Prey capture by *Dionaea muscipula*
A review of scientific literature with supplementary original research

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Abstract: Many descriptions of prey capture by *Dionaea muscipula* (Venus flytrap) in popular publications and educational literature are inaccurate. Here we review well documented literature on prey capture in this plant's natural habitat and add observations on prey capture and attraction mechanisms we have observed in plants cultivated in a greenhouse and garden.

Despite its common name "Venus flytrap" does not specialize in capturing flies. About 70% of the prey it captures in its native habitat consists of spiders, ants, and beetles. Flies are only one-to-eighteen percent of what it captures. In a greenhouse where flies, capable of entering the vents, composed most of the available prey, over 90% of the prey captured were flies. *Dionaea* cultivated in a garden captured a diverse array of animals, only about 37% of which were flies. *Dionaea* is a generalist, capturing a wide variety of prey species. Its capture mechanism does not appear to have a "syndrome" analogous to the Pollination Syndrome in flowers where a specific floral type is pollinated by a specific animal (i.e. Bee Flowers or Fly Flowers).

The measured capture rates of *Dionaea* are low, about one capture/leaf/month in its native habitat. Similar but lower rates were measured in the greenhouse and garden. The single measurements in each habitat need to be repeated, but the low rates are consistent with the observation that wherever it is observed *Dionaea* has nearly all of its traps open. Both the low capture rates and the large number of open traps suggests that alluring agents drawing prey either do not exist or are ineffective.

Despite reports of nectar secretion by *Dionaea* traps, our observations show that unstimulated traps are always dry unless wet by rain, condensation, or a sprinkler system. Secretion occurs only after prey capture. Alluring glands along the outer trap margin have been reported to be visited by small ants that work their mouthparts over the glands. We have photographed a fly exhibiting the same behavior. The exact nature of this behavior needs to be further investigated, but it does not appear that this attractant can act at a distance since flies are as likely to land on the outside of a trap as on the inside.

Darwin proposed that the trap closure mechanism allows small prey to escape, preventing the expenditure of energy on captures likely to be of little benefit. Recent measurements of prey captures indicate that traps show little selectivity based on prey size and that while traps could, in theory, select larger prey, statistically they do not behave this way.

Introduction

What prey does *Dionaea muscipula* capture?

Any carnivorous plant can only capture prey that is present in its environment. If placed in a large terrarium with houseflies it can only capture houseflies. The prey present in the plant's habitat will determine what the plant's traps can capture. However, other factors also determine what prey will be found in traps. Some carnivorous plants have been reported to have extra floral nectaries, attractive scents, and colors analogous to flowers. The relative attractiveness to prey would skew the proportion of each type of prey animal captured. The mechanics of the trap such as the ability to hold large prey, react quickly enough, etc. would also determine the type of prey captured.

It is the object of this paper to review the range of prey that is captured by *Dionaea* in various habitats and determine if characteristics of the trap might favor the capture of specific types of prey.

Most early observations of prey capture were likely conducted on plants cultivated in greenhouses or gardens far away from the plants' natural habitat and usually near human habitations. We will call these the greenhouse habitat and the garden habitat. The first early common name for *Dionaea*, "Catch Fly sensitive", used in a 2 April 1759 letter to Peter Collinson from Gov. Arthur Dobbs of North Carolina, infers that the plants primarily catch flies. Later Dobbs, in a 24 January 1760 letter to Collinson, calls the plant "Fly Trap Sensitive" (Nelson 1990). Subsequent early references to *Dionaea* refer to it as "Tipitiwitchet" which has no reference to the prey captured, but when John Ellis described the plant in the St. James Chronicle in 1-3 September 1773 he called it "Venus's flytrap" even though he knew that it captured many kinds of "little animals, such as Ear-wigs, Spiders and Flies" (Nelson 1990). For its scientific name Ellis proposed "*Dionaea Muscipula*, which may be construed into English, with humble submission both to Critics and foreign Commentators, either as Venus's Flytrap, or Venus's Mousetrap." The Latin species epithet *muscipula* actually means mousetrap, but the common name that took hold with the public was "Venus flytrap".

The name Venus flytrap infers that the prey of *Dionaea* consists of flies, which in a greenhouse with a population of flies, is what most of us who grow the plant observe. Most popular and educational descriptions of *Dionaea* also presume that flies are the major source of prey.

Methods

Prey capture measurements Natural Habitat (Lichtner & Williams 1978).

Leaves were collected in the field (Fig. 1 and Front Cover) from closed traps. For a thorough discussion of *Dionaea* ecology, see Roberts and Oosting (1958). The prey animals were identified in the field and preserved in alcohol. Specimens were reviewed in the laboratory to confirm the order to which they belonged.

Greenhouse Habitat

Two large *Dionaea* plants with traps up to five cm, a selective breeding by Klaus Ivanez (Germany), available in Germany and neighboring countries labeled with the additional designations "Predator" and "Destroyer" (not registered as cultivars) were in 10×10 cm pots (Fig. 2). Entrance of prey into the greenhouse was mostly restricted to the open vents, greatly favoring the entrance of agile fliers such as flies. The two plants had about 25-33 active traps. The eight prey captured previous to our study in reopened leaves were photographed and identified. During the following 36 days, 13 additional prey animals were captured and identified after the traps reopened.

