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Capture Rates of Invertebrate Prey by the Pitcher Plant, Sarracenia purpurea L.

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ABSTRACT —I examined capture rates of invertebrate prey by pitchers of the purple pitcher plant *Sarracenia purpurea*, in western Newfoundland, Canada. While captures were diverse, Hymenoptera (mostly ants), Coleoptera and Gastropoda accounted for 69% of the total dry mass caught. Gastropoda decompose quickly and completely in pitchers, and their importance (20%) implies that prey sampling methods that do not survey freshly caught prey may seriously underestimate resource availability in pitchers.

The average pitcher caught 11 mg dry mass of animal biomass over its lifetime, but capture rates were highly variable (range 0–67 mg). Pitchers opening earlier in the season caught no more or less than those opening late. Larger pitchers caught more than smaller ones, although size accounted for a small fraction of total variance. Capture rates changed with time, peaking in pitchers 12–33 days old; however, pitchers continued to catch prey through their 2nd season (*i.e.*, after overwintering). In an average pitcher, 2nd-season captures made up nearly half of the total.

INTRODUCTION

The pitcher plant *Sarracenia purpurea* L. is one of a number of plants of bogs and infertile soils that capture and absorb nutrients from invertebrate prey (Bradshaw and Creelman, 1984; Juniper *et al.*, 1989). Nutrient uptake from captured prey can increase plant growth rates in *Sarracenia* pitcher plants (Gibson, 1983), as it does in other carnivorous plants (Juniper *et al.*, 1989). Captured prey also constitute the resource base for a community of inquiline bacteria, protozoa, and invertebrates that inhabit the water-filled pitchers. For at least two of these inquilines (the pitcher-plant mosquito *Wyeomyia smithii* Coquillet and the pitcher-plant midge *Metriocnemus knabi* Coquillet) the availability of captured prey limits individual growth, and ultimately population growth (Heard, 1994b) and may indirectly influence oviposition behavior (Heard, 1994a).

The pitcher community is an important model system, having been used to test hypotheses about behavioral ecology (Heard, 1994a), resource processing (Heard, 1994b), life history theory (*e.g.*, Bradshaw and Holzapfel, 1983), toxicology (Fairchild *et al.*, 1987), physiological ecology (*e.g.*, Kingsolver, 1979), population genetics and natural selection (*e.g.*, Bradshaw and Holzapfel, 1986), keystone predation (Addicott, 1974) and community organization (*e.g.*, Harvey, 1996). Because the availability of resources derived from prey capture can potentially control aspects of plant performance, inquiline performance and inquiline community structure, I sought to document the quantity and schedule of prey capture by pitcher-plant leaves.

Several authors have examined patterns in pitcher-plant prey capture and its dependence on factors such as pitcher age (Fish and Hall, 1978; Wolfe, 1981), pitcher density (Cresswell, 1991) and pitcher color, morphology and nectar supply (Cresswell, 1993). However, most studies have not sampled freshly caught prey items before losses to decomposition (except Cresswell, 1991, 1993), and no study has followed prey capture rates for the full lifespan of a pitcher. Here I extend previous reports by reporting patterns in prey capture by pitcher plants in western Newfoundland, Canada. I sampled freshly caught prey in known-aged pitchers (at 3-day intervals) over the 2 full seasons that pitchers survived. Among possible

predictor variables, I chose to focus on pitcher age and opening date and on pitcher size. Despite considerable discussion of pitcher age and its effect on prey capture, no data have been available for 2nd-season pitchers. Opening date is of interest because early-opening pitchers should manage more trapping days. Pitcher size is a particularly important trait because it has been suggested as an oviposition cue for pitcher plant inquiline insects (Heard, 1994a) and because it has predictive value for several other aspects of pitcher plant and inquiline biology (Kingsolver, 1979; Wolfe, 1981; Paterson and Cameron, 1982; Cresswell, 1993; Heard, 1994a, 1994b). Trap size has also been correlated with prey capture rates in other carnivorous plants (*e.g.*, Thum, 1989).

