

Trapping efficiency of three carnivorous *Pinguicula* species

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Summary. In situ trapping efficiencies of *Pinguicula alpina* L., *P. villosa* L., and *P. vulgaris* L. were compared with each other and with those of artificial traps at a subarctic site in northern Sweden. *P. vulgaris* had the highest trapping efficiency i.e., 21–37 µg prey trapped cm⁻² day⁻¹ and apparently has some means of attracting prey. The other two species trapped about 14–18 µg cm⁻² day⁻¹, a value similar to that of paper traps mimicing plant leaves. By weight, *Nematocera* and *Collembola* were the dominant groups trapped by *P. alpina*. *P. villosa* trapped mainly *Collembola*, while small *Nematocera* dominated the prey caught by *P. vulgaris*. Mites (*Acarina*) were caught in high numbers but contributed only a small part of the total captured biomass owing to their low weight.

Key words: Carnivorous plants – Trapping efficiency – Nutrient relations – *Pinguicula*

An unusual method of mineral nutrient acquisition among plants is found in carnivorous species. This group of about 550 vascular plant species (Givnish et al. 1984) are predominantly found in moist, nutrient poor habitats (Lüttge 1983). For almost all species, neither the amount of prey captured nor their efficiency at capturing prey is known (see, however, Dixon et al. 1980; Watson et al. 1982; Wolfe 1981).

The benefits obtained through carnivory by plants have been suggested to increase as the access to vital nutrients in the soil decreases (Givnish et al. 1984). Trapped prey should accordingly provide the most benefit to plants growing in sunny and moist but nutrient-poor environments. Consequently, an investment of resources to increase trapping efficiency should be more profitable for plants in such environments compared with plants in more shady, dry, and nutrient-rich areas.

In northern Fennoscandia three species of *Pinguicula* can be found on contrasting substrates (Osvald 1925; Sjörs 1950, 1965; Persson 1962; Sonesson 1967, 1970). *P. alpina* occurs almost exclusively on calcareous soils. *P. villosa* is found only on acidic, nutrient-poor mires, mainly on *Sphagnum fuscum* hummocks in ombrotrophic sites. The third

species, *P. vulgaris*, shows an intermediate distribution pattern with respect to soil pH, at ombrotrophic as well calcareous sites. These three *Pinguicula* species are considered to be carnivorous (Heide 1912; Lüttge 1983), although possible benefits of trapped prey have only been studied for *P. vulgaris* (e.g. Aldenius et al. 1983; Karlsson and Carlsson 1984). In *Pinguicula* spp. glands on the leaf surface produce a sticky mucopolysaccharide in which the prey is caught (Heslop-Harrison and Knox 1971).

In our study of carnivory, as it relates to ecology of these three *Pinguicula* species in northern Fennoscandia we have compared their relative prey trapping efficiencies. We have also attempted to determine which groups of animals are trapped and the seasonal dynamics in prey capture.

Materials and methods

Study sites

Four types of habitats were selected on open heath and mire areas near Abisko Scientific Research Station in northern Sweden (68°21' N, 18°49' E, 360 m elev.). *Pinguicula alpina* L., *P. villosa* L. and *P. vulgaris* L., were each present in the absence of the other two in habitat types 1, 2, and 3 respectively, *P. vulgaris* and *P. alpina* coexisted in habitat type 4. A short description of each habitat type follows.

1) The vegetation in the *P. alpina* habitat was characterised by *Tomentypnum nites*, *Dryas octopetala*, *Bartsia alpina*, and *Salix reticulata*.

2) *P. villosa* grew on *Sphagnum fuscum* hummocks, where the dominating vascular plants were *Empetrum hermaphroditum* and *Rubus chamaemorus*.

3) In the *P. vulgaris* habitat, *Cladonia* spp., *Loiseleuria procumbens*, *E. hermaphroditum*, *Arctostaphylos alpina*, and *Betula nana* dominated the vegetation.

4) In the habitats where *P. alpina* and *P. vulgaris* coexisted, the vegetation resembled that of the *P. vulgaris* sites above.

Plants were studied at two or more sites for each of the four habitat types.

Seasonal dynamics in prey capture

The numbers of prey attached to the plants were counted periodically throughout the 1985 season. For *P. alpina* and *P. vulgaris* 40 plants were marked and checked at about

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2–3 week intervals. Prey items were not removed from these plants. For *P. villosa*, 20 plants were checked each time. The seasonal turnover of leaves was also recorded.