Garden Pond Habitat

A population of *Dionaea* plants similar to those found in the wild had been established in a large pot with other carnivorous plants for about 20 years was used as the Garden Habitat. Access to prey incapable of flight was limited because the pot was effectively an island in the garden pond (Fig. 3). The population of plants had about 50 active leaves. The five prey captured previous to our study

Figure 1: Natural Habitat. Left: Zone between savannah and pocosin in the Green Swamp in North Carolina. The *Dionaea* in the foreground are marked with stakes for capture rate studies. Right: A close-up of one of the *Dionaea* plants.

in reopened leaves were photographed and identified. During the following 80 days, 58 additional prey animals were captured and identified after the traps reopened. In two captures, pairs of mating mosquitos were captured together. These were each logged as a single capture.

Capture rate measurements Natural Habitat (Williams 1980)

Plants in the field near Supply, North Carolina, USA were marked by placing a numbered potting stake nearby. The leaf nearest the potting stake was leaf 1. The leaves were numbered clockwise around the rosette notating the leaves that were closed (Fig. 1). Enough plants were staked to provide data from about 224 leaves. The leaves were observed just after dawn, at noon, the evening, and the following morning; closures of leaves were recorded. After the final observation the closed leaves were opened to determine if capture of prey had occurred. The traps were then tested to see if they were capable of rapid closure and 201 were. The number of closures with captures and closures without captures were recorded and the number of captures in 24 hours was computed.

Greenhouse Habitat

The traps were photographed daily for 36 days during which there was an average of 29.2 active traps. The observations were ended after 36 days because the weather had cooled enough that the greenhouse vents did not open and insects were not able to easily enter. Monitoring during the next

Figure 2: Greenhouse Habitat. Above: The large *Dionaea muscipula* available in some European countries with the additional designations “Predator” (left) and “Destroyer” (not registered as cultivars) are on the bench in the foreground (white box). Competing carnivorous plants capture more flies than the *Dionaea*. Below: A close-up of the *Dionaea*.

two weeks showed no new captures were made when the vents were closed. Trap reopenings were recorded instead of closures so capture rates were computed as reopenings/day.

Ultraviolet (UV) experiments

Measurements of UV reflection/absorption and fluorescence were made using an ultraviolet lamp (Raytech Versalume UV-lamp with two glass filters for 254nm and 366nm) that emits a spectral curve from approx. 230-420nm with two maxima at 254nm and 366nm. The emission spectrum of the lamp has a visible shoulder from 380-420nm, which appears as dark-blue light. The invisible long-waved UV radiation (around 366nm) is either reflected (impinging light spectrum = reflected spectrum) or absorbed (no reflection, the surface remains dark) or it produces (with some excep-

Figure 3: Garden Pond Habitat. Above: *Dionaea* (white box) similar to that found in the wild growing at the base of *Sarracenia* in the pot to the left rear. The pond is a barrier to prey that cannot fly. Below: Close-up of the *Dionaea*.

tions, i.e. Rhodamine = red fluorescence at 580nm) a bright blue to cyan fluorescence between 420-500nm (The impinging lamp spectrum becomes transferred into a bright visible light, shifted to a longer wavelength by an optical active compound inside or upon the plant tissue). To evaluate such UV studies requires some experience in order to differentiate between UV reflection and fluorescence and to avoid confusion and mistakes; in addition, safety glasses should be used. *Dionaea* and the peristome of *Nepenthes talangensis* × *truncata* were observed for both UV reflection/absorption and fluorescence. As reference for active fluorescence we used writing paper containing optical brightener (Exact composition of the brightener was not labeled on the packaging, but usual for this application is a stilbene derivate mixed with SiO_2 as white filler (also called white body)) that shines super white[1] under UV-radiation.

Review, new results, and discussion

Prey capture in the Natural Habitat

The first person to make an effort to actually see what *Dionaea* captures in its native habitat was Charles Darwin (Darwin 1875, p 312-313). He wrote to Dr. Canby who "visited the native site of the plant, early in the season, before the leaves had grown to their full size, and sent... [Darwin] fourteen leaves, containing naturally captured insects. Four of these had caught rather small insects, viz. three of them ants, and the fourth a rather small fly, but the other ten had all caught large insects, namely, five elaters, two chrysomeles, a curculio, a thick and broad spider, and a scolopendra. Out of these ten insects, no less than eight were beetles, and out of the whole fourteen there was only one, viz. a dipterous insect, which could readily take flight." This amounts to 1/14 flies, 3/14 ants, 1/14 spiders, 8/14 beetles, and 1/14 centipedes. Darwin notes that "only one of the 14 insects could readily take flight but that Drosera ... lives chiefly on insects which are good flyers, especially Diptera, caught by the aid of its viscid secretion". Even at this early date there was strong evidence that *Dionaea* in its native habitat captured a diverse array of insects, most of which could not readily take flight. Darwin also stated in a footnote that Mrs. Treats' cultivated-plants in New Jersey "chiefly caught Diptera". *Dionaea* in the garden habitat of Mrs. Treats captured flies while those in the wild or native habitat captured an array of insects most of which could not readily take flight.

The next observation of prey captured by *Dionaea* in its native habitat was by Frank Morton Jones (1923). Like Darwin, Jones observed a diverse array of insects captured. Jones sample of 50 prey animals, much larger than Darwin's 14, shows 82% to be incapable of agile flight, close to Darwin's observation of 93%. A diverse group of beetles was captured just as Darwin observed but a much smaller portion were beetles... 18% as opposed to Darwin's 57%.

