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The relationship between foraging and shoal position in a mixed shoal of roach (*Rutilus rutilus*) and chub (*Leuciscus cephalus*): a field study

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Abstract. Feeding rates of mixed shoals of juvenile roach and chub were observed in a shallow stream near Cambridge (UK). Roach at the front of the shoal had significantly higher feeding rates than roach at the back and than chub in either front or back positions. Position in the shoal also had a significant effect on the kind of food consumed, with front roach feeding more on plankton and back roach more on bottom food. Altogether 36 fish from the stream were caught and marked. Half of these were deprived of food and the other half well-fed for 3 days in captivity. After release 36% of them joined their old shoal again. Individuals from the starved group occupied front positions significantly more often than well-fed fish, but after 2 days this difference disappeared.

Key words: Foraging in fish shoals – Position preferences – Nutritional state – Juvenile roach – Mixed shoaling

O'Connell (1972) was probably the first to point out a relationship between the position of a fish in a shoal and its food intake (see Lazzaro 1987 for a review). He observed that in northern anchovy (*Engraulis mordax*), a planktivorous species, individuals in the front positions of a shoal had considerably higher food intake rates than fish at the back. The advantage of front positions for planktonic feeders was confirmed by Eggers (1976) who studied the theoretical effects of shoaling on the rate of prey consumption. Further laboratory studies showed that the positioning behaviour of individual fish could be influenced by manipulating their nutritional state (Krause et al. 1992). Food-deprived roach (*Rutilus rutilus*) in shoals of 2 or 4 fish tended to take up front positions very frequently and apparently became shoal leaders. However, all these studies have been done under laboratory conditions and so far differential food intakes in shoals and the consequences for the positioning behaviour of individual fish have not been investigated in the wild.

In this field study I investigated the relationship between an individual's position in the shoal and its feeding rate and the kind of food consumed. In the second part I tested whether positioning behaviour could be manipulated experimentally by introducing fish of different hunger levels into the shoal.

Methods

The study area was a small stream (ca. 1.50 m wide and 10–15 cm deep) with fast-running (the speed of small particles of about 3 mm in size drifting on the surface or underwater was ca. 10 cm/s), very clear water near Newnham (Cambridge, UK). A shoal of about 35–45 roach (*Rutilus rutilus*) and about 15 chub (*Leuciscus cephalus*) and a varying number of minnows (*Phoxinus phoxinus*) (up to 10 individuals) was found almost every day in the same place in the middle of the stream, foraging where the currents were strongest and transported food particles which were picked up by the fish. All fish were juveniles ($\bar{X} \pm SD = 2.7 \pm 0.5$ cm). Observations were made from the river bank during the morning between 9.00 and 12.00 a.m. from 22 March to 25 June 1991 and 15 May to 5 June 1992. For data recording I used binoculars (8 × 21; Ross, London) watching the fish shoal from about 2 m away, which made accurate observations of individual fish possible. Even though the fish were timid and hid under vegetation when approached from the river bank they reappeared quickly and did not appear to be frightened by a motionless observer. Video recordings were used to estimate inter-individual distances and tailbeat frequencies and amplitudes. Scale objects were placed on the bottom of the stream to make exact measurements possible and the camera was positioned almost directly above the fish using a tripod which stood in the water.

Positioning behaviour

A number of roach could be identified individually by differences in individual colouration and marks on fins and distinctive marks on scales presumably left by ectoparasites. The positioning behaviour of these fish was investigated by recording the position (front, middle, back) of each focal fish 10 times (the length of each observation was 1 min) at intervals of 15–20 min in one session (one morning). This was continued until the focal fish disappeared from the shoal which gave an indication of the duration of the 'shoal membership time' for these individuals. Turnover of individuals in the shoal was believed to be frequent, perhaps because the stream was visited regularly by avian predators such as grey herons and kingfishers.

Feeding rates

Three different types of feeding behaviour were distinguished: bites directed at drift food on the surface (mainly insects that had fallen on the surface), at submerged drift food (a variety of animal and plant plankton) and at particles on the bottom (plant material, especially a fast growing species of algae which was very abundant). To investigate the relationship between shoal position and feeding rate I compared biting rates of fish in the first third (referred to as 'front fish') and the last third (referred to as 'back fish') of the shoal. The number of fish in each part was about 15–20 fish, depending on the total number of fish in the shoal on that day. Data were only collected for fish at the front and back of the shoal. Within the front and back parts of the shoal individual fish were randomly chosen and the number of bites recorded over 3 min for each focal fish. Fish that changed their position (into the middle of the shoal, for instance) during that period were disregarded, but this hardly ever occurred.

