

Competition for Pollinators as a Stimulus for the Evolution of Flowering Time

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## Competition for pollinators as a stimulus for the evolution of flowering time

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A study was made of the activities of pollinating insects in relation to the flowering phenology of plants near Banff, Alberta in 1968. From snow-melting time (early May) to the end of May, pollinating insects were abundant and competed actively for relatively scarce pollen and nectar resources. Then, in early June some “cornucopian species” (*Salix* spp. and *Taraxacum officinale* L.) began flowering abundantly offering virtually unlimited supplies of nectar and pollen. Pollinating insects abandoned the spring flowers and were attracted to these cornucopian species. It is postulated that in the presence of cornucopian species natural selection would favour the evolution of earlier- or later-flowering populations of all those species that compete with the cornucopians for pollinators. It was found that in the spring, insects competed for flowers but that after the cornucopian species had completed their flowering (throughout the summer), flowers competed for pollinating insects.

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Исследовали активность насекомых-опылителей в зависимости от фенологии цветения растений в районе Банфф (Альберта) в 1968 г. С момента таяния снега (в начале мая) до конца мая насекомые встречались в большом количестве, и среди опылителей возникала конкуренция из-за пыльцы и нектара, т.к. цветущих растений было немного. Затем в начале июня начинают цвести некоторые “изобильные” виды с большим количеством цветов (*Salix* spp. и *Taraxacum officinale* L.), создавая неограниченные запасы пыльцы и нектара. Насекомые-опылители начинали избегать весенние цветы, привлекаясь больше к этим “изобильным” видам. Предполагается, что при цветении этих “изобильных” растений естественный отбор стимулирует эволюцию видов, цветущих раньше или позднее “изобильных” растений и конкурирующих с последними из-за насекомых-опылителей. Установлено, что весной насекомые конкурируют из-за цветов, но в период цветения изобильных цветами растений (в течение всего лета) цветы конкурируют из-за насекомых-опылителей.

## 1. Introduction

It is common knowledge that most plant species do not flower at the same time. In temperate regions, flowering usually starts even before the spring snows have completely melted and then continues in species after species until late fall, although, of course, the flowering times of many species overlap to various degrees. This paper examines some aspects of the abundance and behaviour of insect pollinators in affecting this wide divergence in flowering phenology. The ideas presented here originated while making field studies of pollinator activities in relation to phenology of flowering of entomophilous species in the Bow River Valley in Banff National Park, Alberta, Canada, during the spring and summer of 1968.

The main thesis examined in this paper is that a principal guiding force causing different flowering times in wild plant species has been the differential ability of flowers to compete for available pollinator resources of an area. When two species come into direct competition for pollinators, one of them often competes more successfully than the other for a particular group of insects or for the most common insects in the area. Those flowers of the poorer competitor that open at the peak flowering period of the more efficient competitor will tend to remain unvisited and natural selection will favour those genotypes of the former that have the potential for a different flowering time (selection might also favour self-pollination or agamospermy).

## 2. Materials and methods

A total of about 2,600 man-hours (two, sometimes three observers) was spent in the field studying insects and flowers beginning 9 May and ending 4 September. The number of man-hours does not include rainy or very cool days when most flower-visiting insects are inactive. Such days accounted for about one-third of the summer. Observations usually began at 8 AM and terminated between 5 and 6 PM. Two observers working more or less together were usually in the field.

Flower-visiting insects were captured with a conventional insect net or with an aspirator.

Every species of flowering plant whether visited by insects or not was examined in the field with a binocular microscope to determine the nectar and pollen availability in the flowers. In each species from 10 up to several dozen flowers, ranging in maturity from the mature bud stage to senescence, were dissected and carefully examined. The precise details of anthesis were described in relation to another project on pollination biology. Careful watch was kept for evidence of insect visitation to the flowers; for example smudged or collected pollen, flower mutilation, etc. Records on manner of presentation and on the quantity of pollen were also kept. Therefore, an accurate, although perhaps

subjective, knowledge of the relative abundance and availability of both pollen and nectar on all plant species was in hand at all times during the study period. Vouchers of all plant species studied are deposited at the herbarium, Plant Research Institute, Department of Agriculture, Ottawa (DAO); insect specimens are deposited at the Canadian National Collection of Insects (CNC), Entomology Research Institute, Department of Agriculture, Ottawa.

## 3. Results

The forests of the Bow River lowlands in the study area are relatively open with many grassy meadows and are considerably disturbed by human activities, fire and elk grazing. The dominant trees are *Pinus contorta* Loudon and *Populus tremuloides* Michx. with a scattering of *Picea engelmannii* Parry and, in the low wet areas, *Populus balsamifera* L.

