

## Optimal foraging: the difficulty of exploiting different feeding strategies simultaneously

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**Summary.** The foraging efficiency of a visually feeding fish, perch (*Perca fluviatilis*) was studied on two prey species (*Daphnia magna* and *Chaoborus obscuripus*) presented either separately or combined. It is shown that when both prey species are present, the foraging efficiency of the predator is reduced. This is due to the predator's inability to simultaneously cope with prey species with different anti-predatory behaviour. In the mixed-meal experiment the predator captured both prey species in equal proportions in disagreement with optimal foraging models assuming that handling time and encounter rate for a prey species are independent of other prey species. The results are, however, in agreement with optimal foraging models assuming that handling time and encounter rate are influenced by short time learning.

Optimal foraging theory has during the last decade been regarded as a powerful instrument to predict foraging in animals (Pyke et al. 1979; Werner and Mittelbach 1981; Krebs and McCleery 1984). Even relatively simple foraging models have generally proven successful both in predicting prey selection of animals (Werner and Hall 1974; Charnov 1976; Krebs et al. 1977) and as an approach to predict resource partitioning between species and between size classes of the same species (Werner 1977; Werner and Hall 1977, 1979; Mittelbach 1981, 1983; Werner et al. 1983). Inclusion of non-profitable prey in the diet is, however, a general phenomenon. This discrepancy between predicted and observed prey utilization has been attributed to a number of factors such as learning (Elner and Hughes 1978; Hughes 1979; MacNair 1980, 1981; Werner et al. 1981) sampling (Werner et al. 1981; Krebs and McCleery 1984), prey crypticity and recognition (Elner and Hughes 1978; Hughes 1979; Erichsen et al. 1981; Houston et al. 1981; Getty and Krebs 1985), nutrient rather than energy constraints (Lacher et al. 1982; Krebs and McCleery 1984) and runs of bad luck (Elner and Hughes 1978) (for a review see Pyke 1984).

Most of the above studies have been based on experiments where the same species of prey has been used and only the size or crypticity of the prey was varied. In this study, I studied the prey selection and capture rate of a visually hunting predator encountering prey of different taxa and with different anti-predator behaviour. I tested whether the prey selection and capture rate were in agree-

ment with that predicted by the classical optimal foraging model developed by Charnov (1976) with special focus on if the presence of one prey species affected the handling time and encounter rate for the other prey species. The results are discussed in relation to theoretical developments of optimal foraging models including short time learning.

### Material and methods

#### *Species studied*

The predator used in the experiments was Eurasian perch (*Perca fluviatilis*). The crustacean zooplankton *Daphnia magna* and the phantom midge *Chaoborus obscuripus* were used as prey species. Sizes and weights of predator and preys are given in Table 1. Being a visual hunter (Disler and Smirnov 1977), perch will feed on zooplankton, macroinvertebrates and fish depending on size and resource availability (Thorpe 1977; Craig 1978; Persson 1983, 1986). Both *Daphnia* and *Chaoborus* are commonly found in the stomachs of perch.

#### *Experimental procedure*

The experiments were carried out in 200 l aquariums at a temperature of 18° C. Three principal experiments were carried out. In the first perch were fed *Daphnia* at a concentration of 2.0 ind l<sup>-1</sup>; in the second, *Chaoborus* at a concentration of 0.4 ind l<sup>-1</sup> and in the third, a mixture of *Daphnia* and *Chaoborus* (2.0 + 0.4 ind l<sup>-1</sup>). In the two first experiments the encounter rates and handling times for perch feeding on the two prey species separately were estimated. An expected return rate when feeding on both prey items simultaneously was then calculated from Charnov's (1976) model:

$$E/T = \frac{a_c E_c + a_d E_d}{1 + a_c H_c + a_d H_d} \quad (1)$$

where  $E/T$  is energy intake per unit time,  $a_c$  and  $a_d$  are the encounter rates for *Daphnia* and *Chaoborus*,  $E_d$  and  $E_c$  are the energy contents of *Daphnia* and *Chaoborus* and  $H_d$  and  $H_c$  are the handling times for *Daphnia* and *Chaoborus* respectively. The expected return rate for perch feeding on both prey species was compared with that when feeding on *Chaoborus* only, to evaluate whether it was expected that perch should include both prey species in the diet in the mixed-meal experiment. The comparison be-

**Table 1.** Sizes and weights of predator (mm and g wet weight) and prey (mm and mg ash-free dry weight) used in the experiments

	Perch		<i>Chaoborus</i>	<i>Daphnia</i>
	Mean	Range	Mean ±95% CL	Mean ±95% CL
Length	102	96–105	12.4±1.1	2.8 ±0.2
Weight	9.5	7.5–11.0	0.76±0.08	0.15±0.04

tween expected and observed diet in the mixed-meal experiment included a comparison of both prey selection and capture rate.

