Pollination in alpine Norway: flowering phenology, insect visitors, and visitation rates in two plant communities

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Pollination studies in European alpine communities are few. The objective of this study was to describe the pollination ecology in two alpine plant communities at Finse, southwestern Norway. Because of late snowmelt and early winter at Finse, the time available for flowering and seed maturation is restricted. Flowering was concentrated at the beginning of the season in both communities, and large overlaps in flowering time were found for most species. In one of the communities, flowering peaks were significantly clumped, whereas in the other they were randomly distributed through the season. However, in this community, five insect-pollinated species flowered simultaneously early in the season. Diptera almost exclusively dominated the visitor assemblage. Most plant species pairs had high overlaps in flower visitor species. Species flowering simultaneously attracted the same visitor species. In one community, eight species pairs flowered sequentially and shared visitors. Visitation rates were highest at the lowest elevated site. The results are compared with those obtained in other alpine areas. It is argued that selection for an early flowering is probably stronger than selection pressures resulting from interspecific interactions.

Key words: alpine, Diptera, flowering phenology, flower visitors, season length, visitation rate.


Il n'existe que peu d'études sur la pollinisation dans les communautés alpines de l'Europe. L'auteur s'est proposé de décrire l'éco logie de la pollinisation dans deux communautés de plantes alpines de la région de Finse, dans le sud-ouest de la Norvège. Parce que la fonte de la neige est tardive et que l'hiver est hâtif à Finse, le temps disponible pour la floraison et la maturation des graines est limité. La floraison survient rapidement au début de la saison dans les deux communautés et on retrouve un important recouvrement des périodes de floraison pour la plupart des espèces. Dans une des communautés, les périodes d'anthèse sont significativement regroupées, alors que dans l'autre ces périodes sont distribuées au hasard tout au long de la saison. Cependant, dans cette communauté, cinq espèces pollinisées par les insectes fleurissent simultanément, et tôt dans la saison. Ce sont exclusivement des diptères qui dominent le cortège des pollinisateurs. Pour la plupart des paires de plantes, on note de forts recouvrements des espèces visitant leurs fleurs. Les espèces fleurissant simultanément attirent les mêmes espèces de pollinisateurs. Dans une des communautés, huit paires d'espèces fleurissant en séquence partagent les mêmes pollinisateurs. Les taux de visites sont plus élevés aux basses altitudes. L'auteur compare ses résultats avec ceux obtenus dans d'autres régions alpines, et il propose que la sélection en faveur d'une floraison hâtive serait probablement plus forte que les pressions sélectionnistes provenant d'interactions interspécifiques.

Mots clés : alpin, diptère, phénologie florale, pollinisateurs, longueur de la saison, taux de visites.

Introduction

The flowering periods of the animal-pollinated plants in a community may be influenced by numerous factors. Interspecific competition for pollination is the most frequently cited explanation for the distribution pattern of flowering times (Mosquin 1971; Pleasants 1980, 1983; Waser 1983). Competitive interactions between species favor divergence in flowering times or flower morphology, such that negative effects of pollinator sharing are minimized. Therefore, if competition for pollination was a sufficiently strong selection pressure in the past, the flowering times within a community should be regularly distributed through the season (Poole and Rathcke 1979; Rathcke 1983, 1984). Conversely, positive interaction for pollination occurs if species experience a higher visitation rate when flowering simultaneously than when flowering sequentially (Thomson 1982, 1983; Rathcke 1983; Laverty and Plowright 1988; Laverty 1992). Such interactions may select for convergence in flowering time or flower morphology. Length of season may influence flowering times (Rathcke and Lacey 1985; Primack 1987). In many alpine areas the time available for shoot development, flowering, pollination, and seed maturation is short. Here, an early season flowering period may be a prerequisite for completion of seed production before winter, particularly when fruits and seeds are relatively large in size (Bliss 1956, 1971; Billings and Mooney 1968), and interspecific interactions for pollination may be less important in explaining the distribution of flowering times within alpine plant communities.

