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Red-spotted Newts: An Unusual Nutrient Source for Northern Pitcher Plants

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Abstract – The northern pitcher plant (*Sarracenia purpurea*) receives some of its nutrients from the decomposition of prey that fall into its pitcher-shaped leaves. The majority of prey consists of ants, beetles, spiders, and slugs, and in rare cases, frogs and lizards. Here we report on the unusual occurrence of 22 Red-spotted Newt larvae (*Notophthalmus viridescens viridescens*) trapped within northern pitcher plants during a nutrient manipulation experiment in a Massachusetts bog in the summer of 2003. Newts were found among the larger of our experimental plants, but were not associated with any particular nutrient-addition treatment. High nitrogen levels in newts could contribute significantly to the nutrient budget of northern pitcher plants. Furthermore, this observation suggests that the trapping of amphibian prey by northern pitcher plants might not be as rare an event as previously believed.

Introduction

The northern pitcher plant, *Sarracenia purpurea* L. (Sarraceniaceae), is a carnivorous plant found in nutrient-poor bogs throughout the eastern United States and Canada (Buckley et al. 2003, Schnell 2002). The plant's pitcher-shaped leaves fill with rainwater and provide habitat for a small group of aquatic larval insects, rotifers, mites, protozoa, and bacteria (collectively referred to as pitcher-plant inquilines; Addicott 1974, Ellison et al. 2003). Potential prey, primarily arthropods, are attracted to the colorful pitchers and to extra-floral nectaries around the opening of the pitchers (Schnell 2002). Once their curiosity has led them inside, the combination of water in the pitcher and downward-pointing hairs on its inside surface make it difficult for prey to escape. The drowned carcasses are decomposed by the inquilines and the pitcher absorbs the mineralized nutrients (Adamec 1997, Bradshaw and Creelman 1984, Chapin and Pastor 1995, Ellison and Gotelli 2001).

Ants, beetles, spiders, and slugs dominate pitcher-plant prey, but the relative composition of the prey varies among bogs (Heard 1998, Newell and Nastase 1998). In rare cases, small frogs and lizards have been trapped by other species of *Sarracenia* (Jones 1935, Schnell 2002), but more commonly frogs sit atop the pitchers and capture insects before the insects enter the pitchers (Jones 1935). Here we report on an unusual

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occurrence of several aquatic larval Red-spotted Newts, *Notophthalmus viridescens viridescens* (Rafinesque) (Salamandridae), trapped within northern pitcher plants in a north-central Massachusetts bog. We discuss the implications of this observation for the nutrient dynamics of northern pitcher plants.

Methods

Study site

Our observations took place at Harvard Pond in Petersham, MA (42°30'N, 72°12'W; elevation 252 m above sea level). Harvard Pond developed from the establishment in the late 1800s of two dams on Riceville Brook (Swan and Gill 1970). This shallow pond (0.2–2.0 m deep) occupies about 50 ha and is dotted with bog islands ranging in size from < 0.1 m^2 to > 50 m^2 (Fig. 1). Just north of the pond is a ≈ 25 ha bog, called Tom Swamp by Swan and Gill (1970). Both the large bog and the bog islands are dominated by leatherleaf, *Chamaedaphne calyculata* (L.) Moench. (Ericaceae), and pitcher plants are abundant throughout the bog-pond complex. All observations reported here were made on the bog islands.

Study species

Sarracenia purpurea is a carnivorous, perennial herb that grows in bogs and poor fens on the eastern coastal plain of the United States, through Atlantic Canada and across the northern mid-western United