Two subsequent field studies have also been done on larger samples of prey captured by *Dionaea* in its native-habitat. One based on captures by 152 traps (Lichtner & Williams 1977) and a second based on captures by 337 traps (Hutchens & Luken 2009, 2015). A comparison of the results of all four studies of captures by *Dionaea* in its native habitat is listed in Table 1. The percentage of flies captured in the field varies from 1% (Hutchens & Luken 2009) and 18% (Jones 1923). The average for all prey captured in the four studies is about 7% Diptera. The differences may be due to differences in the amount of carrion and fecal matter in the vicinity of the plants and thus the ability of the habitat to generate flies.

The predominant prey animals captured in the natural habitat are spiders, ants, and beetles. Spiders constitute approximately one third of the prey captured (18% Jones 1923, 30% Lichtner & Williams 1977, 31% Hutchens & Luken 2009, 2015). They have been reported resting in open traps (Lichtner & Williams 1977) so it seems likely that they walk into the traps and take cover between the lobes. Ants also constitute about one third of the prey (20% Jones 1923, 33% Lichtner & Williams 1977, 26% Hutchens & Luken 2009). The ants must walk into the traps. Jones (1923) reports them being attracted

[1] "Super White" sometimes also "superwhite" is an established term used for paper and laundry treated with an optical brightener that generates a super white appearance due to a blue hue fluorescence usually at approximately 420nm under sunlight (or any light containing UV). Such laundry detergents have been promoted for washing "whiter than white" or super white. The term emerged in the 1960-70s and is still used in optical brightener-related chemistry as well as bright white paper and laundry detergent promotion (Messier *et al.* 2005; https://en.alfakimya.com/textile-optical-brighteners).

Table 1. Percentage of various orders of insects captured by *Dionaea* in its natural habitat in the Carolinas.					
	Darwin	Jones	Lichtner &Williams	Hutchens & Luken 2009	Hutchens & Luken 2015
Citation	1875	1923	1977	Native	Introduced
Arachnid (class)	7.1	18	29.6	31	22.5
Hymenoptera	21.4	20	32.9	28.3	42.8
Coleoptera	57.1	18	11.8	12.3	9.8
Orthoptera*	0	14	14.5	2.5	4.1
Diptera	7.1	18	4.6	1.5	3.5
Other	7.1	12	6.6	24.4	17.4
Total Captures	14	50	152	337**	227**

*Orthoptera used to include Blattodea. The earlier studies by Jones (1923) and Lichtner & Williams (1977) include cockroaches in Orthoptera.
**Capture numbers provided by John J. Hutchens of Coastal Carolina University.

to the "alluring glands" along the edge of the trap. Beetles are the next most common prey captured (18% Jones 1923, 12% Lichtner & Williams 1977, 12% Hutchens & Luken 2009, 2015). Various Orthoptera are also captured in significant numbers (14% Jones 1923, 14.5% Lichtner & Williams 1977, 2.4% Hutchens & Luken 2009). The remaining prey are diverse and captured in small numbers. Both Jones (1923) and Lichtner and Williams (1977) used the older definition of Orthoptera that included Blattodea so their capture numbers for Orthoptera are inflated by a few cockroaches.

Hutchens and Luken (2015) also identified the prey captured by *Dionaea* that were introduced into habitat in South Carolina near already existing established populations. The captures made by these introduced plants were very similar to those made by established plants native to the habitat (Table 1).

It is clear from all the studies done in the natural habitat that flies are of minor importance as a prey animal and that spiders, ants, and beetles are the bulk of the prey captured. Nearly all of the prey animals captured in the natural habitat either are incapable of flight or are clumsy fliers.

Prey capture in the Garden and Greenhouse Habitats

For comparison we made limited observations of prey captured in the greenhouse habitat and garden habitat (Table 2). In both of these habitats flies are a major component of the prey with the garden habitat showing a lot more diversity.

Captures in the Garden Pond

Of the 50 active traps observed in the Garden Pond over 80 days there were 63 (65 prey) captures 37 or 59% Diptera. Thirty seven percent of the total captures were flies. Only two spiders and five ants (four winged) were captured. No Orthoptera and only 2 (3.2%) Blattodea (cockroaches) were captured. The Garden Pond is a 20-year-old stand of *Dionaea* in a large pot with other carnivorous plants that effectively forms an island in a small garden pond. Because of this location flying insects had more access to the traps than those incapable of flight. It is likely that a garden with better access by flightless prey could see larger numbers of ants, spiders and other such flightless animals captured.

Table 2. Orders of insects captured by *Dionaea* in a garden habitat and a greenhouse habitat.			
Habitat GP	Habitat GH	Order	GP= Garden Pond captures, GH= Greenhouse captures
39	19	Diptera	GP (24 flies, 6 mosquitos*, 4 midges, 4 hoverflies, 1 fruit fly), GH (19 flies)
12	1	Hymenoptera	GP (1 ant worker, 4 winged ants, 5 wasps, 1 bee, 1 unknown hymenoptera); GH (1 bee)
3	1	Hemiptera	GP (2 cicadas, 1 green shield bug); GH (1 green shield bug)
2		Blattodea	GP (2 cockroaches)
2		Arachnida (class)	GP (2 spiders)
2		Neuroptera	GP (2 adult antlions)
1		Coleoptera	GP (1 beetle)
1		Gastropoda (class)	GP (1 snail)
1		Unknown	GP (1 larva**)
3		Unknown	GP (3 unidentifiable fragments)
66	21	Total	

*Two times two mating mosquitos were captured together -- 8 mosquitos in 6 captures.
**The larva was likely brought into the trap by an ant that escaped.

