

The influence of prey behaviour on prey selection of the carnivorous plant *Utricularia vulgaris*

Sabine Harms & Frank Johansson

Department of Ecology and Environmental Science, Animal Ecology, Umeå University,
90187 Umeå, Sweden
E-mail: Sabine.Harms@eg.umu.se

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Abstract

The mechanisms underlying differential prey selection of two microcrustaceans by the common bladderwort (*Utricularia vulgaris*) were studied in the laboratory. Functional response experiments with single prey showed that *Utricularia* had a higher attack rate coefficient and a longer handling time coefficient with the cladoceran *Polyphemus pediculus* than with the cyclopoid copepod *Eucyclops serrulatus*. Observation of predation rate, defined as number of prey eaten per unit time, from direct behavioural observation on single prey species, showed a higher predation rate with *Polyphemus* than on *Eucyclops*, at low prey densities. The opposite pattern was found at high prey density. When the two prey were presented simultaneously to the predator, *Eucyclops* was preferred over *Polyphemus*. Results from the situation with two prey and some of the results from the direct behavioural observations support field data on the diet of *Utricularia*, which shows that cyclopoid copepods are selected more frequently than *Polyphemus*.

Introduction

Prey selection by predators affects several important aspects of population dynamics and community patterns (Paine, 1966; Zaret, 1980). A selective prey choice refers to the condition when the relative abundance of a prey in a predator's diet differs from the abundance observed in the environment (Chesson, 1983). Since prey selection has the potential to link the dynamics of species at different trophic levels (Murdoch & Oaten, 1975; Holt, 1977), it is important to know what determines a predator's prey choice.

By analysing prey selection in a mechanistic way, a more thorough understanding of the phenomenon can be attained. One such approach is to compare functional response curves of different prey. The most commonly applied functional response model is the type II functional response (Holling, 1959), where the parameters attack coefficient (a) and handling time (T_h) determine the shape of the curve. Attack rate represents a maximum theoretical rate of attack on a prey,

and on a short time scale it is a useful coefficient for predicting vulnerability of different prey types (Spitze, 1985).

A second mechanistic approach is to directly observe the behaviour that determines prey choice. By looking at behavioural pathways such as encounters, orientations, strikes, captures and ingestions, the predation sequence can be determined. This method can also aid the interpretation of what determines the attack rate and handling time coefficients of functional response models. Sih & Moore (1990) suggested that encounter probability, attack probability, capture success and consumption probability, which can be derived from the behavioural pathway above, are important variables that determine predator diet.

Bladderworts are carnivorous plants that prey on a wide array of aquatic invertebrates, especially zooplankton (Andrikovics et al., 1988; Juniper et al., 1989; Harms, 1999). They capture prey with underwater trap-bladders, sucking in prey upon a dislocation of trigger hairs on the trapdoors. Few studies have in-

vestigated the predator behaviour of these plants. As they are extreme sit-and-wait predators, prey selection probably depends very much on prey characteristics and very little on predator behaviour. Harms (1999) showed in a field study that bladderworts captured prey non-randomly and suggested that, amongst other things, prey activity and movement patterns are important in determining bladderwort diet. Her study showed a mean selection index of 0.02 on *Polyphemus* and 2.31 on *Eucyclops*, where an index >1 indicates selection for, and an index <1 indicates selection against the prey in question.

The purpose of this study was twofold. First we wanted to examine why e.g. cyclopoid copepods are selected more frequently than *Polyphemus pediculus* in the field by bladderworts (Harms, 1999). We did this by performing laboratory studies on the functional response of *Utricularia vulgaris*. Functional response was determined for each prey separately and for the two prey together. Second, we wanted to investigate what determines the shape of the functional response curves obtained from the two prey species. This was done in a separate experiment by direct observation of encounter rate, attack probability and capture success for both prey species.

