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A STUDY OF THE "KILLING PHENOMENON" IN ISOLATED GROUPS OF **ETHEOSTOMA SPECTABILE** (AGASSIZ)¹

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INTRODUCTION

Very little is known concerning the behavior of the Etheostomatinae (darters). The ethology of various other groups of fishes, e. g. Cichlidae, has been studied extensively by European workers (Baerends et al., 1950), but whether or not the results obtained by them are useful in an attempt to analyze the behavior patterns exhibited by darters is highly questionable.

The genus **Etheostoma** contains many species with a wide range of ethological responses, and even within a species, great variation in response to stimuli may be seen, due to differences in environment, genetics, or a combination of the two (Winn, 1958).

It was noted by Strawn (personal communication) that when an adult male and female orangethroat darter, **Etheostoma spectabile** (Agassiz), were placed together in a gallon jar, the male fish would eventually kill the female. Upon further investigation, it was found that this "killing phenomenon" occurred to a greater extent in some populations of **E. spectabile** than in others, and that it was also prevalent in other species of **Etheostoma**.

The object of this investigation was an attempt to characterize this behavior pattern in the orangethroat darter.

METHODS AND MATERIALS

The **E. spectabile** used in this study were obtained from the Little Wildcat tributary of the Illinois River, just below a spring. The average width of the stream was approximately four feet, with depths up to three feet. The stream bed was generally rocky with little siltation occurring, and in places, the channel was choked with watercress. There were few species of fish present, but many individuals. The other darters commonly present besides **E. spectabile** were **E. flabellare**, the fantail darter, and **E. punctulatum**, the stippled darter.

Most male fish used in this study yielded milt when light pressure was applied to the abdominal region. The females varied widely in their degrees of ripeness.

Several collecting trips were made between October 16, 1964, and May 3, 1965. The fish were captured with a ten foot seine of

¹This investigation was carried out in cooperation with the University of Arkansas and the National Science Foundation Undergraduate Research Participation Program under direction of Dr. Kirk Strawn.

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1/4 inch mesh. The greatest concentration of *E. spectabile* was found in pool areas in the fall and winter months, but in early spring more were located in the swift-flowing upstream areas where they bred in great numbers. The captured fish were placed in styrofoam containers for transport to the laboratory.

On arrival at the laboratory, the fish were divided as evenly as possible among three acclimation tanks at 11, 16, and 26°C. The darters were acclimated at these temperatures for at least two weeks before they were used in experiments. Chopped earthworms were fed to the fish once a day, with an occasional supplement of brine shrimp, and city water was added periodically. Tadpoles were placed in the acclimation tanks to act as scavengers.

Three tanks kept at 16, 21, and 26°C, were used for most experiments. Ten one-gallon, widemouth jars, which had been made translucent by sandblasting, were filled approximately 3/4 full of aged tap water and were floated in each tank. The sandblasting was done in order to prevent fish in adjacent jars from seeing each other. A layer of sand and an air stone were placed in the jars. Air stones were also placed in the tanks, among the jars to circulate water and maintain a constant temperature throughout the tank. Additional tests were run at the three previously mentioned experimental temperatures using completely transparent gallon jars.

During most of the tests, temperatures in the experimental tanks varied by no more than 0.1° from the desired levels; however, during one test involving fish acclimated at 26°, the temperature varied by as much as 6° for a short time.

Each test consisted of ten replicates of fish acclimated at one temperature (either 11, 16, or 26°C) and tested at one temperature (either 16, 21, or 26°C). Nine tests were performed using one male and one female per jar, three tests were performed using two females per jar, three tests were made using two males per jar, and three tests used one male and two females per jar. In addition to these tests, one test using one male and one female was performed in transparent glass jars. These fish were acclimated at 16° and were tested in 21° water. Additional experiments were performed at 21° using an entire tank for a single pair of darters.

Each testing period lasted from nine to twenty one days. The jars were checked for deaths at twelve hour intervals, and the fish in them were fed from two to five times during the testing period. Measurements of dead fish were made by means of dividers, and standard length was recorded in millimeters. The temperature in each test tank was recorded at twelve hour intervals.

Chi-square and t-tests for samples with unpaired numbers of observations and unequal variances were employed in statistical analysis of the data.

RESULTS AND DISCUSSION

Dead fish were characterized by shredded fins, chiefly the dorsal and caudal, and by open wounds on the body, especially in the caudal region. Many females were badly mutilated.