The taxa listed in Tab. 1 and 2 include virtually all the entomophilous spring species of the region that have their peak flowering periods prior to 15 June. These taxa produce nearly all of the pollen and nectar resources used by insect pollinators in this area between snow-melting time and mid-June. Six of these taxa, *Primula mistassinica*, *Arctostaphylos uva-ursi*, various *Salix* spp., *Androsace chamaejasme*, *Dodecatheon radicum* and *Taraxacum officinale*, were sufficiently common and flowered at approximately the same time so that comparative observations on flower-pollinator competition could be made. The remainder of the taxa listed in the tables were either rare or extremely local in distribution in the area. They are, however, included to show the nature of their breeding system and because their phenology and pollination biology have a bearing on the interpretation of pollinator activity on other species.

It was discovered that, in the Banff region, three and probably four overlapping but distinctive stages in pollinator-flower competition patterns could be recognized and that these stages replaced each other as the season progressed. The essential elements of the four stages are as follows:

### Stage 1

From snow-melting time to about 10 June. Relatively few entomophilous plant species are in flower and pollinators are usually competing for a relatively scarce nectar and pollen resource.

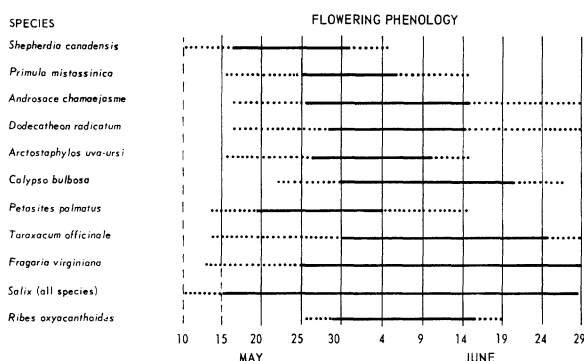
### Stage 2

From about 5 June to 3 July. Several plant taxa that are here called "cornucopian species" (see below) come into full flower. Virtually all pollinators strongly prefer the almost unlimited offerings of these species to other species growing in the vicinity.

Tab. 1. Breeding systems, nectar and pollen resources, and principal pollinators of the entomophilous spring flowers in the Banff region in 1968.

	Breeding system	Principal reward offered	Pollinators
<i>Shepherdia canadensis</i> (L.) Nutt.	dioecious	pollen only	Mainly Diptera (syrphids), few Hymenoptera collecting pollen.
<i>Primula mistassinica</i> Michx.	Heterostyled (distyly); other species have a self-incompatibility system. (Fryxell 1957)	pollen nectar not examined	small Hymenoptera, Diptera, small butterflies.
<i>Androsace chamaejasme</i> Host	hermaphroditic apparently self-incompatible	pollen nectar	syrphids and other Diptera small bees
<i>Dodecatheon radiculatum</i> Greene	Self-incompatible	pollen no nectar	bumblebees only
<i>Arctostaphylos uva-ursi</i> L.	self-compatible	nectar	bumblebees only
<i>Calypso bulbosa</i> L.	self-compatible	none (scent only)	bumblebees only
<i>Petasites palmatus</i> (Ait.) A. Gray	gynodioecious and self-incompatible	nectar pollen	hawk moths, wasps syrphids
<i>Taraxacum officinale</i> L.	apomictic	nectar pollen	virtually all pollinators
<i>Fragaria virginiana</i> Duchesne	not known but other species are self-incompatible or apomictic (Fryxell 1957)	both nectar and pollen	Mainly bumblebees some syrphids
<i>Salix</i> (various species)	dioecious	pollen and nectar	virtually all pollinators
<i>Ribes oxycanthoides</i> L.	not known but other species self-incompatible (Fryxell 1957).	nectar pollen	wasps, bumblebees no information

Tab. 2. Phenology of the principal nectar- and pollen-producing spring flowers in the Banff region, 1968.



<sup>1</sup> Flowers of this species were common in many areas in the region. However, they contained no obvious nectar and the pollinia were not sought by any insect.

### Stage 3

From about 28 June to 1 September. Up to many dozen of plant species are in flower; these grow in many habitats throughout the valley. Nectar and pollen resources are abundant but pollinators *relatively* scarce. Nearly all entomophilous plant species are competing for pollinators.

### Stage 4

Early September to the end of the flowering season. Pollinators are competing for a scarce nectar and pollen resource (assumed; no field evidence available).

