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Recognition of individual black bullheads (Ictalurus melas) by chemoreception

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RECOGNITION OF INDIVIDUAL BLACK BULLHEADS

(*ICTALURUS MELAS*) BY CHEMORECEPTION

By

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CHAPTER I

INTRODUCTION

In the last fifteen years, there has been an increasing amount of interest in chemical communication between animals. Much of the research emphasis has been on insect pheromones, but chemical communicants of other animals are also being studied.

A pheromone is a chemical produced by one animal to communicate with another animal of the same species (Turner & Bagnara, 1971, p. 11). It may act as a relatively long-term, physiological primer or as an immediate behavioral releaser (Cheal & Sprott, 1971). As a releaser, it may serve the following functions: sex attraction, alarm-induction, trail-marking, territory establishment, and individual recognition (Gleason & Reynierse, 1969).

Among the invertebrates, insects have been shown to produce many diverse, highly specific pheromones (Wilson, 1963; Wilson & Bossert, 1963; Johnston, Moulton, & Turk, 1970; Wood, Silverstein, & Nakajima, 1970). Insect pheromones have served as a stimulus for much research because of the possible practical applications of the results. For example, attempts have been made to control pest populations with a combination of sex attractants and pesticides (Beroza, 1970; Wood, Silverstein, & Nakajima, 1970).

Recently some mammalian pheromones have been investigated, e.g. those of rabbits and mice. Rabbits mark their territories and their mates with a chin gland secretion (Mykytowycz, 1965). In mice, the scent of a male can synchronize estrus in a group of females and the odor of a strange male can cause abortion in a newly-conceived female (Gleason & Reynierse, 1969).

The pioneer work in fish pheromones was done by Karl von Frisch. In 1938 von Frisch discovered "schreckstoff" (fear substance) in minnows (von Frisch, 1938, 1941). A fear substance is a chemical released from the skin of a wounded or dead fish which alarms the nearby school and causes its members to flee. This response is called the "schreckreaktion" or fear reaction. Since the discovery of the fear reaction, other types of chemical communication in fish have been studied. Like the work with insects, this study of chemical communication in fish may have practical uses. Among the possible commercial uses of chemicals resembling natural products are shark repellents (Tester, 1963) and attractants for schools of edible fish (Tester, 1952; van Weel, 1952). Hasler's work on the homing of salmon (Hasler, 1957) may lead to a better understanding and more careful management of salmon runs. It may be possible to find "love-in" pheromones similar to those shown to cause aggregations in yellow bullheads (*Ictalurus natalis*) (Todd, 1971) which could be used to control hatchery fishes.

The importance of pheromones may be appreciated when it is realized that only birds and some other mammals match the visual dependency of man. Other animals rely heavily on smell, taste, touch, or audition for their perception of the world. The many experiments on sensory modalities other than sight can only serve to broaden man's understanding of the animal kingdom.

For a final practical consequence of studying pheromones, this greater understanding and awareness of the pervasive role of chemical perception should make laboratory studies of many kinds of animals more exact and significant.

This paper deals with one aspect of the study of chemical perception, the ability of black bullheads (Ictalurus melas), a species of catfish, to discriminate between individuals by means of odor or taste.

CHAPTER II

SURVEY OF THE LITERATURE

Uses of Chemical Recognition by Fish

While many fish species are visually oriented, there are also many which rely primarily on chemoreception and/or audition for their response to stimuli from the environment. Chemoreception refers to the processes of olfaction and gustation. Olfaction is the perception of chemicals by sensory cells in the olfactory epithelium which transmit the information to the brain via the olfactory (I) nerve. Gustation is the perception of chemicals by sensory cells in the taste buds which transmit information to the brain via the facial (VII), the glossopharyngeal (IX), and the vagus (X) nerves (Hara, 1971). By means of olfaction or gustation certain fish can distinguish members of their own species, predators, other species of fish, different plants, and a variety of food.

Recognition of Conspecifics

Among members of their own species, fish are capable of making many distinctions. In a series of reward and punishment conditioning experiments, Göz (1941) determined what distinctions minnows (*Phoxinus laevis*) could make utilizing chemical clues from other fish. Although training required many repetitions, the fish were ultimately able to distinguish between members of two different genera, between two different species, between a pair of like-sexed fish and a pair of opposite-sexed fish, and, finally, between two members of the same species.

Von Frisch's work on the fear substance in minnows (Phoxinus laevis) in 1938 and 1941 started a search for this pheromone among many fish species. Pfeiffer (1960, 1963) found that the ability to produce alarm substance is wide-spread throughout the Ostariophysi (an order which includes minnows and carps, loaches, catfishes, and characins), but it is not evident in other orders of fish. Upon perception of the alarm pheromone, Phoxinus laevis become agitated, form a group, and then flee. Other fish show a variety of responses to their alarm substances. Tench (Tinca vulgaris) and crucian carp (Carassius carassius) stir up the substrate and hide in the murky water. Gudgeons (Gobio fluviatilis) stop moving. Surface-swimming hatchet fish (Carnegiella strigata) dive and form schools. Among the fish shown not to produce schreckstoff are some characins, some poecilids, salmonids, coregonids, Gasterosteus, and Perca (Schutz, 1956).

Some fish can recognize their own young by chemical clues alone, especially fish which care for their young after hatching. Just before hatching and up to the wriggling stage, some cichlids (Cichlasoma nigrofasciatum and C. biocellatum) can distinguish their own young from young of the same or other species by chemical perception (Myrberg, 1966). After the wriggling stage, parents apparently use visual cues to identify their young. The blind goby (Typhlogobius californiensis) can also recognize its own young by chemoreception (MacGinitie, 1939) as can the jewel fish (Hemichromis bimaculatus) (Kühme, 1963).

Chemical perception may be used to identify the sex of a conspecific. The blind goby recognizes members of the same sex and its own mate by olfaction (MacGinitie, 1939). In some blennies, males can distinguish females by olfaction and in other blennies a non-mated ripe male is attracted to a chemical produced by a courting male (Losey, 1969). On the other hand, guppies, some sunfish, and jewel fish seem to rely almost exclusively on senses other than smell in recognizing mates (Breder, 1935; Noble, 1934; Noble & Curtis, 1939).

In fish with a fairly complex social structure, olfaction may function as a means of recognition of group members. Todd, Atema, and Bardach (1967) demonstrated that olfaction was significant in the social life of yellow bullheads.

The maintenance of fish schools may depend in some species on chemical recognition of its members. Hemmings (1963) believes a chemical is responsible for keeping the loach (Rutilus rutilus) in a loose school formation at night when vision is poor. Pheromones seem to help form schools in the blind cave fish of Mexico (Breder & Rasquin, 1943). Cahn and Shaw believe only sight has actually been proven to control fish schooling (Shaw, 1962; Cahn & Shaw, 1963).

Recognition of Predator

Predator-prey relationships among fishes appear to involve chemical recognition in at least two known cases. If water from a tank containing pike (Esox) is introduced to a tank of Phoxinus which have had prior experience with pike, the minnows become agitated and then immobile on the bottom of the tank, or they "freeze" without prior agitation (Göz, 1941). When Esox scent is introduced to the tank of the mosquitofish (Gambusia patruelis), the fish go into a frenzy and sometimes leap out of the tank, regardless of whether they have had prior experience with Esox (Göz, 1941).

Recognition of Another Species

In almost a symbiotic relationship between redfin shiners (Notropis umbratilis) and sunfish (Lepomis cyanellus), scent seems to be important. Hunter and Hasler (1965) demonstrated that redfin shiners spawn over sunfish nests more times than not and the attraction seems to be the scent of the sunfish milt and eggs. The advantage for the shiner seems to be the cleaning of its eggs by the sunfish.

Recognition of Non-Fish Scents

In addition to various pheromones and scents of differing fish species, other odors or tastes provide useful information to certain fish. Food and habitat smells are important to some species.

Hasler (1957) has shown that at least the final part of the journey of salmon returning to spawn is directed by scents from the stream where the salmon hatched. Hasler and Walker (1949) also demonstrated by means of conditioning experiments that bluntnose minnows could discriminate between various plants from their pond habitat.

Black bullheads can locate food by smell and taste (Bardach, Todd & Crickmer, 1967) and respond to various food odors with differing degrees of search activity (Olmsted, 1918). For example, they search most vigorously for bits of earthworm or liver and least vigorously for decaying meat.

Some fish establish symbiotic relationships with non-fish species and recognize their hosts by chemical perception. An example is the recognition of the host sea anemone (Stoichactis) by the damselfish (Amphiprion percula) (Davenport & Norris, 1958).

Bullheads as Experimental Animals in Chemoreception Research

Most vertebrates emphasize one or two senses for their perception of the world. When one sensory modality is poorly developed, damaged, or unusable, other senses function more acutely. Thus, visually-deficient animals rely more heavily on scent, taste, touch, or audition than do sighted animals. (Visual deficiency can result from an actual blindness or be due to habits of the animal, such as living in muddy water.) Hence, pheromones, which are perceived by odor or taste receptors, are utilized by the blind goby, the blind cavefish of Mexico, and loaches which school at night.

Catfish habits and neural anatomy suggest visual deficiency. These fish live primarily in dark, murky water, on or near the bottom, and are most active at night (Trautman, 1957). Vision under these conditions would not be a useful sense. Also, the large olfactory bulbs of catfish are located near the complex nasal apparatus and their optic lobes are small and inconspicuous (Atema, Todd, & Bardach, 1969). The whole body of a catfish is covered with taste buds, which are most concentrated on the barbels around the mouth and on the dorsal surface of the body (Bardach, Todd, & Crickmer, 1967). The nasal apparatus has anterior and posterior openings and many epithelial folds over which water passes (Kleerekoper, 1969). All of these anatomical features suggest a significant use of olfaction and taste and little use of sight by catfish. Experiments have shown that catfish do utilize smell and taste almost exclusively in their perception of their surroundings. Tests have been performed on both blinded and intact animals to show that the test fish could perform the same regardless of the state of their vision.

In experiments with brown bullheads (Ictalurus nebulosus), Parker (1910) suspended two cheesecloth bags into tanks containing a pair of fish. The dummy bag held nothing and the test bag held minced earthworms. The fish would pull at the worm bag and ignore the dummy bag. If the barbels, which contain hundreds of taste buds, were ablated, the fish would still pull at the worm bag. However, if the olfactory tract was cut, the fish would ignore both bags. This seems to suggest that scent is the means by which the bullhead locates its food; however,cutting off the barbels does not destroy the taste buds in the pharynx nor the ones on the surface of the body.

Olmsted (1918) also studied food perception by the brown bullhead. He suspended two cheesecloth bags in the fish tanks, one containing a stone wrapped in cotton and the other containing various food substances wrapped in cotton. Of all the organic materials tested, earthworm and liver were the most stimulating. All decayed flesh, except earthworm, elicited little response. If the barbels were removed from the fish, the animals found the food bag only slightly less rapidly than intact fish. If the anterior nares were sewn shut, there was no searching for the food. Again, this seems to suggest the predominance of the use of olfaction for finding food, with the same reservation as above.

In 1967, Bardach, Todd, and Crickmer investigated location of food by brown and yellow bullheads. The fish were placed in a large tank into which an odorous liquid, such as worm extract, was released. The path of the fish to this "food" was recorded. The fish swam directly towards the "cloud" of scent and performed figure-eights within the cloud until the exact odor source was located. Both barbelless fish and fish with the nares cauterized acted in this manner. The cauterized fish did not move their heads from side-to-side before beginning the search for food, but in other respects their behavior matched that of barbelless or intact fish. A change in search behavior occurred when all the barbels, nares, and taste buds on one side (except the taste buds in the pharynx) were destroyed. Under these conditions, the fish made several small circles towards their intact sides along their path towards the scent cloud. These experiments suggest that olfaction and taste work together in the perception and location of food, since the fish searches normally when either sense organ is removed, but not when both are destroyed.

Chemical perception may be involved in the reproductive behavior of catfish. Both blinded and intact male channel catfish (*Ictalurus* *punctatus*) responded to the scent of a ripe female of the same species by searching around a point source (Timms & Kleerekoper, 1972).

Bowen (1931) attempted to find evidence for a pheromone responsible for maintaining the massive schools of black bullhead young. Transferring the water of one school's tank to an experimental tank containing one fish produced no significant response by the test fish. After further experimentation, Bowen concluded that touch, sight, and pressure were the parameters controlling the schooling of juvenile black bullheads.

Yellow bullheads have been shown to have complex social behavior in the laboratory (Todd, Atema & Bardach, 1967; Todd, 1968; Todd, 1971). They maintain distinct territories usually in areas of the tank containing a hiding place of some sort, and they establish a dominant-subordinate relationship with one fish dominant over the other tank members. Aggression towards strangers is usually violent, but once dominance and subordinance are established only minor, nonviolent skirmishes persist. Destroying the nares of yellow bullheads completely breaks down the order normally maintained in a community tank. The bullheads fight continually and viciously with no establishment of social hierarchies and little recognition of size of other fish; small fish may attack much larger fish (Bardach & Todd, 1970).

Several experiments were performed with yellow bullheads to illuminate the exact role of olfaction in their social behavior (Todd, Atema & Bardach, 1967; Bardach & Todd, 1970). In the first set of experiments, a fish was placed in an experimental tank and presented alternately with the odors of two other bullheads. With one odor, the fish was rewarded with food; with the other odor, the fish was punished with an electric shock. After much training, the fish behaviorally demonstrated an ability to discriminate between odors of two other bullheads. Thus, olfaction can be utilized to recognize other yellow bullheads.

Adult yellow bullheads occasionally form large aggregations. If several newly-trapped bullheads were placed together in a tank, they formed an aggregation. Water passed from the tank of such a group to the tank of two pugnacious territorial yellow bullheads caused the two fish to cease fighting and co-exist, sometimes even in the same hiding place. If left together without the "love-in" water (so named by Todd, 1971), the two fish resumed their battles to establish territories. Todd believes there may be a scent produced by the group of fish which induces aggregation behavior in other bullheads.

