The pollination biology and breeding system of *Monarda fistulosa* (Labiatae)

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Summary. Successful cross-pollination of *Monarda fistulosa* is the result of a complex interaction among flower opening, the pollen-bearing areas of the pollinators and/or their behavior, and the maturation of the stigmas. The flowers open continuously from 0800–2000 h providing a temporally predictable and, if pollinator activity is high, a spatially unpredictable rich source of nectar and pollen. Recently opened flowers may reduce the ability of bees to discriminate between resource rich and poor patches and encourage systematic foraging within patches. The continuous opening of flowers coupled with protandry also results in some flowers of most capitula being in the staminate and others in the pistillate phase. Autogamy is highly unlikely due to strong protandry and the spatial separation of anthers and stigmas. Geitonogamy, at least that mediated by *Bombus* is unlikely because the pollen is spread over a relatively large area of the wings, which reduces the likelihood of a stigma contacting just deposited pollen. Because pollen is transferred from the much smaller coxal area of *Anthophora* and other bees that mistake the stigmas of early pistillate phase flowers for stamens some geitonogamy seems inevitable. However, the delayed receptivity of young stigmas to self-pollen decreases the likelihood of self-pollen germinating on such stigmas. Older stigmas are equally receptive to self- and cross-pollen and the number of pollen grains germinating and pollen tubes reaching the base of the style increases with flower age.

Introduction

The stigmas of self-compatible xenogamous (cross-pollinating) angiosperms are the potential recipients of self-pollen grains due to intraplant movements of pollinators (i.e. geitonogamy). Species that typically have many flowers open at a time with some in the staminate and others in the pistillate phase are especially liable to geitonogamy. In the absence of cross-pollen such pollinations result in inbreeding depression (Darwin 1895). Because of the negative affects of inbreeding depression (Willson and Burley 1983) and the general failure of self-incompatibility to evolve

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secondarily (Whitehouse 1950) it is not surprising that self-compatible xenogamous plants have mechanisms that minimize geitonogamy, e.g., temporal dioecism (Cruden and Herman-Parker 1977), having one or few flowers open at a time (K. Grove personal communication), and the spatial distribution of nectar rewards such that pollinators move from flowers in the pistillate phase to those in the staminate phase (Cruden et al. 1983; Pyke 1978a).

Our interest in *Monarda fistulosa* L. (Labiatae) was stimulated by two observations. First, inflorescences are composed of several capitula, each with ten or more flowers open at a time, with some flowers in the staminate and others in the pistillate phase. Second, *Bombus* appeared to visit staminate and pistillate phase flowers indiscriminately for nectar. The behavior of other common visitors also appeared to favor geitonogamy. These observations led to our initial question: how is pollination effected and geitonogamy avoided or minimized? With the discovery that flowers opened continuously during the day, we expanded the study to include nectar and pollen presentation and their roles in the mating system of *M. fistulosa*.

The plant. In Iowa, *M. fistulosa* is an herbaceous perennial of prairies and forest edges. Plants produce a number of flowering ramets with determinate branched inflorescences. The terminal capitula flower first and flowers within a capitulum open centrifugally. Only occasionally do adjacent flowers open at the same time. The flowers are protandrous and strongly bilabiate with exserted anthers and stigmas that face out and upwards. Approximately 18–20 h after flower opening the styles are 30.5 ± 0.5 mm (n = 20) ($\pm$ one standard error is used throughout the text) long and have elongated such that the stigmas are even with or slightly beyond the anthers. During this period the stigmas become receptive and shortly thereafter the filaments of most flowers reflex and move the anthers away from the stigmas. If pollination does not occur the styles continue to elongate and after 30 h are 32.5 ± 0.6 mm long (n = 20), significantly longer ($t_s = 7.22$, $p < 0.001$) than 20 h styles. The stigmas are now several millimeters beyond the anthers. The style branches of 18–20 h flowers are appressed and the lower is longer than the upper. Over the next 8–10 h the branches slowly reflex such that they form a "y" and if pollination does not occur the lower branch eventually forms a semicircle. Thus, as the flower ages the style elongates and the area of the stigmatic surface exposed to flower visitors increases. Following effective pollination most styles bend

up and backward, thus precluding the reception of additional pollen. Unpollinated flowers retain their color and their stigmas remain receptive for at least four days.

