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Prey capture by three *Pinguicula* species in a subarctic environment

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Abstract The number and biomass of prey captured were estimated for *Pinguicula alpina*, *P. villosa* and *P. vulgaris* in a subarctic environment. Seasonal captures were estimated for one site per species for 4–5 years. Captures were related to reproductive status (reproductive/non-reproductive) and to leaf area. For one species (*P. vulgaris*) the catch was also compared across a range of habitats. Of the seasonal catch, 50–75% was obtained during June and less than 5% during August. For *P. alpina* and *P. villosa* the seasonal catch varied threefold or more between years (means of 89–329 μg dry matter plant^{-1} season^{-1} for *P. alpina*, and 11–91 μg dry matter plant^{-1} season^{-1} for *P. villosa*), whereas the between-year variation for *P. vulgaris* was small (mean c. 600 μg plant^{-1} season^{-1}). Large variations were, however, observed among habitats for *P. vulgaris*. Captured prey may contribute a substantial amount of nutrients to the most successful individuals (up to 85% of the mean seasonal turnover), but prey capture varied greatly and during any given season many individuals obtained only marginal amounts of nutrients through carnivory. *P. vulgaris* trapped almost twice as much per unit leaf area and season as the other two species (224 for *P. vulgaris* versus 127 $\mu\text{g cm}^{-2}$ season^{-1} for the other two species). Reproductive individuals of *P. vulgaris* trapped almost twice as much as non-reproductive individuals (after taking differences in leaf area into account). For the other

two species no differences were observed between reproductive and non-reproductive individuals.

Key words Carnivorous plants · Nitrogen economy · Reproduction

Introduction

Experimental studies have been shown that carnivorous plants benefit from the capture of prey. The benefits are manifested as increases in growth or reproduction or both (Givnish 1989; Juniper et al. 1989). Although the prey composition has been determined for a number of species (see Juniper et al. 1989) there are relatively few cases where the prey has been quantified in terms of trapped dry matter per season. Such analyses are required to evaluate the relative importance of prey in the plants' nutrient economy and the implications for plant performance *in situ*. Two such studies on the same species, *Drosera erythrorhiza*, reported dissimilar findings: Dixon et al. (1980) found that 15% of the annual nitrogen requirements were obtained from prey, whereas Watson et al. (1982) estimated that prey could provide all the N and P required.

Using a different approach, based on the fact that the ^{15}N content of prey N differs from that of soil N, Schulze et al. (1991) estimated the proportion of plant N originating from prey. For a range of south-west Australian carnivorous species they reported that insect nitrogen made up from 15 to over 90% of the nitrogen pool in the above ground plant parts. These results indicate that large variations may occur, both within and between species, in the relative importance of prey capture in the nitrogen economy.

The annual nutrient requirements are higher for reproductive than for non-reproductive *Pinguicula* specimens (Karlsson 1988). However, the nutrient pool remaining in the mother plant after seed production is reduced less than expected from the investment in reproduction when compared with non-reproductive plants, which apparent-

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ly is due to higher resource incomes in the reproductive plants (Karlsson et al. 1990; L. M. Thorén, P. S. Karlsson and J. Tuomi in preparation). Thus reproductive individuals seem to have some means of compensating for the resource investment in reproduction. Differences in the length of the root systems cannot explain the differences in nutrient acquisition (Karlsson 1986). Another possibility is that flowering plants trap more prey than non-reproductive ones.

The purpose of this study was to quantify the seasonal catch or prey for three species of *Pinguicula* in a subarctic environment and determine how it varies with the reproductive status of the plant among years and habitats.

