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# 18 Pitcher Plants (*Sarracenia purpurea*) in Eastern Canadian Peatlands

## Ecology and Conservation of the Invertebrate Inquilines

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**I**n this chapter we review the relationship between the northern pitcher plant (*Sarracenia purpurea*) and its inquilines in northeastern North America. Three species of Diptera (flies) dominate the insect community of the northern pitcher plant. All three are detritivores and feed on the arthropod prey attracted to the pitcher plant. They coexist by partitioning the habitat and food resource spatially. *Wyeomyia smithii*, the pitcher plant mosquito, lives in the water column of the pitcher and feeds by filtering microorganisms (bacteria and protozoa) from the water. *Metriocnemus knabi*, the pitcher plant midge, feeds on the dead organisms that have accumulated at the bottom of the pitcher. *Blaesoxipha fletcheri*, the pitcher plant sarcophagid, feeds at the surface on floating prey items that have drowned in the pitcher fluid. The action of these inquilines apparently speeds up the release of nutrients (mainly nitrogen and carbon dioxide) to the plant, and in turn the plant removes potentially toxic metabolic wastes (ammonia, CO<sub>2</sub>) from the water and infuses oxygen. Pitcher plant habitats, mainly *Sphagnum* bogs, are at risk in some areas of the region, particularly in the more populated zones in the south, to urbanization, agriculture, afforestation, and peat harvest. However, this represents only a small part of the total available peatland habitat in Canada.

## PITCHER PLANTS

Pitcher plants have held a fascination for biologists for centuries because of their carnivorous habits (Juniper et al. 1989). The pitcher-shaped leaves of New World pitcher plants (Sarraceniaceae) collect water and serve as passive insect traps. The insects are attracted to the leaf by UV reflectance and nectar, then slip into the water and eventually drown, providing a nutrient supplement to the plant (Givnish 1989, Chapin and Pastor 1995).

Even more interesting than the predatory habits of the plant is the fact that the plant is also home to an entire community of inquilines (i.e., symbionts which live inside another organism without causing harm to it; Lincoln et al. 1982), including insects, mites, rotifers, protozoa, and bacteria. The water-filled pitcher is referred to as a *phytotelm*, a small aquatic ecosystem formed from a part of a terrestrial plant (Juniper et al. 1989). The ecosystem, although small, supports the full range of foodweb interactions of any other type of aquatic habitat, based upon the breakdown of the arthropod prey attracted to the pitcher by the plant. The small size of the habitat and its isolation from other pitcher habitats provide a relatively simplified system for ecological study or manipulation (Paterson 1971, Addicott 1974). There have been a wealth of studies investigating interactions between the plant and the inquilines (e.g., Bradshaw 1983, Bradshaw and Creelman 1984), interactions among and between inquilines (e.g., Buffington 1970, Addicott 1974, Fish and Hall 1978, Heard 1994a), and the life history and ecology of individual inquilines (e.g. Smith 1902, Paterson 1971, Smith and Brust 1971, Forsyth and Robertson 1975, Farkas and Brust 1986a). The purpose of this chapter is to review the information on the relationship between *Sarracenia purpurea* L., the northern or purple pitcher plant, and its inquilines, particularly with respect to eastern Canada, and to place this relationship into the context of peatland conservation.

## THE NORTHERN PITCHER PLANT (*Sarracenia purpurea* L.)

### Geographic Range

The northern pitcher plant (*Sarracenia purpurea*) is the most widespread of the eight New World species of *Sarracenia* occurring from Brazil to northern Canada (Pietropaolo and Pietropaolo 1974, Juniper et al. 1989). It is found from the Gulf Coast of Florida to Labrador in eastern North America, and from Newfoundland to British Columbia and the Northwest Territories in the northern boreal zone in Canada (Juniper et al. 1989). The species has now also become naturalized in Ireland and Sweden (Juniper et al. 1989). *Sarracenia purpurea* is generally found in moderately to intensely acidic soils (Juniper et al. 1989), although it may live in neutral or alkaline soils in some areas (especially in the south; Pietropaolo and Pietropaolo 1974). The plant

usually grows in *Sphagnum* and sedge wetlands and is generally intolerant of competition or shade (Juniper et al. 1989).

Pitcher plants (*S. purpurea*) are widespread in eastern Canada wherever there is suitable habitat (Wells 1996). They are commonly associated with *Sphagnum* spp. in acid bogs, bog meadows, and boggy lake margins in Nova Scotia (Comeau 1971, Roland and Smith 1969), New Brunswick (Hinds 1986), Prince Edward Island (Erskine 1960), Newfoundland (Pollett and Meades 1970), and Quebec (Marie-Victorin 1964). Frère Marie-Victorin called them "the main ornamentation from our bogs" in Quebec (Marie-Victorin 1964) and pointed out that the local Amerindians called them "grass-toad" because the plant, like the toad, ate insects. The plant is well known for its unique showy leaf and long-stalked flower and has been recognized as the floral emblem of the province of Newfoundland and Labrador.

### Life History of *S. Purpurea*

The purple pitcher plant is a herbaceous perennial which produces pitcher-shaped leaves in a rosette (Pietropaolo and Pietropaolo 1974, Chapin and Pastor 1995). The plant begins producing new pitchers in early spring and on average produces a new leaf every 20 days or so (Fish and Hall 1978). In southern Ontario new leaves appear in early May and open by mid-June (Judd 1959). New leaves do not appear until late May and early June in Manitoba (Farkas and Brust 1986a), New Brunswick (Paterson and Cameron 1982), and Prince Edward Island (Hardwick and Giberson 1996), and these generally do not open until early July (Fig. 18.1). Leaves begin collecting water and attracting insects as soon as they are open, and several new leaves may be produced over a summer (Fish and Hall 1978). Leaves overwinter as intact fluid-filled pitchers. In northern populations (e.g., those throughout Canada) the fluid freezes solid for four or more months inside the pitcher and thaws again in spring (Paterson 1971, Farkas and Brust 1986). Overwintered leaves remain intact for several weeks in the second year, but begin to show signs of rot by mid- to late summer. The rotted leaves lose their integrity and no longer hold water or digest prey (Paterson 1971, Farkas and Brust 1986a).