Autogamous pollination, frequent in alpine populations (Crawford 1989), may suppress interactions between species because individuals are independent of pollinating agents for seed production. Therefore, autogamous populations may have weak, or no, interactions for pollination with other populations, which consequently leads to lower selection pressure for divergence or convergence in flowering time. Autogamous pollination does not obviate early flowering in short-season environments. Regardless of pollination strategy, seed must mature before winter conditions appear.

Diptera are frequent flower visitors in alpine and arctic environments (Hocking 1968; Kevan 1972; Arroyo et al. 1982; Inouye and Pyke 1988; McCall and Primack 1992). The short season in these environments may restrict the establishment of social bee colonies, such as bumblebees. Also, butterflies are rarely recorded as flower visitors in alpine areas. Besides being unselective flower feeders (Faegri and van der Pijl 1979) and inefficient pollen vectors (Kendall and Solomon 1973; Grace and Nelson 1981), a fly-dominated pollinator assemblage has low morphological and behavioral diversity. Consequently, the potential for specialization, in either flowering time or flower
morphology towards a specific pollinator species, may be restricted.

The objective of this work was to describe the pollination ecology in a geographical area that was not previously investigated. I asked the following questions: (i) What patterns of flowering are found in the two communities, and which external factors give the most reasonable explanation of these patterns? (ii) Which flower visitors are the most frequent in the two communities examined, and to what extent do the flowering species share visitor species? (iii) In what aspects is the pollination ecology at Finse similar to, or different from, that of other comparable areas?

Study areas

The study was conducted at two alpine sites at Finse, Hardangervidda, southwestern Norway. Both were south-facing and of equal size (60 x 60 m). They are 2.5 km apart.

Site 1 was sampled in 1991 from June 16 to September 9. It is situated on the south-facing slope of Mount Kvannjolnut (K) (1300 m asl; 60°35’N, 7°33’E) and was exposed to the sun between ca. 07:00 and 21:00 h during the study period. Snow melted away in early June at both sites. Site 1 had a species composition characteristic of the low alpine zone at Finse. Most species at the site flowered abundantly. I measured flowering phenology at both sites every 2–4 days in 1991 by counting the number of open flowers or inflorescences for each species in 22 permanent 2 x 2 m squares. I positioned the squares at random before any species came into flower at both sites. At S in 1990 I measured the flowering phenology only qualitatively by noting every 2nd day which species were in bloom along seven permanent transects, each ca. 60 m long and 3 m wide.

Data analysis

I used Horn’s (1966) niche overlap index to examine differences in plant species niche relationships. Smith and Zaret (1982) showed that this index is little affected by differences in the number of samples, number of species, or evenness in the data set. I used Levins’ (1968) breadth index to quantify niche breadth in visitor use. Bootstrap analysis (Mueller and Altenberg 1985) was used to examine the robustness and bias of the measures. In the niche-breadth and overlap calculations there were large differences in percent bias between some of the species and species pairs (breadth: 0–19.48%; overlap: 1.92–15.15%). Therefore, I present and use bias-corrected values in the analysis.

In the analysis of overlap in flowering time in 1991 I summed all counts of each species in the squares from 1 day. Because flowering phenology was not quantified in 1990, no overlap data are presented for this year. Only visitor species with a total abundance of ≥5 individuals observed were used in the niche analysis of overlap and breadth in visitor species.

All niche measurements were calculated using the computer program Niche written by D. Schluter (University of British Columbia, Vancouver) (see Schluter 1988). Dispersion of flowering peaks was calculated using the program Peak written by J.M. Line (University of Cambridge, Cambridge, England).

Study species

The species studied are presented in Table 1. I concentrated sampling on flower preference of insect visitors and flowering phenology to species that were abundant at the study sites. Only species that received a sufficient number of visits for statistical analysis are presented. All species had a flower morphology that allowed flies to forage in them. No detailed examination was done of breeding systems of the flowering species. The information given in Table 1 should therefore be considered suggestive.

