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Fish in Larger Shoals Find Food Faster

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Summary. Experiments on shoaling cyprinids hunting for food on patches in tanks demonstrate an advantage of foraging in a group. Individual goldfish (*Carassius auratus*) and minnows (*Phoxinus phoxinus*) in a shoal of conspecifics located food more rapidly as shoal size increased from 2 to 20. Although shoaling minnows form polarised schools more readily than goldfish, which rarely do so, both species benefited from the trend of speedier food location with increasing group size.

Introduction

Although the benefits of being a member of a fish school in reducing the effectiveness of predator attack have been clearly demonstrated (Major 1978; Neill and Cullen 1974; Pitcher 1979a; Pitcher and Wyche 1982) there has been relatively little work on other functional aspects of shoaling. Some birds find food more efficiently as members of a flock (Krebs et al. 1972) and it has been thought that shoaling may confer similar advantages on fish (Bertram 1978; Curio 1976). This paper reports experiments which show that individual minnows and goldfish locate food more quickly with increasing shoal size and forms part of a wider experimental investigation of the costs and benefits of shoaling with respect to foraging efficiency. A shoal is defined here as a social group of fish (Pitcher 1979b).

Materials and Methods

Experiments were performed with 5–6 cm minnows and goldfish in order to contrast strong and weakly shoaling cyprinids, respectively.

Four minnows which had been individually marked on the fins with a jet inoculator (Pitcher and Kennedy 1977) and four goldfish with individually recognisable markings were selected. These test fish all had previous experience of foraging with various numbers of conspecifics on artificial food patches similar to those used in this experiment. In the goldfish work the patch consisted of three ice-cube trays with a total of 63 pots which were placed on the bottom of a 1 m × 40 cm × 50 cm deep experiment tank. The minnows were provided with one vertically-hung patch of similar total area comprising 84 pots each fitted with a lip to retain contents. All pots were filled with gravel and patches were cleaned between trials. The goldfish experiments represent pilot work on this topic; the minnow experiments took place at a later date with improved protocol. The vertically-hung food patch was designed to facilitate clear observation of the rapidly-moving minnows.

Goldfish lived in small 50 cm tanks and were carefully transferred to the experimental tank for each trial. In order to standardise handling, the fish were held in a small trough before being introduced to the tank (Kennedy and Pitcher 1975). Minnows lived in the 2 m × 70 cm × 70 cm deep experimental tank into which the patch was introduced for each trial.

During a trial, which lasted 10 min, a group of fish including one test individual searched for small flakes of dried protein fish food placed in the gravel in one randomly selected pot in the patch. The number of seconds the test fish spent searching before finding food was recorded. In goldfish, food searching behaviour was defined as the characteristic nosedown posture within 1 cm of the patch and in minnows, when the fish had placed its snout beyond the entrance of one of the pots.

Each goldfish was tested as a member of a shoal of 2, 4, and 6 fish and each minnow as a member of a shoal of 2, 4, 6, 12 and 20 fish. Four replicates of each test fish in each shoal size were carried out in randomised order to control for the effects of learning. Solitary fish were not included as controls because pilot work indicated that they behaved aberrently, as happens in other species of cyprinids (Pitcher 1979b). To control for hunger, all fish were fed equally about 6 h prior to a trial.

Results

Time spent foraging before food was found decreased as shoal size increased. This effect was true for both species (Fig. 1) and the difference between group sizes was significant (Table 1). There was no significant difference between times for individual test fish and no significant interaction between shoal size and individuals.