Insects are attracted to the leaves by visual and chemical cues (UV light guides and bright purple streaks at the top of the pitcher, and nectar produced in nectaries around the rim of the pitchers; Pietropaolo and Pietropaolo 1974, Juniper et al. 1989). Insects feeding on the nectar may be enticed into the pitcher by accumulation of nectar below the rim, and lose their footing and fall into the fluid. They are prevented from escaping by downward-pointing hairs on the pitcher walls and eventually drown (Pietropaolo and Pietropaolo 1974). Although several species of *Sarracenia* produce digestive enzymes in specialized gland cells (Juniper et al. 1989, Givnish 1989), plant-produced digestive enzymes have not been conclusively shown in *S. purpurea* (Bradshaw and Creelman 1984). Digestion occurs mainly as a result of proteolytic activity from bacteria and autolytic enzymes from the victims themselves

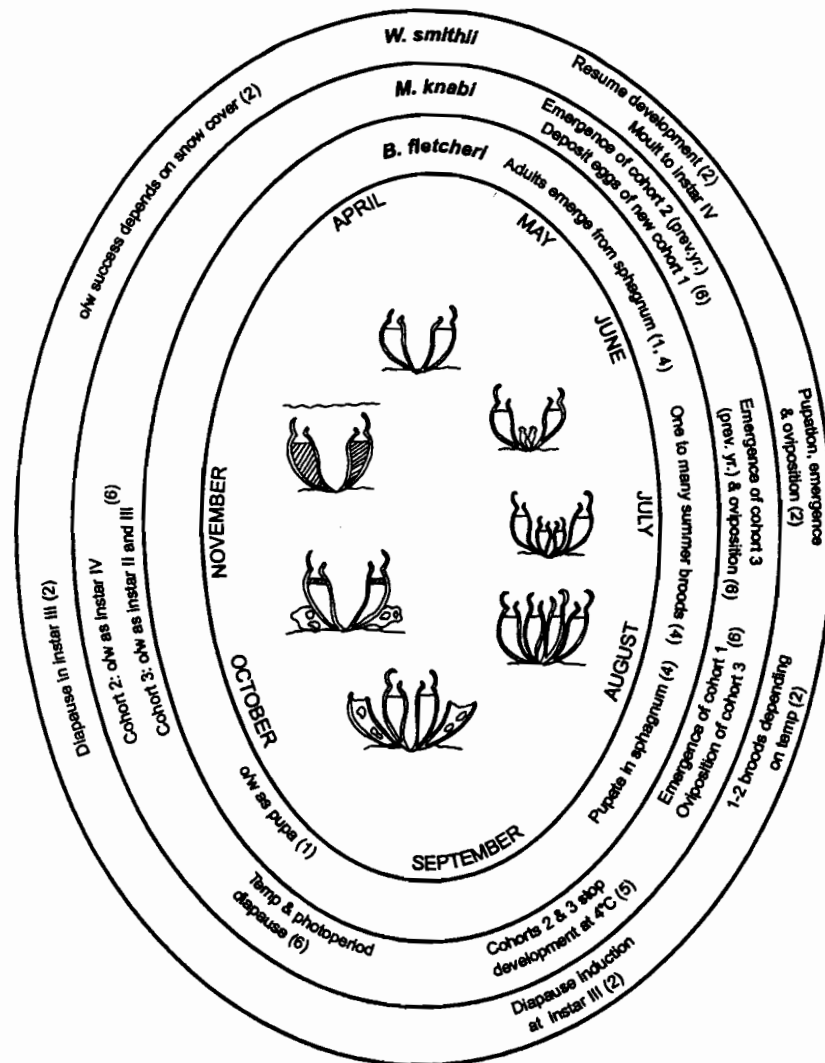


Fig. 18.1. Phenology of the three major pitcher plant inquilines in relation to the life history of the plant. (1) Farkas and Brust 1986b; (2) Farkas and Brust 1986a; (3) Evans and Brust 1972; (4) Forsyth and Robertson 1975; (5) Paterson 1971; (6) Paterson and Cameron 1982.

(Bradshaw 1983). Prey capture is slow at first, but then peaks between 10 and 20 days (after the pitcher fills with water) and then slowly declines. This results in only one to two leaves actively attracting insects at any time (Fish and Hall 1978).

As early as 1875, Charles Darwin noted that carnivorous plants are associated with nutrient-poor conditions (Juniper et al. 1989). However, some researchers have questioned the extent to which carnivorous plants depend on insect prey for nutrient supplementation (e.g., Christensen 1976, Stewart and Nilsen 1971). Chapin and Pastor (1995) showed experimentally that *S. purpurea* was nitrogen- and phosphorus-limited, despite the fact that it was growing in soil nutrient conditions that should not have been limiting. They suggested that soil microbes may compete for nitrogen and other nutrients (especially early in the season), resulting in carnivory being most important to the plant in spring and early summer. Another important competitor may be the *Sphagnum* with which the pitcher plants are usually associated; van Breeman (1995) indicated that *Sphagnum* and other mosses efficiently intercept nutrients from atmosphere, leachates, and litter, reducing the supply of nutrients for other plants. Bradshaw and Creelman (1984) suggested that other benefits of carnivory may be metallic ions and nutrients such as sulphur and phosphorus, rather than just nitrogen alone.

## THE PITCHER PLANT AS A HABITAT FOR AQUATIC INVERTEBRATES

### Limnological Characteristics

Pitchers from pitcher plants form small (generally about 20–30-ml volume), temporary aquatic habitats, characterized by fairly extreme conditions, especially relating to pH and temperature. Each "habitat" (leaf) goes through a recognizable cycle, in which it opens, begins to attract prey and inquilines, then persists for a period of weeks or months with little or no additional food input (Fish and Hall 1978). However, because leaves open throughout the summer, the timing of the cycle may vary among plants or leaves.

Most of the research on the organisms living inside pitchers has focused on ecological interactions between and among inquilines, and relatively little attention has been given to the characteristics of the pitcher habitat. Several researchers have investigated oxygen conditions in the leaf (e.g., Istock et al. 1975, Cameron et al. 1977) or recorded pH over time (Fish and Hall 1978), but we could find no studies that conducted a limnological type of investigation of the pitcher habitat, collecting data on a wide variety of physical factors at the same time. However, some characteristics seem to be common to the pitcher habitat.