Trapping efficiency

Twenty plants in each habitat were marked in late June 1986 and all prey items were removed from the leaves. Each plant was then visited on four occasions, at 4 day intervals. On each occasion all prey attached to the leaves were classified into taxonomic groups (see below) and removed. The leaf areas of the studied plants were estimated at the beginning and end of the study by drawing the outline of the rosette on a sheet of clear plastic for subsequent area determination. Trapping efficiency was calculated using the mean of the values for leaf area before and after the experiment.

Prey items were classified into six groups: 1) small *Nematocera* (<3 mm), 2) large *Nematocera* (≥3 mm), 3) *Collembola*, 4) *Homoptera*, 5) *Hymenoptera*, and 6) *Acarina*. The dry weight of the prey types was estimated by weighing 10–15 specimens of each group: group 1) 0.849 ± 0.094 mg, groups 2) and 5) 0.246 ± 0.058 mg, groups 3) and 4) 0.150 ± 0.031 mg, and group 6) 0.017 ± 0.002 mg (means \pm S.E.).

Two types of artificial traps were constructed and placed close to each studied plant. One type was designed to mimic the leaf rosette of each species (as judged by a human eye); a paper copy of a leaf rosette was cut out, colored, and coated with a sticky, non-drying glue ("Stikem special non-poisonous pest glue" Seabright Enterprises, Emerville, California). This trap type is referred to as a "dummy trap". The second type were made of 2×2 cm sections of transparent plastic covered with the stikem, these traps are called "transparent traps".

Seasonal nutrient gain through carnivory

The trapping efficiency (Fig. 3) were measured during the part of the season when trapping was most successful (Fig. 1). The seasonal catch were thus estimated to be 30 times the daily catch from Fig. 3 (cf also Fig 1 in Karlsson 1986). The nutrient content of the preys were assumed to be $7.8 \mu\text{mol N g}^{-1}$, $0.36 \mu\text{mol P g}^{-1}$ and $0.38 \mu\text{mol K g}^{-1}$ (Spector 1956; Pate and Dixon 1978; Watson et al. 1982). The plants were assumed to assimilate 75% of the nutrients in the preys (Dixon et al. 1980). The trapping surface (projected leaf area) were 1.8, 0.9 and 3.4 cm^2 for *P. alpina*, *P. villosa* and *P. vulgaris* respectively. The estimated nutrient gain based on these assumptions are considered as relatively conservative, i.e., the factual average nutrient gain probably is larger rather than smaller than this estimate.

Statistical analysis

Comparisons between plants species in terms of numbers of each prey group caught and analogous comparisons between plants and traps were performed using a two-way extension of the Kruskal-Wallis analysis of variance by ranks (Zar 1984). The weight of prey trapped by each of the plant species and trap types was compared using a common parametric analysis of variance.

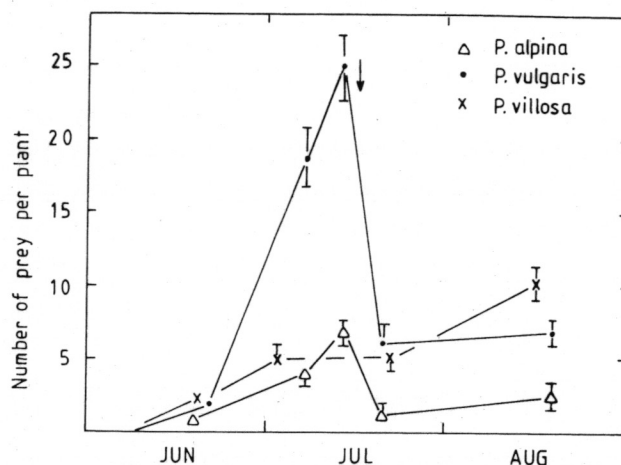


Fig. 1. Number of captured prey per plant at different times of the season. Vertical bars indicate 2 S.E. The arrow indicates a heavy rainfall

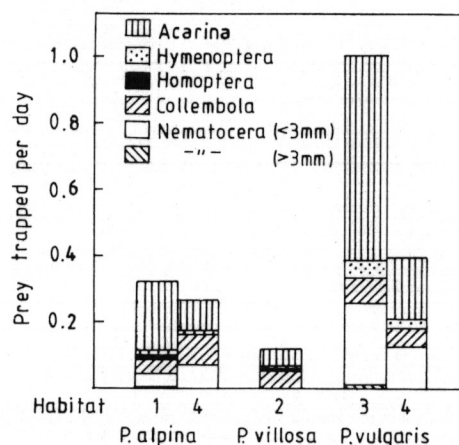


Fig. 2. Number of prey trapped per unit leaf area and day during a 16 day period in early July. Habitat number refers to the description in the methods