A third set of experiments was designed to test the role of olfaction in dominant-subordinate relationships (Todd, 1968; Bardach & Todd, 1970). A pair of yellow bullheads was placed in a tank and allowed to fight until one fish was dominant and the other subordinate. They were then returned to their respective home tanks and twenty-four hours later the water of each was added to the tank of the other fish. In addition, each fish had the water of a "stranger" fish (one with which neither had been in contact) added to its tank. The reactions of the fish were dependent on which water was added. The dominant fish gaped at and searched vigorously for the subordinate's water. The subordinate fish fled from the water of a dominant. Both subordinates and dominants searched throughout the tanks for the stranger water. These results indicate that yellow bullheads can perceive a chemical produced by another bullhead and thereby determine the dominant-subordinate relationship to the test fish.

That this "status" chemical can change was demonstrated when a formerly dominant test fish was beaten by another fish. When the test fish was re-matched with its original partner, it was attacked as though it were a fish of equal or inferior status and not the dominant fish (Bardach & Todd, 1970). Recognition of water from another fish's tank seems to persist for several weeks (Todd, 1971). In one case, a large bullhead jumped into a neighboring tank and so frightened the occupants that all but two leaped from the tank and were killed in the fall to the floor. The surviving fish would quickly flee and hide from the water of the aggressive fish's tank up to four months later, even without coming in contact again with this fish.

Because black bullheads are closely related to yellow bullheads and because preliminary observations demonstrated that their behaviors are similar, it was postulated that black bullheads may also employ pheromones in the maintenance of dominant-subordinate relationships. If, indeed, the black bullheads showed definite dominant-subordinate relationships when paired, the behavior exhibited in the establishment of this relationship could be used as evidence of recognition of a combatant if it appeared when dominant water was added to a subordinate's tank and vice versa.

CHAPTER III

MATERIALS AND METHODS

Tank Set-Up

Fish tanks were set up in the Aquarium Room, Health Sciences Building, University of Montana. Windows were covered with black plastic to prevent excessive algal growth in the aquaria. The fluorescent lights were not maintained on a set photoperiod.

Individual fish were kept in steel-framed aquaria with glass walls and bottoms. Two of these 84-liter tanks were filled with water and had the same filter arrangement as the others but held no fish. They were maintained for isolation of sick fish and for study of the movement of dye in the water. Two tanks contained more than one fish. One of these, the upper holding tank, contained five fish and was a 255-liter aquarium. The lower holding tank of 122-liter capacity held four adult fish and an inch-long juvenile.

The 84-liter aquaria were arranged with two tanks on top and two tanks on the bottom of steel racks. The upper and holding tanks were also kept on a steel rack. (See Fig. 1 for the arrangement of the tanks.)

Black plastic was taped on the ends of all the individual tanks. The tanks rested on wooden blocks on the racks, and the sides of the tanks did not touch. Thus, the fish were isolated both visually and physically from one another.

Each 84-liter aquarium contained two plastic undergravel filters

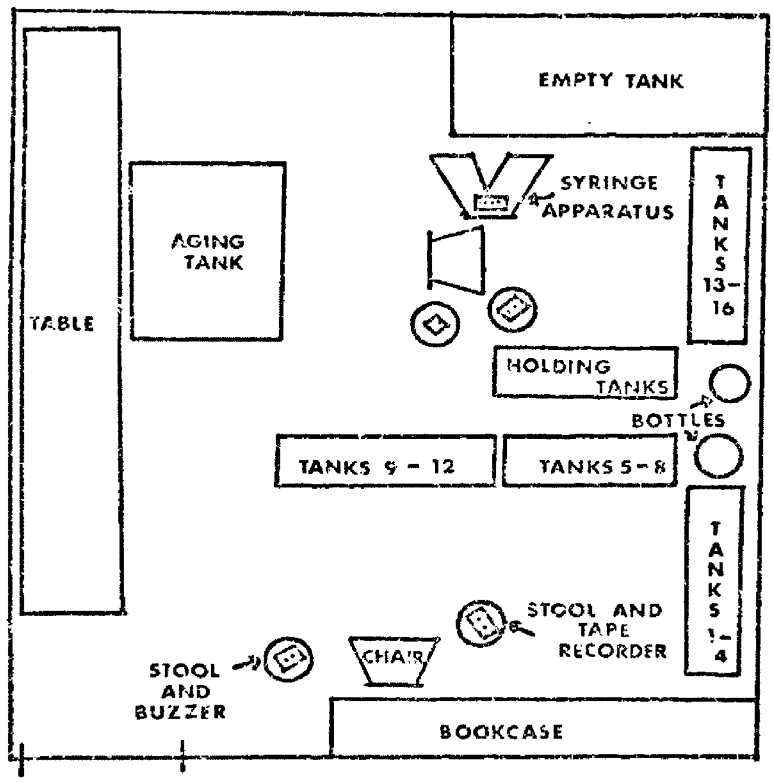


FIG. 1 Arrangement in Aquarium Room

with air input and output tubes in the two back corners (Fig. 2). Also in each tank was a plastic underwater filter. Each underwater filter was filled approximately one-fourth full of charcoal and three-fourths full of polyester quilt batting. The undergravel filters were first covered with nylon screen to prevent clogging and then with a one-inch layer of pea-sized gravel.

Air from jets in the building was first cleaned by passing through a water jar before entering the tubing to each tank.

No snails or algae eaters were utilized to keep the tanks clean because the presence of these animals would have heterotypically conditioned the water.

Water was aged in a fiberglass tank at least 48 hours before being used to allow any chlorine present to evaporate.

Fish Maintenance

Bullheads were captured with a seine in a pond near St. Ignatius, Montana. Eight bullheads were caught July 17, 1973; fifteen were caught September 8, 1973; and thirteen were caught October 20, 1973. The fish were transported to the University in plastic bags filled with water from the home pond. Each bag was aerated briefly before being tied shut.

Before placement in the aquaria, the first batch of fish received a ten-minute salt bath in 2% NaCl solution to loosen existing leeches and to try to alleviate a possibly disease-caused reddening of the fins. All but two of these fish died. A slight fungal growth on the top of the head was the only indication of disease.

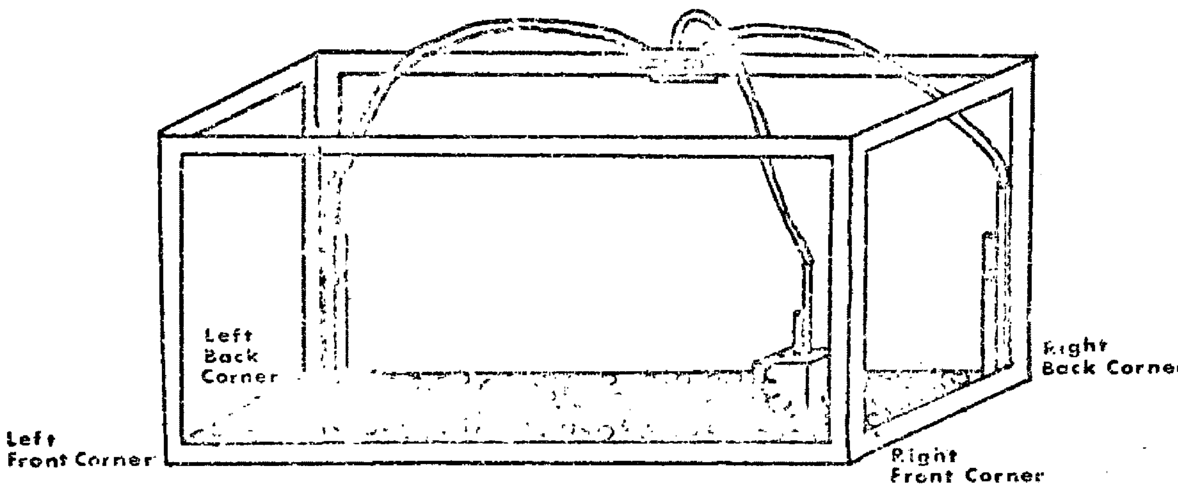


FIG. 2 Aquarium Arrangement

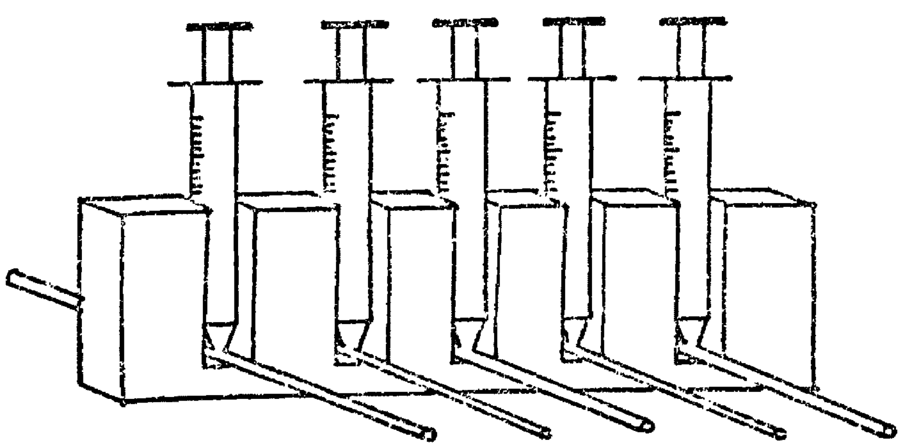


FIG. 3 Syringe Apparatus

Subsequently, newly-caught fish were not given a salt bath, but the leeches were removed with a hemostat. Pea-sized gravel replaced sand which had formerly been used and aged rather than flowing water was used. Five of the fish in the later collections died.

Fungal and algal blooms were controlled largely by restricting the amount of food and reducing the light.

Some disease and damage was evident occasionally among the fish. The red-fin condition noted among incoming fish disappeared for the most part after the fish were kept in isolation for several days. The broken or bent barbels seen on newly caught fish gradually healed and regenerated to slightly smaller than original size. The fish were not treated chemically for disease..

Each bullhead was fed 0.5 gm. of dry, crumb-sized trout food at 9:00 A.M. each day. The animals ate readily and searched the water surface for floating food.

The polyester batting in the underwater filters was changed once every fourteen days. Each time the batting was changed, the charcoal was rinsed and the filter cleaned. The algae on the sides of the tank was removed once a month or as needed.

The lengths of the fish from nose to end of tail were recorded on November 5, 1973, and March 29, 1974. On November 5, the lengths ranged from 13.5 cm. to 18.0 cm., with an average of 15.8 cm. On March 29, the lengths ranged from 16.0 cm. to 19.5 cm., with an average of 18.2 cm. (Table 1). On March 29, the weights were also taken. The weights ranged from 56.5 gm. to 105.0 gm., with an average of 89.2 gm. (Table 1).

TABLE 1

SIZE OF INDIVIDUAL FISH

Fish	Length (cm.) Nov. 5, 1973	Length (cm.) Mar. 29, 1974	Weight (gm.) Mar. 29, 1974
1	17.0	18.5	89.2
3	14.0	17.0	85.0
4	15.5	17.5	86.4
5	16.0	18.0	83.0
6	16.0	18.5	104.7
7	16.0	19.5	104.4
8	16.5	18.0	95.6
10	13.5	16.0	56.5
11	15.0	17.5	69.2
12	18.0	19.5	105.0
13	....	18.5	94.1
14	....	18.5	83.0
15	....	18.5	95.8
16	....	19.0	96.2

NOTE: Fishes 13-16 not used Dec., 1973.

Statistical References

Analysis of Variance (Guenther, 1964) was used as a reference for the statistical tests discussed in Section IV.

Experimental Procedures

Preliminary Experiments

The first experiments were pairings of test fish to establish dominance and subordinance in each pair of fish. Fourteen fish were isolated at least a month before any pairings were undertaken.

The length of each pair was matched as closely as possible. There was no obvious external characteristic which would allow sexing of the fish, so sex did not enter into the choosing of the pairs. Each bullhead possessed some identifying characteristic such as spots on the body or a slightly ragged tail which served to distinguish him from the other bullheads. These characteristics were used to recognize individual fish.

In the first set of experiments, each match was conducted four days apart to minimize stress on the snimals. Each pair was subjected to three matches. If the fish tested were Fish A and Fish B, the three matches would be as follows: A put into B's tank; B put into A's tank; and A and B both put into a neutral tank where no fish lived. The length of the combats varied, ranging from two minutes to sixteen minutes forty seconds, with an average of ten minutes twenty seconds. The fish were left together until one was clearly subordinate to the other. (In the two minute trial, the dominant pushed the submissive from beneath so strongly that the submissive was pushed out of the water. The submissive was then knocked violently into the gravel. Because the submissive appeared in danger and because there was no doubt as to which was dominant, the fish were returned to their own tanks.) These three matches were conducted to determine if a dominant-subordinate relationship depended upon where the fish were paired (in their own tanks, in other fish's tanks, or in neutral tanks) or if this relationship remained the same wherever the combats occurred.

The bullheads were transferred by means of a nylon net. When both fish were moved, two nets were used and the fish were placed simultaneously in the neutral tank.

Observations on the matches were recorded with a portable tape recorder. The activities of the fish and their positions in the tank during the entire experiment were noted. Following each experiment, the recorded data were transcribed. Time was measured by an electric buzzer set to ring every ten seconds. During the transcription, a mark was made whenever the buzzer sounded.

First Water Experiments

The first set of water experiments was performed in December, 1973. There was a four day lapse between the pairing experiments and the first part of the water experiments, and between each water experiment.

Each experimental bullhead was tested with four waters, added in random order: water from the tank of the other member of the pair; water from a stranger fish, i.e. a fish with which the test fish had not been in contact; water from the test animal's own tank; and water from the aging tank. The water from the other pair member was added to see if dominant fish would react the same to subordinate's water as subordinates reacted to dominant's water. The stranger water was added to see if the test fish reacted the same as they did to their partner's water. The "stranger" was a subordinate fish. The water from the fish's own tank was used to see if the fish reacted the same to their own water as they did to other fish waters. Finally, the aged water was added to compare the reaction to water which had had no contact with fish.

