Temporal changes in the pollinator fauna of tristylous *Pontederia cordata*, an aquatic plant

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Temporal changes in the composition of the pollinator fauna of the tristylous aquatic plant *Pontederia cordata* were documented during the flowering seasons of 1982 and 1983. A total of 18 species of insects, mainly bumblebees, and a single species of hummingbird were observed visiting flowers during the 2-month flowering period. The abundance of pollinators within each season varied greatly, with highest densities corresponding to peak flowering in both years. Although overall abundance was similar each year, the diversity of species was greater in 1983 because of the addition of short-tongued bumblebees and the longer residency periods of other species. It is suggested that low summer rainfall in 1983 decreased flowering levels in terrestrial plant communities of the region, resulting in several bee species shifting their feeding onto *P. cordata*. The study demonstrates that changes in the structure of a plant's pollinator fauna occur over time and that despite the possession of a specialized pollination mechanism, tristylous *P. cordata* is visited by a wide range of pollinator species.

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Les changements temporels dans la composition de la faune pollinisatrice de la plante aquatique à trois styles *Pontederia cordata* ont été étudiés au cours de la floraison en 1982 et 1983. Dix-huit espèces d'insectes, surtout des bourdons, et une espèce d'oiseau-mouche ont été observées sur les fleurs durant les 2 mois de la floraison. L'abondance des pollinisateurs a varié considérablement d'une année à l'autre et les densités maximales ont été observées à l'apogée de la floraison les 2 années. Bien que l'abondance totale se soit avérée très semblable les 2 années, la diversité des espèces a été plus grande en 1983 à cause de l'apparition de bourdons à proboscis court et du séjour plus long d'autres espèces. Il est possible que les précipitations peu abondantes au cours de l'été 1983 aient entraîné une diminution de la floraison des communautés de plantes terrestres dans la région, forçant ainsi plusieurs espèces d'abeilles à se nourrir sur *P. cordata*. Il se produit des changements temporels dans la faune de pollinisateurs d'une plante et, bien que munie d'un mécanisme de pollinisation spécialisé, *P. cordata* à trois styles est visitée par un éventail important d'espèces pollinisatrices.

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Introduction

Populations of flowering plants are usually visited by different pollinator species within a flowering season. Variation in the composition of the pollinator fauna can have important implications for plant reproductive success since pollinator species differ in foraging behavior and pollination efficiency (Primack and Silander 1975; Motten et al. 1981; Lindsey 1984; Schemske and Horvitz 1984). While many studies list the visitors to flowers of individual plant species, relatively few have documented how the structure of a pollinator fauna changes within and between seasons.

The genetic floral polymorphism tristyly is a complex outbreeding mechanism which represents one of the most specialized pollination mechanisms in the flowering plants (Ganders 1979; Barrett and Glover 1985). It is therefore of importance for studies in pollination biology to obtain detailed information on the pollinators of tristylous species. *Pontederia cordata* is an emergent perennial aquatic that produces blue zygomorphic tristylous flowers borne on showy spicate inflorescences. The flowers secrete a concentrated nectar (50% sucrose equivalents) for the duration of their 6- to 8-h anthesis period (Wolfe 1985). The plant is self-incompatible and therefore completely dependent on pollinators for reproductive success.

In this paper we examine the composition of the pollinator fauna in a single Ontario population of *P. cordata*. Our specific objectives were to (*i*) determine which species visit flowers and potentially serve as pollinators of *P. cordata*, and (*ii*) document temporal changes in the pollinator fauna within and between two consecutive flowering seasons.

Materials and methods

All work reported here was conducted at Pothole Lake, Leeds and Grenville County, Ontario. Pothole Lake is connected to the Rideau Lake System situated about 50 km north of Kingston, Ontario. The lake is approximately 800 m long and varies from 50 to 300 m in width. *Pontederia cordata* is the most abundant emergent plant in the littoral zone and grows along the shoreline and in shallow areas in the middle of the lake. Further details of the study site are provided in Wolfe (1985).

