

BRIEF COMMUNICATION

The cobra's tongue: Rethinking the function of the "fishtail appendage" on the pitcher plant *Darlingtonia californica*¹

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PREMISE OF STUDY: Carnivorous pitcher plants employ a variety of putative adaptations for prey attraction and capture. One example is the peculiar forked "fishtail appendage", a foliar structure widely presumed to function as a prey attractant on adult leaves of *Darlingtonia californica* (Sarraceniaceae). This study tests the prediction that the presence of the appendage facilitates prey capture and can be considered an example of an adaptation to the carnivorous syndrome.

METHODS: In a field experiment following a cohort of *Darlingtonia* leaves over their growing season, before the pitcher traps opened, the fishtail appendages from half of the leaves were removed. Additionally, all appendages were removed from every plant at two small, isolated populations. After 54 and 104 d, prey items were collected to determine whether differences in prey composition and biomass existed between experimental and unmanipulated control leaves.

KEY RESULTS: Removal of the fishtail appendage did not reduce pitcher leaves' prey biomass nor alter their prey composition at either the level of individual leaves or entire populations. Fishtail appendages on plants growing in shaded habitats contained significantly greater chlorophyll concentrations than those on plants growing in full sun.

CONCLUSIONS: These results call into question the longstanding assumption that the fishtail appendage on *Darlingtonia* is an adaptation critical for the attraction and capture of prey. I suggest alternative evolutionary explanations for the role of the fishtail structure and repropose a hypothesis on the mutualistic nature of pitcher plant–arthropod trophic interactions.

KEY WORDS carnivory; *Darlingtonia*; pitcher plant; prey capture; Sarraceniaceae

Carnivorous pitcher plants (families Sarraceniaceae, Nepenthaceae, and Cephalotaceae) share a number of convergent traits enabling the attraction and capture of animal prey. These include modified fluid-filled pitcher leaves, low-friction cuticles, false exits, trichomes, and extrafloral nectaries (Lloyd, 1942; Juniper et al., 1989). Many other pitcher plant traits, however, have yet to be rigorously verified as critical adaptations to the carnivorous syndrome, despite over a century of literature assigning them such a functional role. In actuality, many unique features of pitcher plants, when closely scrutinized, suggest alternative adaptive scenarios

(e.g., Joel, 1988). For instance, certain morphological characters of *Nepenthes* (Nepenthaceae) pitcher organs have been shown to serve mutualistic, rather than predatory, roles with arthropods and mammals (Clarke et al., 2010; Grafe et al., 2011; Bazile et al., 2012). Likewise, many leaf traits hypothesized to facilitate prey capture in *Sarracenia* (Sarraceniaceae) serve either an alternative or no detectable function upon empirical evaluation (Cresswell, 1993; Green and Horner, 2007; Bennett and Ellison, 2009; Schaefer and Ruxton, 2014).

Darlingtonia californica Torr. (Sarraceniaceae), the sole member of its genus, is the only pitcher plant native to the western United States. It is associated with habitats containing a constant source of cold, flowing water on or downstream of serpentine formations. A recent phylogenetic analysis suggests *Darlingtonia* diverged from the clade giving rise to *Sarracenia* and *Heliophora* sometime during the Oligocene (25–44 million years ago) (Ellison et al., 2012).

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However, due to a paucity of fossil evidence, the phenotype of the common ancestor to these clades is unknown (Wong et al., 2015). While the pitcher leaves of *Darlingtonia* clearly share morphological features with other members of Sarraceniaceae, they are arguably the most complex within the family (James, 1885; Lloyd, 1942; Franck, 1975) (Fig. 1). Foliar traits unique to *Darlingtonia* include the presence of transparent light-transmitting fenestrations, a downward-oriented trap entrance, and the twisting of developing leaves around their vertical axes such that consecutive leaves on a rosette end up facing different directions. Perhaps the most striking feature of the *Darlingtonia* leaf is its “fishtail appendage”—a unique forked structure hanging off the apex of the leaf’s pitcher entrance. This feature has inspired the taxon’s common name: the cobra plant or cobra lily. At its base, the appendage merges with the nectar roll, which encircles the margin of the pitcher entrance. The nectar roll continues along the margins of the fishtail appendage

until terminating distally. The fishtail appendage’s nectar glands, red venation, and short hairs oriented toward the pitcher entrance have led researchers to treat the structure as a prey attractant (Austin, 1875–1877; Lloyd, 1942; Juniper et al., 1989; Schnell, 2002; Ellison and Farnsworth, 2005), but this function has not yet been experimentally verified.