The smallest amount of test water to evoke a response in the first test fish was 250 ml. This amount was added to the right front corner of each tank for each trial.

Test water was added by means of a syringe apparatus (Fig. 3). The four waters were collected just before the experiments in 1,000 ml. flasks. Polyethylene tubing connected the flasks to the syringe apparatus. Each syringe was fitted with a one-way valve that allowed the water from the flasks to be drawn up and pushed out in one direction. The output valves were connected by tubing to the test tank. The apparatus was rinsed with tap water following each set of experiments.

Immediately prior to each experiment, the behavior of the test fish was observed and recorded for five minutes. Then the water was added with as little movement as possible. The time period for adding the water ranged from thirty seconds to four minutes, with an average of one minute twenty seconds. The behavior and position of the fish were recorded while the water was added and for ten minutes following.

Blue ink was added to a tank without fish to trace flow and rate of diffusion. The initial concentration of ink was in the right front corner where the fluid was added. The path of the ink concentrated slightly along the surface towards the upswelling current of the left and right undergravel filters for the first few seconds, then gradually spread evenly throughout the entire tank, diffusing outwards from the right front corner. The ink was homogeneously distributed throughout the tank in two minutes.

Second Water Experiments

The second set of water experiments was conducted in March, 1974.

In these tests, the fish were paired with the same partner as before, but only once in a neutral tank. Again the fish were allowed to fight until dominance was established. The times together ranged from twenty to sixty minutes, averaging 39 minutes.

The day following the match, each member of the pair was tested with its own water and with its partner's water. The next day each was tested with aged water and with the stranger water.

The amount of water added during each trial was increased to 2,000 ml. and the tanks were lowered to two-thirds full. Thus, if a chemical were present in the fish waters. it would be in greater concentration and elicit a potentially greater reaction from the fish than that observed during the first set of experiments.

The underwater filter was moved to the right front corner, beneath where the test water was introduced. The water was thus added to the bubbles above the filter to make the entry of the test water less conspicuous.

The fish were observed quietly without being recorded for at least five minutes at the start of an experiment. When the test animal appeared to be engaging in its normal behavior, the experimental observation was begun. Behavior and position were recorded for five minutes. Water was added for five minutes and behavior was recorded as was the behavior for fifteen minutes after the addition of water.

In these tests, the diffusion pattern of ink appeared to be the same as in the first test.

Sexing

In June, 1974, the 14 test fish were sexed. The ovaries were approximately 3 cm. long, 1 cm. thick, and grainy in appearance. The testes were the same length but thinner and consisted of a duct with fingerlike projections the entire length.

CHAPTER IV

RESULTS AND DISCUSSION

Descriptions of Fish Behaviors

The following is a list of descriptions of the black bullhead behaviors observed throughout this study.

Approach--The orientation and swimming towards a non-swimming fish. The position of the dorsal fin and the speed of the approaching fish do not change during the approach. The approaching fish swims near the bottom and may orient towards any part of the stationary fish.

Arch Up--The curving upwards of the longitudinal axis of a fish lying on the bottom, during which nose and tail lose contact with the bottom. The barbels are extended towards the water surface and the dorsal fin is raised. This position is maintained for five seconds (Fig. 4).

Banging--The vigorous striking of the floor of the tank by the nose of a fish which is head downward behind the tubing of an undergravel filter. The fish wiggles behind the tubing with his ventral surface in contact with the tubing and his dorsal surface in contact with the aquarium corner. In quick succession, the fish first backs up by moving his paired fins toward the substrate while curving his tail right or left and then it swims down by moving his paired fins toward the water surface while straightening his tail. When this up-and-down movement is vigorous and contact is made between the fish's nose and the bottom each time he swims down, this is called Banging.

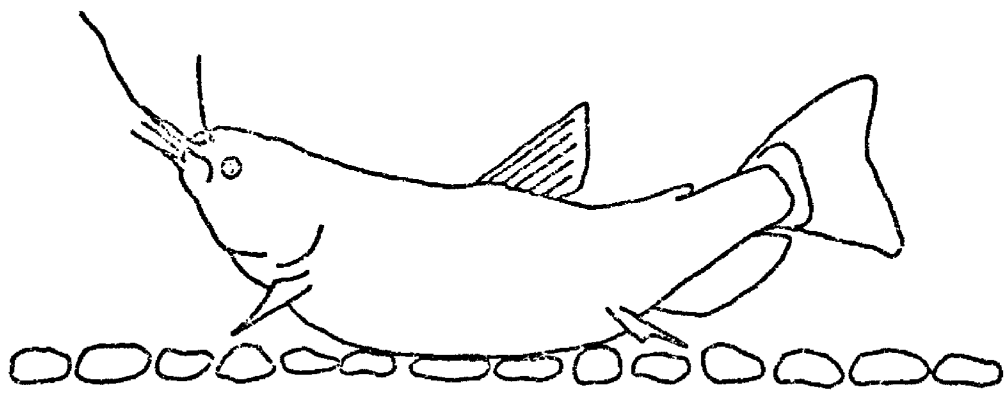


FIG. 4 Arch Up

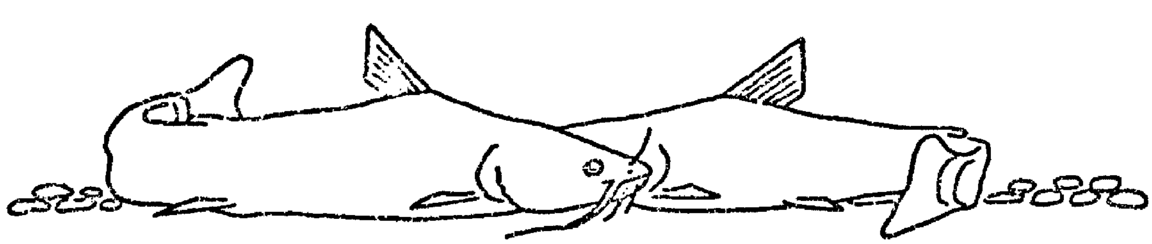


FIG. 5 Curving

Chase--The quick, obvious pursuit of a rapidly swimming fish.

Chew Barbel--The mouthing of a maxillary barbel of one fish by another fish. Only the proximal portion of a barbel is taken inside the mouth of the chewing fish. The end extending beyond the mouth moves up and down in concert with the up and down movement of the chewer's lower jaw. The longitudinal axis of the chewer may be at an angle less than or equal to 90° to the longitudinal axis of the other fish with both fish facing the same direction.

Circling--Two fish swimming in a tight circle with the head of each near the tail of the other. This behavior takes place near the bottom and often lasts for only one complete circle. If the activity level of the fish was high prior to circling, the pace of circling is very rapid. It is comparatively slower if prior activity was low.

Curving--The bending of the tail toward another fish by one or both fish lying parallel on the bottom in a Head-to-Tail position (Fig. 5). If only one fish is curving his tail, the behavior is called "one curving." If both are curving their tails, the behavior is called "both curving." The distance between the long axes of the two fish is usually approximately 4 cm., but occasionally the bodies are next to each other so that the nose of each fish is in contact with the tail of the other fish.

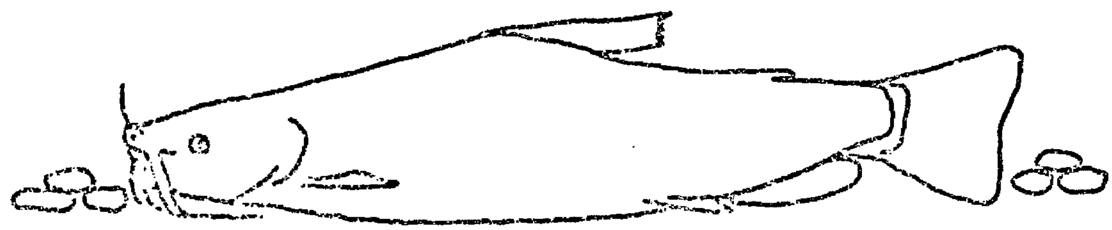
Dance--The up-and-down motion of a bullhead standing on his tail in a corner of the tank. The fish stops swimming while parallel to the back of the tank. He then slowly drifts backward and downward into a corner of the tank, occasionally guiding his course by movements of his paired fins. He stops when his tail touches the tank bottom and his longitudinal axis is perpendicular to the bottom. After a few seconds, he floats upwards a few centimeters and then pushes himself back down by moving his paired fins. This up-and-down bobbing is often repeated three times. Then the fish slowly drifts to a position parallel to the bottom.

Dart--The extremely rapid movement of a fish from one part of the tank to a position lying on the bottom in another part of the tank. The majority of the momentum for this dash seems to come from a quick flexing and straightening of the tail and the posterior third of the body. A dart lasts about one second.

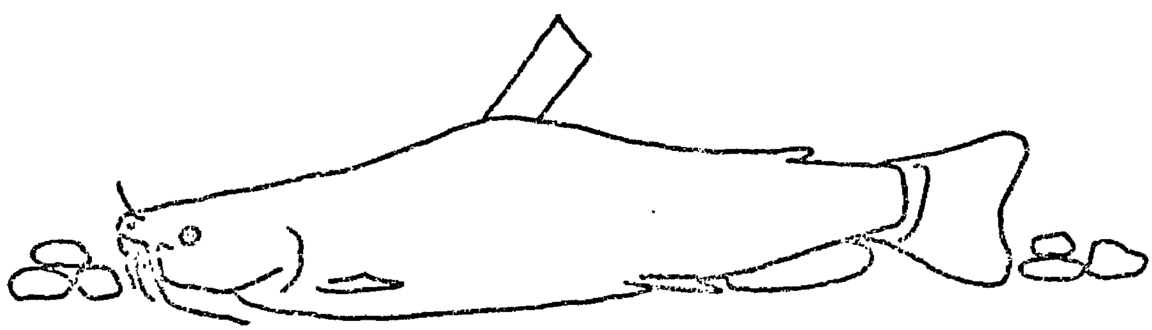
Defecate--The evacuation of fecal material by a swimming fish.

Dorsal Up--The pronounced raising and spreading of the dorsal fin by a swimming or non-swimming fish (Fig. 6). A bullhead has three distinct positions for his dorsal fin: down, relaxed, and raised. In the down position, the dorsal is folded flat against the body so the spine and soft rays are parallel to the longitudinal axis. In the relaxed position, the rays are at approximately a 30° angle. In the raised position, the rays are at approximately a 60° angle. The bullhead can raise his dorsal fin with the rays close together or spread so that each one is distinguishable. The latter situation is designated as Dorsal Up.

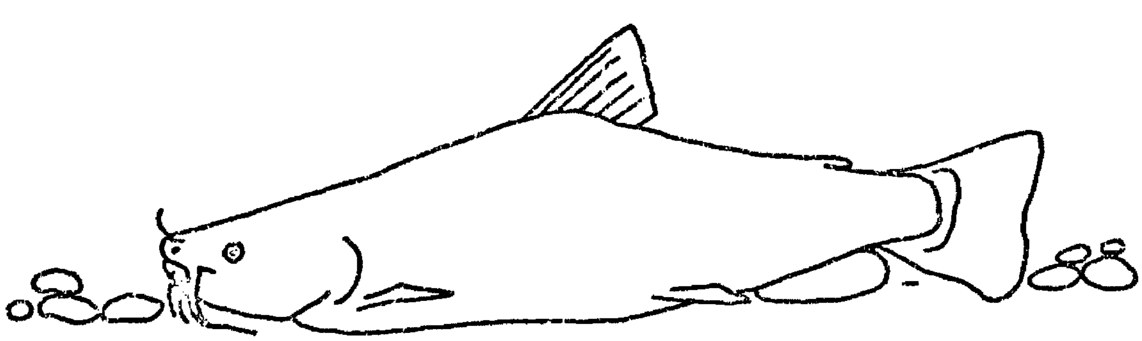
Drift--The sideways movement of a fish lying on the bottom caused by the force of a water current produced by another fish swimming by and not by motion of the drifter's own fins or body.



A. Dorsal Down



B. Dorsal Raised, Not Extended



C. Dorsal Raised and Extended (Dorsal Up)

FIG. 6 Positions of The Dorsal Fin

Eat--A nose stand with the mouth open, the longitudinal axis of the body at an angle between 60° and 90° from the horizontal, the tail curved either right or left, and the paired fins beating anteriorly to maintain this position (Fig. 7). Often the nose is moved slightly right and left to push aside gravel. This nose down position is assumed while searching for food among the gravel.

Face-to-Face--Two fish lying on the bottom facing each other along a straight line (Fig. 8). The noses are usually about 2 cm. apart, but occasionally they are almost touching. Dorsal fins are usually raised.

Fall-to-Bottom--A slow, non-swimming descent to a position lying on the bottom. During the drop, the posterior third of the body is often bent slightly to right or left. The tail is lower than the nose and touches bottom first. The dorsal fin is usually not raised.

Feel--The repeated touching of an object by the chin barbels of a stationary fish. The object felt may be any part of the tank or another fish. If the forward and backward movements of the barbels are very rapid, this type of feeling is noted as "flicking."

Flee--Rapid, erratic swimming by a fish being chased. Direction is often changed quickly in what appears to be attempts to elude the pursuer. Often the fleeing fish bumps into the sides of the tank or the filters during its flight. Respiratory movements following an escape flight are quick and pronounced. The dorsal fin is not raised during the flight.