The flowering phenology of the Pothole Lake population was quantified in 1983. Two transects, each 1 m wide × 10 m long separated by about 7 m, were laid out from the shoreline to the population edge. Transects were censused every 2 days during the entire flowering season and the commencement of flowering was recorded for a total of 379 inflorescences.

The abundance and species richness of visitors to *P. cordata* flowers were determined at regular intervals (about 5 days) throughout the 1982 and 1983 flowering seasons. A record was made of all insects and birds that entered a 2 × 2 m quadrat of high inflorescence density and visited at least one flower of *P. cordata*. Except for the queens of two bumblebee species, which were difficult to distinguish (see Results), all visitors were identified while foraging. Observations were conducted for 30 min of each hour from flower opening (09:00) until 15:00 or 16:00 when flowers closed. Data were used to determine seasonal patterns of abundance and species richness.

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TABLE 1. Visitors to flowers of *Pontederia cordata* during the 1982 and 1983 flowering seasons at Pothole Lake, Ontario

Insects		
Hymenoptera: Apidae		Hymenoptera: Anthophoridae
Apis mellifera		*Melissodes apicata*
Bombus affinus	(Q + W; 1983)	Hymenoptera: Megachilidae
Bombus bimaculatus	(Q + W)	*Megachile mendica*
Bombus borealis	(W; 1982)	Hymenoptera: Halictidae
Bombus fervidus	(W; 1983)	*Dufourea novae-angliae*
Bombus griseocollis	(Q + W)	Lepidoptera: Sphingidae
Bombus impatiens	(Q + W)	*Hemaris diffinus*
Bombus pennsylvanicus	(Q + W)	Lepidoptera: Hesperidae
Bombus perplexus	(W; 1983)	One species
Bombus ternarius	(W; 1983)	Diptera: Syrphidae
Bombus terricola	(W)	One species
Bombus vagans	(W)	
Birds		
Archilocus colubris		

NOTE: For *Bombus* spp.: Q, queen caste; W, worker caste. All visitors were present in both 1982 and 1983 except where indicated.

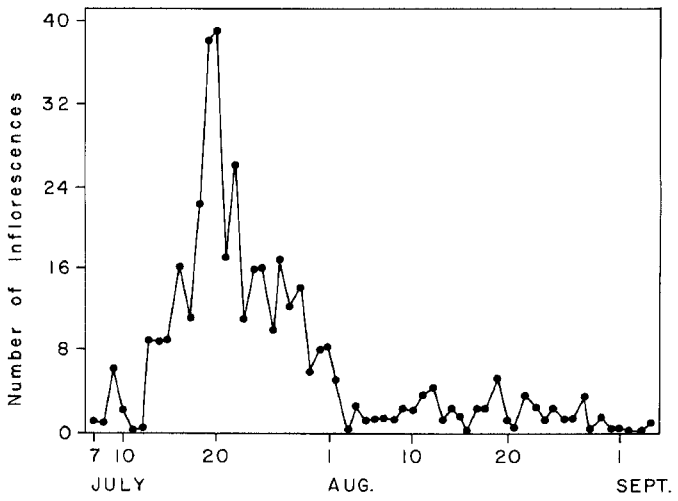

FIG. 1. The flowering phenology of *Pontederia cordata* at Pothole Lake in 1983. Values are the number of inflorescences that commenced flowering in two transects.

Results

In 1983 *P. cordata* began flowering on July 7 and remained in bloom for 60 days. The commencement of flowering of inflorescences through time in the population was positively skewed (Fig. 1; $g_1 = 2.12$, $t = 6.7$, $P < 0.001$) with a peak on July 20. Although quantitative data on phenology were not obtained in 1982, the flowering pattern was very similar to that in 1983, except that flowering commenced on July 1.