Results

For *P. vulgaris*, the largest number of prey attached to leaves was found during early July (Fig. 1). A similar but less pronounced trend was observed in *P. alpina*. Most of the prey at peak catch were small *Nematocera*. However, most of these flies were washed away by a heavy rainfall. The number of prey attached to the *P. villosa* leaves increased slowly throughout the season. Variation between individual plants was large for all species: in mid-July the number of prey per plant ranged from 9 to 69 for *P. vulgaris*, and from 0 to 14 for *P. alpina* and *P. villosa* (not shown).

During the second half of the season the number of prey attached to *P. alpina* and *P. vulgaris* leaves remained almost constant. However, some prey must be captured during the second half of the season, since many leaves had died off during this period. About 30%, 60% and 50% of the leaves of *P. alpina*, *P. villosa* and *P. vulgaris* respectively died during this period, while less than 10% of the leaves died during June and the first half of July (not shown).

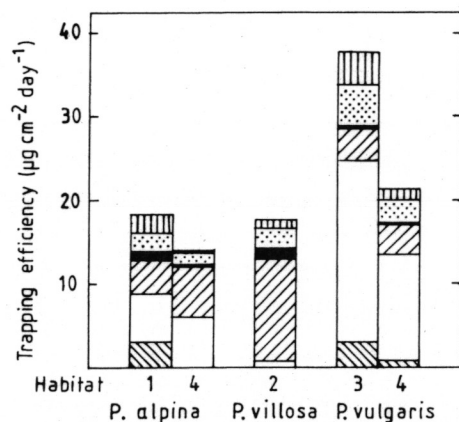


Fig. 3. Dry weight of prey trapped per unit leaf area and day during a 16 day period in early July. Habitat number refers to the description in the methods

The number of prey trapped per plant and day varied almost 10-fold among the species ($P < 0.001$), ranging from 0.11 for *P. villosa* to 1.0 for *P. vulgaris* (Fig. 2). Also, prey composition varied significantly among the *Pinguicula* species ($P < 0.001$). The prey group most frequently found attached to *P. alpina* and *P. vulgaris* was *Acarina* (35–65% of all prey, Fig. 2). Small *Nematocera* and *Collembola* were also relatively frequent (15–31% and 8–32% respectively). For *P. villosa*, *Collembola* (44%) and *Acarina* (40%) were trapped in the largest numbers.

Pinguicula vulgaris trapped an average of 21 and 37 $\mu\text{g cm}^{-2} \text{ day}^{-1}$ at habitats 3 and 4 respectively (Fig. 3). *P. alpina* and *P. villosa* had lower trapping efficiencies than *P. vulgaris* ($P < 0.001$), viz., 14–18 $\mu\text{g cm}^{-2} \text{ day}^{-1}$. By weight, *Nematocera* dominated prey caught by *P. vulgaris*, contributing to about 65% the total. Other well-represented groups on *P. vulgaris* included *Collembola* (9–17%) and *Hymenoptera* (12–13%, Fig. 3). For *P. villosa*, 69% of the catch weight consisted of *Collembola*. *Hymenoptera* was the next best represented group, contributing about 12% of trapped weight. *P. alpina* trapped mainly small *Nematocera* (32–47%) and *Collembola* (21–38%).

P. vulgaris caught significantly more prey than the dummy traps mimicing the *P. vulgaris* plants ($P < 0.001$), whereas the other two species and their corresponding traps caught similar amounts of prey ($P > 0.4$ for both species, Fig. 4). In all three plant-trap comparisons, significantly more prey were found on the plants or on the dummy traps than on the transparent traps ($P \leq 0.006$). This pattern remained consistent when the various prey groups were analysed separately (not shown).

