

Early flowers of *Bartsia alpina* (Scrophulariaceae) and the visitation by bumblebees

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SUMMARY

Phenology and insect visitation of early flowers of *Bartsia alpina*, a perennial herb, in a subalpine population in northern Sweden, were investigated to find causes for low seed set in early flowers. Bumblebees are the only visitors of *B. alpina*; they collect pollen and nectar. Flower phenologies of several bumblebee visited species and their nectar standing crops were measured. Flowering of *Bartsia* started simultaneously with *Astragalus frigidus* while *Pedicularis lapponica* was nearly out of flower. Early blooming flowers of *Bartsia* received fewer visits than later blooming ones. The large volumes of nectar with a high sugar concentration in early flowers indicate that bumblebees neglect or fail to discover early blooming flowers of *Bartsia*. Early in the season seven bumblebees species visited *Bartsia* but later on *Bombus pascuorum* was dominant. This species was also an important visitor of *Astragalus*. A rather low percentage of the pollen loads contained only *Bartsia* pollen, 27–28%, during early and peak flowering of *Bartsia*. Corbicular loads of *B. pascuorum*, the most frequent visitor of *Bartsia*, often contained *Bartsia* but also contained *Astragalus* pollen and to a lesser extent Ericaceae pollen (probably of *Andromeda polifolia*). The large variation in composition of corbicular loads indicated that bumblebees were not faithful to *Bartsia* only and that several plant species were visited by the same individuals. Bumblebee visitation of *Bartsia* and *Pedicularis* during a single trip may result in heterospecific pollen deposition which may lower seed set in *Bartsia*. Bumblebee visitation of *Bartsia* and *Astragalus* during a single trip may not result in heterospecific pollen deposition on *Bartsia* flowers due to the deposition of *Bartsia* pollen on the dorsal and *Astragalus* pollen on the ventral side of the body of bumblebees. Low seed set of early blooming flowers of *B. alpina* was probably due to low visitation rates by bumblebees. In addition, seed set of early flowers may be low due to heterospecific pollen depositions but this also may occur later in the season if the composition of corbicular loads is considered. After artificial heterospecific pollinations seed set decreased as compared with pure pollinations.

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Key-words: *Bartsia alpina*, bumblebees, nectar, phenology, pollen load, seed set.

INTRODUCTION

In entomophilous plants, pollen flow and seed set is determined by the visitation rates of insects and their pollination efficiency. Phenology of both plants and visitors, size and shape of the population and flower density within the population have been demonstrated to be important for visitation rates (Zimmerman 1980; Handel 1983; Rathcke 1983). Visitation of seasonally early flowers when flower density is low and the actual flower population size is small is often unpredictable. According to Thomson (1982) visitation is generally low early in the flowering period, but then increases and remains high for the duration of the flower period. This pattern was observed in *Melampyrum pratense* (Jennersten & Kwak 1991) and *Polemonium foliosissimum* (Zimmerman 1980). However, the reversed pattern, that early flowers received more visits than flowers blooming later in the season, was found for *Viscaria vulgaris* (Jennersten *et al.* 1988) and *Phyteuma nigrum* (Kwak *et al.* 1991).

Visitation rates and also seed set may change during the season due to competition with other flowering species (Motten 1982; Campbell 1985). The conspicuousness of early flowers may influence visitation rate (Jennersten & Kwak 1991), since pollinators fail to discover early flowers of a plant species that just starts to flower. Low seed set of early flowers can also be caused by the negative effects of heterospecific pollen depositions, due to competition with other flowering species (Campbell & Motten 1985). Deposition of heterospecific pollen on stigmas may negatively influence seed set due to several processes, for example limiting space on the stigma or allelopathic effects on conspecific pollen (Feinsinger 1987).

In a study on the mating system and gene flow of *Bartsia alpina* (Scrophulariaceae), Molau *et al.* (1989a) found that fruit abortion was highest early and late in the flowering season. Fruit abortion and low seed set could be due to the lack of conspecific pollen during periods of low visitation rates, or to heterospecific pollen depositions due to the switch in the major food plant of visiting bumblebees. In another paper Molau *et al.* (1989b) emphasized the importance of seed set of early flowers for two reasons: first, seeds produced during low flower density (early and late in the flowering season of a species) are more outcrossed than seeds produced during peak flowering. Secondly, seed production of early flowers contributes largely to the total seed production in *B. alpina* because seed production of peak flowers suffers extremely intensive predation.

