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## Phenological spread in flowering of bumblebee-pollinated plants

ESA RANTA, ILKKA TERÄS and HANS LUNDBERG

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The flowering phenology was studied in bumblebee-pollinated plants in southern Finland (Puumala) and northern Sweden (Abisko). All the plant species which had more than 10 records of bumblebee visits during a summer were included (30 at Puumala, 25 at Abisko). Analysis of pollinator similarity yielded 7 clusters of species at Puumala (2–8 species in each) and 6 clusters at Abisko (2–4 species in each). Most of the species pairs having high overlap in pollinators did not show overlap in their flowering period. However, in only a few cases were the observed spacings of flowering peaks among the cluster members wider than could be expected if the timing of flowering was random (in 2 of the 7 clusters at Puumala, and in 3 of the 6 clusters at Abisko). The number of high-overlap species pairs was 12 (expected 22) at Puumala and 8 (expected 15) at Abisko. Possible ways of pollinator partitioning in these plants are discussed.

Key words: flowering phenology, bumblebees, pollination, niche relations, community structure

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### INTRODUCTION

In boreal and arctic regions there are practically no other pollinators than insects. In a flowering field with a number of insect-pollinated plant species much of the spatial distribution of the plants is undoubtedly due to species-specific reactions to the abiotic conditions. On the other hand, the time of flowering during the summer, differences in pollen dehiscence, nectar production and daily times of flowering may be adaptations to a certain subset of the available pollinators.

A number of studies have demonstrated the ways of coadaptation between plants and pollinators, the mechanism being preference and flower constancy of pollinators (Grant 1950, Manning 1956, Free 1966, Heinrich 1975). Pollinator specialization is an adaptation in evolutionary time, flower constancy is an adaptation in ecological time (Levin 1978). The

rewards given by the plants encourage flower constancy and thus increase the probability of cross-pollination. Many authors have shown that plants compete for pollinators (e.g., Hocking 1968, Levin & Anderson 1970, Mosquin 1971, Pojar 1974, Reader 1975, Lack 1976, Shemske et al. 1978, Thomson 1978, Faegri & van der Pijl 1979, Pleasants 1980, Zimmerman 1980, Bierzychudek 1981). To avoid competition, insect-pollinated plants may thus be expected to reduce overlap in flowering periods (Mosquin 1971), but they can also, for instance, specialize to subsets of pollinators or change the daily time of flowering (Parrish & Bazzaz 1979).

Our aim is to analyse niche relations (measured in terms of pollinator services) in spatially coexisting plant species, and to study to what extent the partitioning of pollinators among plant species is accomplished by phenological spread in flowering. The pollinators in our study are bumblebees (*Bombus* spp.,

Apidae) and the material consists of data on plant-bumblebee interactions in two flowering plant communities in Fennoscandia.

## MATERIAL AND METHODS

The material originates from field work on flower visits paid by bumblebees in two Fennoscandian bumblebee communities, the one in southern Finland (Puumala, 61° 36'N, 27° 58'E) and the other in northern Sweden (Abisko, 68°22'N, 18°47'E). The ecology of the bumblebee communities in these areas has been analysed by Ranta et al. (1981). Thus, only a brief description of the areas is given here. The study area at Puumala (alt. 80–100 m) was an abandoned field (ca. 2 ha) bordered by *Vaccinium*-type pine forest and a farmhouse yard. Field observations of flower visits of bumblebees (queens, workers and males) were made 3–4 times a week from 29 May to 27 August 1968 on test squares (5 x 5 m) and along a transect circling the field (see Teräs 1976 for more details). The study area at Abisko comprised diverse habitats on the slope of Mt Njulla from 340 m to 1050 m above sea level. Three permanent transects (totalling ca. 4 km) were established on the slope, and the material on flower visits by bumblebees was collected by walking along the transects twice a week from 27 May to 15 August 1972. Two 5 x 5 m test squares were also established (see Lundberg & Ranta 1980, Ranta & Lundberg 1981 for more details).

In both areas, notes were made on the phenology of the plant species visited by bumblebees, viz., the beginning and end of flowering and the period when more than 50% of the population was in flower. The visiting frequencies of bumblebee species (sexes and castes) were also recorded for each flower species.