Despite the wide geographical range over which northern pitcher plants are found, conditions inside the pitcher leaf apparently do not vary as much

as equivalent habitats outside the pitcher (Juniper et al. 1989). For example, temperature inside the leaf is less variable than in open bog pools (Juniper et al. 1989), and oxygen levels are usually fairly high, about 5–10 ppm (Istock et al. 1975) or at least 77 percent of saturation (Cameron et al. 1977). However, large diurnal and seasonal fluctuations in all habitat parameters can occur at individual sites, and these result in a highly variable habitat for prospective inquilines.

Midsummer temperatures can vary within the leaf from a nighttime low of about 10°C to >35°C under full sun, even at northern latitudes (Istock et al. 1975, Bradshaw 1980, Paterson and Cameron 1982, Farkas and Brust 1986a). In a single bog, microhabitat features such as shade and sheltering from wind can affect temperature, so that considerable differences in accumulated temperatures (degree days) occur between pitchers usually in shade and those in direct sun (Kingsolver 1979). Temperature patterns should be measured directly in the field because leaf temperatures do not always reflect ambient conditions. In one study in an open bog in New Brunswick (Paterson and Cameron 1982), fluid temperatures during summer and early autumn approximated air temperatures, but in northern Manitoba pitcher temperatures in open bogs in Manitoba were usually warmer than ambient temperatures (Evans and Brust 1972). In late autumn the water in the pitcher begins to freeze (Paterson 1971), and in most locations the pitcher fluid is frozen solid by late November (Fig. 18.1). Any organisms still remaining in the pitchers must be able to tolerate freezing into the solid core. Snow cover at this time plays a crucial role in maintaining the pitcher temperature at just a few degrees below freezing, even in the most northerly locations (Paterson 1971, Smith and Brust 1971, Evans and Brust 1972, Farkas and Brust 1986).

Experimental studies have shown that oxygen conditions are maintained at higher levels than can be accounted for by simple diffusion from the atmosphere, particularly considering the high potential biological oxygen demand (BOD) in pitchers with decaying prey (Cameron et al. 1977, Bradshaw and Creelman 1984). Occasionally, pitchers with high prey volumes do go anoxic (Bradshaw and Creelman 1984), but this is relatively rare in nature (Cameron et al. 1977). Cameron et al. (1977) measured oxygen levels in pitchers in New Brunswick and found that the DO (dissolved oxygen) was usually near saturation, and even their lowest recorded value of 77 percent saturation occurred just above the "wad" of detritus at the bottom of the pitcher. Similarly, Istock et al. (1975) found DO to range between 5–10 ppm at temperatures that fluctuated from 10 to 35°C in a bog in New York State. Cameron et al. (1977) believed that the primary pathway for oxygen to enter the leaf was diffusion through the leaf tissue, since oxygen levels were maintained even in the dark. However, Bradshaw and Creelman (1984) showed that, in light, plants take up CO<sub>2</sub> produced in the fluid by the breakdown of prey and infuse O<sub>2</sub> into the water.

Water in the pitcher is generally very acid (about pH 3.8), although pH may range widely from highly acidic to nearly neutral (Juniper et al. 1989).

Fish and Hall (1978) monitored leaf pH over a period of time and reported that pH increased from 5.8 to 6.3 by day 8 (after filling with water from a sprinkler system). After that the pH declined steadily to pH 3.5 by day 35, after which it was maintained at that level, possibly by physiological control by the plant or by the pattern of prey decomposition.

Nutrient levels in the leaf fluid also depend on time and the amount of prey captured. Levels are low at first, but the process of breaking down the prey increases ammonia and other dissolved nutrients. Action of bacteria and autolytic enzymes provides a steady supply of soluble nitrogen to the plant, even when the inquilines are absent. However, the presence of living insects in the pitchers enhances the rate of nitrogen production and prevents nitrogen from being sequestered in bacteria and protozoa (Bradshaw and Creelman 1984). Despite high ammonia production when inquilines are present, the pitcher habitat does not become toxic, since the plant actively takes up ammonia from the water, especially when temperatures are high and light is bright (Bradshaw and Creelman 1984).

In summary, the pitcher plant provides an aquatic habitat that is often extremely acidic, with large temperature fluctuations both diurnally and seasonally. However, oxygen levels are generally sufficient to support a variety of inquilines that have become specialized to this container habitat, and the plant itself maintains a clean water environment by actively removing potentially toxic waste products from the water.

### Inquilines in Pitcher Plants

A number of organisms live facultatively or obligately in the pitcher fluid of *Sarracenia purpurea*. These range from microscopic organisms (e.g., bacteria, protozoa, and rotifers) to several types of arthropods, although only a few of these are common (Table 18.1). Protozoa identified in a study in Michigan by Addicott (1974) showed a diverse group of nearly 40 taxa, although no information is available on how widespread these are in pitchers in other locations. The arthropods are somewhat less diverse; fewer than 20 taxa have been associated with the pitchers to date (Table 18.1).

Most of the research on pitcher plant inquilines in North America has focused on three flies which have an obligate relationship with *Sarracenia purpurea* (e.g., Judd 1959, Forsyth and Robertson 1975, Fish and Hall 1978, Heard 1994a, Nastase et al. 1995). These are *Wyeomyia smithii*, the pitcher plant mosquito (Diptera: Culicidae), *Metriocnemus knabi*, the pitcher plant midge (Diptera: Chironomidae), and *Blaesoxipha fletcheri*, the pitcher plant sarcophagid (Diptera: Sarcophagidae) (Juniper et al. 1989). These three insects partition the pitcher spatially (Fig. 18.2), and all are detritivores. The mosquitoes filter-feed on fine particulates and microorganisms throughout the water column and return to the surface to obtain oxygen (Bradshaw 1983). The midges feed at the bottom of the pitcher, boring into prey items that have fallen from the surface (Fish and Hall 1978, Bradshaw 1983). However, they