The aim of the present study was to focus on the early flowering period of *B. alpina* to find reasons for low seed set in early flowers. It was hypothesized that competition for bumblebee visitation and heterospecific pollen deposition play a part. Special attention was paid to *Pedicularis lapponica* (Scrophulariaceae), mentioned as possible competitor by Molau *et al.* (1989a).

MATERIALS AND METHODS

Plant species and study site

Bartsia alpina L. and *Pedicularis lapponica* L. (throughout this paper we use generic names for plants and complete names for bumblebees) are perennial, hemi-parasitic

Table 1. Main differences between flowers of *Bartsia alpina* and *Pedicularis lapponica*

Character	<i>Bartsia alpina</i>	<i>Pedicularis lapponica</i>
Flower colour	Deep purple	Light yellow
length	19–20 mm	15–16 mm
life time	5.8 ± 1.2 days (*)	3.3 ± 1.1 days (**)
Fragrance	Weak	Very strong
Corolla tube length	16–17 mm	9–10 mm
Pollen presentation	Visible	Concealed
colour	Whitish	Light yellow
grains per flower	21 600 (*)	55 600 (**)
diameter	32 µm	19 µm
morphology	Tricolpate	Dicolpate
Nectar (***)		
volume after 24 h	0.99 ± 0.16 µl	0.43 ± 0.10 µl
production (mean ± SE)		
concentration after	15.1 ± 0.5%	19.6 ± 1.0%
24 h production		
Visitors (***)	<i>Bombus alpinus</i> <i>B. balteatus</i> <i>B. jonellus</i> <i>B. lapponicus</i> <i>B. pascuorum</i> <i>B. pratorum</i>	<i>Bombus alpinus</i> <i>B. balteatus</i> <i>B. jonellus</i> <i>B. lapponicus</i> <i>B. pascuorum</i> <i>B. pratorum</i>

*From Molau 1991; **from Eriksen *et al.* 1993; ***presented as data in this paper.

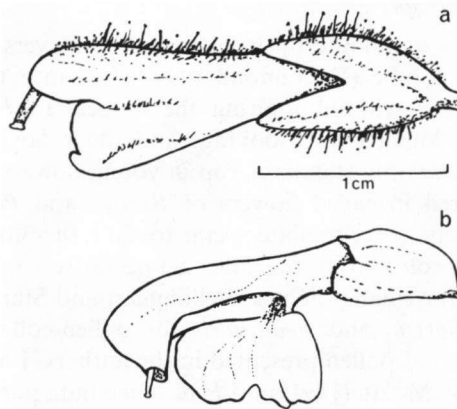


Fig. 1. The flowers of *Bartsia alpina* (a) and *Pedicularis lapponica* (b), both with a protruding pistil.

herbs with zygomorphic flowers. *Bartsia* has an amphi-atlantic and *Pedicularis* a circumpolar distribution. A large population of *Bartsia* was intermingled with *Pedicularis* in the study area. The most obvious difference between the two bumblebee pollinated species is flower colour: deep purple in *Bartsia* and light yellow in *Pedicularis*. Other differences important for pollination are listed in Table 1; the flower morphology is shown in Fig. 1.

The field work was carried out mainly from 22 June to 10 July 1991 during the stay of the first author (phenology records were continued until 24 July) in a subalpine open

field of creeping soil at about 400 m a.s.l. near Abisko Research Station (northern Sweden 68°21'N, 18°49'E), the same population as described in Molau *et al.* (1989a, b).

Flower phenologies of *Bartsia*, *Pedicularis* and the other bumblebee-visited species *Rhododendron lapponicum* L., *Andromeda polifolia* L. and *Astragalus frigidus* L. were recorded every second day in permanent plots of different size depending on the species.

Plant visits, bumblebee behaviour and pollen loads

In an area of about 17,000 m², bumblebee species visiting the plant species *Bartsia*, *Pedicularis*, *Rhododendron*, *Andromeda*, *Astragalus* and *Vaccinium uliginosum* L. were noted. The behaviour of bumblebees on the mentioned species was recorded as nototribically or sternotribically (pollen deposited on the dorsal or ventral side of the body, respectively), collecting pollen and/or nectar. Bumblebee nomenclature follows Løken (1973).

