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Patterns of visitation by animal pollinators

James D. Thomson

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I measured the relative rates of pollination visitation at various points during the blooming periods of several species of animal-pollinated plants in Rocky Mountain subalpine meadows. The most common pattern was for visitation to be low early in the flowering period, but then to increase and remain high for the duration of flowering. Relative visitation rate on a species was uncorrelated with the amount of flowering time overlap experienced from species with similar pollinators; thus overlap is not a good indicator of competition for visits. I also measured visitation rates on three species in artificial and natural competition experiments. In one species, pressure of a potential competitor decreased visitation, but in two others increased it. Whether interspecific overlap increases or decreases visitation probably depends on floral similarity, pollinator constancy, spatial proximity of interactants, and other idiosyncratic characteristics of the interaction. I discuss the role of competition for visits as one component of competition for successful pollination service.

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Мною измерены относительные частоты посещений опылителей в разных точках в период цветения разных видов растений, опыляемых насекомыми на субальпийских лугах Скалистых Гор. Наиболее обычна низкая частота посещений в начале периода цветения, затем частота увелисивается и остается высокой в течение остального периода. Относительная частота посещений вида не коррелирует с величиной перекрывания времени цветения у видов с одинаковыми; таким образом, перекрывание не может быть хорошим индикатором конкуренции за опылителей. Мною также измерена частота посещений трех видов в опытах с искусственной и естественной конкуренцией. У одного вида пресс потенциального конкурента снижает число посещений, но у двух других – улеличивает. Увеличение либо снижение количества посещений при межвидовом перекрывании зависит от сходства цветковых растений, постоянства состава опылителей, пространственной близости взаимодействующих объектов и др. идиосинкразических характеристик взаимодействий. Я обсуждаю роль конкуренции за посещение как компонента конкуренции за эффективную систему опыления.

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1. Introduction

Theoretical treatments (Levin and Anderson 1970, Waser 1978b, 1981) have suggested that interspecific competition by plant species for pollination may result in displacement of flowering times in those plants that share pollinators, and numerous authors have described such displaced patterns and attributed them to competition (Robertson 1895, 1924, Mosquin 1971, Heithaus 1974, Gentry 1974, Frankie et al. 1974, Pojar 1974, Stiles 1975, 1977, Reader 1975, Feinsinger 1976, Pleasants 1977, 1980, Waser 1977, 1978b). On the other hand, more complicated mathematical models have specified conditions where convergence in flowering time, rather than divergence, may be adaptive in increasing pollination success (Straw 1972, Bobisud and Neuhaus 1975, Thomson 1975). Other workers have found aggregated, or nearly random, rather than regular, patterns of flowering peaks (Poole and Rathcke 1979, Rathcke unpubl., Parrish and Bazzaz 1979, Rabinowitz et al. 1981, Thomson 1975, 1978a). Tendencies toward aggregation may be due to various causes, among them convergence. The selective basis for convergence is formally similar to Müllerian mimicry, and convergence in morphology as well as flowering time has also been suggested (Grant 1966, Macior 1971, Proctor and Yeo 1972, Watt et al. 1974, Brown and Kodric-Brown 1979, Thomson 1975, 1978a, 1980, 1981a, 1981b, Schemske 1981; cf. Thien and Marcks 1972, Heinrich 1975, Waser and Real 1979).

Thus, it is by no means clear what interaction to expect between plant species that overlap in time. This paper describes an attempt to study plant-plant interactions directly, by comparing the "pollination success" of a species in situations of different amounts of overlap. I describe (1) the broad temporal patterns of visitation rate and overlap for all major species of a largely perennial herbaceous community, and (2) more detailed studies of interactions of several sets of species, chosen for detailed analysis because they overlap extensively in blooming time and pollinator usage.

2. Materials and methods

2.1. Study site

The study site was a subalpine meadow at 3820 m a.s.l. on the Washington Gulch trail in the East River valley, Gunnison Co., Colorado. The flora of this area is treated by Barrell (1969), the vegetation by Langenheim (1962), and the bumblebee fauna by Inouye (1976, 1978). The particular site, which was chosen for its typicality and relative lack of disturbance, is described more fully as site IB by Thomson (1978a). Fifty-three species of zoophilous plants occurred in this meadow, most of which require animal visits for complete seed set, as demonstrated by bagging experiments (Pleasants 1977, Thoson unpubl.).