I emphasized two main questions in my study. First, what does monitoring of fresh prey items reveal about the importance of gastropods? Gastropods decay rapidly in pitchers, and an important contribution of gastropods to total prey capture would suggest that prey sampling methods that do not examine freshly caught prey may seriously underestimate prey capture (and therefore resource availability) in pitcher communities. Second, how important are prey captures by 2nd-season (post-overwintering) leaves? The prevailing wisdom is that prey capture is negligible in pitchers more than 30–60 days old (*e.g.*, Fish and Hall, 1978; Juniper, 1989), but at least in northern populations *Sarracenia* leaves remain alive much longer.

METHODS

Study site.—I studied pitcher plants in Gros Morne National Park, Newfoundland, Canada (49°34′35″N, 57°52′20″W). The site was a small valley-bottom bog (known locally as Long Marsh) near the park's visitor center.

Natural history of prey capture.—Pitchers (leaves) of *Sarracenia purpurea* fill with rainwater and the water-filled pitchers act as pitfall traps. Prey may simply stumble across a pitcher, or be attracted to nectaries around the pitcher mouth and scattered over the pitcher surface. Pitcher morphology includes a number of features that facilitate trapping, including downward-pointing hairs and a slippery zone above the retained fluid (Juniper *et al.*, 1989). Captured animals include both aerial and terrestrial insects and other invertebrates.

Sampling.—To monitor prey capture by pitcher-plant leaves, in June 1990 I laid a permanent transect through a central part of the bog. Along this transect, I marked a total of 260 pitchers opening in 1990 or in 1991; each year's pitchers were followed through their 1st and 2nd seasons. Typically, pitchers open in midsummer and remain alive and hold water through the winter and into mid- to late summer of the next year.

At 6-day intervals from 26 June to 31 August 1990, I marked a cohort of 10 newly opened pitchers (15 on the first date) with aluminum tags. I recorded the width of the pitcher hood as a measure of pitcher size; this measure is highly correlated with other size measures (Nastase *et al.*, 1995) and has predictive value for other aspects of pitcher plant and inquiline biology (Heard, 1994a, 1994b). Every 3rd day until 24 September I visited each marked pitcher and removed all captured prey items with forceps or wide-mouth plastic disposable pipettes. I visited frequently so that prey items would not begin to decompose before I could remove them. At each visit I recorded the condition of each pitcher: alive, dead (more than ½ pitcher tissue dead), holed (damaged so as not to retain water), or submerged (by standing water in the bog). I also removed any inquiline larvae (*Wyomyia smithii*, *Metriocnemus knabi*, and the sarcophagid *Blaesoxipha fletcheri* Aldrich) to prevent feeding damage to prey items. In 1991, I sampled the same leaves (now in their 2nd season) every 3 days from 19 May to 22 September. When sampling ended, most leaves were dead or moribund. Prey capture was rare at the beginning or end of the sampling season and was

probably negligible between sampling seasons as typically temperatures are low and/or the area is snow-covered for most of this time (Caines and Deichmann, 1990).

In 1991, I marked cohorts of 10 pitchers every 6 days from 9 July until 14 August, sampling for prey every 3 days until 22 September and again in 1992 from 16 May through 10 August. Procedures for sampling these pitchers were the same as in 1990.

Some analyses reported here also include a second set of data from 1990. These data were from extra pitcher cohorts, marked from 29 June through 23 July at 6-day intervals (that is, each extra cohort of 10 pitchers was marked midway between marking dates for the main set of pitchers). I sampled these extra pitchers every 3 days as described above, but after 1 August 1990 I abandoned them to reduce the required sampling effort. I used these data when breaking down prey captures taxonomically or by pitcher age, but excluded them from analyses of lifetime per-pitcher prey capture.

