

Foraging modes of carnivorous plants

Aaron M. Ellison*

Harvard Forest, Harvard University, 324 North Main Street, Petersham, Massachusetts, 01366, USA

Abstract Carnivorous plants are pure sit-and-wait predators: they remain rooted to a single location and depend on the abundance and movement of their prey to obtain nutrients required for growth and reproduction. Yet carnivorous plants exhibit phenotypically plastic responses to prey availability that parallel those of non-carnivorous plants to changes in light levels or soil-nutrient concentrations. The latter have been considered to be foraging behaviors, but the former have not. Here, I review aspects of foraging theory that can be profitably applied to carnivorous plants considered as sit-and-wait predators. A discussion of different strategies by which carnivorous plants attract, capture, kill, and digest prey, and subsequently acquire nutrients from them suggests that optimal foraging theory can be applied to carnivorous plants as easily as it has been applied to animals. Carnivorous plants can vary their production, placement, and types of traps; switch between capturing nutrients from leaf-derived traps and roots; temporarily activate traps in response to external cues; or cease trap production altogether. Future research on foraging strategies by carnivorous plants will yield new insights into the physiology and ecology of what Darwin called “the most wonderful plants in the world”. At the same time, inclusion of carnivorous plants into models of animal foraging behavior could lead to the development of a more general and taxonomically inclusive foraging theory.

Keywords cost-benefit analysis; optimal foraging theory; phenotypic plasticity; sit-and-wait predation

Introduction

Feed me!

—*Little Shop of Horrors*’ [Audrey] Junior, in Griffith (1960: 30)

Carnivorous plants—the subjects not only of numerous fanciful stories, movies, and nightmares, but also of considered ecological and evolutionary study (e.g., Darwin, 1875; Ellison and Adamec, 2018a)—share characteristics of both autotrophs and heterotrophs. Like all plants other than holoparasitic ones, the > 800 species of carnivorous plants obtain carbohydrates from photosynthesis. Like predatory animals, carnivorous plants get their nutrients and some proteins from captured prey. But unlike most predators, including the fictional triffids (Wyndham, 1951), real carnivorous plants are firmly rooted in place. Their small, poorly-developed root systems generally contribute few nutrients and minerals to the plants’ overall metabolism, growth, or reproduction (reviewed in Adamec, 2018; Adamec and Pavlovič, 2018). Rather, the macro- and micronutrients essential for survivorship and reproduction of carnivorous plants are obtained through the attraction, capture, killing, and digestion of mobile, animal prey (Ellison and Adamec, 2018b).

Predatory animals also lure (or stalk), capture, kill, and digest prey. There is ample theoretical understanding of animal foraging modes and behaviors (e.g., Schoener, 1971; Charnov, 1976; Huey and Pianka, 1981). Some of

these have been extended to plants (e.g., Silvertown and Gordon, 1989; Hutchings and de Kroon, 1994; Liu et al., 2016), but carnivorous plants have not been included in theories and syntheses of plant foraging behavior.¹ In fact, the concept of “foraging” was not discussed directly even in the most recent overview of the ecology and evolution of carnivorous plants (Ellison and Adamec, 2018a),² and foraging theory itself has been applied to carnivorous plants only in three recent papers (Crowley et al., 2013; Jennings et al., 2016; Savage and Miller, 2018).

Here, I briefly summarize the parts of foraging theory that are relevant for its application to carnivorous plants; review how carnivorous plants capture prey and acquire nutrients; frame the primary foraging mode of these plants as an extreme example of sit-and-wait predation; and discuss how their foraging “behaviors” can be incorporated into, and used to test, various models of optimal foraging. I close the article with some suggestions

- 1 Carnivorous plants also have been overlooked in other theories and syntheses of ecology and evolution of plant traits (e.g., Wright et al., 2004; Diaz et al., 2016; but see Ellison and Farnsworth, 2005; Ellison, 2006; Farnsworth and Ellison, 2008; Ellison and Adamec, 2011).
- 2 In their contribution to that volume, however, Darnowski et al. (2018) did review data on selectivity of, and specialization on, prey by carnivorous plants (see also Ellison and Gotelli, 2009)

*Corresponding author. E-mail: aellison@fas.harvard.edu

for future research on foraging behavior by carnivorous plants.

Foraging theory for plant ecologists

Foraging [is] the process whereby an organism searches or ramifies within its habitat in the activity of acquiring essential resources.

—Slade and Hutchings (1987: 95)

A quarter-century ago, López et al. (1994) opened a review on parallels between foraging strategies of ants and plants with the pithy observation that “animal and plant ecologists generally follow separate paths.” Their review was timely. The preceding 25 years had seen a flowering of empirical and theoretical research on animal foraging behavior that had defined “optimal” foraging (Schoener, 1971; Charnov, 1976), identified foraging modes (“sit-and-wait” “widely foraging”: Pianka, 1966), and framed a research agenda that occupied many population and community ecologists and animal behaviorists for the next two decades. Concurrently, plant ecologists had moved away from descriptions of plant formations (Braun-Blanquet, 1932) and successional seres (Clements, 1936) to focus on individual- and population-level processes such as growth, demography, and resource allocation (Harper, 1977). It took only a small leap of imagination to ideate a foraging plant (Grime, 1979). The characterization of plants as modular organisms (Harper, 1980) simultaneously provided the lens through which plants—especially clonal ones—could be seen to “behave” through the placement and differential growth of individual modules (“ramets”³) in areas of higher light availability or nutrients (Bell, 1984).