Materials and methods

Functional response

Experiments on prey selection of *U. vulgaris* were done during July and August 1999. As prey, we used two microcrustaceans, a cladoceran zooplankton (*Polyphemus pediculus*) and a cyclopoid copepod (*Eucyclops serrulatus*). Fresh prey were regularly obtained from the field. Both *Polyphemus* and cyclopoid copepods occur at high abundance (124 / l for *Polyphemus*, 288 / l for copepods) in habitats with bladderworts (Harms, 1999). We determined the functional responses for *U. vulgaris* with (a) *Polyphemus* as the only prey, (b) *Eucyclops* as the only prey and (c) both species together in varying proportions. Glass jars (6 cm in diameter), filled with 125 ml water, served as experiment vessels. The water was a mixture of 50% tap water and 50% filtered lake water (mesh size 0.2 mm). In each of the jars, we put a short piece of a shoot of *U. vulgaris* (3–5 cm) with 15 trap-bladders. To synchronise 'hunger level' for the bladderwort traps, all bladderworts were kept devoid of prey in tap water at about 6 °C for at least 1 day, and never longer than a

week, prior to the experiment. All traps of the bladderwort piece were considered to be ready for function at the start of the experiment, and we avoided bladders that contained prey visible from the outside.

In experiments (a) and (b), we added prey at densities of 10, 20, 30, 50, 70, 100, 150 and 200 individuals per jar, with each density replicated eight times. In experiment (c), we added *Polyphemus/Eucyclops* at the proportions of 120/0, 100/20, 80/40, 70/50, 60/60, 50/70, 40/80, 20/100 and 0/120, and each proportion was replicated seven times. The mean size of 40 randomly chosen *Polyphemus* and *Eucyclops* was 0.64 mm (± 0.008 S.E.) and 0.66 mm (± 0.008 S.E.) respectively. Experiments were run for 24 h. We counted prey and replaced prey that were captured, dead or showed unnatural swimming performance every 2–6 h. Furthermore, after 12 h, we replaced about 80% of the water in each jar to guarantee oxygen supply for the prey. All observations were done at room temperature (22 ± 1 °C). After each run, the trapbladders were preserved in ethanol. Bladders were then opened, and all prey that were captured in them and not yet completely digested were counted.

To examine the relationship between number of prey eaten and prey density for the single prey experiments, we used Holling's type 2 functional response model (Holling, 1959):

$$N_e = \frac{aNT}{1 + aT_hN},$$

where N_e is the number of prey eaten, a is the attack rate coefficient, N is prey density, T is total time of exposure, and T_h is the handling time coefficient. The attack rate coefficient determines the initial slope of the curve, while the handling time coefficient determines the level of the asymptote. We estimated the attack rate (a) and handling time (T_h) with non-linear regression using the simplex method in SYSTAT (1992). For the two prey functional response (experiment c), data is presented as the percentage of each prey eaten at each density. All experiments were performed under constant light during the 24 h. We chose this 'light cycle' since the nights at the latitude of the study are very light during the summer.

Functional response experiments were also previously done in a series of experiments in 1995 and 1997. These experiments were performed in exactly the same way as those from 1999. The results of these preceding experiments were to some extent more variable, making the raw r-square of the non-linear regression somewhat lower than for the 1999 experi-

ment. We have, therefore, chosen to present a detailed analysis of the 1999 experiment only. However, to make our case stronger we will present the result of the 1995–1997 experiment graphically since they show the exact same pattern.

Direct observations

Numbers of encounters, attacks and captures, as well as swimming speed of the prey and time a prey spent resting (on the bottom of the jar or on the bladder-worts), were obtained by direct observation. Since a prey has to touch the trigger hairs on a bladder's door to start the prey capturing mechanism, we defined an encounter as a prey's position so close to the trap door (≤ 3 mm) that it potentially came into contact with the trigger hairs. As an attack, we defined each release of the prey catching process, visible as a quick movement and by the change of a bladder's shape from concave to convex, seen from above. We only considered a prey as successfully captured when it was caught within the bladder. Prey that were only squeezed in with their antennae or head in the door were excluded, as they can escape (personal observation) and, therefore, cannot be used as prey by the predator. We calculated encounter rate as the total number of encounters divided by the observation time. Attack probabilities were calculated as the average of the numbers of attacks divided by the numbers of encounters. Capture success was obtained as numbers of prey captured per attack. For swimming speed, we followed one prey for 2 min and drew its path through the jar on paper and noted the time it spent resting. The direct observations were done at two prey densities, 20 and 120 prey/jar, using the same experimental set-up as for the functional response experiments. Each jar was observed for 60 min and replicated 10 times for each prey species and density. Swimming speed and resting time were replicated 12 times and not estimated at densities of 120 prey/jar because it was not possible to keep track of every individual simultaneously.

