuals of different style lengths. Botanists have been interested in the extent that the morphological differences enhance pollen flow between morphs. Such studies are facilitated in many species because thrums usually produce larger (but fewer) pollen grains than pins (Darwin 1877; Vuilleumier 1967; Dulberger 1974). Generally pin stigmas capture more total pollen but a greater proportion of illegitimate (or incompatible) pollen (Ganders 1979). In these populations, neither *C. flava* nor *C. flavoculata* exhibited a noticeable dimorphism in pollen grain size, and the total pollen production per flower was approximately the same for both morphs. Because intermorphic crosses, intramorphic crosses, and self-pollinations are nearly equally successful in producing seeds in both species (Casper 1982) most of the pollen on the stigmas should be compatible. Only in *C. flava* (and only in one year) did pin stigmas capture more total pollen than thrum stigmas.

For both species the number of pollen grains on the stigma usually far exceeds the number of ovules. There is some evidence that a minimum number of pollen grains which is larger than the number of ovules must be deposited to assure that all ovules are fertilized. Cruden (1977) reports that six pollen grains per ovule are required to produce maximum seed set in cleistogamous flowers of *Viola nephrophylla*, for example, and that four grains per ovule are necessary to achieve seed set comparable to that of self-pollination in *Mirabilis jalapa*. Nevertheless, in *Cryptantha* the stigmatic pollen loads appear more than adequate to fertilize four ovules. Foreign pollen was never present in large numbers, so interference from foreign pollen would not be expected (Waser 1978).

Despite the large stigmatic pollen loads not all flowers initiate embryos in all four ovules in either species. Most of the remaining ovules appeared to be unfertilized, but the technique used here, although it provides a better estimate of fertilization rates than the sizes of undeveloped

ovules, does not permit unequivocal detection of fertilization unless it is followed by embryo development. Transmission electron microscopy is probably necessary to determine if ovules without embryos have been fertilized (Mogensen 1975). In addition, only enlarging ovaries were selected for sectioning. The proportions of flowers in which no embryos were present may have been underrepresented in the samples. Thus, I cannot say whether failure of some flowers to produce any seeds is due to lack of fertilization or to post-zygotic abortion.

That the distributions of embryos per flower are different from the distributions of seed numbers does indicate that considerable post-zygotic abortion occurs in both species. The regular abortion of embryos in *C. flava* appears to be related to the mode of seed dispersal and may be genetically controlled (Casper and Wiens 1981; Casper 1982). Abortion in *C. flavoculata* occurs less frequently and is much more variable. Whether the abortion results from a limited availability of resources or whether the genetic constitutions of the embryos are simply inviable is unknown.

Other studies have shown that the source of the pollen may determine the success of a particular cross. In *Campsis radicans* flowers are more likely to mature fruits if they receive pollen from particular individuals (Bertin 1982b), and crosses between certain pairs of individuals are more successful than others in sugar maples (Gabriel 1967). In natural populations of *Phlox drummondii* (Levin 1981), *Delphinium nelsoni* (Price and Waser 1979), *Stylidium elongatum*, and *Stylidium confluens* (Banyard and James 1979) hand pollinations produce more seed if the pollen is obtained from individuals located at some intermediate distance from the seed parent. I did not specifically test the effect of pollen source in this study, but the pattern of seed production is not different in either species when pollen from more than one individual (five) is used to pollinate a single flower. The same results have been obtained in *Cassia fasciculata* (Lee and Bazzaz 1982b). The extent that naturally pollinated flowers receive pollen from more than one source plant is difficult to determine, but there is evidence that considerable pollen carry-over may occur (Schaal 1980). The large number of flowers that failed to mature seeds in these hand pollination treatments could have resulted from the inability to judge stigma receptivity, inadequate pollen transfer, or other difficulties associated with conducting this experiment under field conditions.

Cruden (1977) shows that the number of pollen grains produced per ovule (P/O ratio) increases with the probability of cross-pollination. He relates the pattern to the efficiency of the pollination systems. In this case, both *C. flava* and *C. flavoculata* are self-compatible, have similar floral morphologies, and are visited by the same types of insects, yet *C. flavoculata* produces twice as much pollen per ovule as *C. flava*.