Experimental manipulation of hunger in roach

A total of 28 roach were caught from the above location at night. They were put into 60-1 tanks in the laboratory and given a rest of 3 days to recover from handling and transport and to get used to the conditions in captivity and artificial food. On the 3rd day, 14 fish were marked with a blue spot near the tail and 14 with a blue spot near the head. The former were not fed for the following 3 days and the latter fed in abundance on Tetramin dry food. On their 6th morning in captivity they were released into the stream at the same location where they were caught. Most of them rejoined the shoal within the following hour and the positioning behaviour of these fish was observed for the next 3 days, starting immediately after their release. Individuals were observed for 3-min periods from 9.00 to 12.00 a.m. as described above. The same procedure was repeated with another 12 fish, the only difference being that they were kept in holding tanks in the stream itself to save the fish the stress of transport to and from the laboratory.

For the marking procedure I used Alcyon Blue (DeJonge and Videler 1989) which was tested in a number of laboratory experiments before being applied to the test fish. The dye was injected subcutaneously and remained visible for several weeks or months, and did not seem to affect the performance of the fish. Benzocaine was used to anaesthetize the fish before the injection of the dye.

Results

Positioning behaviour of individuals

On the basis of video recordings a number of general parameters regarding the shoal could be estimated. The shape of the shoal was elliptical most of the time and the mean inter-individual distance between fish was 2.4 cm (SD = 0.64 cm; $n = 30$). Mean tailbeat frequency was about 1 beat/s ($n = 10$) for both roach and chub and mean tail beat amplitudes were 0.4 cm (SD = 0.08 cm; $n = 10$).

Altogether 29 roach were identified individually over the whole study period. Figure 1 shows that more than 50% of those fish disappeared from the shoal within 2–3 days. The longest time that an individual was observed in the shoal was 6 days. It is not known whether the disappearance of individuals was due to mortality or emigration. The two other nearest shoals of roach were about 50 m downstream and 100 m upstream. The shoal I observed never moved from its position in the middle of the stream for more than 1 or 2 m. When disturbed by a predator, fish took shelter under overhanging vegetation near the river bank and usually reappeared after 1–2 min.

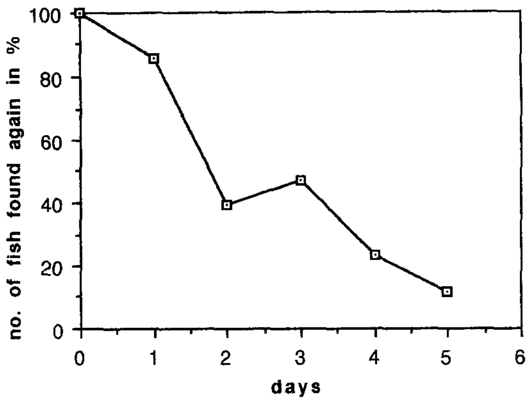

Fig. 1. Over the whole study period of 4 months (2 seasons) 29 fish were identified individually by natural scale marks. The data give an impression of their 'shoal membership time'. The slope of the graph does not decline continually because fish were sometimes absent from the shoal for a day but returned the next

A day-to-day transition matrix for these 29 individually recognizable roach shows that about 50% of the fish at the middle and back of the shoal changed their position from one day to the next. Only fish at the front had a stronger tendency to stay in that position (71.4%). Fish in the middle of the shoal moved equally often to the front and back and movements from front to back (and vice versa) occurred less often than movements from front to middle and back to middle positions (Fig. 2). Some fish showed strong preferences for certain parts of the shoal over 3 days or more, especially five individuals at the front that spent more than 90% time in that part of the shoal (Fig. 3). These data were not statistically analysed because of three problems. It is difficult to state a null hypothesis because the probability that a fish will be found in the front, middle or back is not simply one-third. In the case of 29 individually recognizable fish positioning is not independent. If, say, 15 of them occupy a front position, the others have

position at time t	position at time [t+1]: front	middle	back
front	71.4	19.1	9.5
middle	25	50	25
back	11.1	33.3	55.6

