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THE SENSORY BASIS OF SOCIAL BEHAVIOR IN THE
LARGEMOUTH BASS (MICROPTERUS
SALMOIDES)

By

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LARGEMOUTH BASS (MICROPTERUS
SALMOIDES)

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PREFACE

The objectives of this study on largemouth bass (Micropterus salmoides) social behavior were 1) to qualitatively describe motor patterns and color patterns used by bass in agonistic contexts; 2) to determine the relative importance of olfaction and the lateral line in species recognition when vision is limited; and 3) to determine the relative importance of vision, olfaction, and the lateral line in the establishment of dominance relationships.

I owe much to Dr. R. J. Miller, who served as major adviser and was a constant source of encouragement and intellectual stimulation. His patience in waiting for completion of this manuscript is appreciated. I thank Drs. L. T. Brown, W. A. Drew, and D. L. Weeks who served on the advisory committee. Special thanks is due Dr. D. L. Weeks who gave valuable assistance in design and analysis of this study. I also thank Dr. Helen C. Miller for her constructive criticism of the manuscript.

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CHAPTER I

INTRODUCTION

Since successful social interaction is dependent in large part on the perception of signals provided by conspecific animals, animal communication has been studied as an aspect of biological fitness. However, definition of the term communication has a history of controversy (Frings and Frings 1964). At the most fundamental level, debate centers on whether stimuli responded to must be controlled by the sender and directed at the receiver. Tavalga (1967) dealt with this by suggesting communication can occur at three levels of increasing control and specialization: vegetative, tonic, and phasic. In contrast, Frings and Frings (1964) would exclude from communication vegetative information transfer because of the unspecialized quality of stimuli which are simply the by-product of an organism's presence.

On another level, some ethologists deal with communication only as an intraspecific phenomenon (Frings and Frings 1964; Marler 1967) while others are willing to work with a much broader concept (Burghardt 1970). For purposes of this study, it seems best to approach communication broadly and in terms of the influence which stimuli have on a receiving animal's behavior; thus, Wilson's (1975) definition of communication as the release of stimuli which alter a receiving organism's behavior in a way which benefits one or both organisms is accepted here.

Ethologists approach communication with the tacit assumption that

animals are multichannel senders and receivers which integrate a variety of stimuli produced by other animals into meaningful information. Visual, auditory, chemical, tactile, and electrical stimuli can be combined in many ways to produce compound signals which can increase information concerning identity and internal motivational states of individuals.

However, the relative importance of each sense in a species' communication system has been shown to be dependent on the medium, microhabitat, social context, and diurnal rhythms characteristic of the group (Nelissen 1978). Consequently, study of animal communication often has centered on assessing the relative importance of different senses, and subsequently analyzing those most critical to a particular species or group.

Two experimental approaches have dominated ethological studies of relative importance of sensory systems. Most studies have been based on systematically manipulating stimuli associated with particular sensory systems and assessing the responses of test animals to stimulus configurations lacking key cues (Tinbergen 1948; Keenleyside 1971; Thresher 1976; Wells et al. 1978). Other studies have been done by manipulating sensory systems through obstruction of incoming stimuli, removal of sensory organs, and enervation of sensory systems (Gerking 1950; Todd et al. 1967). Ideally, information obtained from both of these approaches and information about the neurophysiology of the animal's sensory systems should be combined to provide more complete understanding of a communication system.

Although fish are known to communicate using visual, olfactory, tactile, auditory, and electrical signals (see excellent review by Fine

et al. 1977), most ethological studies of fish have emphasized visual and olfactory stimuli. Many studies have established the importance of visual communication in a variety of behavioral contexts. Color patterns, fin displays, body postures, and movement are important in such varied contexts as schooling (Breder and Halpern 1946; Keenleyside 1955; Hemmings 1966), aggregation (Breder and Nigrelli 1935), courtship (Miller 1964), dominance hierarchies (Frey and Miller 1972), and cleaning behavior (Eibl-Eibesfeldt 1955; Losey 1971).

Thorough documentation of visual signals as cues used in sex recognition and communication of motivational states exists for many anabantid species (Forselius 1957; Miller 1964; Picciolo 1964; Hall 1966; Miller and Rainwater 1966; Reser 1969; Wimmer 1970; Robinson 1971; and Jearld 1975) and for poeciliids (Breder and Coates 1935), cichlids (Noble and Curtis 1939; Baerends and Baerends van Roon 1950; Wickler 1964; Fernald 1977), gobiococids (Tavolga 1954, 1955, 1956), nandids (Barlow 1962), and gasterosteids (Tinbergen 1948; Morris 1958). Furthermore, use of highly specific and small scale signals (e.g., eye color and edging and shape of opercular flaps) by lepomine centrarchids has been demonstrated in several studies (Noble 1934; Greenberg 1945; Miller 1963; McDonald and Kessel 1967; Keenleyside 1971; Steele and Keenleyside 1971).

However, use of visual stimuli to organize interactions is possible only if the environment is relatively open and light transmission is sufficient to make signals visible. Yet many fish inhabit waters in which high turbidity or other obstacles obstruct the reception of socially important visual stimuli, making dependence on nonvisual signals necessary.

Until recently, studies of nonvisual communication in fish have focused primarily on the olfactory system. This is understandable since several studies have demonstrated the acuity of this sense (Walker and Hasler 1970); chemical cues will sometimes elicit behavioral responses in fish at dilutions as great as 2×10^{-11} (Pfieffer 1960; Bardach and Todd 1970).

Olfactory cues have been shown to influence a variety of behavioral phenomena in fish. Studies indicate that nest-building, development of nuptial coloration, and courtship can be induced in males by simply exposing them to water from the tank of a conspecific female or to extracts from female ovaries and genital tracts (Tavolga 1956; Mainardi and Rossi 1968; Losey 1969; Rossi 1969; Cheal et al. 1974). Furthermore, both males and females have been shown to respond positively to incurrent water from tanks containing conspecific females or conspecific spawning pairs (Gandolfi 1969; Newcombe and Hartman 1973).

Chemical signals are known to be important in nonreproductive contexts too. Both cyprinids (Von Frisch 1941; Schultz 1956) and cichlids (Kuhme 1963) exhibit a fright reaction to species-specific Schreckstoffes (fright substances) which are released by specialized epidermal cells upon injury to a fish. In addition, the cyprinid, Phoxinus phoxinus, can recognize individuals by olfactory cues (Goz 1941), a capability also possessed by Ictalurus natalis, and shown in the latter to be significant in identification of dominant fish and maintenance of stable dominance hierarchies (Todd et al. 1967; Todd 1968; Atema 1969).

The lateral line is another nonvisual sensory system which has been inferred to be involved in communication among fish. However,

the majority of studies dealing with the lateral line have dealt with physiological and morphological characteristics of the system (Denny 1937-38; Lowenstein 1957; Freihofer 1963; Peters 1971; Roberts and Ryan 1971). Other studies have concentrated on using patterns of innervation and distribution of the lateral line as a taxonomic tool (Branson and Moore 1962; Friehofer 1963).

The biological functions and relative importance of the lateral line have been subjects of controversy, with arguments centering primarily on whether sounds (Kuroki 1976) or water movements (Suckling and Suckling 1964; Dijkgraff 1967) are effective lateral line stimuli. However, most experimental data support Parker's (1903, 1905) original conclusion that lateral line organs are sensors which detect mass movements of water, and, particularly, near-field water displacements (Harris et al. 1962; Bergeijk 1967; Dijkgraff 1967).

The behavioral significance of near-field water displacements has been alluded to in a variety of studies, but little direct evidence has emerged. Detection of conspecific opponents, mates, prey, and predators have been postulated as lateral line functions (Disler 1960; Dijkgraff 1967; Kuiper 1967); yet, no one has shown this to be true. Some data also exist which suggest that the lateral line plays a role in maintaining the organization of fish schools (Hemmings 1966; Shaw 1969; Cahn 1972).

Although communication has been studied in a wide variety of fish species, few systematic studies on the relative importance of sensory systems in centrarchid social behavior have been published. The use of visual, tactile, and auditory signals by Lepomis spp. in species recognition and agonistic interaction has been studied (Miller 1963;

Gerald 1970; Keenleyside 1971), but we have only a limited knowledge about the social importance of these senses in other centrarchid species.