Methods

Seasonal variation in prey capture

In mid-June each year (1989; 1991–1993) 30–60 specimens each of *P. alpina* L., *P. villosa* L. and *P. vulgaris* L. were marked. All were growing on a subalpine heath near Abisko Scientific Research Station (68°21'N, 18°49'E, c. 380 m above sea level). The three species were studied on different parts of the heath: *P. alpina* was growing on mineral soils disturbed by frost heaving. *P. vulgaris* also grew on frost-heaved ground but on more stable sites. The third species, *P. villosa*, was studied on *Sphagnum fuscum* peat substrate (Karlsson 1986). The plants were visited at roughly weekly intervals until the end of August, at which time almost all leaves of all three species were dead. A drawing was made of each leaf, on which each new prey was marked. The prey were not removed, in order to avoid disturbing the leaf surface. Mites (Acarina) occurring on the leaves were recorded but not included in the caught biomass since they may live on the leaves rather than being prey (R.J. Antor and M.B. Garcia unpublished). For all years except 1991, leaf area was estimated for the fully developed leaves from a drawing of the projected leaf area made *in situ*. The area of the drawing was measured using a leaf area meter (Model 3100 LiCor, Inc., Lincoln, Nebraska, USA). Thus the area-based prey capture was expressed in relation to the final leaf area. From 1991 to 1993, reproductive status was recorded for each individual studied. Since it was not always possible to determine the reproductive status of a plant when starting to count prey, the number of replicate plants for each group (reproductive/non-reproductive) varied between 5 and 30 per species during each of the years.

The mean dry weight of Collembola was estimated using a relationship between body length and weight [dry weight (µg) = 2.4 × L^{3.6778}, where L = body length in mm, R. Zamora personal

communication] and length data measured under a dissecting microscope for 49 specimens of *P. vulgaris* (mean dry weight = 21 µg) and 20–45 of *P. alpina* and *P. villosa* (mean = 11 µg for both species). Collembola collected from soil samples from the *Pinguicula* habitats indicated similar weights. Other larger prey were collected while they were still fresh, and then dried and weighed.

The weights used here are lower than those reported previously from the same area (Karlsson et al. 1987). For the Collembola weights in Karlsson et al. (1987) an error must have occurred since the dry weight used in the current paper is 7–14% of that of our previous study. For larger prey groups also, slightly lower mean dry weights were obtained in this study than in our previous one.

Variation in prey capture among *P. vulgaris* in different habitats

To estimate the variation in prey capture among sites a regional survey of the number of prey per plant was conducted for *P. vulgaris*. In mid-August 1988, 10–15 plants from each of six sites were taken into the laboratory. The sites, selected to represent contrasting environments, ranged from Andöya at the Norwegian coast (69°05'N 15°51'E, 30 m above sea level) up to the alpine region in the Abisko area (68°21'N 18°49'E, 900 m altitude). The total projected leaf area was estimated for each plant. In 1993, 30 individuals each in two different habitats were checked for prey regularly from June to August.

Statistical analysis

Unless otherwise stated, all data presented are arithmetic means. To obtain homogenous variances for the ANOVA tests, these analyses were carried out using log₁₀(x+1) or rank-transformed data. However, the results of analyses using untransformed, log- or rank-transformed data were similar. When testing for differences between reproductive and non-reproductive individuals, leaf area was entered as a covariable before the main effects to remove differences owing to the larger leaf area of reproductive plants.

Results

For *P. alpina* and *P. villosa* Collembola were the most abundant prey group in terms of number of trapped individuals (Table 1). For *P. vulgaris* Collembola and Nematocera were about equally abundant as prey. These two prey groups made up 85% or more of the number of prey for all three species (Table 1). They accounted for about 80% of the dry weight of the prey of *P. alpina* and *P. vulgaris* and 100% of the prey of *P. villosa*.

Table 1 Prey capture by three species of *Pinguicula*: taxonomic group composition of captured prey and the relative contributions of the various groups to the trapped dry matter. Based on counts on 60–90 plants per species (data from 1992 and 1993). Mites (Acarina) were not considered as prey (see Methods). The seasonal catch as absolute dry weight is presented in Fig. 5. (Dwt dry weight)

| Prey group | P. alpina | | P. villosa | | P. vulgaris | |
|-----------------|-----------|---------|------------|---------|-------------|---------|
| | n (%) | Dwt (%) | n (%) | Dwt (%) | n (%) | Dwt (%) |
| (Acarina) | 8.2 | — | 1.1 | — | 7.2 | — |
| Collembola | 62.5 | 34.3 | 93.2 | 87.1 | 39.7 | 12.4 |
| Nematocera | 24.3 | 46.6 | 5.7 | 12.9 | 44.9 | 67.2 |
| Other Diptera | 0.6 | 1.4 | 0 | 0 | 0.8 | 1.3 |
| Formicidae | 0.4 | 4.0 | 0 | 0 | 0.8 | 4.3 |
| Coleoptera | 3.1 | 7.7 | 0 | 0 | 4.0 | 5.8 |
| Other Arachnida | 0.6 | 3.4 | 0 | 0 | 2.2 | 7.9 |
| Other | 0.4 | 2.6 | 0 | 0 | 0.3 | 1.1 |
| Total | 720 | 100 | 351 | 100 | 1290 | 100 |