Fig. 2. First-order transition matrix showing the position of an individual at day ($t+1$) as a function of its position at day t, pooled for 29 roach (percentages). Entries in the main *diagonal* indicate constant positioning behaviour from one day to the next

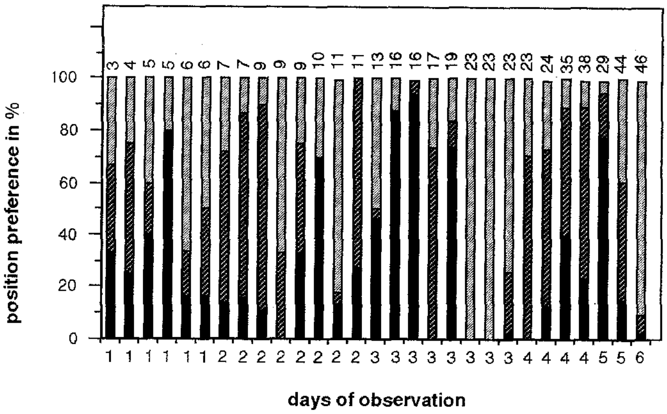

Fig. 3. The position preference in the field (front, *light shading*; middle, *medium shading*; back *solid bars*) of 29 roach that could be identified individually. Each *histogram* represents one individual. They were observed for 1-min periods at intervals of 20 min over a period of ca. 2 h every day. The *numbers* above the columns give the overall number of 1-min scores for each individual fish. Scores are not necessarily correlated with number of days of observation because some fish sometimes disappeared from the shoal for some hours or even days

to be in the middle or back by definition. Another problem is that some individuals were not sighted on certain days, but they may just have been overlooked. Lastly, sample size was small and the day-to-day transition matrix was biased towards individuals that stayed in the shoal for long periods and therefore scored more entries than others. However, despite these problems which complicate statistical analysis there are some clear trends.

Feeding rates

Total feeding rates (surface drift food, submerged drift food and bottom food combined) were higher for roach in the front than for roach in the back and higher for front roach than for front chub (Fig. 4). Roach and chub in the front mainly fed on submerged drift food compared to bottom and surface food whereas roach at the back showed roughly similar intake rates of submerged drift

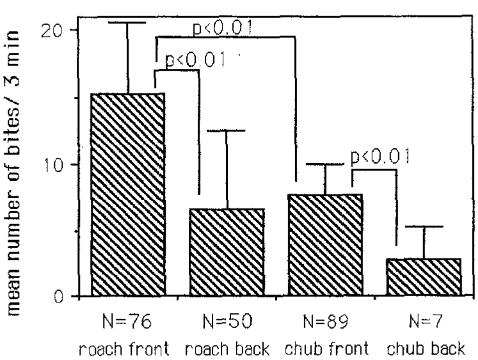

Fig. 4. Total feeding rates (surface drift food, submerged drift food and bottom food combined) of juvenile roach and chub compared for different locations in the shoal. *Error bars* denote standard deviations. Significance was tested by Mann-Whitney *U*-test, two-tailed (SPSS 1988) SPSS/PC+™V2.0 Base Manual, MJ Norusis/SPSS INC., Chicago 1988

food and bottom food. Surface food was almost completely absent in the diet of roach but made up a noticeable proportion for chub. Chub were rarely observed in back positions and the sample size for this group ($n = 7$) was so small that no statistical testing was done to compare with other groups (Fig. 5).

Competition for specific food particles was observed in ca. 5% of the bites and seemed to occur particularly often in the case of surface drift food which mainly consisted of relatively large insects such as Diptera.

Release experiment with roach

A total of 13 marked roach (7 starved, 6 well-fed) were rediscovered after release. Fish could be identified individually in addition to being allocated to the well-fed or the hungry group. On the 1st day of release food-deprived fish spent significantly more time in the front than well-fed conspecifics. On days 2 and 3 after release no differences in positioning between the two groups were observed (Fig. 6).

