

Pollination Ecology of Vernal Angiosperms

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## Pollination ecology of vernal angiosperms

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Pollination interrelationships of vernal, herbaceous angiosperms in a deciduous forest in southwestern Ohio, USA, were studied for 3 seasons with particular emphasis on phenological integration of the bionomics of flowers and the annual colonies of *Bombus* pollinators. Except for *Corydalis flavula*, all plants were insect or bird-dependent for pollination. In general, the spectrum of *Bombus* species on flowers was related to time of emergence from hibernation of bumblebee queens, sequence of anthesis, depth of nectariferous tubes or spurs of flowers in relation to measured proboscis lengths of bumblebee foragers, and site preference for pollinator nesting and foraging. Spectral reflectance from corollas measured spectrophotometrically indicated general correspondence of corolla color and visual spectra of pollinators. Analysis of nectars by refractometry and thin-layer chromatography revealed no preference of pollinators for particular sugars in nectar nor for particular sugar concentrations. Such preference is considered to be related to availability and abundance of nectar. As determined by analysis of corbicular pollen loads from pollinators, fidelity of bumblebee queens to specific flowers was 60%. Only 9.5% of 1457 queens investigated foraged for pollen. Close correspondence of floral form and insect behavior was indentified by means of cinematography and stereophotographic analysis of pollinator activity. Except for possible interactions between *Dicentra* species and *Corydalis*, no clear evidence for competition between pollinators for forage or between plant species for pollinators was observed. The pollination system of the vernal flora is considered to reflect a high degree of coadaptive integration of phenological, ethological, and morphological phenomena in dynamic homeostasis involving constant, but very gradual, change.

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Взаимосвязи при опылении цветущих весной травянистых покрытосемянных растений в лиственном лесу в юго-западной Огайо (США) исследовались в течение 3-х сезонов с особым рассмотрением фенологической интеграции биологии цветов и колоний опылителей *Bombus*. Кроме *Corydalis flavula* все растения опыляются насекомыми или птицами. В целом, состав видов *Bombus* на цветах определяется по времени появлению после зимовки цариц, последовательности цветения, глубиной нектарных трубок или шпор цветов в отношении к длине хоботка фуражиров и территориальной избирательности опылителей при гнездовании и питании. Спектральное отражение от венчика, измеренное спектрофотометрическим методом, показало соответствие окраски венчика и визуального спектра опылителей. Анализ нектара методами рефрактометрии и тонкослойной хроматографии не выявили предпочтения опылителей к отдельным сахарам в нектаре либо к их концентрации. Предпочитаемость цветов определяется доступностью и обилием нектара. Анализ пыльцы из корзиночек опылителей показал, что степень постоянства самок шмелей по отношению к определенным цветам составляла 60%. Лишь 9,54% из 1457 обследованных самок добывали пыльцу. Соответствие формы цветка и поведения животных определено с помощью кинематографии и стереофотографического анализа активности опылителей. За исключением возможности взаимодействия между видами *Dicentra* и *Corydalis* нет доказательство конкуренции между опылителями за корм или между растениями за опылителей. Предполагается, что система опыления весенней флоры отражает высокую степень коадаптивной интеграции фенологических, этологических и морфологических феноменов в динамическом гомеостазисе, включающем постоянные, но очень постепенные изменения.

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## 1. Introduction

The annual cycle of the herbaceous flora of deciduous forests of eastern North America is closely correlated with the vernal cycle of the forest canopy. Sexual reproduction in this cycle is apparently integrated with the bionomics of the fauna responsible for its pollination.

Comprehensive studies of the pollination dynamics of particular plant species (Powell and Mackie 1966, Galil and Eisikowitch 1971, Macior 1968b, c, 1969, 1970a, b, 1973, 1975a) have revealed close mutual associations involving restricted forager spectra and behavior. In general, however, such investigations have failed to place pollination associations in proper perspective within their respective ecosystems.

Although it is beyond the scope of the present study to investigate all aspects of one pollination system, an attempt has been made to study the contemporary ecological and reproductive dynamics of the vernal system in relation to its queen bumblebee pollinators, which exhibit a high degree of phenological integration of their colonial bionomics with anthesis of this flora and constitute its major pollinator component. This association is restricted both temporally and spatially and is largely isolated from the later-blooming flora outside the deciduous forest and even from later-emerging *Bombus* castes.