Study site

The primary study site was Cayler Prairie Preserve, a 64 hectare remnant of virgin prairie in Dickinson County (Section 17, Lakeville Township) in northwestern Iowa (Werner and Platt 1976). Ten plants from Floete Prairie, a small prairie remnant along Iowa Route 32 approximately 3 mile N of US Route 71 (Sec. 26, Lakeville Twp.) were transplanted into large plastic pots and maintained in a screened enclosure at Iowa Lakeside Laboratory.

Methods and results

Pattern of flower opening. Starting at 0800 h the number of flowers that opened during successive 3 h periods was counted. In 1979 the flowers were spotted with a marking pen as they were counted and in 1980 the open flowers were removed as they were counted. The similarity of results (Table 1) using the two methods suggests that removal did not affect the pattern of flower opening.

Most flowers opened between 0800 and 1700 h (Table 1). Analysis of variance of arcsin transformed data indicated significant differences among percentages of flowers opening in the various periods ($F = 37.04$; $p < 0.001$). The means were compared with Student-Newman-Keuls test for equal sample sizes (Sokal and Rohlf 1981). The percentages of flowers opening in the morning (0800–1100 h) and late afternoon (1700–2000 h) were significantly lower than the percentage opening between 1100 and 1700 h. The percentage opening during the night (2000–0800 h) was significantly lower than in any other period. Heavy cloud cover (17 July) and/or light rain (20 July) shifted flower opening toward the afternoon. The effect of cool nights with heavy dew is less clear (compare 21 July with 22 and 23 July).

Pollen viability. To test the ability of pollen grains to germinate following exposure to dew, flowers opening between 1500–2000 h were marked and their pollen applied to the receptive stigmas of caged plants the following morning (0900–1000 h). Pollen from caged plants was used in control pollinations. Pollinated stigmas were collected 6 h later and preserved for examination with fluorescence microscopy. Following exposure to a light dew all of the test ($n = 20$) and control ($n = 15$) pollinations were successful. Following exposure to a heavy dew all the test ($n = 27$) and 19 of 20 control pollinations were successful. In the latter test the numbers of pollen tubes at the base of style after 6 h were also equivalent ($\bar{X} = 15.1 \pm 0.8$ and 14.5 ± 1.1, respectively) ($t = 0.047$).

Stigma receptivity. The responses of stigmas to cross- and self-pollen were tested using plants on Cayler Prairie (1979 and 1980) and the plants from Floete Prairie (1979). To exclude flower visitors on Cayler Prairie cages covered with mosquito netting were placed over the plants. We used 15 and 25 plants on Cayler Prairie in 1979 and 1980, respectively, and different sets of plants in the two years. In 1979 we pollinated flowers of known age and 12–24 h later gently pulled the corollas to determine if they had abscised. To test if abscission reflected successful fertilization we com-

Table 1. Percent of flowers opening every three hours between 0800 and 2000 and during the night (2000–0800 h) in *Monarda fistulosa*. The means for the various time periods (cols 1 and 5, 2 and 3, etc.) are compared with the Least Significant Range for pairs of means (Sokal and Rohlf 1981). The percent opening between 2000–0800 h $<$ 1700–2000 h $<$ 0800–1100 h $<$ 1100–1400 h $=$ 1400–1700 h

Date	n	Percents flowers opening during period				
		2000– 0800 h	0800– 1100 h	1100– 1400 h	1400– 1700 h	1700– 2000 h
4 Aug 1979	289	5	29	38	26	3
5 Aug 1979[a]	391	3	24	28	36	8
17 Jul 1980[b]	358	3	14	30	36	18
18 Jul 1980[c]	600	22	18	31	25	5
19 Jul 1980[d]	761	1	31	33	23	12
20 Jul 1980[e]	628	3	16	29	43	10
21 Jul 1980[f]	573	1	25	31	29	14
22 Jul 1980[f]	620	2	14	37	31	17
23 Jul 1980[f]	656	1	4	35	33	26
24 Jul 1980	882	5	24	36	28	7
25 Jul 1980	1045	12	21	32	25	10

$LSR_{2, \alpha=0.01} = 6.08$; $< 7.68_{(1-5)}$; $< 7.36_{(2-3)}$; $> 1.46_{(3-4)}$; $< 6.61_{(2-5)}$