All collected prey items were preserved in 70% ethanol and later identified, mostly to order (insects and chelicerates) or class (other invertebrates, except nematodes only to phylum). The very large number of captures precluded more precise identifications, although I did draw finer taxonomic and life-stage distinctions where these were ecologically interesting: in Hymenoptera, ants vs. all others; in Diptera, Nematoca adults vs. Brachycera adults vs. larvae; in Lepidoptera, adults vs. larvae; and in Gastropoda, snails vs. slugs. I separated plant material from animal carcasses, dried each to constant mass (72 h at 55–65 C), and weighed them to the nearest 0.1 mg on a Sartorius analytical balance. When a pitcher caught more than one prey item in one sampling period, I recorded the identity of each carcass, but to reduce weighing effort I recorded only total dry mass of all carcasses.

While plant material (almost entirely dead leaf fragments) made up about 15% of "captured" material, I ignore it here for two reasons. First, the nutritional value of plant litter is much less than that of invertebrate carcasses (Southwood, 1973). Second, some of this plant material was probably dislodged by my repeated walking along the transects. Therefore, 15% probably overestimates the real importance of plant material to undisturbed pitchers.

Data analysis.—I conducted three types of analyses. First, I examined the taxonomic composition of all prey, both by number and by dry mass. For prey numbers I was able to include all captured individuals (4780). For dry mass, I used the subset of samples where an individual was captured alone (1715 individuals; here I could assign dry mass unambiguously to a specific taxon). This subsample was representative of the full data set in taxonomic composition: the rank order breakdown by taxon was the same as for the full data set for all taxa represented by 10 or more individuals.

Second, I examined patterns in prey mass captured by individual pitchers over their entire lifetimes. For these analyses, I summed all prey of all taxa captured by a leaf through its 1st and 2nd seasons. In these analyses, I omitted leaves which were not followed for their natural lifespans: the "extra" pitchers marked in 1990 but not followed through 1991, a few pitchers which were lost, and a few that I damaged in removing prey. Pitchers which did not catch prey because they had died or become submerged in standing water were assigned a catch of 0 for all sampling dates after their demise. I used multiple regression analyses to examine the dependence of prey capture success on pitcher size, opening date, and their interaction (using backwards elimination and type III sums of squares).

I also estimated the correlation of total per-pitcher prey capture, including gastropods (snails and slugs), with totals excluding gastropods. This correlation is of interest because common methods for assessing relative resource availability in pitchers (head-capsule counting, and any other method not sampling freshly caught prey) undersample or do not sample gastropod prey. The validity of such methods depends on a high correlation between prey

masses including and excluding gastropods. I used a Monte Carlo procedure to estimate the correlation because I did not have individual body masses for all gastropods. I used snails (119) and slugs (44) captured alone to establish body-mass distributions for these two taxa. I then tabulated for each pitcher the total mass captured and the numbers of snails and of slugs contributing to that mass. I used a computer program written in Quick BASIC to estimate mass totals for each pitcher without gastropods, subtracting for each snail or slug a body mass drawn randomly (with replacement) from the distribution for that taxon. The program calculated the product-moment correlation coefficient r, over all leaves, of capture masses with and without gastropods, repeating the entire procedure 5000 times to estimate the probability distribution of the true (but unknown) r.

Finally, I compared capture success of pitchers of different ages. For these analyses, I excluded only lost pitchers and pitchers I damaged. From the prey capture vs. pitcher age data, I calculated a cumulative prey capture curve, which I used to examine the relative importance of prey capture early and late in the lifetime of a typical pitcher. The sample size for these analyses varies with age (Fig. 3) because new cohorts of leaves were marked through the season. For instance, there were few 90-day leaves because only the first-marked pitchers were 90 days old by the time sampling stopped in the autumn; in contrast, I had 3-day samples from all marked pitchers. I separated capture masses for the 1st sample of the 2nd season; these masses included a few prey actually caught between seasons. I assigned this mass (arbitrarily) to pitchers aged 200 days; any age between the end of the 1st season and the beginning of the 2nd could have been used with identical results.