Flowers of *P. cordata* at Pothole Lake are visited by a wide range of visitors including flies, hummingbirds, moths, and several types of short- and long-tongued bees (Table 1). In terms of abundance, bumblebees were most common while ruby-throated hummingbirds and flies were occasional visitors. Pollinator abundance paralleled the number of inflorescences in the population, peaking on August 2 in 1982 and on July 27 in 1983 (Fig. 2A). While overall pollinator abundance was similar in 1982 and 1983 (Fig. 2A), species richness was higher on almost all sampling dates in 1983 (Fig. 2B). In 1983, 19 species were observed during 1 day (July 27) while the maximum number of species in any 1 day in 1982 was 9 (July 22 and August 5).

The larger number of pollinator species present at Pothole Lake on most sampling dates in 1983 resulted from differences in the phenology of individual species (Figs. 3 and 4). Ten of the 12 species present in both years appeared earlier in the 1983 flowering season and 9 were observed visiting *P. cordata* for a greater portion of the 1983 flowering season. Thus, the residency periods of most species were longer in 1983. In addition, four pollinators (*Bombus perplexus, Bombus affinus, Bombus impatiens* queens, and *Dufourea novae-angliae*) either were not observed or were seen on only a single day in 1982.

Discussion

Pontederia cordata occurs in large monospecific patches that remain in flower for long periods and offer a predictable food source for nectar- and pollen-feeding animals. Bumblebees are the most important pollinators of *P. cordata* at Pothole Lake and in other Ontario populations (Price and Barrett 1982), because of their abundance throughout the flowering period and their effective pollination service (Barrett and Wolfe 1986). Other visitors are either too rare (hummingbirds) or present for too short a period (*Dufourea novae-angliae, Megachile mendica*) to be as important. Honeybees were less abundant than bumblebees and, in addition, because of their nonrandom foraging pattern with respect to floral morph, they may not be as effective as pollinators of *P. cordata* (Wolfe and Barrett 1987).

Although the number of pollinator species was greater in 1983 than in 1982, the overall abundance was not substantially different in the two years. This suggests that regardless of the composition of the pollinator fauna, *P. cordata* can sustain a limited number of visitors. A similar situation was described by Pleasants (1981), who found that the relative number of honeybee and bumblebee species in a Rocky Mountain plant community varied quite dramatically between years, while the total abundance of bees was similar.

The composition of the pollinator fauna at Pothole Lake changed throughout the 1982 and 1983 flowering seasons. Much of the variation within seasons can probably be