2.2. Flower censuses

I laid out a 6 × 18 rectangular grid of fixed sample points, spaced 10 m apart each way, and placed a 4 m^2 plot at each point to count open flowers at 2 or 3 d intervals throughout the flowering season of 1977. For extremely abundant flowers, I used 1 m^2 plots, and for certain species, e.g., composites, I counted heads or inflorescences (see Thomson 1978a). For each plant species, the number of flowers recorded on each day was divided by the number recorded on the peak day of flowering, thus producing a standardized flowering curve. Animals judged capable of pollination were collected by net, except for hummingbirds and bumblebees, which could be identified without capture.

2.3. Measures of visitation

I measured visitation within single 10 × 10 m blocks where the species measured was blooming at high density. Subsequent measures on the same species were made in the same area to equalize as many local effects as possible. In competition comparisons, two or more blocks were employed so the visitation rate on a species growing alone could be compared to the rate when it is growing at similar density but intermingled with other species attracting the same visitors. Details of such comparisons are treated separately in following ections.

Visitation was measured by using finely powdered fluorescent pigments (Helecon®, U.S. Radium Corp.) to track, or at least to imitate, pollen flow (cf. Linhart 1973, Stockhouse 1976, Price and Waser 1979). To measure animal visitation in a patch of flowers, I established a number of test flowers by marking their stems with wire twist ties. Sample sizes were generally 50 or more but varied depending on the time available for marking and the completeness of recovery. The test flowers were spread evenly through the patch and comprised about 15% of the total flowers. Around each test flower I located the nearest conspecific flower in each of the four compass quadrants and daubed its stamens with an aqueous suspension of the pigment. This liquid application greatly reduced wind dispersal of the dust, an otherwise source of error.

After 48 h I harvested the test flowers individually in clean glassine envelopes to prevent contamination from other flowers. I examined each flower microscopically in UV light. Flowers bearing only a speck or two of pigment far from the sexual organs were scored as not visited.

Most of the flowers in the study were shortlived in comparison to the intervals between measurements (B. Thomson, unpubl.). In these cases, results of one measurement are not confounded by residual pigment from previous measures; direct examination showed that pigment vanishes from the system quickly after the source flowers wither. It was rare to find pigment from previous applications when scoring flowers.

The fraction of test flowers and the fraction of marked flowers were not held constant in these measures, but the method is specifically designed to be robust with respect to such variation. The fraction of marked flowers is always high enough (>40%) that animals' pigment pools will almost certainly be refreshed before they are exhausted by grooming. The systematic placement of source flowers around each test flower further reinforces this statistical near-certainty. (If the animals do remove the pigment by assiduous grooming, they probably remove most of their pollen loads as well). Because the pigments are not pollen dyes, their transfer characteristics are probably different (Thomson unpubl.). Estimates of actual pollination rate, or interspecific comparisons, would be dangerous. However, I consider the fraction of test flowers which show pigment to be a robust visitation index which will generally be strongly *correlated* with pollination rate as long as comparisons are made within a plant species, within a meadow, as they are here.

2.4. Overlap calculations

I compute the raw overlap load on each plant species i for day k as

$$o_{ik} = \sum_{j=1}^{s} f_{jk} \cdot a_{ij},\ j \neq i,$$

where s is the number of plant species, f_{jk} is the standardized flowering curve value for species j on day k (see above), and a_{ij} is the faunal overlap between species i and j. Faunal overlaps are calculated, following Schoener (1970), as

$$a_{ij} = 1 - {}^{1}/_{2} \sum_{j=1}^{n} |P_{ih} - P_{jh}|,$$

where p_{ih} and p_{jh} are the proportional representations of pollinator species h on plant species i and j, respectively. Because it uses the standardized flower curve values, this index gives all plant species similar weight. Thus it is essentially a measure of how many of a species' potential competitors for pollinators have strongly overlapping blooming curves. I felt that weighting species by their present abundance in the meadow was unwarranted because (1) the numbers of flowers or heads recorded are not comparable between species because of differences in attractiveness, pollen production, etc. (cf. Pleasants 1980) and (2) the current abundances do not necessarily approximate the prevailing community mixture experienced by these species over evolutionary time.

2.5. Regression analysis

I wished to relate visitation to various variables such as time and overlap for the set of thirty plant species for which at least 15 pollinator observations were obtained. There were 70 measures of visitation for these plants. To render these measures comparable, I standardized each visitation measure, and each of the other variables associated with each measure (see below), by dividing each value by the mean of all the values for the variable in question. This has the effect of "relativizing" the values to a constant sum within each species and correcting for differences in the number of measures per species.