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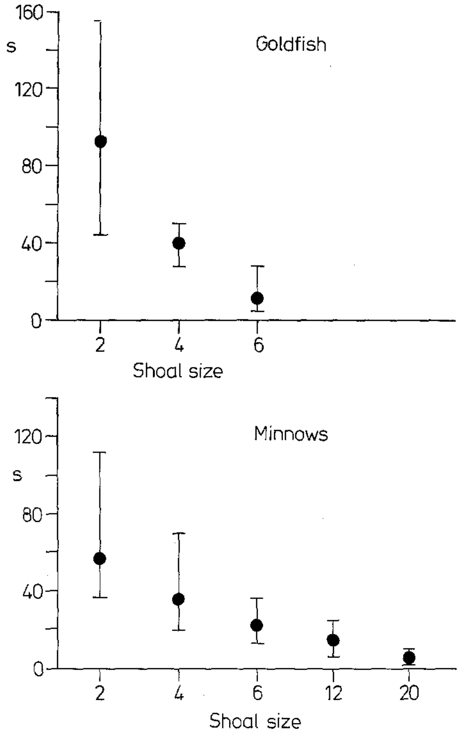

Fig. 1. The relationship between the number of seconds spent foraging before food was found and shoal size in minnows and goldfish. The median and quartiles (based on 16 replicates) are shown for each shoal size

Table 1. Results of the 2-way analysis of variance with replicates carried out on each species (4 individual fish with 4 replicates and 3 shoal sizes in goldfish, 5 shoal sizes in minnows). Data was log transformed to equalise variances

	Goldfish			Minnows		
	df	*F* ratio	*P*	*df*	*F* ratio	*P*
Between fish	3	1.408	>0.25 NS	3	0.849	>0.25 NS
Shoal size	2	6.003	<0.005**	4	23.277	<0.001***
Interaction	6	1.276	>0.25 NS	12	0.275	>0.75 NS

Minnows swam and darted more rapidly than goldfish and formed polarised school units much more frequently. In both species, smaller groups spent less time foraging, possibly because of greater nervousness and vigilance: the present analysis is based on foraging time. Similar but more variable results are given by total elapsed time.

Discussion

Since a known individual in a minnow or goldfish shoal takes less time to locate food with increasing shoal size we can conclude that the foraging fish must be aware that neighbours had found food. If this were not the case the speed of location of food would remain constant in all group sizes. As the shoal size increases the probability of one of its members finding food earlier also increases. In order that shoaling fish can take advantage of this increased searching ability they must be able to recognise a successful fish. Although behavioural cues have not been investigated quantitatively here, it is likely that in minnows the cessation of searching and concentration by a fish on one pot is a cue that food has been found: in addition feeding minnows often wriggled actively with their head in the pot. For goldfish, the more obvious chomping and chewing of flake food may provide the main cue. Once a feeding fish has been identified, other fish attempt to exploit the same source of food. We therefore think that changes in behaviour of foragers was the main cue for test fish in this experiment. Welty (1934) came to a similar general conclusion in experiments designed to demonstrate that speed of learning increased with group size in goldfish. (Our experiments controlled for learning however, and so Welty's specific finding does not apply here.)

However, although behavioural cues are paramount, alternative explanations may be considered. It might be argued that a fish finding food exposes it making it more obvious to others nearby. For the minnows, the design of the pots rules out this possibility, but it cannot be ruled out for the goldfish where a successful fish would occasionally drag a piece of food from the patch. It is also possible that a fish which has found food emits other cues, such as the sound of chewing, which alerts its fellows. In our tanks large air bubblers were employed to provide a 'white noise' background and would probably have masked such eating sounds. The smell of food could be important in guiding a fish to its exact location, perhaps along a concentration gradient. To be effective such an olfactory cue would have to enable the fish to pin-point food within one or two pots, and since such a cue would remain constant across the experiment it is difficult to see how smell alone could account for the differences between group sizes, unless it became more effective when food was initially disturbed by a finder. In fact, this effect is unlikely because searching fish were usually further apart than this.