[a] cloudy until 1000 h
[b] cloudy all day
[c] rain during the previous night
[d] heavy dew and warm
[e] overcast to 1400 h with light rain in morning
[f] heavy dew and cool

pared fruit set in ten hand-pollinated flowers with ten unpollinated controls. The corollas of the pollinated flowers all abscised and all the flowers set fruit. The corollas of the control flowers remained intact and no flower produced a fruit. In 1980, we used a different method to test receptivity. Again flowers of known age were hand-pollinated but were collected and preserved in alcohol 4 h after pollination. Later the styles were stained in 0.1% aqueous aniline blue fluorochrome buffered in 0.1 N K_3PO_4 then examined with a fluorescence microscope (Martin 1959). A stigma was scored as successfully pollinated if one or more pollen grains had germinated. In both years anthers from recently opened flowers were used to apply pollen to the stigmas and the stigmas were exposed to more or less equal amounts of pollen. Cross-pollinations were made with pollen from nearby plants and self-pollinations were made with pollen from the same ramet. Because the 1979 data from Cayler and Floete Prairies are virtually identical we have combined them for analysis. The number of successful pollinations/ number of flowers pollinated from Floete Prairie using cross- and self-pollen are, respectively: 17–19 h: 6/17, 3/18; 22–24 h: 8/10, 9/18; 26–28 h: 14/15, 19/23. The Cayler Prairie data are: 17–19 h: 5/14, 2/12; 22–24 h: 33/38, 22/41; 26–28 h: 52/62, 58/79.

Our data (Fig. 1) indicate that stigmas become receptive to cross-pollen before self-pollen. In 1979 cross-pollen was more successful than self-pollen on 22–24 h and 26–28 h stigmas. The 17–19 h data were consistent with this pattern. In 1980, cross-pollen was more successful than self-pollen on 17–18 h stigmas. The response of 21–22 h stigmas to cross- and self-pollen was similar but not statistically different. The differences between the years may reflect differ-
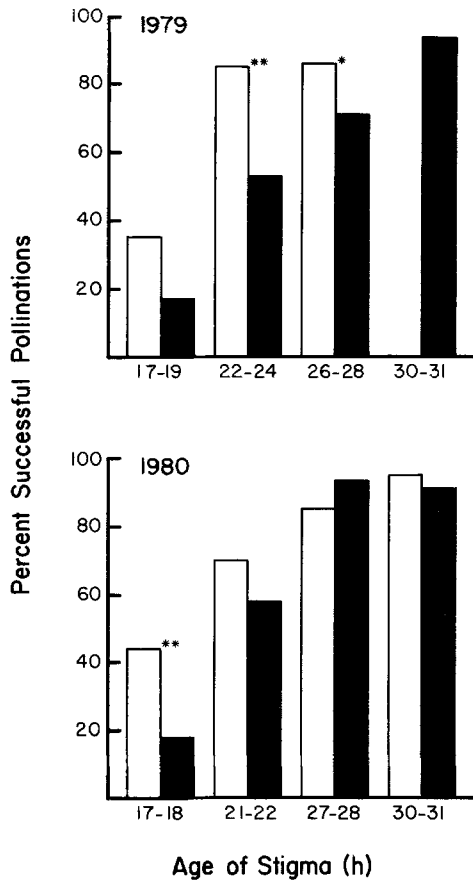
Fig. 1. Success of cross- (*open bar*) and self-pollen (*shaded bar*) on stigmas of different ages. X^2 values for 1979: 2.79, 12.98 ($p < 0.01$), and 5.68 ($p < 0.05$) (*left to right*) and for 1980: 8.68 ($p < 0.01$), 1.42, 0.48 and 0.19. Significance was tested with a 2×2 contigency table (Sokal and Rohlf 1981) and X^2 values are without Yates correction since its inconclusion did not affect significance. Sample sizes are given in the Methods and results

ences in the physiological ages of the stigmas, possibly a consequence of cooler daytime temperatures in 1979 which may have slowed stigma maturation. The mean maximum daily temperatures at nearby Lake Park for the study periods were 26.2 ± 0.8 and $29.6 \pm 0.7° C$ for 25 Jul–15 Aug 1979 and 25 Jul–5 Aug 1980, respectively (US Environmental Data Service).