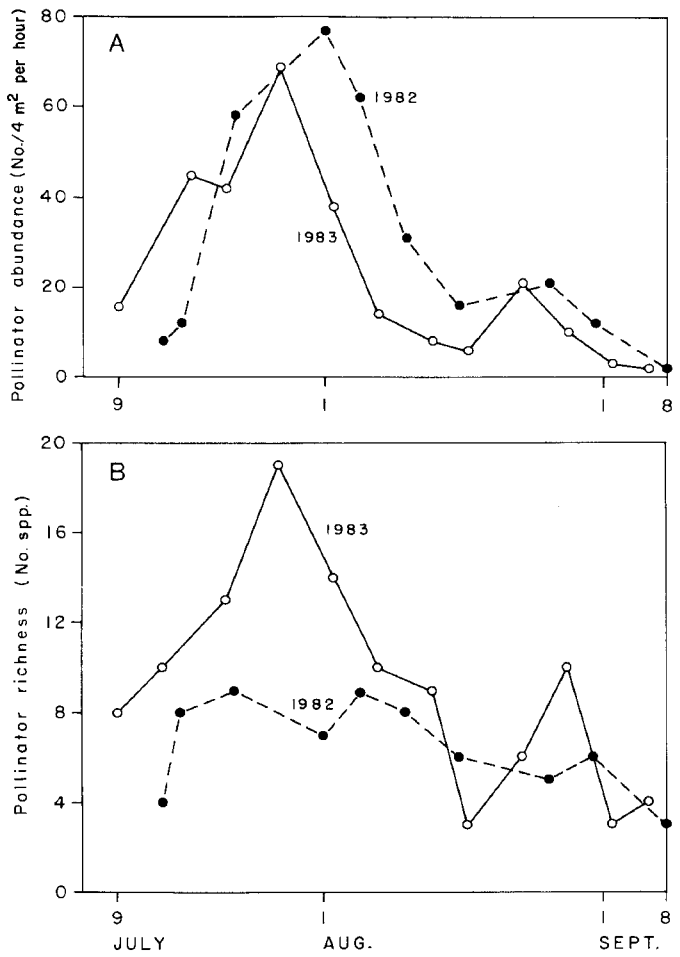

FIG. 2. (A) Abundance and (B) number of pollinator species visiting flowers of *Pontederia cordata* throughout the 1982 (solid circles) and 1983 (open circles) flowering seasons at Pothole Lake.

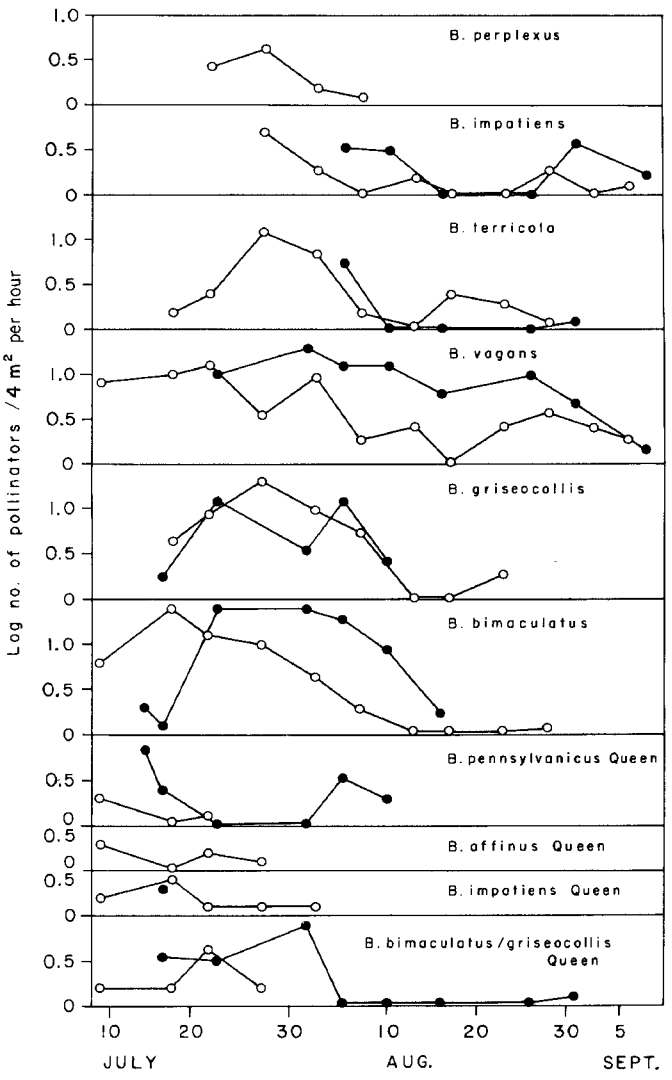

FIG. 3. Seasonal variation in the abundance of bumblebee (*Bombus* spp.) queens and workers visiting flowers of *Pontederia cordata* at Pothole Lake in 1982 (solid circles) and 1983 (open circles).

explained by species-specific nesting times and differences in the schedule of worker production. For example, *B. bimaculatus* queens emerged early in the season, and workers were abundant for most of the flowering period of *P. cordata*. In contrast, *B. impatiens* queens and workers appeared later in the season.