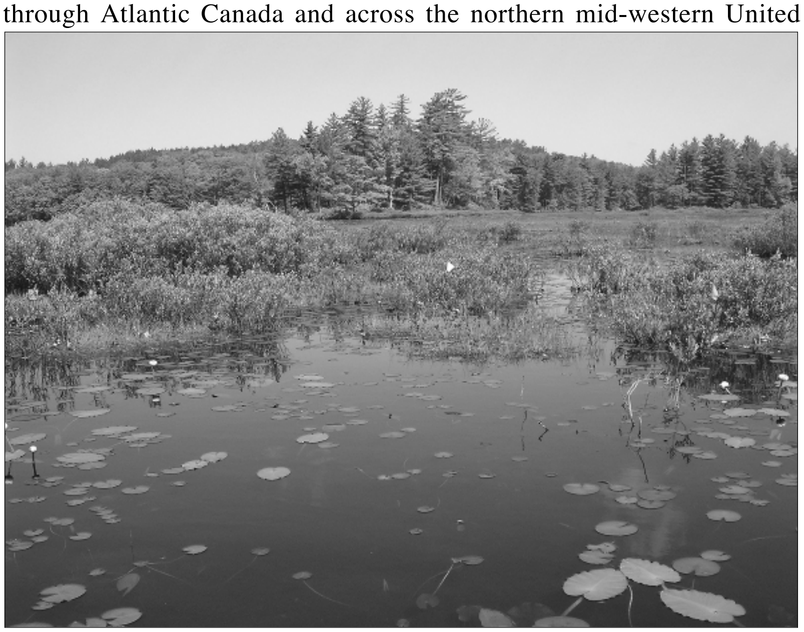

Figure 1. The study site at Harvard Pond, with bog islands.

States and Canada into British Columbia (Schnell 2002). Individual plants are long-lived (> 50 years) and produce 5 to 10 pitcher-shaped leaves each year. New pitchers begin growing in late May, when the danger of frost is past and spring high water levels have receded. The pitchers fill with rainwater and accumulate prey, which are mineralized by the inquilines described above (Ellison et al. 2003, Juniper et al. 1989). However, *S. purpurea* is an inefficient predator (Newell and Nastase 1998), and insect prey accounts for only ≈ 10% of the plant's nutrient budget (Chapin and Pastor 1995, Ellison and Gotelli 2001). In the northeast United States, the balance of a pitcher plant's nutrients come from nitrogen dissolved in precipitation (acid deposition) and from direct excretion of nitrogen and phosphorus by rotifers inhabiting the pitchers (Bledzki and Ellison 1998, Ellison and Gotelli 2002).

Red-spotted Newts inhabit diverse environments throughout much of the eastern United States and southern Canada (Bishop 1969); their range overlaps that of *S. purpurea*. The complex life cycle of the Red-spotted Newt consists of two aquatic stages (egg and aquatic larva) followed by a terrestrial stage (the red eft) and then a final stage as an aquatic reproductive adult (Petranka 1998). Some newts skip the terrestrial stage (Noble 1929). Much less is known about the aquatic larval stage of *N. v. viridescens* than either the red eft or aquatic adult (Petranka 1998).

In the spring, 1 to 2 months before *S. purpurea* begins producing pitchers, female newts attach individual eggs to dead or living plant material (Bishop 1969, Petranka 1998). The aquatic larval stage generally lasts 2 to 5 months, depending on environmental and site conditions (Petranka 1998). Throughout its range, the transition to the terrestrial red eft takes place between August and November (Bishop 1969, Petranka 1998). In Massachusetts, this transition has been reported to occur between August and September (Chadwick 1950, Smith 1920), which is when we observed larval newts trapped in pitcher plants. In Massachusetts, Red Efts live for 2 to 7 years on land before returning to water as adults (Healy 1974).

Context for our observations

The observations reported here were made during an experiment in which we manipulated the nutrient concentration of pitcher fluid. The overall premise of the experiment was to assess the differential uptake by pitcher plants of nitrogen from 2 sources, ammonium nitrate (NH_4NO_3, simulating atmospheric nitrogen deposition) and fruit flies (insect prey). Nutrient treatments consisted of 7 levels of NH_4NO_3 crossed with 7 levels of fruit flies in a response-surface design (Gotelli and Ellison 2004, Inouye 2001) applied to 98 randomly selected plants. The detailed results of this experiment will be presented elsewhere (Ellison et al., in preparation). From June 19 to August 23, 2003, pitchers of each plant were fed twice each week. Each time a plant was fed, we observed if the plant had trapped any additional prey. One half of the plants (one from each NH_4NO_3 x fruit fly combination) were harvested on July 8, and the remaining plants were harvested on August 26. Although we harvested a full complement of 49 plants in July, only 39 were harvested in August; 10 plants had been killed by the root borer, *Papaipema appassionata* Harvey (Noctuidae). The leaves of all harvested plants were measured (pitcher height from base to hood, width at the widest point, and diameters of the pitcher opening ["mouth"], all to ± 1 mm; see Ellison and Gotelli 2002 for details), oven-dried at 65 °C for 48 hours, and weighed (± 0.01 g). Trapped prey were sorted to the lowest taxonomic level possible (usually order, but to genus or species for ants and to species for newts).

