

POLLINATION ECOLOGY OF THE HIGH LATITUDE, DIOECIOUS CLODBERRY (*RUBUS CHAMAEMORUS*; ROSACEAE)¹

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In a 3-yr study, we examined the pollinator guild and intersexual floral characteristics of the dioecious, perennial cloudberry (*Rubus chamaemorus*), which flowers in early spring. The findings contribute to our general understanding of pollination ecology at high latitudes and provide important information for the commercialization of cloudberry. Female flowers were smaller than males but provided more nectar, although this resource was low in both sexes. Insects from 43 families visited cloudberry flowers, yet four families (Apidae, Halictidae, Muscidae, Syrphidae) represented ca. 87% of all visitors observed. Introduction experiments revealed that apids and muscids are significantly poorer pollinators (based on fruit production) than halictids and syrphids, but when fruit mass or seed set was considered, there were no significant differences between families. Pollinator importance, a product of flower visitation frequency and seed set effectiveness, revealed that the dipterans were of paramount importance to the pollination of cloudberry. Furthermore, they are limited to cloudberry because their lapping mouthparts exclude them from accessing the nutritional rewards of competing Ericaceae flowers. While the total number of pollinator families observed suggest a generalist pollination system, if one considers the dominant pollinators (flies) as a functional group, then this insect–flower relationship could be considered a specialized one.

Key words: cloudberry; Diptera; functional groups; Hymenoptera; pollinator effectiveness; pollinator importance; Rosaceae; *Rubus chamaemorus*.

There has been considerable discussion in the recent literature concerning the degree of specialization in the interactions between flowering plants and their pollinators (Johnson and Steiner, 2000; Vázquez and Aizen, 2003; Fenster et al., 2004; Ollerton et al., 2007). While highly specialized interactions do exist (Paulus and Gack, 1990; Schiestl et al., 2004), generalization seems to be the rule, with plants being pollinated by several groups of insects (Herrera, 1987; Waser et al., 1996; Memmott, 1999). However, there has been some debate concerning the actual frequency that pollination generalization occurs in nature (Waser et al., 1996; Vázquez and Aizen, 2003) and how to define it (Johnson and Steiner, 2000; Herrera, 2005; Ollerton et al., 2005), as well as whether the proportion of generalized interspecific interactions increases with increasing latitude (Kevan and Baker, 1983; Ollerton and Cranmer, 2002).

According to Stebbins' "most effective pollinator principle" (1970), a plant should specialize on either its most effective or most abundant pollinator but only when visitation is reliable (Waser et al., 1996). Significant factors that could affect the reliability of pollinators are the density of the vector populations, as well as the limitations imposed by the existing floral structure and the external environment (Stebbins, 1970). Many studies examining the levels of generalization have simply

looked at pollinator species richness (Waser et al., 1996; Oleson and Jordano, 2002; Engel and Irwin, 2003), which may overemphasize the actual importance of some groups because of differences in pollinator effectiveness (Schemske and Horvitz, 1984; Herrera, 1987; Thompson, 2001). A more precise evaluation of the relative importance of each pollinator species would be obtained by combining visitation frequency and the quality of those interactions (pollination effectiveness) to generate an index of pollination importance (Spears, 1983) because such an index reflects the relative contribution of each pollinator group to the fruiting success of a plant species in a given season (Armbruster, 1993).

Plant–pollinator relationships are further complicated by the evolution of dioecy; the nutritional rewards from male and female flowers may vary considerably because the females do not produce pollen. Some dioecious plant species are pollinated by deception, when insect pollinators visit nonrewarding female flowers that resemble the rewarding males (Baker, 1976; Bawa, 1980; Dafni, 1984).

We used pollinator sampling and experimental pollinator manipulation to determine the extent of plant–pollinator generalization in a high latitude plant, the cloudberry (*Rubus chamaemorus* L.), a perennial, dioecious herb with a circumpolar subarctic distribution. Cloudberry fruits are considered a delicacy among northern communities in Russia, Scandinavia, Alaska, as well as in northern Quebec, Newfoundland, and Labrador. While commercial harvests in Scandinavia are in cultivated bogs, North American crops are currently limited to wild harvest. Thus, an understanding of cloudberry pollination ecology would not only contribute to elucidating the role of insect guilds in pollination at high latitudes in early spring, but may also provide valuable information within an applied agricultural context, because of the desire to grow cloudberry commercially in eastern Canada.

Cloudberry plants flower in the early spring, and pollination is entomophilous (Pelletier et al., 2001). Female cloudberry

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flowers are said to offer little or no food reward (Taylor, 1971) and to deceive its insect pollinators (Ågren et al., 1986). The aim of the current study was to describe the structure of its potential pollinator guild of cloudberry in northern Quebec and to determine the relative effectiveness and importance of the principal pollinator groups. In addition, we examined the effects of abiotic factors and the sex of flower on visitation patterns by the principal pollinator groups. We also looked at intersexual differences in pollinator attraction cues and nutrient rewards in cloudberry flowers.

MATERIALS AND METHODS

Study sites—In 1998, as part of a preliminary study to determine the potential pollinators, all insects seen hovering around cloudberry flowers were collected using a sweep net at St. Paul-du-Nord, Baie Comeau, Havre St. Pierre, and Blanc Sablon, representing a latitudinal gradient along the Quebec North Shore, Canada (48°34'N, 69°14'W to 51°25'N, 57°08'W). Subsequently, in 1999, 2000, and 2002, specific experiments, as well as plant and pollinator observations, were carried out in a high-density patch of cloudberry plants (50 × 100 m) in an ombrotrophic bog dominated by *Sphagnum fuscum* Klingg. at Havre St. Pierre, Quebec (50°16'N, 63°34'W). Additional data on flower morphology were also collected in bogs at Aguanish, Quebec in 2004 (50°15'N, 62°31'W).

Flowering phenology—To determine what species of flowers were available during cloudberry's flowering period, we randomly placed ten 0.5 × 2 m quadrats along randomly oriented 50-m transects in the bog opposite our study site at Havre St. Pierre. The open flowers of all plant species were counted in each quadrat every 2 d during the entire cloudberry flowering period (19 d in 1999 and 13 d in 2000). In this study area were two species of *Kalmia* (*K. polifolia* Wang. and *K. angustifolia* L.), and because they had almost identical floral forms and blooming periods, the data were pooled.

Flower size and shape—To examine the degree of variability in cloudberry flower form, we randomly collected fully open male and female flowers ($N = 25$ each) during the flowering period in 2000 and stored them in 70% alcohol. We later measured the length and width of the petals, the length of stamens and pistils, and the width of the androecium/gynoecium using a digital caliper.

In 2002, 20 flowers of each sex were collected randomly, and the petals were immediately glued to a black cardboard sheet and photographed by digital camera. Later, a sample of flowers, which contained examples of both average and extreme flower sizes and shapes, was selected for line drawings to represent the variability in flower forms for both sexes.

To measure the variability in petal number, we counted the petals on all flowers within 1 m on either side of randomly oriented transects through the bogs in Aguanish at two times when female flowers of cloudberry were in bloom (6 and 14 June 2004).

Food rewards—In 2000 and 2002, unopened flower buds were carefully sexed, enclosed in individually labeled, fine-mesh pollinator exclusion bags and checked daily. On the day they were first fully open, flowers were used to measure their available resources during one of five time intervals (0730, 1000, 1230, 1500, and 1730 hours). A maximum of 10 male and 10 female flowers were sampled per interval, and each flower was sampled only once. Males were examined for 4 and 11 d and females for 5 and 9 d in 2000 and 2002, respectively. In male flowers, the proportion of pollen available was estimated from the ratio of dehiscence anthers divided by the total number present. Nectar was collected from the base of male and female flowers with a 5 μ L glass pipette ($N = 369$ male and 227 female flowers for both years). At the beginning of each of the five sampling intervals, we recorded the air temperature and relative humidity using a handheld hygrometer. The volumes of available nectar sampled were too small to obtain reliable sugar concentration measurements by a refractometer.