In the 1970s and 1980s, studies of foraging by animals and plants focused—albeit almost always independently—on nearly identical questions. For animals, these included: defining the types and amount of prey obtained as a function of foraging mode; determining how foraging mode was related to the types and presence of higher-level predators; quantifying the energetic costs and benefits of different foraging modes; and testing whether foraging mode was a fixed or phenotypically plastic trait within individuals, populations, or species (e.g., Schoener, 1971; Huey and Pianka, 1981).

Paralleling the sit-and-wait *versus* widely-foraging strategies of animals (Huey and Pianka, 1981), the extreme

ends of the continuum of clonal plant foraging modes were defined as “phalanx” and “guerrilla” strategies (Clegg, 1978). Phalanx plants have densely packed ramets arising from basal clumps of many branches with short internodes, whereas guerrilla-strategists exhibit predominantly linear growth with little branching, long internodes, and widely-spaced ramets. Plants with these different growth forms would forage for light, nutrients, or water in different ways, and the costs and benefits of these foraging patterns were quantified (reviewed by Hutchings and de Kroon, 1994). Students of plant foraging behavior early on also identified phenotypic plasticity (Schlichting, 1986) as a key trait because of the indeterminate growth of plants, their regular production of identical modules, and their responsiveness to external environmental cues (Slade and Hutchings, 1987; Silvertown and Gordon, 1989; Hutchings and Kroon, 1994).

These common questions eventually led to some unified concepts, models, and theories of foraging strategies and behavior across kingdoms (e.g. Jackson et al., 1986; Rayner and Franks, 1987; López et al., 1994). For example, Rayner and Franks (1987) noted similarities in foraging by fungi and ants for resources dispersed heterogeneously in space; they somewhat fancifully concluded that “[f]urther experimental study and comparison of ants and fungi may help to elucidate some of *biology’s central mysteries*” (p. 132; emphasis added). López et al. (1994) saw similar functional parallels in foraging by animals and resource capture by plants, and outlined a general framework to “link important aspects of animal and plant foraging ecology” (p. 150) that was contingent on identification of a common currency for energetic efficiency of obtaining nutrients, prey, or other resources. Cain’s application of identical and general mathematical models of movement to searching and foraging behavior by herbivorous insects (Cain, 1985) and clonal plants (Cain, 1994; Cain et al., 1996) corresponded well to results of experiments with insects and plants.

As optimality arguments and adaptationist perspectives fell out of favor among ecologists and evolutionary biologists (Gould and Lewontin, 1979; Haccou and Vandersteen, 1992; Belovsky, 1994; Bolduc and Cezilly, 2012), research on foraging strategies slowed and then declined as a proportion of papers published in the ecological and behavioral sciences (Fig. 1). At the time of this writing, foraging by plants is but a small-niche topic of study among only a handful of plant ecologists (McNickle and Cahill, 2009; McNickle et al., 2009; Cahill and McNickle, 2011; Gao et al., 2012; Karst et al., 2012; McNickle and Brown, 2014; Oborny et al., 2017; Benedek et al., 2017). Recent reviews have focused either on parasitic (Mescher et al., 2009) or clonal plants (Liu et al., 2016). Parallels with animals have been neglected for over 20 years (for a notable exception, see Trewavas, 2006) except insofar that parasitic or carnivorous plants, like animals, are recognized as heterotrophs that need to locate hosts or attract prey, respectively, and overcome their defenses (Mescher et al., 2009; Savage and Miller, 2018).

3 Sarukhán and Harper (1973) coined the term “ramet” to mean the functional unit of a vegetatively or clonally reproducing species (such as an individual mushroom, buttercup, or coral polyp) and distinguished it from a “genet,” which is the genetic individual (the product of a spore, seed, or settling larva) and may be a large clone (such as a fairy ring of mushrooms, a mat of buttercups, or a head of a massive coral).

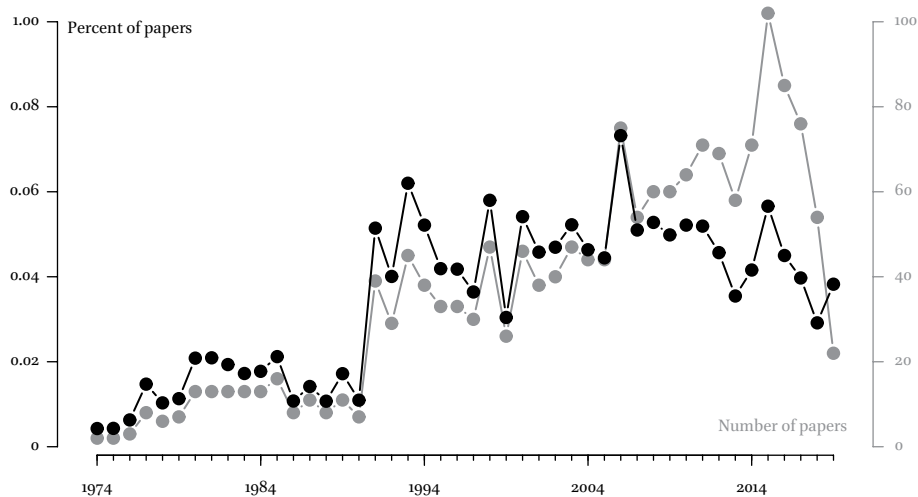


Figure 1. Percent (black) and total number (grey) of papers published annually since 1974 on “optimal foraging” in the Institute for Scientific Information (ISI)/Web of Science (WoS) categories of ecology, evolution, behavior, entomology, zoology, genetics, marine and freshwater sciences, and ocean sciences. An ISI/WoS search on “optimal foraging” (done on 2 May 2019) recovered a total of 1652 papers published since 1974; about 30% of these papers were indexed in more than one of the aforementioned ISI/WoS categories.