Although patterns in prey capture with leaf age were striking, I used a subset of the capture data to assess the statistical significance of age differences. I chose to analyze data for 52 pitchers with complete data for ages 3 to 72 days inclusive [72 days was a compromise between number of samples per pitcher (increasing with age) and number of pitchers (decreasing with age)]. For these pitchers I used a repeated measures analysis of variance to test for effects on prey capture of leaf age, opening date, and their interaction. For within-subjects effects I report results for multivariate tests based on Wilk's λ. Equivalent tests based on Pillai's Trace, Hotelling-Lawley Trace, or univariate statistics did not differ appreciably.

I also compared the breakdown of prey capture by taxon between 1st and 2nd-year (post-overwintering) pitchers, using a G-test of independence (Sokal and Rohlf, 1981). For this analysis, I used all capture records for 9 July through 20 August 1991. In this interval, the 1990 pitchers were in their 2nd year and the 1992 pitchers in their 1st, but both were trapping at once and were exposed to identical suites of available prey.

All statistical analyses except the Monte Carlo correlations and the G-test were conducted with PC-SAS 6.08 (SAS Institute Inc., 1988).

RESULTS

Taxonomic composition of the prey.—Twelve insect orders (Hymenoptera, Diptera, Coleoptera, Homoptera, Collembola, Lepidoptera, Protura, Hemiptera, Trichoptera, Neuroptera and Orthoptera) were represented among the captured prey, as were several other invertebrate groups (Chilopoda, Diplopoda, Acarina, Araneae, Gastropoda, Oligochaeta and Nematoda) (Fig. 1). Of 4780 total captures, Hymenoptera (almost exclusively ants) were most common (1577 individuals; 33%) followed by Diptera (1555; 33%). Gastropoda (378; 8%) and Coleoptera (339; 7%) were a distant third and fourth and other taxa were less common (Fig. 1).

When captures were broken down by dry mass, Hymenoptera (still dominated by ants) remained most important (26% of the total; Fig. 2). However, Coleoptera (23%) and Gas-

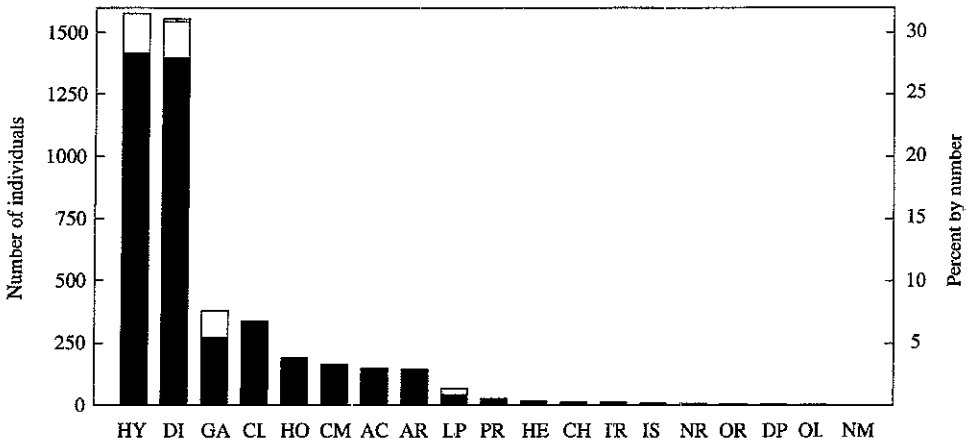

FIG. 1 —Prey captures by taxon, comparing numbers of individuals caught (grand total 4780) Key to taxa: AC, Acarina; AR, Araneae; CH, Chilopoda; CL, Coleoptera; CM, Collembola; DI, Diptera (Nematocera shaded, Brachycera white, larvae hatched); DP, Diplopoda; GA, Gastropoda (snails shaded, slugs white); HE, Hemiptera; HO, Homoptera; HY, Hymenoptera (ants shaded, others white); IS, Isopoda; LP, Lepidoptera (adults shaded, larvae white); NM, Nematoda; NR, Neuroptera; OL, Oligochaeta; OR, Orthoptera; PR, Protura; TR, Trichoptera

tropoda (20%) were second and third; Diptera made up only 12% of captures by mass despite their numbers Other taxa (Fig. 2) were less important (19% all together). The importance of Coleoptera was partly due to occasional captures of a very large (25 mg dry mass) carabid Note that the 20% figure may underestimate the true importance of gastropods, because slugs lack the undigestible exoskeleton that can account for a substantial fraction of an insect carcass.