The 70 visitation measures were treated as the dependent variable in a multiple regression analysis involving four independent variables: the number of flowers of the species in bloom; the overlap load; the cumulative number of flowers of the species to have opened; and the number of days since the species began flowering. In addition to analyzing the entire data set, I also separately analyzed sets of all "early" and "late" visitations. These sets overlap in that both include the visitation measure taken nearest the flowering peak for each species. The early set also includes measures taken earlier, and the late set includes those later, so these sets represent the rise to, and the decline from, peak flowering.

2.6. Single-species competition comparisons

2.6.1. Draba spectabilis Greene/Thlaspi alpestre L.

These two fly-pollinated crucifers are very similar in flower structure, size, and presentation. *Thlaspi* blooms earlier, but there is a substantial overlap period, and the two often grow intermingled. *Thlaspi*'s petals are white to the human eye, *Draba*'s yellow. When they grow together, some insects pass between them without apparent hesitation. *Draba spectabilis* seed set was greatly reduced when visitors were excluded (Thomson unpubl.).

I measured visitation on *Draba* inflorescences in six 100 m² blocks on 15–17 June 1977. All blocks were within 80 m of one another. *Thlaspi* was present in some of the blocks. On 18 July I gathered *Draba* infructescences in these blocks to calculate seed set. Fruits remained attached even if no seeds were set.

2.6.2. Chrysopsis villosa (Pursh) Nuttall/various species

I measured visitation rate on *Chrysopsis villosa* in two 3 × 5 m blocks, 110 m apart, on three occasions. In one block, and in the area surrounding it, *Chrysopsis* occurred alone; the other block was in the most diverse patch of Compositae in the meadow, with *Helianthella quinquenervis* (Hooker) Gray, *Helenium hoopesii* Gray, *Agoseris glauca* (Pursh) Raf., and *Senecio crassulus* Gray blooming concurrently. All of these, *Chrysopsis* included, are yellow composites which are partly or wholly dependent on bumblebee visits for seed set (Pleasants 1977, Thomson unpubl.). Although the flowers share little in common besides "yellow compositeness", short-tongued bumblebees foraging on one of them will often pass to another (Thomson 1981a).

2.6.3. Delphinium barbeyi Hutch/Aconitum columbianum Nutt.

In contrast to the preceding "natural experiments", I used manipulation to determine the effect of *Aconitum columbianum* (Ranunculaceae) on visitation of *Delphinium barbeyi* by bumblebees. *Delphinium* and *Aconitum* flowers are somewhat similar in color to human vision, and both are borne in spikes at about the same height. However, they differ greatly in reflectance spectra, effective corolla tube length, and the maneuvers required to feed from them (Laverty 1978). Both grow in clumps and *Aconitum* seems to prefer moister soils, so the two seldom intermingle. They are mostly visited by different bee species; at my site, *Delphinium* by the long-tongued *Bombus appositus* (Apidae) and *Aconitum* by the medium-tongued *B. flavifrons* (cf. Inouye 1976, 1978). However, *B. flavifrons* will visit *Delphinium* so *Aconitum* is at least a potential competitor for their visits.

Pre-experimental control. At the site described, there was a single patch of *Aconitum* comprising about 290 inflorescences. The nearest *Delphinium* patch (about 300 inflorescences) was 30 m away. On 31 July I spent from 0900 to 0930 hours using powdered Radiant® pigments (Frankie 1973) to dust *B. flavifrons* workers as they backed out of flowers in the *Aconitum* patch. They seemed little affected, often continuing to forage. After dusting the bees, I put five cut spikes of *Delphinium* (in water) among the *Aconitum*. At 1600 hours I collected spikes of *Delphinium* from the nearest patch to see if any of the *Aconitum* bees had transferred the dye. I also examined flowers of *Lupinus* sp., *Mertensia ciliata* (James) G. Don, and *Senecio triangularis* Hooker collected near (<4 m) the *Aconitum* patch.

Experiment and post-control. On 1 August I repeated the above procedure with a different color of pigment. As soon as the dusting period was over, I bagged all the *Aconitum* inflorescences. I did not use cut *Delphinium* spikes in this experiment. At 1600 hours I harvested flowers as before, then uncovered the *Aconitum* spikes. A second control, similar to the first except that cut spikes were not used, was run on 5 August using yet another color of dye.

3. Results

3.1. Patterns of visitation

The 17 plant species can be roughly classified into 5 groups according to the relationship of the flowering curve with the visitation data (Fig. 1). The existence of significant heterogeneity among the visitation measures for each plant can be shown by a 2 × N test of independence; the G values associated with these are also given.