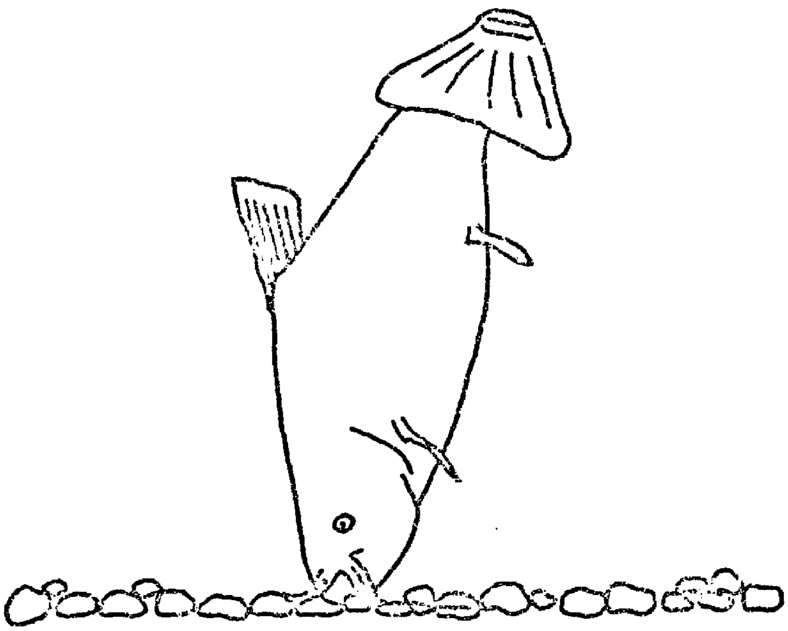


FIG. 7 Eat

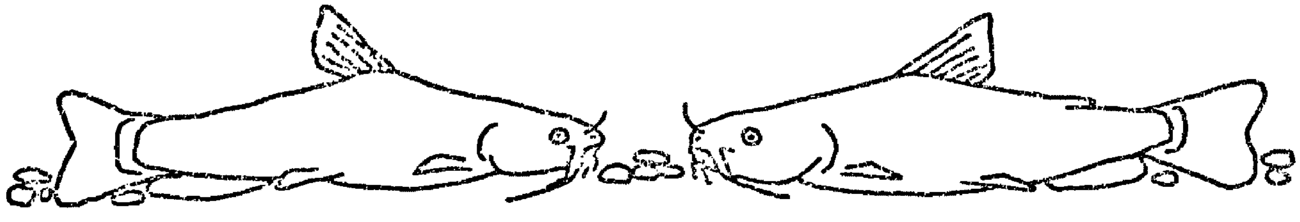


FIG. 8 Face-to-Face

Flutter--Quick, side-to-side swimming with nose against the glass sides of the aquarium and with the longitudinal axis of the fish's body parallel to the horizontal. This behavior is reminiscent of the escape flight against a window by a wild bird trapped inside a building. Fluttering usually occurs near a tank corner.

Follow--Maintenance of an equal distance behind a slowly or moderately swimming fish. If the follower's nose stays in contact with the other fish's tail, this is called "following in contact with tail." If the follower has his mouth open widely, it is called "following with gape." If the follower is about half a tank behind the other fish while keeping his barbels in contact with the path of the other fish along the bottom or sides of the tank, this is called "following the trail."

Gape--A pronounced opening of the mouth by a swimming of non-swimming fish near another fish. If combined with an approach towards the other's side, tail, or top of head, it is considered to be aggressive. If performed by a stationary fish as another fish swims by, it may be defensive. The slight parting of the jaws seen in many swimming fish is not considered to be gaping.

Glance--The same motions as in a Tail Lash except contact is made with the tank instead of another fish. The most frequently glanced objects are the underwater filter and the gravel. When a fish glances the gravel, he leans on his side with his mid-sagittal plane at a 45° angle to the horizontal. Often a fish will glance the bottom about 20 times in succession. This behavior often dislodges food particles. Filter glances are often repeated four to five times. This behavior may dislodge edible algae from the filter.

Gulp--In quick succession, the opening of the mouth and opercula with a lowering of the chin, then the closing of the mouth with a raising of the chin, and finally a closing of the opercula. A gulp seems to force water over the gills, thereby providing added oxygen. Gulps are most frequently performed just before or just after a fish leaves the bottom.

Head-to-Head--Two fish lying parallel on the bottom facing the same way with noses at the same level (Fig. 9). The fish are usually close enough for pectoral fins to be touching.

Head-to-Tail--Two fish lying parallel on the bottom facing opposite directions with the nose of each next to the tail of the other (Fig. 10). The fish are usually about 2 cm. apart.

Jawlock--Two face-to-face fish gripping each other's jaws (Fig. 11). Occasionally one fish will take the whole head of the other fish in its mouth.

Lay Over Top--The bending of one fish on its side over the top of the head of another fish (Fig. 12).

Lean--The tilting of the mid-sagittal plane of a fish lying on the bottom to an angle of 45^o to the horizontal.

Lie Behind Undergravel Filter--A fish nose down between the tubing of the undergravel filter and a corner of the tank.

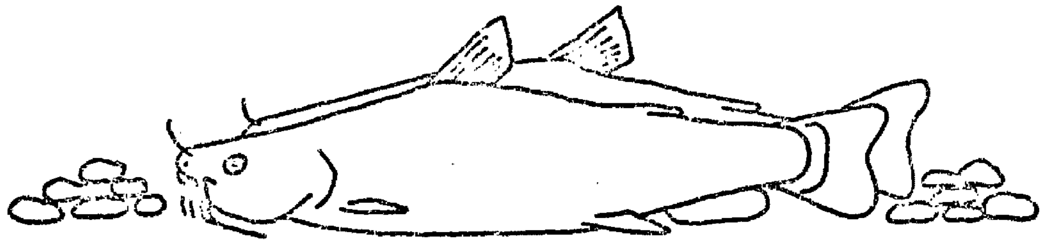


FIG. 9 Head-to-Head

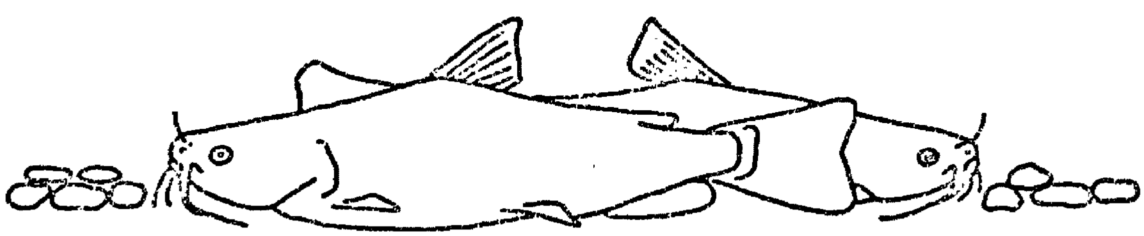


FIG. 10 Head-to-Tail

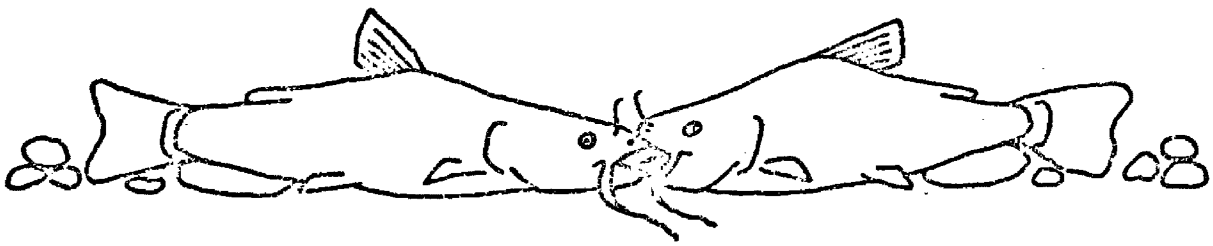


FIG. 11 Jawlock

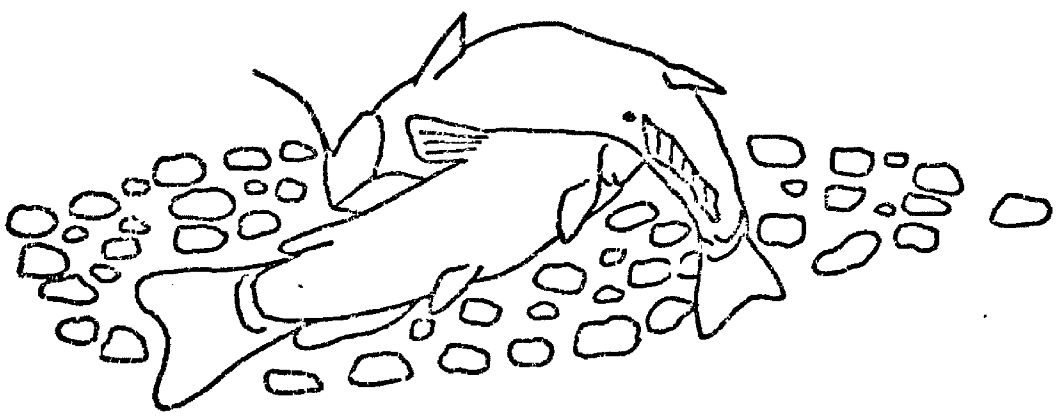


FIG. 12 Lay Over Top

Lie-on-Bottom--A position of recumbency with the caudal fin, anal fin, pelvic fins, and belly touching the gravel.

Nip--Violent contact between the mouth of one fish and the tail, side, or top of head of another fish. A nip is usually preceded by a gaping approach and culminated with a quick flick of the tail which sends the nipping fish quickly towards the side or down on top of the other fish. This behavior is recorded as a "nip" when movement of the nipped fish clearly indicates that contact was made.

Nose Under--Pushing underneath the belly of a stationary fish, displacing this fish upwards. The fish performing the nose under is perpendicular to the other fish with his nose anterior to the anus of the other fish. The fish being displaced generally offers no resistance.

Pass-by--Two fish traveling in opposite directions swimming past each other. The distance between them at the point of passing is about 2 cm.

Perch--Lying on the bottom with all fins extended and no contact between belly and gravel (Fig. 13).

Push into Gravel--The same body position as in Eat with very vigorous side-to-side movements of the nose, noticeably forcing the nose down into the gravel and displacing gravel to the left and right.

Push Jaw--One fish of a pair in Jawlock swimming forward and moving the other fish backward.

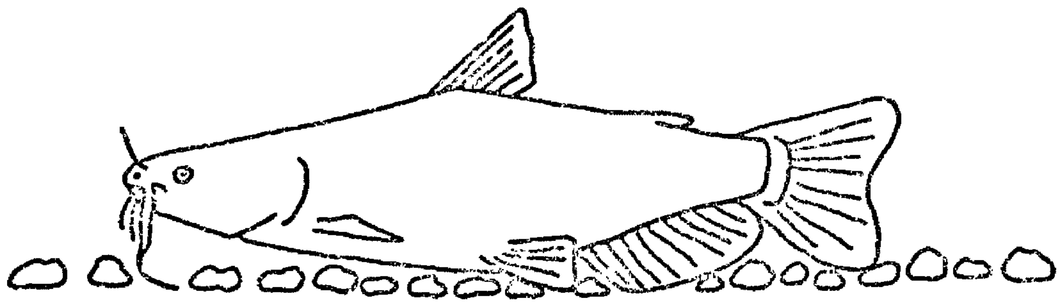


FIG. 13 Perch

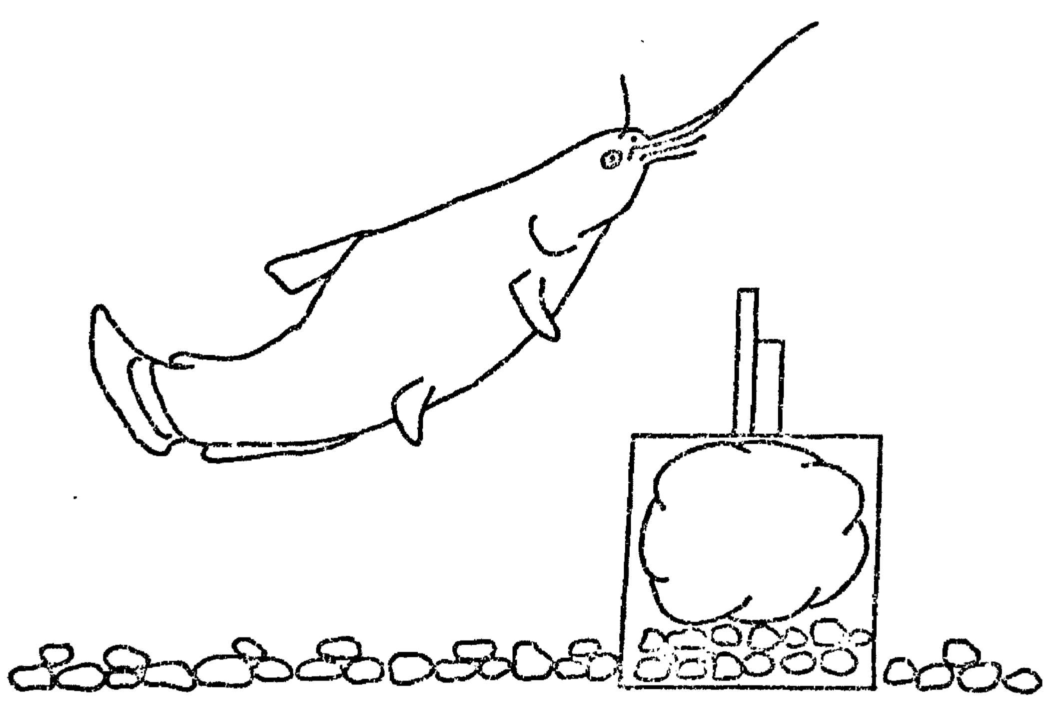


FIG. 14 Swim Up in Water

Push Side--An approaching fish making contact with the sides of and displacing another fish. Often the approach prior to pushing the side is accompanied by a gape.

Quiver--Trembling of the muscles over the body of a fish, especially pronounced near the opercula and pectoral fins.

Rock-Spit--Taking one of more pebbles into the mouth, mouthing them, and ejecting them. The force behind the ejection seems to come from a closing of the opercula which were opened just prior to opening the mouth and from a lifting and forward movement of the floor of the mouth. The fish seem to be gleaning food particles caught between the rocks.

Stand on Tail--Slowly beating the pectoral fins anteriorly to maintain a position in a corner of the tank with the longitudinal axis perpendicular to the bottom and the tail touching the substrate.