In Stage 1 it seemed obvious that, in general, the demand for nectar and pollen resources by the insects much exceeded the supply. This was evident from local

abundance of various pollinators on available plant species, from the active way in which some insects, especially bumble bees, appeared to seek out flowers, and, in some cases, by the intensity or frenzy of the activities, especially on *Dodecatheon*. It was common, for example, to see insects busily engaged in visiting populations of *Salix*, *Dodecatheon* and *Arctostaphylos* in colonies in which most flowers were either damaged or mutilated by bumble bees or bore much evidence of repeated visits by insects. Field examination of flowers in such populations under a binocular microscope showed that most of the nectar and pollen had been collected. At this time (late May and early June) it was relatively easy to capture pollinators even if populations of plants were small. Then, during the week that followed June 5 (the start of Stage 2) a number of cornucopian species (CS's) rapidly came into flower. The most widespread of these was *Taraxacum officinale*, the common dandelion. Large populations of this species began to dominate the roadsides and meadows throughout the lowlands and a number of *Salix* species also began to flower profusely along the Bow River. An important point to note is that within a period of about a week *Taraxacum* or *Salix* began flowering to the extent that the supplies of pollen and nectar offered were essentially inexhaustible. These cornucopian species are characterized by the following combination of features. They are abundant, their flowers are sweetly scented and offer nectar or pollen (or both) of such popularity, in such abundance and in such a convenient manner as to cause a wide spectrum of pollinators to prefer visiting them rather than those

of almost all other species growing in the area. In the case of *Taraxacum*, the flowers have an additional attractance feature, namely, the outer ring of corollas reflects ultraviolet light intensely (Mazokhin-Porshnyakov 1969, Mosquin unpubl.).

With the coming into flower of *Taraxacum* and *Salix*, populations of *Dodecatheon*, *Primula*, *Androsace* and *Arctostaphylos* became virtually abandoned by pollinators which had now presumably gone to obtain the offerings of the CS's, *Taraxacum* and *Salix*. Then at the end of June as flowering of both *Taraxacum* and *Salix* populations began to wane, a third kind of competition phenomenon emerged (Stage 3). This was brought about by the fact that while *Taraxacum* and *Salix* were at the peak of their flowering, many dozens of other plant species had come into flower in many habitats. Thus, by 30 June it often became very difficult to record large numbers of pollinators on any one species. Presumably, pollinators were now dispersed widely over the landscape, a state of affairs that continued with few exceptions until the termination of observations in early September. Stage 3 of the "summer phenomenon" is one in which up to several dozen species are in full flower at one time and nearly all of these contain large stores of nectar and pollen which usually remain uncollected by insects. For example, in *Menziesia glabella* A. Gray, a very common shrub of dense Engelmann spruce forests of the middle elevations, the flowers were one-fourth to one-half filled with nectar, and the nectar is readily accessible. Yet, in many hours of watching large populations of this species only occasional (two or three) bumble bees or other insects were seen visiting the flowers. An abundance of ungathered nectar was also found in many summer-flowering species such as *Fragaria virginiana*, *Vaccinium* spp., *Oxytropis* spp., *Astragalus* spp., *Castilleja miniata* Douglas, *Potentilla gracilis* Douglas, *Epilobium angustifolium* L. and others.

#### 4. Discussion

Conditions favouring a shift in flowering time will naturally vary depending on the amount and kind of competition for pollinators that exists between two or more species. Natural selection will be especially effective in forcing a shift when one of the two or more species is a cornucopian species. In the Banff region such selection apparently operates strongly in early summer in response to *Taraxacum* and *Salix* which flower so abundantly in mid-June. It is postulated that cornucopian species force the flowering peaks of poorer competitors to occur either earlier or later than their own peak flowering times. Another effective way to escape from the selection pressures created by the presence of cornucopian species would be to revert to non-outcrossing methods of reproduction such as self-pollination or apomixis, but it is realized that there may be other causes for the evolution of these forms of reproduction.

There seems little doubt that throughout the "summer phenomenon" period, plant populations were competing for a relatively scarce pollinator resource. Such competition may be widespread in nature. For example, Hocking (1968) in his studies of insect-flower associations in extreme northern Canada found that "there was competition among plants for pollinators rather than among pollinating insects for nectar". At this time of year a large variety of flower types and breeding systems are present in a wide assortment of families in many habitats. Given such a large pollen and nectar supply and a relative scarcity of pollinators, what could be the possible effects on floral mechanisms and breeding systems in other species? One solution to pollinator scarcity is to escape competition by evolving specialized flowers such as occur in *Oxytropis* and *Castilleja*, both of which are rich in nectar but can be pollinated only by long-tongued bees, hawk moths or hummingbirds. Large, specialized flowers would offer special advantages to long-tongued pollinators and, therefore, command the attention of such animals. A second method of escape would be to reduce the need for cross-pollination by reverting to self-pollination or apomixis. A third solution would be to compete more efficiently and hence to flower profusely or otherwise develop a large visual target and at the same time offer large stores of readily accessible nectar or large amounts of pollen. All three of these solutions to pollinator scarcity occur in the species of the Banff area during Stage 3, although as stated above the presence of certain floral structures in some species probably has other explanations.

