Some Preliminary Observations on Hawkmoth Pollination of *Oenothera caespitosa* and *Mirabilis multiflora*

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Abstract

Two sympatric plant species, *Oenothera caespitosa* and *Mirabilis multiflora*, were observed for hawkmoth pollination in 1985 and 1986. These species are shown to be dependent on hawkmoth pollination for their reproduction though either pollinators or resources may limit reproduction in a given year. Additionally, the hawkmoth *Manduca quinquemaculata* begins its foraging on *Oe. caespitosa*, while *Hyles lineata* begins its foraging on *M. multiflora*. This temporal partitioning of hawkmoths reduces competition between both plants and hawkmoths and insures that the visitor best suited for pollinating these plant species visits the plants before other visitors.

Introduction

Oenothera caespitosa and *Mirabilis multiflora* (= *M. froebelii*) have been shown to be hawkmoth pollinated [Gregory, 1963-64; Baker, 1961; Cruden, 1970]. Both of these species are self-incompatible (as I have observed and according to Baker [1964] and Gregory [1963-64]) and are therefore dependent on cross pollination for reproduction. Preliminary observations in the White Mountains, eastern California, showed that these two species were visited primarily by three species of hawkmoths: *Hyles lineata, Sphinx chersis*, and *Manduca quinquemaculata. Oe. caespitosa* and *M. multiflora* are found sympatrically in canyons in the White Mountains and have substantial overlap in their blooming phenologies. Because these two species share pollinators and bloom at the same time, it is possible that they compete for pollinators. While the flowers of both species open late in the afternoon of one day and wilt the following morning, they differ markedly in flower morphology and the size of the nectar reward per flower (Table 1). Such large differences in the packaging of rewards for pollination and the possibility of competition for pollination prompted a detailed examination of the reproduction of these plants.

Seasonal Variation in Pollinator Abundance

Hawkmoth visitation rates to *M. multiflora* in 1985 and 1986 are shown in Figure 1. Average rates were approximately six times greater

Table 1
Characteristics of Hawkmoths and Plants

Plants	Average floral tube length	Average distance to top of nectar	Average nectar volume/flower
Oenothera caespitosa	12.13 cm	8.05 cm	40-50 µl
Mirabilis multiflora	5.74 cm		5-15 µl

Hawkmoths	Average tongue length
Manduca quinquemaculata	11.0 cm
Hyles lineata	4.5 cm
Sphinx chersis	5.5 cm

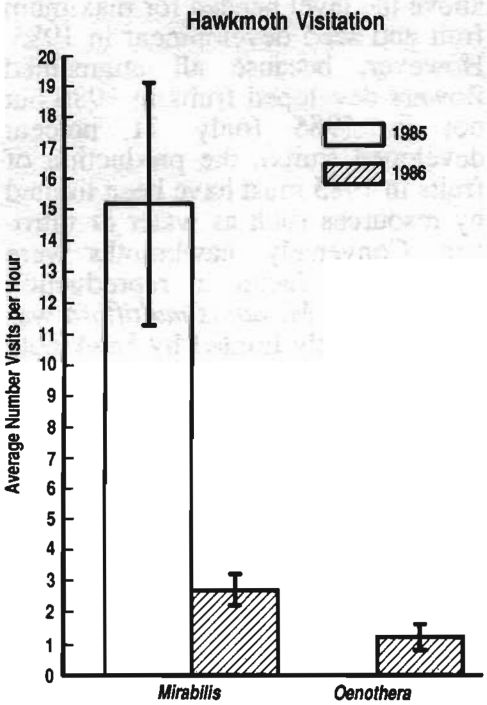


Figure 1. Average number of hawkmoths visiting individual plants of *Mirabilis multiflora* and *Oenothera caespitosa* per hour in 1985 and 1986 (+/- S.E.).

in 1985 than in 1986. Visitation rates to *Oe. caespitosa* were also low in 1986. Plants of *Oe. caespitosa* and *M. multiflora* bloomed profusely in 1986, as did most species in the White Mountains because of a higher than average moisture during the winter months.