Results

Flowering phenology

Figure 1 shows the flowering phenologies. In 1991 the flowering season at K started 2 weeks earlier than that at S. The flowering season terminated at ca. September 10 in both communities. Thus, the flowering season at K was 2 weeks longer than at S. The flowering season at K lasted for 87 days. Peak flowering for five species occurred before midseason, and the mean peak for all species occurred at day 37. At S the
Fig. 1. Flowering phenology at (A) Mount Kvannjolnut in 1991, (B) Mount Sandalsnut in 1991, and (C) Mount Sandalsnut in 1990. In A and B, y-axis values on a given day represent the number of flowers on that day divided by the maximum daily number of flowers for each species. Species names are abbreviated as in Table 1.
### Table 2. Percentage of flower visitors to the plant species at Mount Kvannjolnut in 1991 (K1) and at Mount Sandalsnut in 1990 (So) and 1991 (Si).

<table>
<thead>
<tr>
<th>Insect Order</th>
<th>Plant Species</th>
<th>K1</th>
<th>S1</th>
<th>So</th>
<th>K1</th>
<th>S1</th>
<th>So</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Anthomyiidae</strong></td>
<td><strong>Heterostylodes pilifera Zett.</strong></td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td><strong>Pegoplata aestiva Meigen</strong></td>
<td>29</td>
<td>10</td>
<td>10</td>
<td>11</td>
<td>16</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td><strong>Pegoplata tundrica Schnabl</strong></td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>2</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td><strong>Zaphne barbiventris Zett.</strong></td>
<td>2</td>
<td>11</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>18</td>
</tr>
<tr>
<td></td>
<td><strong>Zaphne frontata Zett.</strong></td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>13</td>
<td>23</td>
</tr>
<tr>
<td><strong>Dolichopodidae</strong></td>
<td><strong>Dolichopus plumipes Scop.</strong></td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td><strong>Dolichopus rupestris Haliday</strong></td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>4</td>
<td>20</td>
<td>3</td>
</tr>
<tr>
<td><strong>Empididae</strong></td>
<td><strong>Empis lucida Zett.</strong></td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td><strong>Rhamphomyia morio Zett.</strong></td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>8</td>
<td>22</td>
<td>15</td>
</tr>
<tr>
<td><strong>Muscidae</strong></td>
<td><strong>Phaonia alpicola Zett.</strong></td>
<td>8</td>
<td>4</td>
<td>5</td>
<td>19</td>
<td>4</td>
<td>36</td>
</tr>
<tr>
<td></td>
<td><strong>Phaonia lugubris Meigen</strong></td>
<td>3</td>
<td>1</td>
<td>0</td>
<td>10</td>
<td>4</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td><strong>Spilogona alpica Zett.</strong></td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>7</td>
<td>11</td>
<td>6</td>
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<tr>
<td></td>
<td><strong>Spilogona nitidicauda Schnabl</strong></td>
<td>0</td>
<td>1</td>
<td>3</td>
<td>0</td>
<td>2</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td><strong>Thricops aculeipes Zett.</strong></td>
<td>8</td>
<td>2</td>
<td>0</td>
<td>16</td>
<td>0</td>
<td>74</td>
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<tr>
<td></td>
<td><strong>Thricops cunctans Meigen</strong></td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>2</td>
<td>1</td>
<td>44</td>
</tr>
<tr>
<td></td>
<td><strong>Thricops furcatus Stein</strong></td>
<td>0</td>
<td>1</td>
<td>7</td>
<td>0</td>
<td>18</td>
<td>119</td>
</tr>
<tr>
<td></td>
<td><strong>Thricops hirtulus Zett.</strong></td>
<td>6</td>
<td>63</td>
<td>65</td>
<td>10</td>
<td>46</td>
<td>71</td>
</tr>
<tr>
<td></td>
<td><strong>Thricops longipes Zett.</strong></td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>3</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td><strong>Thricops nigritellus Zett.</strong></td>
<td>35</td>
<td>1</td>
<td>0</td>
<td>29</td>
<td>0</td>
<td>237</td>
</tr>
<tr>
<td></td>
<td><strong>Scathophagidae</strong></td>
<td><strong>Scathophaga stercoraria L.</strong></td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>1</td>
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<tr>
<td></td>
<td><strong>Syrphidae</strong></td>
<td><strong>Cheilosia sahlbergi Zett.</strong></td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td><strong>Eristalis spp.</strong></td>
<td>0</td>
<td>4</td>
<td>1</td>
<td>0</td>
<td>11</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td><strong>Melanostoma dubium Zett.</strong></td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>3</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td><strong>Platycheirus manicatus Meigen</strong></td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>7</td>
<td>14</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td><strong>Platycheirus subordinatus Becker</strong></td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>5</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td><strong>Hymenoptera</strong></td>
<td><strong>Apidae</strong></td>
<td><strong>Bombus alpinus L.</strong></td>
<td>0</td>
<td>9</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td><strong>Bombus lapponicus Fabr.</strong></td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>3</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td></td>
<td><strong>Lycaenidae</strong></td>
<td><strong>Albulina orbitulus de Prunner</strong></td>
<td>11</td>
<td>0</td>
<td>0</td>
<td>12</td>
</tr>
</tbody>
</table>