Nutrient acquisition strategies of carnivorous plants

The ultimate aim of research into foraging should be to understand the benefits and disadvantages of different resource-acquiring syndromes, and their ecological and evolutionary consequences.

—Hutchings and de Kroon (1994: 161)

Carnivorous plants have evolved independently in at least 10 angiosperm lineages encompassing five orders, a dozen families, and 19 genera (Fleischmann et al., 2018). These plants grow almost exclusively in bright, wet, and nutrient-poor terrestrial, wetland, and aquatic habitats such as ombrotrophic bogs, poor fens, sandy outwash plains, *tepuis* and inselbergs, and dystrophic lakes and streams (Brewer and Schlauer, 2018; Fig. 2). Their restriction to these habitats has been attributed in evolutionary terms to a cost-benefit trade-off: the benefit of being able to live and compete successfully in these “marginal” habitats has come at the cost of lower competitive ability in other habitats (Givnish et al., 1984, 2018)

Form and function of carnivorous plant traps

The prey-capturing traps of these plants all are derived from leaves, exhibit remarkable morphological convergence (Arber, 1941; Ellison and Gotelli, 2009), and include mucilage-covered “sticky” traps in *Byblis*, *Drosera*, *Drosophyllum*, *Philcoxia*, *Pinguicula*, *Roridula*, and *Triphyophyllum*; “pitfall” traps in the bromeliads *Brocchinia* and *Catopsis*, the pipewort *Paepalanthus*, and the pitcher plants *Cephalotus*, *Darlingtonia*, *Heliamphora*, *Nepenthes*, and *Sarracenia*; “eel” (*a.k.a.* “lobster-pot”) traps in *Genlisea* and *Sarracenia psittacina*; “suction traps” in *Utricularia*; and “snap-traps” in *Aldrovanda* and *Dionaea* (Fleischmann et al., 2018). The traps are distinguished either as “active”

or “passive” (Lloyd, 1942)—*a.k.a.* “motile” or “non-motile” (Poppinga et al., 2018; Bauer et al., 2018)—depending on whether all or part of them move.

The active or motile category includes snap- and suction-traps, sticky-traps with curling or snapping leaves, glands, or “tentacles”, and the pitchers of *Nepenthes gracilis* whose hood oscillates when struck by raindrops, bouncing foraging ants from the underside of the hood into the pitcher fluid (Poppinga et al., 2018). The non-motile category includes pitfall- and eel-traps, and sticky-traps without motile leaves, glands, or tentacles.⁴ Regardless of trap type, however, carnivorous plants are best categorized as “sit-and-wait” predators because they are firmly rooted in place or, in the case of unrooted aquatic *Utricularia*, float passively in the water, moved only by wind or currents.⁵

Carnivorous plants acquire nutrients *via* predation through five sequential activities: attracting prey, capturing, killing, and digesting them, and finally absorbing the metabolites from the killed and digested prey (Ellison and Adamec, 2018b). The majority of prey attracted to, and captured by, carnivorous plants are arthropods: insects by terrestrial carnivorous plants and various small crustaceans and zooplankton by aquatic carnivorous ones (Ellison

4 Many non-motile traps have structural characteristics that prevent prey from escaping, such as slippery wax crystals or downward-pointing hairs on the inside of *Nepenthes* and *Sarracenia* pitchers, and viscoelastic fluid in a few *Nepenthes* species (Bauer et al., 2011, 2018).

5 In a study of three potentially competing predators, Jennings et al. (2016) characterized the carnivorous plant *Drosera capillaris* as a “passive” forager, the lycosid spider *Sosippus floridanus* as a “sit-and-wait” forager, and the toad *Anaxyrus quercicus* as an “active” forager. However, in a general mathematical formulation of sit-and-wait *versus* active predation, the purest “sit-and-wait” strategy is to never move (Zoroa et al., 2011).



Figure 2. Examples of dense populations of carnivorous plants in bright, wet, nutrient-poor habitats. **Top:** The California cobra-lily *Darlingtonia californica* grows only in serpentine seeps in northern California and southern Oregon, USA. **Bottom:** The horned bladderwort *Utricularia cornuta*, whose traps, stems, and rhizoids are within the peat, flowers in profusion in bogs and poor fens throughout eastern North America. Photographs © Aaron M. Ellison and used with permission.

and Gotelli, 2009; Darnowski et al., 2018). Attraction is accomplished through visual, olfactory, or acoustic signals, or by providing nectar or carbohydrate-rich mucilage as lures (Horner et al., 2018). Prey are captured in the aforementioned motile or non-motile snares (Poppinga et al., 2018; Bauer et al., 2018).