This is particularly true of Micropterus salmoides, the largemouth bass, a species both widely distributed and economically important. Largemouth bass have been shown to be capable of color perception (Brown 1937) and discrimination between fine monofilaments (R. J. Miller, unpubl.), but we know nothing of how these capabilities are related to social behavior. Brief references to sexually dimorphic color patterns in breeding M. salmoides (Reighard 1906), M. dolomieu (Schneider 1971), and M. punctulatus (L. Vogel, pers. Comm.) exist, but no detailed description of visual signals used by bass has been published. Even less is known about the importance of olfactory and lateral line senses in social behavior of bass.

Since largemouth bass successfully inhabit waters which range from clear to very turbid, information concerning the roles of vision, olfaction, and the lateral line in their behavior is needed to better understand how they accomplish social interactions under low visibility conditions. This study attempts to clarify the importance of vision, olfaction, and lateral line function in species recognition and the establishment of dominance hierarchies in largemouth bass.

CHAPTER II

METHODS AND MATERIALS

Materials

Largemouth bass and bluegill used in this study were captured, as needed, by angling and seining at a local farm pond and Lake Carl Blackwell. All fish were large enough to be sexually mature but displayed some variability in the condition of the reproductive organs. None, however, displayed gonadal development indicative of being in breeding condition. Individual size ranged from 17.8 to 26.0 cm; mean size was 21.24 cm.

Following capture fish were maintained first in 3.0 x 3.7 x 1.0 m concrete outdoor tanks belonging to the Oklahoma Cooperative Fishery Research Unit. Prior to use in experiments, individual fish were isolated for 3-5 days in 15-20 gal laboratory aquaria. During experiment I, fish were kept in observation tanks measuring 180 x 45 x 30 cm; in experiment II, they were kept in 90 x 45 x 30 cm tanks.

Throughout the study fish were supplied a varied diet of minnows, crayfish, frozen shrimp, mealworms, grasshoppers, and earthworms.

Terminology

Terms listed here are defined as follows:

- 1) Conspecific stimulus fish - a bass, M. salmoides, placed in a

test fish's tank as a stimulus for that test fish.

- 2) Dominant - A fish which elicits appeasement from an opponent and characteristically performs greater numbers of aggressive behaviors than an opponent.
- 3) Encounter - The series of interactions occurring between two fish during an observation period.
- 4) Heterospecific stimulus fish - A bluegill, Lepomis macrochirus, placed in a test fish's tank as a stimulus for that test fish.
- 5) "Home" end - The end of an observation tank at which a test fish spends the greatest amount of time.
- 6) Resolution - The point in an encounter at which one fish of a pair exhibits appeasement.
- 7) Subordinate - A fish which exhibits appeasement.
- 8) Test fish - A bass, M. salmoides, belonging to one of the treatment groups in this study.

Design of the Study

This study is divided into two phases: 1) an experiment to determine the importance of visual, olfactory, and lateral line senses in species recognition in M. salmoides; and 2) an experiment designed to elucidate the roles of these senses in the formation of dominance hierarchies in bass.

Experiment I

In this experiment bass were placed in water turbid enough to block vision (approximately 80 formazin units) to determine whether fish could accomplish species recognition, i.e., discriminate between

bluegill and bass despite diminished visual cues.

To assess the importance of nonvisual sensory systems in species recognition, bass in the following four treatment groups were tested on their ability to discriminate between conspecific and heterospecific fish: 1) no operation, 2) occlusion of the nares, 3) enervation of the trunk lateral line, and 4) both operations 2 and 3. Occlusion of the nares was accomplished by injecting enough silicon sealer (Dow-Corning) to completely block the flow of water through the olfactory organs. Enervation of the lateral line was done by severing the branches of the lateralis nerve. The location of the lateralis branches in M. salmoides has been described by Branson and Moore (1962) and Suckling (1967). A small branch runs just under the integument and one scale row beneath the lateral line and a larger branch is located within the transverse septum of the epaxial and hypaxial muscle masses. A small incision was made above the position of the nerves and they were severed with a small scalpel. The smaller branch was severed 2-3 cm posterior to the edge of the opercle; the larger was cut 4-5 cm from this edge. Immediately following treatment, antibiotics were topically applied to all wounds, and fish were placed in tanks for recovery. No fish developed infections or died as a result of treatment.

Prior to treatment all fish were anesthetized by placing them in a .004% by weight solution of ethyl p-aminobenzoate for 5 min. Although this anesthetic is claimed to be nontoxic even at relatively high dosages and requires only a short recovery period (McErlean 1967), several other studies have shown that fish subjected to similar anesthetic and surgical procedures require a period of up to 24 hr before exhibiting normal behavior again (Houston et al. 1973; Hart

and Summerfelt 1973; Shepherd 1970). Consequently, fish in this study were provided a 24-hr recovery period before observations began.

Though test fish were not directly visible to the observer, their behavior was monitored by means of small plastic floats (diameter approximately 1.27 cm) attached by wires and barbless hooks to the dorsum of each fish. Preliminary work demonstrated that particular motor patterns could be identified by the type of float movement occurring. The observer could, therefore, record the number of approaches, chases, and tailbeating bouts, though individual tailbeats were not distinguishable, by recording the number of times the float moved in the manner previously correlated with those behaviors.

Data were recorded on the following measures of test fish behavior: 1) number of approaches to the bass or bluegill, 2) number of times test fish chased bass or bluegill, 3) amount of time spent within 30 cm of bass or bluegill, 4) number of tailbeating bouts performed with bass or bluegill (see Chapter III for motor pattern definitions). This information was recorded in twelve 5-minute observations made at 15-minute intervals, for each fish immediately after the bass or bluegill stimulus fish was released. In addition, qualitative observations on behavior were recorded.

In summary, the general protocol was as follows: 1) four test bass were selected and anesthetized, 2) each test fish was subjected to one of the four treatments, placed in an observation tank, and given 24 hr to recover from handling and establish residency, 3) a stimulus fish, either a bass or bluegill, was placed in the holding compartment opposite each test fish's "home" end of the tank, 4) after min the stimulus fish was released into the tank, and 5) recording data began

immediately. Subsequent to this observation period, all stimulus fish were removed and test fish were left alone in the tanks overnight. The following day steps 3-5 were repeated with the other species of stimulus fish.

Several precautions were taken to avoid confounding treatment effects with other important sources of variability (Frey and Miller 1972): 1) prior to experimental procedures test fish were conditioned as dominants through exposure to smaller conspecific fish in dyadic encounters, 2) test fish were larger than stimulus fish to control size effects, and 3) to eliminate the effects of environmental novelty, test fish were given 24 hours to establish residency before exposure to the stimulus fish.

Resulting data were analyzed using statistical procedures in the SAS and MUSIC computer packages available at the Oklahoma State and Southeast Missouri State Universities.

Experiment II

A second experiment was designed to determine the relative importance of vision, olfaction, and lateral line function in interactions leading to formation of dominance hierarchies in M. salmoides. Bass subjected to identical treatments and of similar size (size differences <1 cm TL) were observed in dyadic encounters to evaluate effects of sensory deficit on development of dominance relationships.

Manipulation of olfactory and lateral line organs was accomplished using techniques described for experiment I. In experiment II, however, fish pairs were maintained in clear water, necessitating an additional experimental procedure to block vision. To simulate a turbid environ-

ment where vision is hindered but not blocked completely, translucent eyecaps were placed over the eyes of each fish. Eyecaps were constructed from commercially available "bead eyes" (WALBEAD) in the following manner: 1) curvature of plastic lenses removed from "bead eyes" was increased with a heated die, 2) lenses were made translucent by rubbing them with an abrasive, and 3) the periphery of each lens was punctured with a pin to permit escape of air trapped during application to fish's eyes. Application of eyecaps was done by anesthetizing test fish and slipping the edge of the cap beneath the bony ridge of the orbit. To reduce the possibility of eye infections, eyecaps were soaked in bactericidal and fungicidal solutions prior to use; in addition, an antiseptic wetting solution was applied to eyecaps and fish's eyes immediately before placing eyecaps in position.

Six operation groups were used: 1) no operation, 2) transparent eyecaps, 3) translucent eyecaps, 4) translucent eyecaps and olfactory occlusion, 5) translucent eyecaps and lateral line enervation, and 6) translucent eyecaps, olfactory occlusion, and lateral line enervation. Control fish (group 1) were anesthetized but otherwise unaltered; fish with transparent eyecaps were included to determine the effect of presence of eyecaps. Strict control groups for all operations were not run because of the prohibitive expense in time and fish. However, goldfish (Carassius auratus) subjected to a sham operation similar to the enervation procedure used here behaved as normal fish did, suggesting these small incisions do not appreciably disrupt behavior (Andrews 1952). A total of 10 fish (5 pairs) per operation were observed.