Pollinator abundance and activity—Using the 1998 data on the potential pollinators of cloudberry at the different sites, we established four principal pollinator groups (those that represented >5% of all pollinators). In subsequent years, we counted all pollinators that were actual flower visitors, but only iden-

tified individuals from within the previously established principal pollinator groups.

To obtain seasonal patterns of pollinator activity, we also collected insects from another cloudberry patch of similar flower density, but at a sufficient distance (>500 m) to ensure pollinator removal did not affect our behavioral observations and pollination experiments (Pelletier et al., 2001). All pollinators that landed on cloudberry flowers within the patch were collected over 30-min sampling sessions at 0730, 1000, 1230, 1500, and 1730 hours throughout the cloudberry flowering period in 1999 and 2000. To test for abiotic effects on pollinator activity, we measured the air temperature and blackbody temperature at shrub level using temperature data-loggers (HOBO H8 #H08-002-02, Onset Computer Co., Bourne, Massachusetts, USA) and wind speed using a handheld anemometer (TA3000T, Airflow Development, Toronto, Ontario, Canada). Blackbody temperatures were obtained from a sensor inside a black metal sphere (diameter ca. 10 cm) because these measures approximate the effect of solar radiation on insect body temperature (e.g., Pivnick and McNeil, 1987). We noted the time, date, and sex of the flower from which each insect was collected. The insects were chilled in a cooler and then frozen for later identification.

Pollinator effectiveness—We measured two indirect indices of an anthophilous insect's potential as a pollinator (Spears, 1983) from the principal groups found visiting flowers in 1999 and 2000. First, the amount of pollen on the body of each individual was counted using a dissection microscope to provide an estimate of pollen carrying capacity ($N = 450$ individuals). Second, pollen was collected from the bodies of individual pollinators ($N = 79$) with a hexane wash and counted using a hemacytometer. Because cloudberry was the only Rosaceae plant in the habitat (A. O. Brown, personal observation), its pollen grains were easily distinguishable from the tetrad pollen of the other (Ericaceae) flowers. Thus, flower constancy of any given individual was determined using the proportion of rosaceous pollen relative to the total pollen present on the body.

We also obtained direct measurements of pollinator effectiveness (fruit set, fruit fresh mass, and percentage seed set) from an individual pollinator's success at pollinating a virgin female flower during a single visit ($N = 192$). A series of cloudberry flowers was isolated in cloth bags prior to opening and was checked daily to determine their developmental stage. Individuals of the major taxa of anthophiles visiting flowers in our collecting site were captured, chilled in a cooler for 15 min, and then allowed one single visit to a flower that had opened within the previous 24 h. This interaction was carried out in a clear plastic cage with mesh windows, so that all insect-flower interactions (e.g., whether stigmatic contact occurred, nectar sought or not) could be noted. The insect was immediately removed at the end of the visit, or the assay was terminated after 1 h if no flower visit was made. The number of ovules in the flower was then counted (which can be inferred from the number of stigma) and the plant immediately rebagged to prevent any further pollinator visits. Approximately 1 month later, fruit were harvested just before maturity (because mature fruits were frequently harvested by local residents, despite signs indicating that experiments were in progress), the seeds counted and fresh mass measured. Percentage seed set was calculated as the number of seeds formed in the fruit divided by the number of ovules originally counted in the flower. We discounted the data from introduction during which the insect groomed extensively before visiting the flower, to reduce the potential for some introductions to underestimate the pollinator's effectiveness.

Pollinator importance—We used the product of flower visitation frequency (the relative abundance of each pollinator group with respect to the whole pollinator community on cloudberry flowers at Havre St. Pierre) and seed set effectiveness for each of the principal pollinator groups to get a realistic measure of the interaction between any given pollinator group and cloudberry. The percentage seed set was used as the index of visit quality because it is the direct measure that is most closely related to the reproductive success of the plant and thus more subject to evolutionary pressures (Schemske and Horvitz, 1984). This index provides a relative scale of each principal pollinator group's contribution to seed set over time:

$$(\text{insects/unit time}) \times (\text{seed set/insect}) = (\text{seed set/unit time}),$$

which allows us to compare their relative importance in the context of this pollination system.

Flower visits—To test whether cloudberry pollinators were preferentially visiting male flowers, in 1999 and 2000, we observed pollinator visits to a series

of male and female flowers using sit-and-wait methods. Although we were able to observe independent flower visits, this approach generated little information or data on sequential flower visits because of the low densities of flowers and pollinators in the bog. Therefore, in 2002, we followed individual insects encountered when walking through the bog. We recorded the family of insect, sex of each flower visited, order of flower visits, and the time spent in each flower until the insect flew out of sight. However, this method proved ineffective for the muscid flies because our movements caused them to leave the patch immediately.

To determine whether the insects were preferentially visiting male flowers, the sex of the flower was noted while the potential pollinators were being collected from cloudberry flowers in 1999 and 2000. We compared the proportion of pollinator visits to male flowers to the proportions of male to female flowers available on that day for both flowering seasons ($N = 22$ d).

Statistical analyses—Variability in male and female flowering phenology was analyzed using a mixed model ANOVA in the program SAS (SAS Institute, 1996), with the year and the number of flowers of each sex per square meter as fixed factors and the day as a random factor. The availability of pollen and nectar was analyzed as a function of the time of day, the year, air temperature, and relative humidity using a four-factor logit model in the GENMOD procedure of SAS. To test for quadratic and cubic flower sex and time of day effects on the availability of nectar in cloudberry flowers, we used a two-factor ANCOVA model with log-transformed data [$\log(x + 0.001)$; Sokal and Rohlf, 1995] in the GLM procedure of SAS. We used Student's t test to test for size differences in male and female flower parts.

To test the effects of abiotic factors (year, time in season, time of day, air temperature, blackbody temperature, windspeed) on the activity levels of the principal pollinator groups, we employed a GENMOD procedure with a Poisson regression model in SAS, and the last four continuous factors were treated as covariables (SAS Institute, 1996). When necessary, data were adjusted for over-dispersion by multiplying the standard error of estimates with a scaling factor. This scaling factor was estimated as $\sqrt{\chi^2/df}$, where χ^2 is the Pearson's goodness-of-fit statistic (Agresti, 1996). We used a two-factor ANOVA with log-transformed data [$\log(x + 0.001)$] to test for differences in the duration of flower visits for each family on both male and female flowers. To see if insects were visiting one sex of flower more often than would be predicted by their relative abundance, we compared these two factors (duration of flower visits and the sex of flower visited) using a χ^2 table.

Indices of pollinator effectiveness were tested for significant differences using ANOVAs by GLM when the data were continuously distributed and by Poisson regression models when the data were in discrete counts. A posteriori tests for pairwise differences were made using the Waller–Duncan comparison.

RESULTS

Flowering phenology—In both 1999 and 2000, male flowers emerged before and were present in the field for longer than females (20 vs. 14 d in 1999 and 16 vs. 12 d in 2000 respectively, Fig. 1) and also were significantly more abundant ($F_{1,49} = 25.57$, $P < 0.0001$). There were significant interyear differences in the number of flowers available ($F_{1,49} = 4.96$, $P = 0.03$) and a significant year \times flower sex interaction ($F_{1,49} = 5.15$, $P = 0.03$) attributable to yearly differences in the abundance of male, but not female flowers (see Fig. 1).

There was an interyear difference in the timing of the onset of cloudberry flowering, with blooms occurring up to 2 wk later in 2000 than in 1999 (Fig. 1). However, in both years, the flowering phenology of *Cassandra calyculata* L., *Kalmia* spp., and *Andromeda glaucophylla* Link. overlapped with that of cloudberry male and female flowers (Fig. 1). The flowering period of *Ledum groenlandicum* Retz., *Vaccinium angustifolium* Ait., and *V. oxycoccos* L. overlapped with that of cloudberry in 1999 but not in 2000.