Questions

We asked 3 questions about the relationship between plant characteristics and trapped newt larvae. Based on the answers to these questions, we speculate on the role of newts in the nutrient dynamics of northern pitcher plants.

First, was the trapping rate of newts (number of newts per pitcher) random? This was addressed by using the Kolmogorov-Smirnov goodness-of-fit test to compare the observed trap rate with that expected if they were trapped according to a Poisson distribution. This test was done using S-Plus version 6.1 (Insightful Corporation, Seattle, WA 2002).

Second, were newts attracted to pitchers of particular sizes? We compared plant morphological attributes of pitchers that captured one or more newts to pitchers that did not trap newts. Because these characteristics are all strongly correlated, multiple tests of the effect of each morphological variable on newt occurrence were inappropriate, so we conducted a principal components analysis (PCA) to determine if the occurrence of newts in pitchers was related to a single, composite morphological score. The PCA was done using S-Plus version 6.1.

Third, were newts found in plants of particular nutrient-addition treatments? To address this, we examined the distribution of newts across treatments using the test of Stapanian et al. (1982). Stapanian's test will be included in EcoSim, version 8.0 (Gotelli and Entsminger 2004).

Results

We first observed a Red-spotted Newt larva in a *S. purpurea* pitcher on August 7, 2003 (Fig. 2). During the next 3 weeks, 22 newts were found in 11 pitchers (9.5% of observed pitchers), and these 11 pitchers were distributed among 8 of the 39 (20.5%) remaining experimental plants. Most newts were found dead and partially decomposed. As plants were fed and observed every 3 days, and decomposition of a newt took approximately 10 days, we are confident that we observed all newts that were trapped within the plants.

Figure 2. A dead Red-spotted Newt (*Notophthalmus viridescens viridescens*) larva in a pitcher plant (*Sarracenia purpurea*).

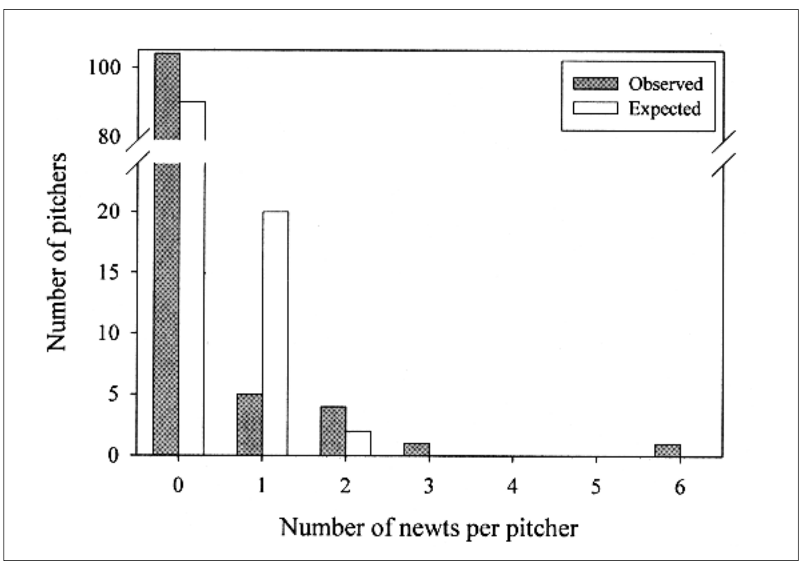

Figure 3. Observed and expected (Poisson) distribution of the number of newts trapped by each pitcher.

The trapped Red-spotted Newt larvae were 2 to 3 cm long and, as evidenced by remnants of gill buds and the majority of the gills already resorbed, they were metamorphosing from the aquatic larval stage into terrestrial red efts (Betsy Colburn, pers. comm.). The larvae were olive-green with orange spots; they had not yet developed the characteristic red color of efts.

