The Scientific Naturalist

Nature's pitfall trap: salamanders as rich prey for carnivorous plants in a nutrient-poor northern bog ecosystem

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Botanical carnivory is an evolutionary marvel of the plant kingdom that has long fascinated general onlookers and naturalists alike. Darwin even dedicated serious study to these "most wonderful plants in the world" (Darwin 1875, Ellison and Gotelli 2009). Carnivory in plants has evolved multiple times across the world, often in wet, open, and nutrient-poor environments, as an alternative pathway of nutrient acquisition (Butler et al. 2005). Among carnivorous plants, the pitcher plants (family Sarraceniaceae), and specifically the northern pitcher plant (*Sarracenia purpurea purpurea* L.), intrigued early natural historians (e.g., Macbride 1815, Riley 1874, James 1883). *Sarracenia purpurea* is found across eastern North America, from the Gulf Coast of Florida north to Nova Scotia and west to the Rocky Mountains (Schnell 2002), making it the subject of early and contemporary observational and experimental studies. Naturally, much research has focused on the ability of these fascinating plants to capture prey and make use of prey nutrients. The specialized bell-shaped leaves of these pitcher plants collect rainwater in which prey dies, decomposes, and breaks down because of both inquiline microorganisms (aquatic larval insects, rotifers, mites, protozoa, and bacteria) that live within the pitcher and digestive enzymes produced by the plant. These digestive actions liberate nutrients for plant growth and reproduction (Adlassnig et al. 2011).

The documented prey assemblage of *S. purpurea* is diverse and comprised almost exclusively of invertebrates. For example, 115 insect families of 14 orders have been found in *S. purpurea* from North Carolina (Wray and Brimley 1943). In Canada, representatives of at least 12 insect orders and seven major invertebrate groups are reported from Newfoundland (Heard 1998), and at least 43 insect families and 13 higher-level invertebrate taxonomic groups have been found in Ontario (Judd 1959). Prey items in the plant's diet are predominantly Diptera, Hymenoptera, and Coleoptera (Cresswell 1993, Heard 1998). Despite an apparently large search effort, there is a conspicuous absence of vertebrate prey (occurring with any level of regularity) reported in these plants. Although rare, vertebrate prey have been reported in tropical pitcher plants (Nepenthaceae; Adlassnig et al. 2011). Rice (2011) remarked that the capture of vertebrate prey by tropical pitcher plants may be the "only example of vertebrate capture and digestion by a carnivorous plant that occurs frequently enough to be considered normal." In the present study, we use a collection of observations in *Sarracenia* to illustrate that vertebrate prey can occur with a striking frequency in Darwin's "most wonderful plants," and our observations generate several new lines of potential research.

Our study site is a small (~4.5 ha), naturally acidic (pH ~4.2–4.6), fishless kettle lake-bog in the low latitude boreal wetland region of western Algonquin Provincial Park, Ontario, Canada (45.6° N, 78.5° W; Appendix S1). The site supports nine species of breeding amphibians and has been home to long-term amphibian research. The bog periphery is ringed by mats of *Sphagnum* moss (*Sphagnum* spp. L.), which supports pitcher-plant (*S. p. purpurea* L.) and typical northern bog vegetation, including black spruce (*Picea mariana* Britton Sterns & Poggenb.), leatherleaf (*Chamaedaphne calyculata* L.), cottongrass (*Eriophorum* sp. L.), and sundew (*Drosera* spp. L.) (Appendix S1). In August 2017 (Survey 1), timed with the onset of salamander metamorphosis, we searched the contents of 144 pitcher plants. Pitcher contents contained predominantly Diptera (88%), Coleoptera (2.3%), and Hymenoptera (4.4%) and a total of eight recently metamorphosed spotted salamanders (*Ambystoma maculatum* Shaw): six live and two dead (Appendix S1: Table S1).

Following 2017 observations, we initiated multiple surveys in August and September 2018 (Appendix S1: Table S1), again timed with metamorphosis but extending across a greater breadth of the juvenile salamander dispersal period. Further, in fall 2017, a drift fence made of sheet metal was installed around the entire ≈ 1-km periphery of the lake, allowing all breeding adults and emergent juveniles to be inventoried from 2018 onward. In early August 2018 (Survey 2), 58 plants were investigated and the majority of the nonsalamander prey items were invertebrate taxa; Diptera (32%), Collembola (20%), and Hymenoptera (16%), with the remainder divided among various true bugs, mites, beetles, and spiders. In addition to these invertebrate prey items, three metamorphic spotted salamanders were discovered in pitcher traps (Appendix S1: Table S1). Subsequent 2018 surveys (Surveys 3 and 4) in late August and mid-September revealed metamorphic spotted salamanders captured in nearly 20% of surveyed plants (Fig. 1; Appendix S1: Fig. S1 and Table S1; Video S1; Video S2). The number of metamorphic salamanders captured in pitcher plants appeared to plateau quickly and was generally consistent with pulses of emergence from the lake, as indicted by concurrent drift fence surveys (Appendix S1: Fig. S1). On multiple occasions, more than one salamander was observed captured within a single pitcher (Appendix S1: Table S1; Video S2).