Once in the traps, prey are drowned in the fluid-filled pitchers of the various pitfall-trapping species or the bladders of *Utricularia*, suffocated in the mucilage and resins of sticky-trappers or the labyrinths of eel-trappers, or crushed and suffocated in the snap-trapping *Dionaea* and *Aldrovanda* (Plachno and Muravnik, 2018). Digestion occurs via glandular secretions of proteases, phosphatases, chitinases, nucleases, and carbohydrate-digesting enzymes (Juniper et al., 1989; Plachno and Muravnik, 2018; Matušiková et al., 2018). In some species of *Darlingtonia*, *Sarracenia*, *Heliophora*,

Nepenthes, and *Utricularia*, commensal bacteria, protozoa, and small arthropods (collectively, “inquilines”) living within the fluid-filled traps partially or completely decompose the prey and mineralize the nutrients that are absorbed by the plant (Ellison et al., 2003; Bittleston, 2018; Miller et al., 2018; Sirová et al., 2018).

Benefits and costs of being a carnivorous plant

Like foraging by animals, predation activities by plants involves handling time and incurs metabolic or energetic costs. For carnivory to evolve among plants, however, the marginal benefits accruing to carnivorous plant from nutrients obtained from captured prey must exceed the marginal costs associated with production, deployment, and functioning of traps to attract, capture, and kill prey,

plus the marginal costs of its subsequent mineralization and digestion (Givnish et al., 1984). Benzing (2000) and Givnish et al. (2018) developed more elaborate models illustrating how optimal allocation to leaves (for photosynthesis), roots, and traps (modified leaves) is a function of trade-offs among water availability, light, and how much carbon fixed by photosynthesis (and hence allocated to growth and reproduction) is augmented by nutrients obtained through captured prey.

Darwin (1875) was the first to demonstrate that carnivorous plants actually absorb and use the nutrients from captured prey. Observational and experimental evidence accumulated in the last 150 years generally has found a positive relationship between prey-derived nutrients and plant growth and reproduction (Ellison, 2006; Adamec, 2018; Adamec and Pavlovič, 2018; Givnish et al., 2018). In at least four unrelated genera (*Dionaea*, *Drosera*, *Pinguicula*, and *Sarracenia*), prey capture by carnivorous traps also stimulates root growth and associated nutrient uptake by these new roots (Hanslin and Karlsson, 1996; Adamec, 2002; Lenihan and Schultz, 2014; Gao et al., 2015; see further discussion below).

The largest cost of being a carnivorous plant is that the traps, which are derived and modified from leaves (or leaf parts), are photosynthetically much less efficient than leaves (Ellison and Gotelli, 2002). Carnivorous plants have significantly lower photosynthetic rates and photosynthetic nutrient-use efficiency than would be predicted by general leaf-trait scaling relationships (Wright et al., 2004; Ellison and Farnsworth, 2005; Ellison, 2006). Feeding carnivorous plants either supplemental prey or inorganic nutrients increases their photosynthetic rates (Knight, 1992; Ellison and Gotelli, 2002) and brings them more in line with general leaf-trait scaling relationships (Ellison, 2006; Farnsworth and Ellison, 2008). There are further energetic costs to producing traps themselves that are compounded by the low rate of photosynthesis by terrestrial carnivorous plants (Ellison, 2006; Karagatzides and Ellison, 2009). Although the aquatic *Utricularia* has very high photosynthetic rates (Ellison and Adamec, 2011) and it responds similarly to manipulation of prey availability (Ellison, 2006; Adamec, 2018), interactions between light availability and

supplemental prey can offset the benefit of each in isolation (Englund and Harms, 2003)

Do carnivorous plants forage optimally?

Animals move when signalled, plants change their phenotype.

—Trewavas (2006: 2)

Carnivorous plants clearly can attract, capture, kill, and digest prey, and use their nutrients for metabolism, growth, and reproduction. But can they be said to “forage” for prey? Foraging implies not only a suite of behavioral traits (Slade and Hutchings, 1987) but also the possibility of altering those behaviors as environmental conditions or prey availability changes e.g., Charnov 1976, Zoroa et al., 2011; Higginson and Ruxton, 2015; Ross and Winterhalder, 2015). In models of selection for foraging strategies, the “goal” of the predator is to maximize net energy intake while minimizing time or resources spent searching for prey (Table 1; Charnov, 1976; Zoroa et al., 2011).

For animals, the probability that a sit-and-wait predator moves from a patch depends on prey availability or the rate at which prey are encountered within the patch, and the energy cost of moving between patches (Charnov, 1976; Huey and Pianka, 1981; Zoroa et al., 2011). Additional parameters that can modify foraging behavior include spatial autocorrelation of favorable (or unfavorable) habitats; aggregation and behavior; state of predators and their prey (Berger-Tal et al., 2010; Mukherjee and Heithaus, 2013; Scharf, 2016; e.g., hunger or propensity to take risks); and sizes of foraging groups (solitary foragers, e.g., wolf packs; Schoener, 1971; Ross and Winterhalder, 2015). Although some real animals can switch between sit-and-wait and active-hunting strategies (Bell, 1991), both classical and recent foraging models assume they do not (e.g., Charnov, 1976; Huey and Pianka, 1981; Scharf et al., 2006; Higginson and Ruxton, 2015; Ross and Winterhalder, 2015).