In type 1 plants (*Lupinus* sp. and *Ranunculus alismaefolius* Geyer), visitation rises and falls closely in step with the flowering curve. *Lupinus* is the only species which has a significantly positive correlation between number of flowers and fraction of flowers visited ($r = 0.96$, $n = 5$, $p < 0.005$). Both species show significant heterogeneity of measurements.

In type 2 plants (*Helenium hoopesii, Chrysopsis villosa, Erigeron peregrinus* (Pursh) Greene, *E. coulteri* Porter (all Compositae), *Draba spectabilis* (Cruciferae) and *Erythronium grandiflorum* Pursh (Liliaceae)), success is lower for the first one or two measurements, then increases and remains high, with no drop in visitation detected near the end of flowering. These species all received high visitation at a time past the peak, when they were rather rare. All except *Chrysopsis* show significant heterogeneity. *Chrysopsis* visitation on the first measurement (16/20) is, however, significantly lower than the subsequent maximum (30/33; $\chi^2 = 7.7$, 1 d.f., $p < 0.01$).

Type 3 plants (*Helianthella quinquenervis, Senecio crassulus* (Compositae), *Delphinium barbeyi* (Ranunculaceae), and *Pseudocymopterus montanus* (Gray) Coulter and Rose (Umbelliferae)) received heavy visitation from the first sampling day to the last. None showed heterogeneity.

Type 4 plants (*Castilleja sulphurea* Rydb. (Scrophulariaceae) and *Arnica mollis* Hooker (Compositae) are frequently visited on their first records, but the last measures show a decline in visits. The first sampling of *Arnica* was not done until its flowering was nearly at its peak, so the lack of an early period of low visitation is understandable. Both showed significant heterogeneity.

Type 5 plants (*Erigeron speciosus* (Lindley) DC., *E. elatior* (Gray) Greene (Compositae), and *Ligusticum porteri* Coulter and Rose (Umbelliferae)) showed apparently random fluctuations in visitation, although some samples were small (Fig. 1). All three were well-visited late in their flowering periods. Heterogeneity was significant in the two *Erigerons*.

3.2. Results of regression analysis

Tab. 1 summarizes the regression analysis of the visitation data for all 17 plant species. The only variable significantly related to visitation is time elapsed since the beginning of bloom, and this is only true of the Early subset. This is apparently due to type 2 plants dominating the sample.

The main conclusion is that an "average" plant species will have its visitation rate increase markedly while it is coming into bloom, but then level off, or decrease only gradually, during the decline of flowering. This pattern seems little affected by overall overlap. Thus such overlap appears unrelated to plant competition for visits. However, overlap thus defined is based on an indiscriminant collection of species which share visitors and flowering time. As suggested in the Introduction, such overlap may subsume both competitive