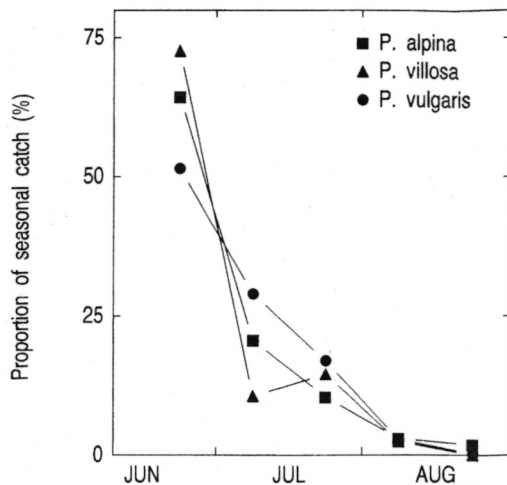


Fig. 1 Seasonal variation in the relative amount of prey trapped by three *Pinguicula* species. Each point represents the mean catch for a 15-day period for 4 years. $SE < 8.5$, $n = 4$ (mean for each year)

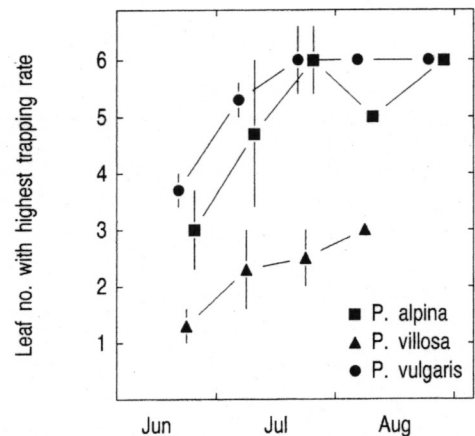


Fig. 3 Seasonal variation in the position of the leaf with the highest trapping effectiveness ($\mu\text{g cm}^{-2}/15\text{-day period}$). Leaf 1 is the first leaf to emerge, while the last leaf to emerge was leaf 7 (*P. alpina* and *P. vulgaris*) or 4 (*P. villosa*). Vertical bars indicate ± 1 SE, based on means for each year ($n = 3$). The position of the symbols for *P. alpina* is slightly shifted to avoid overlap with those of *P. vulgaris*

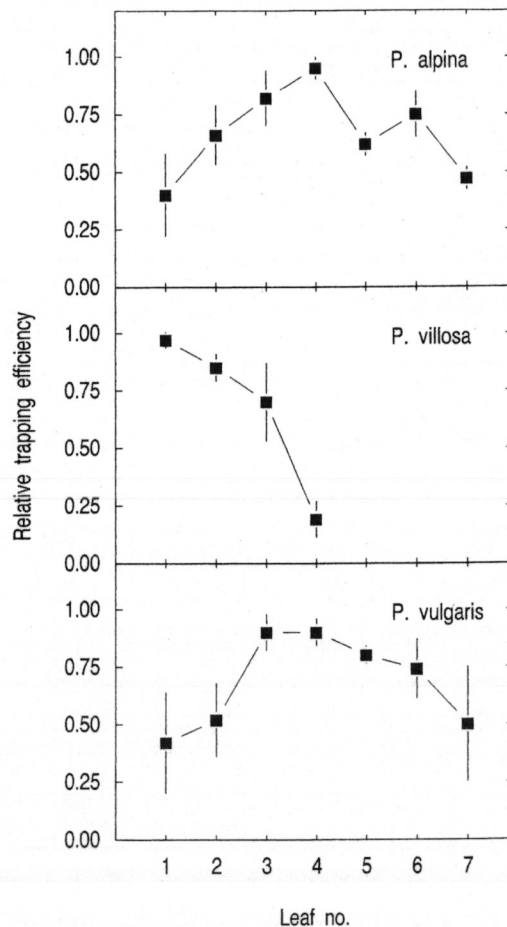


Fig. 2 Relative contributions of the different leaves in the rosette to the total seasonal captured dry weight. For each year the data were normalised so that the leaf with the highest catch ($\mu\text{g cm}^{-2}$) was set to 1.0 and the means for 4 years are presented. Leaf 1 is the first leaf to emerge. Vertical bars indicate ± 1 SE