The leaves of *Darlingtonia* vary in size both within and among individual plants. Pitcher leaves can be classified into two morphological types: juvenile and adult. Juvenile leaves are small and tubular (less than 5 cm in length), and found on plants less than 2 years of age. These lack many of the specialized morphological features of adult leaves (e.g., the bifurcated fishtail appendage) and may function to trap small arthropods (Franck, 1976). The more complex adult leaves produced by mature plants vary considerably in size (5 cm to >1 m tall), but are otherwise morphologically identical. Leaf height, mass, and chlorophyll content tend to increase with shade (D. W. Armitage, unpublished data). During the growing season (early June–October), an individual rhizome continuously produces leaves in a rosette, with each successive leaf decreasing in size. The pitcher entrances remain closed until the leaf reaches its maximum height, then the fishtail appendage rapidly develops and begins producing nectar. Concurrently, the semitransparent distal portion of the leaf swells and forces open the trapping orifice. Small adult pitcher leaves are often recumbent, and their fishtail appendage may function as a ramp for small terrestrial arthropods to access the nectar roll (Lloyd, 1942).

If the presence of the fishtail appendage enhances the luring and trapping prey items, then its removal from an adult pitcher should result in a decrease of successful capture events compared with a pitcher on which it is present. However, this effect may only manifest in small adult pitchers lying prone along the ground. Alternatively, since individual *Darlingtonia* ramets can produce upward of 10 pitcher leaves per growing season, there may be a ramet or genet-level benefit of the appendage that does not manifest at the level of the individual pitcher leaf. For instance, expression of the appendage by an isolated stand of leaves may serve as a long-distance attractant for prey insects, which otherwise may not congregate in the vicinity of the plant. If the absence of these appendages does not negatively impact a plant’s accumulation of prey, then they should not be considered a critical adaptation for prey capture. I tested this hypothesis using a manipulative field experiment in which I removed the fishtail appendages from individual large (erect) and small (prone) *Darlingtonia* leaves before their maturation. I tracked and compared the taxonomic composition and accumulated biomass of captured prey between manipulated and control leaves over a 3-mo growing season. Additionally, I removed all appendages from two small, isolated



FIGURE 1 Mature leaf of *Darlingtonia californica* with fully formed fishtail appendage.

patches of *Darlingtonia* to test whether the presence of the appendage at the population level influenced rates of prey capture.

MATERIALS AND METHODS

The study was done in Plumas National Forest (Plumas County, California, USA), where numerous, patchy populations of *Darlingtonia* occur in spring-fed seeps ranging from between <10 to thousands of individual ramets, each possessing upward of 10 pitcher leaves (exact coordinates are available on request). During late May 2014, I tagged 60 individual developing, unopened pitcher leaves belonging to two size classes: large ($n = 40$, height > 50 cm, erect) and small ($n = 20$, height < 15 cm, growing recumbently). These leaves were located in a small (<1000 total leaves), isolated (>1 km from closest known patch) population of *Darlingtonia* growing in a 30 m² spring-fed seep in the Butterfly Valley Botanical Area, Plumas National Forest. One single leaf was selected per rosette to minimize bias caused by a plant's genotype and to decrease impacts on the organism. These focal leaves were spaced a minimum of 50 cm apart. I removed the developing fishtail appendage using a pair of fingernail clippers from a random sample of half of the leaves. Because insects may also be attracted to the scent of a pitcher leaf's putrefying detritus, I removed fishtail appendages before pitchers opened and commenced trapping.

After 52 d, I harvested 10 large leaves from experimental and control treatments. Prey accumulation in all small leaves was at the limit of detection, and so none were removed. All other large and small leaves were harvested after 104 d. I removed the prey contents of each leaf and stored them in vials of 70% ethanol. Most arthropod prey are rapidly dismembered and digested by the pitchers' associated aquatic food web, leaving only the exoskeleton behind. This digestion prevents the unambiguous identification of prey items, although the remaining material (primarily head capsules and wings) permitted identification of individuals to the level of order, and many to suborder or family. This material was then dried at 60°C for 48 h and weighed. I tested for differences in prey biomass between leaves with and without their fishtail appendages using an analysis of variance (ANOVA) with pitcher size and sampling date as covariates. Additionally, I tested whether the age and presence of the appendage on large pitchers had an effect on the taxonomic composition of prey insects using the permutational analysis of variance algorithm *adonis* implemented in the *vegan* R package (Anderson, 2001; Oksanen et al., 2015). I performed this analysis twice using raw compositional data primarily at the suborder and family levels and the same data grouped at the order level.