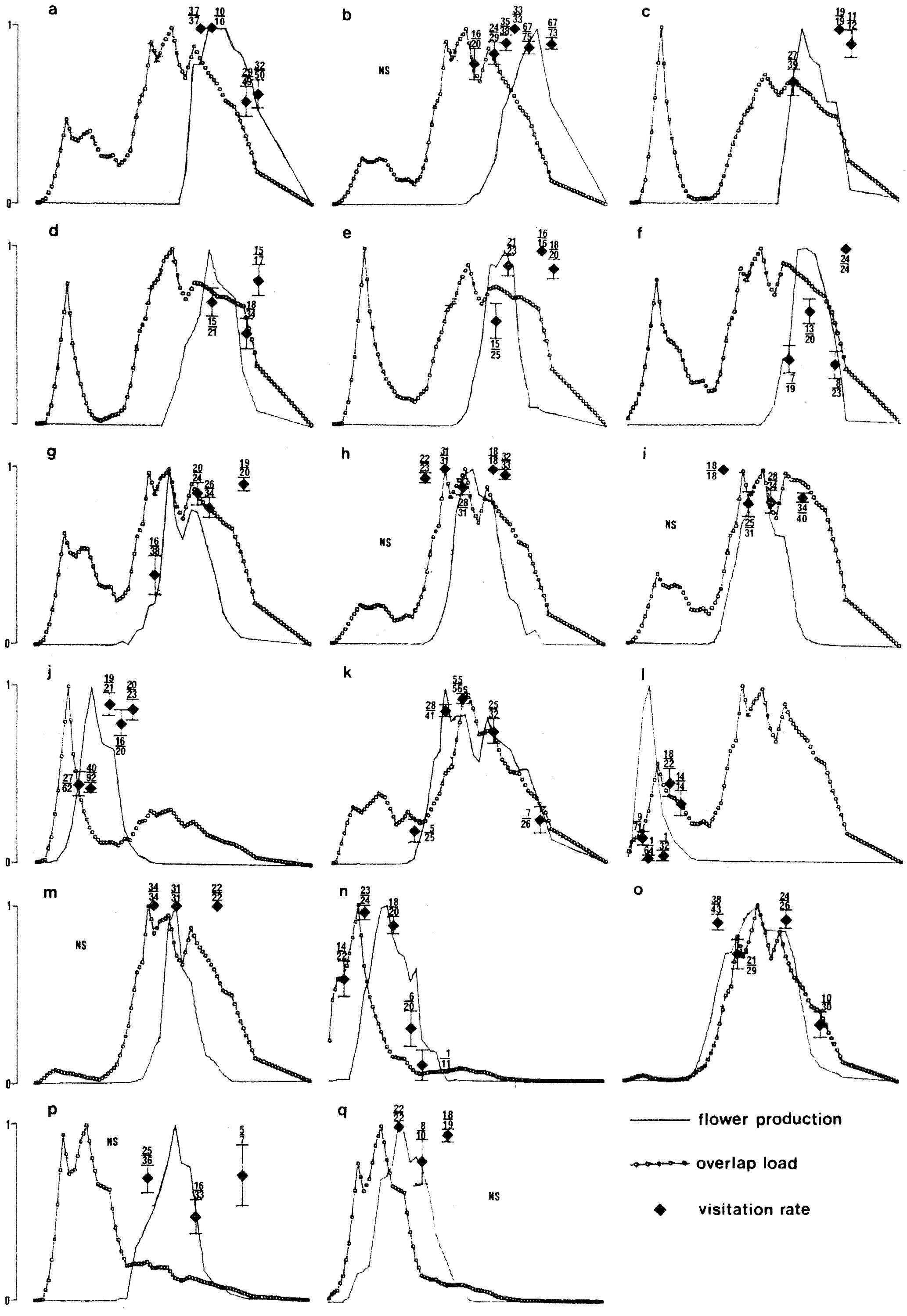

Fig. 1. Summary graphs of flowering curves, overlap, and visitation measures through time on 17 species of zoophilous plants. The horizontal (time) axis is identical for each graph, the 96 days from 29 May 1977 to 2 September 1977. All variables are scaled by the maximum value so they range from 0–1. The sample sizes for each visitation measure are given, in the form (no. visited/no. sampled). Estimated standard deviation bars are shown, as computed by $s = \sqrt{p(1-p)/n}$, where n = no. sampled and p = the proportion visited. For each species, the heterogeneity of the set of N visitation measures was computed as the G statistic for a 2 × N contingency table comparing visited vs. unvisited flowers (or inflorescences, in *Draba spectabilis*). All sets showed significant heterogeneity except those marked "NS". Plant families include Compositae (spp. a–i), Cruciferae (j), Leguminosae (k), Liliaceae (1), Ranunculaceae (m, n), Scrophulariaceae (o), and Umbelliferae (p, q). Major pollinators include bumblebees (spp. a, b, g, h, i, k, o), bumblebees and solitary bees (1), bumblebees and birds (m), solitary bees and flies (c, d, e, f, n), and flies (j, p, q). – Plant species are: a *Arnica mollis,* b *Chrysopsis villosa,* c *Erigeron coulteri,* d *E. elatior,* e *E. peregrinus,* f *E. speciosus,* g *Helenium hoopesii,* h *Helianthella quinquenervis,* i *Senecio crassulus,* j *Draba spectabilis,* k *Lupinus* sp., l *Erythronium grandiflorum,* m *Delphinium barbeyi,* n *Ranunculus alismaefolius,* o *Castilleja sulphurea,* p *Ligusticum porteri,* and q *Pseudocymopterus montanus.*

Tab. 1. Multiple regression analysis of visitation data. Dependent variable is standardized visitation (see text). The only independent variable which predicts a significant portion of visitation is "days elapsed" and this relationship only holds for the Early data subset.

Independent variables	Standardized regression coefficients Entire flowering curve	Early portion of curve	Late portion of curve
Flowers in bloom	−0.069	0.074	−0.246
Overlap load	0.207	0.114	0.178
Cumulative flowers since start of bloom	0.020	−0.537	−0.119
Days elapsed since start of bloom	0.002	0.785**	−0.035

**$p < 0.01$.

and beneficial effects. Thus it is also necessary to consider the results of the specific interactions which were tested experimentally.