Subsequent to treatment, fish with identical operations were

paired and placed in separate holding compartments, each consisting of one-half an observation tank separated by removable opaque plexiglas partitions. After 24 hours, partitions were withdrawn and observations began.

Observation of each fish pair was continuous for 60 min following removal of the plexiglas partition. This observation schedule was used because previous studies have shown resolution of conflicts leading to hierarchy formation is often accomplished within the first 30 minutes of interaction (Frey and Miller 1972; Powell 1972). In addition, qualitative observations were made intermittently throughout several hours following the first observation hour and at the beginning of the second day fish were together.

During observations descriptive data and the following quantitative items (described in Chapter III) were recorded: 1) appeasement, 2) approaches, 3) bites, 4) bite bouts, 5) butts, 6) butt bouts, 7) chases, 8) coughs, 9) flights, 10) follows, 11) latency to approach, 12) latency to resolution, 13) opercle spreads, 14) quivers, 15) shambites, 16) shambite bouts, 17) tailbeats, 18) tailbeating bouts, and 19) withdraws. Observations were recorded with the aid of cassette tape recorders, and data were transcribed later to data sheets.

Statistical analysis of data were accomplished using programs available in the SAS and MUSIC computer systems in the computer center libraries of the Oklahoma State and Southeast Missouri State Universities.

CHAPTER III

DESCRIPTION OF MOTOR PATTERNS AND

COLOR PATTERNS

Motor Patterns

Largemouth bass, for the most part, perform behaviors which are characteristic of the family Centrarchidae; however, several behaviors unique to M. salmoides are described below. The following descriptions are of "typical" performances of movements and postures; during actual interactions between bass more variability in the form of a particular behavior may occur.

Appeasement

Appeasement is a complex of behaviors and may be viewed best as Miller (1963) describes it: an "attitude" which includes several different behaviors. In M. salmoides the components of appeasement include hovering depth, body orientation, pattern of movement, and color pattern. Subordinate bass remain practically motionless in the upper half of the water with fins often folded and the tail slightly elevated. Elevation of the tail is variable but is closely associated with the proximity of the dominant fish and the intensity of interaction. As an approaching dominant nears, the subordinate assumes a more acute angle in the water, lists away from the dominant, and ascends toward the surface. On occasion a subordinate will list so greatly that the body

rolls over completely. In addition, appeasement sometimes includes both an upward curvature in the peduncle, which raises the caudal fin, and a sigmoid body posture.

The behavior which a dominant bass exhibits in response to this "attitude" on the part of the subordinate, creates questions concerning the validity of using the term appeasement to describe the effects of this complex of behaviors. Appeasement implies an attempt to reduce attack behavior in the dominant fish; yet, these subordinate behaviors seem to cause no qualitative change in the tendency of dominant bass to butt, bite, and tailbeat. Even when subordinates assume extreme appeasement postures, the dominant often delivers severe bites and strong tailbeats. However, since the term appeasement has been in general usage for some time it is also used here.

Bite

A bite is a movement in which a fish uses the jaws to grasp or scrape some portion of another fish's body. Bites are directed at a variety of points on the recipient fish's body, but commonly are aimed at the opercular or lateroventral areas. Fins, particularly the anal, and the jaws of the recipient are sometimes grasped. In one instance, a biting fish seized the head of a smaller recipient fish. Biting is the most injurious movement performed by these fish and may lead to shredding of interradiial membranes, removal of scales, and epidermal hemorrhaging.

Butt

A butt is a movement in which an approaching fish terminates its

forward movement by ramming, with the mouth closed or only slightly open, against the body of an opponent. Although a few butts are directed at the opponent's head or caudal peduncle, most are administered to the opercular and lateral body regions. The delivery force of butts varies, ranging from gentle nudges to hard, striking blows which rock the opponent's body. Butting typically follows a slow, deliberate approach.

Quiver

Quivering, which is not reported for other centrarchids in agonistic contexts, is performed almost exclusively by subordinate fish. Quivering is a rapid vibration of the body given while descending. This behavior occurs during rather intense interaction and most often follows a series of rapid approaches and severe bites by the dominant fish. In a typical sequence of events leading to quivering, the dominant fish approaches and bites the subordinate, which then assumes or accentuates an appeasement posture; the dominant fish then delivers several butts and bites and swims to a position beneath the subordinate which then quivers and descends upon the dorsum of the dominant fish. Quivering sometimes continues after contact with the dominant's dorsum. The position of the dominant varies and occasionally the dominant may bite or butt the side of a quivering fish.

Sham Bite

A sham bite occurs when an approaching bass stops approximately 2-3 cm from another bass and performs a biting movement which does not make contact. In this movement, the jaws may be slowly closed or

snapped sharply together. No attempt is made by the approaching fish to grasp any part of the recipient fish's body. During sham biting, the biting fish faces the lateral anterior region of the recipient fish, bringing the jaws in proximity to the recipient's lateral line. This behavior occurs following establishment of dominance.

Spit

Spitting is another behavior not described for other centrarchids. A spit, which usually occurs following a slow approach, is an expulsion of water from the buccal cavity. The propulsive force of the ejected water is provided by a quick snapping movement which opens the jaws widely while the opercles are appressed. A spitting fish characteristically swam to within approximately 2-3 cm of the lateral portion of the recipient fish's body, and quickly snapped the jaws open. The force of the ejected water sometimes rocked the recipient fish's body. Spitting was performed only by dominant fish.

Tailbeat

A tailbeat is a forceful undulation of the caudal peduncle and fin, presumably to direct a wave of water toward an opponent. Sometimes, tailbeating results in the caudal fin slapping against an opponent's body. Although the power and number of these strokes are variable, a tailbeating sequence of 2-4 strokes is most common.

During tailbeating, the relative positions of the two fish fall primarily into two categories, the parallel head-to-head and parallel head-to-tail positions. Of these two categories, the parallel head-to-head occurs most frequently. However, once the dominant-subordinate

relationship has been established, the dominant may perform tailbeats from a position beneath and at approximately a 90° angle to the subordinate. In this position, the dominant may list slightly to direct the displaced water upward at the subordinate fish. This change from the more typical parallel positions seems to be required because subordinate fish are often near the surface of the water.

During especially forceful tailbeating, the body of the fish tends to become elevated at the head and to move upward and forward. This movement is counteracted by opposing movements of the pectoral fins.

Bout

A bout consists of a series of one motor pattern which is preceded and succeeded either by other motor patterns or time intervals sufficiently long to make the series appear clustered. Bouts may consist of a motor pattern series performed by only a single individual or a sequence of motor patterns performed alternately or simultaneously by both fish in a pair.

Withdrawal

During agonistic interaction either the dominant or subordinate bass, more often the former, may turn and slowly swim away without being chased. Withdrawals usually occur well after a hierarchy has been formed.

In dominant fish withdrawal separates bouts of agonistic activity into discrete units. A dominant fish will approach the subordinate, perform an agonistic behavior, then turn and withdraw to the far end

of the observation tank. Subsequently, the dominant reapproaches and the sequence is repeated. Withdrawal by a subordinate fish is very slow, is limited to the upper water levels, and is accomplished with a minimum of fin and body movement.

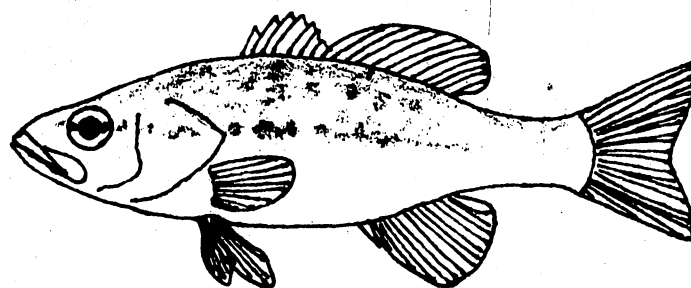
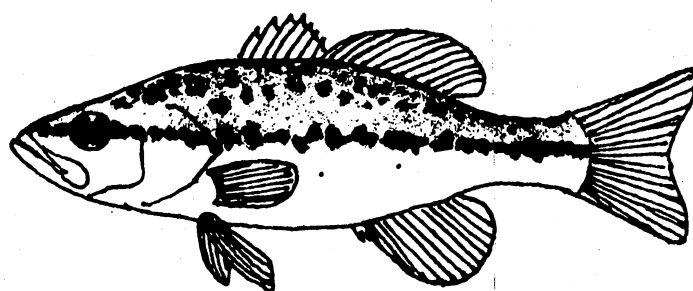
Color Patterns

As in other centrarchid species, bass color patterns are closely linked to particular complexes of behaviors. During agonistic interactions changes in color pattern and accompanying behavior are indicative of the position of that fish in the dominance hierarchy. Subordinate fish characteristically display a dark iris, mottled upper body, and a dark lateral stripe (see Figure 1). Change to this color pattern begins gradually and is first noticeable in the darkening of the lateral stripe followed by an increasingly visible pattern of mottling over the body. The fully developed coloration of a subordinate can be described as a heavy pattern of black mottling on a greenish background, a distinct black lateral stripe, and a black iris.

