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Prey capture in the Venus flytrap: collection or selection?

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Abstract: Charles Darwin first proposed that the Venus flytrap (*Dionaea muscipula* Ellis) functions optimally by capturing and digesting large prey, the small prey escaping through openings at the trap margins. This hypothesis, although intuitively sound in the context of trap mechanics or plant allocation theory, has not been tested adequately with populations of plants growing in the field. Here, with traps collected in the endemic habitat over 9 months, we show that prey capture in the Venus flytrap is opportunistic rather than selective. While there was no effect of trap size on prey capture success, there was a significant but weak positive relationship between trap length and prey length. Prey sizes were well below the theoretical maximum holding capacities of traps and relatively small insects were represented across the range of trap sizes. Our results show that prey capture was not biased toward large invertebrates. Instead, we suggest that nonselective prey capture across the observed range of trap sizes is the best-fit explanation of trap function in the context of relatively limited ability to change allocation in response to sudden increases in resource availability.

Key words: carnivorous plant, *Dionaea muscipula*, optimal function, plant allocation, prey capture, Venus flytrap.

Résumé : Charles Darwin a le premier proposé que la dionée attrape-mouche (*Dionaea muscipula* Ellis) fonctionnerait le mieux en capturant et en digérant de larges proies, les petites proies s'échappant par les ouvertures au pourtour de la trappe. Cette hypothèse, bien qu'intuitivement sensée lorsqu'on la place dans le contexte de la mécanique de la trappe ou théorie de l'allocation de la plante, n'a jamais été vérifiée adéquatement sur des populations vivant en nature. À partir de trappes récoltées dans un habitat endémique pendant neuf mois, les auteurs montrent que la capture des proies par la dionée est opportuniste plutôt que sélective. Alors que l'on n'observe aucun effet de la dimension de la trappe sur le succès de capture des proies, on retrouve une relation faible, mais positive entre la longueur de la trappe et la longueur des proies. On observe une capture des proies bien en deçà de la capacité des trappes et des insectes relativement petits se retrouvent sur l'ensemble des dimensions de la trappe. Les résultats montrent que la capture des proies n'est pas biaisée en faveur de grands invertébrés. On suggère plutôt qu'une capture non sélective sur l'ensemble des dimensions des trappes constitue la meilleure adéquation du fonctionnement de la trappe, lorsqu'on se place dans le contexte d'une capacité relativement limitée pour changer l'allocation en réaction à des augmentations subites de la disponibilité de la ressource.

Mots-clés : plante carnivore, *Dionaea muscipula*, fonctionnement optimal, allocation à la plante, capture des proies, dionée attrape-mouche.

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Introduction

Disparate lines of evidence dating from the late 1800s to the present suggest that relatively large insect prey are an integral part of optimal function in the Venus flytrap (*Dionaea muscipula* Ellis), a carnivorous angiosperm with leaves modified into snap traps (Darwin 1875; Jones 1923; Lloyd 1942; Schulze et al. 2001; Volkov et al. 2008; Ellison and Gotelli 2009). The origin of this idea is traced to Charles Darwin (Darwin 1875), who maintained that the costs of capturing small insects exceeded the benefits and thus traps

acting like filters allowed the "small and useless fry to escape". The elegance of this idea was firmly established when new data seemed to fit the old model (Jones 1923). More recently, ^{15}N was used to estimate the contribution of insects to *Dionaea* nitrogen budgets, with the conclusion that the capture of large insects (i.e., grasshoppers) may contribute to an increase in growth rate of *Dionaea* (Schulze et al. 2001). Reanalysis of the meager prey data for *Dionaea* gave mixed results in terms of whether or not the plant selectively captures relatively large insects (Ellison and Gotelli 2009). The elegant and long-standing idea that *Dionaea* functions optimally by capturing relatively large prey has not been adequately studied in the context of ecological processes operating in the endemic habitat (Luken 2005).

Prey capture in carnivorous plants has broad relevance for understanding the integration of nutrient acquisition, photosynthesis, and biomass allocation (Givnish et al. 1984; Ada-

Table 1. Mean (SE) values for each variable describing *Dionaea* prey acquisition by plant size class and date of collection.