Some salamanders were observed to deteriorate in physical condition quickly following capture. In as little as 3 d, some salamanders went from alert and active in pitcher fluid (e.g., swimming, responsive to touch, natural skin coloration; Video S1, Video S2) to dead. We witnessed other captured salamanders survive at least 19 d. Spotted salamanders were observed trapped in pitchers that varied from ~1/4 full to completely full of fluid (Fig. 1), and in pitchers that were nearly recumbent (with the long axis of the pitcher at angles of <10° relative to the *Sphagnum* substrate) to nearly vertical (pitcher long axis >70° relative to substrate). In some cases, salamanders may have simply fallen into pitcher pitfalls (i.e., recumbent pitchers that had mouths flush with the substrate surface), whereas others would have had to climb plant leaves >8–10 cm off the substrate to enter the elevated mouths of some pitchers. Preliminary observations suggest that salamanders can escape, perhaps facilitated by rainfall and pitcher flooding, and further, that dead salamanders decompose rapidly (10 d or less; Butler et al. 2005, Regester and Whiles 2006). Instances of foul odor associated with pitcher traps containing vertebrates, suggesting prey overloading and putrefaction (Adlassnig et al. 2011), were recorded in 2017, but not in 2018. In total, eight individual salamanders were found trapped in pitcher plants during survey efforts in 2017
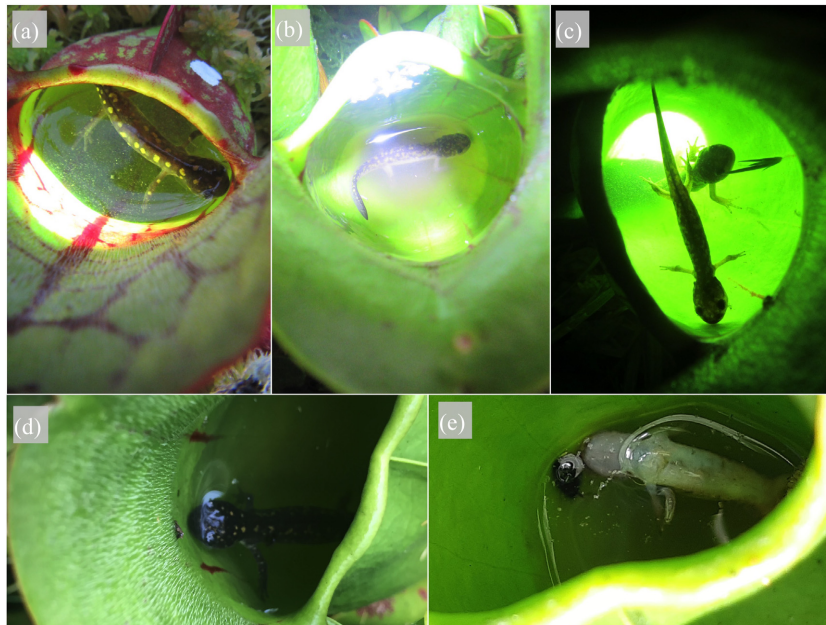

Fɪɢ. 1. Recently metamorphosed spotted salamanders (*Ambystoma maculatum* Shaw) trapped inside the leaves of northern pitcher plants (*Sarracenia purpurea purpurea* L.). (a), (d) Live salamander trapped within pitcher full of fluid, and (b) pitcher approximately half-full of fluid. (c) Two live salamanders trapped within a pitcher approximately four-fifths full of fluid. (e) Dead spotted salamander metamorph floating in half-full pitcher. Photos (a)–(c) by Patrick David Moldowan; photos (d), (e) by M. Alex Smith and Hannah Wynen.

and an additional 35 individuals were recorded with increasing survey effort in 2018.

The high frequency of salamander captures in pitcher plants suggests that salamanders might be a substantial nutrient source for pitcher plants. In 2018, average snout–vent length (SVL) of metamorphic spotted salamander at our site was 29.7 ± 2.8 mm SD ($n = 1,273$). Based on the relationship between SVL and dry mass for spotted salamanders given by Regester et al. (2006), we estimate that the average dry mass of metamorphic spotted salamanders at our site was 155 mg, of which $\approx$ 18.5 mg (11.9%) was nitrogen (Regester and Whiles 2006). Assuming *S. purpurea* pitchers are an average of 500 mg dry mass, of which 5 mg (1%) is nitrogen (Butler et al. 2005), a single salamander could contribute to the plant an amount of nitrogen equivalent to that contained in three pitchers (Appendix S1: Table S2).