I conducted a second experiment to test the hypothesis that fishtail appendages play a role in prey attraction or capture at the level of individual plants or small founding populations. Early in the 2015 growing season, I located two small, isolated patches of *Darlingtonia* comprising between 100 and 250 pitchers and located at least 500 m downstream from the nearest neighboring populations. Because *Darlingtonia* populations tend to expand downstream along spring-fed seeps, these small founding populations probably represented a single genet dispersed as a seed from larger populations growing upstream. From these populations, I removed the fishtail appendage from all leaves. I marked 20 unopened leaves of equivalent developmental stage and returned to the site approximately every 20–30 d to remove the appendages from developing leaves. After 104 d, I removed the 20 marked pitchers from each

plot and took them to the laboratory for prey biomass measurement. I compared the per-leaf prey biomasses from these "population-level" removal treatments to those of the 2014 "leaf-level" removals and control treatments using ANOVA. The 2014 data were necessarily used as controls because no other unmanipulated and similarly isolated plots of *Darlingtonia* could be located in the region. However, there were no interannual differences in prey capture rates among unmanipulated leaves sampled from larger nearby populations (D. W. Armitage, unpublished data). To increase statistical power, I pooled data from the two experimental populations because there were no significant differences between the populations' means and variances.

Because *Darlingtonia* can grow in shaded habitats, its fishtail structure may also serve a photosynthetic role. To investigate this possibility, I removed an additional 20 fishtail appendages from 10 leaves growing in full sunlight and 10 plants growing in heavy shade for chlorophyll analysis. These leaves were taken from a medium-sized population growing upstream of the 2015 experimental plots. I estimated the total chlorophyll [Chla + Chlb] concentration of each appendage using an Apogee CCM-200 chlorophyll content meter (Apogee Instruments, Logan, Utah, USA). This device outputs a chlorophyll content index (CCI) that I converted into total chlorophyll content (mg/cm²) using a standard calibration equation ($R^2 = 0.96$) (Richardson et al., 2002). Each fishtail appendage was measured in triplicate (at its midpoint and along both wings), and I compared the averaged estimates using a Student's *t* test. I performed all data analysis in R (v. 3.1.1) (R Core Team, 2015). When necessary, data were log-transformed to meet the assumptions of homogeneity and normality of residual variances.

RESULTS

Prey biomass increased with leaf age, but removal of appendages did not impact prey biomass accumulation (Table 1, Fig. 2A). Likewise, I did not detect an effect of population-level appendage removals on prey biomass ($F_{2,56} = 2.1$, $P = 0.133$) (Fig. 2B). Despite marked interleaf variability in prey composition, I found no evidence for discrimination in prey taxa between *Darlingtonia* leaves with and without fishtail appendages, but prey composition differed significantly between 52-d- and 104-d-old leaves (Table 1; Appendix S1, see Supplemental Data with the online version of this article). The majority of prey in all large pitchers belonged to the orders Hymenoptera (11.4 ± 2.0 /leaf; primarily families Vespidae and Ichneumonidae), Coleoptera (9.9 ± 2.3 /leaf; primarily family Cerambycidae), and Diptera (3.9 ± 0.9 /leaf). However, individual large-bodied lepidopterans and orthopterans occasionally greatly contributed to prey biomass. Small pitchers contained far fewer prey than large pitchers, and the prey assemblage contained only small dipterans and coleopterans <3 mm in body length (Appendix S1). Chlorophyll content was relatively low in fishtail appendages growing in both full sun and shade, but appendages from shaded plants contained significantly higher chlorophyll concentrations than plants in full sun ($t = 4.6$, $df = 16.9$, $P < 0.0005$) (Fig. 3).

DISCUSSION

Contrary to expectations, removal of the fishtail appendage from leaves of *Darlingtonia* did not hinder the plant's ability to lure and

TABLE 1. ANOVA and PERMANOVA models and test statistics for the effects of appendage removal, pitcher leaf age (days), and pitcher leaf size (mg) on prey biomass (mg) and prey composition in *Darlingtonia californica* leaves. No significant interactions were found among any covariates.

