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Some aspects of the schooling behaviour of fish

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Document Version

Publisher's PDF, also known as Version of record

Publication date:

1955

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Keenleyside, M. H. A. (1955). *Some aspects of the schooling behaviour of fish*. Martinus Nijhoff/Brill.

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self, has consummatory value. is threshold lowering. Preventing an animal reacting to less and more in the so-called "vacuum" when no external stimulus is applied to a constant stimulus (TINBERGEN) for the presence of internal stimulus to respond to a given stimulus in rudd (Table XVI) show that it does not affect the intensity of flocking together again. However, the need for it is clear.

Instinctive activities of the same kind and motivation of instinctive behaviour are "another pattern" (TINBERGEN, 1951). Schooling sticklebacks provide confirmation that feeding motivation is correlated with food, although they group more readily when food is present. Reproductive motivation leads to cessation of group formation. Mated females group less closely than unmated ones to closer schooling. The main difficulty is the lack of support for assigning specific functions which can be compared to the levels of motivation centres (see below).

The central nervous system of fish and the brain removal has led to cessation of schooling (WIEBALCK, 1937) and has had similar effects (BERWEIN, 1941). However, schooling in the form it takes among different species, is indirect and involves mechanisms in the central nervous system.

The social instinct in animals. "There are social instincts that are not part of some instinctive system of centres controlling behaviour when it strives to be in the neighbourhood when performing some, or all, of its activities" (MOYNIHAN and MOYNIHAN, 1951, p. 112). MOYNIHAN and MOYNIHAN (*Lonchura punctulata*) show appetitive behaviour when isolated and also that these

birds flock together when they are not engaged in any other activity. They consider, therefore, that there is a partially independent general social motivation in some birds, comparable to incubation motivation, in which the consummatory situation, as with flocking, consists of being in a certain relation to objects in the environment.

The question of whether there is a separate schooling instinct can be answered tentatively in the affirmative. Schooling behaviour of fish clearly has some of the characteristics of an instinctive activity, although evidence for the presence of some other features is inadequate. There is, however, no superordinated, mystical "social centre" which is at a higher level than other centres and which controls all other types of behaviour. Schooling should probably be placed at a low level in the organization of behaviour because, while some instincts (feeding, escape and others) influence and make use of schooling, the latter does not directly influence other instincts.

SUMMARY

The purpose of this paper is to present a hypothesis on the nature of the schooling behaviour of fish based on an ethological investigation of schooling. Recognizing the disadvantages of a limited amount of data and of the use of different species for different parts of the study, the following tentative picture is suggested.

Schooling may be considered an instinct as defined by TINBERGEN and is at a relatively low level in the hierarchical organization of behaviour. It has typical appetitive behaviour and a consummatory situation. A single fish separated from its school searches until perceiving a group of fish. It then approaches the group. In most cases vision is the only sense involved in this approach. If more detailed specific stimuli are then perceived (possibly through any of the sense organs) the fish ceases searching and remains with the school; if not, it soon leaves, and appetitive behaviour continues until the appropriate consummatory situation (being in a school of the same species) is attained. This hypothesis is based on the following points:

1. A school of fish is an aggregation formed when one fish reacts to others by remaining near them.
2. Typical features of *Gasterosteus aculeatus* and *Scardinius erythrophthalmus* schools are: performance of the same activity at the same time by all fish, lack of aggressiveness between members and equality of rank of all members.
3. Blinded *Scardinius* fail to show typical schooling but remain in an area where odours from other *Scardinius* can be detected. This response may keep schools of this species from scattering widely at night.
4. Visual perception of a school of fish releases approach in single *Scardinius* and *Pristella riddlei*.
5. When presented with two different-sized schools of their own species single *Gasterosteus*, *Scardinius* and *Leuciscus rutilus* prefer the larger to the smaller group.
6. A small *Gasterosteus* prefers six large to six small *Gasterosteus*.
7. A single *Gasterosteus* prefers a school of its own species to a school of *Rhodeus amarus* but shows no consistent preference when either *Pygosteus pungitius* or *Leuciscus* are presented together with *Gasterosteus*.
8. A single *Pristella* prefers a school of unoperated *Pristella* to a school with amputated dorsal fins. The dorsal fin with its conspicuous black patch is jerked more

rapidly after alarm. This structure and its special movement may be considered a social releaser.

9. Increased feeding motivation leads to limited dispersal of a school of *Gasterosteus*. The head-down feeding posture is a signal attracting others in a school to a source of food.

10. Alarm causes an increase in density of a school of *Gasterosteus*.

11. With increasing reproductive motivation male *Gasterosteus* cease schooling and try to hold territories. Females disperse to a limited extent.

ACKNOWLEDGEMENTS

This work was carried out during the two years the author was a guest at the Zoological Laboratory, The University of Groningen. The author wishes to express his sincere gratitude to Professor G. P. BAERENDS, Director of the laboratory, for making it possible for him to study there and for guidance, advice and criticisms during the course of the work.

The ready cooperation and assistance of the members of the scientific and technical staff of the laboratory are deeply appreciated.

Thanks are extended to Miss A. F. TUCKER for reading and criticizing parts of the manuscript and to Dr H. F. R. PRECHTL for translating the summary into German.

Two Canadian Government Overseas Scholarships, awarded annually by the Royal Society of Canada, are gratefully acknowledged. Without this financial assistance the author would have been unable to study in The Netherlands.

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