In Puumala altogether 59 plant species were visited by bumblebees (9 species, Teräs 1976) and the total number of observations was ca. 5900. The corresponding figures at Abisko were 50 plant species, 9 bumblebee species and ca. 1700 observations (Ranta & Lundberg 1980). For the purposes of the present study we have, however, excluded all the flowers that had less than 10 observations of flower visits by bumblebees. Thus, our data consist of 30 plant species and ca. 5800 observations at Puumala, and of 25 plant species and ca. 1600 observations at Abisko (Table 1).

The pollinator similarity between the flower species *i* and *j* was calculated by the percentage similarity method

$$PS_{ij} = \sum_h \min(p_{ih}, p_{jh}),$$

where  $p_{ih}$  is the proportion of the  $h^{\text{th}}$  pollinator in the visits of all the pollinators to the  $i^{\text{th}}$  plant species and  $p_{jh}$  is the corresponding value for the  $j^{\text{th}}$  plant species. The closer the value of  $PS_{ij}$  is to unity, the more similar are the flower species for their bumblebee pollinators ( $PS_{ij}$  ranges from 0 to 1). The similarity matrices (435 items at Puumala and 300 at Abisko) were then reduced to dendrograms (group average method; Sneath & Sokal 1973) to reveal possible clusters of similar species.

## RESULTS

The plant species included in this study are listed in Table 1 together with the numbers of pollinating bumblebee species (sexes and castes separated) and the total number of visits. A complete picture of the flowering pattern of these plant species can be found in Ranta et al. (1981: Fig. 1). The following plant species are shared by the two communities: *Geranium sylvaticum*, *Geum rivale* and *Solidago virgaurea* (*Epilobium angustifolium*, *Vaccinium myrtillus* and *V. vitis-idaea* grew at Puumala, too, but had less than ten records of visits by bumblebees).

All the plant species in this study are visited by at least two, frequently by more, bumblebee pollinators: when the sexes and castes are considered separately, the mean of the pollinators for a plant species was 8.5 (S.D. 5.0) at Puumala and 8.7 (S.D. 4.9) at Abisko. The records of the distances between the midpoints of the flowering periods (more than 50% of the plant population in flower) of neighbouring plant species gave a community mean of 3.2 days at Puumala and 2.5 days at Abisko. When the corresponding number of flowering midpoints of plant species were allocated at random over the flowering period (93 days at Puumala, 60 days at Abisko) in each community, and the mean of 100 randomizations was then calculated as above, the expected distance was 3.0 days (S.D. 0.14) at Puumala and 2.3 days (S.D. 0.10) at Abisko. The difference between the observed and expected values at Abisko is suggestive ( $t=1.98$ ,  $p<0.1$ ) and provides modest support for the interpretation that the flowering peaks in this community are evenly distributed.

The overall mean of the pairwise pollinator similarities between the plant species was 0.495 at Puumala and 0.443 at Abisko (Fig. 1). The level of similarity chosen for separating the species clusters is the mean plus one standard deviation (0.720 for Puumala and 0.676 for Abisko). All the species groups above this level have been included in the analyses below. The flower community at Puumala clustered into 7 groups (PA-PG, Fig. 1), each comprising 2 to 8 species. The corresponding figures at Abisko were 6 groups (AA-AF, Fig. 1) with 2 to 4 species.

The hypothesis tested here is that diffuse competition (see MacArthur 1972) for pollina-

Table 1. List of plant species visited by bumblebees in the two study areas. Only the species having a frequency  $\geq 10$  are included (f= frequency of visits, number of bumblebee pollinators: Q= queens, W= workers, M= males are also indicated). Abbreviations of species names are given.