The perch were starved for 12 h prior to each experimental trial to standardize hunger. In all three experimental sets perch were trained for 9 days on the diet and concentration to avoid any long time learning effects (Werner et al. 1981). Before the trial started, the fish was confined to a smaller section of the aquarium by a partition. After this, the prey was introduced and the experiment was initiated by removing the partition and allowing the fish to feed. Depletion of resources during the trials was always less than 20%. Data recorded during the feeding experiments were swimming speed while feeding, number of attacks, number of successful attacks and, in the mixed-meal experiment, the species of prey captured. Encounter rate was operationally defined as the number of captures during the trial divided by total trial time minus time spent handling (Mittelbach 1981). As the handling times were too short to be accurately measured, these were estimated as the time/prey in experiments where perch were fed at an excess density of *Daphnia* and *Chaoborus* respectively (Werner 1977; Mittelbach 1981).

## Results

### Single meal experiment

The two prey species differ significantly with respect to their anti-predator behaviour. The anti-predator behaviour of *Daphnia* is restricted to the pre-predator attack phase (visibility, shape etc.) and a *Daphnia* once encountered will generally be captured by the fish if profitable. In contrast, *Chaoborus* may have a considerable success in evading an attack (O'Brien 1979). To circumvent the post-attack, anti-predator behaviour of *Chaoborus*, perch put in considerable effort pursuing each *Chaoborus*. Perch feeding on *Chaoborus* swam twice as fast as perch feeding on *Daphnia* (Table 2). This difference in swimming speed reflects the different feeding techniques for the two prey species.

The time/prey was similar for both prey species at the prey densities used in the experiments (Fig. 1, left). The encounter rates and handling times for *Daphnia* and *Chaoborus* respectively were also similar (Table 3). Due to the difference in weight, the capture rate (mg/s) was higher when feeding on *Chaoborus* than on *Daphnia* (Table 3).

### Mixed-meal experiment

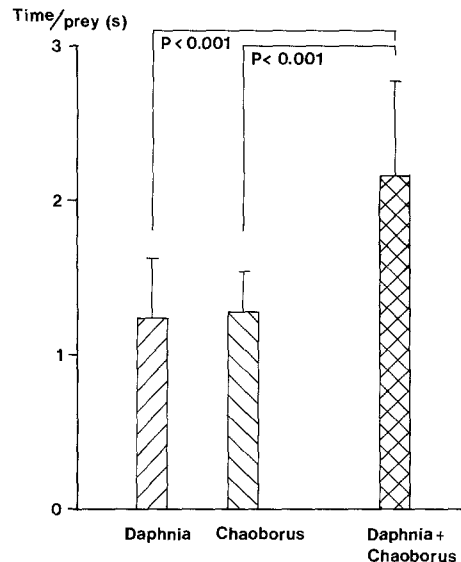
*Daphnia* were included in the diet in the mixed-meal experiment and both species of prey were consumed in equal proportions (percentage *Daphnia* of total = 52%). None of the perch specialized totally in either prey, although the

**Table 2.** Swimming speed of perch feeding on *Daphnia*, *Chaoborus* and *Daphnia* plus *Chaoborus*

	Swimming speed (cm/s)	
	Mean ± 95% CL	n
<i>Daphnia</i>	4.67 ± 0.45	54
<i>Chaoborus</i>	11.50 ± 1.42	30
<i>Chaoborus</i> + <i>Daphnia</i>	7.81 ± 2.51	15

**Table 3.** Capture rate (ind·s<sup>-1</sup> and mg·s<sup>-1</sup>) for perch feeding on *Daphnia* (2.0 ind·l<sup>-1</sup>), *Chaoborus* (0.4 ind·l<sup>-1</sup>) and *Chaoborus* plus *Daphnia* (2.0+0.4 ind·l<sup>-1</sup>). For the single prey experiments handling time (s) and encounter rate (ind·s<sup>-1</sup>) are also given

	Handling time ±1 SD (s)	Capture rate ±1 SD		Encounter rate ind·s <sup>-1</sup>	n
		ind·s <sup>-1</sup>	mg·s <sup>-1</sup>		
<i>Daphnia</i>	0.92 ± 0.1	0.81 ± 0.31	0.12 ± 0.05	1.41	15
<i>Chaoborus</i>	0.96 ± 0.1	0.78 ± 0.20	0.59 ± 0.15	1.36	15
<i>Daphnia</i> + <i>Chaoborus</i>		0.46 ± 0.28	0.21 ± 0.12		15

**Fig. 1.** Time/prey (s) for perch feeding on *Daphnia* (2.0 ind·l<sup>-1</sup>), *Chaoborus* (0.4 ind·l<sup>-1</sup>) and *Daphnia* and *Chaoborus* (2.0+0.4 ind·l<sup>-1</sup>). Means with 1 SD are given. *P* from Mann-Whitney twotailed test

proportion consumed by individual perch varied (range for *Daphnia*, percentage of total = 22–82%). The time/prey in this experiment was almost twice that for perch feeding on the prey species separately (Fig. 1, right). This in turn resulted in a lower capture rate (0.21 mg/s) (Table 3) than was theoretically expected (0.43 mg/s).