Flower size and shape—The androecia of male flowers were significantly wider than the gynoecia in female flowers (2.95 ± 0.09 vs. 2.52 ± 0.06 mm, respectively, $t = 4.14$, $df = 28$, $P =$

0.0003). However, there was no significant difference in the length of stamens in male flowers and the pistils in females (3.96 ± 0.19 vs. 4.39 ± 0.30 mm respectively, $F_{1,452} = 1.44$, $P = 0.24$).

Petals from male flowers were significantly longer (11.68 ± 0.32 vs. 9.39 ± 0.21 mm, respectively, $t = 6.22$, $df = 105$, $P < 0.0001$), wider (10.69 ± 0.24 vs. 7.23 ± 0.19 mm, respectively, $t = 11.31$, $df = 106$, $P < 0.0001$), and had a greater surface area (127.04 ± 5.32 vs. 70.08 ± 3.39 mm², respectively, $t = 9.48$, $df = 105$, $P < 0.0001$) than those from female flowers (Fig. 2).

Cloudberry flowers with four petals are more abundant in both sexes than those with five. However, five-petaled flowers were more common in male (26.7 and 20.7% of 176 and 121 flowers) than female plants (19.3 and 9.5% of 88 and 95 flowers) on both sampling dates.

Food rewards—Pollen—There were significant annual and daily effects on the availability of pollen in male flowers. Pollen presentation in male cloudberry flowers, as measured by the proportion of anthers dehiscent, was greater in 2000 than in 2002 (0.77 ± 0.02 vs. 0.61 ± 0.02 respectively; $\chi^2 = 21.66$, $df = 1$, $P < 0.0001$). As there was no time of day \times year interaction with respect to the proportion of dehiscent anthers the data from the two years were pooled. Significantly less pollen was available in midmorning than later in the day ($\chi^2 = 13.42$, $df = 4$, $P = 0.01$), but not less than early in the morning (Fig. 3A). Once an anther has dehiscent, it should always be evident, so we believe this apparent drop is an artifact of sampling error.

Nectar—When nectar was found, it was in tiny droplets within the ring of stamens, on the inner rim of the receptacle in male flowers and at the base of the gynoecium and between adjacent ovules in the female flowers. In 2000, 32% (43/135) of all male and 25% of all female (36/143) flowers sampled contained no measurable quantities of nectar. When nectar was present, it was there in small quantities; however, female flowers produced significantly more than males (0.143 ± 0.036 vs. 0.046 ± 0.013 μ L; $F_{1,266} = 7.98$, $P = 0.01$). The temporal patterns of nectar production varied throughout the day, showing a cubic relation for the females ($F_{3,271} = 9.10$, $P < 0.0001$) and a quadratic one for the males ($F_{2,271} = 4.51$, $P = 0.01$). Female flowers had peaks of production in the early morning and in the middle of the afternoon, while in male flowers nectar accumulated over the course of the day and then declined in the late afternoon (Fig. 3B). Because these flowers were bagged and thus unavailable to pollinators, the decrease in nectar production after the early morning in female flowers and at the end of the afternoon in both sexes suggests possible reabsorption of the standing nectar, as reported in other species (Búrquez and Corbet, 1991).

There were no effects of air temperature on pollen or nectar availability ($\chi^2 = 1.80$, $df = 1$, $P = 0.18$ and $F_{1,266} = 0.73$, $P = 0.39$, respectively), but both variables showed a significantly negative correlation with relative humidity ($\chi^2 = 23.27$, $df = 1$, $P < 0.0001$ and $F_{1,266} = 7.04$, $P = 0.01$, respectively). High relative humidity can negatively affect stigmatic receptivity and thus decrease the efficacy of pollinator visits (Corbet, 1990), so the observed humidity-related effects may be an adaptation by cloudberry plants to reduce the attractiveness of its flowers to pollinators during periods of unsuitable humidity conditions.

In 2002, we found a very different pattern, with almost no measurable quantities of nectar found in either sex. Only 4 of 84 female and 12 of 235 male flowers contained any measurable quantities of nectar. Thus, an interyear comparison with respect to volume was not possible.

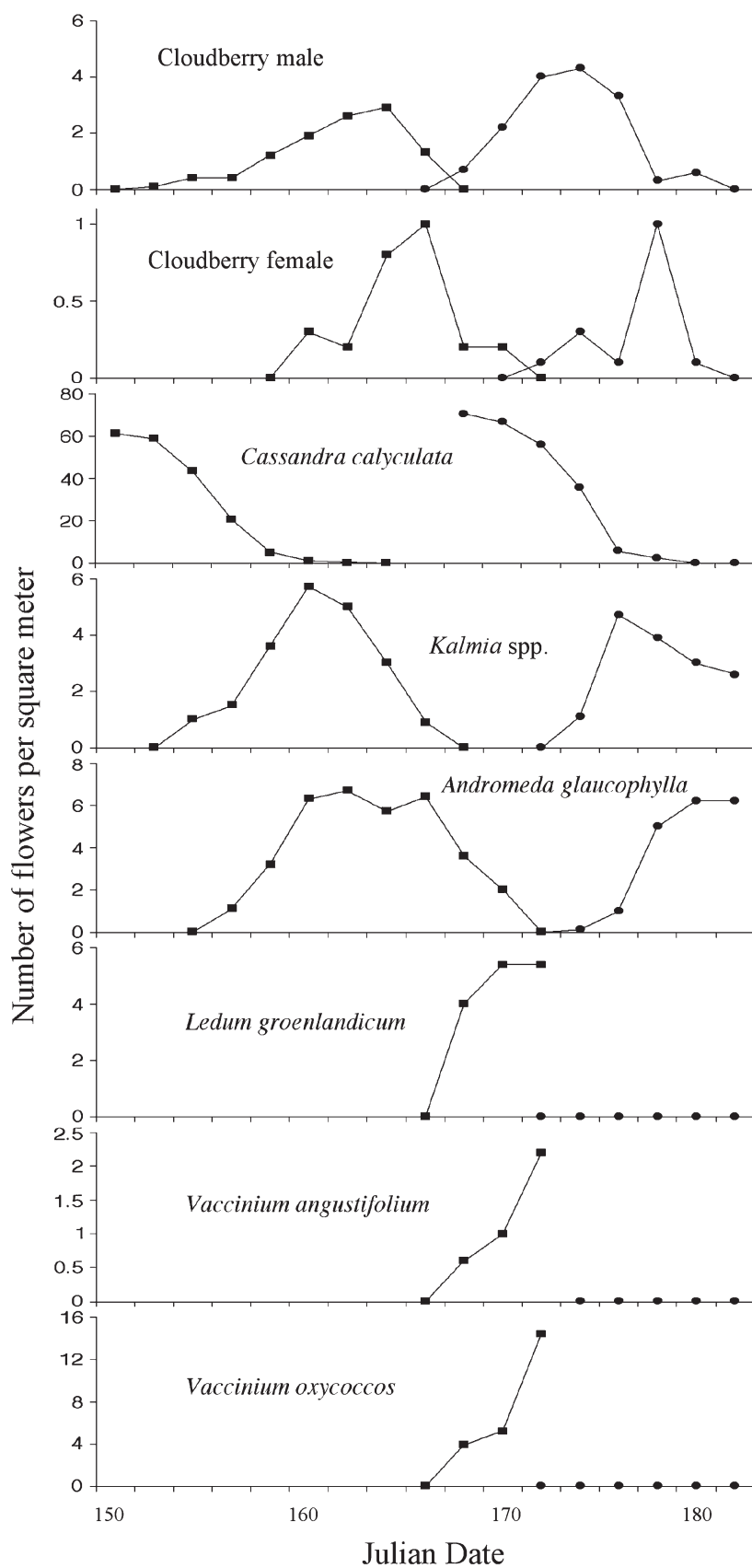


Fig. 1. The mean number of flowers/m² at Havre St. Pierre, Quebec, Canada, from 10 quadrats on every second day of flowering of plants of *Rubus chamaemorus* (cloudberry) and other species in 1999 from 30 May to 18 June (squares) and in 2000 from 14–29 June (circles).