Patterns in lifetime prey capture.—The average pitcher caught a total of 11 02 mg dry mass

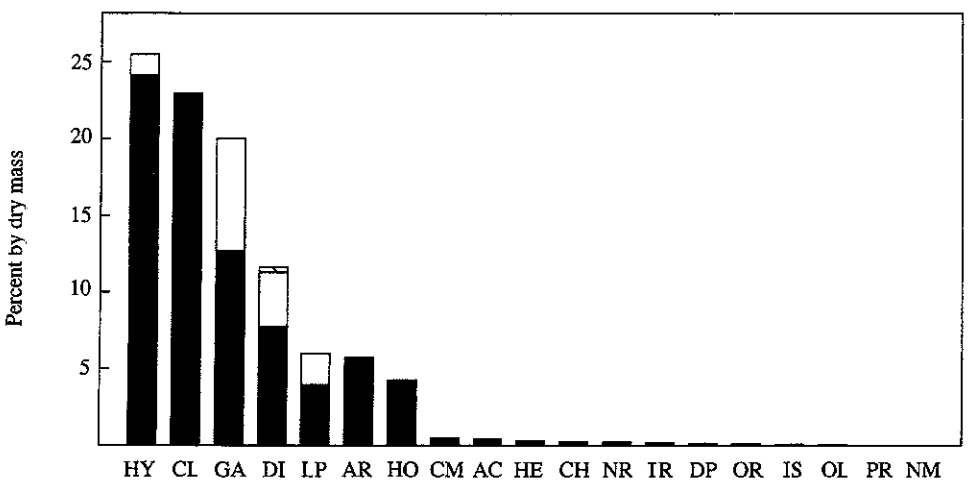

FIG 2 —Prey captures by fraction of total dry mass. Taxa as in Figure 1

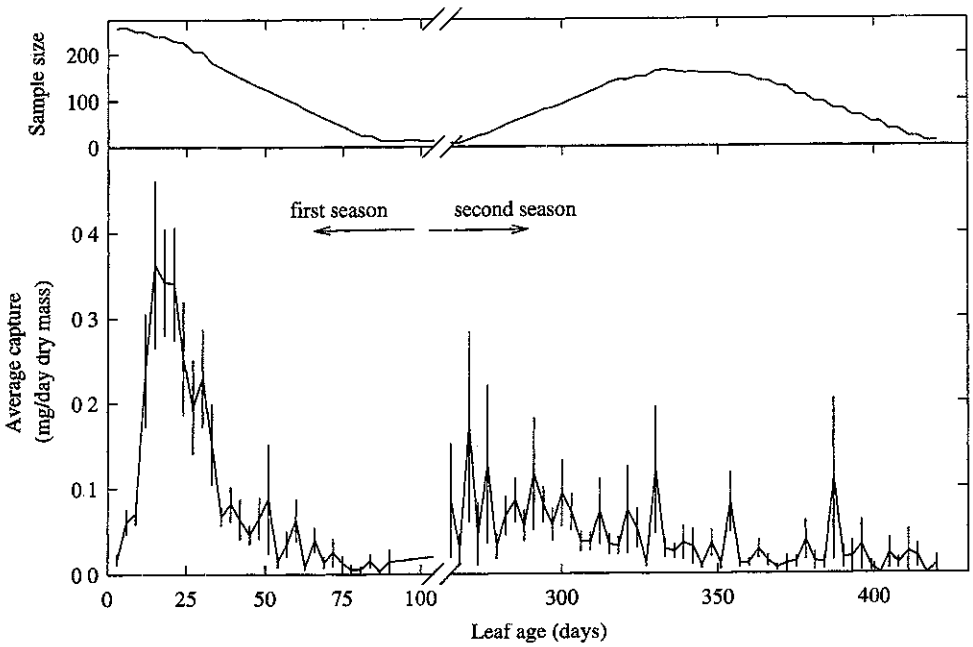

FIG 3 —Average prey capture rates vs age of pitchers Bottom panel shows capture rates, expressed as mg dry mass per day but calculated only every 3 days; error bars are ± 1 standard error Top panel shows number of pitchers included for each age

of animal prey over its lifetime Captured mass did not differ significantly between early- and late-opening pitchers, but larger pitchers caught significantly more prey than did smaller ones (Table 1) However, pitcher size explained only 3.5% of the variance in total prey capture