| Abbrev.        | f  | Q           | W | M | Abbrev.       | f        | Q  | W           | M |   |   |
|----------------|--|-------------|---|---|---------------|----------|--|-------------|---|---|---|
| <b>PUUMALA</b> |  |             |   |   | <b>ABISKO</b> |          |  |             |   |   |   |
| Asyl           | <i>Angelica sylvestris</i> L.              | 23          | 1 | 3 | -             | Apol     | <i>Andromeda polifolia</i> L.              | 27          | 6 | 2 | - |
| Cvul           | <i>Calluna vulgaris</i> (L.) Hull          | 135         | 1 | 3 | 2             | Aarc     | <i>Angelica archangelica</i> L.            | 41          | 4 | 6 | 2 |
| Cglo           | <i>Campanula glomerata</i> L.              | 12          | - | 3 | -             | ARal     | <i>Arctostaphylos alpina</i> (L.) Sprengel | 18          | 5 | 1 | - |
| Csca           | <i>Centaurea scabiosa</i> L.               | 26          | 2 | 5 | -             | ASal     | <i>Astragalus alpinus</i> L.               | 300         | 8 | 6 | 5 |
| Chel           | <i>Cirsium helenioides</i> (L.) Hill       | 59          | 6 | 5 | 3             | Balp     | <i>Bartsia alpina</i> L.                   | 18          | 3 | 4 | 1 |
| Clpa           | <i>Cirsium palustre</i> (L.) Scop.         | 361         | 5 | 7 | 6             | Ctet     | <i>Cassiope tetragona</i> (L.) D. Don      | 15          | 1 | 1 | - |
| Esp.           | <i>Euphrasia</i> sp.                       | 22          | - | 2 | -             | Eang     | <i>Epilobium angustifolium</i> L.          | 82          | 2 | 4 | 3 |
| Fulm           | <i>Filipendula ulmaria</i> (L.) Maxim      | 23          | 1 | 3 | -             | CRpa     | <i>Crepis paludosa</i> (L.) Moench         | 14          | - | 4 | 3 |
| Gsyl           | <i>Geranium sylvaticum</i> L.              | 23          | 4 | 4 | -             | Dlap     | <i>Diapensia lapponica</i> L.              | 30          | 6 | - | - |
| Griv           | <i>Geum rivale</i> L.                      | 380         | 5 | 4 | -             | Gsyl     | <i>Geranium sylvaticum</i> L.              | 84          | 4 | 5 | 3 |
| Hspp           | <i>Hieracium</i> spp. <sup>1</sup>         | 176         | 6 | 4 | 5             | Griv     | <i>Geum rivale</i> L.                      | 31          | 2 | 2 | 3 |
| Hmac           | <i>Hypericum maculatum</i> Crantz          | 94          | 1 | 4 | -             | Plap     | <i>Pedicularis lapponica</i> L.            | 44          | 4 | 4 | 1 |
| Karv           | <i>Knautia arvensis</i> (L.) Coulter       | 408         | 4 | 5 | -             | Pcae     | <i>Phylodoce caerulea</i> (L.) Bab.        | 17          | 3 | 1 | 1 |
| Lpra           | <i>Lathyrus pratensis</i> L.               | 402         | 4 | 5 | -             | Ppal     | <i>Potentilla palustris</i> (L.) Scop.     | 41          | 1 | 2 | 1 |
| Lsyl           | <i>L. sylvestris</i> L.                    | 17          | 1 | 2 | -             | Ralp     | <i>Rhododendron lapponicum</i> (L.)        |             |   |   |   |
| Laut           | <i>Leontodon autumnalis</i> L.             | 52          | 2 | 3 | 1             | Wahlenb. |  | 112         | 9 | - | - |
| Lvis           | <i>Lychnis viscaria</i> L.                 | 95          | 6 | 5 | -             | Sspp     | <i>Salix</i> spp. <sup>3</sup>             | 275         | 9 | 1 | - |
| Mpra           | <i>Melampyrum pratense</i> L.              | 59          | 1 | 4 | -             | Salp     | <i>Saussurea alpina</i> (L.) DC.           | 45          | 2 | 5 | 4 |
| Pere           | <i>Potentilla erecta</i> (L.) Rauschel     | 10          | - | 3 | 1             | Saiz     | <i>Saxifraga aizoides</i> L.               | 23          | 1 | 4 | 2 |
| Rida           | <i>Rubus idaeus</i> L.                     | 254         | 6 | 6 | -             | Saca     | <i>Silene acaulis</i> (L.) Jacq.           | 13          | 3 | 1 | 1 |
| Sspp           | <i>Salix</i> spp. <sup>2</sup>             | 60          | 3 | - | -             | Sdio     | <i>S. dioica</i> (L.) Clairv.              | 12          | 2 | - | 1 |
| Svul           | <i>Silene vulgaris</i> (Moench) Garcke     | 15          | 1 | 4 | -             | Svir     | <i>Solidago virgaurea</i> L.               | 152         | 5 | 6 | 6 |
| Svir           | <i>Solidago virgaurea</i> L.               | 609         | 5 | 6 | 5             | Teur     | <i>Trollius europaeus</i> L.               | 19          | 4 | 3 | - |
| Toff           | <i>Taraxacum officinale</i> Weber, s. lat. | 31          | 4 | 3 | -             | Vmyr     | <i>Vaccinium myrtillus</i> L.              | 89          | 8 | 3 | 1 |
| Thyb           | <i>Trifolium hybridum</i> L.               | 30          | 1 | 5 | -             | Vuli     | <i>V. uliginosum</i> L.                    | 64          | 5 | 5 | - |
| Tpra           | <i>T. pratense</i> L.                      | 732         | 6 | 6 | 3             | Vvit     | <i>V. vitis-idaea</i> L.                   | 32          | 1 | 4 | 2 |
| Trep           | <i>T. repens</i> L.                        | 154         | 2 | 7 | -             |          |  |             |   |   |   |
| Vcha           | <i>Veronica chamaedrys</i> L.              | 12          | 1 | 4 | -             |          |  |             |   |   |   |
| Vera           | <i>Vicia cracca</i> L.                     | 1087        | 5 | 6 | 3             |          |  |             |   |   |   |
| Vsep           | <i>V. sepium</i> L.                        | 436         | 7 | 5 | -             |          |  |             |   |   |   |
|                | <b>Total</b>                               | <b>5836</b> |   |   |               |          | <b>Total</b>                               | <b>1600</b> |   |   |   |