The color pattern of a dominant bass is opposite the coloration of subordinates. Dominant bass maintain a rather silvery body with a slight amount of mottling and an extremely diffuse or absent lateral stripe. The iris is never completely black and often displays reddish brown areas.

At the initiation of agonistic interactions both fish exhibit color patterns similar to those described for dominant bass. However, as interaction proceeds, color patterns progressively change in the direction of the coloration associated with the hierarchy position each fish eventually assumes.

Figure 1. Typical color patterns in subordinate (top)
and dominant (bottom) Micropterus salmoides.



CHAPTER IV

QUALITATIVE DESCRIPTION OF ACTIVITY IN

EXPERIMENT I TEST FISH

After being subjected to treatments and placed in observation tanks for recovery, qualitative observations on all test fish were begun. Shortly after entering the tanks, all test fish began to swim up and down the length of the tank for up to 30 min. The fish appeared to be exploring the observation tank environment. As time passed, they usually spent increasing amounts of time at one end of the tank, and finally positioned themselves there. For the remainder of the 4-hr observation period, test fish tended to use this end of the tank as a "home" position.

The only consistent exception to the pattern of behavior occurred in deolfacted-lateral line-enuvated fish. Although these fish established a "home" end of the tank, they patrolled the tank for longer periods of time, sometimes continuing this behavior for the total observation period. Only one test fish in this group remained relatively inactive and at one end of the tank.

No qualitative differences in swimming motions could be detected among test fish groups. However, lateral line-enuvated and deolfacted-lateral line-enuvated fish tended to swim along the sides of the tank rather than in the center of the tank as control and deolfacted fish did. Other than this, swimming motor patterns of normal and treated

fish appeared similar.

All test fish were provided minnows for food prior to the release of stimulus fish in the tanks. To restrict swimming of the minnows, their caudal fins were removed, resulting in rapid beating of the peduncle without propulsion. All control and deofactored fish located minnows with ease and ingested them. Most of the lateral line enervated fish and deofactored alteral line enervated fish were slower locating the minnows, but once they determined the position of a minnow, they almost always captured it.

Although description of the behavior of the stimulus fish was not a major objective of this study, several differences between the two groups were noted. Upon release from the holding compartment, bluegill typically moved about the tank until nearing the test fish.

Following release, stimulus bass also moved about the tank; however, when approached by the test fish these stimulus fish tended to interact rather than flee. During early encounters with the test fish, conspecific stimulus fish often engaged in tailbeating bouts and sometimes initiated activity by approaching the test fish. Subsequent to be dominated by the test fish, however, stimulus bass usually remained at the end opposite the "home" position of the test fish. Thereafter, stimulus bass rose to the surface when approached by test bass or fled when attacked severely.

Comparison of Test Fish Groups

Responses of test fish groups to stimulus fish differed qualitatively. Control and deofactored fish responded quickly to both types of stimulus fish. In addition, they approached stimulus fish in a

direct manner, i.e., rapidly and linearly. Once stimulus fish were restricted to a particular corner opposite the "home" end of the tank, control and deolfacted fish would rapidly approach this corner, locate the stimulus fish, and initiate interaction.

Approaches of lateral line-enuvated and deolfacted-lateral line-enuvated fish were slower and less direct. These test fish also had more difficulty locating stimulus fish which were not actively moving about; several times approaching test fish did not detect slowly withdrawing stimulus fish. During later observations, however, all test fish approached in a rather deliberate, direct manner.

Differences existed in the way test fish from different groups accomplished these approaches, however. Control and deolfacted test fish performed these approaches by swimming toward the stimulus fish's end of the tank, orienting to and nearing the stimulus fish. Lateral line-enuvated and deolfacted-lateral line-enuvated fish seemed to direct their later approaches to the location most frequently occupied by the stimulus fish, even though the stimulus fish may have moved elsewhere.

Differences also existed between test fish in their performance of tailbeating bouts. Control, deolfacted, and deolfacted-lateral line-enuvated bouts with bass were more intense than those with bluegill. On several occasions, conspecific bouts in each of these groups resulted in the water surface being broken. Lateral line-enuvated test fish engaged in tailbeating bouts much less frequently and never at the intensity demonstrated in other test fish groups.

Patterns of chasing also suggest qualitative differences between

test fish groups. Chases performed by control and deolfacted fish usually effectively restricted stimulus fish to one corner of the tank. During chases, these test fish rapidly pursued stimulus fish at a distance of approximately 5 to 10 cm for the complete length of the tank, eventually cornering them. In contrast, chases performed by lateral line-enervated and deolfacted-lateral line-enervated fish were of shorter duration and often were terminated when a distance of more than 15-20 cm separated the two fish. At distances greater than this, these test fish seemed to become disoriented with respect to the position of the stimulus fish.

The effectiveness of butts and bites, determined by severity of injuries to the body of the stimulus fish, also varied among groups. Control test fish generally inflicted more injury on stimulus fish than other test fish did. On one occasion, a bluegill was killed within the first hour by a control fish; on others, stimulus fish had many scales removed and displayed epidermal hemorrhaging. No other test fish group killed or so extensively injured stimulus fish.

Description of Typical Encounters

A short time after release of the stimulus fish, control fish oriented to and slowly approached this fish. Approach was typically followed by the stimulus fish withdrawing while the test fish swam almost parallel to or slightly behind it. Subsequently, test fish usually returned to the "home" end of the tank and reapproached the stimulus fish several times. These subsequent approaches tended to become more rapid and direct and began to terminate in tailbeating bouts. Bouts with bluegill characteristically were of short duration

due to flight of the stimulus fish; bouts with bass were longer because these stimulus fish responded initially with reciprocal tailbeats.

After a period of approaching and tailbeating, control fish usually began to direct butts and bites at stimulus fish. Though these were not always observable in float movements, some butting and biting could be detected when fish were interacting near the surface. In every case, this led to appeasement by stimulus bass and flight by stimulus bluegill.

During subsequent observations, control test fish would alternately swim to the "home" end of the tank and reapproach the stimulus fish, reinforcing the dominant-subordinate relationship. Once dominated, stimulus bass generally remained still near the surface in one corner of the tank. In contrast, bluegill sometimes wandered into the "home" area.

Deolfacted test fish interacted with stimulus fish in a manner similar to control fish. These fish approached both types of stimulus fish soon after their release and began tailbeating bouts. Chasing, butting, and biting also were qualitatively similar to these behaviors in controls.

Lateral line-enervated fish interaction sequences with stimulus fish differed in several ways from those of control fish. First, though test fish in this group often began approaching active stimulus fish within the first 5 min of observation, they did not do so when stimulus fish were relatively inactive. Furthermore, these test fish seldom progressed to tailbeating, but continued to approach and withdraw, with some intermittent butting and biting, for the duration of

the observation period. Unlike control fish, there also seemed to be no qualitative difference in the intensity of interactions of lateral line-enuvated fish with bass and bluegill. In general, this test fish group was less active than any other group.

Encounters of deolfacted-lateral line-enuvated test fish with stimulus fish were distinctly different from all other test fish groups. Since these fish spent a considerable amount of time traversing the length of the tank, all but three individuals moved into proximity of stimulus fish within the first two 5-min observations. However, first approaches were sometimes due to encountering a stimulus fish on one of these traverses, rather than the result of orienting to and swimming directly toward a stimulus fish. Subsequent approaches to bass led to tailbeating, but unlike control fish interactions did not result in rapid domination of stimulus fish. Instead, stimulus bass moved more freely through the tank, even occasionally, during later observations, approaching test fish and initiating tailbeating bouts. In one test fish encounter with a stimulus bass it was difficult to determine which fish was dominant.

In contrast to other test fish groups, interactions involving deolfacted-lateral line-enuvated fish and stimulus bass tended to increase in intensity over the observation period. In later observations, butting and biting by test fish appeared to become more forceful, sometimes jolting the stimulus fish. Moreover, bouts of what appeared to be rapid circling and reciprocal biting occurred between test fish and stimulus bass during hours 3 and 4.