Prey masses excluding gastropods were well-correlated with total prey masses including gastropods: of the 5000 Monte Carlo resamplings, 95% had $r > 0\ 75$ (mean $r = 0\ 86$, 95% confidence interval 0 73–0 96)

Changes in capture rates with pitcher age—Prey capture rates depended strongly on pitcher age (Fig 3) Newly opened pitchers caught little prey Capture rates peaked sharply for pitchers ca 25 days old, and then fell off to very low levels in pitchers older than 50 days The repeated measures ANOVA confirmed that this pattern was highly significant (Table

TABLE 1 —Multiple regressions for total prey capture (mg dry mass) Total model r^2 is only 3 6% (size alone, 3 5%)

Source[1]	Slope	df	MS	P
Size	0 259	1	743 3	0 014
Open	−0 019	1	23 7	0 66
Error		191	120.3	

[1] "Size" is width of pitcher hood (mm); "Open" is opening date of pitcher (Julian day) The non-significant ($P > 0\ 25$) size*open interaction has been pooled with the error

TABLE 2.—Repeated measures ANOVA results for prey capture by pitchers up to 72 days old

A. Within-subject effects

Source[1]	Wilk s λ	df	F	P
Age	0 2046	23, 24	4 06	0 0006
Age × Open	0 1162	92, 97	0 77	0 90

B. Between- subject effects

Source[1]	df	MS	P
Open	4	5 860	0 057
Error	46	2.364	

[1] "Age" is days since pitcher opened; "Open" is date of leaf opening

2), although there were no significant effects of opening date or its interaction with pitcher age In the 2nd season, capture rates actually increased compared to the end of the 1st season (Fig. 3), although they tended to fall off again as the season progressed Even though per-day capture rates peaked sharply early in the 1st season, the average leaf caught 46% of its prey during the (longer) 2nd season (Fig. 4)

The prey of 2nd-year pitchers differed taxonomically from that of 1st-year pitchers (G = 110 9, 7 df, P ≪ 0 001; Table 3) Most of the difference was due to Diptera being much less common in 2nd-yr pitchers

DISCUSSION

Taxonomic composition of the prey.—Prey captures by pitcher plants were diverse. However, a few taxa (Hymenoptera, Coleoptera and Gastropoda) dominated in terms of dry mass