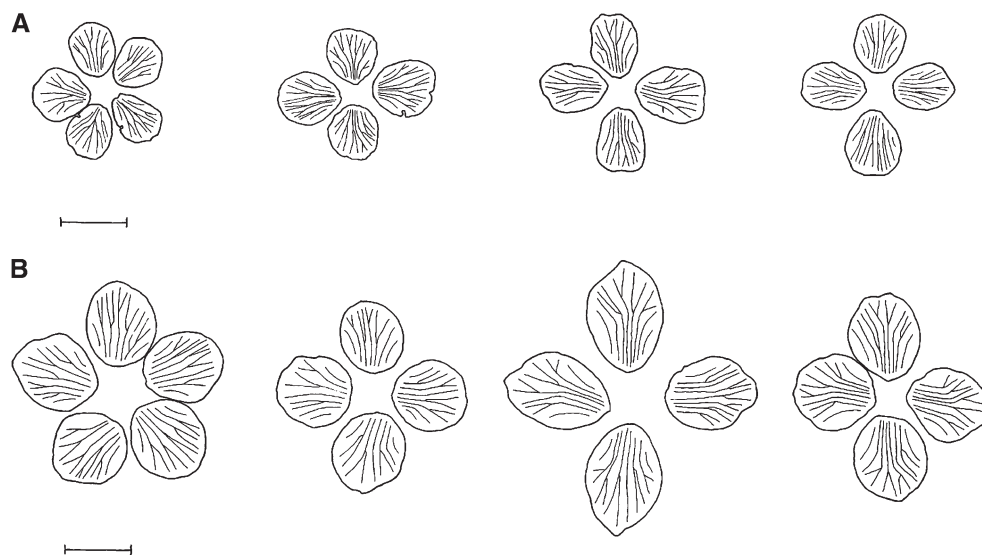


Fig. 2. Representative variability in the size and shape of (A) female and (B) male flower forms, taken at Havre St. Pierre, Quebec, in 2002. The bar indicates a scale of 1 cm.

Pollinator abundance—In 1998, 332 anthophiles from nine insect orders and 43 families were found among cloudberry flowers (Table 1) together with a few flower spiders (Arachnida; Aranea). The relative abundance of the pollinator groups was similar across the four sites (Table 2). Four families represented 62.3% of the total: Apidae (*Bombus ternarius* Say, *B. terricola* Kirby, *B. sylvicola* Kirby, *B. sandersoni* Franklin, *B. frigidus* Smith, and *Psithyrus ashtonii* Cresson), Halictidae (*Halictus* sp.), Muscidae (*Helina* sp.) and Syrphidae (*Sphaerophoria* sp., *Eristalis tenax* L., *Parasyrphus* sp., *Platycheirus holarcticus* Vockeroth, *Eupodes americanus* Wiedemann, *Chrysogaster* sp., *Toxomerus marginata* Say, *Meliscaeva cinctella* Zetterstedt, and *Melanostoma mellinum* L.). Within the Syrphidae, *M. mellinum* was the most common, representing ca. 74% of all specimens caught.

The structure of the pollinator guild actually observed visiting cloudberry flowers was similar in 1999 and 2000, with the four major families observed in 1998 comprising 87.6 ($N = 305$) and 83.7% ($N = 170$), respectively, of the total. There were considerable interyear differences in the abundance for each of the four principal pollinator groups, although Diptera were always significantly more abundant than the Hymenoptera, using a log-linear model (Fig. 4). Overall, the structure of the cloudberry pollinator guild in Quebec resembles that of those found elsewhere in Scandinavia (Ågren et al., 1986).

Pollinator activity—Bumblebees (Fig. 5A, $\chi^2 = 14.42$, $df = 2$, $P < 0.001$) and syrphids (Fig. 5D, $\chi^2 = 7.24$, $df = 2$, $P < 0.05$) declined in the latter part of the season, while the Muscidae numbers increased continuously (Fig. 5C, $\chi^2 = 56.47$, $df = 2$, $P < 0.0001$) and halictid numbers remained constant over the flowering period (Fig. 5B, $\chi^2 = 3.57$, $df = 2$, $P = 0.17$). Thus, despite the temporal change in different families within the pollinator guild, cloudberry flowers had relatively constant visitation levels over the flowering period. The maximum number of pollinators from any given taxonomic group observed during any sampling session was 12 (Syrphidae) but often pollinator densities were <1 individual/30 min (see Fig. 5).

The bumblebees did not show any significant daily activity pattern (Fig. 6). The three other principal pollinator groups exhibited a significant quadratic pattern in their daily activity (Fig. 6), with peak activity levels occurring just after noon, when air temperature and solar insolation are maximal. Black-body temperature best described the variability in cloudberry flower visiting patterns in the apids, halictids, and syrphids (Table 3). The activity of the Muscidae is best described by the variability in air temperature (Table 3).

Over the range of wind velocities that permitted pollinator activity, variations in windspeed did not significantly influence the presence of any pollinator group on flowers (Table 3). However, at >10 m/s very little flight activity occurred. At windspeeds >4 m/s pollinators would remain on the flowers when we approached, but under less windy conditions they would fly off at the slightest movement by the observer. We also noted that at the higher wind speeds the small syrphids would approach the edge of the flower several times but return to the center before taking off when the wind abated. These observations suggest that, when active, the pollinators delay take off during periods of high winds, and this behavior would increase their residence time in flowers.

Pollinator effectiveness—The four principal pollinator groups not only had different activity patterns, they also differed significantly in two indirect indices of pollinator effectiveness (Table 4). The hymenopteran pollinators carried significantly more pollen on their bodies than did the dipterans, but because a significant quantity was buried deep within the body hair or in pollen baskets, these may be unavailable for pollination (Harder and Wilson, 1998). Furthermore, analyses of pollen counts show that flies and halictids have a high fidelity for cloudberry flowers (on average 95%) compared with bumblebees (~65%).

The halictids and syrphids were significantly more effective at inducing fruit set during a single visit than the apids, whereas the muscids showed no difference from any other group (Table 4). However, when pollination was successful, the type of pollinator had no significant effect on the quality of fruit produced, as measured by fresh weight or percentage of seeds set (Table 4).