The number of newts trapped within pitchers was not different from random (question 1). There was no significant difference between the observed capture rate and that predicted by a Poisson random variable ($P = 0.96$; Fig. 3).

Table 1. Pitcher plant morphological features (mean ± 1 SD) of pitchers with ($N = 11$) and without ($N = 104$) newts. Pearson's correlation coefficient (r) of each morphological feature with the first principal component (PC-1) in the principal components analysis (PCA) is given in the last line of the table. This principal component accounted for 87% of the variance in plant morphology.

	Morphological attributes			
	Dry mass (g)	Mouth area (mm^2)	Width (mm)	Height (cm)
Newts found	1.05 (0.07)	733.3 (49.7)	49.5 (1.6)	17.6 (0.6)
Newts not found	0.66 (0.35)	521.5 (20.8)	40.2 (1.0)	15.2 (0.4)
Correlation (r) with PC-1	0.51	0.49	0.51	0.49

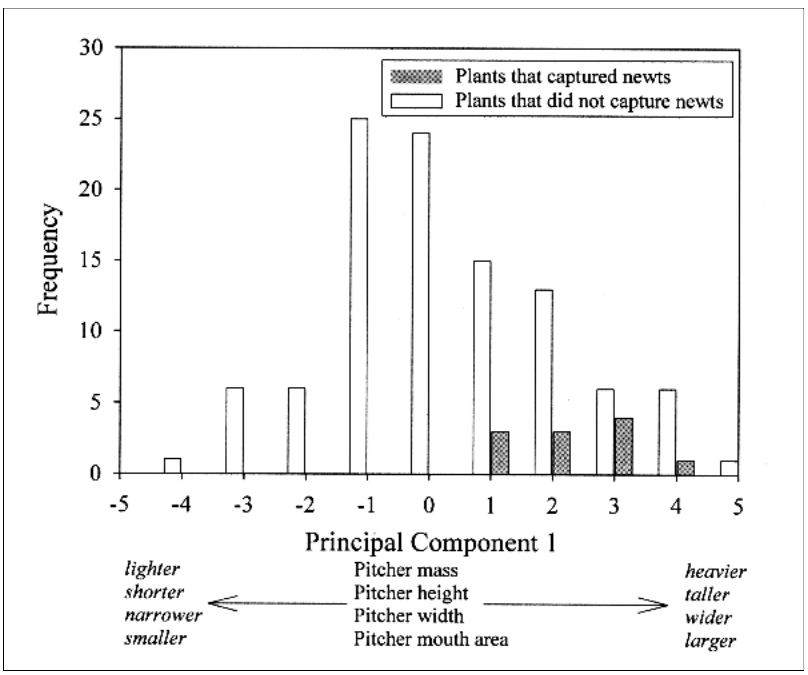

Figure 4. Relationship between the size of each pitcher (expressed as principal component 1) and the frequency of newts trapped by the pitcher.

Comparison of morphological attributes between pitchers that trapped at least one newt and those that did not (question 2) revealed that pitchers with trapped newts were larger in terms of height, width, and mouth area, and had greater dry mass (Table 1, Fig. 4). These 4 morphological characteristics were strongly and positively correlated with the first principal component (PC-1) of the PCA (Table 1), and presence or absence of trapped newts was significantly associated with PC-1 ($P = 0.0008$, Kruskal-Wallis rank test). In contrast, and in accordance with the results of the Poisson analysis, there was no relationship between pitcher size and the number of newts captured, for those plants that actually captured newts ($P = 0.9$, Kruskal-Wallis rank test).

Finally, nutrient manipulation did not affect the presence or absence of newts (question 3), as newts were distributed randomly across treatments ($P = 0.21$).

Discussion

The discovery of dead newt larvae in pitcher plants has not been previously reported in the published literature, and we can only speculate on the sequence of events that led them to enter the pitchers and subsequently die. It is not possible that females deposited their eggs within the pitchers where larvae were found because newts lay their eggs 1 to 2 months before pitchers are produced. It is possible, however, that in the spring, when the plants were still under water (a result of the high snowfall of the winter of 2002 and a new beaver dam), eggs were deposited on the bog islands near pitcher plants where larvae were subsequently found. Larvae might have remained in the pond in close proximity to the bog islands while searching for safe places on land where the newts could metamorphose.