To examine if the data from the observation experiments could predict the outcome of the single prey functional response curves, we calculated how many prey that should be eaten by the *Utricularia* during 24 h given the numbers from the behavioural observation. We call this parameter 'predation rate' and it was calculated as the number of captures in the 60 min multiplied by 24 (h). Predation rate, therefore, refers to the number of prey captured by 15 *Utricu-*

laria bladders in 24 h at densities of 20 and 120 prey/jar.

The highest zooplankton densities used in our experiment (200/jar) correspond to a density of 1600 l^{-1} . Although reported mean zooplankton densities are usually lower, such high densities are not unusual within littoral zooplankton communities (Smyly, 1957; Straškraba, 1965). Further, Butorina (1986) reported a mean density of 806 *Polyphemus pediculus* per l. Since zooplankton show considerable patchiness (Butorina, 1986; Folt & Schulze, 1993), the *Polyphemus* mean value reported probably implies much higher densities in swarms given that the value of 806 is a mean value.

Results

Functional response

The functional response type II curve provided a good fit to the data on number of prey eaten as a function of prey density; raw r-square for the nonlinear fit was 0.88 (df = 64) and 0.92 (df = 64) for *Eucyclops* and *Polyphemus*, respectively (Figure 1). A qualitative interpretation of the shape of the curve suggests that *Utricularia* had a higher attack coefficient and longer handling time coefficient for *Polyphemus*. This interpretation was statistically supported by an approximate comparison of the mean estimated values of attack rate and handling time on *Polyphemus* ($a = 0.126 \pm 0.032$ S.E., $T_h = 0.657 \pm 0.041$ S.E.) and on *Eucyclops* ($a = 0.043 \pm 0.009$ S.E., $T_h = 0.449 \pm 0.054$ S.E.); $p < 0.02$, $t = 2.50$, df = 62 and $p < 0.01$, $t = 3.06$, df = 62 for attack rate and handling time t -tests, respectively.

Results from the two prey experiment showed that *Eucyclops* were selected over *Polyphemus* (Figure 2a), and a t -test at a prey density of 60 prey/jar showed that more *Eucyclops* were consumed at equal prey densities ($p = 0.05$). In contrast, plugging the estimates of the attack rate and handling time of the two prey species into the two prey functional response equation (Lawton et al., 1974):

$$Ne_1 = a_1 N_1 T / (1 + a_1 T_{h1} N_1 + a_2 T_{h2} N_2)$$

(prefix 1 and 2 correspond to the two prey species) predicts that *Polyphemus* should be selected over *Eucyclops* (Figure 2b). For example, at equal prey densities of 60 prey per jar, the zooplankton should be taken in