Surface Creep--Slow swimming near the surface with the barbels spread out and forward.

Swim--Coordinated movement of all fins carrying the fish from one part of the tank to another. If this is very slow so that the movement of the pelvic and pectoral fins is pronounced, this swimming resembles the movement of a terrestrial quadruped and is called "walking." If the fish swims rapidly around the tank, this is called "quick swimming." Quick swimming if most often seen after a disturbance. Swimming at a pace between walking and quick swimming is called "moderate swimming."

Swim Up in Water--An upward lifting of the anterior two-thirds of a slowly swimming fish while the barbels are raised towards the water surface (Fig. 14).

Swim with Barbels in Contact--Swimming with the barbels held out and down in contact with the gravel and/or sides of the tank.

Tail Lash--One fish swimming next to another, bending towards it, then bending away, making contact so that the other fish is noticeably pushed aside (Fig. 15). Three intensities of tail lash are seen: mild, in which the lashed fish is barely moved; moderate; and severe in which the lashed fish is knocked several centimeters from his previous position.

Touch--A stationary fish extending its barbels forward and making contact with the tank or another fish, then drawing the barbels back. As distinguished from the term Feel, a Touch is a single contact.

Wiggling--Quick, sinusoidal movement across the tank with the fish's belly in contact with the gravel. This behavior seems to dislodge food buried in the gravel.

Yawn--A gradual, broad opening of the mouth and the opercula and a momentary holding of the wide open position, before closing the mouth and the opercula. Often a yawn is followed by a slight gulp.

Results and Discussion of Pairing Experiments

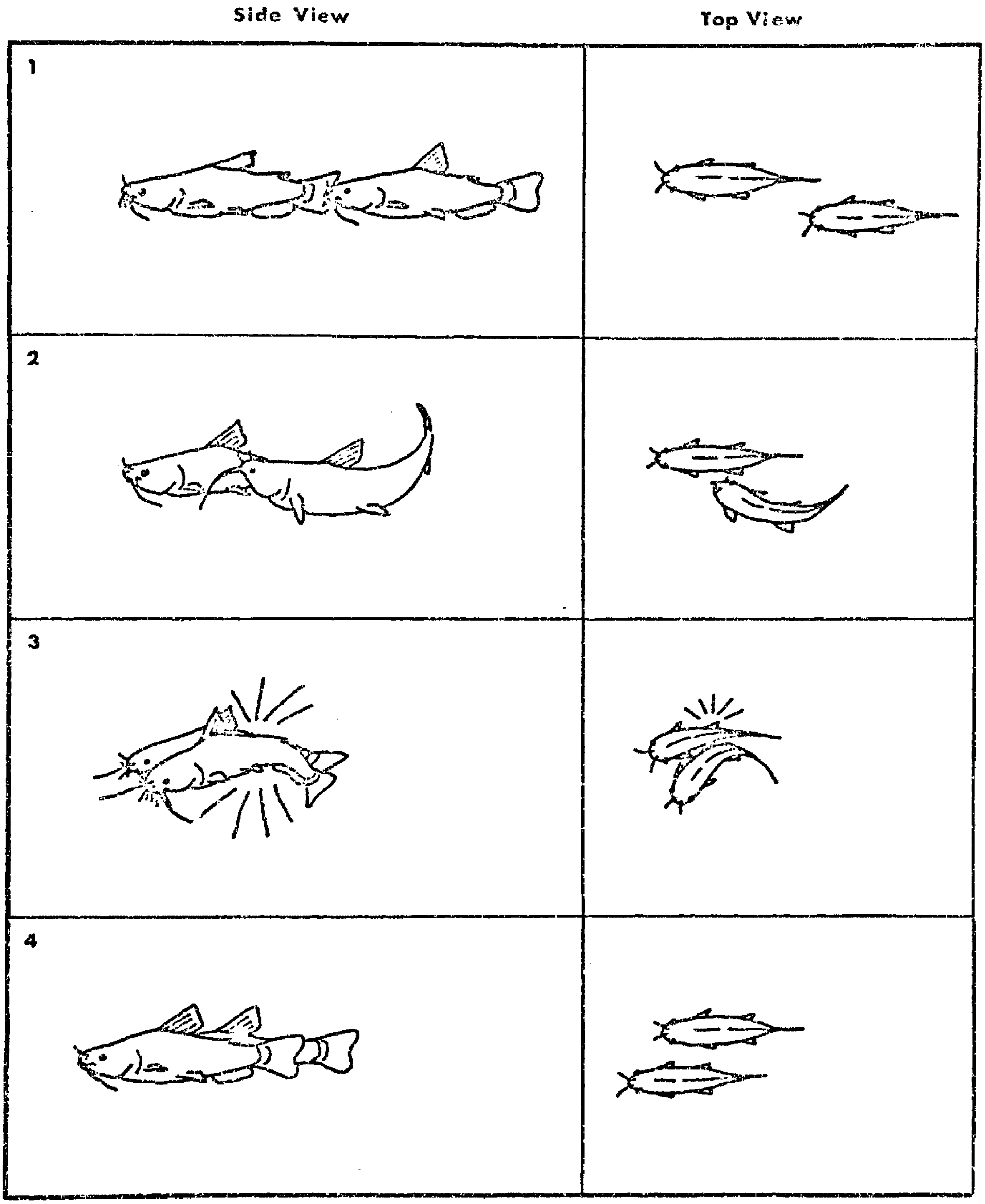


FIG. 15 Tail Lash

Results of Pairing Experiments

The purpose of the preliminary pairing experiments was to determine if the bullheads would establish dominant-subordinate relationships following isolation and, if so, to use the resultant behavior if it appeared in the subsequent water experiments as evidence of the recognition of fish-produced substances in the test water.

Bullheads do fight violently following a period of isolation. When first put together, the two fish lie on the bottom for a minute or two, sometimes with the dorsal fins raised. Then one will begin to swim around the tank, often encountering the other fish in its first circle of the tank. The battle frequently begins at this point and may continue intermittently for 15 minutes. During this time, the fish may inspect, tail lash, follow, and nip each other. Dominance and subordinance were assumed to be established when one fish quickly and definitely fled the other fish at each approach of the latter.

The following is an excerpt from the record of a pair's encounter to illustrate the behaviors observed:

> 1 in left back center, 12 in right back corner. 1 approaching 12--touching 12's tail. 12 turning around. Face-to-Face. 12 gaping right side of 1. 12 following 1 in contact with 1's tail. Side-by-Side (head-to-tail)--12 violent tail lash but missed as 1 swam forward. 12 gaping left side of 1 beneath 1's dorsal fin. 1 is fleeing...

The three encounters of each pair of fish were used to see if a relationship could be established and maintained in any tank, regardless of which fish normally lived there, or if dominance was a function of residency. The former situation was the result. The dominant-subordinate relationships established during the first encounters remained the same during the other encounters except in two cases where a fish that fled during the first encounter emerged dominant in the second two encounters. In addition, out of seven first encounters, the resident fish won three times and the non-resident won four times (Table 2). This approximately equal distribution of dominance between resident and non-resident fish differs from experiments by Braddock (1949) in which resident platyfish (Platypoecilis (Xiphophorus) maculatus) won significantly more often than non-resident fish.

Sex could possibly have affected the outcome of battles but this also did not seem to be a decisive factor. Table 3 shows that out of six pairs of opposite sexes, males were dominant three times and females were dominant three times. This, again, is a one-to-one ratio of males to females, similar to the ratio of resident and non-resident dominant fish and indicates that being a member of one or the other sex does not confer dominance.

When size of the fish is considered, a possible cause of dominance is found (Table 4). In every pair, the dominant fish was the heavier fish. When both fish were the same length, the heavier fish won. In the first pairing experiments, one pair which did not establish definite dominance and subordinance had close to the same weights (Table 4, Fishes 13 and 16). In another pair, dominance was reversed in the second encounter to the heavier fish, which remained dominant

TABLE 2

DOMINANCE VS. RESIDENCY

Pair	Resident During First Encounter	Dominant Fish
6 & 8	6	8
1 & 12	1	12
*3 & 4	4	4
10 & 11	10	11
*14 & 15	15	15
*13 & 16	16	16
5 & 7	7	5

*Resident Fish = Dominant Fish

TABLE 3

SEXES OF EXPERIMENTAL PAIRS

Dominant		Subordinate	
Fish	Sex	Fish	Sex
12	Male	1	Female
4	Male	3	Male
7	Female	5	Male
6	Male	8	Female
11	Female	10	Male
16	Male	13	Female
15	Female	14	Male
Total	4 Males* 3 Females	Total	4 Males* 3 Females

*One pair was male-male.

TABLE 4

SIZES OF EXPERIMENTAL PAIRS

Dominant Fish	Length (cm.)	Weight (gm.)	Subordinate Fish	Length (cm.)	Weight (gm.)
12	19.5	105.0	1	18.5	89.2
4	17.5	86.4	3	17.0	85.0
7	19.5	104.4	5	18.0	83.0
6	18.5	104.7	8	18.0	95.6
11	17.5	69.2	10	16.0	56.5
16	19.0	96.2	13	18.5	94.1
15	18.5	95.8	14	18.5	83.0

in the third encounter (Table 4, Fishes 5 and 7). In one instance, dominance was reversed between the first and second pairing experiments and Table 1 shows that the fish involved also reversed their size relationship (Table 1, Fishes 6 and 8). Todd (1968) believed that size was the determining factor for dominant-subordinate relationships in yellow bullheads; Baerends and Baerends-van Roon (1950) observed this for cichlids; Braddock (1949) felt size was important in deciding dominance in platyfish; and Gibson (1968) observed that the larger blenny (Blennius pholis) in a pair always became dominant.

In addition to subordinate fish being smaller than dominant fish, they also exhibit fewer aggressive behaviors and more submissive behaviors. The individual behaviors which the fish perform were counted and summed for each encounter. The acts were classified as aggressive (behaviors causing or potentially causing harm to the other fish), submissive (behaviors showing deference to the other fish), interactive (not clearly aggressive behaviors involving one fish acting upon another), and non-contact (behaviors performed by one fish involving no contact with another fish).

Table 5 shows the results of three encounters for five pairs of fish (two pairs were not included in the Table because for one pair dominance was not established during the three encounters and for the other pair, dominance changed from one fish to the other in the last two encounters). When the numbers of behaviors performed by dominants and subordinates for each encounter are compared, dominant fish performed more aggressive and less submissive behaviors than

TABLE 5

RESULTS OF PAIRING EXPERIMENTS
(Three Encounters for Five Pairs of Fish)

A. Aggressive Behaviors

Act	Dominant				Subordinate			
	Encounter				Encounter			
	1*	2	3	Total	1	2	3	Total
1. Gape..........	3	8	14	25	2	0	6	8
2. Gape side.....	44	15	29	87	25	1	2	28
3. Follow with Gape..........	1	4	9	14	4	0	0	4
4. Tail Lash.....	43	11	43	97	13	8	8	29
5. Push Side.....	10	3	12	25	1	2	0	3
6. Tail-nip......	8	8	4	20	3	0	0	3
7. Side-nip......	6	8	7	21	10	0	1	11
8. Top-nip.......	1	2	0	3	3	0	0	3
9. Chase.........	4	1	3	8	5**	0	0	5
10. Jawlock.......	2	1	4	7	0	1	4	5
11. Push Jaw......	1	1	1	3	0	0	0	0
12. Bump..........	4	1	1	6	3	0	0	3
13. Lay Over Top..	0	1	2	3	1	0	0	1
Total	127	64	128	319	70	12	21	103

B. Submissive Behaviors

Act	Dominant 1*	2	3	Total	Subordinate 1	2	3	Total
1. Flee..........	7**	2	0	9	24	18	16	58
2. Fall-to-Bottom	3	0	0	3	0	4	5	9
3. Lean..........	0	0	0	0	0	0	3**	3
4. Drift.........	0	0	0	0	0	0	2**	2
5. Quiver........	0	3**	2**	5	0	5**	20**	25
6. Flutter.......	4	2	5	11	23	18	10	51
Total	14	7	7	28	47	45	56	148

*Total time (5 pairings): Encounter 1--50 min.; Encounter 2--48 min.; Encounter 3--56 min.
**One fish

C. Interactive Behaviors

Act	Dominant				Subordinate			
	Encounter				Encounter			
	1*	2	3	Total	1	2	3	Total
1. Chew barbel...	1	0	0	1	0	2	0	2
2. Feel other....	0	1	4	5	0	3	0	3
3. Follow tail...	2	3	0	5	2	0	0	2
4. Dart away.....	2	1	1	4	1	0	2	3
5. One curving...	5**	3**	3	11	4**	4**	11	19
6. Touch other...	3	16	13	32	4	4	7	15
7. Follow........	37	9	12	58	30	3	3	36
8. Follow trail..	1	3	2	6	1	0	0	1
9. Nose under....	1	2	9	12	1	0	1	2
10. Approach......	20	5	20	45	3	3	8	14
Total	72	43	64	179	46	19	32	97

D. Non-Contact Behaviors

1. Lie on Bottom.	29	31	40	100	18	22	36	76
2. Swim..........	42	28	77	147	47	37	72	156
3. Raise dorsal..	15	5	20	40	9	3	15	27
4. Eat...........	2	0	8	10	2	1	3	6
5. Rock-spit.....	0	0	2	2	0	3	2	5
6. Feel tank.....	8	10	19	37	11	6	7	24
7. Touch tank....	0	0	4	4	1	5	0	6
8. Defecate......	0	0	1	1	1	0	0	1
9. Arch up.......	0	1	0	1	0	0	0	0
10. Tail lash water.........	0	3	5	8	0	0	0	0
11. Swim-barbels..	0	0	3	3	2	0	0	2
Total	96	78	179	353	91	77	135	303

*Total time (5 pairings): Encounter 1--50 min.; Encounter 2--48 min.; Encounter 3--56 min.
**One fish

E. Simultaneous Acts by Two Fish

Act	Encounter 1*	2	3	Total
1. Both curving...	5**	1**	0	6
2. Circling.......	5	4	2	11
3. Pass-by........	8	4	15	27
4. Face-to-Face...	10	3	8	21
5. Head-to-Head...	2	5	8	15
6. Head-to-Tail...	1	6	3	10
7. Wiggling.......	0	2	0	2
Total	31	25	36	92

*Total time (5 pairings): Encounter 1--50 min.; Encounter 2--48 min.; Encounter 3--56 min.