Captures in the Greenhouse

Of the 33 active traps in the greenhouse observed over 36 days there were 21 captures over 90% of which were flies. One true bug and a bee were also captured. The strong impression, held by many, that the main prey of *Dionaea* is flies is, no doubt, strengthened by similar observations by those of us who grow this plant in our greenhouses.

The primary objective of Darwin (1875), Jones (1923), and Hutchens and Luken (2009) was to test Darwin's hypothesis that the structure and closure mechanism of *Dionaea* traps allow smaller prey to escape so an emphasis was placed on the size of the prey captured rather than its type. The analysis of the prey captured by *Dionaea* in its native habitat done by Lichtner and Williams (1976) and Williams (1980) emphasized the type of prey captured. Looking at the data this way leads to some important conclusions.

1. *Dionaea* captures a wide array of prey species.
   The species captured are primarily determined by the species available in the habitat. There does not seem to be a specific syndrome[2] that defines the captures such as flying insects, prey attracted to nectar, or prey that might be lured by a sex attractant. The capture mecha-

[2] In flowers, a pollination syndrome is a suite of flower characteristics that result either in the attraction of specific animal pollen vectors such as bees, hummingbirds, butterflies, or flies, often to the exclusion of other vectors, or characters that allow physical vectors such as wind to be more effective. An example is the fly pollination syndrome, which has a smell that attracts flies and often a trap that temporarily holds them (i.e. *Amorphophallus* species) while they pollinate the flower. Some flowers are generalists and have many pollinators (Faegri & van der Pijl 1979).

nism of *Dionaea* is not specific for flies. It is likely that most of the prey captured in its native habitat walks up the leaf petiole into the trap. The common name "flytrap" is misleading. In the various studies only between 1.5% (Hutchens & Luken 2009, 2015) and 18% (Jones 1923) of the captured prey are Diptera while the rest are either non-fliers or clumsy fliers. The presence or absence of animal carcasses or droppings nearby probably causes the fly populations to fluctuate greatly but, in general, where *Dionaea* is native, relatively few flies are captured. By contrast in the human related garden habitat and greenhouse habitat many flies are captured.

2. *Dionaea* is a generalist in terms of the prey captured.
This brings into question suggestions of elaborate systems analogous with pollinator attractants in flowers such as alluring glands that act as nectaries (Jones 1923), UV patterns (Joel *et al*. 1985), and attractive scents (Kreuzwieser *et al*. 2014). The descriptions of captures by the "flytrap" and many of the proposed attractants may have been influenced by observations of *Dionaea* capturing flies in its greenhouse and garden habitats and by analogies with fly pollinated flowers as opposed to looking at the plant in its native habitat where the evolutionary pressures that led to development of its capture mechanism exist. Of the proposed methods of attraction only Jones' (1923) observation that ants are attracted to "alluring glands" (Fig. 4) is documented.

While studying plants in the greenhouse habitat, a fly was observed moving to various points on a trap working its mouthparts over the area with alluring glands in the same way that the small ants described by Jones (1923) did (Fig. 4). This fly may have been attracted to the same thing that Jones' ants were but the attraction does not seem to act over longer distances since flies enter traps only infrequently. A BBC ONE video (2009) shows a fly lapping abundant nectar from the area of the alluring glands of a *Dionaea* trap. Our trap was dry (Figs. 4 & 5) and Jones (1923) does not mention abundant secretion in the area where the ants he observed were attracted. In our experience unstimulated traps that have not been wet by an outside source are always dry unlike those in the WildFilmHistory (1974) and the BBC ONE video (2009).

Prey capture rates in various habitats

If *Dionaea* plants are observed in almost any setting, the majority of the traps are open, often untouched by prey. This suggests that prey is captured infrequently. Captures and leaf closures without capture by 201 functional *Dionaea* traps in the field were measured during 24 hours in its native habitat by Lichtner and Williams (published in Williams 1980, see Table 3). Only six prey were captured by the ten traps that closed during this period. At this rate about 0.9 prey captures would occur per month so a plant with 6 functional traps would capture an average of approximately 5.5 prey a month. Capture rates may vary from day to day and according to conditions, but unless a large source of prey becomes available or adverse weather occurs, we would expect this measurement is in the normal range. This single observation should be supplemented by many more field measurements of capture rates in order to be considered representative, but a low rate like this is what would be expected if most the traps in the field are open.