## 2. Study site and methods

This study was carried out in the spring of 1971, 1972, and 1973 in mixed deciduous forest of the Fort Ancient State Memorial, a prehistoric Hopewell Indian site near Lebanon, Warren County, in southwestern Ohio. The study areas extended along the slopes of a plateau rising 83 m above the Little Miami River. *Dicentra cucullaria* inhabited the east-facing slope of the plateau along with scattered plants of *Hepatica acutiloba*, *Dentaria laciniata*, *Claytonia virginica*, *Anemonella thalictroides*, *Sanguinaria canadensis*, *Trillium grandiflorum*, and a small population of *Corydalis flavula*. The south slope was covered with *Mertensia virginica* and *Phlox divaricata* above merging below into populations of *Delphinium tricorne*, *Camassia scilloides*, and *Hydrophyllum appendiculatum* with scattered plants of *Silene virginica* and *Tradescantia ohiensis*. A large population of *Dicentra canadensis* with fewer *D. cucullaria* plants intermixed covered part of the western slope. Moderately extensive populations of *Pedicularis canadensis* inhabited the top of the plateau on the margin of woodlands. A population of *Aquilegia canadensis* bordered the woodland at the base of the south slope. Scattered individuals of *Aesculus glabra* formed part of the overstory for all the other woodland species, which are spring ephemerals. Field investigations extended from early April until the end of May in each season. Terminology in this report follows that of Gleason (1952) for plants and Mitchell (1962) for insects.

To determine the ability of plants to produce seed in the absence of insect pollen vectors, five insect enclosures of rigid 18 × 14 mesh galvanized window screen were placed over plants of each species while flowers were still in bud. Enclosures were made sufficiently large to accommodate extension of scapes and pedicels during flowers and fruiting to avoid accidental pollination through contact with the enclosure. When blooming was completed, fruiting of flowers under the enclosures was compared with that of a similar number of flowers on uncaged control plants in the immediate vicinity of the experimental ones.

The spectrum of pollinators on each plant species was determined by collecting and preserving insects and by observing ruby-throated hummingbirds *Archilochus colubris* L. without collecting. Attention was directed primarily to those native plant species sufficiently abundant for study and frequently visited by bumblebees *Bombus* spp. The annual colonies of these insects are established in abandoned rodent nests in the spring by queens fertilized the previous summer and hibernating over the winter in the ground. Queens searching for nesting sites hover near the earth and investigate openings in its surface. Such hunting queens were collected to estimate the relative numbers of individuals of each species nesting in the area. Since foraging activity of bumblebees is not necessarily confined to a restricted area until the colony is established, the removal of transient queens from a limited study site was not considered a significant change in the pollination system during the research period. This assumption appeared correct from the relative frequency of early *Bombus* species collected on plant species blooming later.

The significance of pollen as a forager attractant was determined by microscopic analysis of pollen removed from corbicular loads of pollinating bumblebees. Pollen loads were dissociated in 70% ethanol and mounted in glycerin jelly tinted with methyl green. Pollen constituents were identified as proper to the plant on which the insect was foraging or foreign to that plant species. *Bombus* colonies are initiated by the queen's making and provisioning one or more honey pots filled with honey after which she establishes a first cluster of brood cells provisioned with pollen as well as honey. A pollinator with corbicular pollen loads is thus presumed to have established brood cells. A queen without corbicular pollen is presumed to have no colony at all or at most an incipient colony with a honey pot only. Pollen may still be an attractant for such an individual since emergent queens feed abundantly on pollen in preparation for egg laying.

Nectars were analyzed for component sugars by thin-layer chromatography using a technique modified after Jeffrey and Arditti (1969). The method was preferred because it identifies sugars by a combination of *R<sub>f</sub>* values and specific colors for individual sugars following spray visualization. Total sugar content of nectars was determined by a Bausch and Lomb portable refracto-

meter. All nectar samples were removed from fresh flowers by 5- $\mu$ l micropipettes and analyzed in the field in all *Bombus*-related flowers in which it was sufficiently abundant. Insufficient quantities of nectar were found in *Camassia* and *Hydrophyllum*.

Spectral reflectance from corollas of fresh flowers was determined in the field by means of a Bausch and Lomb Spectronic 20 reflecting spectrophotometer. Light of 10 spectral wavelengths was used, and the values obtained were converted by means of trichromatic coefficient computation of the coordinate values of a Maxwell color diagram from which a composite color was determined. Only the fundamental color of the corolla was identified except for the distinctly different colors of the nectariferous spurred petals of *Aquilegia* and *Delphinium* and the variation in the upper lip (galea) of *Pedicularis*.

Possible correlations between lengths of pollinator probosces and corolla tubes and spurs were studied by measurements from fresh flowers and preserved bumblebees collected the first season. Fifty corollas for each plant species were measured. Length was determined from the point of petal fusion distally to the apex of the spur or base of the corolla tube. Probosces were removed by microdissection from pollinator heads soaked overnight in 10% potassium hydroxide solution. The probosces were then rinsed in water and mounted in clear glycerin jelly for microscopic examination. Proboscis length from the tip of the glossa to the base of the prementum was measured with a calibrated ocular micrometer. Fifty probosces were measured for each species except *Bombus griseocollis* (18), *E. impatiens* (42), *B. pennsylvanicus* (19), and *B. vagans* (18).