In contrast, foraging responses by plants in response to changing resource availability reflect phenotypic plasticity (sensu Schlichting, 1986) that could be characterized

Table 1. Key components of foraging activity after Schoener, 1971; Charnov, 1976; Higginson and Ruxton, 2015; Ross and Winterhalder, 2015) and generalized responses by sit-and-wait animal predators and carnivorous plants.

| Foraging traits | Sit-and-wait animals | Carnivorous plants |
|---------------------------------|---|---|
| Pursuit (including search) time | Optimize giving-up time or movement between patches with different prey densities to maximize encounter rate while minimizing energetic costs. | Evolution of a variety of visual and olfactory attractants; provisioning of food and other lures for prey. |
| Handling time | Optimize energy obtained per time spent handling (e.g., capturing, killing, caching). Specialization on prey species or size may be common or rare. | “Passive traps”: Selection optimizes: adhesiveness (e.g., <i>Byblis</i> , <i>Drosera</i> , <i>Pinguicula</i>); near-frictionless surfaces (e.g., <i>Nepenthes</i> , <i>Sarracenia</i>); one-way “lobster-pot” trap morphology (e.g., <i>Genlisea</i> , <i>Sarracenia psittacina</i>). “Active traps”: Selection for: rapid speed of closure and energetic efficiency (<i>Aldrovanda</i> , <i>Dionaea</i> , <i>Utricularia</i>); biomechanical novelties (e.g., <i>Drosera glanduligera</i> , <i>Nepenthes bicalcarata</i>). Prey specialization is rare. |
| Feeding rates and eating time | Different functional responses. | Most have Type I functional response. Most have evolved digestive enzymes that are modified from compounds used for defenses against herbivores; some have digestive mutualisms with inquilines (in <i>Sarracenia</i> , <i>Nepenthes</i> , <i>Utricularia</i>). |

as a switch between sit-and-wait and more active foraging behavior. For example, plants respond to reduction in light availability by etiolation—the elongation of internodes produced between leaves or branches—and reduced branching (reviewed by Hutchings and de Kroon, 1994). Increased light, and especially increased nutrient availability, can stimulate branch and root production by activating lateral buds (Slade and Hutchings, 1987; Hutchings and de Kroon, 1994). In extreme cases, plants faced with rapid decline in resource availability may flower, fruit, and disperse seed to new habitats just before the plants die (Bazzaz, 1991).

Evolutionary canalization and ecological plasticity of carnivorous plants

The central organizing principle for the evolution of carnivory by plants is that the carnivorous traps provide sufficient net benefits in nutrient-poor habitats to offset the costs of producing the traps and any concomitant reduction in photosynthetic rates (Givnish et al., 1984; Ellison and Gotelli, 2002; Givnish et al., 2018). The structure and predictions of this cost-benefit model have been supported by observational and experimental evidence (reviewed thoroughly in Givnish et al., 2018), but the model itself is focused on the *evolution* of carnivory by plants as a fixed nutrient-acquisition mechanism for plants growing in particular habitats. That is, once a carnivore, always a carnivore. In an unchanging environment with a predictable supply of prey, we would predict—in line with the model of Zoroa et al. (2011)—that carnivorous plants would maintain a fixed foraging strategy as sit-and-wait predators with a constant production of traps and consistent rate of prey capture dependent only on the local density and movement patterns of insects. But environments do vary and prey populations grow, crash, or move, and real carnivorous plants are not triffids that uproot themselves and move to another site when they are hungry.

Most carnivorous plants are solitary or have “phalanx” growth forms.⁶ However, phenotypic plasticity associated with foraging occurs in carnivorous plants that switch from production of carnivorous traps to non-carnivorous leaves within seasons or ontogenetically; take up additional nutrients through their roots after capturing prey; or temporarily activate traps at irregular intervals in response to environmental or other external cues. These responses mirror those expected by the cost-benefit model for the evolution of carnivory but occur in ecological time and within the lifetime of a single plant. Thus, they can be considered to be analogous to behavioral changes observed by predators that switch to alternate prey, move to another patch, or change from sit-and-wait foragers to actively-hunting ones.

⁶ The Asian pitcher plants (*Nepenthes* species) and some bladderworts (*Utricularia* species) have “guerrilla” growth forms but there has been no work on whether species in either of these genera can alter their Baupläne.

Variation in production of carnivorous traps

The cost-benefit model for the evolution of carnivorous plants implies that they should be most prevalent in very bright, moist, and nutrient poor-habitats (Givnish et al., 2018). A prediction of this model relevant to plant foraging behavior is that when carnivorous plants are shaded by neighbors, habitats dry up, or nutrient supply changes, the plants should shift to alternative, non-carnivorous methods of obtaining nutrients. Observations and experiments on many different species of carnivorous plants have supported this prediction.

Ellison and Gotelli (2002) showed that within a single growing season, the northern (or purple) pitcher-plant *Sarracenia purpurea* shifted from producing carnivorous pitchers to non-carnivorous but photosynthetically more efficient flattened leaves (“phyllodia”) (Fig. 3). Similar phenotypic plasticity has been observed in the yellow pitcher plant (*S. flava*) and the Venus’ fly-trap (*Dionaea muscipula*) fed supplemental prey (respectively by Weiss, 1980; Gao et al., 2015); *Nepenthes talangensis* and *Dionaea muscipula* fertilized with inorganic nutrients (respectively by Pavlovič et al., 2010; Gao et al., 2015); and *S. purpurea* across an experimental sun-shade gradient (Mandossian, 1966). Shading and fertilization reduced the stickiness of leaf traps of the the round-leaved sundew, *Drosera rotundifolia* (Thorén et al., 2003), whereas trap (bladder) production in *Utricularia* declined in low light conditions in spite of high prey availability (Englund and Harms, 2003).