<sup>1</sup>) Mostly *Hieracium umbellatum* L., but includes *Pilosella officinarum* F.W. Schultz & Schultz Bip.

<sup>2</sup>) *Salix caprea* L. and *S. phylicifolia* L.

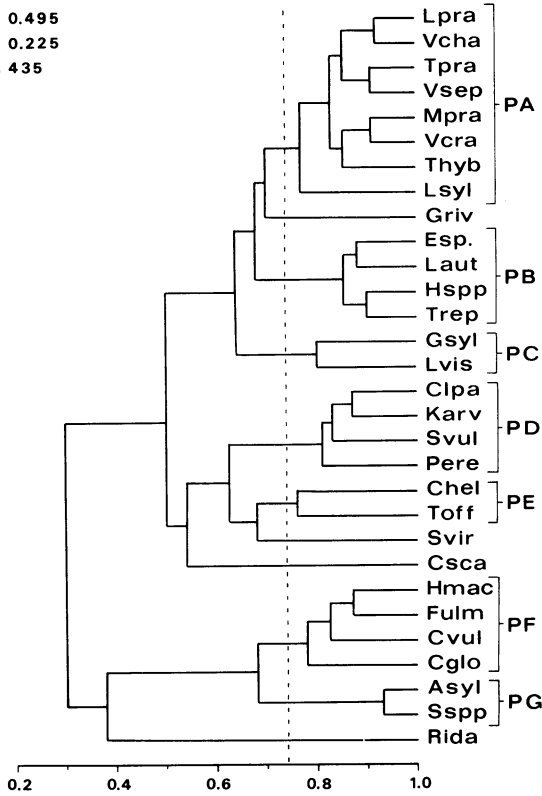
tors among the species in the clusters (PA-PG, AA-AF) affects the distribution of their flowering times in the season (Fig. 2). The non-competitive null hypothesis is that the pairwise spacing of flowering peaks within each species cluster does not deviate from the spacing of a corresponding number of species drawn at random from the total number of species (30 at Puumala, 25 at Abisko). The random draws for each cluster were made 100 times, and for each draw the mean was calculated for all the distances between pairs of flowering peaks. The grand mean of these figures (with standard deviation) is the estimate of the expected spacing in each cluster. At Puumala the observed figures were greater than expected in 3 out of 7 cases (2

statistically significant differences, PA, PG); at Abisko the observed spacing was greater than expected in 4 out of 6 cases (statistically significant differences in AC, AD and AA) (Table 2).

The statistically significant differences give some support to the competitive hypothesis, but a fair number of them is not significant (Table 2). Although most of the species pairs having high pollinator similarity have no overlap in their flowering periods (Fig. 2), 12 species pairs (expected number 22) at Puumala, and 8 species pairs at Abisko (expected number 15) show high overlap for both pollinators and flowering periods. To permit an analysis of these species pairs, we have listed some characters of the plants in Table 3.