An example of weather conditions affecting prey captures occurred on a day when it rained continuously (Table 3). No captures were made. Interestingly 15 traps of 202 that were capable of closing were closed without capturing prey as opposed to the 4 that closed on a day with no rain. Raindrops striking the trigger hairs could have closed these. Those of us who have watered *Dionaea* plants in a greenhouse probably agree that Darwin's observation that "Drops of water or

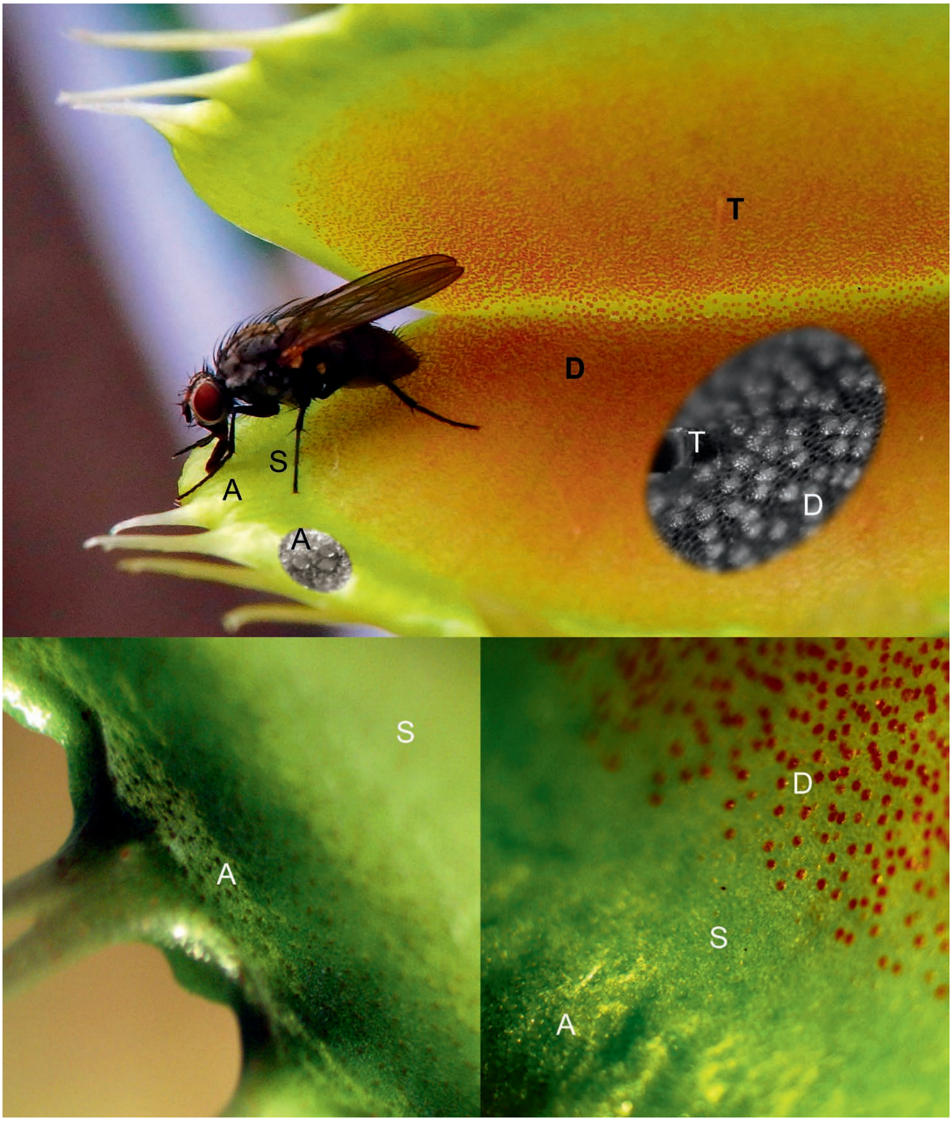

Figure 4: Close-up of a *Dionaea* trap. A= Alluring glands (green). S= Smooth area where the trap seals when digesting prey. D= Digestive glands that secrete fluid and digestive enzymes after prey is captured. T= Trigger hair, the sensory organ that triggers closure of the trap. The fly has its mouthparts on the alluring glands that are dry.

a thin broken stream, falling from a height on the filaments did not cause the blades to close" is usually accurate, although we have seen traps close on occasion when we watered them. However, his statement that "no doubt as in the case of *Drosera*, the plant is indifferent to the heaviest shower of rain" seems unlikely since a day of intermittently heavy showers resulted in 15 closures of 202 traps exposed to rain but probably not to prey animals while only 4 were closed on a clear day with exposure to prey animals.

Figure 5: A single observation of a fly landing on a large *Dionaea* trap in the greenhouse. It moved about the periphery of the leaf working its mouthparts on the area where the alluring glands are located in a manner similar to the small ants observed by Jones (1923). The trap is dry with no obvious nectar visible. This fly landed on the petiole and walked into the trap.

Captures in the Greenhouse and Garden Habitats

The capture rates computed for the Greenhouse and Garden Pond Habitats are listed in Table 4. Though lower than capture rates in the natural habitat they were of the same magnitude. The Greenhouse capture rates are lowest, about 34% of that of *Dionaea* in its natural habitat. This is likely partly because access to the greenhouse by insects was limited during periods of cooler temperatures when the greenhouse vents were closed. During two weeks of observations of greenhouse *Dionaea* after the vents were closed no captures occurred so when the vents were closed the capture rate was zero. The few flies that were able to enter when the vents were closed were captured by large *Nepenthes*, *Sarracenia*, and *Drosera*. These other carnivorous plants located near the *Dionaea* reduced the prey available to the Greenhouse *Dionaea* (Fig. 2) at all times and contributed to the low capture

Table 3. Prey capture in 24 hrs. by *Dionaea* in its native habitat during periods of heavy rain and no rain.*		
Weather	Rain	No Rain
Total Traps	244	224
Traps that could close**	202	201
Captures	0	6
Closures without capture	15	4

*The study was done in late June near Supply, NC.
**Measured by triggering open traps after observations.