Throughout the research period phenological records of blooming were maintained for the plant species under investigation and other vernal species with conspicuous flowers not primarily visited by bumblebees.

Pollinating behavior of foragers on flowers was recorded on 16 mm color film by cinematography using a single-lens reflex hand-held camera equipped with a 90 mm f/1.5 telescopic lens, a 10 mm extension ring and

electric drive for continuous operation. Filming speed was 32 frames/s, and individual frame exposure was 1/320 s. All cine filming was done in available light. This system provided sufficient mobility to follow individual pollinators from one flower or plant to the next and sufficient working distance (45 cm) from the flower to avoid disturbance of the pollinator. Where greater detail in ethological records was required, a custom-built 35 mm stereoscopic camera was used with a color-balanced electronic flash at a distance of 90 mm from the subject.

### 3. Results

#### 3.1. Insect dependence of plant species

*Self-pollination potentials.* Fruiting of flowers under insect exclosures demonstrates their self-compatibility and ability to self-pollinate provided the exclosure is effective in eliminating all potential pollinators, but it does not distinguish internal from external reproductive barriers. No insect activity was observed at any time within the exclosures.

Only *Corydalis flavula* (Tab. 1) was perfectly fruitful with and without pollinators indicating its insect-independence. The bilateral symmetry of its fumariaceous flower and the behavior of one *Bombus bimaculatus* and one *B. impatiens* queen briefly probing the flower spur with their tongues are similar to the form and pollination of *Dicentra canadensis* and *D. cucullaria* in the same plant family, which are completely insect-dependent.

The complete or virtual insect dependence of *Camassia scilloides*, *Delphinium tricornis*, *Dentaria laciniata*, *Dicentra canadensis*, *Dicentra cucullaria*, *Mertensia virginica*, and *Pedicularis canadensis* contrasts with their wide range (41–99%) of success in fruiting when open-pollinated. *Delphinium*, *Pedicularis*, and *Aquilegia canadensis*, however, are also frequently pollinated by hummingbirds. Bumblebees are the primary and almost exclusive pollinating insects on *Delphinium*, *Di-*

Tab. 1. Fruiting of experimental (caged) and control (open-pollinated) plants.

Plant species	Experimental			Control		
	Flowers	Fruits	%	Flowers	Fruits	%
<i>Aquilegia canadensis</i> .....	38	27	71	38	32	84
<i>Camassia scilloides</i> .....	65	0	0	66	60	91
<i>Claytonia virginica</i> .....	42	6	14	42	40	95
<i>Corydalis flavula</i> .....	115	115	100	115	115	100
<i>Delphinium tricornis</i> .....	103	0	0	108	91	84
<i>Dentaria laciniata</i> .....	46	0	0	46	44	96
<i>Dicentra canadensis</i> .....	120	0	0	115	47	41
<i>D. cucullaria</i> .....	125	0	0	123	54	44
<i>Hydrophyllum appendiculatum</i> ...	484	75	15	514	480	93
<i>Mertensia virginica</i> .....	383	4	1	411	326	79
<i>Pedicularis canadensis</i> .....	1138	1	<1	1155	1140	99

Tab. 2. *Bombus* queens on plant species and total collecting time (h).

Plant species	Time	<i>Bombus</i> species									Total
		<i>affinis</i>	<i>bimaculatus</i>	<i>fervidus</i>	<i>griseocollis</i>	<i>impatiens</i>	<i>nevadensis auricomus</i>	<i>pennsylvanicus</i>	<i>perplexus</i>	<i>vagans</i>	
<i>Aesculus glabra</i> .....	17	1	4	0	4	28	0	2	0	2	41
<i>Aquilegia canadensis</i> .....	17	10	0	0	0	0	0	0	0	1	11
<i>Camassia scilloides</i> .....	21	6	20	0	5	75	1	3	6	1	117
<i>Delphinium tricornes</i> .....	75	187	39	0	5	12	74	14	10	19	360
<i>Dicentra canadensis</i> .....	51	68	42	0	2	15	2	0	6	0	135
<i>D. cucullaria</i> .....	59	60	60	1	2	8	1	0	31	1	164
<i>Hydrophyllum appendiculatum</i> .....	25	9	25	0	22	22	0	1	5	58	142
<i>Mertensia virginica</i> .....	38	56	55	0	4	5	3	2	35	2	162
<i>Pedicularis canadensis</i> .....	69	20	235	1	3	31	2	14	0	19	325
Total .....	372	417	480	2	47	196	83	36	93	103	1457

*centra*, *Mertensia*, and *Pedicularis*, but many solitary bees and small flies along with bumblebees pollinate *Aquilegia*, *Camassia*, *Claytonia*, *Dentaria*, and *Hydrophyllum*. Moderate to substantial fruiting of *Claytonia*, *Hydrophyllum*, and *Aquilegia* under exclosures suggests a comparable degree of pollinator-independence.