To determine if there were differences in the success of self- and cross-pollen, we used the Mann-Whitney U-test to compare the number of pollen grains that germinated

and the number of pollen tubes that reached the base of the style in those flowers that had receptive stigmas (Table 2). First, at each age the number of cross- and self-pollen grains germinating ($U = 144.5$, $t_s = 0.94$; $U = 975$, $t_s = 0.88$; and $U = 101.5$, respectively) and number of cross- and self-pollen tubes at the base of the style were equivalent ($U = 163$, $t_s = 1.66$; $U = 902$, $t_s = 0.22$, and $U = 97$, respectively). Second, for both cross- and self-pollen the number of pollen grains germinated and pollen tubes to the base of the style increased significantly with flower age.

Flower visitors. Most of the flower visitors were bees (Table 3) which began to forage between 0900–0930 h and continued to forage until 2000–2100 h, although activity decreased considerably after 1700 h. *Bombus* and *Anthophora walshii* were the most common visitors. The number of *B. nevadensis* visiting *Monarda* was consistently higher than that of *B. vagans* and *B. fervidus*. Butterflies occasionally visited the flowers and the two specimens of *Papilio* examined carried no pollen. The smaller bees, including *Lasioglossum* and *Agapostemon*, were infrequent visitors that foraged only for pollen and were rarely observed on pistillate phase flowers.

The larger bees can be divided into two groups based on their foraging behavior. Individuals of *Anthophora*, *Megachile*, *Melissoides*, and small individuals of *B. vagans* hovered in front of the staminate phase flowers and dropped down onto the anthers which they manipulated with the lower segments of their second and third legs, perhaps the coxae, and then lifted up and away from the anthers. Pollen was transferred from the area of the coxae to the stigmas when they visited pistillate phase flowers. When these bees visited a flower for nectar, they darted beneath the anthers or stigma and contacted neither.

Our data indicate that *Anthophora*, *Megachile*, and *Melissoides* discriminate between staminate and pistillate phase flowers and avoid late pistillate phase flowers (Table 4). The visits of these species to staminate (1st day) and pistillate phase (2d and 3d day pooled) flowers deviated significantly from that expected if the bees visited flowers indiscriminately ($X^2 = 142.8$, 17.00 and 11.80 for the three species respectively; for all $p < 0.005$).

Individuals of *Bombus* foraging for nectar visited flowers of a capitulum sequentially with no apparent regard to the sexual phase of the flowers. Most *B. nevadensis* and larger individuals of *B. vagans* fluttered their wings continuously while foraging. Careful observation showed that the wings struck the anthers or stigmas of adjacent flowers as

Table 2. Number of cross- and self-pollen grains germinated and cross- and self-pollen tubes at the base of the style in receptive flowers of different ages (1980 data only). The differences between the number of cross- and self-pollen grains germinated or pollen tubes at the base of the style for each time period are not significant. $\bar{X}$'s within columns are significantly different at the level indicated (see text for further explanation)

Age of flower	Number pollen grains germinated				Number pollen tubes at base of style			
	Cross-pollen		Self-pollen		Cross-tubes		Self-tubes	
	n	$\bar{X} \pm SE$	n	$\bar{X} \pm SE$	n	$\bar{X} \pm SE$	n	$\bar{X} \pm SE$
17–18 h	24	5.8 ± 1.3*	10	5.9 ± 1.3**	24	2.9 ± 0.6***	10	4.9 ± 1.5****
21–22 h	45	12.6 ± 1.6	39	11.5 ± 1.8	45	6.3 ± 0.8	39	7.0 ± 1.0
27–28 h	11	20.9 ± 3.1*	13	14.1 ± 3.2**	11	15.4 ± 2.1***	13	11.5 ± 2.0****

* $U = 245$, $t_s = 4.02$, $p < 0.001$; ** $U = 95$, $p < 0.05$; *** $U = 256$, $t_s = 4.41$, $p < 0.001$; **** $U = 89.5$, $p < 0.05$

Table 3. Number of foraging bouts, which included two or more capitula, by visitors to flowers of *Monarda fistulosa* in 1979. Nectar was taken from both male and female phase flowers

Species	Nectar only	Pollen only	Pollen and nectar
Anthophora walshii Cresson	31	55	66
Megachile latimanus Say	5	12	10
Melissoides tepaneca Cresson	0	4	0
Bombus vagans Smith	39	7	8
Bombus nevadensis Cresson	106	1	2
Bombus fervidus (Fabricius)	11	0	0
Lasioglossum forbesii Robertson	0	22	0
Agapostemon virescens (Fabricius)	0	3	0
Apis mellifera Linnaeus	32	0	0