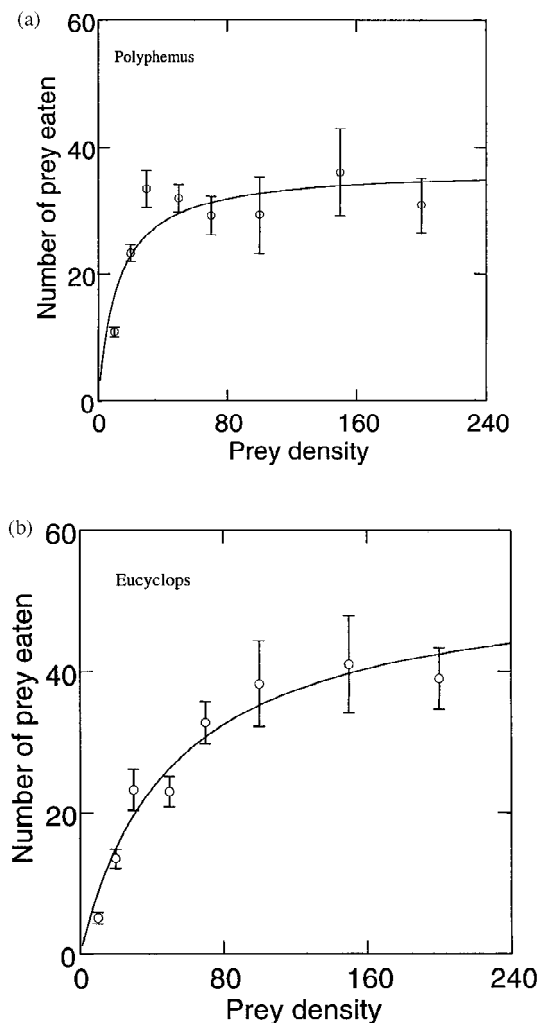


Figure 1. Functional response curve fits of *Utricularia vulgaris* feeding on (a) *Polyphemus pediculus*, and (b) *Eucyclops serrulatus*. Each point represents the mean number of prey eaten and error bars show S.E. The line shows the curve fit estimated from the functional response equation.

the proportion: 74.4% *Polyphemus* and 25.6% *Eucyclops*. Hence, the two prey functional response equation could not predict the observed outcome of predation when the two prey were presented together.

Direct observations

Behavioural observation results are given in Table 1. *Utricularia* had a much higher encounter rate with *Polyphemus* at a prey density of 20/jar, but no difference was found at a prey density of 120/jar. Attack probability was higher on *Eucyclops* at the high prey density, but no difference was found at the low prey

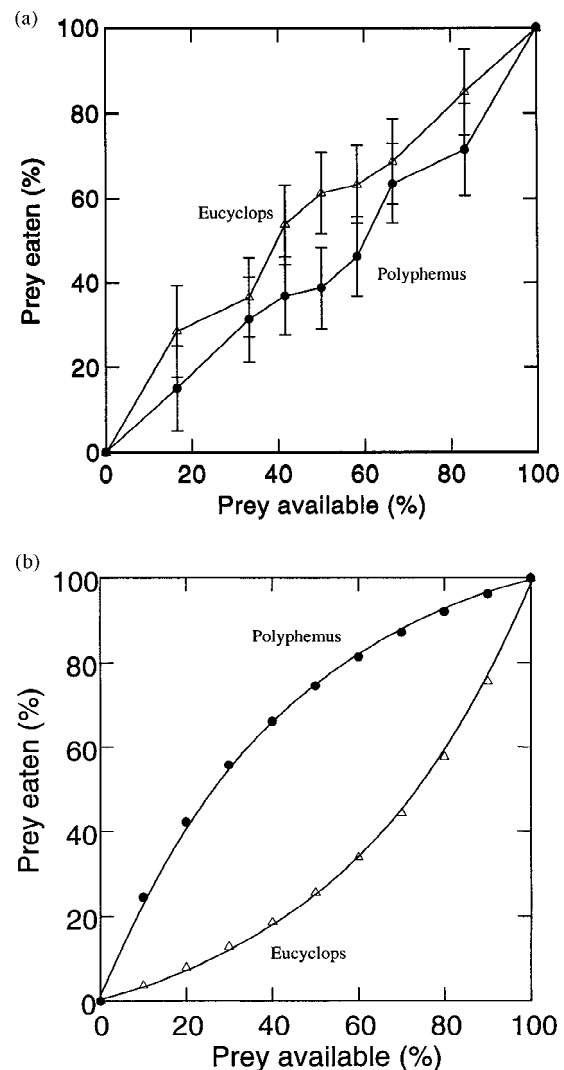


Figure 2. (a) Proportion of *Polyphemus pediculus* and *Eucyclops serrulatus* eaten by *Utricularia vulgaris* when presented at different relative proportions at a total density of 120 prey/jar. Error bars show standard error. (b) Predicted proportion of prey eaten based on the two prey functional response equation.

density. Capture success did not differ between the two prey at either prey density, and no differences in swimming speed were found at a prey density of 20/jar. *Eucyclops* spent 38% of the time resting on the plants and the glass jars. Since this behaviour was never observed in *Polyphemus* it resulted in a highly significant difference in resting time.