**Spectrum of *Bombus* pollinators.** Of the 9 *Bombus* species (Tab. 2) occurring in the research area *B. fervidus* was rare, and *B. griseocollis* and *B. pennsylvanicus* were uncommon. All but *B. fervidus* and *B. nevadensis auricomus* hunted nesting sites in the deciduous woodland (Tab. 3) and may be assumed to nest there. The three commonest species on flowers (*B. affinis*, *B. bimaculatus*, and *B. impatiens*) were also the earliest to emerge from hibernation and the commonest hunters of nesting sites. With the exception of *B. griseocollis*, the latest species to emerge (*B. fervidus*, *B. nevadensis auricomus*, and *B. pennsylvanicus*) were also the least common as foragers and hunters of nesting sites. Total figures for foragers and nest site hunters are considered adequate indicators of the relative abundance of queens for each *Bombus* species in the research area.

Calculated as foragers per hour of collecting time for each plant species, the frequency of foragers ranged from 0.6 on *Aquilegia* to 5.6 on *Camassia* and 5.7 on *Hydrophyllum*. Frequencies were moderately low on *Aesculus* (2.4), *Dicentra canadensis* (2.6), and *D. cucullaria* (2.8) to moderately high on *Mertensia* (4.3), *Pedicularis* (4.7), and *Delphinium* (4.8).

In relation to particular plant species, not all *Bombus* species were effective as pollinators in proportion to their abundance. *B. affinis* is the only corolla perforator, and its high frequency on *Aquilegia*, *Delphinium*, *Dicentra*, *Mertensia*, and *Pedicularis* was associated with perforation of corolla tubes and spurs. Although *Aquilegia*

Tab. 3. *Bombus* queens hunting nesting sites.

<i>Bombus</i> species	Total	% Total
<i>affinis</i> .....	27	24.5
<i>bimaculatus</i> .....	38	34.6
<i>fervidus</i> .....	0	0.0
<i>griseocollis</i> .....	4	3.6
<i>impatiens</i> .....	31	28.2
<i>nevadensis auricomus</i> .....	0	0.0
<i>pennsylvanicus</i> .....	1	0.9
<i>perplexus</i> .....	6	5.5
<i>vagans</i> .....	3	2.7
Total .....	110	100.0

*ilegia* can be pollinated by perforators (Macior 1966), such forager behavior does not effect pollination in other species.

Among *Bombus* pollinators the most frequent species was *B. bimaculatus* on *Dicentra canadensis* (31%), *D. cucullaria* (37%), *Mertensia* (34%), and *Pedicularis* (72%); *B. impatiens* on *Aesculus* (68%) and *Camassia* (64%); *B. nevadensis auricomus* on *Delphinium* (21%); and *B. vagans* on *Hydrophyllum* (41%). Pollinators that were not the most abundant species on any plant species but were found more frequently on one plant species than on others included *B. griseocollis* on *Hydrophyllum* (47%), *B. pennsylvanicus* on *Delphinium* (39%) and *Pedicularis* (39%), and *B. perplexus* on *Dicentra cucullaria* (33%) and *Mertensia* (38%). The highly non-random distribution of pollinator species suggests particular, but not exclusive plant-pollinator associations.

### 3.2. Floral attraction of pollinators

**Pollen.** Of the 1457 bumblebee queens collected on flowers only 139 (9.5%) carried pollen (Tab. 4). Of the latter 84 (60%) carried proper pollen only, 33 (24%) carried proper mixed with foreign pollen, and 22 (16%) carried foreign pollen only. If we assume that insects with no proper corbicular pollen were foraging for nectar only, then the total of pollen foragers on the flowers studied is reduced to 117 or 8% of the total foragers. This figure may be somewhat higher if some of these insects had just begun to forage and had not yet accumulated corbicular pollen of the plant species on which they were collected.

The numbers of pollen foragers are rather small for the determination of the degree of fidelity of a *Bombus* species to a particular plant species based upon the degree of purity of pollen loads, but they are suggestive. The percentage of corbicular loads of pure pollen ranges from 25% in *B. impatiens* to 100% in *B. nevadensis auricomus* and *B. pennsylvanicus*. The overall fidelity of *B. bimaculatus* is 73% for 84 individuals, and its fidelity to *Pedicularis* is 82% for 61 foragers. The data suggest that bumblebee queens are primarily nectar-foraging pollinators with a low degree of fidelity to plant species in the vernal flora.

**Nectar.** Thin-layer chromatography indicated that no two nectars analyzed were identical (Tab. 5), but virtually all of them contained both fructose and sucrose at least in trace amounts. The majority of nectars had three sugar components, but *Aesculus* nectar contained only sucrose. Little is known about the abilities of bumblebee queens to discriminate between kinds of sugars, but if trace amounts of nectar components are not significant then *Aquilegia* nectar would resemble that of *Aesculus*; *Delphinium* and *Pedicularis* nectars would be similar; and nectars of *Dicentra canadensis*, *D. cucullaria*, and *Mertensia* would be distinct.