Table 4. A comparison of capture rates in different habitats.	
Habitat	Captures/leaf/month
Garden Pond	0.55
Greenhouse	0.30
Natural	0.89

rate. The Garden Pond *Dionaea* population captured prey at about 61% of the rate of *Dionaea* in its natural habitat. It is likely that the pond water acted as a barrier to prey incapable of flight with only reduced access over the lily pads on the water (see Fig. 3) thus reducing the number of captures. Unfortunately it is impossible to make firm conclusions based on single samples of the capture rate in each location. An additional problem in comparing the capture in the Greenhouse with those in the Garden Pond arises because the plant forms of *Dionaea* are different. In the greenhouse, the locally-named "Predator" and "Destroyer" plants had large traps ranging up to 5 cm in size, while the plant in the Garden Pond was the common form of *Dionaea muscipula* similar to those found in the wild. More extensive sampling under better-controlled conditions needs to be done. In addition, in the future, controlled experiments on the comparative attractiveness of various carnivorous plants to different types of prey should be made. Also other carnivorous plants in the greenhouse were in competition with *Dionaea* for the flies. The competing *Nepenthes* species attracted prey with abundant nectar drops and *Drosera fragrans* and *Drosera* aff. *indica* "Africa" have a noticeable fragrance produced by their leaves, both of these attractants are lacking in the *Dionaea* we observed.

Alluring prey to traps

Numerous flowers have various mechanisms that attract pollinators (Faegri & van der Pijl 1979). There is strong evidence that some carnivorous plants have similar mechanisms that attract prey (Jürgens *et al.* 2009; Moran & Clark 2010). Such attraction or alluring mechanisms have been proposed to exist in *Dionaea*, but much of the information is from secondary sources without citations or from selected poses from educational videos, such as the BBC ONE video (2009). Many statements about such mechanisms have been made with little evidence to support them. Those that seem reasonable are often accepted as accurate and get widely repeated in popular literature and educational material on *Dionaea*. Some of the alluring mechanisms may even exist, but far more rigorous observation and experimentation should occur before we accept descriptions of them as accurate.

The following alluring mechanisms have been proposed to exist in *Dionaea*:

1. Alluring glands, a name assigned to glands structurally identical to digestive glands, were named by Jones (1923). They are located just beyond the smooth area around the edge of the trap inside the "cilia" along its rim (Fig. 4). These are not pigmented like most digestive glands and are slightly smaller in size. Jones (1923) reported that in its native-habitat small ants were attracted to these glands and that they move their mouthparts over them as if taking

up nectar. He also reported that a large wasp exhibited the same behavior. There are numerous undocumented secondary sources that state that nectar is secreted by these glands and possibly a scent. There are also impressive educational videos of flies attracted to these glands. We have never seen secretion from these glands and other than Jones' paper, there is little scientific work to indicate that they act as nectaries. When we observed the glands under the microscope, no secretion was visible. Except when wet by external sources, such as misting systems, the glands in unstimulated traps were always dry. The dry traps of *Dionaea* are probably an advantage since it makes most captures in hot and sunny weather. By comparison, in such weather the nectar secreted by *Nepenthes* pitchers becomes very viscous, finally crystallizing (Fig. 6). In *Dionaea* such incrustations would prevent smooth sealing when the traps close and complicate digestion by drying out the trap contents.

2. Alluring scents have been proposed. Jürgens *et al.* (2009) studied volatiles emitted from the traps of a number of carnivorous plants. In three species of *Sarracenia*, compounds typically found in flowers or fruits were found, suggesting that together with other features such as color and nectar production, the emitted volatiles may allow the traps to act as flower or fruit mimics. However, they found that the leaves of *S. purpurea*, *Dionaea muscipula*, and *Drosera binata* emitted much weaker scents with lower numbers of components, consisting mainly of volatiles typically emitted from green leaves. This does not support the notion of a scent acting as a part of a suite of attractants in *Dionaea*.

   In a more recent study, Kreuzwieser *et al.* (2014) found that *Dionaea* releases volatile organic compounds including terpenes, benzenoids, and aliphatics that attract fruit flies (*Drosophila melanogaster*). They concluded that *Dionaea* attracts insects using food smell mimicry "since the scent released has strong similarity to the bouquet of fruits and plant flowers". This does not sound like the "weaker scents with lower numbers of components, consisting mainly of volatiles typically emitted from green leaves" described by Jürgens *et al.* (2009).

   In addition, fruit flies are not typical prey of *Dionaea*. Only one fruit fly was captured during our observations. Would spiders, grasshoppers, and many of the range of prey in *Dionaea* traps be attracted by floral or fruity scents? This seems unlikely.

3. Red coloration mimicking meat such as fly pollinated flowers has been said to attract flies. Carrion flowers actually do attract fly pollinators in this way and some, such as skunk cabbage (*Symplocarpus foetidus*) and *Aristolochia* have a red color resembling carrion in addition to the appropriate scent (Faegri & van der Pijl 1979). Red coloration of pitcher plants has been reported to attract prey (Schaefer & Ruxton 2008), but more recent experiments show that nectar rather than color is the attractant (Bennett & Ellison 2009). There is evidence that the red coloration of *Drosera* is not involved in prey attraction (Foot *et al.* 2014; Schaefer & Ruxton 2008). In *Dionaea* there is no evidence that the red coloration of the traps are involved in prey capture. The presence of both red and green traps in the wild and the lack of red color's involvement in other carnivorous plants makes it unlikely that *Dionaea* traps red coloration plays an important role in attracting prey. *Dionaea* traps lack the potent carrion smell or fecal smell often present in fly pollinated flowers and is not likely to be a carrion mimic.