Pollen loads on the body of bumblebees were investigated on microscope slides; bumblebees visiting *Bartsia* were caught, anaesthetized slightly with carbon dioxide and cleaned with a piece of a sticky gel, prepared according to Beattie (1972).

Corbicular loads were collected from all flower-visiting bumblebees and the colour of the load noted. Loads were stored for later microscopical analysis.

Although loads containing *Astragalus* pollen were orange-coloured, the amount of *Bartsia* and *Pedicularis* pollen could not be determined in the field due to the similarity in colour. However, pollen of the two species differed both in size and morphology (Table 1). A reference collection of pollen from bumblebee-visited plant species was prepared.

Attractiveness of the plant species

Nectar was measured as standing crop in open visited flowers ($n=30$ per species) by inserting a 1 μ l capillary tube (Drummond microcaps) into the corolla and gently moving around the ovary without injuring the tissues. In *Bartsia* and *Pedicularis* standing crop in both young (fresh looking) and older flowers, was measured; in *Astragalus* and *Andromeda* only standing crop in young flowers was measured. Nectar production was measured in caged flowers of *Bartsia* and *Pedicularis*, by allowing previously emptied flowers to accumulate nectar for 24 h ($n=30$). The sugar content (% sucrose = g sucrose/100 g solution) of the collected nectar was measured using a pocket refractometer modified for small volumes (Bellingham and Stanley, Tunbridge Wells).

The attractiveness of *Bartsia* and *Pedicularis* for pollen-collecting bumblebees was considered as the amount of pollen presented in the anthers. For this purpose we used *Bartsia* data published by Molau (1991) and *Pedicularis* data published by Eriksen *et al.* (1993).

Artificial pollination and seed set

To detect the possible effect of foreign pollen on the seed set of *Bartsia*, virgin, caged flowers were hand-pollinated with both *Bartsia* and *Pedicularis* pollen or only with *Bartsia* pollen. *Bartsia* pollen was taken from flowers at a distance of at least 5 m, although Molau *et al.* (1989a) found no influence of distance on seed set. Each plant has two flowers on the same node so both treatments could be applied on flowers on the same inflorescence. Pollen of both species was applied until stigmas were light coloured. In order to prevent predispersal seed predation, which can destroy many of the seeds

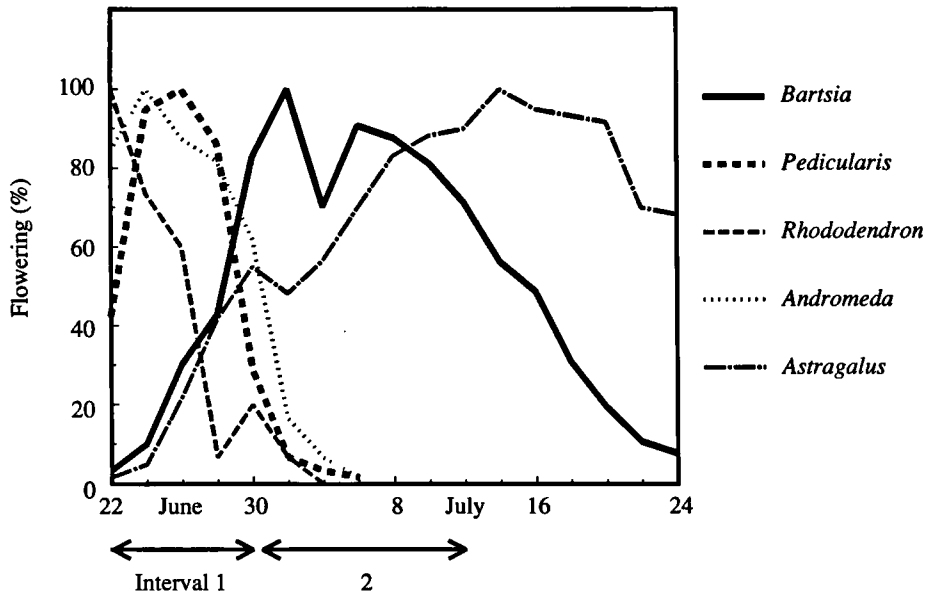


Fig. 2. Phenology of bumblebee visited plant species in the subalpine meadow in 1991. The highest number of blooming flowers per day is 100%. The two intervals (22–30 June and 1–10 July) compared in this study are indicated. Note that phenology of *Bartsia alpina* and *Astragalus frigidus* is followed after time interval 2.

produced (Molau *et al.* 1989b), the pollinated flowers remained caged for 5 weeks until seed capsules were collected. The number of well developed fruits and seeds was counted.