Mean values of total sugar content of nectars (Tab. 6) range from 16.3% in *Dicentra canadensis* to 54.2% in *Aesculus*, while variations within a species range from 4.6% in *D. canadensis* to 14.0% in *Aesculus*. Thus the lowest concentration shows the least variation, and the nectar with the highest sugar concentration is most variable in percent sugar.

**Corolla color.** The attractiveness of floral colors for animal pollinators is a function of corolla reflection in relation to the animal's visual spectrum. Bumblebees are known to have trivariant color vision (Daumer 1956, 1958, Mazokhin-Porshnyakov 1962) in which yellow (588 nm), blue-violet (440 nm), and ultraviolet (360 nm) are mutually complementary and especially attractive to them. Yellow is evident (Tab. 7) in the

Tab. 4. Types of pollen in corbicular loads of *Bombus* queens.

Plant species	Load type*	<i>Bombus</i> species									Total
		<i>affinis</i>	<i>bimaculatus</i>	<i>fervidus</i>	<i>griseocollis</i>	<i>impatiens</i>	<i>nevadensis auricomus</i>	<i>pennsylvanicus</i>	<i>perplexus</i>	<i>vagans</i>	
<i>Aesculus glabra</i> .....	1	0	0	0	1	0	0	0	0	0	1
	2	0	1	0	0	0	0	0	0	0	1
<i>Aquilegia canadensis</i> .....	1	2	0	0	0	0	0	0	0	0	2
<i>Camassia scilloides</i> .....	1	0	1	0	1	1	0	0	2	0	5
	2	0	2	0	1	4	0	0	1	0	8
	3	1	4	0	0	3	0	0	0	0	8
<i>Delphinium tricornes</i> .....	1	0	4	0	0	0	4	0	0	1	9
	2	0	1	1	0	0	0	0	1	0	3
	3	5	2	0	1	0	0	0	0	0	8
<i>Dicentra canadensis</i> .....	1	0	0	0	0	0	0	0	1	0	1
	2	0	1	0	0	0	0	0	1	0	2
<i>D. cucullaria</i> .....	1	0	1	0	0	0	0	0	0	0	1
<i>Hydrophyllum appendiculatum</i> .....	1	1	5	0	1	1	0	0	0	1	9
	2	0	1	0	5	2	0	0	1	1	10
<i>Pedicularis canadensis</i> .....	1	2	50	0	1	1	0	1	0	1	56
	2	1	7	0	0	0	0	0	0	1	9
	3	0	4	0	1	0	0	0	1	0	6
Total .....		12	84	1	12	12	4	1	8	5	139

- \* 1 = proper pollen only  
 2 = proper + foreign pollen(s)  
 3 = foreign pollen(s) only.

Tab. 5. Composition of floral nectars.

Plant species	Sugars present			
	Dextrose	Fructose	Sucrose	Xylose
<i>Aesculus glabra</i> .....	—	—	+	—
<i>Aquilegia canadensis</i> .....	T	T	+	—
<i>Delphinium tricornes</i> .....	—	+	T	—
<i>Dicentra canadensis</i> .....	—	+	+	+
<i>D. cucullaria</i> .....	T	+	+	—
<i>Mertensia virginica</i> .....	+	+	+	—
<i>Pedicularis canadensis</i> .....	—	+	T	—

T = trace  
+ = present  
— = absent.

Tab. 6. Total sugar content (%) of floral nectars.

Plant species	Mean	Range
<i>Aesculus glabra</i> .....	54.2	44.5–58.5
<i>Aquilegia canadensis</i> .....	24.7	18.9–30.8
<i>Delphinium tricornes</i> .....	43.7	38.8–52.6
<i>Dicentra canadensis</i> .....	16.3	14.4–19.0
<i>D. cucullaria</i> .....	17.8	14.7–20.6
<i>Mertensia virginica</i> .....	38.7	31.4–42.2
<i>Pedicularis canadensis</i> .....	34.9	31.3–41.4

mouth of *Dicentra* and *Aquilegia* corollas and is the ground color of *Aesculus* and *Pedicularis*. Blue-violet is strongly reflected from *Camassia*, *Delphinium* (lower petals and sepals including the spur), *Dicentra*, *Geranium*, *Hydrophyllum*, *Mertensia*, *Phlox*, and *Tradescantia*. *Delphinium* is known to be highly reflective in the ultra-violet (Macior 1975b). All of these flowers are chromatically attractive to bumblebees but may not sustain foraging interest if resources in them are meagre or unavailable to the insects. The red flowers of *Aquilegia* and

*Silene* were pollinated primarily by hummingbirds, which prefer red flowers (Raven 1972) but are not restricted to them (Grant and Grant 1968). They were also frequent pollinators of the purplish blue flowers of *Delphinium*. Since bumblebees are red-blind (Mazokhin-Porshnyakov 1969), flowers which reflect red and blue-violet simultaneously such as those of the blue *Mertensia*; purplish blue *Delphinium*, *Hydrophyllum*, and *Tradescantia*; bluish purple *Phlox*; purple *Geranium*; and reddish purple *Camassia* attract bumblebees primarily, if at all, with the blue-violet component but not with the red component.