Despite the differences in protocol between the experiments on the 2 species we think it is of interest that similar trends of speedier location of food with shoal size are observed in minnows and goldfish (a 2-way ANOVA gave no significant differences between species, although the test is invalid due to the different sizes of tank etc.). In both species there is a remarkable reduction in foraging time as the shoal increases from 2 to 6 fish. This implies that shoaling species which have only a weak tendency to form polarised synchronised schools are nevertheless at no disadvantage in exploiting the benefits of social behaviour. The separate definitions of shoaling (meaning a social group) and schooling (meaning a polarised shoal) introduced by Pitcher (1979b) are therefore useful in this respect.

Competition between fish was deliberately made negligible in these experiments, but could have been investigated by increasing the numbers of fish while decreasing the quantity of food and altering tank and patch dimensions. In the wild, the benefits of a very large shoal size, such as efficiency of locating food in an unpredictable habitat, must therefore be balanced by the costs to fish which are successful in finding food but cannot prevent their unsuccessful companions from exploiting it as well. Conversely, a very small shoal size bears costs not only in slower food location but also in less time devoted to food gathering because of vigilance. For a given species one might expect an optimal shoal size and this point is currently being investigated further (Pitcher 1980). Other benefits of shoal foraging such as circumventing territory-holding fish on coral reefs (Robertson et al. 1976), have not been investigated with a view to determining the optimal numbers in a shoal.

The transfer of information between fish results from their observation of one another's behaviour and can be termed *passive* information exchange. For example, Krebs et al. (1972) found that great tits (*Parus major*), trained to search for hidden food adapted their searching pattern according to the success or failure of other birds. This passive information exchange differs from the *active* information exchange shown for instance by honeybees (Heinrich 1978) or by nectar-feeding bats (Howell 1979). The foraging patterns of the cyprinid fish described here are less complex than those of higher mammals with well developed social behaviour. They do however provide an example of one simple way in which it is an advantage to forage as a member of a group.

References

Bertram BCR (1978) Living in groups: predators and prey. In: Krebs JR, Davies NB (eds) Behavioural ecology. Blackwell, Oxford, pp 64–96

Curio E (1976) The ethology of predation. Springer, Berlin Heidelberg New York

Heinrich B (1978) The economics of insect sociality. In: Krebs JR, Davies NB (eds) Behavioural ecology. Blackwell, Oxford, pp 97–128

Howell DJ (1979) Flock foraging in nectar-eating bats: advantages to the bats and to the host plants. Am Nat 114:23–49

Kennedy GJA, Pitcher TJ (1975) Experiments on homing in shoals of the European minnow. Trans Am Fish Soc 104:454–457

Krebs JR, MacRoberts MH, Cullen JM (1972) Flocking and feeding in the Great Tit, *Parus major* – an experimental study. Ibis 114:507–530

Major PF (1978) Predator-prey interactions in two schooling fishes, *Caranx ignobilis* and *Stolephorus purpureus*. Anim Behav 26:760–777

Neill SR StJ, Cullen JM (1974) Experiments on whether schooling by their prey affects the hunting behaviour of cephalopods and fish predators. J Zool (Lond) 172:549–569

Pitcher TJ (1979a) The role of schooling in fish capture. International Commission for the Exploration of the Sea. CM 1979/B:15:1–17

Pitcher TJ (1979b) Sensory information and the organisation of behaviour in a shoaling cyprinid. Anim Behav 27:126–149

Pitcher TJ (1980) Some ecological consequences of fish school volumes. Freshwater Biol 10:539–544

Pitcher TJ, Kennedy GJA (1977) The longevity and quality of fin marks made with a jet inoculator. Fish Mgmt 8:16–18

Pitcher TJ, Wyche C (1982) Predator-avoidance tactics of sand-eel schools: why schools may be reluctant to split. Environ Biol Fish (in press)

Robertson DR, Sweatman HPA, Fletcher EA, Cleland MG (1976) Schooling as a means of circumventing the territoriality of competitors. Ecology 57:1208–1220

Welty JC (1934) Experiments on group behaviour of fishes. Physiol Zool 7:185–128