**One pair

subordinate fish in 51 of 57 comparisons (Table 5A, 5B). Dominants performed more interactive behaviors than subordinates in 18 of 30 comparisons (Table 5C). Dominants performed more non-contact behaviors than subordinates in 16 of 33 comparisons (Table 5D). (Table 5E shows behaviors which the fish were performing together rather than as individuals and because both fish are performing the behaviors at the same time there is no basis for comparison between the fish; only a basis for studying the nature of the encounters.) Thus dominant fish for the most part exhibit more aggressive and less submissive behaviors than subordinate fish. Dominant and subordinate fish perform interactive and non-contact behaviors with about equal frequency. Statistical tests were not used to show significance or non-significance in these results because of the differences in duration of the encounters.

Discussion of Pairing Experiments

A general picture of winning or dominance and losing or subordinance is apparent. It seems as though greater size, and hence greater strength, is the key determinant as to which member of a pair will be dominant. Several aggressive and interactive behaviors could serve as size determinants. Pushing the side, being tail lashed, pushing the jaw, feeling, and nosing under could tell a fish how heavy or large the other fish is. Atema, Todd, and Bardach (1969) and Baerends and Baerends-van Roon (1950) believe that mouth fights (involving jawlocks and pushing of the jaws) are a test of strength and that holding the upper jaw in such a fight often leads to winning (though mouth fights are rare and not necessary to establish dominance). After a number of strength tests, one fish begins to flee and the other begins to chase. Subsequent encounters between the pair are usually neither as violent nor as complex as the first encounter and the submissive behavior is seen earlier in the fight, sometimes at the very beginning.

In the second pairing experiments, the length of the encounter, determination of the dominant fish, and any unusual events were recorded.

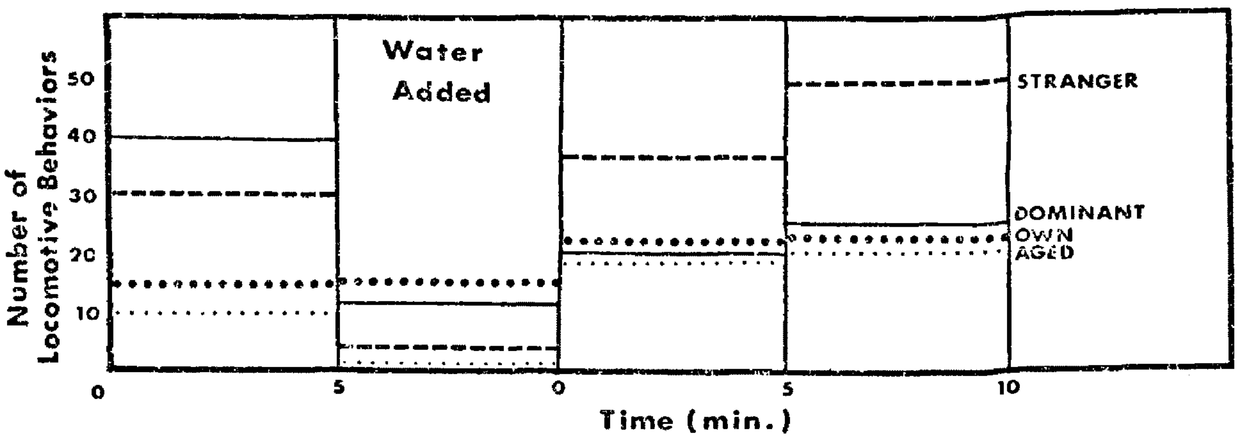
Results and Discussion of First Water Experiments

If the waters from the partner and stranger fish tanks contained no discernibly different odors or tastes from the test fish's own water or from aged water, there would be no behavioral difference in the reaction to the addition of any of the four waters. Thus, the null hypothesis was that the four treatments, i.e. waters, would elicit the same response or lack of response from the fish tested.

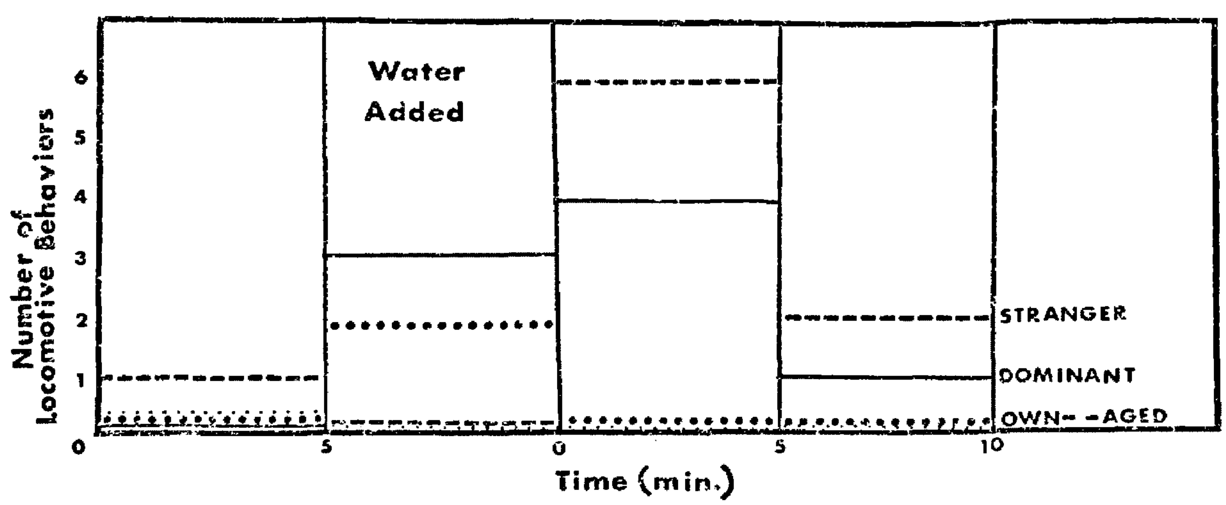
Results of First Water Experiments

In the first set of water experiments, there were clear indications that the null hypothesis was false, that, instead, the fish were reacting differently to the four waters being added. When aged or self waters were added, the experimental fish would lie on the bottom while the water was added, then gradually resume behaviors typical of those seen during most of the day, such as slow circling of the tank or resting on the bottom. When partner or stranger waters were added, however, the fish responded differently. They performed behaviors rarely, if ever, seen before the waters were added. These behaviors included: arching up, raising the dorsal fin, swimming up in the water, falling to the bottom, pushing vigorously into the gravel, and banging behind the undergravel filters. They also increased the frequency of four other behaviors: swimming with barbels in contact, rock-spitting, feeling, and touching. After lying on the bottom during the addition of the water, the fish often began what appeared to be searching movements, in which they swam quickly throughout the tank and felt and touched particularly the corners and the underwater filter. Often the dorsal fin was raised prior to leaving the bottom and sometimes it remained raised during the searching.

Unfortunately, the timing of the addition of the waters was not held constant in these first water experiments and, hence, a statistical comparison of the different experiments could not be undertaken. Figures 16 and 17, however, show the results of these experiments. The ordinate values of these graphs were obtained by counting the number of times the test fish performed the behaviors graphed in each time period. For Figures 16A and 17A, all the locomotive behaviors performed during the experiments by the subordinate and dominant fish were tabulated. Thus, these graphs represent the general activity levels of the fish throughout the experiments. In Figures 16B and 17B, the behaviors described above as those which

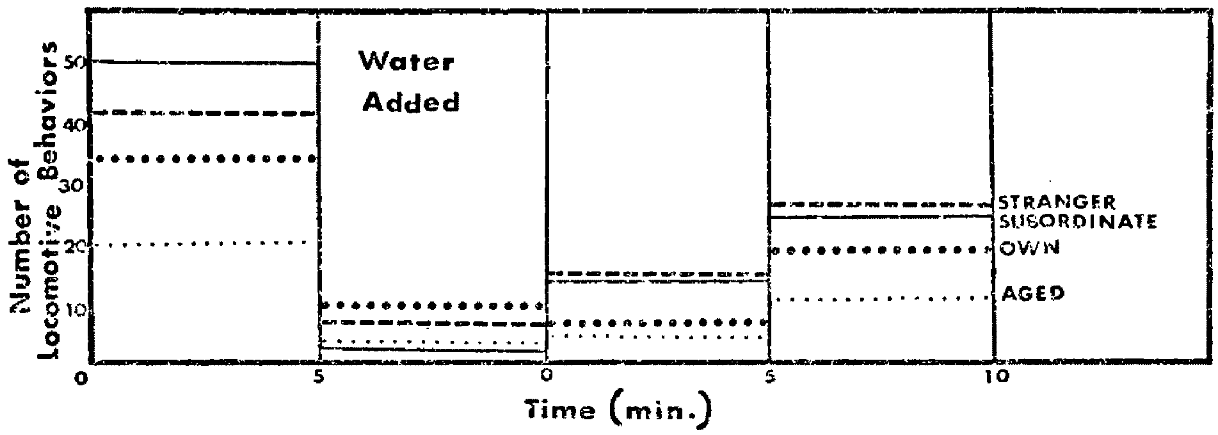


A. Total Locomotive Behaviors for 7 Fish

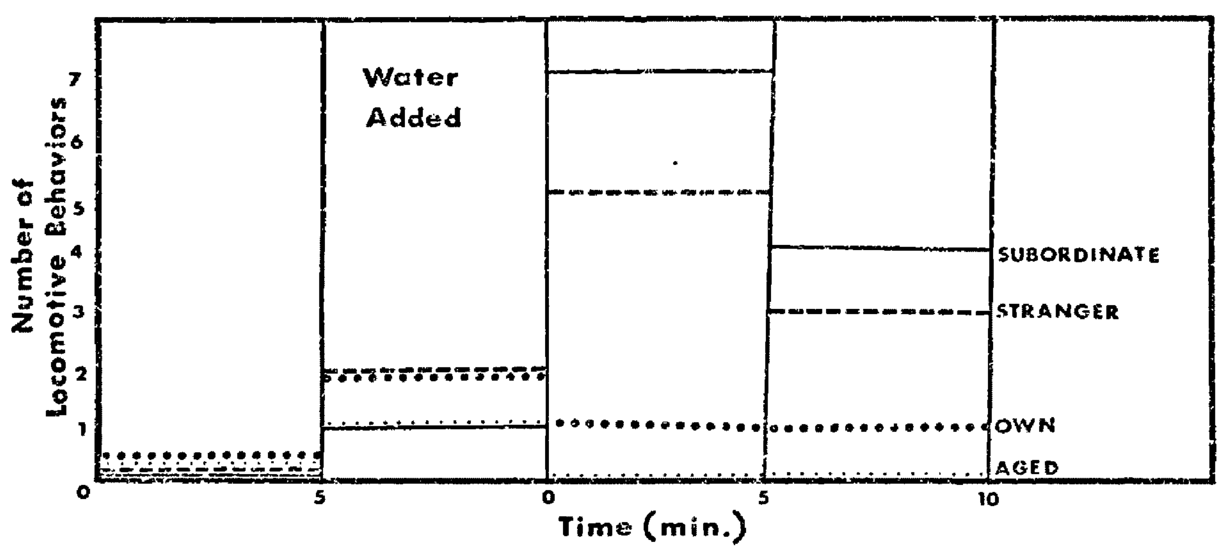


B. Ten Locomotive Behaviors Which Increase When Dominant or Stranger Waters Are Added (Total for 7 Fish)

FIG. 16 Locomotive Behavior of Subordinate Fish in Response to Introduction of Water from Dominant Fish, Stranger Fish, Own Tank, and Aging Tank (First Water Experiments)



A. Total Locomotive Behaviors for 7 Fish



B. Ten Locomotive Behaviors Which Increase When Subordinate or Stranger Waters Are Added (Total for 7 Fish)

FIG. 17 Locomotive Behavior of Dominant Fish in Response to Introduction of Water from Subordinate Fish, Stranger Fish, Own Tank and Aging Tank (First Water Experiments) increased greatly after the partner and stranger waters were added are graphed. These graphs represent a response specifically to the addition of other fish waters.

Discussion of First Water Experiments

These graphs show a depression of activity caused by the addition of any water, with a gradual recovery in the level of locomotive activity. If just the behaviors seen after the addition of water are considered, the fish show a greater response to the partner and stranger waters than to the aged or self waters.

While there is a distinguishable difference in the responses to partner and stranger waters as compared to aged and self waters, the difference is not pronounced. Thus, it was decided that a second set of experiments should be performed which incorporated certain changes from the first set of water experiments.

Results and Discussion of Second Water Experiments

In the second set of water experiments, a larger quantity of test water was added to a smaller amount of tank water. Hopefully, the response seen in the first experiments would thus be enhanced. Also, the water addition time was kept constant, so that each five-minute period in one experiment could be compared statistically with the corresponding time period in the other experiments. Finally, observations were recorded for an additional five minutes to see if activity levels would return to normal fifteen minutes following addition of water.