TABLE 18.1. Organisms Reported to Inhabit Pitchers of *Sarracenia purpurea*

Protozoa <sup>b</sup>	Rotifers	Arthropoda
Flagellates	unknown loricates <sup>a</sup> and illoricates <sup>a</sup>	Acarina, <i>Histiostoma</i> sp. <sup>b,c,*</sup>
Chrysoomonadida	<i>Habrotrocha rosa</i> <sup>d</sup>	<i>Anoetus gibsoni</i> <sup>f</sup>
<i>Monas vulgaris</i>		<i>Anoetus hughesti</i> <sup>f</sup>
<i>Monas</i> sp.		Crustacea, Copepoda <sup>d,*</sup>
Cryptomonadida		Insecta, Plecoptera, <i>Leuctra maria</i> <sup>e</sup>
<i>Cryptomonas</i> sp.		Odonata, Libellulidae nymph <sup>f</sup>
<i>Chilomonas paramecium</i>		Megaloptera, <i>Sialis joppae</i> <sup>g</sup>
Euglenida		Lepidoptera, <i>Exyra rolandiana</i> <sup>f</sup> (consume the leaves)
<i>Euglena</i> sp		<i>E. semicroceae</i> <sup>f</sup> (consume the leaves)
<i>Astasia klebsi</i>		Diptera, Culicidae, <i>Wyeomyia smithii</i> <sup>b,c,*</sup>
<i>Scytomonas pusilla</i>		Chironomidae <i>Metriocnemus knabi</i> <sup>b,c,*</sup>
<i>Anisomonema emarginatum</i>		<i>Metriocnemus cf. fuscipes</i> <sup>h</sup>
<i>Notosolenus</i> sp.		Lynnophyes sp. <sup>h</sup>
Volvocida		unknown Pentaneurini <sup>h</sup>
<i>Chlamydomonas</i> sp.		Ceratopogonidae, <i>Culicoides</i> sp. <sup>h</sup>
<i>Chlorogonium</i> sp.		Sarcophagidae <i>Bleasoxipha fetcheri</i> <sup>b,i,*</sup>
<i>Carteria</i> sp.		Sarcophaga sarraceniae <sup>f</sup>
<i>Polytomella agillis</i>		Phoridae, <i>Dohrniphora cornuta</i> <sup>f</sup>
Kinetoplastida		unknown phorid <sup>h</sup>
<i>Bodo</i> sp.		Sciariidae, <i>Bradysis macfarlanei</i> <sup>f</sup>
<i>Cercomonas</i> sp.		unknown sciarid <sup>i</sup>
Trichomonadida		Hymenoptera, <i>Polistes fasciatus pallipes</i> (paper wasp, nests in dry pitchers) <sup>f</sup>
<i>Urophagus rostratus</i>		
Ciliates		
Gymnostomatida		
<i>Urotricha ovata</i>		
<i>Urotricha agilis</i>		
<i>Platyphyra spumacola</i>		
<i>Prorodon</i> sp.		
<i>Rhopalophrya</i> sp.		
<i>Spathidium</i> sp.		
<i>Litonotus</i> sp.		
<i>Chilodonella</i> sp.		
<i>Dysteria</i> sp.		
Trichostomatida		
<i>Colpoda inflata</i>		
<i>Colpoda steini</i>		
<i>Colpoda</i> sp.		
<i>Bresslauna</i> sp.		
<i>Leptopharynx sphagnetorum</i>		
unknown microthoracid		
Hymenostomatida		
<i>Colpidium campyllum</i>		
<i>Pseudoglaucomo muscorum</i>		
<i>Paramecium bursaria</i>		
<i>Cyrtolophosis elongata</i>		
<i>Cyclidium elongatum</i>		
Peritrichida, <i>Vorticella</i> sp.		
Oligotrichida, <i>Halteria</i> sp.		
Hypotrichia, unknown spp.		

<sup>a</sup>Refers to taxa that are frequently reported.

<sup>b</sup>Addicott 1974 (Mich.).

<sup>c</sup>Judd 1959 (Ont.).

<sup>d</sup>Juniper et al. 1989 (several locations).

<sup>e</sup>Hardwick and Giberson 1995 (P.E.I.).

<sup>f</sup>Turner et al. 1996 (W. Virg.)

<sup>g</sup>Wray and Brimley 1943 (N. Carolina).

<sup>h</sup>Mather 1981 (New Jersey).

<sup>i</sup>de la Rosa and Nastase 1987 (Penn.).

<sup>j</sup>Forsyth and Roberston 1975 (Ont.).

<sup>k</sup>Farkas and Brust 1986b (Man.).

<sup>l</sup>Bateman 1987 (Nfld.).

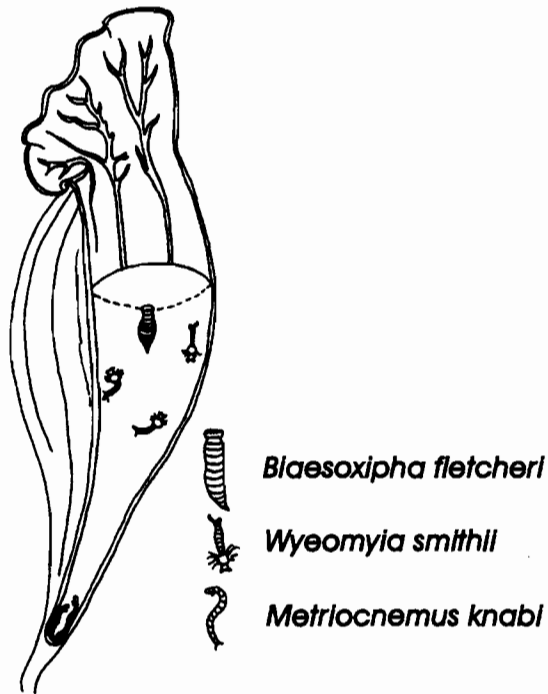


Fig. 18.2. The spatial distribution of the three major inquilines in the pitcher of the northern pitcher plant.

respire cutaneously and are dependent upon adequate oxygen supplies in the water at the bottom of the pitcher (Cameron et al. 1977). The sarcophagid feeds on newly drowned insect prey at the surface of the pitcher by piercing the prey cuticle and macerating the tissue. Like the mosquitoes, they obtain their oxygen at the surface (Forsyth and Robertson 1975).