3.3. Morphological, ethological, and phenological coadaptations

*Floral structure.* Actinomorphic flowers in this study had nectar freely exposed to foragers (*Camassia*, *Claytonia*, *Hydrophyllum*), concealed between the bases of free petals (*Dentaria*), within the tips of long-spurred petals (*Aquilegia*), or at the base of a long corolla tube (*Mertensia*, *Phlox*, *Silene*).

Tab. 7. Spectral reflectance (%) from flower corollas.

Plant species	Wavelength (nm)									
	415	445	475	505	535	565	595	625	655	685
<i>Aesculus glabra</i> .....	17	25	32	33	44	42	44	42	41	39
<i>Aquilegia canadensis</i> spur .....	18	18	17	14	15	16	21	32	38	49
<i>Aquilegia canadensis</i> mouth .....	25	25	26	35	43	43	43	43	43	43
<i>Camassia scilloides</i> .....	30	30	40	37	22	28	32	32	36	36
<i>Delphinium tricornes</i> spur .....	27	20	17	11	11	9	9	11	19	29
<i>Delphinium tricornes</i> mouth .....	34	34	34	25	37	45	41	47	47	41
<i>Dicentra canadensis</i> .....	29	40	51	46	51	49	49	48	46	51
<i>D. cucullaria</i> .....	19	45	49	47	51	48	48	51	53	49
<i>Geranium maculatum</i> .....	34	44	40	31	23	21	27	36	56	51
<i>Hydrophyllum appendiculatum</i> .....	23	30	31	29	22	19	20	26	34	37
<i>Mertensia virginica</i> .....	29	38	43	33	26	18	18	19	21	42
<i>Pedicularis canadensis</i> galea .....	12	12	13	18	18	16	23	32	37	40
<i>Pedicularis canadensis</i> lower lip .....	22	22	27	37	37	54	56	50	50	39
<i>Phlox divaricata</i> .....	36	38	41	34	30	28	30	40	40	55
<i>Silene virginica</i> .....	15	14	13	12	12	15	29	49	60	54
<i>Tradescantia ohiensis</i> .....	49	45	41	26	22	16	19	27	46	59

Tab. 8. Length (mm) of corolla tubes and spurs.

Plant species	Mean	Range
<i>Delphinium tricornes</i> .....	18.0	16–20
<i>Dicentra canadensis</i> .....	10.1	9–11
<i>D. cucullaria</i> .....	7.4	7– 8
<i>Mertensia virginica</i> .....	12.8	12–15
<i>Pedicularis canadensis</i> .....	10.7	10–12

Zygomorphic flowers consistently concealed nectar. *Delphinium* secretes nectar in two upper petal spurs surrounded by a sheathing sepal. *Dicentra* nectar is contained in two spurred outer petals, and its anthers are concealed between the tips of two inner petals. *Pedicularis* nectar is at the base of a long corolla tube, and its anthers are contained in the tip of the galea. *Aesculus* nectar is at the base of a short corolla tube, and its anthers are exposed. The length of narrow, deep tubes and spurs from which nectar is removed by bumblebees ranged from 7.4 mm in *Dicentra cucullaria* to 18.0 mm in *Delphinium* (Tab. 8). All length ranges are mutually distinct except for that of *Pedicularis*, which overlaps the range of *Dicentra canadensis*.

**Structure of insect probosces.** Nectar is gathered by bumblebees by extension of the glossa and its protrusion by forward rotation of the base of the prementum at the mandibular hinge so that the combined length of prementum and glossa is available for insertion into a flower. The total effective foraging length is determined by adding the length of the head and even part of the thorax if the mouth of the corolla is sufficiently wide to accommodate them. Measured proboscis lengths (Tab. 9), therefore, tend to be less than the effective foraging length on particular flowers but are useful for comparing nectar-foraging capacity of *Bombus* species. The species with the shortest proboscis (*B. affinis*) is the only corolla perforator in the area. Mean proboscis lengths of other species range from 10.36 mm in *B. griseocollis* to 12.69 mm in *B. nevadensis auricomus*, and their dimensional ranges overlap considerably. Furthermore there is a very close similarity between dimensions of pairs of species: *B. griseocollis* and *B. impatiens*, *B. nevadensis auricomus* and *B. pennsylvanicus*, and *B. perplexus* and *B. vagans*. The range of *B. fervidus* is close to that of *B. nevadensis auricomus*, while that of *B. bimaculatus* is relatively distinct from all the others.