In the Banff region the principal cornucopian species is the introduced *Taraxacum officinale*. It seems clear that prior to the time of its introduction, only various *Salix* species played the role of CS's. It is probable that, together, *Salix* and *Taraxacum* species react only slightly if at all to the poorer competitors but, rather the latter respond to the former. Since both *Salix* and *Taraxacum* produce nectar and pollen in great abundance, and since the populations themselves are common, there would appear to be little selection pressure exerted on such species to alter their flowering phenology. In contrast, in the poorer competitors, selection pressure to alter flowering would be strong. Furthermore, since *Taraxacum* is apomictic in many regions (Fryxell 1957) and also in the Banff region where it sets full seed when isolated from insects (Mosquin unpubl.), this would also indicate that it lacks a good mechanism for responding to pollinator pressures.

Of considerable theoretical interest is the fact that those spring species flowering earlier than the CS's have the kind of genetic systems that provide for a great deal of outcrossing (Mosquin 1966), and, therefore, for the creation and maintenance of high levels of heterozygosity. These early-flowering species are either dioecious, heterostyled, self-incompatible, or gynodioecious, or they combine several of these features (Tab. 1). In the case

of *Arctostaphylos* and *Calypso*, the plants are self-compatible (Mosquin 1970 and unpubl.) but probably are often outcrossed in view of the visits by bumble bees. In comparison, mechanisms that would promote homozygosity, such as self-pollination are absent from the spring flora. The fact that so many of the components of the genetic systems that characterize the spring plants are of the flexible type suggests that only such systems can respond effectively to selection and yet retain the advantage of being pollinated by the abundant pollinators available at this time of the year. It certainly does not seem to be a coincidence that systems that would promote homozygosity are absent from the spring flora.

One factor that would influence the insect-flower competition patterns is the flower constancy of bees, a phenomenon discussed by Grant (1950). Flower constancy means that a bee, once it becomes accustomed to visiting one species of flower in an area will continue to visit that species to the exclusion of flowers of other species nearby. The more flower constant a pollinator is, the less likely will competition of plants for pollinators lead to a divergence in flowering time, since "constant" pollinators do not readily abandon one species for another. Honey-bees are strongly flower constant while bumble bees and most wild bees are not. Honeybees were not present in the study area at Banff. Bumble bees and other wild bees often visit several or more species of plant in a single foray although strong flower constancy seems to be the rule when a cornucopian species is providing the reward.

Abandonment of one source of nectar or pollen for another has been described by Free (1968) between dandelions and apple trees and between dandelions and plum trees in commercial orchards in England. In a paper describing the effects of competition of different plant species for pollinators of the wild bee genus *Megachile* in southern Alberta, Hobbs and Lilly (1954) state that "a preferred source (nectar and pollen) early in the season may be abandoned for another source later on". They cite examples showing that wild bees have strong preferences although the preference is determined to an important degree by the distance of the bee's nest from the source of nectar or pollen. So the general pattern in the wild is probably one in which bees are

normally relatively inconstant, a phenomenon that would promote divergence in flowering time.

It seems reasonable that fall-flowering species might come under selection pressures that would force later flowering. Pollinators in the fall are often very common and active; they would compete actively for the few plant species still in flower at this time. However, the fall patterns would be complicated by selection for earlier flowering in order to insure seed ripening prior to killing frosts. Since observations at Banff terminated on 4 September, no conclusions concerning fall patterns can be made.

The presence of large stores of ungathered nectar in numerous species during the summer months suggests that there exists an open niche for the evolution of new species of pollinators or for the increase in populations of already existing ones.

## 5. Acknowledgements

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## References

- FREE, J. B. 1968. Dandelions as a competitor to fruit trees for bee visits. – *J. Appl. Ecol.* 5: 169–178.
- FRYXELL, P. A. 1957. Mode of reproduction of higher plants. – *Bot. Rev.* 23: 135–233.
- GRANT, V. 1950. The flower constancy of bees. – *Bot. Rev.* 16: 379–398.
- HOBBS, G. A. and LILLY, C. E. 1954. Ecology of species of *Megachile* Latreille in the mixed prairie region of southern Alberta with special reference to pollination of alfalfa. – *Ecology* 35: 453–462.
- HOCKING, B. 1968. Insect-flower associations in the high Arctic with special reference to nectar. – *Oikos* 19: 359–387.
- MAZOKHIN-PORSHNYAKOV, G. A. 1969. Insect vision. – Plenum Press, N.Y. 306 pp.
- MOSQUIN, T. 1966. Reproductive specialization as a factor in the evolution of the Canadian flora. – In: *The Evolution of Canada's Flora*, ed. R. L. Taylor and R. A. Ludwig, University of Toronto Press. 137 pp.
- 1970. The reproductive biology of *Calypso bulbosa* (Orchidaceae). – *Can. Field-Nat.* 84: 291–296.