Response variable	Covariate	df	SS	F	P
Prey biomass	Fishtail appendage	1	5.71	1.952	0.168
	Pitcher age	1	142.3	48.679	<0.0001
	Pitcher size	1	5.8	1.984	0.165
	Residuals	56	163.7		
Prey composition (orders)	Fishtail appendage	1	0.230	1.131	0.324
	Pitcher age	1	2.489	12.236	<0.0001
	Residuals	36	7.324		
Prey composition (raw)	Fishtail appendage	1	0.497	1.558	0.101
	Pitcher age	1	2.033	6.377	<0.0001
	Residuals	36	11.479		

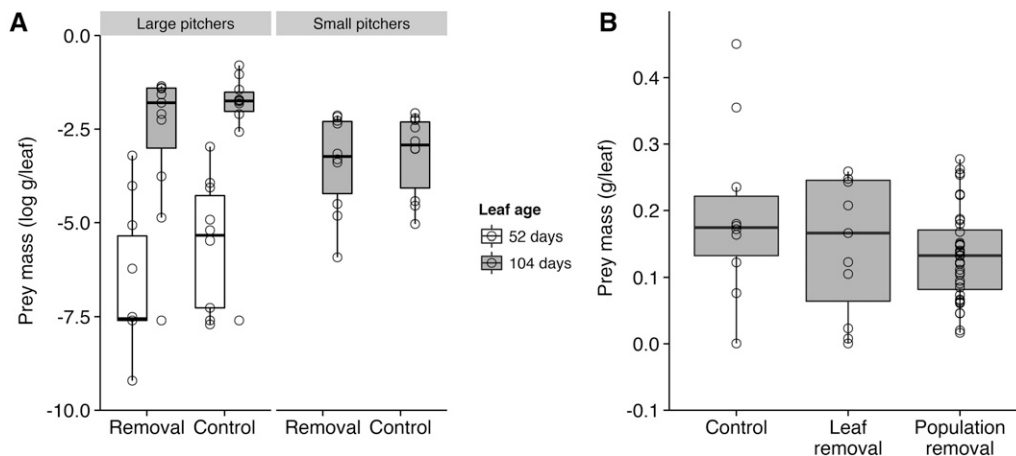
capture prey items, nor did it change the taxonomic composition of the captured prey. This outcome was observed in both large and small adult pitchers and was not influenced by the leaf's age. Furthermore, the complete removal of fishtail appendages from entire isolated patches of *Darlingtonia* did not negatively impact individual leaves' abilities to trap prey compared to both untreated populations and experimental leaves surrounded by neighbors possessing the appendage. In concert, these findings suggest that the presence of fishtail appendages within relatively isolated, small populations of *Darlingtonia* may not function to attract prey into the patch nor into a leaf's trapping orifice. These results call into question the assumption that all nectary-bearing structures on pitcher plant leaves are critical adaptations to the carnivorous syndrome.

The fishtail appendage of *Darlingtonia* may instead represent a vestigial or exapted structure. Members of the sister genus *Sarracenia* possess an offshoot of the nectar roll that forms an operculum "hood", replete with extrafloral nectaries along its outer rim, red venation along the medial axis, and hairs on its underside. Similar, convergent structures can also be found on the majority of *Nepenthes* (Nepenthaceae) and *Cephalotus* (Cephalotaceae) species. In these genera, the operculum shows remarkable interspecific variation but is generally believed to function both in prey capture and the prevention of flooding and dilution of the pitcher chamber

from rainwater (Juniper et al., 1989). Within Sarraceniaceae, *Sarracenia purpurea* and members of the neotropical genus *Heliamphora* lack an operculum, although derivatives of this structure manifest in *S. purpurea* as a vertical extension of the nectar roll possessing all of its characteristic traits and in *Heliamphora* as a reduced appendage possessing enlarged nectar glands and no hairs (Adams and Smith, 1977). In the latter, flooding is mitigated via a small slit in the leaf's keel serving as a drain (Lloyd, 1942). In *Darlingtonia* and the morphologically similar *Sarracenia psittacina*, the flooding problem is ameliorated by the species' downward-facing pitcher openings. In these taxa, an inflated, semitransparent, hairless "hood" wraps over the entire upper portion of the pitcher leaf, and the operculum covering is either lost completely (as in *S. psittacina*) or remains as the fishtail appendage on *Darlingtonia* (Lloyd, 1942).