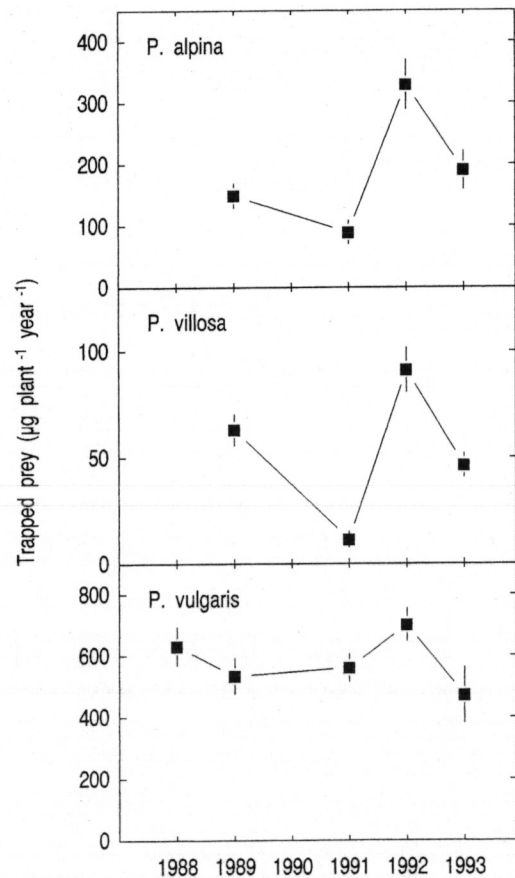


Fig. 4 Variation among years in the amount of prey captured per plant and season. Vertical bars indicate ± 1 SE, $n = 30-60$. The value from 1988 for *P. vulgaris* was obtained from Table 2

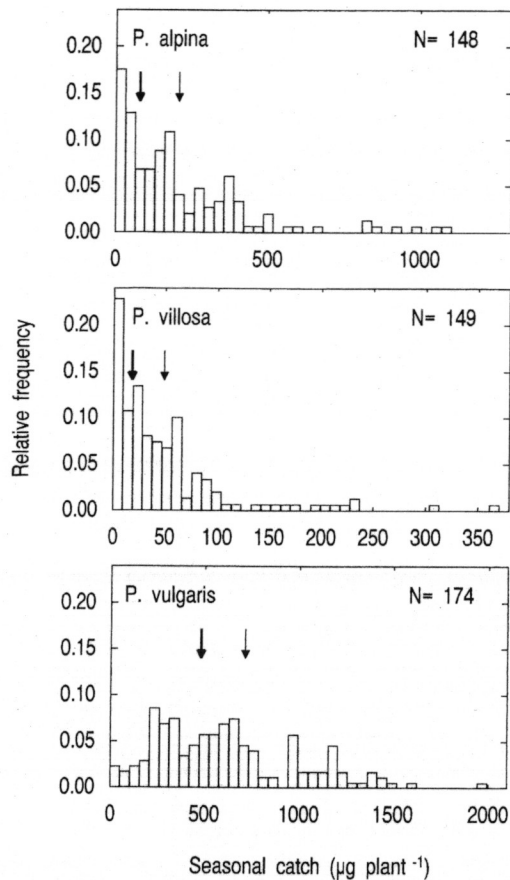


Fig. 5 Frequency distribution of the seasonal catch, based on all plants studied during 1989–1993. Arrows indicate mean catch based on $\log_{10}(x+1)$ transformed data (thick arrow) and untransformed data (thin arrow)