If the interpretation of Cruden and Miller-Ward (1981) is correct the likelihood that a pollen grain will reach a stigma also depends on the size of the stigma relative to the size of the area on the pollinator on which the pollen is carried. They find a negative correlation between P/O ratios and the ratios of the stigmatic surface areas to the pollen-bearing areas of the pollinators. Because the stigmatic surface area of *C. flavoculata* is smaller than that of *C. flava*, these two species follow this general trend.

Charnov (1979, 1982) has proposed an alternative expla-

nation for the decline in P/O ratios with increased inbreeding. Using a model of sex allocation, he suggests that seed production is not generally limited by the availability of pollen and that increased inbreeding in plants is comparable to local mate competition in animals (Hamilton 1967, 1979). The sex ratio in animals is predicted to become female-biased in situations where genetically related males compete for mates (Hamilton 1967, 1979). Thus the relative allocation to pollen production would increase as competition among unrelated pollen grains increases and would not be determined solely by the efficiency of getting pollen to ovules. If sex allocation theory can be applied to plants, the proportions of resources allocated to pollen and seeds will depend on such factors as the spatial arrangement of individuals within populations and the mating patterns among them. The relative dispersal distances of pollen and seeds, for example, are predicted to influence the relative proportion of resources allocated to male and female function (Bulmer and Taylor 1980).

The relative biomass allocated to pollen and seed production in *C. flava* and *C. flavoculata* is not consistent with the P/O ratios. Approximately 2.3 nutlets with a mean weight of 3.22 mg mature per flower in *C. flavoculata*. The individual nutlets of *C. flava* are smaller (2.43 mg) and, on the average, slightly less than one seed is produced per flower. The pollen grains of the two species are approximately the same size. Thus, even though *C. flavoculata* produces twice as much pollen per flower as *C. flava*, it allocates a greater proportion of resources, as measured by biomass, to female function. It should be noted that using biomass as a measure of resource allocation may also be an oversimplification since the production of pollen and seeds probably requires different resources (Lovett Doust and Harper 1980).

Sexual selection theory – the idea that the pattern of sex allocation is primarily shaped by male function – is generally applicable to plants if seed production is not limited by the availability of pollen. An extension of the theory predicts that plants should be able to select the pollen parents of their offspring by such means as selective abortion of fruits or ovules (Janzen 1977; Charnov 1979). This study shows that the abortion of fertilized ovules is common in both *C. flava* and *C. flavoculata* and that large numbers of pollen grains are normally deposited on the stigmas. The data suggest that seed production is not limited by the quantity of pollen available. Competition among pollen grains for ovules to fertilize would be expected. The floral morphologies of many species of *Cryptantha* are similar. A comparison of P/O ratios, the sizes of the stigmas, the number and sizes of nutlets, and the number and sizes of pollen grains in several additional species of *Cryptantha* with the same breeding and pollination systems would provide useful data with which to test the pollinator efficiency (P/O ratio) and sex allocation theories.

Acknowledgments. I am grateful for the advice of D. Wiens, R. Charnov, and J. Ehleringer. I also thank T. Burns, G. Cook, P. Fordyce, C. Geerlings, and T. LaPine who assisted with field work and A. Chapa who spent hours counting pollen grains. This paper is a portion of a doctoral dissertation submitted to the University of Utah. It was supported in part by two Sigma Xi grants-in-aid.

References

- Banyard BJ, James SH (1979) Biosystematic studies in the *Stylidium crassifolium* species complex (Stylidiaceae). *Aust J Bot* 27:27–37