Natural variation in production of pitchers and phyllodia by *S. purpurea* occurs across geographic gradients in atmospheric nutrient deposition (Ellison and Gotelli, 2002) and smaller-scale gradients in nutrient availability in different types of wetlands (Bott et al., 2008). Shifts to production of phyllodia also occur in response to drought (in *S. flava*, *S. oreophila*, *S. leucophylla*: Christiansen, 1976; Weiss, 1980), onset of winter (in *Di. muscipula* and the Australian pitcher plant *Cephalotus follicularis*: Slack, 1979), or shade (in some *Nepenthes* species: Slack, 1979). Stickiness of sticky traps (i.e., investment in the glands or mucilage that trap and digest prey) also varies across gradients in availability of light (in the butterwort *Pinguicula vallisneriifolia*: Zamora et al., 1998) or nutrients (in *P. moranensis*: Alcalá and Dominguez, 2005). Some Mexican *Pinguicula* species shift from producing carnivorous sticky leaves to succulent, non-carnivorous ones during the dry winter season while others cease producing leaves altogether and form overwintering resting buds (Alcalá and Dominguez, 2005). The West African liana *Triphyophyllum pelatatum* is both ontogenetically and seasonally heterophyllous. Juvenile and adult leaves are, respectively, only photosynthetic or photosynthetic and hooked to support the growing vine, whereas carnivorous glandular (sticky) leaves are produced only at the beginning of the annual rainy season (Menninger, 1965; Green et al., 1979).

Carnivorous plants also may compete with animals for prey. For example, bladderworts (*Utricularia vulgaris*) competes with bluegill (*Lepomis macrochirus*) for shared zooplankton prey. Presence of *Utricularia* reduced prey abundance, but its removal had no significant effect

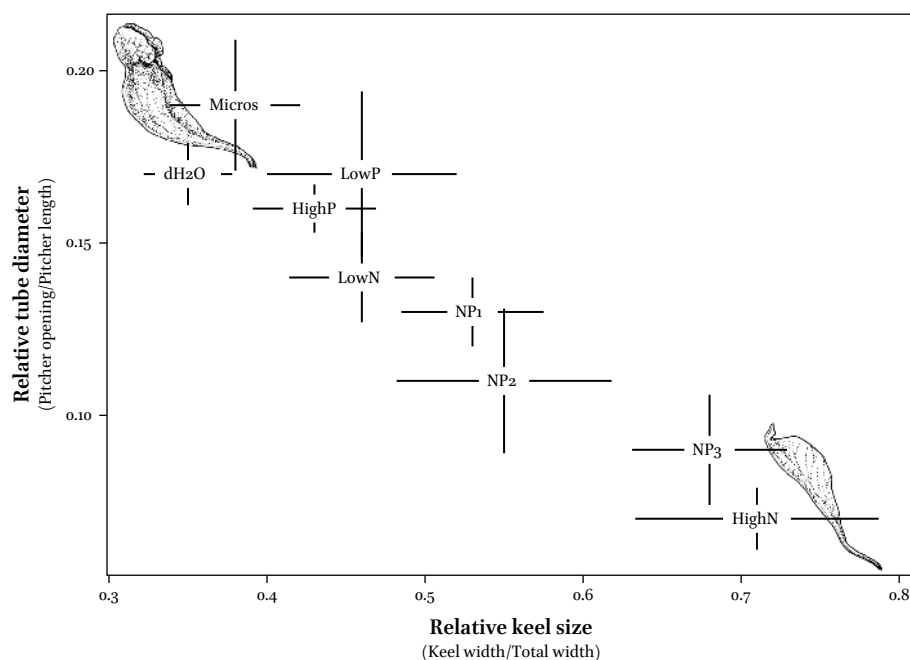


Figure 3. Relative size of leaves produced by *Sarracenia purpurea* as a function of inorganic nitrogen (as 0.1 [LowN] or 1.0 [HighN] mg $\text{NH}_4\text{-N/L}$ as $\text{NH}_4\text{Cl/L}$), phosphorus (as 0.025 [LowP] or 0.25 [HighP] mg $\text{PO}_4\text{-P/L}$ as NaH_2PO_4), or micronutrients (10% Hoagland's solution [Micros]) added weekly in one of nine combinations (LowN, LowP, HighN, HighP, Micros; three stoichiometric manipulations: LowN + LowP [NP1], HighN + HighP [NP2], and HighN + LowP [NP3]; and distilled water controls [dHzO]) to replicate sets of ten pitchers. Figure redrawn from Ellison and Gotelli (2002).

on bluegill survivorship or growth (Davenport and Riley, 2017). Spiders and the pink sundew *Dr. capillaris* also have high dietary overlap in the field (Jennings et al., 2010). A mathematical model of this interaction suggested that competitive interactions between these two species could alter trichome density (a measure of trap stickiness) on the leaves of the sundew (Crowley et al., 2013). This prediction was tested and supported in mesocosms: increased spiderweb density at ground-level led to an increase in trichome density (i.e., investment in traps) on sundew leaves (Jennings et al., 2016).

Stimulation of root uptake by prey capture

The observed stimulation of nutrient absorption by roots of several carnivorous plant species after they have captured and digested prey with their foliar traps may represent an adaptive foraging "switch." Three species each of sticky-trapping *Drosera* (Adamec, 2002) and *Pinguicula* (Haslin and Karlsson, 1996) fed supplemental prey subsequently absorbed from the soil relatively large amounts of potassium (K), calcium (Ca), and magnesium (Mg) but less nitrogen (N) or phosphorus (P). The preferential uptake of K, Ca, and Mg from soils may have occurred because relatively small amounts of these macronutrients are derived from prey (Adlassing et al., 2009), whereas N and especially P routinely are taken up from prey (Ellison, 2006; Ellison and Adamec, 2011; Adamec, 2018).