**PUUMALA**

$\bar{x}$  0.495  
s 0.225  
n 435



**ABISKO**

$\bar{x}$  0.443  
s 0.233  
n 300

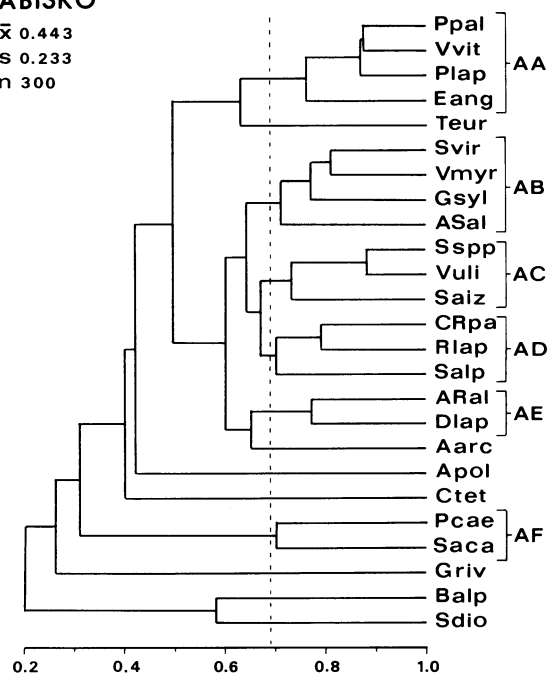
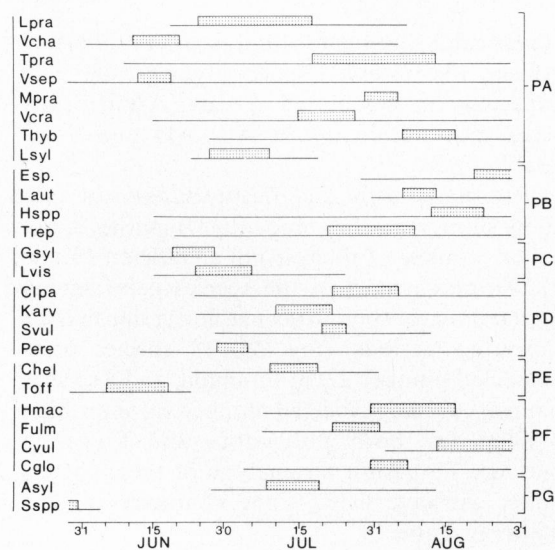


Fig. 1. Dendrograms of the pollinator similarities between the 30 plant species at Puumala and the 25 plant species at Abisko. For species names see Table 1. The clusters of species having high overlap in pollinators are indicated with capital letters (PA-PG for Puumala, AA-AF for Abisko). The dotted line shows the similarity at the level of the mean plus one standard deviation (0.720 and 0.676, Puumala and Abisko, respectively). For both communities the mean ( $\bar{x}$ ) and standard deviation (s) of pairwise overlaps (n) are given.

**PUUMALA**



**ABISKO**

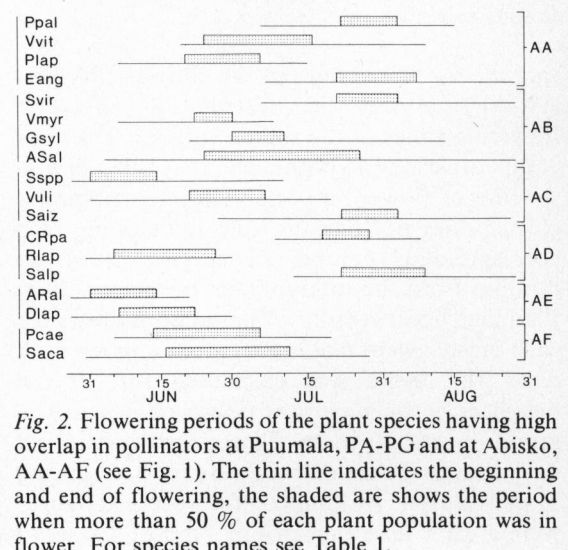


Fig. 2. Flowering periods of the plant species having high overlap in pollinators at Puumala, PA-PG and at Abisko, AA-AF (see Fig. 1). The thin line indicates the beginning and end of flowering, the shaded are shows the period when more than 50 % of each plant population was in flower. For species names see Table 1.