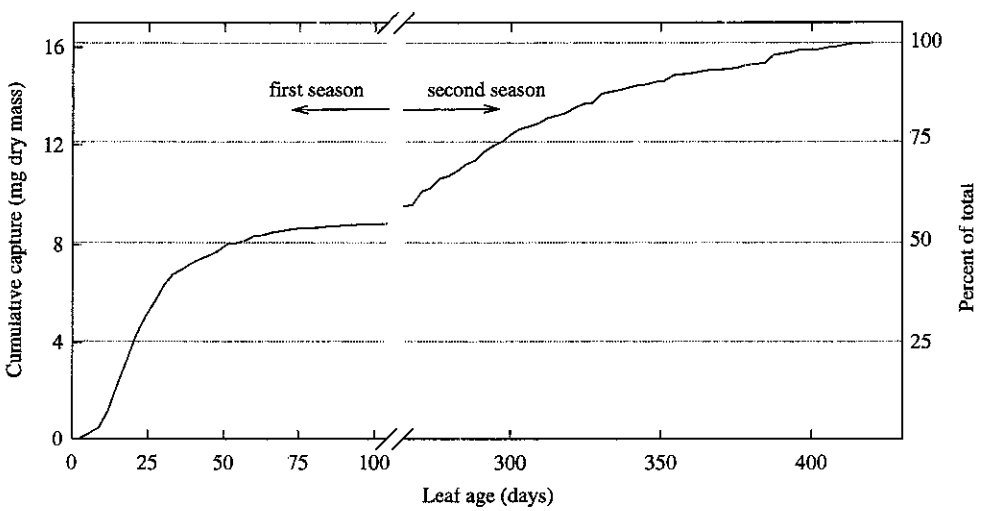

FIG. 4.—Cumulative average prey capture by pitchers The first prey sample for each pitcher from its 2nd season (with pitcher age depending on the opening dates for that pitcher) is separated and applied between the 2 seasons; this sample includes remains of prey caught any time between the last sample of the 1st season and the first sample of the 2nd The end of the curve (16 2 mg prey) exceeds the figure for average total prey capture (11 mg) because pitchers included there survived longest

TABLE 3.—Prey capture for 1st- and 2nd-yr leaves, 9 July to 20 August 1991

Taxon	1st year	2nd year[1]	2nd year expected[2]
Diptera	294	12	64
Hymenoptera	171	54	37
Gastropoda	63	11	14
Coleoptera	43	17	9
Acarina	31	2	7
Araneae	11	11	2
Homoptera	8	7	2
Others	9	15	2

[1] 1st-year and 2nd-year taxonomic distributions are significantly different ($G = 110.9$, $df = 7$, $P \ll 0.001$

[2] Expected based on 1st-year taxonomic distribution with 2nd-year total captures

(Fig. 2), and presumably therefore in terms of nutritional importance both to the plant and to the inquiline community. Other studies of *Sarracenia purpurea* have found similar results, but the particular taxa dominating captures differ among sites. In two studies in Michigan, Cresswell (1991, 1993) found dry mass of captures dominated by Diptera (45%), Orthoptera (20%), and Coleoptera (13%); Hymenoptera made up only 4% and gastropods were entirely absent (J. Cresswell, pers. comm.). Three other studies have relied on sampling all dead and decomposing prey from a leaf on a single sampling date, rather than recovering fresh prey captures; therefore, they could not estimate masses. First, Judd (1959) sampled pitcher prey in southwestern Ontario. From his frequency lists, the dry mass of Judd's capture would probably have been dominated by Diptera, Coleoptera, Orthoptera and Hymenoptera (mostly ants). Second, for *S. purpurea* pitchers in North Carolina, Wray and Brimley's (1943) data suggest Hymenoptera (ants and others) and Coleoptera as dominant. Finally, for pitchers in eastern Newfoundland (about 450 km ESE of my site), Laird (1988) found Gastropoda, Isopoda, Diplopoda and Hymenoptera (ants) "common" to "abundant" (and all these taxa are relatively large-bodied). Variation in the local abundance of different potential prey must surely account for much of the difference among study sites; unfortunately, the data required to test this idea are not available.

The substantial representation of Gastropoda (both snails and slugs; 20% of capture mass) at my site is of particular importance for studies of pitcher-plant communities. This is because, unlike arthropod prey, gastropods are entirely digested in pitchers; this includes snail shells, which eventually dissolve in the acid pitcher fluid. Several workers have sought to reconstruct past prey capture from decomposed remains (Wray and Brimley, 1943; Judd, 1959; Laird, 1988), and others have counted arthropod head capsules (which do not decompose) as a measure of past prey capture [Lounibos *et al.*, 1982; Bradshaw, 1983; Bradshaw and Holzapfel, 1983, 1986; and Naeem (1988) in the related pitcher plant *Darlingtonia californica*]. Both methods will underestimate, and may miss completely, the importance of Gastropoda. While gastropods are unimportant at some sites (Cresswell, 1991, 1993, and pers. comm.), they are common at others (this study and Laird, 1988, in Newfoundland) and have been reported from others (S. Newell, pers. comm., in Michigan; J. Rango, pers. comm., in New York; Wray and Brimley, 1943, in North Carolina).