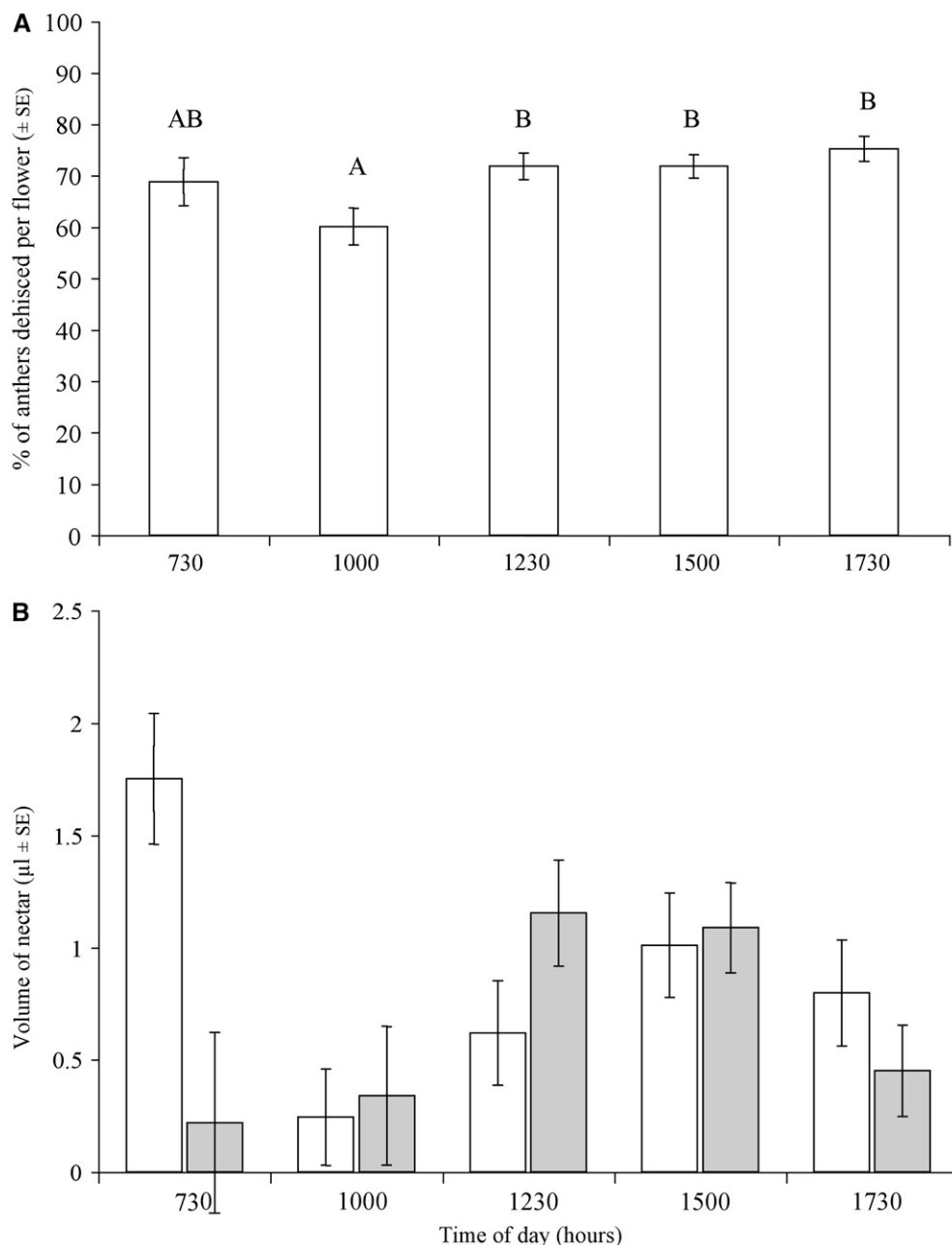


Fig. 3. (A) Pollen presentation, expressed as percentage of anthers that have dehiscing, on bagged male flowers of *Rubus chamaemorus* as a function of the time of day at Havre St. Pierre, Quebec, in 2000 and 2002. Both years were pooled due to a lack of year \times time of day interaction effect ($P = 0.3492$). Columns denoted by different letters are significantly different ($P < 0.01$) using the protected least significant differences method. (B) The amount of nectar available (μ L \pm SE) as a function of the time of day for bagged female (white bars, $N = 143$) and male flowers (gray bars, $N = 135$) at Havre St. Pierre in 2000. Nectar production showed a significant cubic relation for the female flowers ($P < 0.0001$) and a significant quadratic one for the males ($P = 0.0118$).

Pollinator importance—The calculation of pollinator importance using a product of flower visitation frequency (see Fig. 4) and a direct measure of pollinator effectiveness (seed set, see Table 4) reveals that in both 1999 and 2000 the flies are the most important pollinators in this system (Fig. 7). As in other studies (e.g., Montalvo and Ackerman, 1986; Herrera, 1987; Olsen, 1997; Vázquez et al., 2005; Sahli and Conner, 2006; Ollerton et al., 2007), the most influential variable is the relative abundance, as the principal pollinator groups did not differ significantly in

their seed set effectiveness. If one uses fruit set rather than seed set as the measure of pollinator effectiveness the importance of flies is further accentuated, with a 2.2- and 1.9-fold increase for Syrphidae and Muscidae compared with only 1.3- and 1.5-fold increase for the Apidae and Halictidae.

Flower visits—*Time in flowers*—There were significant effects of the family of pollinator ($F_{3,77} = 6.76$, $P = 0.0004$) and the sex of the flower ($F_{1,84} = 10.77$, $P = 0.0015$) on the duration

TABLE 1. Orders and families of insects found visiting cloudberry flowers on the Quebec North Shore in 1998 ($N = 332$). The most abundant families are in boldface and considered the principal pollinators of cloudberry in this study.

Order	Family	Relative abundance (%)
Hemiptera	Mesovellidae	<1
	Miridae	<1
Homoptera	Cicadellidae	1.2
	Acrididae	3.3
Orthoptera	Tetrigidae	<1
	Byrrhidae	<1
Coleoptera	Cantharidae	2.7
	Carabidae	<1
	Chrysomelidae	<1
	Cucujidae	1.2
	Curculionidae	<1
	Elateridae	1.5
	Eucmenidae	1.2
	Helodidae	<1
	Lampyridae	<1
	Nitidulidae	<1
	Scarabaeidae	<1
	Tenebrionidae	<1
Diptera	Anthomyidae	3.9
	Asilidae	<1
	Bombyliidae	1.5
	Muscidae	8.7
	Ceratopogonidae	<1
	Chironomidae	<1
	Dolichopidae	<1
	Empididae	2.4
	Calliphoridae	4.5
	Sarcophagidae	<1
	Syrphidae	33.4
	Tachinidae	2.4
	Therevidae	<1
Hymenoptera	Apidae	13.9
	Braconidae	<1
	Eumenidae	<1
	Formicidae	2.1
	Halictidae	6.3
	Ichneumonidae	2.1
	Perilampididae	<1
	Siricidae	<1
	Tenthredinidae	<1
	Vespidae	1.5
Lepidoptera	Geometridae	<1
Thysanoptera	Thripidae	<1

of visits by insects. Furthermore, there was a significant family \times sex of flower interaction ($F_{2,84} = 3.26$, $P = 0.04$), indicating the different groups of principal pollinators of cloudberry visited male and female flowers in different ways. Syrphid flies spent more time in male cloudberry flowers than any other insects did in the flowers of either sex, although the time syrphids spend on male and female flowers did not differ (Table 5). Halictid bees spent significantly less time in female than in male cloudberry flowers, whereas the bumblebees (Apidae) spent the

same amount of time in flowers of both sexes. The lack of data for Muscidae represents their propensity to take flight in response to the presence of observers.

Proportion of male to female flower visits—The insect pollinators of cloudberry visited male flowers more often than would be predicted from the ratio of male to female flowers in the field at any given time ($\chi^2 = 54.15$, $df = 22$, $P = 0.0002$). Whereas these flowers represented only 86% of the plant population ($N = 348$ flowers), 99% of the visits to cloudberry flowers were on males ($N = 359$ visits).

Insect-flower interaction—Dozens of visits by individuals from each of the principal pollinator groups were observed closely on both male and female flowers. In male flowers, the bumblebees (Apidae) vibrated their thoracic muscles and turned radially with ventral contact on the anthers. They often inserted their tongues into the base of the flower. Their interaction with the female flowers simply involved turning around with ventral contact on the stigma and some tongue probing around the base of the ovaries. The solitary bees (Halictidae) visited male and female flowers in much the same way as the bumblebees, although leg-rubbing over the anthers rather than vibration was employed as the main pollen-collecting mechanism. Individuals from both families often hovered over female flowers without landing and moved on to an adjacent male flower.

On male flowers, both groups of flies (Muscidae, Syrphidae) ingested pollen, often clearing the entire flower of nearly all available pollen while moving about through the anthers and on the petals. They also probed for nectar at the base of the flower while moving around, and during this process, many parts of the body touched the anthers (see Fig. 8). Although they often groomed extensively and ingested the pollen obtained using this behavior, considerable amounts remained on their body surfaces. In female flowers, the flies imbibed nectar, moved about on the pistils and petals in the same manner as they did when searching for pollen on males. In some instances, they ate pollen directly from the stigmatic surface, possibly reducing pollination success.