#### *Wyeomyia smithii* (Coquillett)

*Wyeomyia smithii* is the best studied of the pitcher plant inquilines. It has been reported from the Florida Gulf Coast to Labrador and westward to northern Manitoba (Juniper et al. 1989). The life cycle is considered to be univoltine in the north (Farkas and Brust 1986a), although bivoltinism and multivoltinism have been reported farther south (Kingsolver 1979, Bradshaw and Holzapfel 1983). *Wyeomyia smithii* is autogenous (i.e., it does not require a blood meal for maturation of the eggs) for the first ovarian cycle throughout its range. In the north females produce only one clutch of eggs and are not known to bite, but those in southern latitudes will take a blood meal to mature

further batches of eggs (Bradshaw 1986). *Wyeomyia smithii* appears to be restricted to the northern pitcher plant in the north, but will oviposit in other species of pitcher plant in the south (Juniper et al. 1989).

The phenology of *W. smithii* is shown in relation to the plant phenology in Fig. 18.1. Females preferentially oviposit into new pitchers (Fish and Hall 1978, Mogi and Mokri 1980, Bradshaw 1986), but will lay in older pitchers as well (Farkas and Brust 1986a). Istock et al. (1975) have shown that the mosquitoes distinguish natural pitchers from artificial ones by using a chemical cue, and believe that this cue may also help them distinguish between new and old pitchers. Over much of the north the timing of the first opening of new pitchers corresponds to the period when the adults are on the wing and looking for oviposition sites (Judd 1959, Farkas and Brust 1986a, Heard 1994a). A preference for new leaves at this time ensures that eggs are laid in pitchers that have the highest probability of (1) attracting prey to provide food for developing larvae (Fish and Hall 1978, Bradshaw 1986) and (2) successfully overwintering, since previously overwintered pitchers begin to rot within a few weeks of oviposition (Farkas and Brust 1986a).

Adults are highly susceptible to desiccation. Wallis and Frempong-Boadu (1967) found that adults did not survive long enough to oviposit at humidities of less than 70 percent, and observed that females did not travel far from the pitcher they emerged from. Many pitchers can be found in a small area, however, and Bradshaw (1983) has observed females visiting, and even rejecting, several pitchers before ovipositing. Eggs are laid singly, either on the surface of the water or on the sides of the pitcher (Smith 1902, Wallis and Frempong-Boadu 1967, Fish and Hall 1978), but are susceptible to desiccation (Fish and Hall 1978). Oviposition rates are very low, with many females depositing only a single egg in a pitcher (Heard 1994c).

Eggs are deposited about a week after emergence and hatch in four to six days at 23°C (Wallis and Frempong-Boadu 1967). Larvae require about three weeks to develop at 23°C and under optimum food conditions, but will slow or stop development when food is limiting (Wallis and Frempong-Boadu 1967). *Wyeomyia smithii* is resource-limited over most of its range, with larvae having higher growth rates and more synchronous development when given a nutritional supplement than when grown under natural food conditions (Farkas and Brust 1985, Heard 1994a). Larval development is also affected by temperature. Kingsolver (1979) notes that pitchers growing in open sun accumulated more degree days than those growing in the shade in the same bog, and that differences in the accumulated degree days determined whether there would be one or two generations of mosquitoes in a year in Michigan.

*Wyeomyia smithii* overwinter as third-instar larvae in the northern part of their range (Smith and Brust 1971, Evans and Brust 1972) and in the fourth instar in the south (Bradshaw and Lounibos 1972). Diapause is induced by photoperiod, but the critical photoperiod varies with latitude, ranging from 13.8–14.6 hours per day in Massachusetts (Bradshaw 1980) to 14.5–15 hours in southern Manitoba (Smith and Brust 1971) and about an hour later in

northern Manitoba (Farkas and Brust 1986a). The latitudinal differences in diapause induction result in larvae entering the third-instar diapause at about the same calendar date in northern and southern Manitoba (Farkas and Brust 1986a). Interestingly, *W. smithii* require the same critical photoperiod for terminating diapause as they do for diapause induction (Smith and Brust 1971). Photoperiod is a well-known cue for inducing diapause but is less common in ending diapause (Beck 1968).

The diapausing larvae overwinter encased in ice in the pitcher leaf, but are not tolerant of very cold temperatures. Most diapausing larvae cannot survive any subzero temperatures for more than a few months (Paterson 1971, Evans and Brust 1972), yet they are found in climates (e.g. northern Manitoba, Labrador) where air temperatures may dip to  $-30^{\circ}\text{C}$  and colder for extended periods. Evans and Brust (1972) found that only about 50 percent of larvae could supercool to  $-5^{\circ}\text{C}$ , although a few larvae could supercool to  $\leq -10^{\circ}\text{C}$ . Paterson (1971) found that all larvae died in less than a month at  $-16.5^{\circ}\text{C}$ . Survivorship in the northern parts of the range appears to be highly dependent on snow cover, which lays an insulating blanket over the pitcher, preventing the pitcher temperature from falling below about  $-3$  to  $-5^{\circ}\text{C}$ . Paterson (1971) reported nearly zero mortality in a population in New Brunswick where snow covered the bog early in the winter and winter temperatures persisted for only four months. Mortality was considerably higher (30–91 percent) in Manitoba where winter temperatures persisted for up to six months. Interestingly, survivorship was higher in northern locations than in the south in Manitoba (Farkas and Brust 1986a), probably because of earlier and more extensive snow cover in the northern site, which insulated the pitchers from cold temperatures in early winter. Heard (1994b) found that wind exposure was the most important factor affecting distribution of pitcher plant mosquitoes in Newfoundland, and he also attributed this pattern to snow cover, since sites with high wind exposure experienced high winter mortality from lack of snow.

In the spring diapause is terminated by a resumption of long days (Smith and Brust 1971) and warm enough temperatures for development to be resumed. Mosquitoes moult to the fourth instar in early spring, and pupation occurs (in northern populations) around the time that new leaves are just opening on the plant (Fig. 18.1).