The lack of hawkmoth visitation may be explained by the fact that hawkmoths migrate (see Grant [1983]). Perhaps in years of exceptional bloom, food sources are abundant and hawkmoths therefore do not need to migrate as far. Because *Oe. caespitosa* and *M. multiflora* are both on the north and west edges of their ranges in the White Mountains and because 1986 was an exceptional year for flower production, a reduction in hawkmoth migration would account for the decreased visitation observed. Also, both increased parasitism or predation of hawkmoths, or a decrease in larval food sources could all account for the dearth of pollinators in 1986.

Table 2
The effect of pollen augmentation on fruit development in *Oenothera caespitosa* in two years that differed in natural pollinator visitation (1985 was a year of high pollinator visitation, and 1986 was a year of low pollinator visitation)

	Number of Fruits			
	1985		1986	
Mature Fruit	Augmented	Unaugmented	Augmented	Unaugmented
Developed	20	17	25	2
Undeveloped	8	10	0	26
	$X^2 = 0.45$, $p = 0.50$		$X^2 = 45.67$, $p << 0.0001$	

Fruit and Seed Set

Variation in pollinator abundance (Fig. 1) had a direct effect on fruit and seed set in *Oe. caespitosa* and *M. multiflora* (Table 2, Figs. 2 and 3). Table 2 shows the effect of augmenting stigmas of *Oe. caespitosa* with outcrossed pollen after hawkmoth visitation. In both 1985 and 1986, stigmas of *Oe. caespitosa* were either augmented with addtional outcrossed pollen after pollinator visitation or were unaugmented (only receiving pollen from natural visitation). In 1985, which was a year of high hawkmoth abundance (Fig. 1), augmentation did not significantly increase fruit set. Additionally, augmentation did not significantly increase the average number of seeds per fruit (Fig. 2). However, in 1986, a year with low lawkmoth activity (Fig. 1), fruit set was substantially increased with augmentation. In *M. multiflora,* which bears only one ovule per ovary, the average minimum estimated seed set in 1985 was more than twice that found in 1986, while the maximum estimated seed set in 1985 was nearly seven times greater (Fig. 3).

Augmentation of stigmas with additional pollen in *Oe. caespitosa* (Table 2, Fig. 2) indicates that the abundance of hawkmoths was at or above the level needed for maximum fruit and seed development in 1985. However, because all augmented flowers developed fruits in 1986 but not in 1985 (only 71 percent developed fruits), the production of fruits in 1985 must have been limited by resources such as water or nitrogen. Conversely, hawkmoths were the limiting factor in reproduction during 1986. *Mirabilis multiflora* was also apparently limited by hawkmoth abundance in 1986 (Fig. 3). Hawkmoth visitation is therefore crucial for reproduction in these plant species, and factors which limit reproduction are highly variable between seasons in the White Mountains.

Temporal Variation in Visitation

Frequency distributions of the time of visitation for each species of hawkmoth at *Mirabilis multiflora* are shown in Figure 4. Peak visitation by *Hyles lineata* is between 8:15 and 8:30 p.m., while *Sphinx chersis* and

Manduca quinquemaculata show peak visitation near 8:45 p.m. However, *M. quinquemaculata* visitation to *Oe. caespitosa* peaks between 8:15 and 8:30 p.m. (Fig. 5). Frequency distribution of visitation times of *Manduca quinquemaculata* to *M. multiflora* and *Oe. caespitosa* are significantly different (Kolmogorov-Smirnov test, D_{max} = 0.68, p = 0.01) while the distributions of *Hyles lineata* to *M. multiflora* and *Manduca quinquemaculata* to *Oe. caespitosa* are statistically indistinguishable (K-S test, D_{max} = 0.14, p = 0.80).

Because the top of the nectar column is approximately 8.0 cm from the top of the hypanthium tube in *Oe. caespitosa* (Table 1), to extract any nectar a hawkmoth would need a tongue of at least 8.0 cm in length. In order to extract all of the available nectar, a tongue length of 12.0 cm is needed. In contrast, to extract nectar from *M. multiflora,* a tongue approximately 5.7 cm long is necessary. The