A one sample runs test showed that in 7 of the 15 trials, there was a significant difference ( $P < 0.05$ ) from random capture, i.e. the probability of the predator capturing a *Daphnia* after a *Chaoborus* and vice versa was significantly lower than 0.5. At least one miss on *Chaoborus* was recorded in more than 50% of the mixed-meal trials (Table 4). This contrasts to the experiment using only *Chaoborus* as

**Table 4.** Comparison of hunting success for *Chaoborus* when perch were fed *Chaoborus* only and when fed *Chaoborus* and *Daphnia*

	<i>Chaoborus</i>	<i>Chaoborus</i> + <i>Daphnia</i>	Significance of difference
Number of experiments where all attacks were successful	15 (n=15)	7 (n=15)	$P < 0.01$ (Fisher's test)
Number of successful attacks of total	225 (n=225)	136 (n=147)	$P < 0.001$ ( $X^2$ )

prey where no unsuccessful attack was recorded. The swimming rate of perch while feeding on the mixed-meal was intermediate between that when feeding on *Daphnia* and *Chaoborus* respectively (Table 2).

The expected capture rate (0.43 mg/s), using Charnov's (1976) model, for perch feeding on the mixture of *Daphnia* and *Chaoborus* (2.0+0.4 ind/l) was considerably lower than that for perch feeding solely on *Chaoborus* (Table 3). According to Charnov's model, perch should thus have excluded *Daphnia* from the diet in the mixed-meal experiment.

## Discussion

The perch were unable to simultaneously utilize feeding techniques that were maximally efficient for *Daphnia* and *Chaoborus* respectively. This resulted in a reduced capture rate and, for *Chaoborus* also in a decreased capture success. That an individual using a generalist strategy will have a lower maximum feeding efficiency compared to an individual using a specialist strategy has been suggested in other studies (Werner et al. 1981) and is consistent with the principle of allocation (Levins 1968).

Why did perch include *Daphnia* in their diet in the mixed-meal experiment? The prey species used in the experiments were both present in the water column to reduce any effects of crypticity (Erichsen et al. 1981; Houston et al. 1981) or travelling time between patches (Heller 1981). Long term learning effects (Werner et al. 1981) were also avoided in the present experiments. The significant difference from random capture in many trials in the mixed-meal experiment, however indicates that short time learning was present. It has been shown theoretically (McNair 1980, 1981) that short time learning will cause partial preferences and non profitable prey items to be included in the diet. McNair (1981) showed that training on encounter rate alone had different consequences for the optimal diet than training on handling or handling and encounter rate. In either case, however, an increase in total prey abundance (rule 3; McNair 1981) broadened the diet of the predator. In my study, the presence of two prey species simultaneously affected both the handling (pursuit, capture, swallowing) and encounter rate as is demonstrated by the lower capture success (Table 4) and the intermediate swimming speed (Table 2) in the mixed-meal experiment. In the experiment *Daphnia* and *Chaoborus* were captured in equal proportions. This suggests that the presence of two prey species affected handling and encounter rate combined similarly for both prey species as the handling time and encounter rate for *Daphnia* and those for *Chaoborus* were similar in the single meal experiments (Table 3).

Partial preferences have also been observed in previous laboratory studies (Werner and Hall 1974; Krebs et al. 1977; Elner and Hughes 1978). The predator, however, was much more likely to take the more profitable prey than the less profitable, in contrast to the result of my study where perch captured *Daphnia* and *Chaoborus* in equal proportions. This discrepancy could be due to the fact that by capturing prey of different sizes but of the same taxa, as was the case in the above studies, will allow the predator to use the same feeding technique. This is not possible with prey of different taxa and anti-predator behaviour (see swimming speeds while feeding; Table 2). As animals in nature encounter a large number of different prey species, we expect the discrepancy between the observed diet of animals in nature and that predicted by classical foraging models (i.e. Charnov's model) to be larger than the discrepancy between the optimal diet and the diet in laboratory experiments where prey only differed in size. The poor resemblance between the observed diet of animals in nature and the diet predicted by classical optimal foraging models (Schluter 1981) is thus not surprising but rather expected. In view of this, there seems to be few reasons to continue to compare the observed diet of animals in nature with that predicted by optimal foraging models that assumes handling time and encounter rate for a prey type to be independent of other prey types. Instead we should direct our interest towards experimental testing of models that are more realistic with respect to how animals judge their prey (i.e. McNair 1980, 1981).

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