3.3. Results of single-species competition comparisons

Visitation on *Draba spectabilis* increased as flower density increased (Tab. 2). *Thlaspi alpestre* was present in large numbers in one block, and *Draba* received higher visitation there. In fact, visitation on *Draba* was more highly correlated with the total inflorescence density than with the density of *Draba* alone (Tab. 2), which suggests that the insects may respond mainly to increased general resource density, showing little discrimination between the flowers. Tab. 2 also gives the mean number of seeds per fruit for each block. These means are weakly correlated with visitation ($r = 0.75$, $n = 6$, $p < 0.1$, two-tailed test).

Chryopsis heads were more abundant in the block where it occurred alone, but the visitation was higher in

Tab. 2. Relation of *Draba* visitation to seed set and *Draba* and *Thlaspi* densities. Pearson product-moment correlations are given. Significance levels are for two-tailed tests.

Block	No. visited infls. / No. sampled infls.	Mean no. seeds/fruit (s, no. fruits)	*Draba* density (infls. m^{-2})	*Thlaspi* density (infls. m^{-2})	*Draba* + *Thlaspi* densities summed
1	16/54	3.02 (2.55, 361)	3.870	0.056	3.924
2	22/52	3.23 (2.32, 295)	7.827	0	7.827
3	14/52	3.66 (3.15, 216)	4.080	0	4.080
4	31/53	3.95 (2.17, 116)	5.811	4.774	10.585
5	32/53	4.37 (2.66, 275)	10.264	0.077	10.340
6	17/42	3.73 (2.12, 60)	6.905	0.167	7.072
Correlations with visitation (transformed as $\sqrt{p}$):			$r = 0.751$ $0.1 > p > 0.05$	$r = 0.542$ ns	$r = 0.986$ $n = 6$, $p < 0.01$

Tab. 3. Visitation on *Chrysopsis villosa* (CV), with and without potential competitors. Total visitation was significantly higher in block 1 (2 × 2 contingency table, $\chi^2 = 7.83$, 1 d.f., $p < 0.01$).

Date	Block 1 Flower densities: CV	Others	Visitation on CV	Block 2 Flower densities: CV	Others*	Visitation on CV
29 Jul	7.09 m^{-2}	0	14/17 (0.824)	5.27 m^{-2}	7.22 m^{-2}	21/21 (1.0)
6 Aug	6.94 m^{-2}	0	36/44 (0.818)	6.05 m^{-2}	5.13 m^{-2}	31/31 (1.0)
14 Aug	6.26 m^{-2}	0	29/32 (0.906)	4.63 m^{-2}	2.10 m^{-2}	38/41 (0.927)
Total			79/93 (0.849)			90/93 (0.968)

*Summed densities of *Helenium hoopesii, Helianthella quinquenervis, Senecio crassulus, Agoseris glauca* (all Compositae).

the mixed block (Tab. 3) on each of the three sampling dates. The difference between the visitation rates is lowest on the last day. By this time, the numbers of the other species had declined considerably, while the later-blooming *Chryopsis* was still blooming strongly in both blocks. The overall difference between the blocks was highly significant (χ^2 = 7.84, 1 d.f., $p < 0.005$).

In the pre-experimental control; no dye was transferred to the *Delphinium* patch (Tab. 4). A small amount of dye was transferred to the five cut spikes, but direct observation showed that most of the visits to those spikes were not well enough directed to achieve fertilization (cf. Laverty 1978). No dye was found on *Mertensia,* very little on *Senecio* and *Lupinus.*

When the *Aconitum* was covered, at least some bees responded by beginning a "searching" behavior. I saw one marked bee 150 m away from the *Aconitum* patch, alternately visiting *Senecio crassulus* and the extremely different *Gentiana calycosa* Grisebach. Another visited *Senecio triangularis, Castilleja rhexifolia* Rydb., *Erigeron peregrinus,* and *Pedicularis groenlandica* Retz. All the tested species showed more dye (Tab. 4) than the day before although the differences were significant only in *Delphinium* (both flowers and inflorescences). The observed differences may be considered conservative underestimates because fewer bees carried dye during the experiment. At least one marked *B. flavifrons* worker was seen foraging "skillfully" in the *Delphinium* patch.

While samples are small for the post-experimental control, it appears that *Aconitum* did not regain sole use of its visitors (Tab. 4). In fact, visits to other species are higher than during the experiment in some cases. The bees' inconstancy may have been facilitated by the exposure to different flowers during their enforced infidelity four days before, but the *Aconitum* bloom was declining rapidly at this time and the bees may have simply depleted the available flowers and left. Certainly bees were working the remaining bloom.