The fishtail appendage of *Darlingtonia* and the opercula of *Sarracenia* and *Heliamphora* share many developmental and morphological features. The pitcher leaves of Sarraceniaceae undergo nearly identical patterns of early histogenesis wherein the apical tissue of the leaf primordium gives rise to the operculum in *Sarracenia* or the hood and fishtail appendage in *Darlingtonia* (Lloyd, 1942; Franck, 1975; Fukushima et al., 2015). Arber (1941) observed that the leaves of Sarraceniaceae share a similar pattern of venation wherein the majority of veins

converge at the midrib's apex at exactly the point where the opercula and fishtail appendage originate. The author hypothesized that this clustering of veins results in a disproportionate supply of nutrients and localized hypertrophy, which, in turn, initiates the development of the pitcher's operculum or fishtail appendage (Arber, 1941). On adult leaves of *Darlingtonia* and *Sarracenia*, nectar glands ring the margins of their appendages, and the positioning and location of hairs on the undersides of both structures is identical, although the hairs are reduced in *Darlingtonia* (Adams and Smith, 1977). In *Sarracenia*, these hairs are hypothesized to

**FIGURE 2** (A) Prey biomass as a function of fishtail appendage presence (x-axes), pitcher size (facets), and pitcher age (shading); (B) prey biomass as a function of appendage removal treatment. Boxes denote 25th through 75th percentiles; bolded lines denote median values.

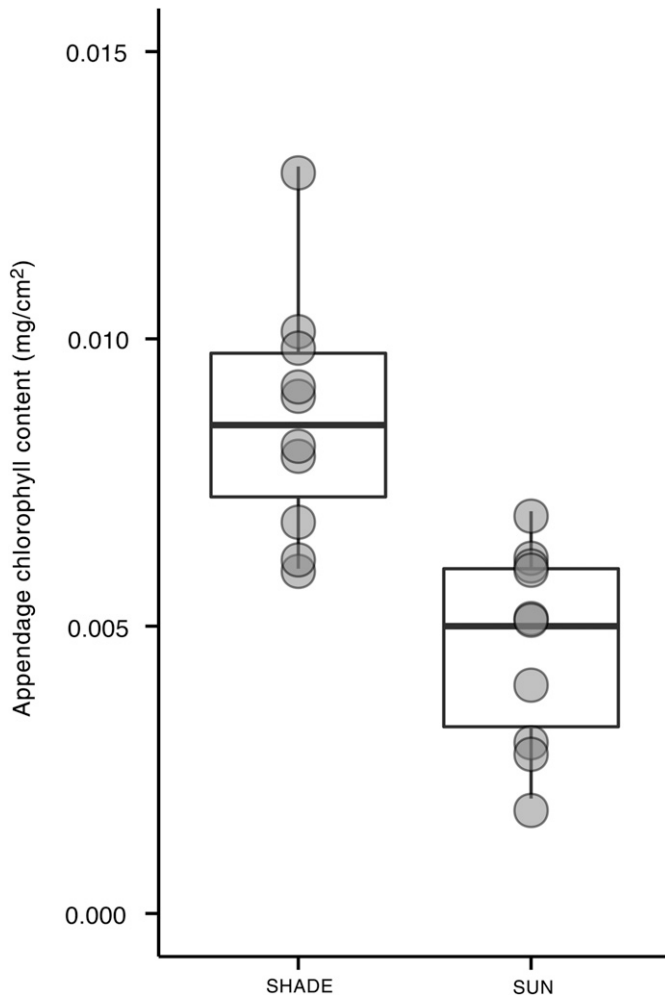


FIGURE 3 Total chlorophyll content of fishtail appendages from sun- and shade-growing *Darlingtonia* populations. Boxes denote 25th through 75th percentiles; bolded lines denote median values.

inhibit the foothold of insects, which then fall directly into the pitcher trap (Lloyd, 1942). In *Darlingtonia*, however, these hairs would cause potential prey to fall from the leaf. These observations are consistent with the fishtail appendage of *Darlingtonia* being homologous with the operculum of *Sarracenia* and the nectar spoon of *Heliophora*.