RESULTS

Phenology

When the observations started on 22 June both *Bartsia* and *Astragalus* had just opened their first flowers (Fig. 2). During time interval 1 (22–30 June 1991), *Pedicularis* and *Andromeda* had their peak flowering. *Rhododendron* was nearly out of flower when *Bartsia* started to flower. Interval 2 (1–10 July) contained the flowering peak of *Bartsia* while the number of flowers of *Astragalus* continued to increase during interval 2. Note that in Fig. 2 observations on the phenology were continued after interval 2.

Plant visits, bumblebee behaviour and pollen loads

Bumblebee observations were made between 22 June and 10 July. The abundance of bumblebees, and hence the number of observations, were low at the beginning of the observation period. The main reason for this was the absence of workers. Although the first worker (belonging to the species *B. jonellus*) was observed on 24 June, workers were not abundant until 2 July. The percentages of workers observed during the first two and the last two days in this study ranged between 0–14 and 51–55, respectively. Thus, early flowers of *Bartsia* were visited and pollinated only by bumblebee queens.

In total, the 576 observations of foraging bumblebees included eight plant and eight bumblebee species (Table 2). The most frequent bumblebee species in the study area were *Bombus pascuorum* (314 observations) and *B. lapponicus* (120 observations),

Table 2. Bumblebee species, caste (Q=queen, W=worker) and proboscis lengths in mm (after Ranta & Lundberg 1980) and the number of individuals visiting various plant species; Ba = *Bartsia alpina*, Af = *Astragalus frigidus*, Pl = *Pedicularis lapponica*, Vu = *Vaccinium uliginosum*, Ap = *Andromeda polifolia*, Vv = *Vaccinium vitis-idaea*, Rl = *Rhododendron lapponicum*, Pc = *Phyllodoce caerulea*

<i>Bombus</i>	Case	Proboscis length	Ba	Af	Pl	Vu	Ap	Vv	Rl	Pc	Total
<i>balteatus</i>	Q	17.8	23		1						24
<i>pascuorum</i>	Q	15.1	140	75	3	13	13		2		246
<i>hortorum</i>	Q	14.6	7								7
<i>pratorum</i>	Q	13.1	3			2	1				6
<i>alpinus</i>	Q	12.9	4	1		6	4			1	16
<i>lucorum</i>	Q	12.1	1	1		3	2	1			8
<i>jonellus</i>	Q	11.5	2	1	1	2	2				8
<i>pascuorum</i>	W	11.5	32	33		3					68
<i>lapponicus</i>	Q	11.2	10	1	4	30	17	2		1	65
<i>balteatus</i>	W	10.8	10	7			1				18
<i>pratorum</i>	W	9.6		2		6					8
<i>alpinus</i>	W	9.2				1					1
<i>lapponicus</i>	W	8.7			2	45	6	2			55
<i>jonellus</i>	W	6.8	7		2	32	3	2			46
			239	121	13	143	49	7	2	2	576

followed by *B. jonellus* (54 observations) and *B. balteatus* (42 observations). During the study time the plant species *Bartsia*, *Vaccinium*, *Astragalus* and to a lesser extent *Andromeda* were important for bumblebees (Table 2).

Plant species with long corollas (*Astragalus*, *Bartsia* and *Pedicularis*) were visited by bumblebee species or castes with long probosces. Plant species with short corollas (*Andromeda* and *Vaccinium*) were visited by species with short probosces, namely *B. lapponicus* and *B. alpinus* (Table 2).

Early in the flowering season bumblebees collected pollen on *Bartsia* by buzzing (Michener 1962; Buchmann 1983) to release pollen grains out of the anthers. However, later in the season bumblebees stopped buzzing but were still collecting pollen on *Bartsia*. In the latter case the heads of these bumblebees were white-coloured with pollen and *Bartsia* pollen was found in the corbiculae (Table 3).