The high frequency of captures also suggests that pitcher plants are a considerable mortality source for young salamanders. Between 17 August and 7 October 2018, 1,530 metamorphic spotted salamanders were captured at the on-site drift fence (Appendix S1: Fig. S1). The 35 salamanders caught by pitcher plants represent 2.3% of emerging metamorphic individuals from the breeding site. In 2018, we estimate that we sampled, at most, 50% of plants at the site (Appendix S1: Table S1) so it is conceivable that with full sampling effort, plant captures may approach 4–5% (nearly 1 in 20) of metamorphic individuals. If true, pitcher plants serve as a nontrivial source of mortality for salamanders and salamanders may serve as an appreciable seasonal nutrient pulse for pitcher plants.

Although there are many instances of carnivorous plants trapping small vertebrates (Skutch 1928, Cresswell 1993, Adlassnig et al. 2011), there are very few substantiated instances of vertebrate trapping in *Sarracenia* despite a wealth of study. Butler et al. (2005) reported juvenile red-spotted newt (*Notophthalmus viridescens* Rafinesque) in pitcher plants (Appendix S1: Table S1) and hypothesized that the frequency of *Sarracenia* pitchers containing small vertebrates, and potentially feeding upon them, may not be as rare as was thought. Our observations support this hypothesis. Salamanders may be underreported prey items in pitcher plants because of a relatively narrow detectability period during metamorphic amphibian emergence (late summer/early fall, in this case) and the rapid rate of decay of soft-bodied prey.

How and why do these salamanders enter the pitchers? One hypothesis is that metamorphic salamanders utilize pitchers as a refuge upon their emergence into terrestrial habitats. When plants were approached or disturbed, most salamanders rapidly swam to the bottom of the pitcher (Video S1) and tightly wedged themselves out of sight in the narrow, tapered stem of the pitcher. Individuals often remain submerged for several minutes and repeatedly dive to the pitcher bottom as long as the perceived threat remained. Another possibility is that the salamanders are attracted to the pitcher by small insect prey visiting to feed from the plant nectaries. This latter hypothesis seems more likely, given that the salamanders have ample and more readily accessible refugia within the complex vegetative mat at the aquatic–terrestrial interface, although explicit testing is required. Alternatively, salamanders may randomly encounter, fall into, and become trapped in recumbent pitchers. However, the capture of multiple salamanders in a single pitcher on more than one occasion (Appendix S1: Table S1; Butler et al. 2005) in relatively open habitat suggests that the capture of salamanders by pitcher plants may be nonrandom.

What causes the eventual death of the salamanders? We documented a wide-ranging survival period following entrapment (3–19+ d). Butler et al. (2005) hypothesized that newts killed in pitcher traps ultimately drowned through the debilitating effects of low pH (pH < 4; pH-physiology hypothesis), and they considered this effect to be more important than the deleterious effects of the plant's digestive enzymes. Given that enzymatic activity and pitcher fluid pH varies with leaf age (Fish and Hall 1978, Gallie and Chang 1997), it would be very interesting to know the age of the leaf and pitcher fluid pH for those plants containing salamanders. Perhaps salamanders are better able to tolerate entrapment under certain conditions (e.g., younger leaves that are less acidic, but can contain more digestive enzymes) permitting their survival and possible escape. We propose that temperatures inside the pitcher fluid may exceed the tolerable thermal maximum of trapped salamanders (thermal stress hypothesis), as some pitchers are fully exposed to sunlight. Observers have commented on the anesthetic properties of pitcher fluid on captured prey (Mellichamp 1875, James 1883, Juniper et al. 1989, p. 242), suggesting that inebriation and paralysis upon exposure may be another mode of mortality (intoxication hypothesis). Infection by environmental (inquiline) pathogens may be a cause of mortality during the immunosuppressed period of metamorphosis (immunocompetence hypothesis). Alternatively, if circumstances do not permit escape, energy reserves will become depleted and the salamander could succumb to starvation (exhaustion hypothesis).

Finally, and more broadly, our observations have led us to ask what the proportional biomass contribution of a salamander prey item(s) is to a plant relative to other captured prey? Do pitcher plants in amphibian-rich habitats (e.g., fishless bogs) reap benefits (greater growth, reproduction and/or densities, for example) from a larger and particularly nutrient-rich prey base, such as small vertebrates? Do fishless bogs in general generate relatively high productivity in the surrounding forest by virtue of extreme amphibian biomass?

