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Some aspects of the schooling behaviour of fish

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

instinctive activities of the same tivation of instinctive behaviour another pattern" (TINBERGEN, ooling sticklebacks provide con- feeding motivation is correlated r food, although they group more ductive motivation leads to ces- d females group less closely than o closer schooling. The main dif- he lack of support for assigning ich can be compared to the levels ntres (see below).

he central nervous system of fish brain removal has led to cessation 6; WIEBALCK, 1937) and has had 1936; BERWEIN, 1941). However, arying in the form it takes among r within one species, is indirect mechanisms in the central nervous

e social instinct in animals. "There that are not part of some instinct. of a system of centres controlling when it strives to be in the neigh- ies when performing some, or all, r, 1951, p. 112). MOYNIHAN and (Lonchura punctulata) show appe- k 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.

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