It was generally true that males which killed females were in bright breeding coloration and exhibited a ripe condition, whereas those that did not kill females were usually poorly colored, small, and not ripe. In a very few cases, males were killed by females, and in tests using individuals of the same sex a considerable number of kills resulted.

Experiments carried out in clear jars showed no significantly different results than those run in sandblasted jars.

Four tests were run in which one male and one female were placed by themselves in an experimental tank at 21°C. A female was never killed by a male in any of these tests, possibly because there was ample room for the female to escape the attacks of the male. However, when the tank was checked, the two fish were often very close to each other.

A definite correlation exists between difference in size and non-occurrence of killing. In other words, a ripe male is more likely to kill a female if she is closer to his size than if a large size difference exists between the two. A t-test which was significant at the .01 level of probability indicates that this is true.

In tests involving one male and two females per jar nineteen males killed females; of these, ten killed two females.

In all tests involving one male and one female per jar, 33 males killed females, while four females killed males. To be certain that this phenomenon involves males killing females almost entirely, rather than random numbers of kills between the sexes, a chi-square test of significance was performed. This test was highly significant, and supported the previous conclusion.

Any explanation of the "killing phenomenon" exhibited by the orangethroat darter would be highly tentative on the basis of the above data. It is known that individual aggressiveness, as shown by threatening or fighting, plays a central role in vertebrate societies and populations. Individual aggression in vertebrates is frequently expressed in two special forms: (1) defense of a given area, and (2) hierarchies of precedence within social groups (Collias, 1944).

Defense of a given area involves territoriality, which is generally concerned with breeding season. In territorial fishes, the male will defend his breeding area from the intrusions of all other males, but will be receptive to females. Dominance relations between the sexes must often be established for harmony, but excessive aggressiveness toward the opposite sex is probably an obstacle to mating. Courtship

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frequently serves to ameliorate the dominance relations and promote tranquility between the sexes. Therefore, male darters would not be expected to kill females when they are in breeding condition.

In nature, the breeding of *E. spectabile* occurs on riffles with many other darters around. The males migrate to the breeding riffles first, to be followed by the females later. When the female enters an area occupied by a male, he follows her and defends an area around her. This chase is usually terminated by the spawning act (Winn, 1958). In this study, the darters were subjected to confinement and environmental conditions entirely unlike those encountered in nature. It could be speculated that the killing of the female by the male is a displacement activity (Tinbergen and Iersel, 1947) resulting from frustration. Bastock et al. (1953) state that a displacement activity may be performed by an animal in which one drive is, at the same time, both activated and thwarted. A drive may be thwarted in several ways. The consummatory act may be physically prevented by some factor in the external environment, or possibly, the indispensable releasing stimuli may be entirely absent. The primary function of a displacement activity seems to be the relieving of surplus excitation in the central nervous system.

Braddock (1945) found that a male *Platyopocilus*, if frustrated in its attempt at copulation, may punish the female.

Winn (1958) states that the dominated school, the dominated territorial school, and the hierarchical school are not represented in the darters. Yet it seems probable that some sort of hierarchical arrangement occurs in *E. spectabile* since females were observed to kill males in rare instances, and, more commonly, to kill other females.

The difference in aggressive behavior of males and females is partly explainable by differences in sex hormones (Collias, 1944). Male pugnacity is probably not completely dependent upon male hormone from the gonads: this is more true of some species than others. Castrated male swordtails are said to maintain their social position from one to six and one half months. Treatment with androgens stimulated aggressive behavior in spayed and normal female swordtails (Noble and Borne, 1940).

Few morphological effects of sex hormones are so consistent in the vertebrate series as is this stimulation of aggressive behavior by androgens. However, in some species the importance of psychological and extra-gonadal factors may outweigh the usual effects of sex hormones.

SUMMARY

It was noted by Strawn (personal communication) that when an adult male and female orangethroat darter, *Etheostoma spectabile* (Agassiz), were placed together in a gallon jar, the male would eventually kill the female.

The object of this investigation was an attempt to characterize this "killing phenomenon" exhibited by the orangethroat darter.

It was concluded that in close confinement, males show a strong tendency to kill females, although a few females killed males. A correlation is indicated between degree of breeding condition of the male and the occurrence of killing.

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