Most bumblebee species visited the same plant species in a similar way: either upright resulting in pollen deposition nototribically (dorsal site of the body, *Bartsia*, *Pedicularis*) or upright with pollen deposition sternotribically (ventral side of the body, *Astragalus*, *Andromeda* and *Vaccinium*). *B. jonellus* was the most important exception, visiting *Bartsia* flowers upright with pollen deposition nototribically and *Pedicularis* flowers upside down with pollen deposition sternotribically (ventral side of thorax and abdomen). Thus on *B. jonellus* pollen of the two species are deposited on two different sites of the body, and on all other bumblebee species pollen of *Bartsia* and *Pedicularis* were expected on the head-thorax.

Pollen from *Bartsia* was found on the bodies (corbicular loads excluded) of all 15 bumblebees visiting *Bartsia* (number of pollen grains 788 ± 121 , mean \pm SE). The mean percentage of *Bartsia* pollen in the body load of bumblebees was 86 (range 30.0–99.8%). *Bartsia* pollen was present both on the dorsal and ventral side of the body. Pollen of

Table 3. Composition of corbicular loads, collected during two time intervals; % loads containing various species are given for all bumblebee species foraging on *Bartsia alpina*, and for the bumblebee species *Bombus pascuorum*

Date	<i>Bartsia</i>	<i>Pedicularis</i>	<i>Astragalus</i>	<i>Ericaceae</i>	<i>Salix</i>
All bumblebee species					
24–30 June (n=36)	94.4	25.0	22.2	44.4	2.8
1–10 July (n=30)	93.3	10.0	46.7	36.7	0
<i>Bombus pascuorum</i>					
24–30 June (n=12)	91.7	16.7	50.0	58.3	0
1–10 July (n=18)	100	11.1	55.6	38.9	0

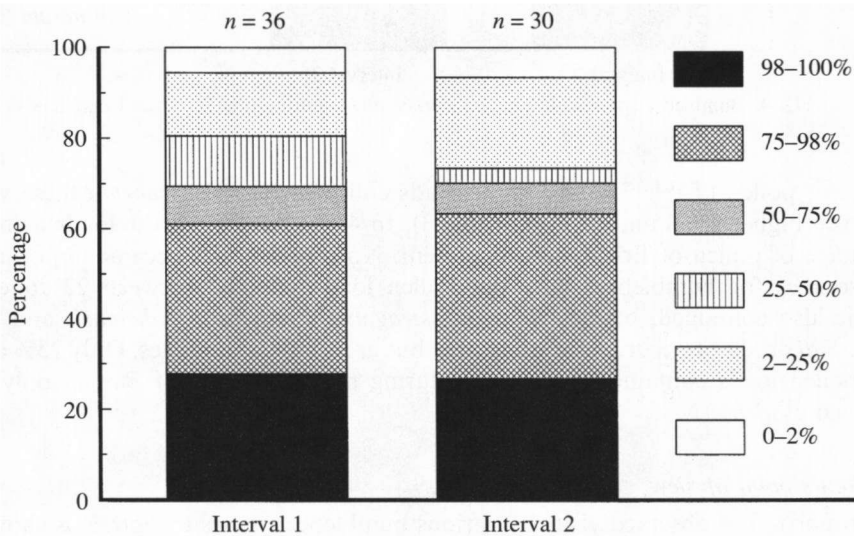


Fig. 3. Frequency of pollen loads with different contributions of *Bartsia* pollen, collected from bumblebees foraging on *Bartsia alpina* during two time intervals (22–30 June and 1–10 July).

several other plant species was present: the tetrads of pollen characteristic of Ericaceae, in this study represented by *Andromeda* and *Vaccinium*, were found mostly as foreign species both on the dorsal and ventral side of the body. *Pedicularis* and *Astragalus* pollen grains were also found: *Pedicularis* on the dorsal and *Astragalus* on the ventral side of the body.