Table 4. Number of visits to first, second, and third day flowers of *Monarda fistulosa* during which either the anthers or stigmas were contacted. Data for 1978 and 1979 are combined

Species	Number of foraging bouts	Staminate (1st day)	Early pistillate (2d day)	Late pistillate (3d day)
Anthophora walshii	60	569	200	31
Megachile latimanus	3	51	13	4
Melissoides tepaneca	2	39	12	2
Augochlorella striata	1	8	2	0
Bombus vagans	4	30	19	13
Lasioglosum forbesii	8	47	9	6

Table 5. Pollen loads of primary visitors to the flowers of *Monarda fistulosa* in 1980

Species	Position of pollen	n	Number of *Monarda* grains $\bar{X} \pm$ S.E.
Anthophora walshii	between coxae	21	225 ± 46
	abdomen	2	400, 6
Bombus vagans	wings	9	773 ± 179
	abdomen	9	90 ± 77
	thorax	2	363, 696
Bombus nevadensis	wings	26	2684 ± 353
	abdomen	25	521 ± 85
	thorax	5	182 ± 85

the bees half-crawled, half-flew from flower to flower and the inner one-quarter of the wings carried large numbers of pollen grains (Table 5). As the larger bees moved to the next flower they frequently pulled the flower they were leaving beneath them. This may explain the presence of small numbers of pollen grains on the abdomens of most *Bombus*. Only a few individuals had pollen on the underside of the thorax. Because most individuals of *B. vagans* passed beneath the anthers or stigmas as they foraged they picked up less pollen than individuals of *B. nevadensis* and presumably were less effective as pollinators.

We determined the number of pollen grains carried by the bees from slides prepared in the field. We removed the pollen from the pollen bearing areas with small blocks of fuchsin-gelatin held with tweezers and prepared the slides as described by Beattie (1971). The bees were chilled prior to removal of the pollen and released afterwards.

Self-pollination. We tested the ability of flowers to self-pollinate in two ways. In 1978, 10 pairs of capitula, usually on the same ramet, were tagged and one of each pair bagged. In 1979, capitula of caged plants were compared with capitula of nearby plants. In both years fruit set, seed set, and fecundity were significantly higher in open pollinated flowers (Table 6).

Evidence of pollination. To determine if the bees actually transferred pollen, we collected the stigmas of previously unvisited flowers following visits by pollen-bearing bees. Six foraging *Anthophora* females were netted and placed sequentially with plants that had been caged for 24 h. Most of the bees began to forage in a normal manner within a minute or two and continued to forage following removal of the cage. The bases of early and late pistillate phase flowers were color coded prior to the introduction of the bees. The number of pollen grains per stigma was determined from stigmas mounted in fuchsin-gelatin. Stigmas of 106 of 154 marked flowers received pollen grains. Of 65 barely exserted stigmas 39 received pollen grains ($\bar{X}$ = 6.2 ± 1.1 grains per stigma) compared to 67 of 89 strongly exserted stigmas ($\bar{X}$ = 8.5 ± 1.2 grains per stigma). A test for the equality of two percentages (Sokal and Rohlf 1981) shows the percentage of strongly exserted stigmas that received pollen grains to be significantly higher than the percentage of barely exserted stigmas receiving pollen grains (t_s = 1.97, $p < 0.05$). However, the number of pollen grains received by barely and strongly exserted stigmas was equivalent (U = 157.5, t_s = 1.739, $p > 0.05$).

Table 6. Percent fruit set, seed set and fecundity in open pollinated and bagged (1978) or caged (1979) flowers of *Monarda fistulosa*. Differences between percentages were compared with a t-test for paired comparisons (Sokal and Rohlf 1981). Between year differences for open pollinated and bagged vs caged are not significant. All within year contrasts are significant ($p < 0.001$)