Calculated predation rate for the prey density of 20/jar was 60.0 for *Polyphemus* and 14.4 for *Eucyclops*, i.e. a 4.2 times higher predation rate on *Polyphemus*. Based on this, we expected more *Polyphemus*

Table 1. Mean values of observed behavioural variables for the two prey *Eucyclops serrulatus* and *Polyphemus pediculus* at densities of 20 and 120/jar when together with the predator *Utricularia vulgaris*. Numbers of replicates for both prey species, are given in brackets after the entries of the behavioural variables. Standard errors are given within brackets after the mean values. Significant *p*-values (Mann–Whitney *U*-test) are given in bold

	<i>Eucyclops</i>	<i>Polyphemus</i>	<i>p</i> -value
20 individuals			
Behavioural variable			
Encounter rate (10, 10)	1.80 (0.20)	4.70 (0.79)	0.009
Attack probability (10, 10)	0.40 (0.14)	0.55 (0.09)	0.355
Capture success (5, 9)	1.0 (0)	0.96 (0.04)	0.456
Swimming speed			
(mm/s) (12, 12)	2.49 (0.26)	3.46 (0.26)	0.386
Resting time (%) (12, 12)	38.2 (0.51)	0	<0.001
120 individuals			
Behavioural variable			
Encounter rate (10, 10)	4.7 (0.77)	4.4 (0.70)	0.760
Attack probability (10, 10)	0.59 (0.07)	0.21 (0.07)	0.002
Capture success (10, 6)	1.0 (0)	0.94 (0.05)	0.197

than *Eucyclops* to be captured in the functional response experiments at a density of 20 prey/ jar when prey were presented alone. The observed values in the single prey functional response experiments (23.2 for *Polyphemus* and 13.5 for *Eucyclops*) were in the same direction, but lower than predicted for *Polyphemus* (Figure 1a, b). In contrast, the calculated predation rate was 2.4 times lower on *Polyphemus* than on *Eucyclops* at a prey density of 120 prey/jar; 26.4 for *Polyphemus* and 64.8 for *Eucyclops*. Again, the predicted values were in the same direction, but the observed number of prey eaten in the single prey functional response experiments was lower than expected for *Eucyclops* (*Polyphemus* (31), *Eucyclops* (40)).

The result from the direct observation experiments suggests that more *Polyphemus* than *Eucyclops* should be consumed at low prey densities, and the reverse at high densities when the two prey are presented together. Hence, the observations at high prey density, but not those at low density agree with results observed in the two prey experiment. Given that 15 bladders were available the result from the high density was probably no effect of satiation. For example, only a mean number of 0.87 *Polyphemus* per hour was

captured during the one hour observation period (encounter rate \times attack probability \times capture success for 120 prey/jar, Table 1).

Functional response experiment from 1995 and 1997

The functional response curves were of a similar shape in the 1995/1997 experiment as in the 1999 experiment. The *Polyphemus* curve showed a steeper rise and an earlier levelling off than the *Eucyclops* curve (Figure 3a, b). Similarly, the 1995/1997 two-prey experiment showed that *Eucyclops* was selected over *Polyphemus* (Figure 3c).

Discussion

This study showed that when prey were presented together, *Eucyclops* was preferred over *Polyphemus*. This is in accordance with the field data on prey selection of *Utricularia vulgaris* found by Harms (1999). In contrast, the single prey functional response experiment and the direct observation experiments did not explain this pattern. Nevertheless, we will start our discussion with interpretation of the results and predictions made by the single prey experiments. We will then compare and discuss these in relation to the results from the two prey functional response experiment and the 1995/1997 experiment.