Given the morphological plasticity of the fishtail and opercular appendages in Sarraceniaceae, these structures may serve roles contingent upon their local environments. It was hypothesized that plants' investments in traits that facilitate carnivory come with a cost to photosynthetic efficiency such that they can only thrive in habitats where they will not experience strong competition with noncarnivorous plants for light, water, or nutrients (Givnish et al., 1984). Thus, plants should reduce their investment in carnivorous organs in low-light environments and instead reallocate growth to photosynthetic tissues (Zamora et al., 1998; Thorén et al., 2003). Using the size of the fishtail appendage as a proxy for a plant's investment in prey capture, Ellison and Farnsworth (2005) concluded that, contrary to their expectations, *Darlingtonia* plants were unable to regulate the size of the fishtail appendage under changing photosynthetic conditions. The authors also detected remarkably

low overall photosynthetic rates for all plants measured (Ellison and Farnsworth, 2005). Unlike other members of Sarraceniaceae, however, *Darlingtonia* can be found growing in shaded habitats (D. W. Armitage, personal observations), where the plants' fishtail appendages contain greater chlorophyll concentrations than plants growing in full sun. This finding suggests that the fishtail appendage might serve a photosynthetic role in light-limited habitats. Therefore, the structure should not be assumed to be independent of a plant's photosynthetic abilities nor a proxy for investment in carnivory.

The fishtail appendage of *Darlingtonia* may instead be involved in supporting local insect populations—a phenomenon that has also been observed in the genus *Nepenthes* (Bazile et al., 2012). Rebecca Austin (1875–1877), the first botanist to study the natural history of *Darlingtonia* in the wild, noted that flies would regularly alight on the fishtail appendage and feed on its nectar, while only a very small minority were drawn into the leaf and trapped. The low capture probability of *Darlingtonia* was later estimated to be approximately 1.7% of vespulid wasps that had already landed on a pitcher leaf (Dixon et al., 2005). The probability of successful prey capture (compared with the overall number of visits) in other pitcher plant species is similarly low, and experimental and observational studies have failed to support the hypothesized roles of numerous other foliar traits in prey capture (Cresswell, 1993; Green and Horner, 2007; Bennett and Ellison, 2009; Schaefer and Ruxton, 2014). These findings, along with the common observation of insects feeding on pitcher leaves and avoiding capture, beg an alternative explanation for the fishtail appendage's role. Joel (1988) hypothesized that the relationship between pitcher plants and insects represents a mutualistic, rather than a predator–prey interaction. The author reasoned that because pitcher plants are commonly found in hydric, sunny habitats, their liberal nectar offerings do not negatively impact a plant's water and carbon budgets. Pitcher plants in the family Sarraceniaceae are often the dominant nectar-bearing members of their local communities and supply nectar to insects continuously throughout the growing season. Nectivorous insects quickly learn to exploit this resource, and the behavior is maintained as long as insect mortality via entrapment is not common enough to be selected against. With its bountiful nectar glands, the fishtail appendage on *Darlingtonia* may facilitate insects' feeding on the plant's nectar while remaining incidental to prey capture. Additional sources of “unsafe” nectar along the margins of the pitcher entrance may tempt the occasional insect into entering the trap while the “safe” nectar presented on the fishtail appendage may promote and maintain visitation by nectivorous insects. The plant would then benefit from the small proportion of insects lured into the pitcher trap. However, my data do not support this hypothesis, since the per capita prey biomass in isolated, appendage-free populations was not significantly lower than in control populations, although a nonsignificant negative trend was observed. An alternative approach toward testing this hypothesis would involve quantifying the relative contributions of pitcher nectar to the diets of the local insect community. Such a study could be carried out using stable isotope ratios of nitrogen, which are anticipated to differ between the nectars of carnivorous and noncarnivorous plants and likewise between insects selectively feeding on either nectar source (e.g., Zanden and Rasmussen, 2001).

In conclusion, by experimentally removing the unique fishtail appendages on leaves of *Darlingtonia californica*, I demonstrated that the absence of the structure does not hinder a leaf's ability to

capture prey. This finding contrasts with over a century of descriptive literature categorizing the structure as an adaptation to the luring and trapping of prey. There are at least three potential alternative explanations for this structure's evolutionary persistence: (1) as a vestigial homologous structure under little to no selection; (2) as a facultatively photosynthetic structure facilitating carbon acquisition in shaded habitats; and (3) as a source of "safe" nectar encouraging visitation by nectivorous insects and supporting their local populations while entrapping a small proportion of visitors. These alternative roles need not be mutually exclusive and likely depend on environmental factors. Adaptive explanations for the unique morphological and physiological traits possessed by carnivorous plants pervade the literature. However, barring experimental verification, these adaptive hypotheses remain speculative. Going forward, researchers are encouraged to take a more pluralistic approach in their treatments of carnivorous plants by considering alternative evolutionary explanations for the unique foliar features of these plants.

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