Fortunately, while absolute measures of prey capture are unreliable if gastropods are not sampled, relative rankings of leaves by prey capture are not. I found that lifetime prey capture ignoring gastropods was well-correlated with total lifetime prey capture. Therefore,

head capsule counts are appropriate as an indirect measure of resource availability in pitcher-plant communities

Patterns in lifetime prey capture.—The failure of pitchers to open early in the season to catch more prey over their lifetimes may seem surprising, as these pitchers had more potential trapping days. However, these extra trapping days are not very productive ones; a longer 1st season (for an early-opening pitcher) adds only more "old-but-still-1st-season" days (the tail of the 1st-season hump in Fig. 4), where the average capture rate is only on the order of 0.01 mg/day. The earliest and latest opening pitchers differed by 66 days (expected capture 0.66 mg) in 1990 and by only 36 days (0.36 mg) in 1991, and so the extra days would be unlikely to contribute significantly compared to an 11 mg expected lifetime capture. In more southerly populations, *Sarracenia purpurea*'s growing season is longer. If pitcher lifespan is similar, then opening date might well have more explanatory power in the south than it does for northern, short-summer populations.

Pitcher size explained a significant but very small fraction of variance in prey capture among pitchers (3.5%; Table 1). This result is consistent with two other studies. Cresswell (1993) found a significant effect of pitcher size explaining at most 10.5% of variance in capture rate (reported statistics were for a multiple regression with two other independent variables). Wolfe (1981) found that for plants in a greenhouse catching deliberately released *Drosophila*, leaf size explained 42% of the variance in prey capture for "old" leaves (>30 days) but no significant variance for younger leaves. The higher r^2 is unsurprising for a greenhouse study where variables such as sun and wind exposure, surrounding vegetation, and microtopography were all controlled. Such factors influence capture success of other carnivorous plants (Karlsson *et al.*, 1987; Thum, 1986; Zamora, 1995).

The limited explanatory power of pitcher size has important implications for the pitcher-plant inquiline community. Pitcher-plant mosquitoes and midges both lay more eggs in larger pitchers (Wiens, 1972; Mogi and Mokry, 1980; Bradshaw, 1983; Heard, 1994a; Nastase *et al.*, 1995), and I have previously suggested (Heard, 1994a) that leaf size might provide ovipositing inquilines with a cue indicating expected prey capture, and therefore resource availability. Because resources limit growth of both midge and mosquito (Heard, 1994b), such a cue would be valuable, but the consensus of this and related studies is that while pitcher size does predict resource availability, it does not predict it very well.

Patterns in capture rates with pitcher age.—The strong peak in prey capture rate for pitchers 12–33 days old (Fig. 3) confirms the pattern reported from field data by Bradshaw and Holzapfel (1983; with only ranked pitcher ages) and from greenhouse data by Fish and Hall (1978). It is unknown what changes in leaf characteristics might account for declining capture rates, although Wolfe (1981) has speculated that changes in nectar quality or quantity may be involved.

No previous study has examined prey capture by leaves in their 2nd season. My 2nd-yr leaves caught different prey than 1st-yr leaves (Table 3). This could be because nectar production is reduced or ceases in 2nd-yr leaves, although there are apparently no data on this point. Second-year prey capture is still substantial in quantity, however. Despite claims that most or all prey are caught in the 1st 30–60 days after a pitcher opens (Fish and Hall, 1978; Juniper, 1989), my pitchers caught roughly as much prey in their 2nd season as in their 1st (Fig. 4). This result is important, because pitcher-plant midges and mosquitoes are limited in growth and therefore in reproductive success by resource availability in both 1st- and 2nd-season leaves (Heard, 1994b). Second-season captures may also account for a substantial fraction of resource availability to the plant, although studies of nutrient uptake and the fate of absorbed nutrients in *Sarracenia* (Plummer and Kethley, 1964; Christensen,

1977; Bradshaw and Creelman, 1984) have not included 2nd-season *Sarracenia purpurea* leaves.

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