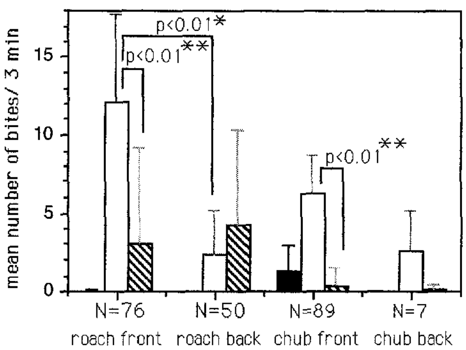

Fig. 5. Feeding rates of juvenile roach and chub compared for different types of food and different locations in the shoal. *Error bars* denote standard deviations. Significance was tested with (*) Mann-Whitney *U*-test, two-tailed, and (**) Wilcoxon Matched-Pairs Sign-Rank test (the data on consumption of drift food and bottom food forming a pair for each individual roach; SPSS 1988). *Solid bars*, surface food; *open bars*, drift food; *shaded bars*, bottom food

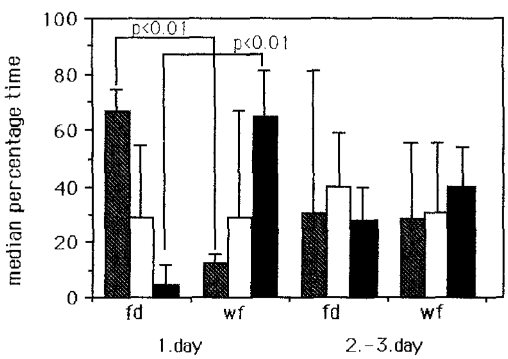

Fig. 6. A total of 36 roach were caught and marked, and half of them starved for 3 days and the other half well fed for 3 days. After release 7 food-deprived (fd) and 6 well-fed (wf) fish were found again. The position behaviour of these fish was observed for 3 days starting directly after release. *Error bars* denote quartiles. Significance was tested with Mann-Whitney *U*-test, two-tailed (SPSS 1988). *Shaded bars*, front; *open bars*, middle; *solid bars*, back

Discussion

Roach and chub

Chub were noticeably absent from back positions in the shoal for most of the time. Their total feeding rate was significantly lower than that of roach at the front. However, chub consumed most of the surface drift food which is probably the food source of the highest energetic value since it consists almost entirely of insects. Roach were found at all shoal positions about equally often and varied their diet composition with shoal position. Roach are known to be omnivorous and to respond quickly to short-term changes in the abundance of prey (Niederholzer and Hofer 1980). Competition between roach and chub, especially for surface drift food, was observed regularly which suggests that roach at the front might increase their proportion of surface drift food in the absence of chub.

Roach

This study shows that feeding rates of roach varied considerably across the shoal. However, from the recording of feeding rates alone it is not possible to decide whether prey density was lower at the back than at the front of the shoal. Indirect evidence for higher prey densities at front positions comes from the release experiment where the fish's nutritional state was manipulated. Hungry fish showed a strong preference for front positions directly after release, and this preference had disappeared 2 days later when fish had probably replenished their energy reserves. Studies on the same species in captivity showed that hungry fish had strong preferences for front positions and also that food intake was highest at the front provided that prey density was below a critical threshold (Krause et al. 1992).

Recent studies on juvenile cyprinids demonstrated that fish show an initial increase in O_2 consumption and spontaneous swimming activity in response to starvation (Wieser 1991; Wieser et al. 1988) which suggests a simple mechanism leading to the positioning of hungry fish at the front of the shoal.

However, it still remains to be explained why all fish do not try to get to the front. According to theory the benefits of front positions in terms of higher energy intakes may be offset by considerable costs which only some fish are willing to pay, so that others adopt positions which are suboptimal for foraging but better in other respects. It is interesting to note in this context that some roach at the front of the shoal had strong tendencies to stay in their part of the shoal for longer periods (in one case over a sustained period of 6 days). The connection between starvation and increase in metabolic activity suggests that front positions have higher costs in hydrodynamic terms, an issue which has been controversial over the last two decades (Weihs 1973; Partridge and Pitcher 1979; Fields 1991). It is also controversial whether front position in fish shoals are subject to higher predation risks (Hamilton 1971; McKaye and Oliver 1980; Parrish 1989; Parrish et al. 1989; Krause in press). However, for some social species of animals tradeoffs between higher feeding rates at the group periphery and lower predation risks in the group centre have been reported (Okamura 1986: mussels, *Mytilus edulis*; Rayor and Uetz 1990: colonial spiders, *Metepeira incrassata*).

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