Several hours after conclusion of the regular observation procedure, two 10-min qualitative observations of test fish activities were

conducted. These indicated that test fish in control, deolfacted, and lateral line-enuvated groups were no longer interacting with stimulus fish as much as in early observations. Deolfacted-lateral line-enuvated fish, which were the only group to continue approaching stimulus fish with frequency, did so in a rhythmic pattern. Hierarchy relationships established during earlier observations persisted through later observations.

CHAPTER V

QUANTITATIVE ANALYSIS OF EXPERIMENT I

Initially, overall means for each variable were compared using an analysis of variance to determine main effects and interactions for the 4(operation) x 2(sex) x 2(order of presentation of stimulus fish) factorial design. Subsequently, T tests were used to compare mean test fish responses per 5-minutes to conspecific and heterospecific stimulus fish within each operation group. In addition, regression of mean number of responses per 5-min on hour during which the observations were made was determined for each operation group to reveal any time dependent qualities of the data. Statistically significant differences ($p = .05, .01$) are followed with the associated p-value in parentheses. Differences which are not statistically significant, but which appear to have biological meaning, are noted as data trends.

Eight dependent variables were analyzed: number of approaches to bass (APC), number of approaches to bluegill (APH), number of tailbeating bouts with bass (TBC), number of tailbeating bouts with bluegill (TBH), number of chases with bass (CHC), number of chases with bluegill (CHH), time spent within 30 cm of bass (TMC), and time spent within 30 cm of bluegill (TMH). In addition, behavior rates (e.g., APC/TMC) were computed and compared.

Approach

Approach is obviously a necessary component of exploratory behavior; thus, test fish responsive to the introduction of a stimulus fish into the tank were expected to approach both bass and bluegill. However, test fish which recognized differences between the two stimulus fish were expected to approach bass more often than bluegill. APC and APH means are presented in Figure 2.

Analysis of variance for APC showed no statistically significant main effects or interactions. However, APC means for operation groups reveal a trend, consistent with other variables, which appears to be biologically meaningful. Although control test fish were expected to approach bass most frequently, deolfacted-lateral-line-enuvated test fish exhibited the highest mean number of approaches to conspecific fish ($\bar{X}=5.00$). Control and deolfacted test fish performed slightly fewer approaches than this ($\bar{X}=3.5486$ and 3.4091 , respectively), while lateral line-enuvated test fish approached conspecific fish the least number of times ($\bar{X}=2.0347$).

These data suggest that deolfacted-lateral line enuvated test fish had a higher tendency to approach bass than any other group did. However, since APC values do not reflect the possibility that two fish with identical APC means may differ in the number of approaches performed per unit TMC, these ratios were computed to determine whether rate of approaching differed among test fish groups (Table 1). This transformation reveals that control test fish displayed the highest APC/TMC (17.04). Remaining test fish groups now assume the following decreasing order of APC/TMC values: deolfacted (14.91), deolfacted-lateral line-enuvated (13.21), lateral line-enuvated (7.79). Con-

Figure 2. Bar graph of APC and APH means for the 4-hour observation period (C=control, DO=deolfacted, LE=lateral line-enervated, DOLE=deolfacted-lateral line-enervated).

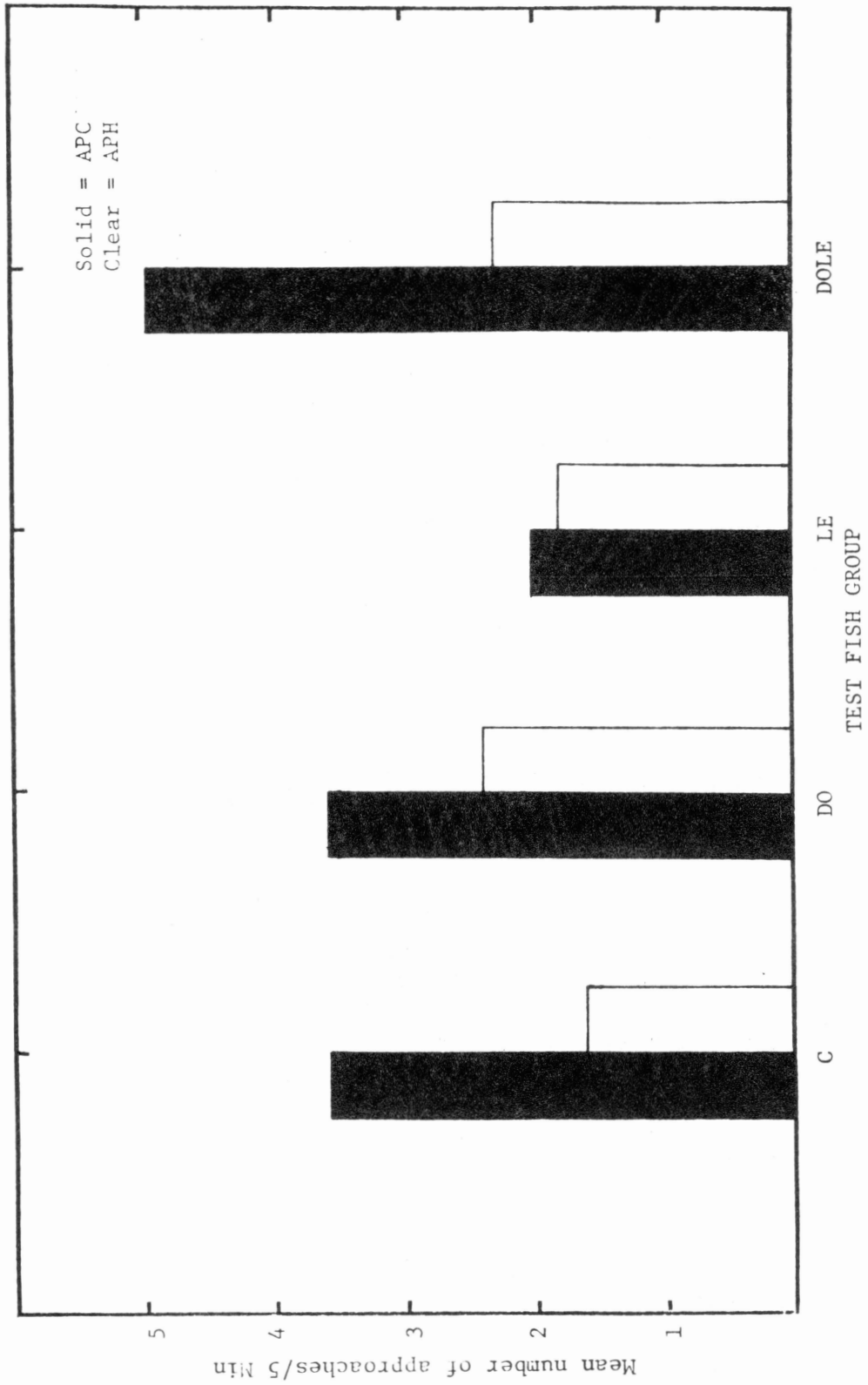


Table 1. Mean number of approaches per 5 minutes spent together.

Group	APC/TMC	APH/TMH
Control	17.04	9.43
Deolfacted	14.91	8.47
Lateral line enervated	7.79	9.80
Deolfacted-lateral line enervated	13.21	7.76

sequently, although control and deolfacted test fish performed fewer conspecific approaches than deolfacted-lateral line-enuvated fish, they used less time per approach.

Analysis of variance for APH values also detected no statistically significant main effects or interactions. Comparison of APH means for operation groups reveals that considerably less difference exists between these values than between APC means (Figure 2).

As with APC means, rates were compared by computing APH/TMH for each operation group (Table 1). Differences among operation group APH/TMH values are small, suggesting that operation groups treated heterospecific fish quite similarly.

Comparison of APC and APH means within operation groups demonstrates that, with the exception of lateral line-enuvated fish, test fish tended to approach bass more often than bluegill. T test results (Table 2) for within group comparisons indicate that only control and deolfacted-lateral line-enuvated test fish exhibited APC and APH means sufficiently different to achieve statistical significance ($T=2.064$, 2.433 , $p=.049$, $.025$, respectively). Deolfacted test fish also tended to approach conspecific fish more often, but this difference is not statistically significant. In contrast to these test fish groups, lateral line-enuvated test fish treated the two types of stimulus fish almost identically.

Consideration of overall APC and APH means alone may mask differences in the way in which fish distributed these behaviors over the 4-hr observation period. To determine whether such differences did exist, regression of APC and APH on hour was computed and least squares lines of best fit were drawn for each test fish group (Figures 3, 4, 5,

Table 2. T test results from comparisons of APC and APH means.