Single prey

When prey were presented alone, the functional response experiments showed a higher attack coefficient and a longer handling time coefficient with *Polyphemus* than with *Eucyclops*. This suggests that *Polyphemus* should be selected for at mixed prey densities (see results from the two prey functional response prediction, Figure 2b). The calculated predation rate predicted that more *Polyphemus* than *Eucyclops* would be caught at a prey density of 20/jar, but the reverse at a prey density of 120/jar. Because of the result from the high prey density we suggest that the direct observation experiments provided a slightly better, though not accurate, predictor for the two-prey outcome than the single prey functional response experiment. It could be argued that more *Polyphemus* should be eaten at a prey density of 120/jar since the functional response experiment estimated a higher attack rate on this prey. However, calculating attack rate from the direct observation experiments (number of prey captured/(time \times number of prey available)) suggests that attack rate

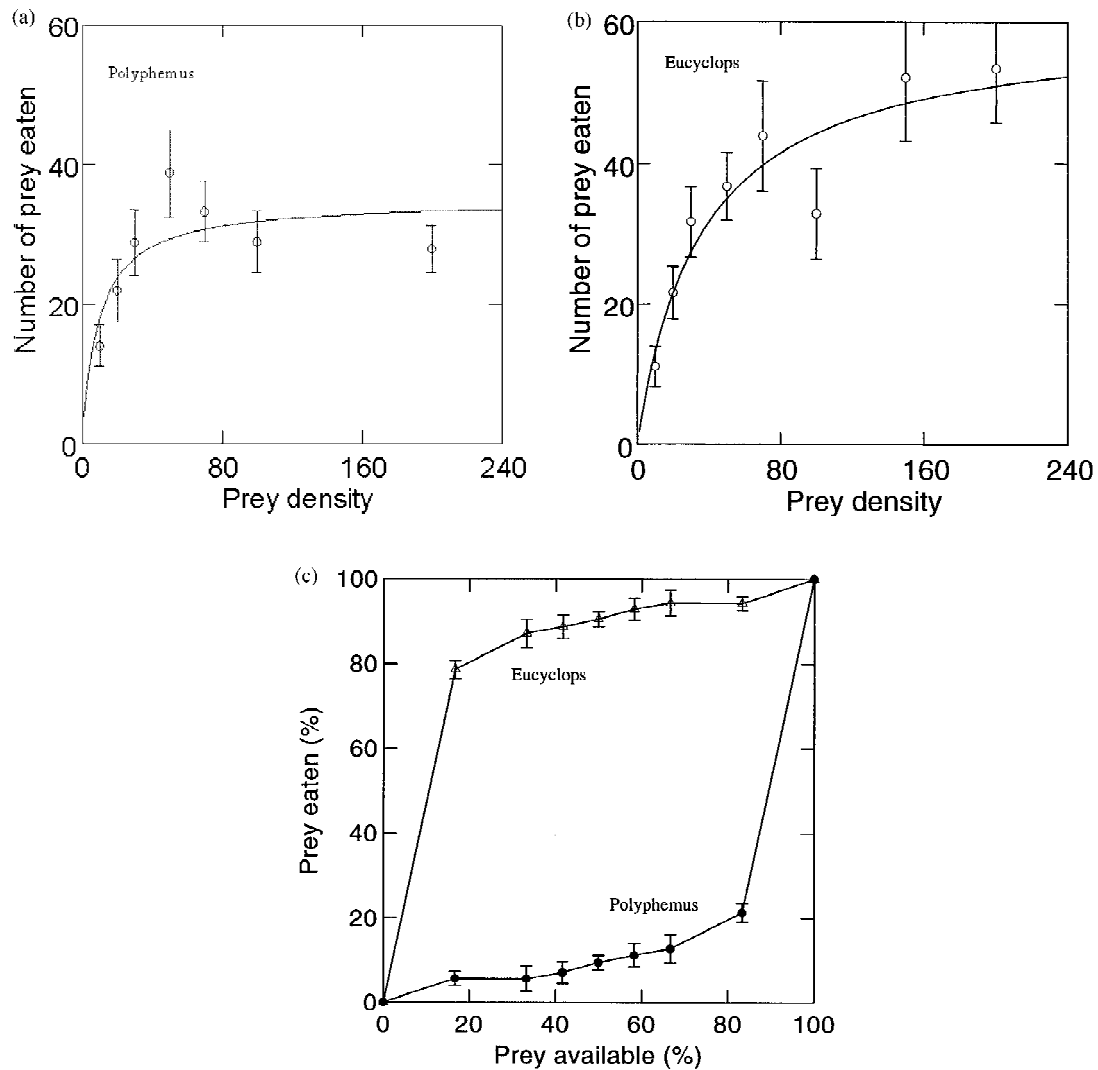


Figure 3. Functional response curve fits from 1995/97 of *Utricularia vulgaris* feeding on (a) *Polyphemus pediculus*, and (b) *Eucyclops serrulatus* in. Each point represents the mean number of prey eaten and error bars show S.E.; (c) proportion of *Polyphemus pediculus* and *Eucyclops serrulatus* eaten by *Utricularia vulgaris* when presented at different relative proportions at a total density of 120 prey/jar. Error bars show standard error.