#### *Metriocnemus knabi* Coquillett

*Metriocnemus knabi*, the pitcher plant midge, has not been as well studied as *W. smithii*, the pitcher plant mosquito. Their geographical ranges overlap, but the midge appears to be more widespread and abundant in the north than the mosquito. The midge lives in the mixed detritus that accumulates in the bottom of the pitcher (Fish and Hall 1978) and scavenges for particulate material or bores into drowned insects (Bradshaw 1983). It obtains its oxygen directly from the water and so is restricted to pitchers with sufficient oxygen for them to respire. Cameron et al. (1977) found that it was relatively intolerant of low

oxygen, but observed that oxygen conditions in the leaves was generally high enough that strategies for dealing with low oxygen would rarely be needed.

Paterson and Cameron (1982) give the seasonal phenology of the midge for a location in New Brunswick. This is summarized, along with the phenology of the plant and other inquilines, in Fig. 18.1. In New Brunswick overwintered fourth-instar larvae began developing into pupae and adults by early May. Adults from this generation oviposited into overwintered leaves, and first-instar larvae were noted about a month after adult emergence. A second generation, which had overwintered as second- and third-instar larvae, matured by late June and July, giving a second emergence peak at that time, although low numbers of adults were seen throughout the rest of the summer. These adults oviposited in both old and new leaves, and early-instar larvae from this generation began to appear in late July. Larvae from the spring generation grew through the summer and began pupating by August, giving another emergence peak in late summer. Pupation occurred in a gelatinous mass on the sides of the pitcher, above the water line. Pupae were still observed as late as September, but development to the pupal stage was arrested by a critical photoperiod (Paris and Jenner 1959). There were apparently two cohorts present in New Brunswick (Paterson 1971), each producing three generations every two years; i.e., they emerged in May and August one year and July the next year. Some overlap of these cohorts was considered likely.

Development of the midges, like that of the mosquitoes, likely depends strongly on temperature, since in Newfoundland, which is farther north than New Brunswick, Heard (1994a) found that the midges were univoltine (one generation per year) and showed a similar life cycle to that of the mosquito, presumably overwintering as late-stage larvae. Paterson (1971) recorded high tolerance of *M. knabi* larvae to cold; his field populations showed very little overwintering mortality, and in the lab 75 percent of larvae tested were still alive following freezing to  $16.5^{\circ}\text{C}$  for 116 days. In contrast, mosquito larvae tested at the same time showed 100 percent mortality at that temperature after only 26 days. Both the mosquitoes and midges stopped feeding and voided their guts completely before their habitats froze, and Paterson (1971) felt that this strategy aided supercooling, since gut contents may serve as a site for ice-crystal formation in supercooled insects. The critical temperature for cessation of feeding in *M. knabi* was  $4^{\circ}\text{C}$ .

Since *M. knabi* show little or no preference for ovipositing in new pitchers, they may oviposit in previously overwintered pitchers that cannot overwinter a second time in an intact state. Paterson and Cameron (1982) note that midge larvae can migrate (by crawling) from older, rotten pitchers into adjacent new ones before entering diapause to overwinter. In contrast, mosquito larvae oviposited into old pitchers are not capable of migrating to new habitats and will not survive the winter (Farkas and Brust 1986a).

Abundance of pitcher plant midges appears to be related to pitcher volume (Paterson and Cameron 1982, Nastase et al. 1995), although not in all cases (Hardwick and Giberson 1996). This pattern is probably related to intraspe-

cific competition, since larval mass (Heard 1994a) and pupation success (Bradshaw 1983) decline with increasing larval density in pitchers. Competition is probably food-related, since midges were found to be nutrient-limited in a study in Newfoundland (Heard 1994a).

### *Blaesoxipha (Fletcherimyia) fletcheri* (Aldrich)

*Blaesoxipha fletcheri* larvae are apparently restricted to the leaves of the northern pitcher plant, and as with the other inquilines of this species, its range is potentially as large as the range of the plant. Its reported range, however, is from Georgia to Newfoundland and westward to Manitoba (Forsyth and Robertson 1975). The larvae are maggot-like and are the largest of the pitcher plant inquilines, with third-instar larvae reaching 15–20 mm in length. They breathe at the water surface through posterior spiracles. The spiracle area is enlarged, with a cup-like structure that can be spread to take advantage of the surface tension layer and keep them suspended (Fish and Hall 1978, Juniper et al. 1989). Larvae will drown if submerged for any period of time. They feed voraciously at the surface on newly drowned insect prey still floating on the water surface (Forsyth and Robertson 1975).

Adult females are viviparous (i.e., bear live young), and “larviposit” directly into the water while sitting on the rim of the pitcher (Juniper et al. 1989). In Ontario *B. fletcheri* begins development in early June in synchrony with the initial openings of new pitchers (Fig. 18.1) (Forsyth and Robertson 1975). Adults prefer to larviposit in new pitchers, and larvae are only found in older pitchers at peak densities (Forsyth and Robertson 1975, Farkas and Brust 1986b). Their strategy to colonize new pitchers may relate to their pattern of feeding, since pitchers attract most of their prey very soon after they open (Fish and Hall 1978) and the larvae require fresh, floating food to survive. The larvae leave the pitchers to pupate in the surrounding *Sphagnum* (Farkas and Brust 1986b). In Ontario (Forsyth and Robertson 1975) development from first instar to pupation occurred in less than two weeks, so there is potential for several generations to occur during the summer, depending on temperature and food availability. They apparently overwinter as pupae in the sphagnum moss (Fig. 18.1).

Females produce a clutch of 8–14 larvae, but larviposit single larvae into pitchers, and rarely is more than one larva found in a pitcher. This pattern relates to the aggressive behaviour of the larva; when a *B. fletcheri* larva encounters another, it coils around it and/or pierces it with its mouthparts to try to submerge and drown it (Forsyth and Robertson 1975). The larger larvae are most successful in these encounters, either killing the smaller ones or driving them from the pitcher. Larvae are able to migrate limited distances to move to an unoccupied pitcher. Density estimates of this species tend to be somewhat misleading (since densities are rarely more than one per leaf), and it may be more appropriate to refer to frequency of occurrence in pitchers, rather than density (Hardwick and Giberson 1996).