Discussion

The trapping efficiency of these *Pinguicula* species (0.2–0.4 prey $\text{cm}^{-2} \text{ day}^{-1}$, Fig. 4) is low as compared to the Australian *Drosera erythrorhiza*, which has been found to trap 7–9 prey $\text{cm}^{-2} \text{ day}^{-1}$ (Watson et al. 1982). The weight of the catch, however, depends greatly on the types of preys caught. In this study, the large numbers of trapped *Acarina* contributed about 10% or less to the total dry weight, while the few large *Nematocera* caught were each about 50 times heavier than the average acarid and conse-

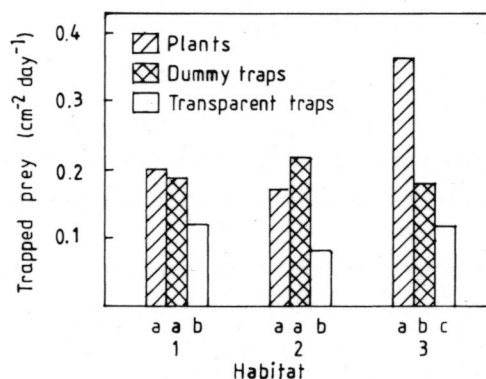


Fig. 4. The trapping efficiency of plants compared with that of dummy traps mimicing leaves and transparent traps at three sites (see methods for description of the traps). Habitat 1 = *P. alpina*, 2 = *P. villosa*, and 3 = *P. vulgaris*. Bars labelled with the same letters are not significantly different from each other ($P = 0.05$, only within habitat comparison)

quently contributed proportionally more for the dry matter per individual.

Prey digestion in *P. grandiflora* has been studied by Heslop-Harrison and Knox (1971): enzyme secretion was initiated within 1 h after prey have capture, after 2 h metabolites from the prey had started to be assimilated by the plant. Assimilate transport out of the leaf began about 12 h later. It can therefore be assumed that such plants need a few days to fully utilize the nutrients in a prey item. Heavy rainfall could therefore cause a substantial loss of potential nutrients for these plants if it occurred during a successful trapping period (cf. Fig. 1). In addition, such an event would probably also decrease plant trapping efficiency since the secretory glands used to trap and digest the lost prey cannot be regenerated (Heslop-Harrison 1978, Heslop-Harrison and Helsop-Harrison 1981).

In contrast to the other two species, *P. vulgaris* caught more prey than the dummy trap (Fig. 4). Thus *P. vulgaris* apparently has some means of attracting prey which is lacking in the other two species. One factor that might help explain the difference in trapping efficiency could be leaf color. *P. vulgaris* and *P. villosa* have yellowish-green leaves while *P. alpina* leaves are reddish-green. *P. vulgaris* may also produce attractive odours. There are some notes in the literature about *Pinguicula* exhaling a fungus-like odor (Lloyd 1942; Slack 1979) but there are no tests of possible effects of the odor. The differences between the dummy traps and the transparent traps (Fig. 4) indicate that leaf shape and/or color is one factor attracting animals to the traps.

The efficiency of the trapping organs has been found to decrease with age in *Sarracenia purpurea* (Wolfe 1981). In *Pinguicula* species trapping ability decreases as the leaf catches prey since the secretory glands on the leaf surface cannot regenerate after use. A decreased trapping efficiency could be one cause for the successive die off of leaves during the season. Another reason could be a decreased photosynthetic capacity as a result of trapping: the leaves fold over preys thus decreasing the intercepting leaf area.

The short subarctic growing season, being ca. 60–90 days for these species (Karlsson 1986), limits the time available for capturing prey in this environment. Nevertheless, the capture of 5–7 small *Nematocera* per season has

Table 1. Comparison between the estimated seasonal nutrient gain through trapped preys and the nutrient pool size of flowering specimens (μmol per plant). See methods for assumptions for estimating the nutrient gain through carnivory. Plant nutrient pool sizes are from Karlsson unpublished work

Species	Site	Nutrient					
		N		P		K	
		gain	pool	gain	pool	gain	pool
<i>P. alpina</i>	1	4.1	19	0.26	0.68	0.28	6.2
	4	3.2		0.21		0.22	
<i>P. villosa</i>	2	2.1	6.3	0.13	0.38	0.14	1.0
<i>P. vulgaris</i>	3	16	26	1.0	1.1	1.1	3.8
	4	9.1		0.61		0.61	

been shown to increase growth and nutrient contents in *P. vulgaris* (Aldenius et al. 1983; Karlsson and Carlsson 1984).

According to the hypothesis that the potential to benefits from trapped prey should be highest in nutrient poor environments (Givnish et al. 1984), the largest effect would be expected for *P. villosa* followed in decreasing order by *P. vulgaris* and *P. alpina*. No such differences were found, however. *Pinguicula vulgaris* growing on the intermediately rich habitat was most efficient, while the species growing on the poorest and richest substrates had similar efficiencies that were lower compared to *P. vulgaris* (Figs. 2–3).