Table 2. Observed (OBS) and expected (EXP) spacings (in days) of the midpoints of flowering periods among the cluster members in the two study areas (see Fig. 2). The expected spacings and standard deviations (SD) are based on 100 randomizations (see text); t-test results with statistical significances are indicated, S= number of species (ns, statistically nonsignificant difference).

| Cluster | S | OBS | EXP  | SD  | t     | p      |
|---------|---|-----|------|-----|-------|--------|
| PUUMALA |   |     |      |     |       |        |
| PA      | 8 | 26  | 18.7 | 2.8 | 2.607 | <0.005 |
| PB      | 4 | 15  | 20.6 | 5.0 | 1.120 | ns     |
| PC      | 2 | 10  | 20.9 | 7.9 | 1.380 | ns     |
| PD      | 4 | 15  | 20.6 | 5.0 | 1.120 | ns     |
| PE      | 2 | 33  | 20.9 | 7.9 | 1.532 | ns     |
| PF      | 4 | 17  | 20.6 | 5.0 | 0.720 | ns     |
| PG      | 2 | 50  | 20.9 | 7.9 | 3.684 | <0.01  |
| ABISKO  |   |     |      |     |       |        |
| AA      | 4 | 20  | 14.5 | 3.2 | 1.719 | <0.1   |
| AB      | 4 | 16  | 14.5 | 3.2 | 0.469 | ns     |
| AC      | 3 | 33  | 14.9 | 4.4 | 4.114 | <0.001 |
| AD      | 3 | 30  | 14.9 | 4.4 | 3.432 | <0.001 |
| AE      | 2 | 9   | 17.5 | 7.5 | 1.133 | ns     |
| AF      | 2 | 9   | 17.5 | 7.5 | 1.133 | ns     |

## DISCUSSION

The diverse flower structures and pollinator mechanisms found in angiosperms represent adaptive radiation into plants suited to different pollen vectors or suited in different ways to the same vector (Stebbins 1970). The first requirement for efficient pollination of many species of simultaneously flowering plants is flowering constancy in the individual pollinators (Heinrich 1975). In most cases constancy is gained by offering rewards. The amount of food provided by a flower should be sufficient to attract foragers, yet low enough to keep them moving from one plant to another (Heinrich & Raven 1972).

Many authors suggest that plant species having a high pollinator similarity in local communities divide the pollinator resource by flowering during more or less non-overlapping periods (e.g., Levin & Anderson 1970, Heinrich & Raven 1972, Heinrich 1975, Pleasants 1980). In most cases this was true in our communities, too. However, both communities contained species pairs which had considerable overlap of both pollinators and flowering times (Table 3). These pairs will be examined more closely to discover their ways of achieving pollination.

Table 3. Some characters of the pairs of plant species having high overlap in pollinators and flowering times in the two study areas. (PS= pollinator similarity, height in cm, flower colour, shape of the flower and C= corolla tube depth in mm are indicated).

| Species pair                   | PS       | Height | Colour | Shape | C  |
|--------------------------------|----------|--------|--------|-------|----|
| PUUMALA                        |          |        |        |       |    |
| <i>Lathyrus pratensis</i>      |          | 20—50  | yellow | tube  | 5  |
| vs.                            |          |        |        |       |    |
| <i>L. sylvestris</i>           | 0.77     | 20—50  | red    | tube  | 5  |
| <i>Vicia cracca</i>            | 0.84     | 20—50  | blue   | tube  | 11 |
| <i>Veronica chamaedrys</i>     | vs. 0.84 | 10—30  | blue   | open  | 2  |
| <i>Vicia sepium</i>            |          | 30—50  | blue   | tube  | 10 |
| <i>Trifolium pratense</i>      |          | 20—40  | red    | tube  | 11 |
| vs.                            |          |        |        |       |    |
| <i>Melampyrum pratense</i>     | 0.84     | 10—40  | yellow | tube  | 13 |
| <i>Vicia cracca</i>            | 0.83     | 20—50  | blue   | tube  | 11 |
| <i>Trifolium hybridum</i>      | 0.87     | 20—70  | pink   | tube  | 3  |
| <i>Leontodon autumnalis</i>    |          | 10—30  | yellow | head  | 6  |
| vs.                            |          |        |        |       |    |
| <i>Hieracium</i> spp.          | 0.87     | 5—40   | yellow | head  | 1  |
| <i>Trifolium repens</i>        | 0.87     | 10—30  | white  | tube  | 3  |
| <i>Geranium sylvaticum</i>     | vs. 0.80 | 30—40  | red    | open  | 5  |
| <i>Lychnis viscaria</i>        |          | 30—70  | red    | tube  | 10 |
| <i>Silene vulgaris</i>         |          | 20—50  | white  | cup   | 4  |
| vs.                            |          |        |        |       |    |
| <i>Cirsium palustre</i>        | 0.82     | 40—100 | red    | head  | 4  |
| <i>Knautia arvensis</i>        | 0.83     | 30—80  | red    | head  | 6  |
| <i>Hypericum maculatum</i>     | vs. 0.72 | 30—40  | yellow | open  | 1  |
| <i>Campanula glomerata</i>     |          | 20—70  | blue   | tube  | 4  |
| ABISKO                         |          |        |        |       |    |
| <i>Potentilla palustris</i>    | vs. 0.73 | 30—100 | red    | open  | 0  |
| <i>Epilobium angustifolium</i> |          | 50—100 | red    | open  | 0  |
| <i>Vaccinium vitis-idaea</i>   | vs. 0.87 | 10—30  | white  | cup   | 5  |
| <i>Pedicularis lapponica</i>   |          | 15—30  | yellow | tube  | 8  |
| <i>Astragalus alpinus</i>      |          | 10—30  | blue   | tube  | 6  |
| vs.                            |          |        |        |       |    |
| <i>Vaccinium myrtillus</i>     | 0.78     | 15—50  | red    | cup   | 6  |
| <i>Geranium sylvaticum</i>     | 0.67     | 30—40  | red    | open  | 0  |
| <i>Solidago virgaurea</i>      | 0.68     | 30—50  | yellow | head  | 7  |
| <i>Crepis paludosa</i>         | vs. 0.72 | 30—100 | yellow | head  | 4  |
| <i>Saussurea alpina</i>        |          | 20—40  | red    | head  | 6  |
| <i>Arctostaphylos alpina</i>   | vs. 0.77 | 1—5    | white  | cup   | 6  |
| <i>Diapensia lapponica</i>     |          | 5—30   | white  | cup   | 6  |
| <i>Phyllodoce caerulea</i>     | vs. 0.68 | 10—20  | red    | cup   | 9  |
| <i>Silene acaulis</i>          |          | 1—5    | red    | cup   | 7  |