**Pollinator behavior.** On open, actinomorphic flowers pollinators randomly traverse the flower contacting stigmas and anthers while foraging. On *Aquilegia* hummingbirds hover beneath the flower and insert their tongues into the spurred petals from below. Bumblebee pollinators of *Aquilegia* grasp the exerted anthers and stigmas and collect pollen or occasionally probe the

spurs for nectar from below. *Bombus affinis* does not do this, but it is effective in pollination when it lands on the essential parts before climbing to the tips of the spurs where it removes nectar by perforation.

The zygomorphic flowers of *Delphinium* are pollinated sternotribically by the heads of bumblebees and hummingbirds (Macior 1975b) as they enter the mouth of the nectariferous, spurred petals and depress the two lower petals, which cover the anthers and stigmas. *Dicentra* species are pollinated by bumblebees contacting anthers and stigmas after deflecting the inner protective petals (Macior 1970a) as they probe the spurred petals for nectar.

**Phenology of anthesis.** All plants studied confined their blooming to the months of April and May except *Aquilegia*, which continued into early June. All species grow on the forest floor beneath large, deciduous trees except *Aquilegia*, which prefers open borders of these woodlands, and *Aesculus*, a tree. The blooming periods for plant species are listed in Tab. 10 according to sequence of bloom beginning with the earliest.

The tree canopy begins expansion at the end of April and is completed by mid-May. In 1973, for example, canopy cover was estimated at 20% on 29 April and 80% on 11 May.

Blooming periods varied from one season to another. The blooming period was earliest in 1973 for all species recorded, but in 1971 and 1972 blooming periods were not consistent for all species. Thus *Delphinium* and *Pedicularis* bloomed earlier in 1972 than in 1971, while *Dicentra canadensis*, *D. cucullaria*, and *Mertensia* bloomed earlier in 1971 than in 1972. Variations also occurred in the duration of bloom between plant species and within a species in different seasons. In general, the extension of more favorable weather prolonged the blooming period, while periods of inclement weather either delayed flowering or shortened the blooming period. The most ephemeral species were *Hepatica* and *Sanguinaria*, which bloomed for less than two weeks, and *Dicentra* species, which bloomed for about two weeks. All other species had blooming periods ranging from more than two weeks to four weeks. Among the earliest blooming species were *Hepatica*, *Dentaria*,

Tab. 9. Length (mm) of probosces of *Bombus* queens.

<i>Bombus</i> species	Mean	Range	S.D.
<i>affinis</i> .....	9.42	8.87–10.09	0.31
<i>bimaculatus</i> .....	11.09	10.53–12.19	0.38
<i>fervidus</i> .....	12.25	11.49–13.66	0.46
<i>griseocollis</i> .....	10.36	9.39–11.14	0.43
<i>impatiens</i> .....	10.54	9.83–11.14	0.33
<i>nevadensis auricomus</i> ....	12.69	11.05–13.57	0.43
<i>pennsylvanicus</i> .....	12.60	11.14–13.57	0.42
<i>perplexus</i> .....	10.92	9.50–11.92	0.61
<i>vagans</i> .....	10.93	9.66–11.49	0.35



Tab. 10. Blooming phenologies of plant species.

Plant species	First flowers	Full bloom	Last flowers	Season
<i>Hepatica acutiloba</i> .....	5 April	10 April	15 April	1972
<i>Dentaria laciniata</i> .....	8 April	18 April	28 April	1972
	5 April	13 April	23 April	1973
<i>Claytonia virginica</i> .....	14 April	1 May	18 May	1972
	7 April	20 April	30 April	1973
<i>Dicentra cucullaria</i> .....	13 April	17 April	27 April	1971
	14 April	22 April	30 April	1972
	7 April	13 April	21 April	1973
<i>Anemonella thalictroides</i> .....	8 April	18 April	28 April	1972
<i>Sanguinaria canadensis</i> .....	10 April	13 April	15 April	1972
<i>Mertensia virginica</i> .....	12 April	17 April	29 April	1971
	15 April	26 April	7 May	1972
	10 April	18 April	25 April	1973
<i>Dicentra canadensis</i> .....	18 April	24 April	30 April	1971
	23 April	30 April	7 May	1972
	10 April	20 April	26 April	1973
<i>Corydalis flavula</i> .....	15 April	24 April	30 April	1971
	14 April	21 April	30 April	1972
<i>Aesculus glabra</i> .....	19 April	8 May	20 May	1971
	22 April	5 May	19 May	1972
	15 April	10 May	21 May	1973
<i>Delphinium tricornes</i> .....	7 May	14 May	21 May	1971
	26 April	8 May	19 May	1972
	15 April	4 May	15 May	1973
<i>Trillium grandiflorum</i> .....	18 April	24 April	30 April	1972
<i>Pedicularis canadensis</i> .....	1 May	8 May	19 May	1971
	26 April	6 May	16 May	1972
	18 April	28 April	11 May	1973
<i>Silene virginica</i> .....	28 April	7 May	16 May	1972
	28 April	12 May	28 May	1973
<i>Camassia scilloides</i> .....	29 April	12 May	24 May	1972
	28 April	7 May	14 May	1973
<i>Aquilegia canadensis</i> .....	12 May	20 May	27 May	1971
	4 May	13 May	23 May	1972
	4 May	12 May	7 June	1973
<i>Hydrophyllum appendiculatum</i> .....	10 May	15 May	20 May	1972
	7 May	15 May	25 May	1973