Group	APC	APH	df	T	P
Control	3.548	1.597	22	2.06434	.049
Deolfacted	3.409	2.409	20	0.78210	.4
Lateral line enervated	2.035	1.819	22	0.24684	.5
Deolfacted- lateral line enervated	5.000	2.271	22	2.43274	.025

Figure 3. Plot of regression of APC (solid line) and APH (dashed line) on hour for controls. Circles are observed hourly means (solid=APC, clear=APH).

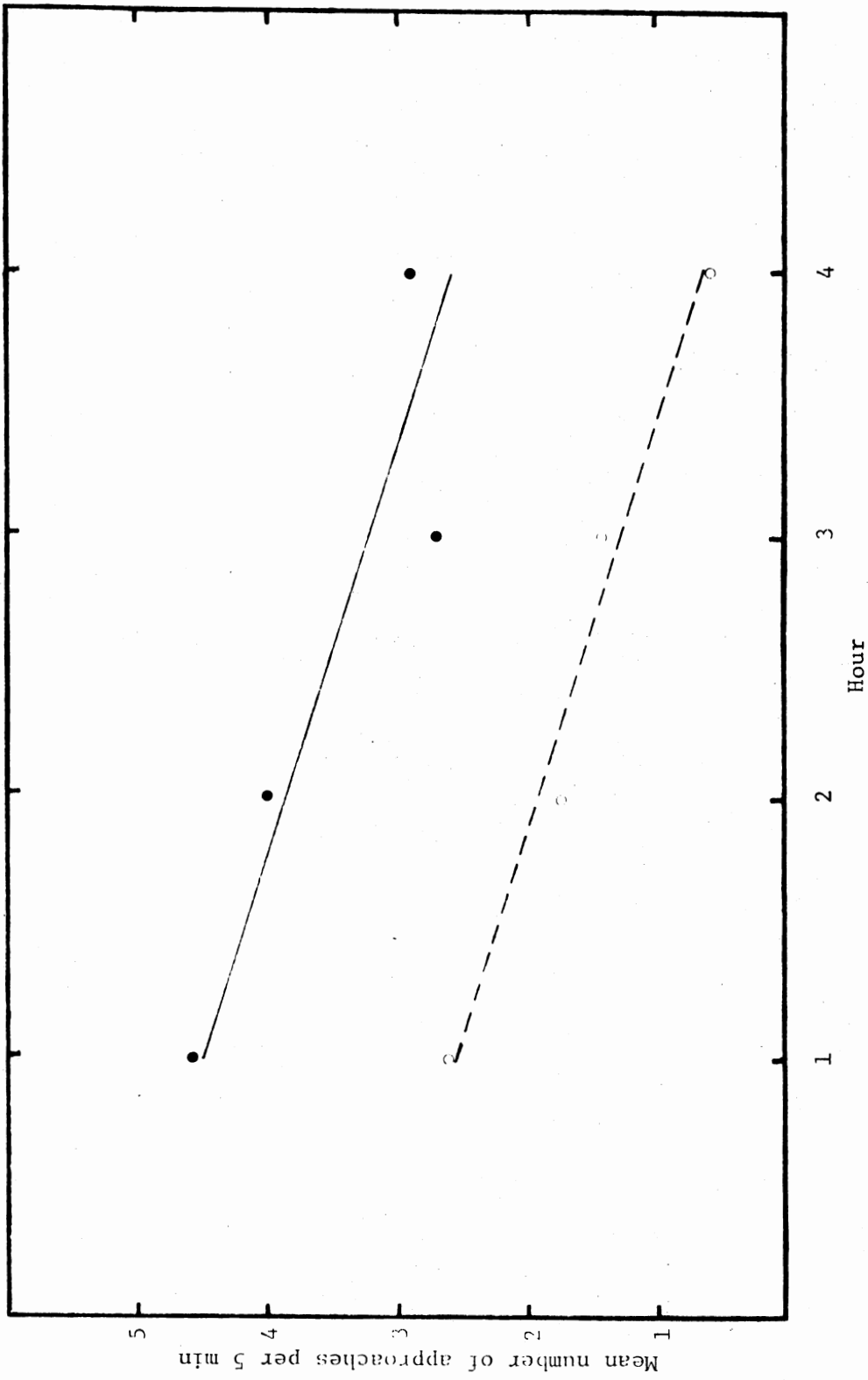


Figure 4. Plot of regression of APC (solid line) and APH (dashed line) on hour for deolfacted fish. Circles are observed hourly means (solid=APC, clear=APH).

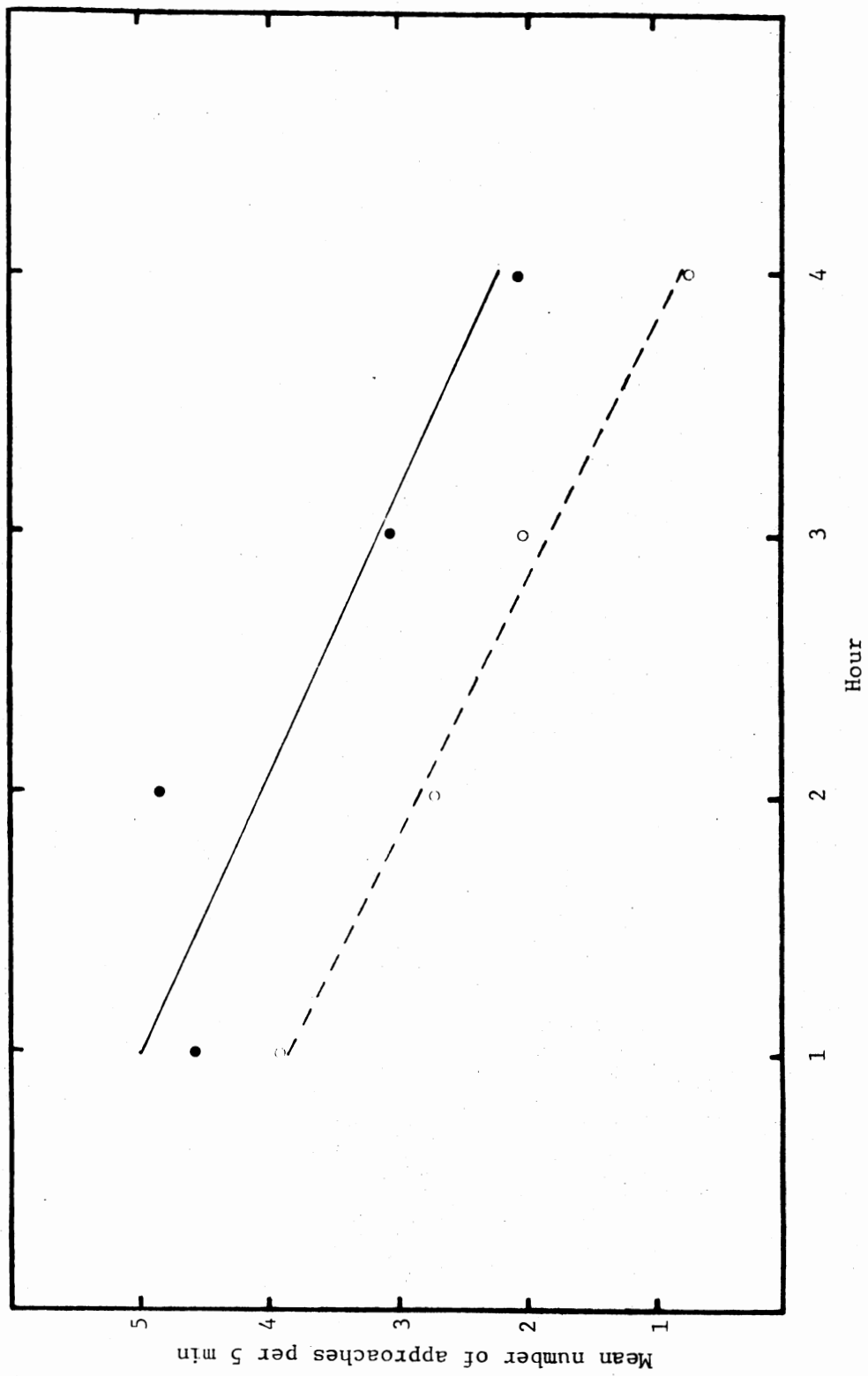


Figure 5. Plot of regression of APC (solid line) and APH (dashed line) on hour for lateral line enervated fish. Circles are observed hourly means (solid=APC, clear=APH).