At least 65% of all observed bumblebees carried pollen loads in their corbiculae (Fig. 3, Table 3). Both during early and peak flowering of *Bartsia* the percent of pure *Bartsia* pollen loads was low. Only 27–28%, respectively, of the loads sampled from bumblebees foraging on *Bartsia* contained only *Bartsia* pollen (less than 2% pollen grains of other species). *Astragalus* was an important pollen resource both during early and peak flowering of *Bartsia*, 22 and 47%, respectively, of the loads contained

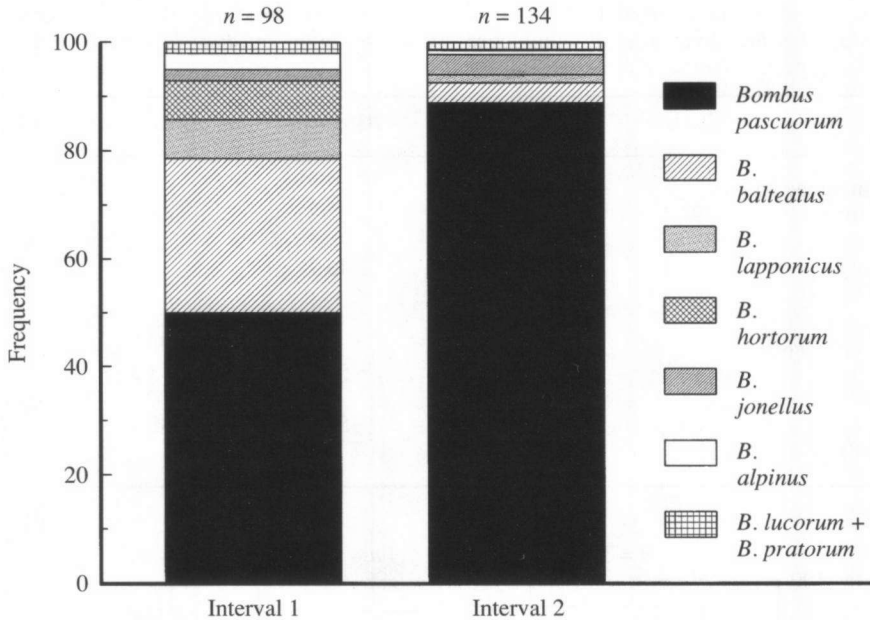


Fig. 4. Bumblebee species foraging on *Bartsia alpina* during time intervals 1 and 2.

Astragalus pollen (Table 3) and for the loads collected by *B. pascuorum* these values were even higher (50.0 and 55.6%) (Table 3). In 44% and 37% of the loads a smaller percentage of pollen of Ericaceae was present. No other species became important as food sources for bumblebees later on. Pollen loads sampled between 22 June and 30 June also contained, besides *Bartsia*, *Astragalus*, Ericaceae, *Pedicularis* and *Salix* pollen. *Salix* did not occur in the study area but grew beside the edges. Only 25% of the early pollen loads contained *Pedicularis*; during peak flowering of *Bartsia* only 10% contained *Pedicularis*.

The plant's point of view

The proportion of observed visits by various bumblebee species to *Bartsia* is shown in Fig. 4. Early flowers of *Bartsia* were visited by seven bumblebee species. Two bumblebee species, *B. balteatus* (only early in the season) and *B. pascuorum*, showed the highest visitation frequencies on *Bartsia*. However, due to the low number of visits spent by *B. balteatus* ($n=34$, 16% of the total number of bumblebees visiting *Bartsia*, Table 2), *Bartsia* is more important as a food source for *B. balteatus* than this bumblebee species is for the pollination of *Bartsia*. With time, the dominance of *B. pascuorum* as main visitor became evident (Fig. 4).

The number of observations of bumblebee visits to *Pedicularis* was low (Table 2), due to the progress in flowering. The proportion of observed visits by bumblebees to *Astragalus* showed a similarity in visitation pattern with *Bartsia*. Early in the season (interval 1) several bumblebee species visited *Astragalus*, but later on the flowers were exclusively visited by the main visitor, *B. pascuorum*. Altogether, 72% of all visits to *Bartsia* and 89% of all visits to *Astragalus*, during the total observation period, were made by *B. pascuorum* (Table 2).