A more significant finding of our study was the difference in the pollinator fauna of *P. cordata* between years. The number of bee species visiting *P. cordata* on most sampling dates in 1983 was greater than in 1982. A possible cause of the difference in pollinator richness may be the contrasting patterns of summer rainfall in the two years. Little precipitation fell in the spring and summer of 1983 in contrast to 1982 (total June and July rainfall: 1982, 166 mm; 1983, 85 mm). The dry spring and summer of 1983 in southern Ontario were associated with decreased flowering in many terrestrial plant communities (L. M. Wolfe, personal observation). Since *P. cordata* inhabits a permanently flooded environment, its flowering was not affected by the dry conditions. The higher diversity and longer residency periods of pollinators in 1983 may have resulted from pollinators shifting onto *P. cordata* as a result of decreased floral rewards available in terrestrial plant communities.

Bombus terricola provides an example in our data of a shift in feeding between the two years of observation. During 1982 this species commonly visited terrestrial plants and was only observed on *P. cordata* for 2 days in that year. In 1983, however, it was a common visitor to the plant community. *Pontederia cordata* may be a suboptimal source of forage for *B. terricola* since, on average, these bees spend more than twice as long probing individual flowers for nectar as *B. vagans* (2.2 vs. 1.0 s; Wolfe 1985). The difference is most likely a consequence of the relatively short tongue of *B. terricola* compared with that of *B. vagans*.

Although we suggest that rainfall patterns influenced the faunal composition via the availability of floral resources, it is also possible that rainfall directly affected colony establishment. For example, Harder (1986) suggested that different rainfall patterns in successive years on Amherst Island, Ontario, influenced year-to-year changes in individual bumblebee species abundance by affecting nest site availability and colony development.

It is unclear whether differences in the pollinator fauna have any significant consequences for the reproductive fitness of *P. cordata* at Pothole Lake. Although the plant received a wide diversity of visitors during the 1982 and 1983 seasons, percentage seed set was near maximal in both years (Wolfe 1985). High seed set arises because the uniovulate flowers

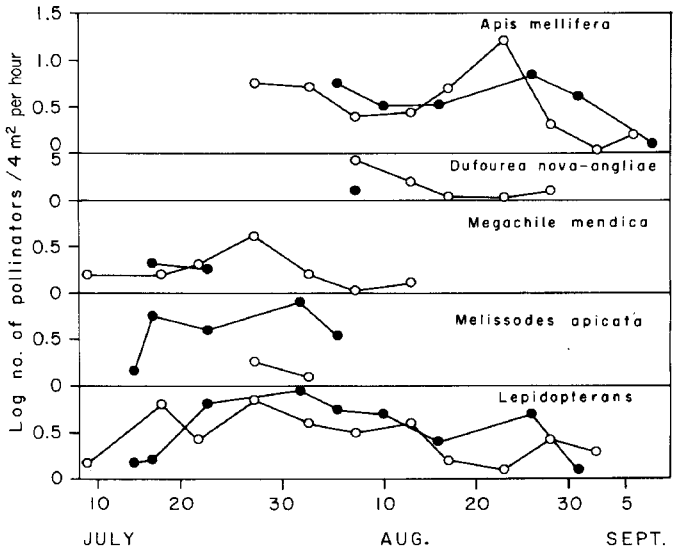

FIG. 4. Seasonal variation in the abundance of common species of pollinators visiting flowers of *Pontederia cordata* at Pothole Lake in 1982 (solid circles) and 1983 (open circles).

require relatively few pollen grains (three to five) to ensure fertilization, and high pollinator densities ensure that seed set is not pollen limited (Wolfe 1985). Although *P. cordata* possesses a specialized pollination mechanism, at Pothole Lake the species is visited by a diverse and changing pollinator fauna which does not appear to limit seed production. To what extent temporal changes in the species composition of the pollinator fauna affect other aspects of plant reproduction, such as gene flow and mating patterns, will require further study of *P. cordata* and its pollinators.

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