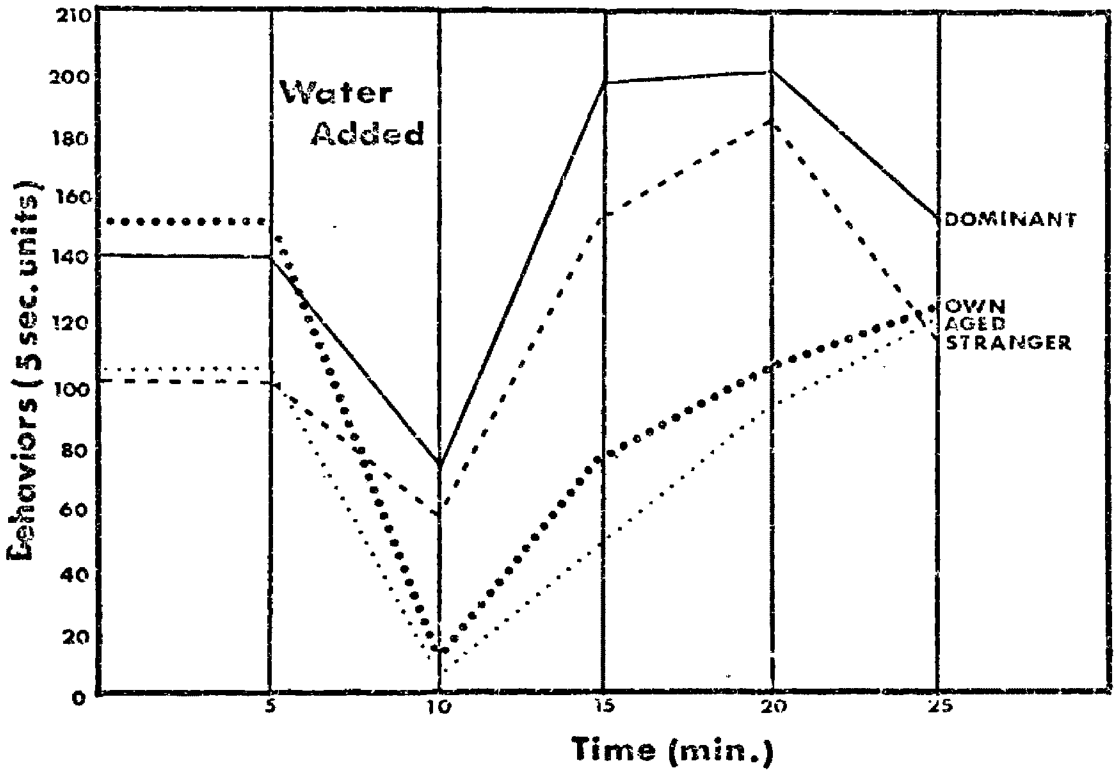
Results of Second Water Experiments

Locomotive and stationary behaviors for subordinate and dominant fish before, during, and after the addition of test water are shown in Figures 18, 19, and 20. The ordinate values represent the number of 5-second time periods the fish spent performing the behaviors graphed and the abscissa values are the time intervals from start to finish of the experiment.

In Figure 18A, all locomotive behaviors observed for the subordinate fish during the four experiments are graphed. The fish were more active following the addition of stranger or dominant waters than after the addition of aged or self waters. There seemed to be a slightly greater response to dominant than to stranger water. All four levels of locomotive activity approached the levels observed prior to the addition of water fifteen minutes after the water was added.

The ten behaviors which increase greatly during and after the addition of dominant and stranger waters were the same as those described for the first water experiments (p. 53). Subordinate fish showed a great increase in these ten behaviors in response to dominant or stranger water and practically no increase in response to aged or own water (Fig. 18B).

By contrast, the locomotive behaviors other than the ten discussed above exhibit similar changes in response to the four different waters (Fig. 18C). All are depressed during and after addition

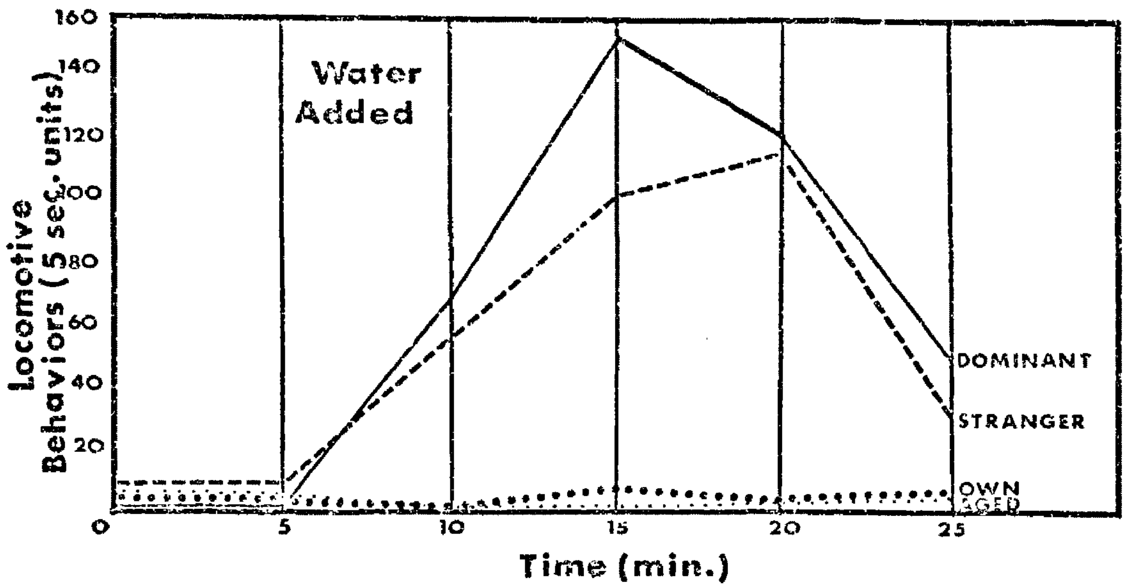


A. Total Locomotive Behaviors (23 behaviors)

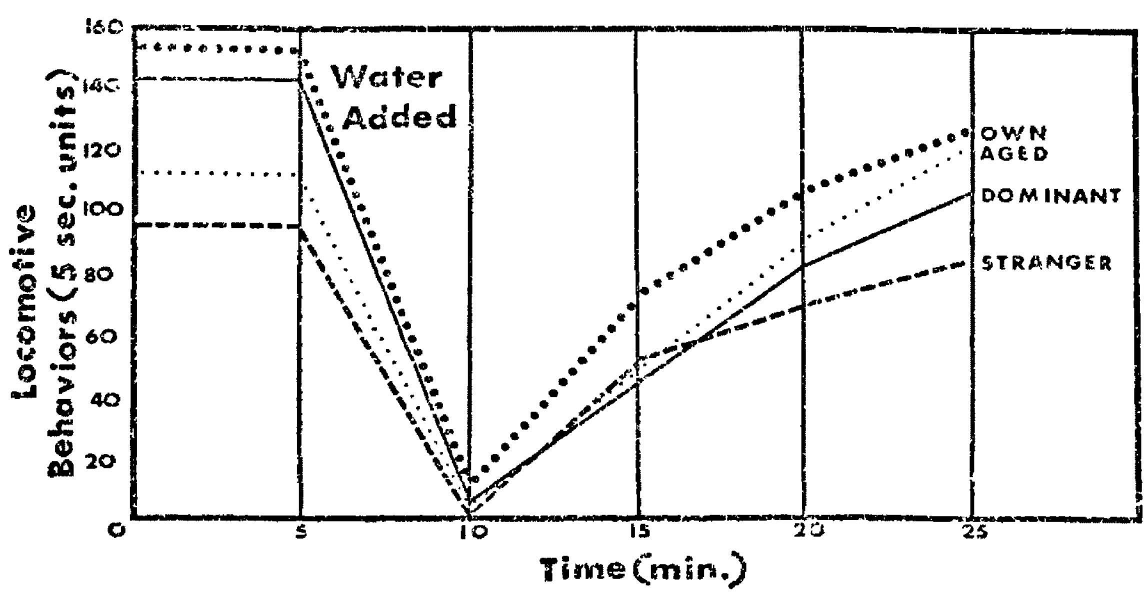
Note: Each of the 4 Values in Every 5-Minute Time Period Represents A Total of All the Locomotive Behaviors Treated in the Graph for All the Fish Under Consideration and Is Expressed As the Number of 5-Second Time Periods Spent Performing These Behaviors. This Applies to All Following Graphs.

FIG. 18 Locomotive Behavior of Subordinate Fish in Response to Introduction of Water from Dominant Fish, Stranger Fish, Own Tank and Aging Tank (Second Water Experiments; Total for 6 Fish)

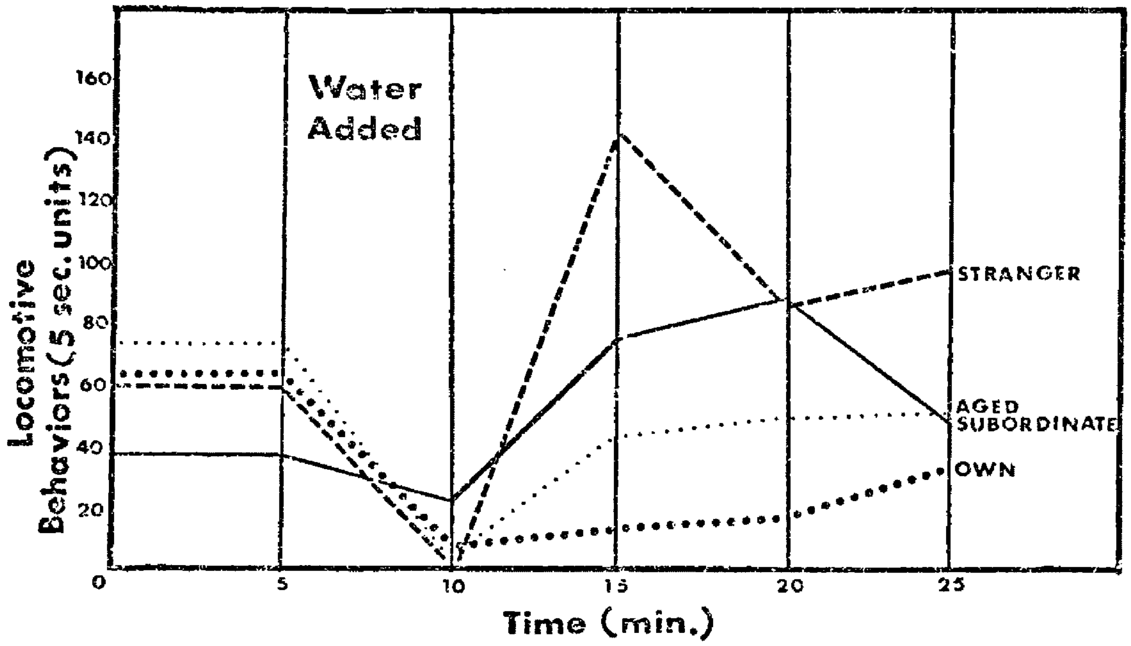
FIG.18--Continued



B. Ten Locomotive Behaviors Which Increase When Dominant or Stranger Waters Are Added (Total for 6 Fish)



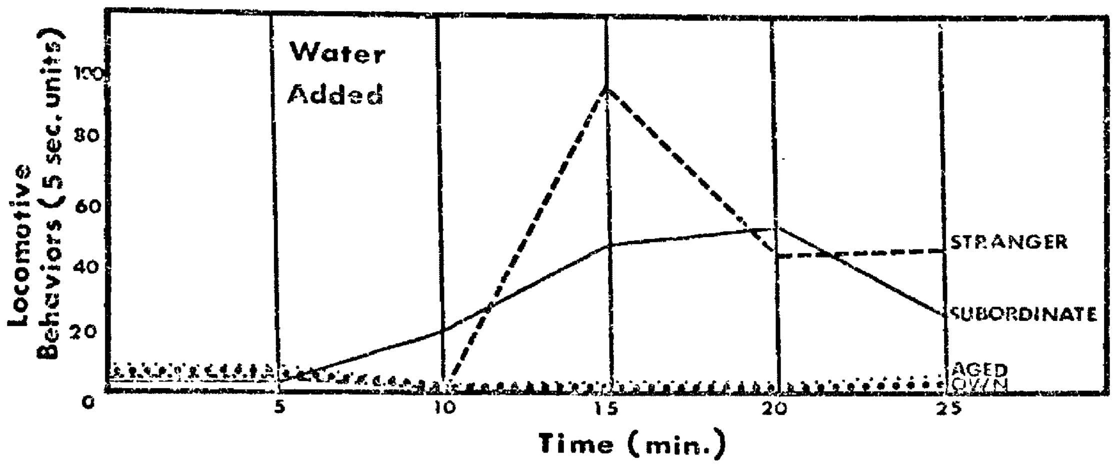
C. Thirteen remaining Locomotive Behaviors Indicating No Reaction to Test Waters Except Depression of Activity (Total for 6 Fish)



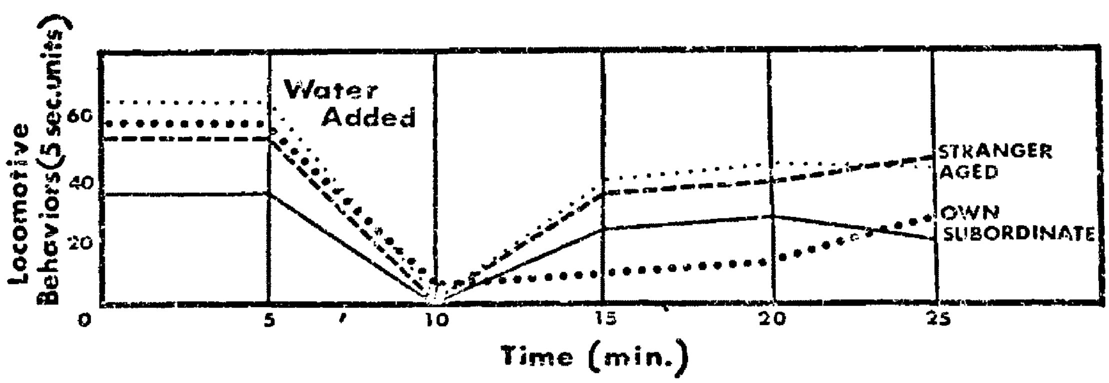
A. Total Locomotive Behaviors (23 Behaviors)

FIG. 19 Locomotive Behaviors of Dominant Fish in Response to Addition of Water from Subordinate Fish, Stranger Fish, Own Tank and Aging Tank (Second Water Experiments; Total for 6 Fish)