**Note:** The values in the table are the percentage of visits by the insect taxa to each plant species. Percentage values do not always add up to 100 due to rounding errors. Only visitor taxa observed on five or more occasions are included. The niche breadth values (Levin's index) for each plant species are bias corrected by bootstrapping (1000 resamples).

<table>
<thead>
<tr>
<th>Plant Species</th>
<th>Total no. of visits observed</th>
<th>Niche breadth (bias corrected)</th>
</tr>
</thead>
<tbody>
<tr>
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<td></td>
<td></td>
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<tr>
<td></td>
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</tbody>
</table>

**NOTE:** The values in the table are the percentage of visits by the insect taxa to each plant species. Percentage values do not always add up to 100 due to rounding errors. Only visitor taxa observed on five or more occasions are included. The niche breadth values (Levin's index) for each plant species are bias corrected by bootstrapping (1000 resamples). Plant species names are abbreviated as in Table 1.

Includes Eristalis tenax L. and Eristalis pertinax Scop.
Flowering season lasted for 74 days. Here, four species peaked flowering before midseason, and also here, the mean peak for all species, day 33, occurred before midseason. In both communities, all species had started to flower before midseason. The two species first in bloom at K, *Ranunculus acris* and *Potentilla crantzii*, flowered only very sparsely during the first 2 weeks when temperatures and snowfall were low. Visual inspection of Fig. 1A suggests that the species at K are divided into two groups that flowered at different times through the season; no such separation of flowering times was evident at S in 1991 (Fig. 1B). An analysis of the dispersion of flowering peaks in the two communities reveals that the peaks at K were randomly dispersed along the time axis (expected variance / sample variance = 1.01, $\chi^2 = 7.07$, df = 7, $P = 0.42$; see Poole and Rathcke (1979) and Rabinowitz et al. (1981), whereas the flowering peaks at S were significantly clumped (expected variance / sample variance = 2.40, $\chi^2 = 16.78$, df = 7, $P = 0.02$). Figure 1C shows the flowering phenology at S in 1990. The initiation and sequence of flowering were about equal for all species both years. At S, the species were in flower for extensive periods (Fig. 1). *Ranunculus acris* and *Silene acaulis* flowered for nearly the whole season in both years, and all species at S flowered for more than half the season. At K, only *R. acris* and *Parnassia palustris* were in flower for more than half the season.