Variable	Size class			$F_{2,71}$	P	Date	P
	1	2	3	$F_{2,71}$	P	$F_{2,71}$	P
Total number of traps*	7.4 (0.6)	6.7 (0.5)	7.4 (0.4)	1.69	0.192	33.40	<0.001
Total number of traps with prey*	1.8 (0.2)	1.4 (0.1)	1.6 (0.2)	1.67	0.195	10.84	<0.001
% of total traps closed[†]	47.8 (2.2)	45.0 (3.2)	46.4 (2.5)	0.13	0.880	7.14	0.002
% of total traps with prey[†]	24.5 (2.0)	23.5 (3.4)	23.1 (2.7)	0.16	0.851	6.77	0.002
% of closed traps with prey[†]	52.4 (4.3)	51.2 (4.9)	48.2 (4.7)	0.30	0.743	4.02	0.022
Mean trap length (mm)*	8.8 (0.3)a	13.7 (0.5)b	17.2 (0.6)c	221.12	<0.001	19.29	<0.001
Mean trap width (mm)*	5.3 (0.2)a	7.9 (0.3)b	10.2 (0.4)c	153.01	<0.001	7.75	0.001
Mean prey length (mm)*	2.6 (0.2)a	5.1 (0.7)b	6.3 (0.5)b	26.48	<0.001	0.29	0.748

Note: Data were analyzed statistically using a randomized block analysis of variance, using site of collection as the block. No significant interactions between size class and date were found for any variable. Means by date are not shown because our primary focus was on differences by size class. Different letters in the same row indicate significant differences among size classes based on Tukey's test.

*Log$_{10}$ transformed.

[†]Arcsine square root transformed.

mec 2002; Ellison 2006). Of the approximately 600 species of carnivorous plants, only two (*Dionaea muscipula* and *Aldrovanda vesiculosa* L.) use snap traps produced from modified leaf blades. In *Dionaea*, trap production is a relatively inflexible trait. The cost in photosynthetic capacity must be balanced against nutrient return that varies depending on trap size, trap number, trap efficiency, prey availability, prey nutrient content, season, and other factors. Over 9 months we harvested traps from plants growing in the endemic habitat of northeast South Carolina, USA. Our goal was to examine the composition of prey items, trapping success, and the relationship between trap size and prey size. If prey size was optimized in the field, we expected trapping success to be higher for larger plants and for larger traps and we expected prey sizes to be scaled very near the maximum holding capacities of traps.

Materials and methods

Venus flytraps were studied at Lewis Ocean Bay Heritage Preserve in Horry County, South Carolina (lat 33°47′N, long 78°52′W), a 3640 ha protected area that includes 22 Carolina bays and extensive pine savanna. Flytraps were found at the ecotone between Carolina bays and pine savanna, a diverse habitat supporting shrubs, herbs, grasses, sedges, ferns, and vines. Complete enumeration of two relatively large Venus flytrap populations occurred in June 2002. This census provided data on lengths of 861 traps and allowed us to compare the size distribution of traps in entire populations with the size distribution of traps from our more limited sampling done to examine prey capture in many populations.

Ten populations of *Dionaea* were sampled in winter (4 February 2006), spring (17 May 2006), and autumn (26 October 2006). Sampling in summer was omitted because plants were dormant owing to drought. Within each population, two Venus flytraps in each of three size classes were selected for prey assessment (total $n = 60$ plants per sampling date, except for spring when two plants in the largest size class in one population were unavailable). Although individual plants were selected haphazardly, plants had to have at least one closed trap to be selected. Our sampling of captured prey in the field was guided by petiole length on individual plants, a leaf characteristic correlated with

trap length (Pearson $r = 0.61$, $n = 234$ leaves from June 2002 survey). Size classes consisted of (1) petioles (= phyllode) < 1 cm long, (2) petioles > 1 and < 2 cm long, and (3) petioles > 2 cm long. These size classes spanned the typical size range of Venus flytraps at Lewis Ocean Bay Heritage Preserve (Luken 2007). On each plant, the numbers of open and closed traps were counted. Closed traps were removed from petioles and preserved in 95% ethanol. In the laboratory, trap length, trap width, and prey length (if present) were measured to the nearest millimetre using electronic calipers and a dissecting microscope with a stage micrometer, respectively. Prey items were usually identified to order, although ants (Formicidae) were distinguished from Hymenoptera because of their abundance. Identification was sometimes limited by specimen decomposition within traps.

Differences in trap size and prey capture success among the three size classes and among the collection dates were compared statistically with a randomized block analysis of variance (ANOVA) using the General Linear Model in SYSTAT (version 12, Systat Software Inc.). Populations of *Dionaea* served as the blocking factor. Statistical assumptions (i.e., normality and equal variance) were tested and appropriate transformations applied. Differences in prey assemblages among the three size classes were compared using a randomized block permutation-based multivariate ANOVA (PerMANOVA, Anderson 2001) in PC-ORD (version 5.15, MjM Software). Prey assemblages were described as presence or absence of 15 prey taxa for each size class after combining data for all collection dates. The Sorensen distance measure was used for the PerMANOVA and P values were obtained with 4999 permutations. A posteriori pairwise comparisons among size classes were made using t tests with 4999 permutations (Anderson 2001). The relationship between size of individual traps and size of prey was assessed using linear regression. Statistical differences between the calculated regression slope and slopes of 0.5 and 1.0 were assessed (Sokal and Rohlf 1995). All tests were considered significant at $\alpha = 0.05$.