4. Ultraviolet (UV) patterns similar to those that attract flower pollinators have been described by Joel *et al.* (1985). Included in their account is a photograph and description of the UV pattern on a *Dionaea* trap. It shows the zone of the trap with the alluring glands absorbs ultraviolet light and the zone with digestive glands reflects it. A pattern would therefore be visible to insects with UV vision, such as bees. They state that this is evidence in favor of Jones'

Figure 6: A = The trap of *Nepenthes bicalcarata* with attracting nectar drops on the outside. B = During the hot season the secreted nectar becomes very viscous and forms incrustations of crystallizing sugar. C = The open trap of *Dionaea* is always dry, smooth and shiny.

(1923) idea of a baited system over Lichtner and Williams (1977) proposal that traps are not baited and prey capture is non-specific. Our observations with a 230-420nm UV-lamp with peaks at 254nm and 366nm show a pattern that results from a difference in reflection of UV by the inner digestive zone and absorption on the upper margin of the trap zone with alluring glands (Figs. 4 & 7). While this pattern agrees with the data of Joel *et al.* (1985), compared with the patterns of flowers that are known to attract insects, this pattern lacks contrast and is unspectacular. In addition, we found no visible fluorescence from *Dionaea* traps similar to that observed from traps of other carnivorous plants such as peristomes of *Nepenthes* and

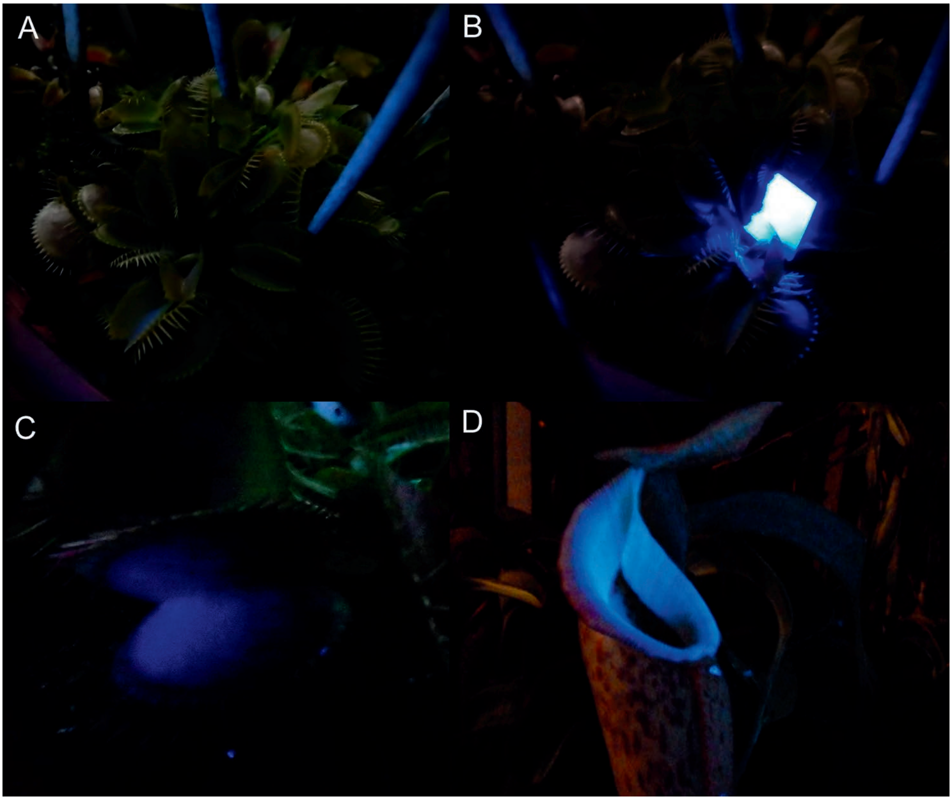

Figure 7: A = *Dionaea* under UV showing no luminescence. B = *Dionaea* under UV with a piece of super white paper (containing fluorescent optical brightener) as reference. The very bright luminescence of the super white paper as reference proves that enough UV-light is given to excite fluorescence when present. C = The dark blue light (approx. 380-420nm) that is emitted by the UV-lamp is reflected from the digestive zone together with invisible UV (maximum at 366nm). The margin with alluring glands shows very low to no reflection. This confirms a UV-pattern as shown by Joel *et al.* (1985). But it is not very spectacular compared with the patterns of attractive flowers. D = The peristome of this *Nepenthes talangensis* × *truncata* shows a bright and clear fluorescence under UV. The UV from the lamp (366nm) is transferred into bright visible light, which is shifted to the longer wavelength at approx. 490nm (blue-cyan).

Sarracenia (Fig. 7, Kurup *et al.* 2013; Hartmeyer *et al.* 2013). This lack of active fluorescence and the rather inconspicuous pattern due to reflection and absorption suggests that UV is not involved in attracting prey.

Does the size of prey matter?

Darwin (1875) noticed that when an insect enters a *Dionaea* trap and touches a trigger hair twice or two trigger hairs once, the trap rapidly closes such that the marginal projections ("cilia") on each of the opposing lobes bar the escape of larger prey. Struggles against the trigger hairs cause the trap to completely close, sealing the lobes along the smooth areas on the surface of the trap near its rim.