does vary with prey density. For example, attack rate for *Polyphemus*, when calculated from the direct observation experiment, was 0.12 at a prey density of 20/jar and 0.009 at a prey density of 120/jar.

The calculated predation rate was higher than observed in the functional response experiments for both prey species at high densities. There could be several explanations for this discrepancy. First, the longer experimental period in the functional response should result in more bladders firing. Since it takes some time for bladders to 'recharge', the bladders cannot capture prey during this time. Hence, the time until a

bladder is 'recharged' will constrain prey capture. In contrast, during a short experimental period most of the bladders will be ready for prey capture. Second, the prey in the functional response were refilled to their initial densities every 2–6 h causing somewhat lower prey densities occasionally. In contrast prey were replaced immediately in the direct observation experiment. Consequently, realised mean prey density was somewhat higher in the direct observation experiment.

The higher handling time with *Polyphemus* in the functional response experiment was not due to prey

size, as both prey species were of about the same size. Other, not studied, differences in body shape or composition might make *Polyphemus* harder to digest. It seems more plausible, however, that a reduction in encounter rate on *Polyphemus* at higher prey densities could have caused a lower attack and capture rate. Swarm building behaviour of *Polyphemus* might have the potential to decrease encounter rate at higher prey densities. While *Polyphemus* may hide in vegetation (the bladderwort piece) at low densities, swarm building outside the vegetation should reduce their risk of encountering and being captured by *Utricularia* at higher densities. Hence, *Polyphemus*'s tendency to build swarms (Butorina, 1986) might explain the sudden levelling-off (longer handling time) and decline of the single-prey curve for *Polyphemus* at a prey density of 30/jar, because at these densities they might encounter the bladders less often. The direct observation studies give some support to this since an increase in prey density from 20 to 120/jar did not cause an increase in encounter rate. In contrast, such an increase was found in *Eucyclops* which did not seem to form swarms. We are currently investigating the consequences of swarm building for the shape of the functional response curve in *Polyphemus* (Harms in prep.).

Two prey

The two-prey experiment showed that a higher proportion of *Eucyclops* was preyed upon at all prey densities used. Hence, the information from the functional response experiment and the direct observation was not a good predictor for the two-prey system. We suggest that interactions between the prey could cause *Eucyclops* to be more vulnerable than suggested from the one prey functional response experiments. Such interaction modifications are common in aquatic systems (Huang & Sih, 1990; McNeely et al, 1990; Johansson, 1995). One possible mechanism could be that the presence of *Polyphemus* causes *Eucyclops* to spend more time resting on the bladderwort. Another could be that *Polyphemus* spends more time outside the vegetation (the bladderwort piece) when copepods are present. Nevertheless, we believe that the results from the functional response experiments are not experimental artefacts because both study years showed the same pattern with respect to functional response shapes.

Other studies that have tried to predict two prey functional responses from one prey functional responses have also failed to predict a correct response

for the two prey situation (Lawton et al., 1974; Akre & Johnson, 1979; Reynolds & Geddes, 1984; Spitze, 1985; Colton, 1987). We can only agree with Colton (1987) who states that a good understanding of the three species can only be achieved from experiments where all three species are present. The reason is that multi-species interactions very often lead to interactions between species not present in a two species system (Werner, 1992; Wootton, 1993).

To our knowledge, this is the first attempt to study the factor determining prey choice in a carnivorous plant. Based on field data, we predicted that *Eucyclops* should be chosen, and we found support for this. *Eucyclops*, generally, seems to be at a higher risk of being caught by bladderworts than *Polyphemus*. Whether this prey selection has the potential to influence the dynamics of the prey populations is currently under investigation.

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