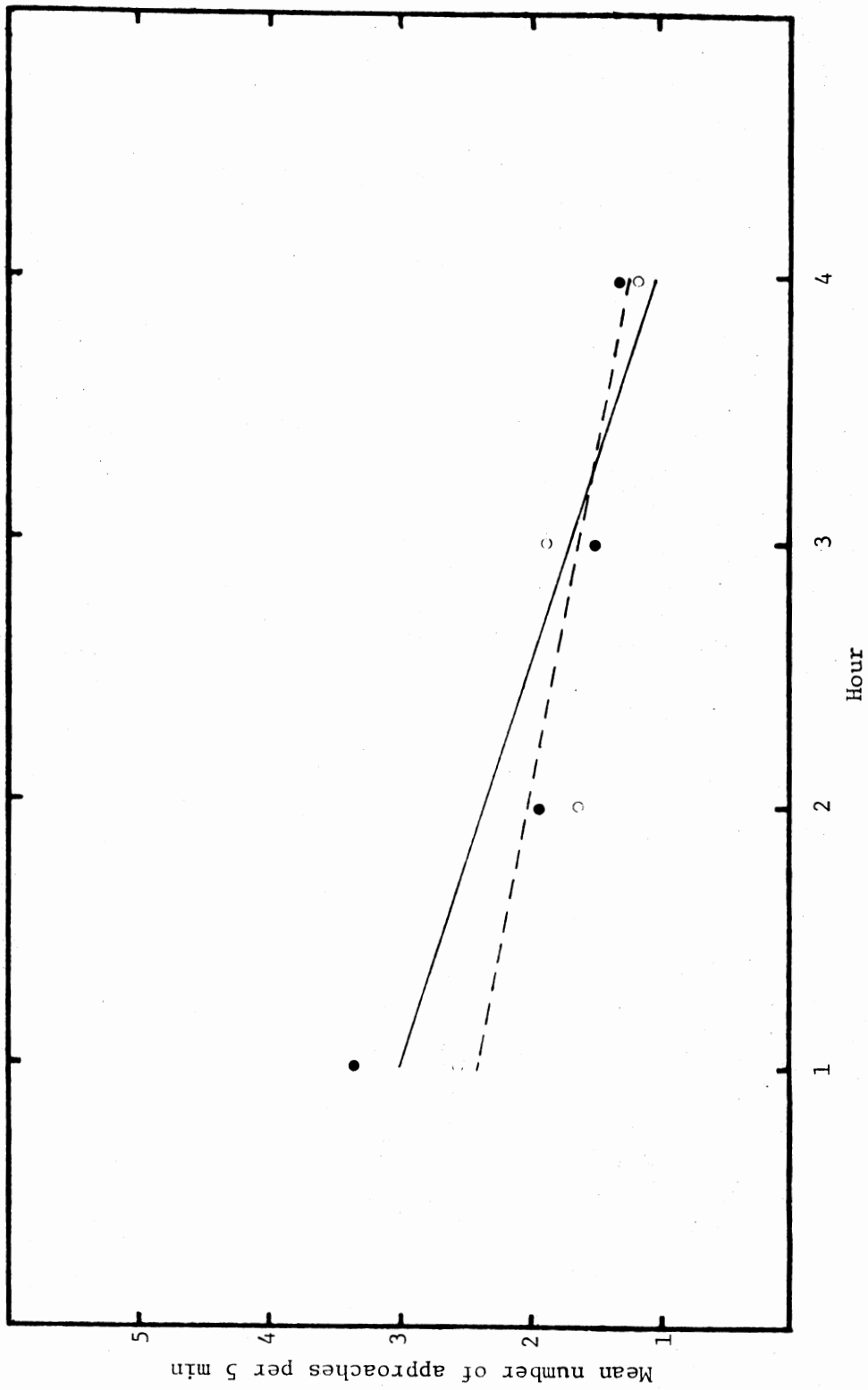
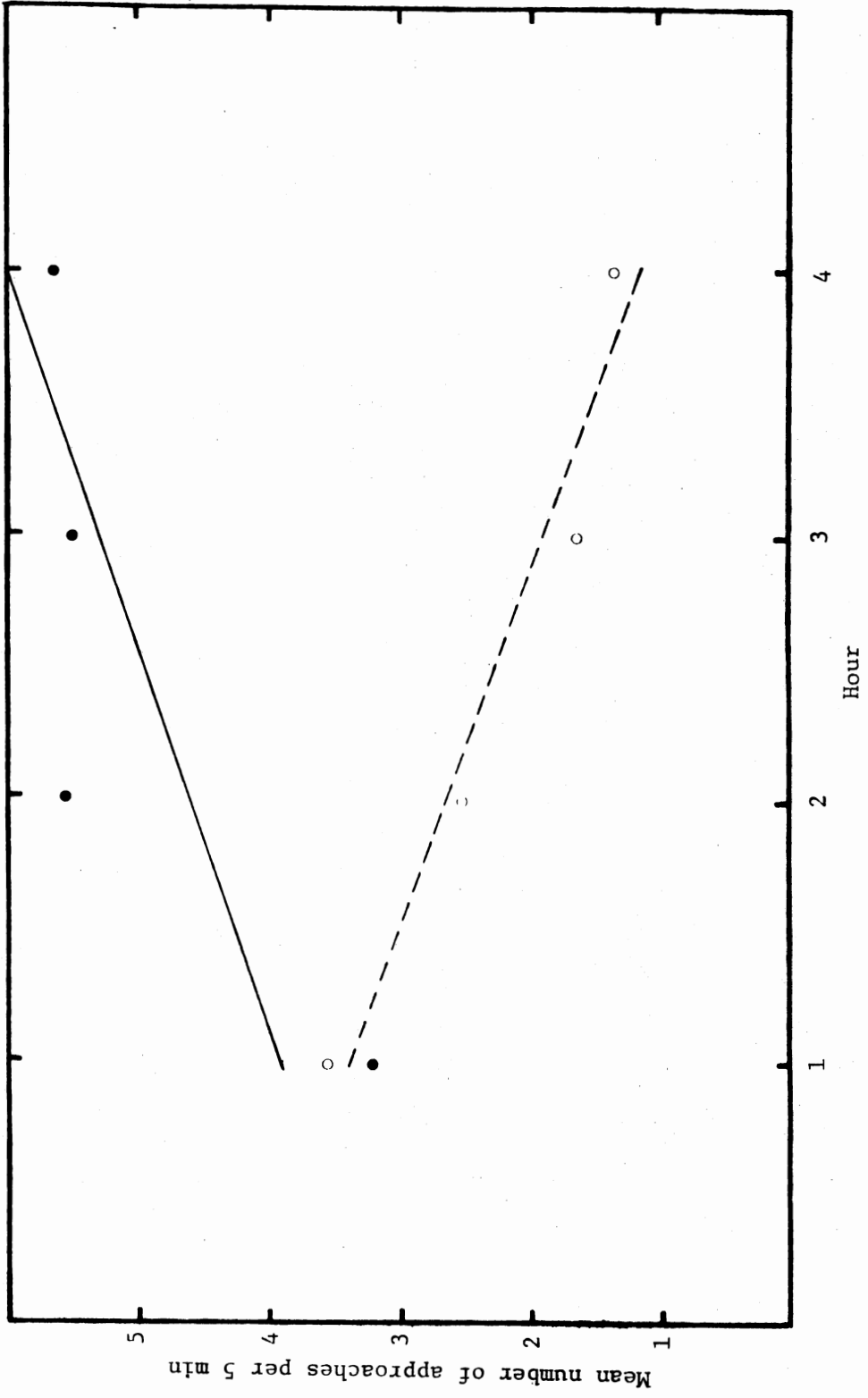


Figure 6. Plot of regression of APC (solid line) and APH (dashed line) on hour for deolfacted-lateral line-ennervated fish. Circles are observed hourly means (solid=APC, clear=APH).



and 6). Regression coefficients were then compared among groups using the F test to determine whether slopes for the 4-test fish groups were significantly different.

Regression analyses show that distinct differences did exist in the way in which test fish from different groups distributed approaches over time. Differences among APC slopes are significantly different ($p < .05$) and reflect the fact that test fish tended to fall into two groups. Control, deolfacted, and lateral line-enuvated test fish were similar and exhibited a rather consistent decline in mean APC values over the 4-hr period ($r = -.9187, -.9144, -.9148$; $b = -1.915, -2.791, -1.957$ approaches/5-min, respectively). In striking contrast, deolfacted-lateral line-enuvated test fish were characterized by an hourly increase in mean APC values ($r = .7918$; $b = 2.182$). Thus, these fish appear to be qualitatively different from the first three groups in their tendency to interact with conspecific stimulus fish.