**Flower visitors**

Table 2 summarizes the percentage of visits by insect taxa to each plant species. Dipterans constituted almost the entire visitor assemblage at both sites and in both years. Most of the plants were visited by many insect species. However, only a few taxa were common on each plant species.

At K, the most common flower visitor was *Thricops nigrirritellus*. Flies of this species showed preference for *R. acris* early in the flowering season and later switched to *Leontodon autumnalis* and *Parnassia palustris*. The abundance of Syrphidae was low; only 4.1% of all visits were by this family. *Bombus lapponicus* (10 visits) was the only bumblebee recorded at K. Towards the end of the flowering season, workers of *B. lapponicus*, although in small numbers, were very active on *Geranium sylvaticum* and *L. autumnalis*. The only butterfly observed was *Albulina orbitulus*, which only occurred at K.

Most visits by this species were to *Parnassia palustris* and *Cerasitum alpinum*.

At S in 1991, *Thricops hirtulus* was the most frequent visitor. *Bombus alpinus* visited *L. autumnalis* in low numbers. Syrphids, *Eristalis* spp., were more frequent on this species compared with the previous year. Some of the species (e.g., *Thricops aculeipes* and *Thricops nigrirritellus*) differed greatly in abundance between the two sites sampled in 1991.

At S in 1990, *Thricops hirtulus* was more than twice as frequent as any other visitor. It was the most frequent flower visitor on all species, except for late-flowering *L. autumnalis* and *Parnassia palustris*. The second most frequent visitor was *Zaphne frontata*, especially on *L. autumnalis*. Earlier in the season it frequently visited *Taraxacum croceum*. *Eristalis* spp. were very active on flowers late in the season but in low numbers. No bumble bees were recorded as visitors in 1990.

Table 2 also shows the visitor niche breadths for each plant species. For some of the plants, the niche breadth showed large differences both between areas and between years. In 1991, populations of the same species had wider breadth at K than at S, with the exception of *Parnassia palustris* and *L. autumnalis*. From 1990 to 1991 at S, the niche breadth for *L. autumnalis* increased markedly, whereas it decreased sub-
stantially for Taraxacum croceum and C. alpinum.

Niche overlaps in visitor species

Figure 2 shows the plants’ mean niche overlaps in visitor species. In general, large overlaps were found. All species sampled in both sites in 1991 had the highest mean overlap at K. At S, all species had the highest mean overlap in 1990. In 1991, L. autumnalis had the highest mean overlap of all species at K, whereas it had the lowest at S. The correlation between overlap for species pairs at S in 1990 and 1991 was positive and highly significant (df = 19, r = 0.69, t = 4.16, p = 0.0005). This close correlation did not exist between the substantially for Taraxacum croceum and C. alpinum.

Flowering phenology

The synchronous early flowering is probably best explained by the short time available for shoot and flower development and seed maturation. Early flowering is well known from other studies in short-season environments. Bliss (1956, 1971) and Billings and Mooney (1968), in their reviews of plant development in arctic and alpine environments, stated that flowering occurred shortly after the occurrence of favorable temperatures and that flowering was synchronous among species. Holway and Ward (1965) showed that snow cover was the primary factor influencing phenology and that species initiated flowering early after snowmelt in the Rocky Mountains. Inouye and Pyke (1988), in an investigation of the pollination biology in alpine Australia, found that most species flowered early in the season. Helenurm and Barrett (1987), working with boreal forest herbs in Canada, also found flowering to be more prominent early in the season and argued that abiotic factors such as climate and season length may have influenced the flowering phenology. Kudo (1991) showed that rapid-flowering alpine species are more successful seed producers in Japan. Finally, Galen and Stanton (1991) showed that differential snow accumulation influenced fitness in Ranunculus adoneus A. Gray. Plants with delayed flowering, because of a thicker snow pack, suffered a reduction in seed set and seed weight. They concluded that the time available for seed development was too short for these plants. Thus, in short season environments, the timing of reproductive events is probably most influenced by the limited time available for seed maturation, which selects for early flowering individuals. I found (unpublished data) that the flower visiting activity at S in 1990 is highest early in the flowering season. This may also favor early flowering because of the increased possibilities for pollination at this time.