DISCUSSION

We found a diverse community of insect pollinators visiting cloudberry flowers, a high latitude plant, indicating generalization in its pollination system. However, four families represented up to 88% of the pollinator community. Of these four, the muscid and syrphid flies are obligate visitors (discussed later), whereas the apid and halictid bees are relatively rare. Furthermore, the bumblebees are not very constant cloudberry visitors, and these bees were overrepresented in 1998 because they were collected while hovering over cloudberry flowers. Our findings support previous observations concerning the

TABLE 2. The relative abundance (%) and number of individuals of the four principal pollinator families (Insecta) of cloudberry (*Rubus chamaemorus*) collected at each of the four preliminary study sites along the Quebec North Shore in 1998.

Study site	Apidae	<i>N</i>	Halictidae	<i>N</i>	Muscidae	<i>N</i>	Syrphidae	<i>N</i>
St. Paul du Nord	7.7	4	17.3	9	11.5	6	28.8	15
Baie Comeau	17.2	21	5.7	7	5.7	7	28.7	35
Havre St. Pierre	13.2	17	3.9	5	10.1	13	36.4	47
Blanc Sablon	13.8	4	0	0	10.3	3	48.3	14

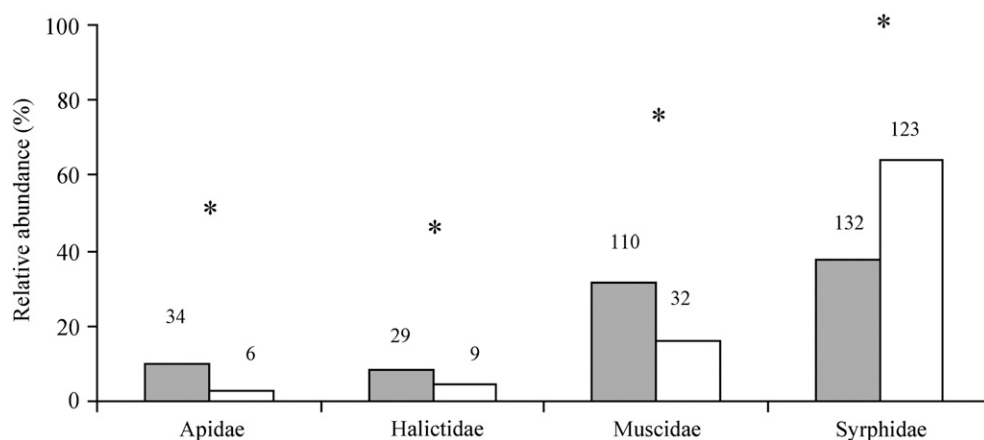


Fig. 4. The relative abundance of the four principal Insecta pollinator families of *Rubus chamaemorus* flowers at Havre St. Pierre, Quebec, for 1999 (solid bars) and 2000 (open bars). The numbers above each column represent the sample sizes; asterisks denote significant interannual differences for each group (likelihood ratio χ^2 test, $P < 0.0001$). In both years, there were significantly more flies than bees (likelihood ratio χ^2 test, $P < 0.0001$).

importance of flies to the pollination ecology of flowering plants in higher latitude environments (Downes, 1964; Hocking, 1968; Kevan, 1972; Elberling and Oleson, 1999).

The high levels of cloudberry flower constancy seen in the flies, and their abundance at all sites along the Quebec North Shore, suggests that the Diptera constitute the principal pollinators

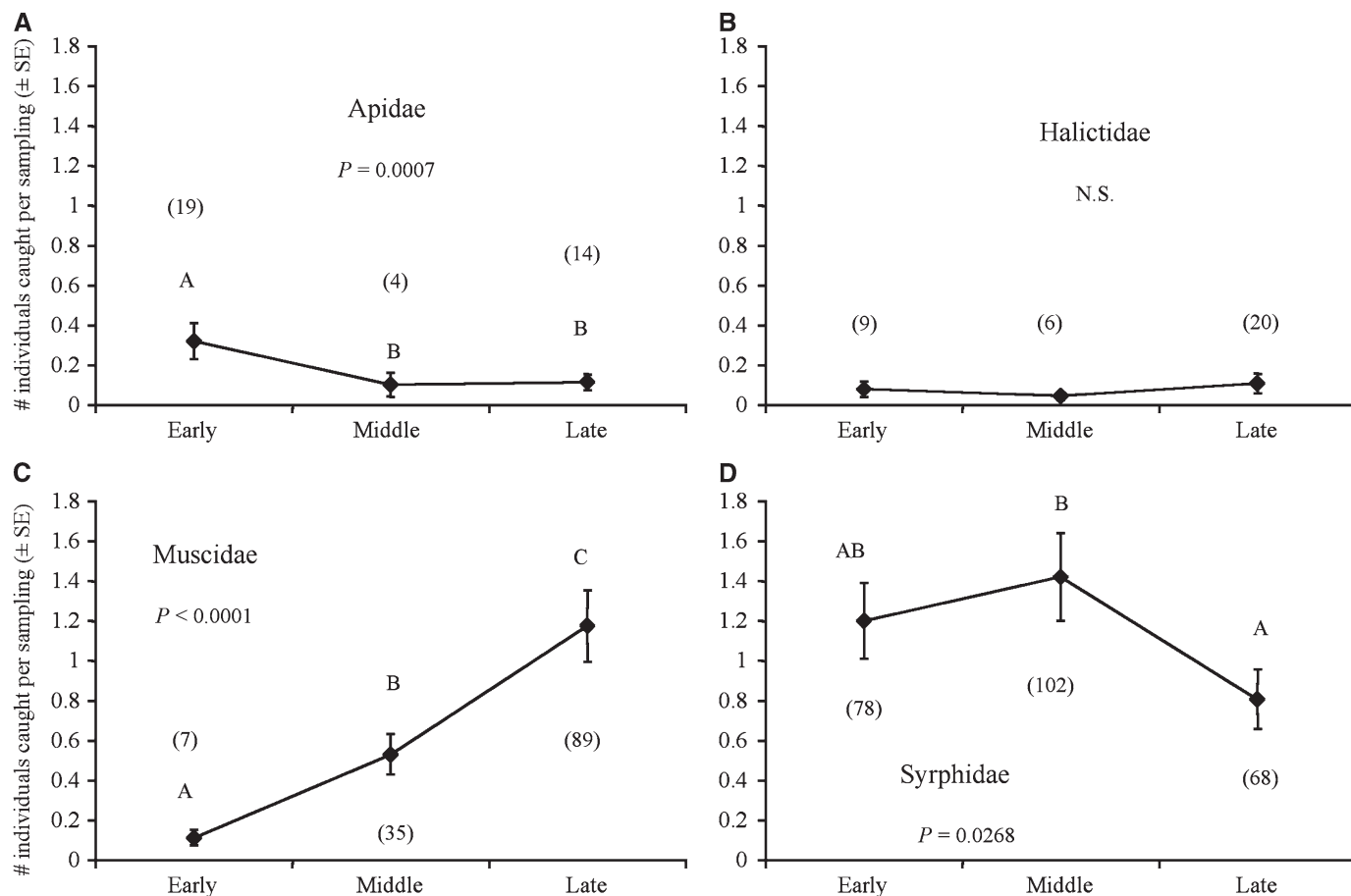


Fig. 5. Activity (mean number of individuals caught per 30 min sampling session at five times per day \pm SE) of the principal Insecta pollinator families of *Rubus chamaemorus* as a function of the time in the flowering season at Havre St. Pierre, Quebec in 1999 and 2000. The data for both years were pooled, due to a lack of year \times time in season interaction ($P > 0.05$). The numbers in parentheses are the sample sizes for each family and time in season. Values denoted with different letters are significantly different ($P < 0.05$) by the protected least significant difference method.