FIG. 19-- Continued



B. Ten Locomotive Behaviors Which Increase When Subordinate or Stranger Waters Are Added (Total for 6 Fish)



C. Thirteen Remaining Locomotive Behaviors Indicating No Reaction to Test Waters Except Depression of Activity (Total for 6 Fish)

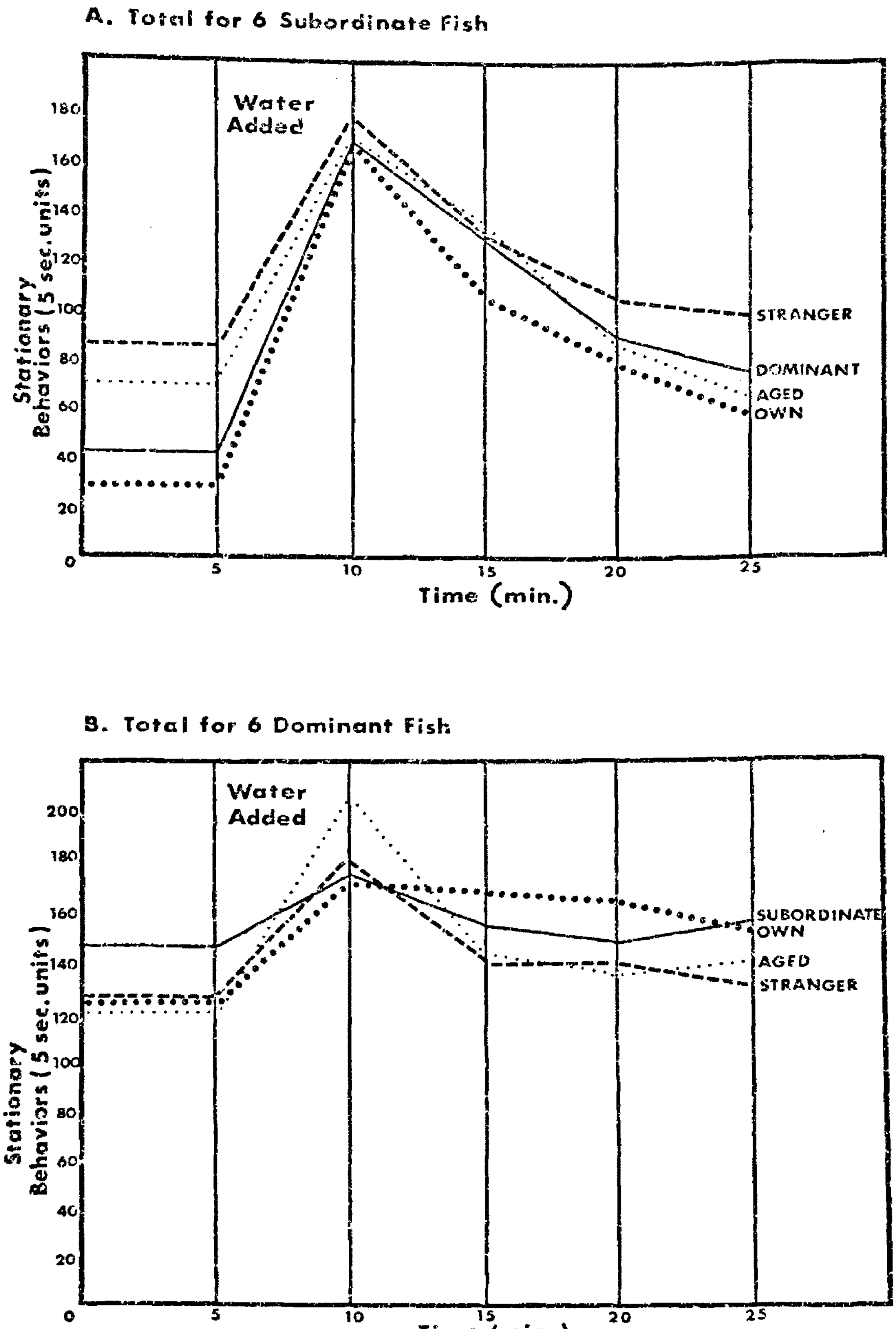


FIG. 20 Changes in Stationary Behaviors with Addition of Experimental Waters

of test water, then gradually return to levels close to levels prior to the addition of water.

Trends similar to those observed for subordinate fish are seen for dominant fish with one exception (Fig. 19). Again the activity of the fish is depressed by the addition of any water and the subordinate and stranger waters cause a marked increase in activity following the addition of these waters. However, the stranger water rather than the subordinate water causes the greatest increase in activity, whereas for subordinate fish the dominant water elicited the greatest response.

Stationary behaviors of the fish (Fig. 20) are approximately reciprocals of the locomotive behaviors other than the ten locomotive behaviors which increase in response to other fish waters (Fig. 18C, 19C). The stationary behaviors increase with the addition of water and gradually decrease thereafter.

Analysis of Variance

An analysis of variance was determined for the total locomotive behaviors of subordinate and dominant fish, for the ten behaviors seen in response to partner and stranger waters, and for the remaining locomotive behaviors after the results for the ten behaviors are subtracted (Table 6). For total locomotive behaviors, this test shows significant differences in responses to different test waters in the first and second 5-minute periods after the water was added to subordinate fish tanks and in the first and third 5-minute periods after water was added to the dominant fish tanks.

TABLE 6

RESULTS OF ANALYSIS OF VARIANCE
(Second Water Experiments)

A. Total Locomotive Activity

	Subordinate	Dominant
1. 5 minutes before water added	Accept H_o* $p>.05$	Accept H_o $p>.05$
2. Water added	Accept H_o $p>.05$	Accept H_o $p>.05$
3. First 5 minutes after water added	Reject H_o $p<.05$ Dom>Aged Dom>Own Stranger > Aged Dom+Stranger > Aged+Own	Reject H_o $p<.05$ Stranger>Own Sub+Stranger>Aged+Own
4. Second 5 minutes after water added	Reject H_o $p<.05$ Dom+Stranger> Aged+Own	Accept H_o $p>.05$
5. Third 5 minutes after water added	Accept H_o $p>.05$	Reject H_o $p<.05$ No discernible difference

*H_o (null hypothesis) = No difference in behaviors when four test waters (partner, stranger, own, and aged) are added

B. Reaction to Water
(Locomotive Behaviors 1-10)

	Subordinate	Dominant
1. 5 minutes before water added	Accept H_o $p > .05$	Accept H_o $p > .05$
2. Water added	Accept H_o $p > .05$	Accept H_o $p > .05$
3. First 5 minutes after water added	Reject H_o $p < .05$ Dom > Aged Dom > Own Stranger > Aged Stranger > Own Dom+Stranger > Aged+Own	Reject H_o $p < .05$ Stranger > Aged Stranger > Own Sub+Stranger > Aged+Own
4. Second 5 minutes after water added	Reject H_o $p < .05$ Dom > Aged Dom > Own Stranger > Aged Stranger > Own Dom+Stranger > Aged+Own	Accept H_o $p > .05$
5. Third 5 minutes after water added	Reject H_o $p < .05$ No discernible difference	Accept H_o $p > .05$

C. Non-Reactive Behaviors
(Locomotive Behaviors 11-23)

	Subordinate	Dominant
1. 5 minutes before water added	Accept H_o $p > .05$	Accept H_o $p > .05$
2. Water added	Reject H_o $p < .05$ Dom+Own > Stranger+Aged	Accept H_o $p > .05$
3. First 5 minutes after water added	Accept H_o $p > .05$	Accept H_o $p > .05$
4. Second 5 minutes after water added	Accept H_o $p > .05$	Accept H_o $p > .05$
5. Third 5 minutes after water added	Accept H_o $p > .05$	Accept H_o $p > .05$

According to Scheffe's method (Guenther, 1964) of determining which treatments differed and in what way, in subordinate tanks the dominant water caused greater activity than the aged or own waters, the stranger water caused greater activity than the aged water, and the dominant and stranger waters caused a greater combined response than the aged and own waters.

Also according to Scheffe's method, the dominant fish reacted with greater activity in the first five minutes after stranger water was added than after their own water was added. In addition, the combined response to subordinate and stranger waters by dominant fish showed a higher level of activity than the response to aged and own waters. The difference in response detected by analysis of variance in the four waters in the third five minutes after water was added was so slight it could not be detected by Scheffe's method.

The analysis of variance for the ten behaviors which increased upon addition of other fish waters shows results similar to the analysis of variance for total locomotive behaviors. The null hypothesis that there was no difference in treatments was rejected for the three consecutive 5-minute periods following addition of water to the subordinate tanks and it was rejected for the first 5-minute period following water addition to the dominant tanks.

For the first and second 5-minute periods after addition of water to tanks with subordinate fish, Scheffe's method shows these behaviors to be performed more during the addition of dominant or stranger water than during the addition of aged or self water. The difference in treatments in the third 5-minute period was not ascertainable by Scheffe's method.

The dominants perform the ten behaviors believed to be a response to the water of another fish more after stranger water is added than after aged or own water is added. The responses to subordinate and stranger waters were together significantly greater than the responses to aged and own water.

Analysis of variance indicates that for locomotive behaviors other than the ten behaviors observed as a reaction to water of other fish, there are no significant differences among responses to test waters except just as the water is added to subordinate fish tanks. Scheffe's method finds no difference between responses to each individual type of water, but does indicate that activity is greater in response to dominant plus own waters than to stranger plus aged waters. All of the activity levels are so low at this point, however, that this difference may not be significant because of the small number of behaviors performed and the relatively small sample size.

Discussion of Second Water Experiments

Following the addition of test waters, both dominant and subordinate fish react more to the addition of partner or stranger waters than to the addition of aged or self waters. This indicates that the fish can recognize a different quality in the waters from other fish that is not characteristic of their own water or aged water. In some way, water from a fish previously encountered and water from a stranger fish differ from water out of the test fish's own tank and water out of the aging tank.

Furthermore, although there seems to be no qualitative difference between dominants and subordinates in their response to other fish waters, there does seem to be a temporal and quantitative difference. Subordinate fish have a more pronounced, longer, and more continuous response compared to the dominants' response. This difference in response may be caused by a difference in the waters or by behavioral differences between dominant and subordinate fish.

A definite recognition of a difference between two fish waters would be evident if there were a different behavioral response to partner than to stranger water. This has been reported for yellow bullheads (Todd, 1968; Bardach & Todd, 1970). The dominant bullheads attacked subordinate water and subordinate bullheads avoided dominant water. Thus the aggressive and submissive behaviors seen in the pairing of the yellow bullheads were also seen in their responses to test waters. No such qualitative difference in response to partner versus stranger waters or such aggressive or submissive behaviors were seen in the water experiments with the black bullheads. If black bullhead responses are plotted on a graph, the results indicate that the subordinates are more active when water of a dominant fish is added than when water of a fish they have previously not encountered is added (Fig. 18A, B). Conversely, the dominant fish show a greater increase in activity when the water of a fish they have not encountered is added than when the water of a fish they have already dominated is added (Fig. 19A, B). However, the statistical tests do not indicate a significant quantitative difference in either dominant or subordinate responses to partner versus stranger waters. If these experiments had been performed for several more pairs of fish, this trend may have proven to be statistically discernible. Also, the experiments were performed in March which is two months from the beginning of the black bullhead spawning season. The gonads of both sexes were larger than those of fish dissected in mid-winter. Magnuson (1962) noted a change in medaka dominant-subordinate relationships with the onset of the breeding season. It could be that a more pronounced reaction by the bullheads in March was prevented by hormonal changes beginning to occur with the approach of the breeding season.

These experiments indicate that a black bullhead can derive some information from the water that enables it to distinguish water that has contained other bullheads from water that has contained only itself or no bullhead. This information must be a chemical (either an odor or taste). Further, there is a definite difference in the response of subordinate fish to test waters compared to the response of dominant fish to test waters. There is also an indication that the bullheads can distinguish water from a fish previously encountered as opposed to water from a fish never before encountered.

If the fish are detecting a specific chemical produced by other black bullheads which transmits information, then this chemical may be called a pheromone. It would be wise, however, to refrain from discussing pheromones in black bullheads until further research has satisfied as yet unanswered questions.

Suggestions for Future Research

Further laboratory and field research is necessary to learn the role of chemoreception in the social life of black bullheads in ponds and rivers. The experiments performed for this study should be done during all seasons of the year to see if the responses change with time of year or breeding condition. They should be repeated with first the olfactory apparatus and then the taste buds ablated to see if the response is olfactory or gustatory. It may be important to perform the experiments soon after capture of the fish since at least one set of researchers reports diminished olfactory and gustatory responses in catfish following a period of captivity (Tucker, 1973).

Experiments to locate the source of the chemical could be carried out by testing the fish's slime, urine, or organ extracts in place of water from another fish's tank.

Observations in the field are needed to establish the social life of bullheads in natural habitats and then ablation of olfactory and gustatory apparatuses could be performed on fish in these natural conditions.

CHAPTER V

CONCLUSIONS AND SUMMARY

1. When two black bullheads fight, the larger bullhead becomes the dominant fish. The sex of the fish and the resident status do not determine which fish will be dominant.

2. Both dominant and subordinate bullheads can distinguish water of other fish from their own or non-fish waters. Both exhibit higher levels of activity and more specific reactive behaviors when water of other fish is added to their tank, as compared to when their own or aged water is added; the specific reactive behaviors are arching up, swimming up in the water, raising the dorsal fin, pushing vigorously into the gravel, falling to the bottom, and banging behind the undergravel filter.

3. Subordinate bullheads respond with heightened behavioral activity levels more continuously, more vigorously, and for a longer time when water from other bullheads is added to their tanks than dominant fish do.

4. Black bullheads can recognize individual differences in other black bullheads because they respond predictably differently to water from two other bullheads. Subordinate bullheads respond with higher activity levels to dominant water than to stranger water, but dominant bullheads respond more actively to stranger water than to subordinate water.

5. Black bullheads respond differently to water from the home tanks

of other bullheads and, hence, must be able to recognize these differences by chemoreception.

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