The estimated amount of nitrogen gained through the captured preys during one season corresponds to 21%, 33%, 63% of the plant pool size for *P. alpina*, *P. villosa*, and *P. vulgaris* respectively (Table 1). The phosphorus gain was proportionally somewhat larger while the potassium gain was smaller. These figures are lower than corresponding comparison for *Drosera erythrorhiza*, where the catch were sufficient to supply 100% of the nutrient pools of N and P (Watson et al. 1982). A more relevant comparison would however be between the catch and the plant annual nutrient turnover, such a comparison will be made in Karlsson (in prep). In any way, the carnivoric habit apparently can contribute with a substantial part of the nutrient recruitments of these plants.

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References

- Aldenius J, Carlsson B, Karlsson S (1983) Effects of insect trapping on growth and nutrient content of *Pinguicula vulgaris* L. in relation to the nutrient content of the substrate. *New Phytol* 93:53–59
- Dixon KW, Pate JS, Bailey WJ (1980) Nitrogen nutrition of the tuberous sundew *Drosera erythrorhiza* Lindl. with special reference to catch of arthropod fauna by its glandular leaves. *Austr J Bot* 28:283–297
- Givnish TJ, Burkhardt EL, Happel RE, Weintraub JD (1984) Carnivory in the bromeliad *Brocchinia reducta*, with a cost/benefit model for the general restriction of carnivorous plants to sunny, moist and nutrient poor habitats. *Am Nat* 124:479–497
- Heide F (1912) *Lentibulariaceae (Pinguicula)*. In: The Structure and Biology of Arctic Flowering Plants I. Meddelser om Grønland XXXVI: 441–481
- Heslop-Harrison Y (1978) Carnivorous plants. *Sci Am* 238:104–115
- Heslop-Harrison Y, Heslop-Harrison J (1981) Digestive glands of *Pinguicula*: Structure and cytochemistry. *Ann Bot* 47:293–320
- Heslop-Harrison Y, Knox RB (1971) A cytochemical study of the leaf-gland enzymes of insectivorous plants of the genus *Pinguicula*. *Planta* 96:183–211
- Karlsson PS (1986) Seasonal pattern of biomass allocation in flowering and non-flowering specimens of three *Pinguicula* species. *Can J Bot* 64:2872–2877
- Karlsson PS, Carlsson B (1984) Why does *Pinguicula vulgaris* trap insects? *New Phytol* 97:25–30
- Lloyd FE (1942) Carnivorous plants. *Chronica Botanica Co.* Waltham
- Lüttge U (1983) Ecophysiology of carnivorous plants. In: Lange OL, Nobel PS, Osmond CB, Ziegler H (eds) *Encyclopedia of Plant Physiology NS 12C* Springer Berlin, pp 489–517
- Osvold H (1925) Zur Vegetation der Ozeanischen Hochmoore in Norwegen. *Svenska Växtsociologiska Sällskapet Handlingar VII*
- Pate JS, Dixon KW (1978) Mineral nutrition of *Drosera erythrorhiza* Lindl. with special reference to its tuberous habit. *Austr J Bot* 26:455–456
- Sjörs H (1950) Regional studies in north Swedish mire vegetation. *Bot Not* 2:173–222
- Sjörs H (1965) Northern mires. In: The Plant Cover of Sweden. *Acta Phytogeographica Suecica* 50:180–188
- Slack A (1979) Carnivorous plants. *Edbury Press*, London
- Sonesson M (1967) Studies on mire vegetation in the Torneträsk area, northern Sweden. I. Regional aspects. *Bot Not* 120:272–296
- Sonesson M (1970) Studies on mire vegetation in the Torneträsk area, northern Sweden. III. Communities of the poor mires. *Opera Botanica* 26, p 120
- Spector WS (ed) (1956) *Handbook of biological data*. Saunders Co. Philadelphia
- Watson AP, Matthiessen JN, Springett BP (1982) Arthropod associates and macronutrient status of the red-ink sundew (*Drosera erythrorhiza*) – *Aust J Ecol* 7:13–22
- Wolfe LM (1981) Feeding behaviour of a plant: Differential prey capture in old and new leaves of the pitcher plant (*Sarracenia purpurea*). *Am Midl Nat* 106:352–359
- Zar JH (1984) *Biostatistical analysis*. Prentice-Hall Englewood Cliffs. 2nd ed

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