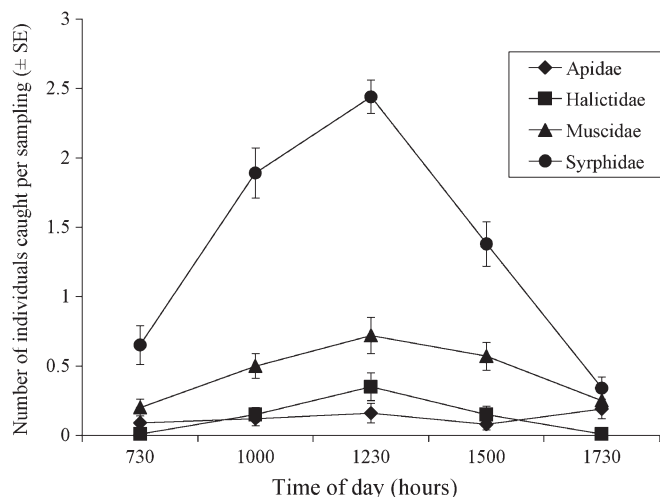


Fig. 6. Diurnal activity of the principal Insecta pollinator families of *Rubus chamaemorus* as a function of the time of day at Havre St. Pierre, Quebec, in 1999 and 2000. The data for both years were pooled, due to a lack of year \times time of day interaction ($P > 0.05$). All the daily activity terms show significant quadratic patterns, except for Apidae ($P < 0.0001$, by the protected least significant difference method).

of cloudberry. Nevertheless, because of their comparable effectiveness, bees may be important, especially in years when overall pollinator populations are low. Also, the bees' relative behavioral independence from climatic factors (Heinrich, 1974) would allow them to visit cloudberry flowers under conditions that may restrict dipteran activity, especially early in the morning and in late afternoon when temperatures are often suboptimal for flight for most insects. Bumblebees may forage over several kilometres (Walther-Hellwig and Frankl, 2000; Knight et al., 2005), while flies such as syrphids are much more restricted in their movement (Wratten et al., 2003), so differential foraging ranges must also be taken into consideration when evaluating the selective forces favoring outcrossing as a result of the high degree of relatedness in adjacent plants of a clonal species (Nuortila et al., 2002).

The plant species competing with cloudberry for pollinators in the subarctic bogs are all Ericaceae (see Fig. 1), whose rewards are reserved for either long-tongued (*C. calycuta* and *A. glaucophylla*) or big-bodied pollinators (*Kalmia* spp.; Reader, 1977). During spot observations on principal cloudberry pollinators visiting coflowering species (*Kalmia* spp., $N = 17$; *C. calyculata*, $N = 16$; *V. angustifolium*, $N = 9$; and *A. glaucophylla*, $N = 9$), we observed 38 *Bombus* spp. and 13 *Halictus* sp. but only one dipteran (*Muscidae*). However, the fly was not able to access any food rewards during the visit to the flowers of *Kalmia* spp. This observation suggests that, in the habitat,

TABLE 3. Four-factor ANCOVA table for the level of activity (number of individuals caught per sampling session) of the principal pollinator families (Insecta) of cloudberry (*Rubus chamaemorus*) as a function of the measured abiotic factors (air temperature [T_{air}], blackbody temperature [T_{blk}], windspeed, and time of day) recorded at Havre St. Pierre, Quebec in 1999 and 2000.

Family	Factor	df	χ^2	P
Apidae	T_{air}	1	0.01	0.934
	T_{blk}	1	4.03	0.0448
	Windspeed	1	3.07	0.0797
	Linear effect of time of day	4	3.61	0.4614
Halictidae	T_{air}	1	0.10	0.7577
	T_{blk}	1	6.31	0.012
	Windspeed	1	0.02	0.876
	Linear effect of time of day	1	23.95	<0.0001
Muscidae	T_{air}	1	10.0	0.0016
	T_{blk}	1	0.02	0.8796
	Windspeed	1	0.70	0.4025
	Quadratic effect of time of day	1	22.53	<0.0001
Syrphidae	T_{air}	1	1.45	0.2291
	T_{blk}	1	21.25	<0.0001
	Windspeed	1	0.29	0.5905
	Quadratic effect of time of day	1	43.17	<0.0001

cloudberry flowers represent major sources of energy and protein for flight and gametogenesis for these small flies (ca. 5–10 mm in length) because of their limited foraging range (Wratten et al., 2003) and the lack of other plant species with open flowers whose rewards are accessible to insects with lapping mouthparts.

Considering the hypothesis of selection along the lines of least resistance (Stebbins, 1970), the effectiveness and abundance of small flies in this system may have been the selective forces that led to "economical" adaptations of cloudberry that favor pollination by Diptera: the basic open flower shape, with the anthers and stigma positioned to maximize body contact with these small visitors (see Fig. 8) and small quantities of nectar rewards provided by both sexes (Ollerton et al., 2007; see Fig. 3B). This relationship would have been reinforced by the exclusion of these pollinators from other flowers during the cloudberry flowering period.

Male flowers are larger than females, and they have a higher frequency of 5- over 4-petaled flowers, suggesting there is greater selection on male than on female flower display (Delph et al., 1996). Our data suggest that these differences are detected by the pollinators because all groups showed overall preferences for male flowers. Furthermore, our behavioral observations on both families of bees in the field suggest that they often inspect, but do not land on, female flowers.

TABLE 4. The indirect (pollen carrying capacity, flower constancy \pm SE) and direct (fruit set, fresh fruit mass, and seed set per visit \pm SE) measures of effectiveness for the four principal Insecta pollinator families of cloudberry (*Rubus chamaemorus*). Values denoted with different letters within a same row are significantly different ($P < 0.05$) using the protected least significant difference (LSD) method.

Trait	Apidae	Halictidae	Muscidae	Syrphidae	P
Pollen carrying capacity (no. grains)	1144.2 \pm 291.0 b	1737.3 \pm 221.8 a	841.9 \pm 155.6 c	418.7 \pm 116.2 d	<0.0001
Flower constancy (%)	67.7 \pm 4.8 a	93.8 \pm 3.7 b	97.5 \pm 3.1 b	99.7 \pm 2.3 b	<0.0001
Fruit set (%)	33.3 \pm 19.2 a	84.6 \pm 10. b	76.2 \pm 9.3 ab	92.3 \pm 5.2 b	0.0007
Fresh mass (g)	0.42 \pm 0.15	0.31 \pm 0.06	0.33 \pm 0.05	0.28 \pm 0.04	0.7666
Seed set (%)	25.0 \pm 13.7	54.8 \pm 9.3	40.0 \pm 7.3	41.6 \pm 6.7	0.3270