Given that salamanders are several orders of magnitude larger than the invertebrate prey and are largely

comprised of soft flesh, the nutritional benefit of a salamander for a pitcher plant is likely to be substantial (Appendix S1: Table S2). Despite the brief window in which salamander prey are available to pitcher plants, it remains possible that salamanders are an important seasonal prey source for pitcher plants, at least in some areas. Future research may wish to address (1) to what degree nutrients from potentially nutrient-rich prey are absorbed by the plant, (2) nutrient allocation to plant tissues, and (3) consequences for plant fitness (growth and reproduction). Conversely, if salamanders are attracted to pitchers because of invertebrate prey, salamanders may undermine the nutrient acquisition of pitcher plants. The ecology of salamanders and pitcher plants may thus be unexpectedly interrelated.

Overall, our observations of salamanders as pitcher-plant prey provide exciting new avenues of research, especially as aquatic–terrestrial nutrient vectors in nutrient-poor and fish-free habitats. Vertebrate prey may be more common in the pitcher plant than was previously thought, and it is surprising that this report arises from an investigation of two widely distributed and well-studied species.

LITERATURE CITED

Adlassnig, W., M. Peroutka, and T. Lendl. 2011. Traps of carnivorous pitcher plants as a habitat: composition of the fluid, biodiversity and mutualistic activities. Annals of Botany 107:181–194.

Butler, J. L., D. Z. Atwater, and A. M. Ellison. 2005. Red-spotted newts: An unusual nutrient source for northern pitcher plants. Northeastern Naturalist 12:1–10.

Cresswell, J. E. 1993. The morphological correlates of prey capture and resource parasitism in pitchers of the carnivorous plant *Sarracenia purpurea*. American Midland Naturalist 129:35–41.

Darwin, C. 1875. Insectivorous plants. D. Appleton and Company, New York, New York, USA.

Ellison, A. M., and N. J. Gotelli. 2009. Energetics and the evolution of carnivorous plants–Darwin's "most wonderful plants in the world." Journal of Experimental Botany 60:19–42.

Fish, D., and D. W. Hall. 1978. Succession and stratification of aquatic insects inhabiting the leaves of the insectivorous pitcher plant, *Sarracenia purpurea*. American Midland Naturalist 99:172–183.

Gallie, D. R., and S. C. Chang. 1997. Signal transduction in the carnivorous plant *Sarracenia purpurea* (Regulation of secretory hydrolase expression during development and in response to resources). Plant Physiology 115:1461–1471.

Heard, S. B. 1998. Capture rates of invertebrate prey by the pitcher plant, *Sarracenia purpurea* L. American Midland Naturalist 139:79–89.

James, J. F. 1883. Pitcher plants. American Naturalist 17:283–293.

Judd, W. W. 1959. Studies of the Byron Bog in southwestern Ontario X. Inquilines and the victims of the pitcher-plant, *Sarracenia purpurea* L. Canadian Entomologist 91:171–180.

Juniper, B. E., R. J. Robins, and D. M. Joel. 1989. The carnivorous plants. Academic Press, London, UK.

Macbride, J. 1815. On the power of *Sarracenia adunca* to entrap insects. In a letter to Sir James E. Smith, President of the Linnean Society, from James Macbride, M.D. of South Carolina. Transactions of the Linnean Society of London 12:48–52.

Mellichamp, J. H. 1875. Notes on *Sarracenia variolaris*. Pages 113–133 in Proceedings of the American Association for the Advancement of Science, 23rd meeting.

Regester, K. J., K. R. Lips, and M. R. Whiles. 2006. Energy flow and subsidies associated with the complex life cycle of ambystomatid salamanders in ponds and adjacent forest in southern Illinois. Oecologia 147:303–314.

Regester, K. J., and M. R. Whiles. 2006. Decomposition rates of salamander (*Ambystoma maculatum*) life stages and associated energy and nutrient fluxes in ponds and adjacent forest in southern Illinois. Copeia 2006:640–649.

Rice, B. A. 2011. Reversing the roles of predator and prey: A review of carnivory in the botanical world. Pages 493–518 in J. Seckbach and Z. Dubinsky, editors. All flesh is grass, plant–animal interactions. Springer, New York, New York, USA.

Riley, C. V. 1874. Pitcher-plant insects. Nature 10:463–465.

Schnell, D. E. 2002. Carnivorous plants of the United States and Canada. Second edition. Timber Press, Portland, Oregon, USA.

Skutch, A. F. 1928. The capture of prey by the bladderwort: A review of the physiology of the bladders. New Phytologist 27:261–297.

Wray, D. L., and C. S. Brimley. 1943. The insect inquilines and victims of pitcher plants in North Carolina. Annals of the Entomological Society of America 36:128–137.

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