### Interactions between Pitcher Plant Inquilines

The three major pitcher plant inquilines mentioned above are all detritivores and depend on the prey captured by the plant. Some early researchers (e.g., Buffington 1970, Paterson 1971) speculated on how communities are maintained despite the potential for competitive interactions. Both Buffington (1970) and Paterson (1971) suggested that the various inquilines fed on different stages of the detritus breakdown process and therefore partition the resource in order to avoid competitive exclusion. Fish and Hall (1978) further noted that the inquilines also partitioned the resource temporally, timing their life cycles to take advantage of the stage of decomposition of the prey. However, these interactions were not quantitatively tested until relatively recently. Bradshaw (1983) confirmed experimentally that the three inquilines tended to be “self-limited” (i.e., showing intraspecific competition) rather than being limited by each other (interspecific competition).

In fact, there is evidence that the presence of the midges actually enhances the mosquito populations. Bradshaw (1983), Nastase et al. (1995), and Heard (1994a) found that mosquito abundance was positively correlated to midge abundance. Heard (1994a) showed that this was an example of a processing-chain commensalism, where consumers specialize on food at different stages of processing. The feeding action of the midges speeds the breakdown of the prey and accelerates production of the bacteria and protozoa that make up the major food of the mosquito, so that the presence of midges enhances production of the mosquitoes. Mosquito abundance had no effect on midge abundance, however, indicating that the chain is unidirectional (Heard 1994a).

Another question concerns whether competition occurs between the inquilines and the plant itself, for example, in a sort of resource parasitism. Although the plant can survive without prey, growth rates are higher when prey are present (Chapin and Pastor 1995). It is clear that the insect inquilines that live in the plant intercept some of these resources, and potential energy is lost to the plant when the insects respire and emerge out of the pitcher. However, the insect larvae may benefit the plant by speeding up the decomposition of the resource and/or converting the nutrients into a form more easily used by the plant (Paterson and Cameron 1972). Bradshaw and Creelman (1984) confirmed experimentally that the relationship between the plant and the inquilines was mutualistic. The inquilines inject nitrogen (as ammonia) into the leaf fluid, which is taken up by the plant. This in turn prevents the build-up of toxic waste products in the water, which would have a harmful effect on the inquilines. Further, the leaves take up CO<sub>2</sub> (in light) and infuse oxygen into the water. Although bacterial and enzyme breakdown of prey occurs even in the absence of the inquilines, the inquilines speed up the process and also prevent the dissolved nutrients from becoming sequestered in microbial populations (by feeding on the bacteria and protozoa). Since pitcher plants in open bogs can experience very high temperatures and light conditions, even in the far north (e.g., Evans and Brust 1972), plant growth

may become carbon-limited (Bradshaw and Creelman 1984). These same physical conditions may increase O<sub>2</sub> demand (and subsequent CO<sub>2</sub> release through respiration) by the inquilines in the water, so Bradshaw and Creelman (1984) suggest that the mutualistic interaction relating to O<sub>2</sub> and CO<sub>2</sub> may be as important as the ammonia/nitrogen one.

There is still no evidence, however, that the interaction between pitcher plants and its inquilines results in higher growth rates or production by the plant. The three main inquilines in northern pitcher plants require the plant to survive, but the degree of importance of the inquilines to the plant remains to be quantified.

### CONSERVATION ISSUES RELATING TO PITCHER PLANT INQUILINES

Many pitcher plant inquilines are obligate inhabitants of pitcher plants and so are obviously dependent on the presence of the pitcher plant to survive. Pitcher plants in turn are dependent on the survival of the bog habitat. Peatlands may be disturbed by agriculture, urban development, afforestation, and peat harvest (Keys 1992).

#### Wetlands in Canada

European settlers in North America long considered wetlands wasted land, but that viewpoint is gradually being replaced by an understanding of the value of wetlands as wildlife and biodiversity refuges and carbon sinks and in maintaining water quality (Keys 1992). More than 70 percent of the wetland areas in southern Canada have been altered for agriculture, urban expansion, and forestry, and the percentages are much higher in some heavily populated areas of the country (Keys 1992). However, peatlands, the habitats where pitcher plants flourish, are far more common in the sparsely populated north, where there has been relatively little disturbance. This is in sharp contrast to northern Europe, where few peatlands have not been altered. Peat in those areas is harvested for fuel and for horticultural purposes, and drained peatlands may also be used to support forestry or agriculture (Keys 1992).

#### Status of Peatlands in Atlantic Canada

Peatlands cover 111 million ha (12 percent) of Canada's territory, and occur mostly in the Boreal Forest Biome (Keys 1992). Total peatland area and its percentage of the total land area are given for each of the eastern Canadian provinces in Table 18.2. Less than 0.02 percent of the total peatland area in Canada is currently being harvested, and most of the harvest operations have been centered in Quebec, Alberta, and New Brunswick (Keys 1992, Price 1996). Peat harvest operations are important employers in these regions, and

TABLE 18.2. Area Classified as Peatlands in the Five Eastern Provinces of Canada

Province	Peatland Area (ha)	Percent of Total Area
New Brunswick	120,000	2
Newfoundland and Labrador	6,429,000	17
Nova Scotia	158,000	3
Ontario	22,555,000	25
Prince Edward Island	8,000	1
Quebec	11,713,000	9

the value of the industry (>\$180 million in sales per year; Price 1996) has prompted a steady growth in harvesting operations over the past decade (Keys 1992). Although the area involved is small, peatlands tend not to be managed as sustainable resources, since they are simply abandoned once they are exhausted and are left to regenerate naturally. However, fewer than 10 percent of the abandoned bogs in Quebec show *Sphagnum* regeneration even after up to 20 years (Price 1996). Interest in conservation and restoration strategies has been increasing in recent years in Canada, resulting in studies on the effects of peat extraction on bog vegetation (Jonsson-Ninniss and Middleton 1991), physical characteristics of cutover bogs (Price 1996), and natural revegetation of harvested peatlands (Lavoie and Rochfort 1996). Machine-harvested peatlands (as are usually found in Canada; Keys 1992) do not readily return to their preharvest conditions after cutting, because the harvesters destroy the capillarity of the organic layer, making it difficult for *Sphagnum* to reestablish (Price 1996). During peat extraction the water table drops and the compression of the drained peat alters the pore structure, so that even when these areas are reflooded the water relations are changed (Schouwenaars 1993, Price 1996).