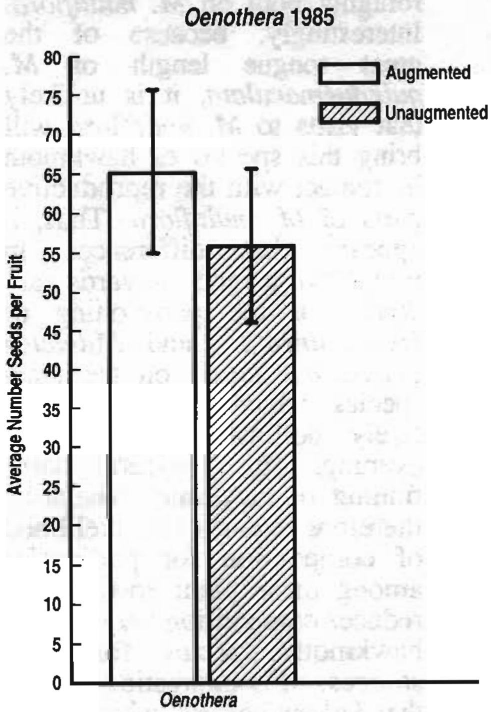


Figure 2. Average number of seeds per fruit from flowers of *Oenothera caespitosa,* either augmented with additional pollen or unaugmented (+/- S.E.).

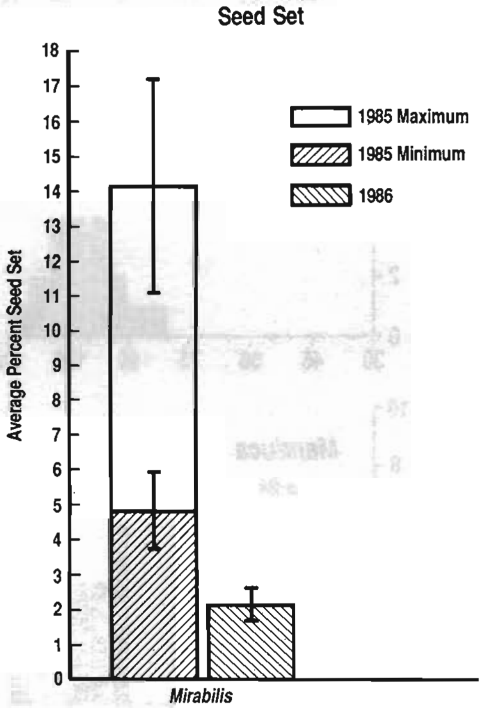
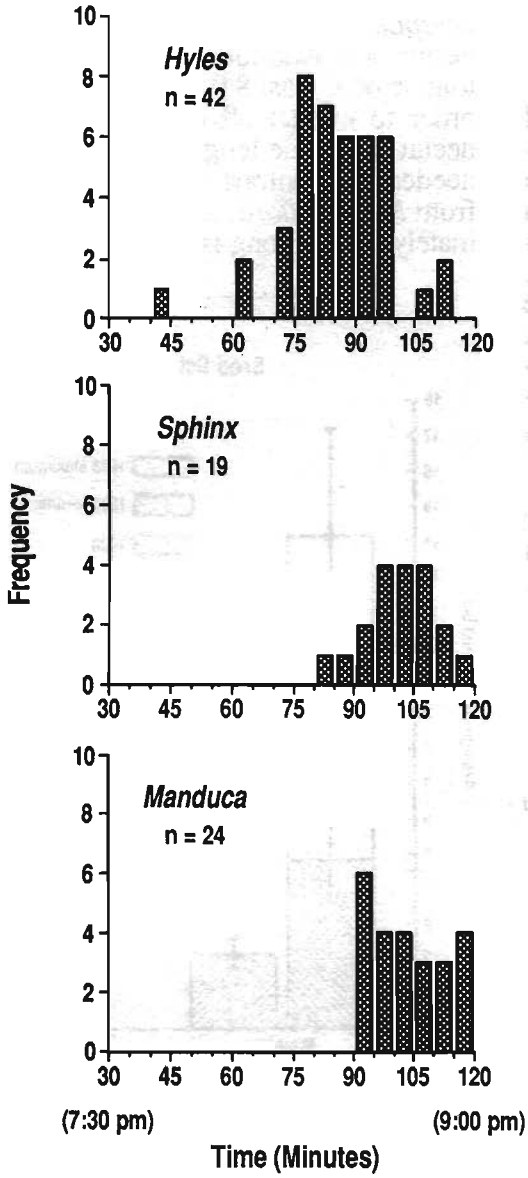


Figure 3. Average percentage of flowers producing seed in four plants both in 1985 and 1986 (+/- S.E.). In 1985 seed was collected late in the season when dehisence may have already occurred, resulting in some flowers without an aborted ovary or seed. If all unknown flowers are assumed not to have produced seed, then the resulting 1985 minimum average percent seedset would have occurred. If all unknown flowers are assumed to have produced seed, then the 1985 maximum average percent seedset would have occurred. Seed was collected early in 1986, and therefore the actual average percent seed set is reported.