The means of ensuring pollination include the following: (1) The plants may differ from each other in some other respect than flowering time (e.g., shape, height, colour of flower, time of day at which they flower, quality and quantity of

nectar and/or pollen, habitat). (2) The plants depend more on other pollinators than on bumblebees (e.g., solitary bees, hover-flies, butterflies or moths). (3) The plants are, at least partly, self-pollinated or wind-pollinated, or they reproduce vegetatively.

Thomson (1978) showed that a plant species may benefit by sharing pollinators with an apparent competitor when both species are relatively rare (neighbour influence). Further, Bobisud & Neuhaus (1975) suggested that rare species may benefit by the inconstancy of pollinators. At Puumala *Lathyrus sylvestris* was the rarest bumblebee-pollinated species, and it had high overlap of pollinators and flowering time with *L. pratensis*. Thus it is tempting to assume that it gained by the presence of *L. pratensis*. At Abisko a similar pair of species was *Crepis paludosa* and *Saussurea alpina*.

At Puumala the most abundant of the species listed in Table 3 were *Vicia cracca*, *Lathyrus pratensis* and *Trifolium pratense*. Sometimes these species were visited by the same bumblebee individual during a single foraging trip (Teräs 1976). But it is probable that some individuals in a bee colony were constant to, say, *V. cracca*, while others visited *T. pratense* more frequently. A corresponding example at Abisko was the pair *Astragalus alpinus* and *Vaccinium myrtillus*, both growing abundantly on the slope. Following Heinrich (1976) and Ranta & Vepsäläinen (1981), we suggest that specialization by individual bumblebees may account for the successful pollination of these plant species. However, controlled field experiments are needed for a better understanding of this question.

Levin & Kerster (1973) and Faulkner (1976) observed that honeybees tend to maintain a given height in inter-plant flights, and the authors assume that pollinator discrimination by height is likely to be the rule in dense plant populations, as it is the most economic foraging strategy for pollinators. If this holds for bumblebees as well, height constancy would explain the overlaps at Puumala in the pairs *Lathyrus pratensis* — *Vicia cracca*, *L. pratensis* — *L. sylvestris*, *Trifolium pratense* — *V. cracca*, *T. pratense* — *T. hybridum*, *T. repens* — *Leontodon autumnalis*, *Geranium sylvaticum* — *Lychnis viscaria* and *Cirsium palustre* — *Knautia arvensis*. Corresponding

examples from Abisko would be *Vaccinium vitis-idaea* — *Pedicularis lapponica*, and *Geranium sylvaticum* — *Solidago virgaurea*. But there is little evidence of height constancy in bumblebees. On the contrary, Free (1966) and Eisikowitch (1978) reported that bumblebees did not discriminate between stunted and tall plants of the same species.