Table 2 Comparison of seasonal *P. vulgaris* catches between habitats. The data for 1988 were estimated by counting the prey obtained from 12 specimens under a dissecting microscope. Plants were collected at the end of July. The order of the sites in the list indicates their relative position along an west-east gradient

| Site | Year | Caught wt ($\mu\text{g}/\text{plant}$) | Catch per unit leaf area ($\mu\text{g}/\text{cm}^2$) |
|------------|------|---|--|
| Andöya dry | 1988 | 256 | 69 |
| Andöya wet | 1988 | 1203 | 101 |
| Katterjokk | 1988 | 845 | 127 |
| Njulla | 1988 | 353 | 92 |
| Abisko dry | 1988 | 631 | 377 |
| Abisko dry | 1993 | 503 | 147 |
| Abisko wet | 1993 | 151 | 44 |
| Lapporten | 1988 | 227 | 69 |

For all three species 50–75% of the total mass of trapped prey was obtained during the second half of June, i.e., the first 2 weeks of the growing season in this subarctic area, whereas less than 5% was caught during August (Fig. 1). The different leaves in the rosettes of these plants varied in terms of their proportional contribution to the total captured biomass (Fig. 2). For *P. alpina* lower prey capture were found for the first- (leaf 1)

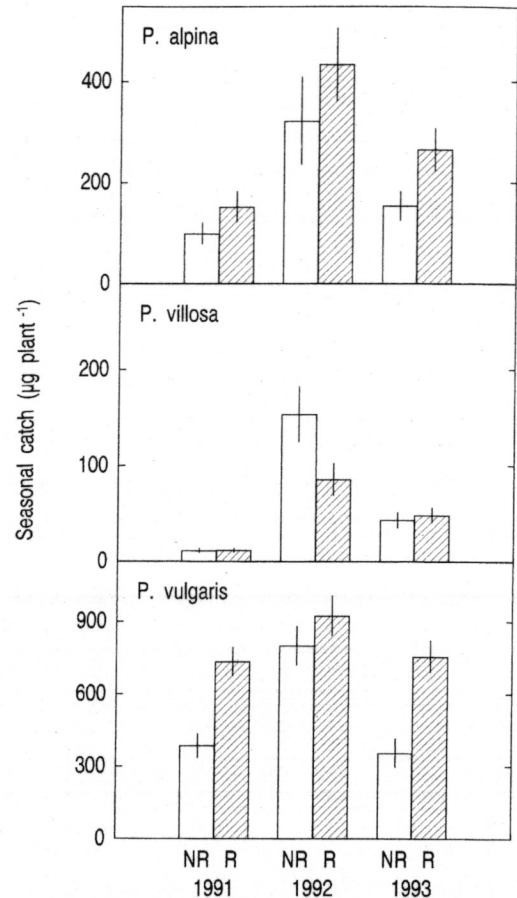


Fig. 6 Seasonal trapped dry weight for reproductive (R) and non-reproductive (NR) individuals. Vertical bars indicate ± 1 SE, $n=5-30$ per reproductive type, species and year. A statistical analysis for the 1992 and 1993 data is presented in Table 3

and the last-developing (leaf 7) leaves in the rosette than for intermediate ones ($P=0.042$, one-way ANOVA). A similar pattern was found for *P. vulgaris* although differences among leaves were not significant ($P=0.18$). For rosettes of *P. villosa*, which only contain three or four leaves, the trapping rate declined with leaf number ($P=0.003$). Within the leaf rosette, the prey trapping efficiency shifts successively towards more recently expanded leaves (higher leaf number) as the season progressed (Fig. 3).

For *P. alpina* and *P. villosa* the seasonal catch varied considerably between years (Fig. 4), ranging from 89 to 329 μg per plant for *P. alpina* and from 11 to 91 for *P. villosa*. For *P. vulgaris* the mean captured mass was relatively constant at c. 600 μg per plant and season. Variation among individuals was large: for *P. alpina* it varied from 0 to 1080 μg , for *P. villosa* from 0 to 365 and for *P. vulgaris* from 0 to 1971 μg (Fig. 5). For *P. vulgaris* both the seasonal catch per plant and the catch per unit leaf area varied up to 8-fold among habitats (Table 2).