Results

In *Dionaea*, all leaves regardless of developmental stage produce traps. Plants maintained, on average, 7 leaves/plant (Table 1); populations of leaves showed a normal (Shapiro–

Wilk normality test, $W = 0.98$, $n = 861$ traps) distribution of trap sizes (Fig. 1a).

Our harvesting of traps for prey assessment yielded 580 traps in three clearly defined length and width size classes separated by approximately 3 mm increments (Table 1). Trap display, as indicated by the number of traps per plant, did not differ significantly among the size classes (Table 1). Trapping success, as indicated by the total number of traps with prey, the percentage of traps closed, the percentage of traps with prey, and the percentage of closed traps with prey, did not differ significantly among size classes (Table 1). Prey length differed significantly among size classes, with mean prey length in the smallest size class approximately half that of the other two size classes.

Over our 9-month study, prey composition spanned six classes and 13 orders of invertebrates. Predominant prey items across all dates and size classes were spiders (31% of total prey items), ants (26%), and beetles (12%). Prey assemblages were significantly different among size classes (PerMANOVA, $F_{2,18} = 2.35$, $P = 0.013$), with the largest size class significantly different (1 vs. 3: $t = 2.10$, $P = 0.004$; 2 vs. 3: $t = 1.59$, $P = 0.018$) than the two smaller classes. Assemblage differences were driven by the presence of infrequently captured taxa (i.e., Blattoidea [1% of total prey items in all size classes], Diptera [1%], and Gastropoda [1%]) in the largest size class.
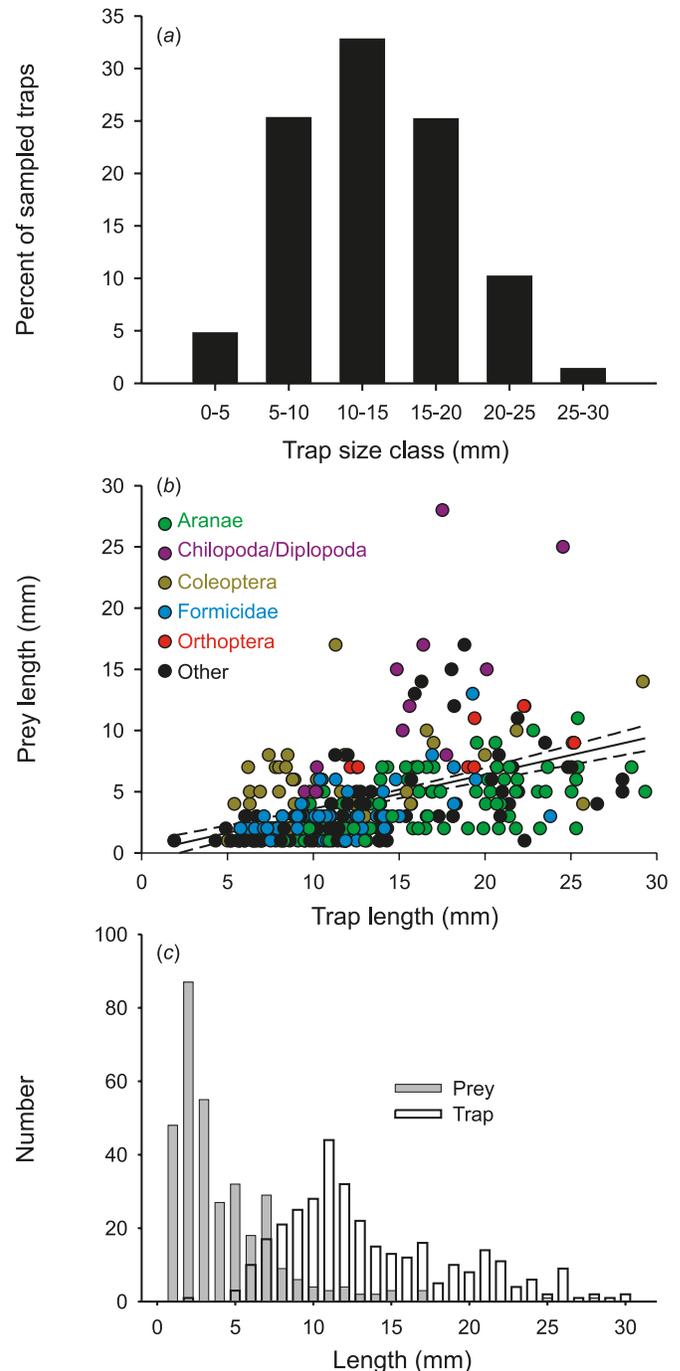
Individual traps of all sizes were capable of prey capture (Fig. 1b). However, this sample of traps underperformed, with a regression coefficient of 0.32 for the relationship between trap length and prey length. Deviations from the trend were observed for centipedes and millipedes captured in traps of intermediate length. Furthermore, the distribution of prey lengths was significantly different than the distribution of trap lengths (Fig. 1c, $P < 0.001$, Kolmogorov–Smirnov test), with the prey lengths positively skewed (skewness = 2.52).