In the two communities examined, flowering peaks were either clumped (S) or randomly distributed (K). Therefore, on the basis of Poole and Rathcke’s (1979) method, there are no indications that past interspecific competition influenced flowering times to minimize overlap. Competitive selection pressure was probably too infrequent, nondirectional, or weak to produce character displacement in flowering times because of the probable high degree of environmental stochasticity in these areas and the reliance on autogamous pollination or asexual reproduction. However, care should be taken when interpreting data for species interactions because no experimental testing or measurements on fitness were done. Furthermore, it must be pointed out that flowering curves for only seven species were analyzed. These species represent only a proportion of all species in the communities, and inclusion of more species into the analyses could give different results. Rabinowitz et al. (1981) found that the dispersion of flowering peaks of wind- and insect-pollinated prairie plants did not deviate from a random assemblage. These authors suggested several causal scenarios to explain the lack of a community-wide pattern but pointed out the difficulties of explaining properties of flowering times distribution from purely observational studies like this one.

Table 3. Visitation rates (VR) to the species at Mount Sandalsnut (S) in 1990 and 1991 and at Mount Kvanndjofn (K) in 1991

<table>
<thead>
<tr>
<th>Species</th>
<th>VR</th>
<th>SD</th>
<th>n</th>
<th>Σ vis</th>
<th>Σ fl</th>
<th>VR</th>
<th>SD</th>
<th>n</th>
<th>Σ vis</th>
<th>Σ fl</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cerastium alpinum</td>
<td>0.33</td>
<td>0.69</td>
<td>60</td>
<td>42</td>
<td>1024</td>
<td>0.42</td>
<td>0.48</td>
<td>41</td>
<td>109</td>
<td>655</td>
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<tr>
<td>Leontodon autumnalis</td>
<td>0.36</td>
<td>0.57</td>
<td>46</td>
<td>43</td>
<td>741</td>
<td>0.15</td>
<td>0.24</td>
<td>52</td>
<td>45</td>
<td>1040</td>
</tr>
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<td>Parnassia palustris</td>
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<td>0.78</td>
<td>32</td>
<td>31</td>
<td>372</td>
<td>0.57</td>
<td>0.69</td>
<td>33</td>
<td>86</td>
<td>388</td>
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<tr>
<td>Potentilla crantzii</td>
<td>0.18</td>
<td>0.39</td>
<td>36</td>
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<td>504</td>
<td>0.69</td>
<td>0.99</td>
<td>53</td>
<td>134</td>
<td>568</td>
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<tr>
<td>Ranunculus acris</td>
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<td>0.99</td>
<td>115</td>
<td>97</td>
<td>1436</td>
<td>0.72</td>
<td>0.90</td>
<td>77</td>
<td>232</td>
<td>1144</td>
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<tr>
<td>Taraxacum croceum</td>
<td>1.20</td>
<td>1.62</td>
<td>92</td>
<td>106</td>
<td>681</td>
<td>1.05</td>
<td>1.44</td>
<td>64</td>
<td>96</td>
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<td>Silene acaulis</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.03</td>
<td>0.06</td>
<td>47</td>
<td>49</td>
<td>3695</td>
</tr>
<tr>
<td>Geranium sylvaticum</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1.83</td>
<td>1.53</td>
<td>34</td>
<td>277</td>
<td>3075</td>
</tr>
</tbody>
</table>

**NOTE:** VR is presented as the mean ±SD of the number of visits per flower per hour in all periods. The number of visits observed during sampling periods from 1990 at S and from 1991 at both sites was multiplied by six and three, respectively, because observation periods lasted for 10 min in 1990 and for 20 min in 1991. n, number of 10- or 20-min observation periods; Σ vis, total number of visits observed; Σ fl, total number of flowers observed in all periods.