Attractiveness of the plant species

Standing crop of nectar in *Bartsia* decreased during the season both in young (0.72 ± 0.21 – 0.04 ± 0.02 μl , means \pm SE) and old flowers (0.18 ± 0.03 – 0.06 ± 0.01 μl). Only 6.7% of the early flowers were empty, and 56.7% of the later flowering *Bartsia* flowers were empty. Concentration of nectar in old flowers on 24 June was $44.2 \pm 1.8\%$, the concentration of nectar in young flowers dropped from $49.3 \pm 0.7\%$ to $19.9 \pm 0.8\%$ (24 June and 27 June). This is an indication that until 24 June the nectar was accumulated and water evaporated during a longer time period. This was also indicated by the low sugar concentration of freshly produced nectar ($15.1 \pm 0.5\%$).

Nectar standing crop and concentrations did not differ between uncaged flowers of *Pedicularis* and *Bartsia* (27 June). Nectar production during 24 h (caged flowers) was two times larger in *Bartsia* (0.99 ± 0.16 μl , mean \pm SE) than in *Pedicularis* (0.43 ± 0.01 μl). On 27 June standing crop of nectar in flowers of four bumblebee visited plant species was measured. *Andromeda* had large volumes (3.87 ± 0.36 μl per flower), significantly higher than the other three species (Student–Newman–Keuls test, $P < 0.05$). *Bartsia* had a volume of 0.18 ± 0.05 μl , *Pedicularis* 0.53 ± 0.12 μl and *Astragalus* 0.18 ± 0.05 μl . The four species did not differ significantly in the concentration of the nectar (range: 19.9–26.9%). The amount of energy per flower was highest in *Andromeda*, due to its large volume.

Pedicularis flowers contained 2.6 times more pollen grains than *Bartsia* flowers but due to the small sizes of *Pedicularis* grains (Table 1) the total volume in pollen per flower (a possible measure for the value of the plant species as pollen source) in *Bartsia* was only 1.8 times that of *Pedicularis*.

Artificial pollination and seed set

Percentage fruit set after pollination was higher than after mixed (with *Pedicularis* pollen) pollination, 82.2 and 70.1%, respectively. Seed set after artificial pollination of *Bartsia* flowers was also significantly influenced by the presence of *Pedicularis* pollen (t -test, $P < 0.05$); seed set was reduced from 36.7 ± 6.3 (mean \pm SE) seeds per capsule for pure pollinations to 20.3 ± 4.8 for mixed pollinations. Caging of the experimental flowers did not entirely prevent predispersal seed predation, and 32% of the capsules were lost.

DISCUSSION

Early in the flowering period of a species when its flower density is low, insect visitors sometimes fail to detect, or neglect to visit a certain plant species. At a certain moment bumblebees start to visit flowers as the minor species while majoring on another one (Heinrich 1979). For *Bartsia* and also for the related species *Melampyrum pratense* (Jennersten & Kwak 1991) there was a delay of some days after the start of flowering before bumblebees started to visit the plant species. In other species, bumblebees visited first flowering inflorescences intensively (Kwak *et al.* 1991). Direct observations on foraging bumblebees early in the flowering period of *Bartsia* revealed a low visitation rate. This may result in a lack of conspecific pollen and thus lower the seed set.

The lack of visitation early in the season resulted in a high standing crop of nectar with an unusually high sugar concentration (49%) when compared with flowers with nectar produced during 24 h (15%). In the present study we used the combination of nectar standing crop, nectar production rate and sugar concentration as a measure for

bumblebee visitation. Standing crop is not only a function of the underlying secretion pattern but also of the foraging of previous visitors in combination with post-secretion evaporation or dilution.