The prey trapping efficiency of *P. vulgaris*, expressed as the amount of prey captured per unit leaf area, was about twice that of the other two species (224 $\mu\text{g cm}^{-2}$ season $^{-1}$ for *P. vulgaris* versus 127 $\mu\text{g cm}^{-2}$ season $^{-1}$ for the other two species; $P=0.002$ for differences among

Table 3 Effect of plant reproductive status (*Rep.st.*, *R.s.*; reproductive or non-reproductive) and year on seasonal prey capture of three *Pinguicula* species, assessed using analysis of variance. Data for 2 years (1992, 1993) where both plant

reproductive status and leaf area were recorded are included in the analysis (see Fig. 6 for means). Leaf area was entered before the other factors in the analysis. Based on $\log(x+1)$ transformed data; a corresponding analysis using ranked data yielded similar *P* values

| Species | Source of variation | | | | | Adj. r^2 |
|--------------------|---------------------|----------------|------------|---------------|-------------|---------------|
| | Area SS | Rep. st. SS | Year SS | R.s.×Yr SS | Total SS | |
| <i>P. alpina</i> | 0.12 | 0.19 | 1.61** | 0.16 | 10.60 | 0.13 |
| <i>P. villosa</i> | 0.27 | 0.00 | 4.60*** | 0.47 | 18.45 | 0.25 |
| <i>P. vulgaris</i> | 0.83** | 1.39*** | 1.41*** | 0.54* | 11.27 | 0.38 |

* $0.05 < P \leq 0.01$; ** $0.01 < P \leq 0.001$; *** $P < 0.001$

Table 4 Mean dry weight (μg per plant \pm SE) of prey captured on flower stalks of three *Pinguicula* species, $n=30$. All *P. vulgaris* prey were small Nematocera

| Species | Year | Mean | Minimum | Maximum |
|--------------------|------|------------|---------|---------|
| <i>P. alpina</i> | 1991 | 0 | 0 | 0 |
| <i>P. villosa</i> | 1991 | 0 | 0 | 0 |
| <i>P. vulgaris</i> | 1991 | 30 ± 6 | 0 | 136 |
| <i>P. vulgaris</i> | 1993 | 51 ± 7 | 0 | 260 |

species, two-way ANOVA with year and species as factors, not shown).

The amount of prey trapped by *P. vulgaris* was higher in reproductive plants than in non-reproductive ones (Fig. 6; Table 3). After correction for differences in leaf area the mean seasonal catch was estimated at $362 \mu\text{g}$ for non-reproductive individuals and the reproductive individuals $691 \mu\text{g}$ (decoded means for $\log_{10}(x+1)$ transformed data; not shown). No significant effect of reproductive status was found for *P. alpina* or *P. villosa*. In addition to the catch of the leaf rosette some prey was found on the flower stalk of one of the three species, *P. vulgaris* (Table 4). The proportion of total prey captured on the flower stalk was small (5–6%).

Discussion

The seasonal variations in prey capture reported here are the combined result of variations in plant trapping potential and prey abundance. The fast decline in prey capture over the season (Fig. 1) could have resulted from a decline in trapping potential and/or prey abundance. However, the pattern of change in prey abundance seems to be different. Koponen (1977) recorded the highest densities of Nematocera in light-traps in August–September. The biomass of Collembola is also likely to increase from June to August (E. T. Persson personal communication). The successive shift over time in trapping efficiency in favour of younger leaves (Fig. 3) indicates that individual leaves successively lose their ability to trap prey with age. Similar patterns have been observed previously for *P. vulgaris* (Darwin 1897, p. 370), where the number of insects caught declined as the season progressed, and for *Sarracenia purpurea* (Wolfe 1981) where the trapping rate declined with leaf age.

A decline in trapping efficiency with leaf age could have at least two causes: (1) a decrease in the ability of the leaf to attract prey and (2) a decrease in the ability to trap animals coming to the leaf. In *Pinguicula* a fungus-like odour emitted from the leaves has been suggested to be a prey attractant (Lloyd 1942). The emission of such odours may be highest in young leaves. In *Pinguicula*, only the part of the leaf with intact stalked glands, which produce mucopoly-saccharides, can trap prey (Heslop-Harrison and Knox 1971). Glands on the surface of the *Pinguicula* leaves cannot be regenerated and thus can only be used to trap prey once (Heslop-Harrison 1978; Heslop-Harrison and Heslop-Harrison 1981). However, gland wear due to prey capture could only be part of the reason for the decline in trapping rate over the season found for the *Pinguicula* species at Abisko, since only a small proportion of the leaf surface comes into contact with prey. More likely explanations are that the glands may have a limited period of function or that the leaf gradually loses its ability to attract prey.