In contrast, the snap-trapping *Di. muscipula* showed increased uptake of N (as ammonium: NH_4^+) and glutamine following foliar feeding of prey or inorganic NH_4^+ (Gao et al., 2015). This response by *Di. muscipula* to foliar

feeding is unlike that seen in noncarnivorous plants, for which inputs of foliar N reduce (down-regulate) its uptake by roots (Gao et al., 2015). Further, the fed traps appeared to become sinks for root-derived carbon (Gao et al., 2015), which is unsurprising given the energetic cost of digestion of prey and assimilation of mineralized nutrients. One could hypothesize that the switch to root uptake of N following prey capture is an adaptive response that provides additional nutrients needed for subsequent increases in photosynthesis. Photosynthesis would also increase with the increase in petiole length observed in fed *Di. muscipula* plants (Gao et al., 2015).

Sarracenia purpurea also increases root-uptake of N following foliar feeding, and by inference, in response to atmospheric deposition of nitrogen oxides (NO_x) (Leihan and Schultz, 2014). In parallel with the observed reduction in trap production and increase in phyllodia production described above (see *Variation in production of carnivorous traps*, above), *S. purpurea*, like *Di. muscipula*, rapidly shifts its foraging phenotype in response to external stimuli (Ellison and Gotelli, 2002).

Transient and temporary activation of traps

Traps rarely function continuously or collect prey at a constant rate. For example, prey capture by *S. purpurea* pitchers peaks 2–3 weeks after they open, coincident with their brightest color or peak in nectar production (Fish and Hall, 1978; Wolfe, 1981; Cipollini et al., 1994). Pitchers of several *Sarracenia* species are produced sequentially or in cohorts, and pitchers produced later in the season tend to be smaller (Juniper et al., 1989; Butler and Ellison, 2007;



Figure 4. *Nepenthes rafflesiana* growing in Borneo, with its enlarged and conspicuous peristome. Photograph © Aaron M. Ellison and used with permission.

Horner et al., 2012), less attractive (Bhattarai and Horner, 2009), and trap fewer prey than pitchers produced at the beginning of the growing season (Bhattarai and Horner, 2009; Horner et al., 2012). The higher abundance of prey late in the growing season may offset the reduction in capture rate by smaller pitchers (Horner et al., 2012). Whether these canalized developmental patterns in pitcher size reflect selection for maximizing foraging success, however, remains unexplored.

In contrast, some species of *Nepenthes* temporarily activate their traps in response to external cues. In most *Nepenthes* species, the “lip” (peristome) of the pitcher is replete with extrafloral nectaries whose secretions attract foraging ants who then recruit their nest-mates to this abundant source of sugars (Juniper et al., 1989; Merbach et al., 2001). The peristome is normally dry, but when it is moistened by condensing fog, rain, or the nectar itself, it becomes nearly frictionless (Bauer et al., 2008). Ants foraging on a wetted peristome lose their footing and “aquaplane” into the fluid-filled pitcher in which they drown (Bohn and Federle, 2004). The intermittent and unpredictable activation of the peristome as a wet-

table surface led Bohn and Federle (2004) and Bauer et al. (2008) to hypothesize that it would facilitate ant recruitment when dry and maximize prey capture (as “batches of ants”) when wet, relative to a continuously wet peristome. Field observations and experiments with *N. rafflesiana* in Brunei supported this hypothesis (Bauer et al., 2015; Fig. 4).

Bauer et al. (2015) went on to show mathematically that intermittent batch captures would maximize nutrient intake if the batch-captured prey was reliably both the predominant prey species and abundantly recruited to the lure. For many *Nepenthes* species growing in the lowland wet tropics of Southeast Asia, ants are the dominant prey and recruit to nectar sources in abundance (Adam, 1997; Merbach et al., 2001). Additional support for this hypothesis comes from observations that lichen-feeding termites (*Hospitalitermes bicolor*) recruiting to, and feeding on, the white lichen-mimicking trichomes produced just beneath the peristome of *N. albomarginata* also are captured in large batches (Moran et al., 2001; Merbach et al., 2002). It is plausible, therefore, that the activation of the *Nepenthes* peristome represents an adaptive foraging strategy for this genus of sit-and-wait predators.

Other foraging adaptations

Two other potential foraging strategies merit attention. First, intraspecific variation in shapes and positions of *Nepenthes* pitchers expands the spectrum of prey available to and captured by the plants (Clarke and Moran, 1994; Moran, 1996; Rembold et al., 2010). Most *Nepenthes* species produce two kinds of pitchers. Seedlings and young plants produce rosettes of “lower” pitchers that rest on the ground. As the *Nepenthes* vines grow upward, they produce aerial “upper” pitchers that, like leaves, are suspended in the air. Perhaps unsurprisingly, lower pitchers captured far more walking, crawling, or otherwise flightless arthropods (such as mites, spiders, springtails, and termites) than the upper pitchers, which tended to capture flies, beetles, and butterflies (Moran, 1996; Rembold et al., 2010). Ants were captured by both upper and lower pitchers, but sexual (alate) ants usually were present only in the upper ones (Rembold et al., 2010). In the extreme, some species produce pitchers with peculiar morphological adaptations associated with unusual foraging strategies. These include the “toilet”-shaped upper pitchers of *Nepenthes lowii* that attract tree shrews and assimilate nutrients from their accumulating feces (Clarke et al., 2009), and the mostly detritivorous lower pitchers of *N. ampullaria* (Moran et al., 2003). To my knowledge, however, there has been no exploration of switching between production of pitcher types in response to external cues.