*Flower density within squares not quantified for S 1990.
**Flower visitors**

The dominance of flies in the visitor assemblage agrees with the open flower morphology of the plants. Zygomorphic flowers, often associated with bumblebees, are rare in the Finse area. A survey of Faegri’s (1967) plant list from Finse reveals that only 10% of the species have this flower form, and visits by Bombus spp. were observed to only 18 of 119 flowering species growing naturally at Finse (wind-pollinated species excluded). No other bees have been observed in the Finse area (personal observation). The dominance of Diptera as flower visitors has also been recognized in other alpine areas (Australia: Inouye and Pyke 1988; New Zealand: Primack 1983; White Mountains, United States: McCall and Primack 1992; Andes: Arroyo et al. 1982) and in arctic Canada (Kevan 1972). Compared with these areas, the Finse area is different in its complete lack of bees others than Bombus spp., in the very low abundance of Bombus spp., and in the scarcity of syrphids.

Each plant species was visited by many insect species. This observation corresponds with the floral morphology of the species studied. All of them had a flower morphology permitting visits by a large range of species. A generalist flower form, e.g., bowl shaped, is interpreted as an adaptation to unpredictable pollination conditions (e.g., Rathcke 1988), such as those at Finse. The potential for pollinator-restrictive flower morphologies, e.g., zygomorphic flowers, would seem to be low because of the scarcity of specialized pollinators.

**Niche overlaps in visitor species**

In general, the flowering species shared visitor species to a large extent. This reflects the large similarity between the species, both in flower morphology and flowering time. At S, species pairs with a high overlap one year also had a high overlap the next year, indicating that the same species may be pollinated by the same insects in consecutive years. Such similarity between species pairs was not found on a spatial scale. Species pairs having a high overlap in visitor species at one site in 1991 did not necessarily have a high overlap at the other site. This indicates that the visitor fauna is more variable in space than in time and that a population’s visitor assemblage is determined by its location more than by its flower morphology. At K in 1991, overlap in flowering time was not a good predictor of overlap in visitor species because of sequential sharing of visitors in eight species pairs. Such sharing of visitors might benefit individuals in both species because presence of one species results in an increase in visitation rate to the other species (Waser and Real 1979; McGuire and Armbruster 1991).

The positive correlation between overlap in flowering time and visitor species at S shows that species flowering simultaneously are visited by the same insect species available in that period.

**Visitation rates**

The average visitation rate values for all species at the two sites correspond to those found in other alpine areas. McCall and Primack (1992) found a visitation rate of 1.32 visits per flower per hour in alpine North America. In alpine Australia, Inouye and Pyke (1988) measured a visitation rate of 0.87 visits per flower per hour. Arroyo et al. (1985) measured a decrease in visitation rate with increasing altitude in Andes. They found visitation rates of 0.41, 0.25, and 0.19 visits per flower per hour at the low-, middle-, and high-elevation sites, respectively. Also at Finse, a decrease in visitation rate with altitude was found. The large difference between the two sites is a result of a lower density of flower visitors at S, coupled with a higher flower density at this site. The differences in visitation rates at S between years is most easily explained by differences in climatic conditions during time of sampling and fluctuations in the insects population densities between years. Taraxacum croceum was much more attractive to the insects than the other species studied, probably because of its showy floral display and the large quantities of nectar and pollen it produces (personal observation). The species assemblage studied showed no divergence away from this species, either in time of flowering or in visitor species.

Community studies on pollination ecology have usually been carried out in species-rich tropical and temperate floras and often on species with highly specialized pollination modes. More work is needed in communities in which unspecialized pollinators dominate and in which the influence of abiotic factors like length of flowering season and climate is likely to govern community-wide patterns of flowering times, pollination mode, and reproductive success.

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