It appears that competition for visits may occur in the *Delphinium/Aconitum* case, but the other cases are more indicative of interspecific facilitation for visits.

4. Discussion

4.1. Overlap, visitation, and competition

The use of overlap data to draw inferences about interspecific competition has been questioned ever more strongly in recent years (see Connell 1980 for a recent treatment), and the techniques of measuring overlap have also been debated (e.g., Colwell and Futuyma 1971, Abrams 1975, 1980, Armstrong 1977, Hurlbert 1978, Case 1981). The overlap measures used in this paper represent only one set of formulations out of many possible, and I do not defend them as being better than other choices. For instance, the indices I used give all plant species similar weight, rather than reflecting

Tab. 4. Flowers showing the dye applied to *Bombus flavifrons* workers foraging in the *Aconitum* patch (see text). Table entries are in the form: no. with dye/no. sampled (proportion visited). χ^2 values are given for those measures which differ significantly from the Experiment (2 × 2 contingency tables, 1 d.f.).

	No. bees marked	*Delphinium* in *Delphinium* patch	*Delphinium* in *Aconitum* patch	*Lupinus* sp.	*Mertensia ciliata*	*Senecio triangularis*
Pre-experimental control .... 31 Jul	15	0/53 infls (0.0)** 0/126 fls (0.0)**	5/5 infls (1.0) 15/59 fls (0.254)	1/11 infls (0.091) 1/245 fls (0.004)	0/19 infls (0.0) 0/95 fls (0.0)	2/38 heads (0.053)
Experiment .... 1 Aug	11	10/56 infls (0.179) 22/142 fls (0.155)	not done	not done	5/45 infls (0.111) 5/162 fls (0.031)	8/48 heads (0.167)
Post-experimental control .... 4 Aug	9	6/7 infls (0.857)** 12/25 fls (0.480)**	not done	2/14 infls (0.143) 16/155 fls (0.103)	2/4 infls (0.500) 2/13 fls (0.154)*	6/36 heads (0.167)

*$p < 0.05$.
**$p < 0.01$

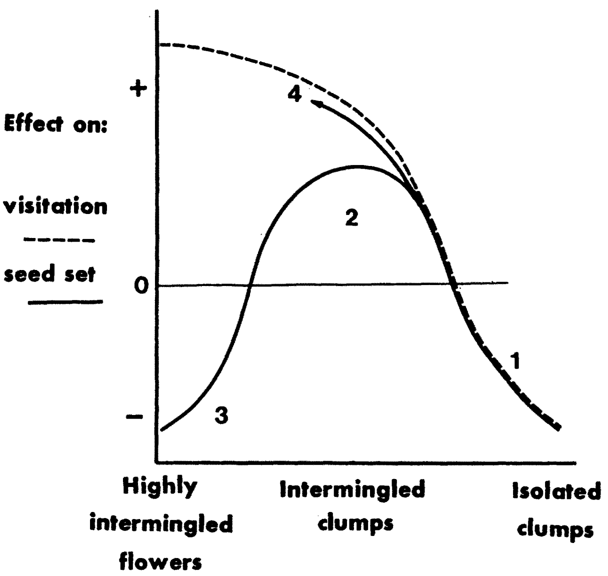

Fig. 2. A conceptual model of the effect of spatial intermingling on the relationship between two species which share inconstant pollinators. When the curves are above the neutral line, the species relationship is cooperative; when below, competitive. When intermingling is low (right-hand part of the graph), competition is mainly exploitative. As intermingling increases, interference competition through heterospecific pollinator visiits becomes dominant. Points 1–3 refer to specific examples mentioned in the text. Point 4 represents the additional possibility of an interaction in which a diel separation of bloom times or differential pollen placement on vectors allows extensive spatial intermingsling without extensive heterospecific pollen transfer.

their abundance in the meadow. Ideally, perhaps, plant species should be weighted by their average abundances over evolutionary time, since adaptations should reflect these abundances. With no way to estimate these it is simpler to weight species equally. From inspection of the data, I do not believe that different overlap indices would reveal correlation of visitation and overlap. This suspicion is reinforced by the pairwise interactions studied experimentally. In some cases overlap decreased visitation, in another, increased it. There may well be other species pairs where overlap has no effect. With these diverse possibilities it is hardly surprising that composite indices of generalized overlap, which may include overlaps from mutualistic, competitive, and neutral species, show no relationship to visitation. It will usually be more constructive to examine the components of specific interactions to see what factors determine the nature of the interaction.