Analysis of corbicular loads gives information on the plant choice by bumblebees over a long period of foraging. Loads may contain pollen from plants mainly visited for pollen, from plants visited for pollen and nectar and probably to a lesser extent from plants visited for nectar only. In the case of low bumblebee frequencies, analysis of corbicular loads may be very useful to collect more information about flower visitation by bumblebees. However, the analysis of corbicular loads is seldom used. The composition of the corbicular loads indicated that *Bartsia* was visited very often, also during peak flowering, in combination with other plant species. The percentage of pure corbicular loads was rather low during both early and peak flowering of *Bartsia*, compared with other studies. In particular, the low percentage of pure loads during peak flowering was not expected. *Astragalus* appeared to be an important second species although the loads were taken from bumblebees foraging on *Bartsia*. Macior (1982) found in only three of a total of 24 samples (populations of species) of *Pedicularis* a lower purity percentage than 30%. In a recent paper Macior (1995) mentioned that *Pedicularis racemosa*, out of five *Pedicularis* species, had the lowest percentage of pure loads: 59%. Corbicular loads thus often contained more than one plant species indicating that more than only *Bartsia* was visited during the foraging trips. Bumblebees could have visited specific plant species during longer periods or could have switched continuously. Continuously switching between plant species may possibly lead to heterospecific pollen deposition. We found stigmas contaminated with foreign pollen (6–12%, unpublished data) during both periods. It is unlikely that heterospecific pollen deposition is the main reason for low seed set of early flowers.

Bartsia flowers intermingled with flowering *Astragalus* or *Pedicularis* may be visited earlier than flowers in pure stands. However, in general switching between two plant species may lead to heterospecific pollen deposition and lead to a lower seed set. This risk of heterospecific pollen transfer was obvious for bumblebee species switching between *Bartsia* and *Pedicularis*, except for *B. jonellus*, a bumblebee species occurring in very low numbers on *Bartsia* and *Pedicularis*. Switching between *Bartsia* and *Astragalus* resulted in pollen deposition on two different sites of the body, respectively, on the dorsal and ventral side of the bumblebee's body. The ventral side did not touch the stigma of *Bartsia*. Thus, *Bartsia* flowers intermingled with *Astragalus* may receive more and earlier visits than flowers in pure stands without the risk of heterospecific pollen transfer. Bobisud & Neuhaus (1975) calculated that two plant species with morphologically similar flowers may, under certain circumstances, gain more visitation by pollinators when occurring together compared with when they grow separately. Pollen of *Pedicularis* was not so often found in the corbicular loads as *Astragalus*, indicating that sharing of visitors between *Astragalus* and *Bartsia* occurred more often than between *Pedicularis* and *Bartsia* at least in 1991, in contrast to the hypothesis of Molau *et al.* (1989a). This was especially true for the main visitor of *Astragalus* and *Bartsia*, *B. pascuorum*. The rate of sharing visitors is also influenced by the number of flowers present. For *Pedicularis* it is known that both the start and the total number of flowers produced may differ between years (Molau 1993) whereas the start and number of flowers of *Bartsia* remains fairly constant. Therefore, the number of flowers of *Pedicularis* and *Bartsia* present, simultaneously, the sharing of visitors, and hence the risk of heterospecific pollen deposition may change from year to year.

After the peak of flowering of *Pedicularis*, both *Bartsia* and *Astragalus* flowers were present and bumblebees had to make their choice between the two species, which were increasing in number of flowers. *Bartsia* was probably in a disadvantageous position because the appearance of flowers is not as conspicuous as in *Astragalus*, at least for man. *Bartsia* provides both nectar and pollen. Some bumblebee species, *B. pascuorum* included (Prýs-Jones & Corbet 1987) prefer to collect pollen and nectar during the same visit. Thus for *Bartsia* competition with other pollen and/or nectar providing species may have occurred, for instance with *Astragalus*, or with *Andromeda* for nectar. Pollen of the latter species was often found on the bodies of bumblebees, but not in large numbers.

The most important bumblebee species throughout the season visiting *Bartsia* was *B. pascuorum*; queens were the most important early foragers; later on the workers became dominant. This long- to medium-tongued species also showed a preference for *Astragalus* (Table 3) and, to a lesser extent, for *Vaccinium* species. Early in the season seven bumblebee species visited *Bartsia*, indicating that more species were minoring or majoring on *Bartsia* and that *B. pascuorum* was not the only visitor of early flowers.

In conclusion, low seed set in seasonally early flowers of *Bartsia* was probably due to a low visitation rate resulting in a lack of conspecific pollen, hence a quantitative aspect. In addition, seed set of early flowers may be low as a result of heterospecific pollen (*Pedicularis*) deposition, a qualitative aspect of pollination but it is not likely that this had occurred in 1991. *Pedicularis* shows a great variation in flowering phenology. There may occur years with a greater flowering overlap than in 1991 (according to Molau). In such years the chance on heterospecific pollen deposition may also be larger.

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