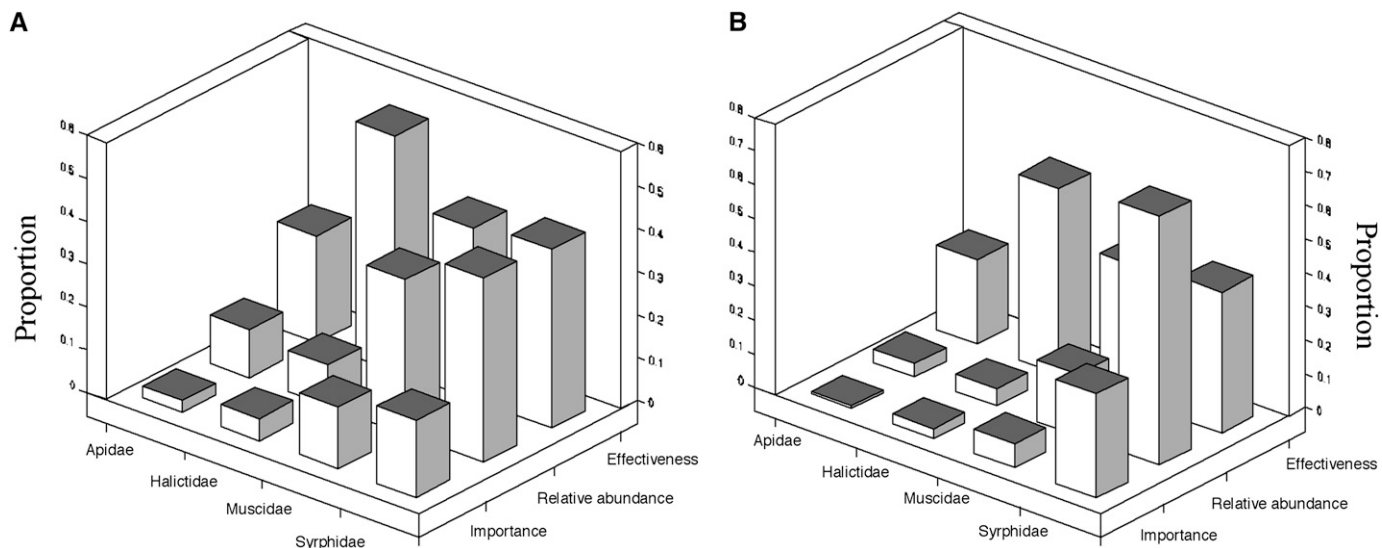


Fig. 7. Pollinator importance (seed set/unit of time) as estimated by the product of pollinator effectiveness (seed set/insect) and relative abundance (insects/unit of time) for the four principal Insecta pollinator families of *Rubus chamaemorus* at Havre St. Pierre, Quebec, in (A) 1999 and (B) 2000.

Full export of pollen may be more limited by visits from pollinators than full fertilization of ovules in female flowers (Delph et al., 1996), possibly optimizing male reproductive potential because the proportion of pollen reaching conspecific stigma is maximal when small amounts are removed per pollinator visit (Wilson et al., 1994). Thus, sexual dimorphism in cloudberry flower size may favor the evolution of larger males; they require more than one pollinator visit to export all of their pollen because dehiscence is gradual (Fig. 3A), and one single visit by muscid and syrphid flies to a virgin female flower results in fruit production 76.2 ± 9.3 and $92.3 \pm 5.2\%$ of the time, respectively (see Table 4). Despite the differences in flower size, the height of anthers and stigma do not differ, and their positioning is such that body contact between them and small pollinators occurs readily (see Fig. 8). Preliminary data obtained on possible intersexual differences in UV-reflectance and volatile bouquets emitted do not suggest that these would provide reliable cues for foragers to discriminate between male and female cloudberry flowers.

Although nectar production in cloudberry flowers is patchy in time and space, female flowers produce significantly more nectar than males. However, in years like 2002, when very few flowers produced nectar, it is possible that deceit, as proposed by Ågren et al. (1986), may act as a component of the pollination process. Otherwise, flowers with small quantities of nectar, like cloudberry, may not provide sufficient energy to make visits by large-

bodied hymenopteran pollinators worthwhile (Heinrich, 1975), thus explaining their preference for the abundant coflowering Ericaceae that do provide important quantities of nectar (Reader, 1977). However, small flies, the most important pollinators in this system, are obligate visitors to the open flowers of cloudberry in the early spring and clearly exploit the small amounts of nectar in cloudberry flowers with their lapping mouthparts. The higher discrimination between male and female flowers by the hymenopteran pollinators, when compared to the dipterans, may be the result of the overall low amounts, together with the high variability in nectar rewards offered by female flowers.

Several studies mention the temporal variability of nectar within populations of flowers over the course of a day or flowering season (Langenberger and Davis, 2002; Pacini et al., 2003), but we have found no mention of interannual variation in nectar production within populations of plants. A long-term study is required to elucidate the causes behind the marked variability in the nectar production by cloudberry flowers and to test the hypothesis that, in situations of low nectar availability, female cloudberry flowers that most resemble males would have a greater reproductive success. In addition, it would be important to determine the impact of nectar availability on the population dynamics of the principal pollinators. Furthermore, because female cloudberry flowers contained higher quantities of nectar in the early morning samples, such studies should include the importance of nectar availability on the flower visiting behavior of nocturnal pollinators (see Pelletier et al., 2001).

The interannual uncertainty of the abiotic conditions (e.g., rain, wind, frost) threatens cloudberry's pollination via effects on pollinator activity or flower longevity. For example, during three years (1999, 2000, 2002), intense rainstorms reduced the duration of cloudberry's flowering period by eliminating all available blooms when no floral buds were left to give rise to additional flowers. Also, in 1998 many female flowers were killed by late periods of frost in Baie Saint-Ludger, Quebec (Pelletier et al., 2001). The higher risks associated with uncertain environmental conditions would not favor specialization as a pollination strategy (Levins, 1968). However, clonal growth, a slow but dependable mode of reproduction, may help buffer against impacts from

TABLE 5. Time in seconds (\pm SE) that individuals of the principal pollinator families spent on male and female cloudberry flowers (*Rubus chamaemorus*) at Havre St. Pierre in 1999, 2000 and 2002. Values denoted by different letters are significantly different ($P < 0.05$) using the protected least significant difference (LSD) comparison method.

Family	Pollinator time on flowers (s, \pm SE)			
	N	Male flowers	N	Female flowers
Apidae	34	2.37 (0.59) ac	15	2.29 (0.52) ac
Halictidae	27	2.67 (0.46) a	21	1.19 (0.35) bc
Muscidae	0	(NA)	16	2.49 (0.39) a
Syrphidae	28	4.23 (0.39) d	28	3.32 (0.32) ad



Fig. 8. Typical positions of a small syrphid fly while visiting a (A) male and a (B) female flower of *Rubus chamaemorus*.

environmental disturbance by providing a persistent survival mechanism until the conditions favoring sexual reproduction reoccur (Bond, 1994). Investment in clonal growth is well documented in cloudberry, because around 95% of the plant's biomass occurs underground, mostly in the form of slow-growing rhizomes (Dumas and Maillette, 1987; Jean and Lapointe, 2001). In fact, cloudberry's clonal investment is so large that it often takes around seven years of vegetative growth from the seed stage before the first flower is formed (Østgard, 1964).

Traditionally, the definition of pollination specialization considers the number of species involved; however, Fenster et al. (2004) have suggested that it may be more pertinent to look at the level of functional groups in such interactions. In this study, direct behavioral observations of flower visits in the natural environment and in experimental introduction arenas showed that the nature of the cloudberry flower visits by all groups of dipteran pollinators are almost identical. Thus, due to the similarity in their body sizes, nutritional and energetic needs, as well as pollination effectiveness, they could be considered as a single functional group because they would exert similar selection pressures on cloudberry's reproductive strategies. From the plant's perspective, a visit from any fly within the functional group is essentially the same, and therefore, any adaptation favoring the attraction of one fly group should also act on others. Fenster et al. (2004) have suggested that a pollination system should be considered as specialized when greater than 75% of all flower visits are effected by a single functional group. Based on this criterion, we could consider cloudberry to have a specialized pollinator guild; flies represented 69.5 and 76.4% of all cloudberry flower visits in 1999 and 2000, respectively. For these reasons, we believe it could be argued that the pollination of cloudberry is functionally specialized on small flies (Ollerton et al., 2005).

From a fundamental perspective, our findings suggest that there may be a high proportion of flower specialists at high latitudes from a lack of generalist flower visiting opportunities for certain functional groups of pollinator in these species-poor en-

vironments. In addition, our results provide a baseline data set for the development of practical management practices that exploit native pollinators in cultivated cloudberry fields. The introduction of hives of honey and bumblebees may not be ideal to maximize pollination services, because of their preference for coflowering ericads as a result of the low quantity of nectar rewards available from cloudberry. Our results show that habitat management promoting healthy fly populations would be the best way to maximize yields of cloudberry.

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