Second, for carnivorous plants that have a more “phalanx” growth morphology, Savage and Miller (2018) suggested that groups of *Sarracenia flava* pitchers might forage and accumulate prey like a pack of wolves or other group-foraging species, with similar advantages (Clark and Mangel, 1986). Observational data of *S. flava* plants growing in Florida showed that identifiable ramets had 1–5 pitchers, but it was difficult to distinguish genets

(Savage and Miller, 2018). Experimental groupings of potted *S. flava* plants placed in the field differed in total mass of prey captured (larger groups had more total prey mass) but per-leaf capture rate of all prey and numbers of individuals from different insect orders (or ants; family Formicidae) were statistically indistinguishable among groups of different sizes (Savage and Miller, 2018). These results are not especially surprising, as *Sarracenia* and other carnivorous plants rarely are selective in the taxa of prey that they capture (Ellison and Gotelli, 2009) and have Type-I (less frequently, Type-II) functional responses (*sensu* Holling, 1959) to prey availability (Ellison and Gotelli, 2009; Darnowski et al., 2018; Horner et al., 2018).

Future research directions

Elsewhere immense research into the nature, habits and constitution of the triffid went on. Earnest experimenters set out to determine in the interests of science how far and for how long it could walk; whether it could be said to have a front, or could it march in any direction with equal clumsiness; what proportion of its time it must spend with its roots in the ground; what reactions it showed to the presence of various chemicals in the soil; and a vast quantity of other questions, both useful and useless.

—*The Day of the Triffids*, Wyndham (1951: 30)

This review of foraging strategies by carnivorous plants suggests several lines of research that could yield new insights into their physiology and ecology, and additional contributions to general theories of foraging behavior applicable to both animals and plants.

Future research on foraging by carnivorous plants

Carnivorous plants have evolved traps and foraging strategies that maximize energetic benefits and minimize costs of trapping (Givnish et al., 2018). These constraints occur in ecological time, and phenotypically plastic responses that increase benefits and decrease costs have been observed within single growing seasons. Overall, benefits have been quantified for many species but costs have not (Ellison, 2006).

The observation that carnivorous plants increase (switch to) their uptake of nutrients by roots after they have captured prey with their leaf-derived traps suggests an adaptive response that could further promote photosynthesis and growth. Testing this hypothesis will require simultaneous and sequential measurements of nutrient uptake and transport, and photosynthesis coupled with new understanding of mechanisms of regulation and induction of digestive enzymes by carnivorous plants (Matušíková et al., 2018).

Research on prey capture by carnivorous plants has focused on documenting prey spectra and specialization, usually over entire growing seasons and at coarse

taxonomic levels (insect prey are routinely distinguished only by order, with ants separated out of Hymenoptera). Description of temporal patterns in prey availability and short-term capture rates are less common, but could help to explain why many carnivorous plants produce smaller traps later in the growing season. Better taxonomic resolution of prey could also clarify whether co-occurring species of carnivorous plants really are: foraging randomly or whether they specialize on particular prey types; competing for available prey; or can shift their foraging strategies in response to external cues.

Most carnivorous plants have “phalanx” growth forms that mirror the sit-and-wait strategy of animal predators. But some carnivorous plants, including the vining *Nepenthes* spp. and *Triphyphyllum peltatum*, and many aquatic *Utricularia* spp., are more “guerrilla”-like. Whether these species can, like other clonal plants (Hutchings and de Kroon, 1994), adjust their internode length or trap density in response to prey availability remains unexplored. Specific to *Nepenthes*, which produce dimorphic traps, is the question of whether they can alter the production or location of different trap types in response to seasonal or other temporal changes in prey availability.

A reunification of plant and animal foraging theory

General models of animal foraging assume pure strategies: either sit-and-wait or actively-hunting. Plants, with their plastic responses to resource availability, illustrate the existence of a continuum between these pure strategies that merits more general exploration in foraging theories for both animals and plants.

Plants also can be considered the purest form of sit-and-wait predator: they sit and never move (*cf.* Zoroa et al., 2011). In this way, plants are more like sessile filter-feeders. Some filter-feeders are solitary (e.g., barnacles, clams, oysters), but others are colonial (e.g., bryozoa, hydrozoa, corals, sponges). The modular construction of plants and colonial animals suggests similar foraging strategies and plastic responses that have been explored in taxonomic isolation for over three decades (Harper, 1986). Bringing these back together could lead to a foraging theory that is taxonomically inclusive and includes solitary, colonial, sessile, mobile life forms.

Acknowledgements

I thank Ofer Ovadia and Inon Scharf for inviting me to present a perspective on sit-and-wait predation from the point of view of a carnivorous plant. Useful discussions with Brita Svensson, Gustaf Granath, and Robert Muscarella helped me to focus attention on salient traits of carnivorous plants relevant to this review. I am grateful for two decades of continuous support by the US National Science Foundation and the Harvard Forest for my research on carnivorous plants.

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