The changes in the hydrology of cutover bogs result in a change in vegetation as well, favoring well-rooted plants rather than *Sphagnum* moss, which relies on capillary action to obtain water (Jonsson-Ninniss and Middleton 1991, Price 1996). We had difficulty finding information on regeneration of pitcher plants (*Sarracenia*), mainly because most of the work that has been done on revegetation of harvested bogs comes from Europe, where *Sarracenia* is not native. However, no pitcher plants were found in revegetated bogs in Quebec (Lavoie and Rochfort 1996) or Ontario (Jonsson-Ninniss and Middleton 1991) after 20 years postharvest, although they were apparently present, in the Ontario bog at least, prior to harvest.

Pitcher plants (*Sarraceniaceae*) possess numerous small, winged seeds (Zomlefer 1994) and so may be dispersed on wind currents, but presumably they require a nearby source of colonists to recolonize revegetated areas. Peat harvesting generally removes all the surface vegetation and destroys any seeds that may be in the peat (Lavoie and Rochfort 1996), so recolonization of

cutover bogs by *Sarracenia* may be very slow. Lavoie and Rochfort (1996) suggest that restoration attempts should include addition of fertilizer and deliberate dispersal of seeds and spores from bog plants. In addition, pitcher plants are easily transplanted from existing bogs and will reestablish in bogs as long as hydrological conditions are suitable (Hardwick and Giberson 1996).

#### Reestablishment of the Inquiline Community Following Disturbance

Bogs are generally isolated and localized habitats, a tendency which results in discrete, isolated populations of inquilines (Forsyth and Robertson 1975). What this means for dispersal of inquilines into bogs which have been disturbed and subsequently restored is difficult to say, as we could not find published studies of bog revegetation attempts that considered the invertebrate communities associated with the bog plants in North America. Recently, in Prince Edward Island (P.E.I.), we had the opportunity to evaluate how transplanting of pitcher plants *prior* to peat harvest (rather than during postharvest recovery) affected subsequent performance of the inquilines (Hardwick and Giberson 1996).

Due to impending drainage and harvest of an important bog near Miscouche, P.E.I., a local environmental group organized a "rescue" of "rare and/or interesting" bog plants from the bog to a number of other bogs in the region (Keys 1992). The pitcher plants appeared healthy and vigorous two years following the transplant, but the inquilines did not fare as well (Hardwick and Giberson 1996). Mosquitoes were extremely rare or absent from all transplanted pitchers, although they were present in at least some pitchers in all other bogs investigated in the province. Midge numbers were also reduced, though not to the same degree as mosquito numbers, and only in the bogs where there was not a local source of colonizing adults. Only the sarcophagid appeared to be unaffected by transplanting. We concluded that mortality of inquilines was very high during the transplant process since most of the transplanted pitchers lost their fluid during transport, and that the subsequent differences in their abundance were related to recolonization abilities. Adult pitcher plant mosquitoes are apparently very poor dispersers (Wallis and Frempong-Boadu 1967), and Heard (1994b) has also noted that they do not readily return to sites where they have been displaced due to poor overwintering success. The midges appear to be able to disperse short distances to colonize empty pitchers (within the bog; Hardwick and Giberson 1996), but may be slow at colonizing isolated habitats. Sarcophagids are strong flyers, however, and should recolonize quickly after the pitcher plants themselves reestablish following disturbance.

#### CONCLUSIONS

Very little of Canada's total peatland habitat is at risk at the present time, largely because of the general distribution of this habitat away from major

population centers. However, because most of the harvest activities are concentrated in the southern regions of the country, where suitable habitat is relatively rare, these activities have the potential to threaten both the pitcher plants and their associated inquilines, at least on a local scale. Transplanting has proven to be a successful method of preserving pitcher plants, given suitable habitat, but may not be adequate for preserving pitcher plant invertebrates. More experimental work is needed to determine the success of various restoration strategies following peat harvest.

#### ACKNOWLEDGMENTS

Funding for the study on the Pitcher Plant transplant was provided by a University of Prince Edward Island Senate Research Grant, and the Island Nature Trust of Prince Edward Island was very helpful in providing information on the transplant. Sylvie Desormeaux translated the information on Quebec pitcher plants from the French in the book by Frère Marie-Victorin. Pat Crawford helped guide the figures through CorelDraw.

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# 19 Constructed Marshes in Southeast Pennsylvania

## Invertebrate Foodweb Structure

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LYNNETTE L. SAUNDERS

**W**e compared the taxonomic and trophic structure of aquatic invertebrate communities in 11 recently created freshwater marshes to communities at 7 nearby reference sites. Our purpose was to determine which features of the created sites most influence the invertebrate community and to evaluate the rates at which key elements of the community are acquired during early succession following site construction. The created and reference sites were all semipermanent, shallow ponds (<1.5 m mean depth) in the Northern Piedmont ecoregion of southeast Pennsylvania. We sampled the invertebrates using both a 0.2-m<sup>2</sup> quadrat and 82-cm<sup>2</sup> core tube at 10 locations in each wetland. Invertebrates were identified and weighed, then allocated to 1 of 57 families and to 1 of 7 trophic groups. We also obtained concurrent measurements of fish presence, vegetation abundance, physical habitat features, and water chemistry. Based on canonical correspondence analysis, the presence of fish had the greatest effect of any habitat variable on the invertebrate community. Mean invertebrate biomass was ca four times higher in wetlands with few or no fish ( $n = 6$ ) than at sites with a well-established fish community ( $n = 12$ ) ( $p < 0.001$ ). Macroinvertebrate predators were the most strongly reduced of the 7 trophic groups in wetlands with fish. The created wetlands were rapidly colonized by most trophic groups, but macrocrustacean scavengers (amphipods and isopods) and consumers of aquatic macrophytes (primarily chrysomelid and curculionid beetles) were notably absent at several created sites. Using family-level taxonomic richness as one criterion of successful site construction, we found that “failures” (with fewer than the 95 percent confidence interval of 18.8–28.9 families based on the reference

*Invertebrates in Freshwater Wetlands of North America: Ecology and Management*, Edited by Darold P. Batzer, Russell B. Rader, and Scott A. Wissinger  
ISBN 0-471-29258-3 © 1999 John Wiley & Sons, Inc.