- Bateman AJ (1948) Intrasexual selection in *Drosophila*. *Heredity* 2:349-368
- Beattie AJ (1971) A technique for the study of insect borne pollen. *Pan-Pac Entomol* 47:82
- Bertin RI (1982a) Floral biology, hummingbird pollination and fruit production of trumpet creeper (*Campsis radicans*, Bignoniaceae). *Amer J Bot* 69:122-134
- Bertin RI (1982b) Paternity and fruit production in trumpet creeper (*Campsis radicans*). *Amer Nat* 119:694-709
- Bierzuchudek P (1981) Pollinator limitation of plant reproductive effort. *Amer Nat* 117:838-840
- Bulmer MG, Taylor PD (1980) Dispersal and the sex ratio. *Nature (London)* 284:448-449
- Casper BB (1982) Ecological studies of ovule abortion and seed dispersal in *Cryptantha* (Boraginaceae). Dissertation. University of Utah, Salt Lake City, Utah, USA
- Casper BB, Wiens D (1981) Fixed rates of random ovule abortion in *Cryptantha flava* (Boraginaceae) and its possible relation to seed dispersal. *Ecology* 62:866-869
- Charnov EL (1979) Simultaneous hermaphroditism and sexual selection. *Proc Natl Acad Sci USA* 76:2480-2484
- Charnov EL (1982) The theory of sex allocation. *Princeton Monographs in Population Biology*, No. 18. Princeton, NJ: Princeton Univ. Press
- Cruden RW (1977) Pollen-ovule ratios: a conservative indicator of plant breeding systems in flowering plants. *Evolution* 31:32-46
- Cruden RW, Miller-Ward S (1981) Pollen-ovule ratio, pollen size, and the ratio of stigmatic area to the pollen-bearing area of the pollinator: an hypothesis. *Evolution* 35:964-974
- Darwin C (1877) The different forms of flowers on plants of the same species. London: John Murray
- Dulberger R (1974) Structural dimorphism of stigmatic papillae in distylous *Linum* species. *Amer J Bot* 61:238-243
- Gabriel WJ (1967) Reproductive behavior in sugar maple: self-compatibility, agamospermy, and agamocarpy. *Silvae Genet* 16:165-168
- Ganders FR (1979) The biology of heterostyly. *N Z J Bot* 17:607-635
- Hamilton WD (1967) Extraordinary sex ratios. *Science* 156:477-488
- Hamilton WD (1979) Wingless and fighting males in the fig wasps and other insects. MS Blum, NA Blum (eds) *Reproductive competition and sexual selection in insects*. New York: Academic Press, Inc
- Janzen DH (1977) A note on optimal mate selection in plants. *Amer Nat* 111:365-371
- Lee TD, Bazzaz FA (1982a) Regulation of fruit and seed production in an annual legume, *Cassia fasciculata*. *Ecology* 63:1363-1373
- Lee TD, Bazzaz FA (1982b) Regulation of fruit maturation pattern in the annual legume, *Cassia fasciculata*. *Ecology* 63:1374-1388
- Levin D (1982) Dispersal versus gene flow in plants. *Ann Mo Bot Gard* 68:233-253
- Lovett Doust J, Harper JL (1980) The resource costs of gender and maternal support in an andromonoecious umbellifer, *Smyrniolum olusatrum* L. *New Phytol* 85:251-264
- Mogensen HL (1975) Ovule abortion in *Quercus* (Fagaceae). *Amer J Bot* 62:160-165
- Price MV, Waser NM (1979) Pollen dispersal and optimal outcrossing in *Delphinium nelsoni*. *Nature (London)* 277:294-297
- Schaal BA (1980) Measurement of gene flow in *Lupinus texensis*. *Nature (London)* 284:450-451
- Stephenson AG (1979) An evolutionary examination of the floral display of *Catalpa speciosa* (Bignoniaceae). *Evolution* 33:1200-1209
- Udovic D (1981) Determinants of fruit set in *Yucca whipplei*: reproductive expenditure vs. pollinator availability. *Oecologia (Berl)* 48:389-399
- Udovic D, Aker C (1981) Fruit abortion and the regulation of fruit number in *Yucca whipplei*. *Oecologia (Berl)* 49:245-248
- Vuilleumier BS (1967) The origin and evolutionary development of heterostyly in angiosperms. *Evolution* 21:210-226
- Waser NM (1978) Competition for hummingbird pollination and sequential flowering in two Colorado wildflowers. *Ecology* 59:934-944
- Willson MF (1979) Sexual selection in plants. *Amer Nat* 113:777-790
- Willson MF and Price PW (1980) Adaptive design of the floral display in *Asclepias syriaca* L. *Amer Midl Natur* 92:47-57

Received December 9, 1982