*Claytonia*, and *Anemonella*, which are neither primarily nor regularly pollinated by bumblebees. The latest blooming species included those which are pollinated regularly (*Delphinium* and *Pedicularis*) or almost exclusively (*Silene* and *Aquilegia*) by ruby-throated hummingbirds.

**Phenology of pollinator activity.** The ruby-throated hummingbird is the only bird pollinator in the research area. It was observed pollinating *Delphinium*, *Pedicularis*, *Silene*, and *Aquilegia* and was first observed on 8 May 1971, 5 May 1972, and 4 May 1973. It is a secondary pollinator of *Delphinium* and *Pedicularis*, the primary pollinator of *Aquilegia*, and the sole pollinator observed on *Silene*. Because of its late arrival it is not available for pollinating *Dicentra* and *Mertensia*, which conceal nectar as do other flowers regularly pollinated by hummingbirds.

The foraging season of bumblebees begins with the consistently earliest species observed or hunting nesting sites, viz., *Bombus affinis*, *B. bimaculatus*, *B. griseocol-*

*lis*, *B. impatiens*, and *B. perplexus*. *Bombus fervidus* and *B. vagans* varied from one season to another, while *B. nevadensis auricomus* and *B. pennsylvanicus* are generally later emerging species (Fye and Medler 1954, Medler and Carney 1963, Macior 1968a).

As determined by their carrying corbicular pollen loads, the earliest bumblebee species to establish nests were *B. bimaculatus* and *B. perplexus*, which were also the most abundant pollinators (Tab. 2) of the earliest bumblebee-pollinated plants, viz., *Dicentra cucullaria* and *Mertensia*, *Bombus bimaculatus*, however, was also the most frequent pollinator of *Pedicularis*, which blooms late in the season. *Bombus impatiens* was the next earliest to nest, and after *B. bimaculatus*, was the most abundant pollinator of *Dicentra canadensis*, the next earliest bumblebee-pollinated plant species. *Bombus nevadensis auricomus* was late to establish nests and was the most frequent pollinator of *Delphinium*, a later blooming plant. About the last bumblebee to nest was *B. vagans*, which was the most abundant pollinator of *Hydrophyllum*, the last species to bloom.

#### 4. Discussion

In general, there is a correspondence of chronologies of blooming and pollination in the vernal flora, but there is no exclusive conspecific adaptation involving bumblebee queens, which exhibit relatively little foraging fidelity to particular plant species. Simultaneous flowering and insect emergence is a direct consequence of the influence of the same microclimatic factors on plants and insects (Siivonen 1942, Vezina and Grandtner 1965, Jackson 1966).

Floral diversity among vernal species is the direct consequence of the interaction between floral expression and pollinator selection. Nevertheless, no single structural, behavioral, or environmental characteristic of flower or pollinator can be identified as being responsible for the plant-pollinator association. Since color in itself is not an inducement to successive floral visits, the behavior of the visitor must be reinforced by other floral characteristics. There is no obvious relationship of differences in nectar concentrations related to blooming phenologies or floral morphology. The primary characteristic of nectar as a pollinator attractant appears to be a combination of its quantity and availability in relation to specific foragers. Availability, in turn, is dependent upon accessibility and rate of production of nectar. The accessibility of nectar to specific foragers is an interrelational function of form and behavior of flowers and pollinating foragers. Among *Bombus* species differences in proboscis length are definitely associated with parameters of phenology and floral morphology. In the vernal pollination system there is obviously a close coadaptive integration of the form and behavior of flowers, their pollinators, and their phenologies.

In the vernal flora there is no conclusive evidence that competition for pollinators is effective in excluding plant species from the ecosystem.

The reproductive success and wide geographic dispersion of vernal angiosperms throughout the deciduous forests of eastern North America reflect the high degree of coordination existing in their pollination system. The plant-pollinator community exhibits a dynamic balance of morphological, behavioral, and phenological factors so closely interdependent that a change in any one is likely to affect the entire system. Pollination systems are highly coordinated associations of plants and animals evolving through coadaptive integration.

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