Smaller insects should be able to escape during the period that the trap is partially closed. Darwin said one of his sons actually observed this. He thought allowing the small prey to escape would save the plant a great deal of energy expenditure on a capture that was of little value to the plant. Darwin's letters to Canby and his request for captured insects were explicitly done to test this hypothesis (Jones 1923). Of the 14 insects captured, 3 were small and 11 were large enough to have been retained by the marginal projections blocking their way. He considered this adequate evidence for his model despite 21% of the captures in the small sample being of a size that should have escaped. However, Jones (1923) did not accept the model on this basis. Jones looked at captures by 50 traps and found of the 50 captures only one was less than 5 mm in length and only 7 were less than 6 mm. Ten were 10 mm or more in length with a maximum of 30 mm. Jones (1923) concludes that in the mature traps he studied, prey less than 1/4 in (= 6.35 mm) escape while others are captured. Sixteen percent of his larger sample was small enough to have escaped compared to 21% of Darwin's. Jones accepted Darwin's model presuming that most of the smaller prey had escaped.

A more elaborate experiment was done by Hutchens and Luken (2009) with a much larger sample of 337 captured prey. They compared leaf size with capture size in large, medium, and small sized traps. With the exception of a few infrequently captured large prey animals captured by large traps, all three sizes of traps captured the same range of sizes of animals. Large, medium, and small traps all tend to catch relatively small prey. Larger traps can let small prey escape, but it does not appear that they are very good at the task of primarily collecting large prey. Hutchens and Luken's data does show that the larger size traps collect larger prey on average due to a few very large captures, so a larger trap is better able to capture larger animals than the smaller traps. However, it is not clear if this advantage is due to letting small ones escape or just being able to hold onto a larger prey item compared to a smaller trap. They conclude that "Carnivory in *Dionaea* is not size selective" and that "Large insects were not preferentially captured". Perhaps Darwin's elegant idea about the efficiency of letting the "small ones get away" may occur but may not be the general case.

How is prey captured by *Dionaea* traps?

The answer depends on where the observation is made. A *Dionaea* plant in a greenhouse will likely have a fly land directly on its leaf. The fly in Figure 4 landed on the petiole of the trap and walked into it. The prey then moves around in the trap, possibly visiting the area of the alluring glands. If it brushes the trigger hairs twice the trap will snap shut. Its struggles will lead to trap narrowing and the digestion of the prey. After digestion, the trap will reopen and only the exoskeleton of the fly will remain. This scenario is well illustrated by Attenborough (1995) in a video that shows a beetle walking up a trap growing wild in the Carolinas into the trap that is then triggered and closes and digests the insect as described above.

A *Dionaea* plant growing wild in the sandy soils of the coastal regions of the Carolinas in the open sun with pine trees nearby is likely to have an ant or beetle walk up its petiole into the trap or to have a spider select it as a hiding place. If any of these animals stimulates two trigger hairs (or one hair twice) the trap will close on it, the struggle of the prey will cause narrowing, and the prey will be digested except for the exoskeleton which will remain after the leaf opens.

It is possible that ants are lured into the trap (Jones 1923), or that they just blunder in, as the beetles certainly must. The spiders appear to be attracted to the traps as a hiding place (Williams 1980). Other than Jones' observation, there is no evidence of alluring prey into *Dionaea* traps except in the popular and educational literature and videos. There may be lures of some type but convincing evidence is lacking.

Both in the greenhouse and the wild, the trap will remain partly open for a while with the way out barred by the marginal spikes (cilia) along the edge of the leaf. During this period small prey can escape from large traps but according to Hutchens and Luken (2009), statistically most do not.

The Venus flytrap is the first thought to come to most people's mind when someone says "carnivorous plant". It is unfortunate that we do not have better information on the interaction with the prey captured by the plant in its native-habitat. Descriptions and even careful experiments based on this plant's behavior in greenhouses and gardens far away from its native habitat have led to a great deal of lore about its behavior right down to the notion that it is primarily a fly-catching plant. Once established, this lore takes on a life of its own. Not all of it is necessarily false, but far more rigorous observations with reference to the plant in its native habitat needs to be done before we accept it as fact. We have to ask, should *Dionaea muscipula* even be called a flytrap?

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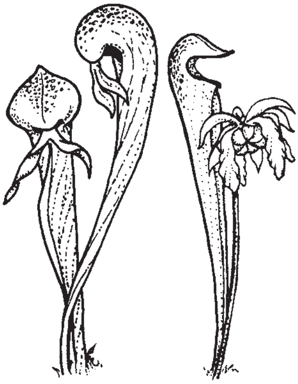

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Front Cover: Upper half: *Dionaea* habitat in the zone between a pocosin and longleaf pine savannah in the Green Swamp, Brunswick County, North Carolina in 1974. The young man in the photograph is Frank Lichtner studying the prey captured by *Dionaea*. Lower right: Another *Dionaea* habitat area, overgrown by grass that will eventually shade out the *Dionaea* if there is no fire. Lower left: A *Dionaea* plant in the Green Swamp (Cover of *Science* 1218(4577)10/12/1982. Reprinted with permission from AAAS). Article on page 44.

Back Cover: A three-year-old juvenile specimen of *Roridula gorgonias* in cultivation. Photo by Barry Rice. Article on page 74.

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