I have also found increases in visitation with overlap in two-species mixtures of *Hieracium* (Thomson 1978b), and *Potentilla* (Thomson 1981b), and a mixture of several Compositae (Thomson 1981b). In all these cases the flower species were similar in flower structure, somewhat similar in appearance, and were intermingled. It seems likely that these conditions cause pollinators to concentrate in local areas of high floral density, without necessarily discriminating among the different species in assessing density (Thomson 1981b). True competition for visits is more likely to occur when the species in question are dissimilar in appearance, require different foraging behaviors, and do not intermingle, as in the *Delphinium/Aconitum* case. This importance of intermingling is depicted in Fig. 2, where the dotted line shows the hypothesized shift from competition to mutualism for visits as the interacting plants become more intermingled.

As Waser (1978a, b, 1981) stressed, however, visitation is only one component of pollination success, and it is possible that visits which include deposition of heterospecific pollen may be harmful rather than beneficial. At extremes of intermingling, heterospecific visits will tend to increase (Levin and Anderson 1970), which may cause pollen wastage, stigmatic clogging, or active inhibition of fertilization by foreign pollen (Waser 1978a, b, Wissel 1977, Sukada and Jayachandra 1980, Thomson et al. 1981). Thus seed set may decline even as visitation is enhanced (solid line in Fig. 2). The numbered regions of Fig. 2. represent different measurements of reproductive success by potentially competing plant species. Area 1 describes the competition for visits noted in the *Delphinium/Aconitum* experiment above, area 2 the various mutualistic interactions described above (*Draba/Thlaspi*, etc.), and area 3 depicts the depression of seed set found by Waser (1978b) in highly intermingled artificial arrays of *Delphinium nelsonii* Greene and *Ipomopsis aggregata* (Pursh) V. Grant.

4.2. Implications for community structure

Given that interactions between pollinator-sharing plant species may in theory be beneficial, neutral or harmful, one might not expect to find the blooming periods of such plants displaced in time as if in avoidance of competition. However, as mentioned in the introduction, regularly spaced flowering peaks have been described by several authors who attribute the phenomenon to interspecific competition. There are various possible explanations for the disparity between these reports and the present results.

First, it may be that mutualistic enhancement of visitation rate shown here is routinely overpowered by negative effects of heterospecific pollinations, i.e., the solid curve in Fig. 2 seldom if ever enters the positive region. Few data bear on this balance of visitation rate and visitation purity. Waser's (1977, 1978b) clearest demonstration of seed set reduction due to heterospecific pollinations was obtained in artificial arrays of plants that were more intermingled than in nature. His field data, which purport to show the same phenomenon in natural populations, remain subject to other interpretations because visitation rate was neither held constant nor measured (Thomson 1978a).

A second possibility is that regular patterns of flowering time, where they exist, are not engendered solely by competition for pollination, but reflect other aspects of flower, fruit, or seedling biology (cf. Snow 1965, Ågren and Fagerström 1980).

A third possiblity is that some reports of regularly spaced flowering peaks, most of which derive from simple inspection of census data, may be incorrect. In only a few communities have the patterns revealed by flower censuses been compared to null hypotheses (see Poole and Rathcke 1979, Cole 1981). In the majority of these cases (Poole and Rathcke 1979, Anderson and Schelfout 1980, Rathcke unpubl., Rabinowitz et al. 1981, Parrish and Bazzaz 1979, Thomson 1975, 1978a), the overall pattern of flowering was clumped or close to random. Pleasants (1977, 1980) reports significantly regular timing of flowering peaks in Colorado subalpine meadows, but these findings were not confirmed by similar analyses in the similar but more diverse meadows described here, in the same part of Colorado (Thomson 1978a).

In summary, displaced flowering patterns are not universally found and the data presented here suggest that they should not be universally expected.

4.3. Overall patterns of visitation

The visitation data displayed in Fig. 1 and the regression analysis, lend partial support to the hyposthesis that visitation tends to be relatively low early in the blooming period of a species but that after it rises it remains high, as if there is a lag in flower-abundance tracking by the pollinator fauna. Although not all species showed this pattern, it was the most common. In some of the cases where the pattern was not detected, it may have occurred but not been found because the first measurements were made too late (e.g., *Arnica mollis*), or because the fractions visited were so near unity on all days that possible differences in visitation intensity would necessarily be unapparent (e.g., *Heliantehlla quinquenervis*). While not universal (Schemske 1977), it appears that increasing visitation through time may characterize a number of systems (Inouye 1978, Stephenson 1979, Free and Ferguson 1980, Tepedino 1981, Thomson, unpubl. data on *Diervilla lonicera* Mill.).

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