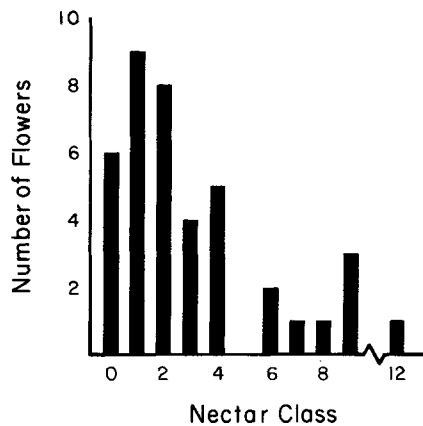|	1978			1979		
	Open $\bar{X} \pm$ S.E.	Bagged $\bar{X} \pm$ S.E.	t_s	Open $\bar{X} \pm$ S.E.	Caged $\bar{X} \pm$ S.E.	t_s
Number of capitula	10	10		18	18	
Number flowers/ capitulum scored	51.4 ± 5.8	52.1 ± 4.47		48.5 ± 2.0	35.1 ± 3.5	
%Fruit set (fruits/flower)	74.1 ± 5.8	16.9 ± 4.1	7.70	82.1 ± 2.6	32.9 ± 5.4	7.84
%Seed set (seeds/fruit)	81.2 ± 3.4	53.9 ± 5.4	4.42	85.2 ± 2.3	58.4 ± 4.8	4.23
%Fecundity (fruit set × seed set)	60.6 ± 5.6	9.0 ± 2.7	8.77	70.8 ± 3.7	20.2 ± 3.7	8.10

Fig. 2. Frequency of flowers ($n=40$) per nectar class. The classes represent 0, 0.01–0.05, 0.06–0.10, ... 0.56–0.60 μl of nectar, respectively

Because similar manipulations with *Bombus* failed we collected stigmas from previously unvisited flowers of uncaged plants. The stigmas of 23 of 45 flowers visited just once by *B. nevadensis* received pollen grains ($\bar{X}=14.5\pm2.9$ grains; range$=1$–45). The stigmas of 2 of 3 flowers visited by *B. vagans* received 2 and 5 pollen grains respectively.

Available nectar. Nectar was removed from flowers with one μl capillary tubes and the volume determined by dividing the length of the column of nectar by the length of the tube. Sugar concentrations were determined with a Bellingham and Stanley pocket refractometer. Where sugar content is given, the value has been corrected using the method suggested by Bolten et al. (1979). The amount of sugar reported per flower may be overestimated due to the refractive activity of amino acids (Inouye et al. 1980) and/or electrolytes (Hiebert and Calder 1983) in the nectar.

The volumes of nectar in just opened and older flowers just prior to the initiation of foraging by bees (0915–0945 h) were equivalent ($\bar{X}=0.31\pm0.05$ μl, n$=17$, and 0.24$\pm$0.04 μl, n$=16$, respectively; t$=1.200$). The percentage of dissolved solids was greater in the nectar of just opened flowers at this time ($\bar{X}=26.7\pm0.8$ and $23.9\pm1.1\%$, respectively; t$=2.145$, $p>0.05$). By early afternoon (1300–1400 h) there was a significant difference between the volumes of nectar from recently opened ($\bar{X}=0.24\pm0.03$ μl, n$=14$) and older flowers ($\bar{X}=0.07\pm0.02$ μl, n$=14$) (t$=4.944$, $p<0.001$). The sugar concentrations were equivalent (39.7 ± 1.6 and $43.9\pm2.6\%$, respectively; t$=1.442$).

The rate of nectar secretion following removal by bees is sufficient to replenish the original nectar in 5 h. Following removal by *Bombus* and *Anthophora* there was a residual of 0.04 ± 0.01 μl (n$=18$) of nectar per flower and five hours later flowers from those plants, which had been caged, contained 0.19 ± 0.04 μl (n$=6$) of nectar with a concentration of 55%. An hour later, six hours after removal, flowers held equivalent volumes of nectar ($\bar{X}=0.18\pm0.02$ μl, n$=16$). Some older female phase flowers produced no nectar following removal by bees.

Because flowers opened throughout the day and foraging bees depleted the nectar in older flowers, we expected a few flowers to contain large amounts of nectar and a large number to contain little nectar. This was tested by measuring the nectar from one flower from each of a number of uncaged individuals on two afternoons. The data

were pooled for analysis. The distribution of nectar volume per flower (Fig. 2) was significantly skewed ($g_1=1.362$, t$=3.603$, $p<0.001$) and the mean (0.14 μl) and standard deviation (0.15 μl) were almost equal.