When on bog islands, it is possible that the newts were attracted to pitcher plants as protective cover from frogs, turtles, birds, or other common predators. Alternatively, the newts might have been attracted into the pitchers while searching for food. Newts are generalist carnivores (Petranka 1998), and would find much to choose from in pitchers, ranging from the inquilines to recently captured prey. In the majority of our observations, however, the newt larvae ultimately became prey for the pitcher plant.

The mortality of newt larvae in general is quite high; less than 2% survive to metamorphosis (Petranka 1998). Predation by leeches has been suggested as the leading cause of mortality of larval Red-spotted Newts (Petranka 1998). It is unlikely that the pitcher-plant inquilines actually killed newt larvae given the size differences between the newts and inquilines. The largest of the inquilines are ≈ 1 cm-long larvae of the sarcophagid fly, *Fletcherimyia fletcheri* (Aldrich) (Sarcophagidae).

Alternatively, bacteria and autolytic enzymes in the pitcher fluid (Bradshaw and Creelman 1984) may have killed the newts.

It is more likely that the low pH of the pitcher water (usually < 4.0 by mid-summer; Fish and Hall 1978) contributed to newt morbidity or mortality. Acidic conditions can weaken or kill amphibians, including larval Red-spotted Newts and other salamanders (*Ambystoma jeffersonianum* [Green] and *Ambystoma maculatum* [Shaw] [Ambystomidae]), due to electrolyte imbalances (Robinson 1993, Sadinski and Dunson 1992). Newts weakened by low pH then could have drowned in the pitcher. Chadwick (1950) observed complete mortality of 31 metamorphosing larval newts placed in pond water with no access to land, suggesting that larvae must have access to air in order to complete metamorphosis. Similarly, the newts we found were close to metamorphosis and may have been unable to escape the water-filled pitchers to complete metamorphosis. Either directly or indirectly, pitcher plants appeared to trap larval Red-spotted Newts and to influence their subsequent death.

Prey trapped by northern pitcher plants serves as a valuable source of nitrogen for the plant and its associated inquiline community. In Massachusetts, the most common prey trapped by pitcher plants are ants, primarily *Myrmica lobifrons* Pergande (Ellison et al. 2002) and, in general, pitcher plants trap between 1 to 5 ants each day (A.M. Ellison and N.J. Gotelli, unpubl. data; Newell and Nastase 1998). Moreover, larger pitchers have been observed to trap more prey (Heard 1998), consistent with our observations of newts trapped within the larger of our experimental pitchers.

The quantity of prey is not nearly as important to plant nutrient supply as is its mass and percentage of nitrogen (N). The mean dry mass of the ant *M. lobifrons* is 0.3 mg, of which ≈ 0.04 mg (14%) is N (J.L. Butler and A.M. Ellison, unpubl. data). In contrast, the average dry mass of a metamorphic larval newt is 63 mg (Burton and Likens 1975b, University of Rhode Island 2001), of which ≈ 5 mg (8%) is N (Burton and Likens 1975a). Although ants contain a higher percentage of N, a single newt contains > 100 times the amount of N in an ant. Because *S. purpurea* pitchers at Harvard Pond average 500 mg dry mass, of which 5 mg (1%) is N (J.L. Butler and A.M. Ellison, unpubl. data), a single trapped newt could account for the entire N content of an average pitcher.

Pitcher plants respond to increasing N inputs by changing pitcher structure in the current season (Ellison and Gotelli 2002) and by increased probability of flowering in the subsequent growing season (Ellison and Gotelli 2001). Prey trapped late in one growing season, such as newts, are most likely to affect reproduction in the next season (Shreve 1906).

Although trapping of Red-spotted Newts by northern pitcher plants has not previously been documented, it is unlikely that our observation in the summer of 2003 represented a unique event. It is more likely that trapped Red-spotted Newt larvae in pitcher plants have been overlooked. Although the ecological implications of our observations require further study, our observations provide new data on the patterns of prey capture by pitcher plants and their potential impacts on plant nutrient dynamics.

Acknowledgments

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