Pollinators often remain constant to a single searching image (Levin & Kerster 1973, Heinrich 1975), and the chances of a species becoming pollinated would be greater if it flowered slightly after one of similar appearance. This may apply with closely related species like *Lathyrus pratensis* and *L. sylvestris*, and *Trifolium repens* and *T. hybridum* at Puumala (in both cases the first started to flower a little earlier than the second).

The constancy of pollinators to a given colour has been studied by comparing the visits to a species which has flowers of more than one colour (Free 1966, Cruden 1972, Kay 1978, Mogford 1978), but the results obtained are contradictory. Pollinators may become conditioned to one colour, or they may ignore colour as a distinguishing factor, and even confuse similar plant species of the same flower colour (e.g., the yellow-flowered *Leontodon autumnalis* and *Hieracium* spp. at Puumala). The scent of the flowers may also differ and have selective advantage in attracting pollinators (Leleji 1973, Macior 1978).

The sugar concentration, quality and volume of nectar, or the amount of pollen produced can differ between simultaneously flowering plants (Kwak 1978, Corbet 1978, Corbet et al. 1979). It is not certain whether small differences in the quality of nectar are sufficient to provide differential attractive stimulus for different nectar foragers (Macior 1978). However, the frequency of bumblebee visits increases with the amount of nectar and pollen (e.g., Kevan 1978, Heinrich 1979), and diel fluctuations in caloric rewards cause fluctuation in the foraging behaviour of pollinators (Corbet et al. 1979). According to Kämpylä (1978), there are great differences between the amount of nectar produced by *Hypericum maculatum* and *Campanula* species, and between the sugar types of *Geranium sylvaticum* and *Lychnis viscaria*. Further, at Puumala Teräs (1976) observed that

*H. maculatum* and *Melampyrum pratense* were most frequently visited in the morning, which suggests diel segregation between these species and *Campanula glomerata* and *Trifolium pratense*, respectively.

We have deliberately limited our study to bumblebee-pollinated plants. However, it is possible that some of the plants also depended on other pollinators. For example, of the plants present at Puumala, *Veronica chamaedrys* is often pollinated by flies, *Lychnis viscaria* by flies and butterflies, and *Silene vulgaris* by moths. At Abisko *Silene acaulis*, *Solidago virgaurea*, *Saussurea alpina* and *Crepis paludosa* were also frequently visited by butterflies.

### Concluding discussion

If pollinators visit different plant species indiscriminately, the frequency of within-species cross-pollination is inversely proportional to the numbers of other flower species in flower at the same time. This makes it necessary for plants to improve flower fidelity in pollinators. This can be attained by increasing the benefits for pollinators. The rewards offered to pollinators are extra supplies of pollen and/or nectar, the production of which demands energy. Thus, minimization of expenses is to be expected. This may take several forms and act as a powerful selective force in establishing differences in (1) structural morphology, colour and scent of pollination units (flowers, blossoms), (2) amounts and kinds of rewards supplied, and (3) flowering periods of plants. In case (1) pollinators are excluded: a complicated flower structure enables plants to specialize on a subset of pollinators. Structural differentiation is often associated with point (2): flowers relying on

specialized pollinators produce abundant and/or high quality nectar. It is noteworthy that plant species producing only pollen (not nectar) for pollinators seldom have a complicated floral structure (Faegri & van der Pijl 1979).

On the ecological time scale, plants cannot be expected to react to local competition for pollinators by altering their floral structure or the kinds of rewards supplied for pollinators, or by shifting their flowering times. Instead, we suggest that the observed phenological spread in flowering between most of the species pairs having high pollinator overlaps in the communities studied by us are probably due to exclusive interspecific interactions. In other words, local competition for pollinators may have excluded part of the congeners of some plant species. However, we lack direct evidence for competition, but indirectly competition should lead to a wider spacing of flowering midpoints in the coexisting species sharing pollinators as compared to random flowering (Poole & Ratchke 1979). The difference between the observed and random spacing of flowering midpoints in some clusters of species in both communities agrees with this hypothesis. However, there are a number of species pairs with high overlaps (for both pollinators and flowering time) in both of the communities. To gain insight into the pattern, more data are needed on the plant-pollinator interactions, and on the reproductive options open to plants.

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