Just opened flowers, nine per plant, from caged individuals were used to test for interplant variation in nectar volume (μl). The $\bar{X}$'s$\pm$S.E.'s were: 0.08 ± 0.01, 0.31 ± 0.07, 0.55 ± 0.11, 0.57 ± 0.09, 0.59 ± 0.08, and 0.64 ± 0.04. A single classification ANOVA indicated a significant difference among means ($F_{5,48}=12.60$; $p<0.001$). Student-Newman-Keuls test showed the volume of nectar per flower from the first plant was significantly lower than that in the other individuals ($LSR_{[1-2;\,a=.01]}=0.326<0.59$). Nectar per flower in the second plant was significantly lower than that in three other plants ($LSR_{2-3,\,a=0.05}\approx0.244<0.26$; $LSR_{2-4}\approx0.294\approx0.29$; $LSR_{2-5}\approx0.324<0.33$; $LSR_{2-6}\approx0.345<0.39$). We used log transformed data in the analysis to correct for heterscedasticity.

Discussion

The successful cross-pollination and outbreeding of *M. fistulosa* are due, at least in part, to the continuous opening of the flowers during the day and the stigmas becoming receptive to cross-pollen before they are receptive to self-pollen. We are unaware of any previous discussion of either trait (Cruden et al. 1983; Nettancourt 1977).

The continuous opening of flowers produces a skewed distribution of rewards which may reduce the ability of bees to discriminate between resource rich and poor patches. In general foraging by flower visitors produces a mosaic of nectar rich and nectar poor patches (Pleasants and Zimmerman 1979; Zimmerman 1981) and a standing crop of nectar with a skewed distribution (Gill and Wolf 1977; Pleasants and Zimmerman 1979). It is no surprise that flower visitors recognize and either reject or move out of nectar poor patches (Gill and Wolf 1977; Heinrich 1979; Pyke 1978b; Waddington and Heinrich 1981). In *M. fistulosa* if the capitula are visited but once or twice an hour [a rate exceeded in an Iowa City population (Cruden personal observation)], recently opened flowers, which contain large rewards relative to other flowers, although temporally predictable, will be few in number and unpredictable in space. The random distribution of such "bonanza" flowers should dampen the ability of bees to detect differences between patches and/or maintain systematic foraging within patches (Feinsinger 1978).

If a skewed nectar distribution has ecological or evolutionary significance, as Feinsinger (1978) suggests, it should be maintained by the plant, rather than being an artifact of pollinator foraging. The pattern of flower opening of *M. fistulosa* does exactly that. The skewed distribution of nectar per flower resulting from the foraging of flower visitors, a relatively low rate of replenishment, and interplant variation in nectar production is maintained and amplified by the continuous opening of flowers. However, if the bees monitor resource availability as a function of patch, rather than flower or capitulum, they may perceive the available reward as more or less constant. Thus the response of the bees to the reward distribution may combine elements that appear to be contradictory, i.e., pollinators visit more flowers if the distribution is skewed (Feinsinger 1978) vis-à-vis their preference for a constant distribution (Real 1981; Waddington et al. 1981). Finally, the distribution of

pollen probably approximates that of nectar and the response of pollen collecting bees should parallel those of nectar collecting bees.

A second consequence of the pattern of flower opening is the attraction of foraging bees throughout most of the day, even though the volume of nectar per flower is low relative to other bee-pollinated species (Cruden et al. 1983) and many flowers contain little or no nectar. The attractiveness of *M. fistulosa* may reflect the relatively large number (15–20%) of "bonanza" flowers; approximately twice the number reported for *Asclepias, Glechoma* (Southwick et al. 1981) and *Delphinium* (Pleasants and Zimmerman 1979).

Bee activity parallels the daily rhythm of flower opening and was subject to some environmental regulation. The first flowers opened about 0800 and the first bees were seen within the hour. The level of activity increased during the morning. There was a noticeable reduction in flower visitors after 1700–1800 h, which mirrored a decrease in flower opening. Southwick et al. (1981) observed a similar response in *Lonicera*. The initiation of flower opening and the foraging of bees was shifted toward the afternoon on days with heavy cloud cover and/or rain or following cool nights with heavy dew. Parallel delays in flower opening and foraging by pollinators in response to these environmental conditions has been noted before (Cruden 1972 b; Cruden et al. 1983; Estes and Thorp 1975).

Because water soluble proteins that are necessary for pollen grain germination (Heslop-Harrison 1975, 1979) are easily leached from the pollen (Kirby and Vasil 1979), and *M. fistulosa* pollen is frequently exposed to heavy dew, we tested the ability of the pollen to germinate following exposure to heavy dew. The ability of *M. fistulosa* pollen to germinate after exposure to dew is consistent with Eisikowitch and Woodell's (1974) suggestion that pollen normally exposed to moisture will be protected in some manner.