Kolmogorov-Smirnov Test		
	D-MAX	p
Hyles vs. *Sphinx*	.57	<.001
Hyles vs. *Manduca*	.64	<.0001
Sphinx vs. *Manduca*	.13	>.05

Figure 4. Frequency distributions of the time of visitation for *Hyles lineata*, *Sphinx chersis*, and *Manduca quinquemaculata* to *Mirabilis multiflora*.

wide perianth of *M. multiflora* allows even a large visitor to crawl deep within the flower, reducing the needed tongue length even further.

Apparently because the reward offered by *Oe. caespitosa* flowers is much greater than that of *M. multiflora* flowers (Table 1), and because *M. quinquemaculata* has a tongue that enables it to extract the reward, *M. quinquemaculata* visits *Oe. caespitosa* early in the evening and only subsequently visits *M. multiflora.* Conversely, because of the morphological restrictions of *Oe. caespitosa* flowers, *Hyles lineata* is able to extract little or no nectar from *Oe. caespitosa* flowers and therefore begins its foraging bout on *M. multiflora.* Interestingly, because of the great tongue length of *M. quinquemaculata,* it is unlikely that visits to *M. multiflora* will bring this species of hawkmoth in contact with the reproductive parts of *M. multiflora.* Thus, it appears that differences in morphology and rewards account for the partitioning of *Hyles lineata* and *Manduca quinquemaculata* on the plant species which they are most likely pollinate early in the evening. This temporal partitioning of hawkmoth visitation therefore reduces the likelihood of competition for pollinators among these plant species and reduces competition between the hawkmoth species for food sources. It is interesting to note that *Sphinx chersis,* which has a relatively short tongue, does not visit *M. multiflora* until approximately 8:45 p.m. Perhaps there is an additional plant

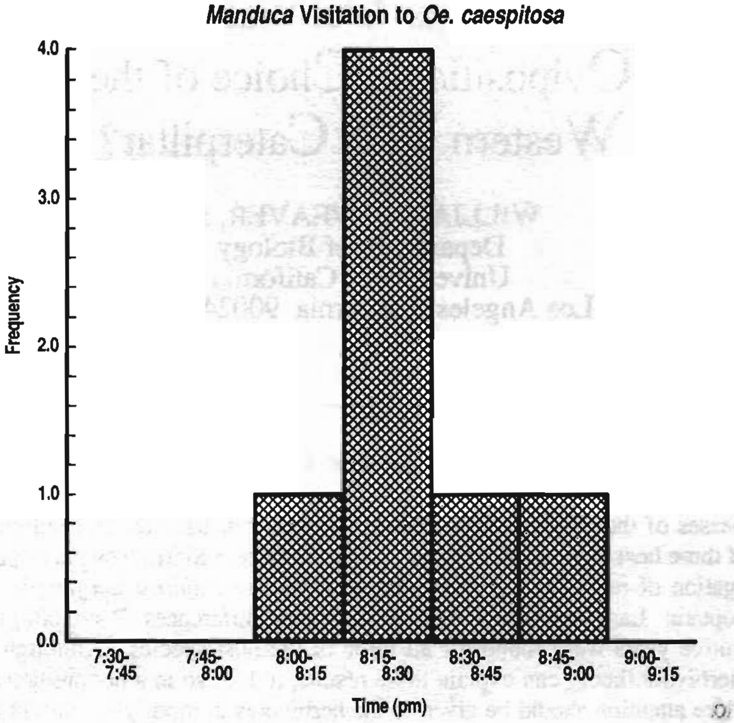


Figure 5. Frequency distribution of the time of visitation for *Manduca quinquemaculata* to *Oenothera caepspitosa.*

species at which *Sphinx chersis* begins foraging early in the evening.

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