Discussion

Our results, based on a relatively large sample of traps collected over three seasons, did not support the hypothesis that large prey are captured selectively or that trap size influences trapping success, even though prey composition was similar to that found in previous studies (Darwin 1875; Lichtner and Williams 1977). Instead, we found that trapping success was similar across trap size classes and that trap size explained a small but significant amount of the variation in prey length. Although prey composition in the largest size class differed from that in the two smaller size classes owing to the presence of a few taxa that were seldom encountered, prey composition was still dominated by spiders and ants in all size classes. Because we lacked data on prey availability, it was possible that larger prey simply were not present.

Any explanation for prey composition in the Venus flytrap must ultimately focus on trap mechanics. The most recent review of processes controlling trap closure in *Dionaea* describes three physiological phases: the silent phase with no movement although the trap is open, the accelerated phase lasting about 0.3 s as the trap closes, and the relaxation phase when the trap is closed and insect digestion oc-

Fig. 1. Lengths of traps and prey collected from Venus flytraps growing in the endemic habitat. (a) Size distribution of lengths of 861 traps sampled on 3 June 2002 at Lewis Ocean Bay Heritage Preserve. (b) Relationship between lengths of traps and lengths of invertebrate prey found in 278 closed traps. The solid line (±95% confidence intervals represented by dashed lines) represents significant regression between trap and prey lengths in millimetres (prey length = 0.317 × trap length + 0.055, $P < 0.001$, $R^2 = 0.239$, df = 332). Traps containing multiple prey were included as independent samples for the purposes of this relationship. Different-colored symbols represent dominant prey taxonomic categories. (c) Distributions of prey and trap lengths.

curs (Volkov et al. 2008). The accelerated phase is well studied and is started by generation of a receptor potential when trigger hairs, three on each lobe surface, are twice mechanically stimulated by live prey. The resulting action potential, electrical charge transduction, and sudden change in hydrostatic pressure cause the accelerated phase (Volkov et al. 2008), but there is no evidence that prey size affects triggering. However, selective capture of large prey depends on the universally described, relatively slow, but poorly explained end point of the accelerated phase, previously described as partial closure (Volkov et al. 2008) or damped closure (Forterre et al. 2005), that allows a window of escape for small prey. In the absence of data to support such escape, we alternatively suggest that partial trap closure is simply the result of physical forces that emerge as trap lobes are appressed (Stuhlman 1948; Lichtner and Williams 1977; Forterre et al. 2005) and that prey selection is nominal, with the most likely selective force being the ability of the trap to hold captured prey rather than the ability of the trap to allow escape of small prey.

Carnivory in *Dionaea* was not size selective (i.e., large insects were not preferentially captured), and traps were functional regardless of size; this functionality occurs year-around. The spreading of nonselective insect capture across all leaves regardless of developmental stage may represent the best potential return on investment considering the limited growth response to sudden large increases in resource availability (Roberts and Oosting 1958; Brewer 1999; Luken 2007) and the potential whole-plant benefits of any insect capture (Schulze et al. 2001; Adamec 2002). If growth is scaled to existing nutrient capital and maintenance costs are low, then increasing trap size (a trait correlated with petiole size) provides only marginal benefit in terms of trapping success or trapping function.

The elegant idea that *Dionaea* selects large prey may be a further example of the Panglossian paradigm, where it is often erroneously assumed that natural selection forges every facet of complex biological structures (Gould and Lewontin 1979). In the current research, traps previously thought to select prey become traps that more simply and more generally collect prey. Traps once thought to be fine-tuned plant structures become parts of whole plants that may express limited biomass allocation and growth (Ellison 2006). Future research on carnivorous plants, and in particular *Dionaea*, should now shift to the universal observation that such plants are rare even when suitable habitat is available and they remain rare even when traditional plant resources are supplemented (Luken 2007). Successful adaptive management may entail learning more about what such plants cannot do or what factors allow them to simply persist, rather than focusing on their positive growth responses to increased resource availability (Brewer 1999; Luken 2007).

Acknowledgements

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