For the most successful individuals prey capture apparently contributes significantly to the nutrient economy (Table 5). Differences among individuals, years and habitats were large, however (Figs. 4 and 5, Table 2). During any given season many individuals receive only small or negligible amounts of nutrients in the form of prey. Even larger differences among individuals have been reported for *Sarracenia purpurea* (Cresswell 1993) where c. 8% of the plants caught 66% of the prey biomass and over 50% of the plants did not trap any prey.

In a previous study we estimated that prey could supply these *Pinguicula* species with nitrogen and phosphorus corresponding to 20–100% of their pool size, depending on the species and on whether the plant produces seed (Karlsson et al. 1987; Karlsson 1988). These estimates were too high due to an error in the estimating dry weight of a collembolan (see Methods). In the present study the average contribution of N was estimated to be 7–15% for *P. alpina* and *P. villosa* whereas for *P. vulgaris* the average N gain from prey corresponded to about 26–40% of the annual turnover (Table 5). The contribution for the most successful individuals was 2–4 times higher than the average, i.e., 18–85%.

The fact that the trapping success was higher for reproductive *P. vulgaris* than for non-reproductive individuals explains why the somatic cost of reproduction

Table 5 Estimated seasonal nitrogen gain ($\mu\text{mol N plant}^{-1}$) from trapped prey for reproductive and non-productive individuals as related to annual nitrogen turnover. Based on the assumption that prey have a 10% N content (Riechle et al. 1969; Spector 1956; Watson et al. 1982) and 76% of the prey N is transferred to the plant (Dixon et al. 1980). Mean maximum is the mean of the most successful plant each year. Seasonal nitrogen turnover from Karlsson (1988)

| Species Reprod. st. | N income ($\mu\text{mol N plant}^{-1}$) | | Seasonal turnover |
|------------------------|---|------------------|----------------------|
| | Mean | Mean max. | |
| <i>P. alpina</i> | | | |
| Non-reproductive | 1.1 ^a | 4.0 ^a | 8.0 |
| Reproductive | | | 13 |
| <i>P. villosa</i> | | | |
| Non-reproductive | 0.3 ^a | 0.8 ^a | 2.0 |
| Reproductive | | | 4.4 |
| <i>P. vulgaris</i> | | | |
| Non-reproductive | 2.9 | 6.2 | 7.3 |
| Reproductive | 4.2 | 10.2 | 16 |

^a Reproductive and non-reproductive individuals are pooled, since there was no difference in trapping success between reproductive and non-reproductive plants (Table 2)

(Tuomi et al. 1993) was less than predicted from reproductive effort (Karlsson et al. 1990, L.M. Thorén et al. in preparation). However, a similar discrepancy between reproductive effort and somatic cost was also observed for the other two species (Karlsson et al. 1990) although no differences in trapping success were observed between reproductive and non-reproductive individuals. It is thus possible that these species have other mechanisms for compensating for the costs of reproduction.

One aspect that may affect the seasonal capture is robbing of prey by ants (Zamora 1990; Zamora in preparation). Robbing by ants was observed at Abisko during experimental feeding of *Pinguicula* plants with *Drosophila* flies, but no natural prey were observed to be removed by ants (L. M. Thorén and H.-M. Hanslin personal observation). Prey robbery is mainly restricted to large, relatively fresh prey (Zamora 1990). Since most prey caught at Abisko are small and since our surveys of prey capture were at roughly weekly intervals, we assume that the proportion of robbed prey at Abisko was small and that most the prey robbed had been removed from the plant in the period between capture and the following survey, i.e., such items were rarely, if ever, recorded as prey in our surveys.

Thus, for the *Pinguicula* species at Abisko, carnivory is an unreliable source of nutrients. Some individuals trap large amounts of prey while others obtain little or none. Like most carnivorous plants, these species can apparently maintain growth and reproduction with the soil as their only source of nutrients (Aldenius et al. 1983; Karlsson and Carlsson 1984; Karlsson et al. 1991). It remains to be determined whether the differences in trapping success observed between individuals would even out with time, the alternative being that inherent differences in prey trapping efficiency exist between individuals.

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