Cross-pollination

Cross-pollination in *Monarda* is the result of floral behavior and interactions between the flowers and pollinators that 1) facilitate the movement of pollen between plants while minimizing autogamy and geitonogamy and 2) favor cross-pollen over self-pollen on young stigmas. Autogamy is avoided by strong protandry and the spatial separation of stigmas and anthers. Geitonogamy is minimized by the large pollen-bearing area of the *Bombus* and the avoidance of late pistillate phase flowers by *Anthophora, Megachile,* and *Melissoides*. Because pollen is broadly distributed on the wings of *Bombus* it is quite unlikely that pollen picked up from one flower would be deposited on the stigma of an adjacent flower. Geitonogamous pollinations of early pistillate phase flowers, which are visited with reasonable frequency by *Anthophora*, etc., may be ineffectual due to the differential receptivity of young stigmas to cross- and self-pollen.

We know of no other species in which the stigmas of early pistillate phase flowers are first receptive to cross-pollen and then become receptive to self-pollen. Our data are not consistent with cryptic self-incompatibility as described in *Cheiranthus cheiri* (Bateman 1956) and *Amsinckia grandiflora* (Weller and Ornduff 1977). In *A. grandiflora* cross-pollen tubes grow faster than self-pollen tubes and only a small proportion of the latter reach the bases of the styles. In *M. fistulosa*, if self-pollen germinated, the numbers of self- and cross-pollen grains germinating were equivalent as were the number of self- and cross-pollen tubes that reached the base of the style. Likewise our results can not be explained by the breakdown of self-incompatibility due to age, an environmental factor such as high temperature, or other factors discussed by Nettancourt (1977).

Our observation that *Anthophora* and *Megachile* recognize and avoid pistillate phase flowers with well exserted stigmas seems inconsistent with the fact that a greater percentage of strongly exserted stigmas received pollen grains than barely exserted stigmas. Flowers with well exserted stigmas, although visited less frequently, were more efficient in capturing pollen grains because of the larger stigmatic area that was exposed to the pollinators. Early pistillate phase flowers may be visited more frequently than older flowers because they resemble staminate phase flowers, but the appressed stigmatic lobes must limit pollen deposition.

Self-pollination

Our data show quite clearly that *M. fistulosa* is xenogamous, not autogamous as reported by Gill (1980). Fecundity is consistent with other xenogamous species (Cruden 1972a) but is much lower than that of facultatively autogamous species in which fecundity is frequently 95–100 percent (Cruden 1977, personal observation). The relatively high fecundities in the bagged inflorescences and caged plants (9% and 20%, respectively) probably do not occur under field conditions in which pollen is removed from most anthers before the stigmas are receptive, at least 50–60% of the stigmas are cross-pollinated, and a typical flower lasts two or three days. In contrast pollen is not removed from the anthers of bagged flowers and the stigmas remain receptive for at least four to five days. Given the abnormally high density of pollen bearing anthers and receptive stigmas within bags some contact between the anthers and stigmas of adjacent flowers may be inevitable. Although our data do not reveal how much self-pollination or geitnonogamy occurs in flowers exposed to pollinators, it is probably minimal.

Pollinators

The pollination of *Monarda fistulosa* is effected by bees with one of two quite different behaviors. *Anthophora, Melissoides,* and *Megachile* carried and transferred pollen from the coxal area whereas pollen was carried and transferred from the wings of *Bombus*. The ability of these bees to transfer pollen was confirmed by exposing flowers with "virgin" stigmas to *Bombus* and *Anthophora*. More than sixty percent of the stigmas received pollen grains. Our observations contrast sharply with Robertson's (1982) report that butterflies were the primary pollinators in southern Illinois.

Our observations parallel those of Whitten (1981) on *M. clinopodia*. Floral behavior is similar; both species are strongly protandrous, self-compatible, produce equivalent volumes of nectar and are pollinated by *Bombus* that carry pollen on their wings. In contrast to our observation of limited and probably ineffectual pollen foraging by *B. vagans*, Whitten (1981) reported regular foraging for pollen on *M. clinopodia* by *Bombus*, which utilized the "drop-on" behavior we observed in the "anthophorid" guild.

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