APH regression slopes were also different ($p < .05$). Here, however, all test fish groups performed a decreasing number of approaches to bluegill over time. The general pattern of distribution of approaches to heterospecific fish was at least somewhat similar.

Examination of APC and APH regression lines within each test fish group establishes that control, deolfacted, and deolfacted-lateral line-enuvated fish consistently tended to approach bass more often than bluegill. Unlike control and deolfacted fish, however, deolfacted-lateral line-enuvated fish began to do this at hour 2 rather than hour 1. APC and APH regression lines for lateral line-enuvated test fish lie close together, suggesting that they did not approach bass and bluegill at dissimilar rates.

Tailbeating Bouts

Since the actual number of tailbeats could not be observed, only the number of tailbeating bouts were recorded. Consequently, although comparative information concerning the tendency of different test fish to engage in tailbeating is available, this measure does not reveal whether one group performed more tailbeats per bout than any other group did. Tailbeating bouts are, nevertheless, a useful measure of the tendency of fish to participate in agonistic activities with a stimulus fish.

When overall TBC means for test fish groups are compared, the relative differences among groups are similar to those for APC means (Figure 7). This is to be expected since an approach generally precedes a tailbeating bout. Deolfacted-lateral line-enervated test fish performed the highest mean TBC ($\bar{X}=1.18$). Control and deolfacted test fish exhibited very similar TBC means ($\bar{X}=.75$ and $.73$, respectively), while lateral line-enervated fish had a very low TBC mean ($\bar{X}=.11$).

Conversion of TBC means to TBC per unit TMC shows that control test fish performed the highest mean number of bouts per 5-minutes spent with another bass (Table 3). As with APC data, the similarity between control, deolfacted, and deolfacted-lateral line-enervated fish group means, and their difference from the lateral line-enervated group mean, suggests that enervation of lateral line has the greatest effect on the total number of bouts performed by a fish.

TBH means for all test fish groups are similar and very small, indicating a low tendency in all test fish to tailbeat with bluegills (Figure 7). Transformation of TBH means to TBH per unit TMH values also indicate that all test fish groups seemed to perform tailbeating

Figure 7. Bar graph of TBC and TBH means for the 4-hour observation period (C=control, DO=deolfacted, LE=lateral line-enervated, DOLE=deolfacted-lateral line-enervated).

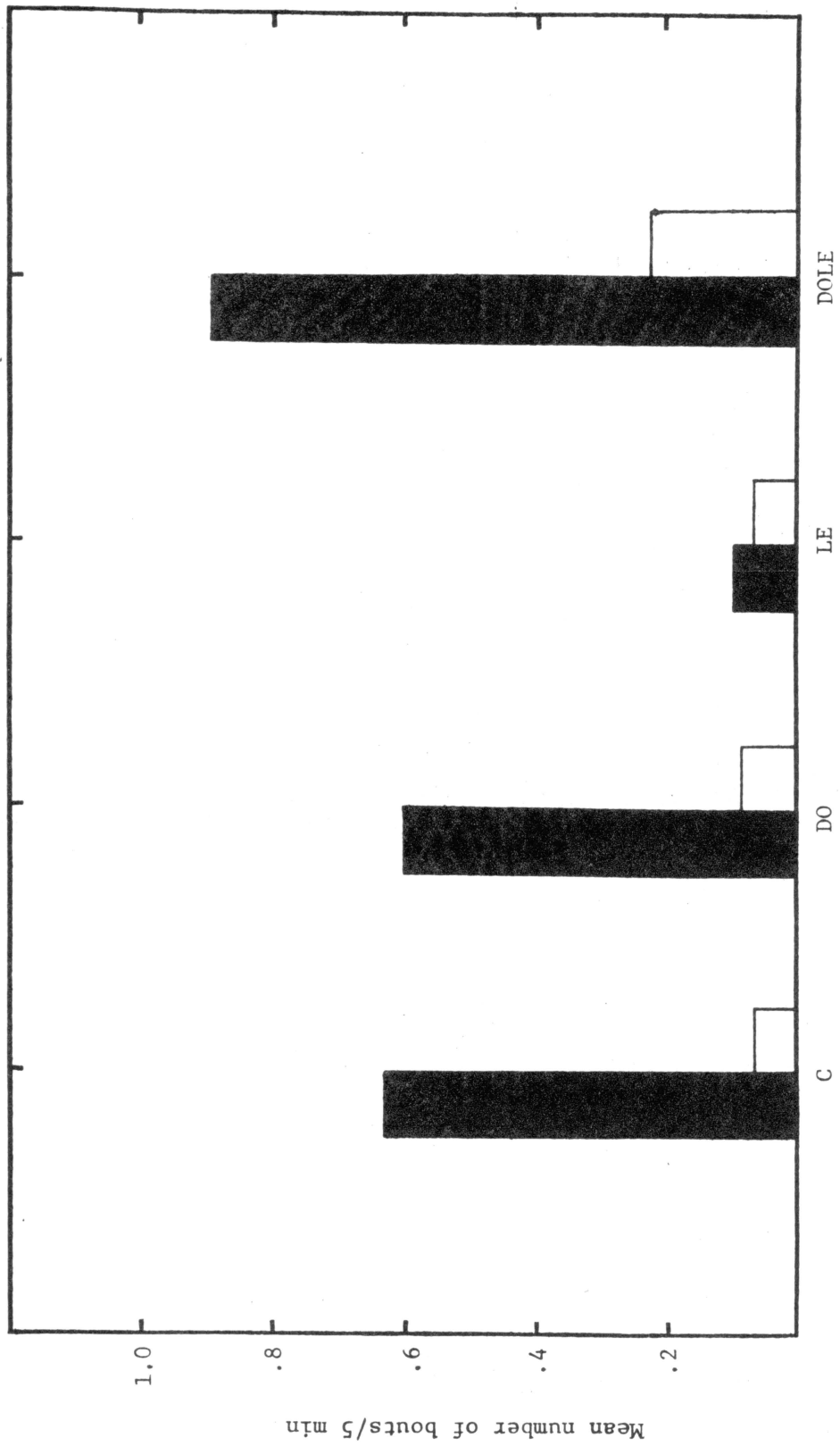


Table 3. Mean number of tailbeating bouts per 5-minutes spent together.

Group	TBC/TMC	TBH/TMH
Control	3.47	0.37
Deolfacted	3.23	0.31
Lateral line enervated	0.44	0.43
Deolfacted-lateral line enervated	3.13	0.92

bouts with bluegill at approximately the same rates (Table 3).

Since tailbeating is a behavior which occurs typically between conspecifics, test fish were expected to perform more bouts with bass than with bluegill. T tests (Table 4) computed to evaluate differences between TBC and TBH means within test fish groups, reveal that only control and deolfacted-lateral line-enervated test fish exhibited statistically significant differences ($T=2.302, 2.313; p=.05, .05$, respectively). Although this difference is not statistically significant for deolfacted fish, this group appears to be somewhat similar to control and deolfacted-lateral line-enervated groups. Lateral line-enervated test fish exhibited the smallest difference between TBC and TBH means.

To reveal any patterns of distribution of bouts performed per 5-min over the 4-hr period, regression of TBC on hour was calculated and least squares lines of best fit were drawn (Figures 8-11). Using an F test, slopes for test fish groups were then compared.

Analysis of TBC data revealed that regression coefficients differed significantly among groups ($p<.01$). Control and deolfacted test fish exhibited a decrease in mean number of bouts performed over the 4 hours ($r=-.8925, -.9444; b=-.2557, -.3137$, respectively). Lateral line-enervated test fish also performed a decreasing number of bouts over time ($r=-.7924; b=-.0469$) but differ from the first two groups in their considerably lower hourly means. Unlike other groups, deolfacted-lateral line-enervated fish engaged in an increasing number of bouts over time ($r=.9713; b=.1780$), indicating again that this group was different from the others in the pattern of distribution of motor patterns over time.

Table 4. T test results from comparisons of TBC and TBH means.

Group	TBC	TBH	DF	T	
Control	.750	.067	18	2.3024	.05
Deolfacted	.725	.092	18	1.8799	.10
Lateral line enervated	.108	.075	18	0.6236	.60
Deolfacted- lateral line enervated	1.183	.258	18	2.3131	.05

Figure 8. Plot of regression of TBC (solid line) and TBH (dashed line) on hour for control fish. Circles are observed hourly means (solid=TBC, clear=TBH).

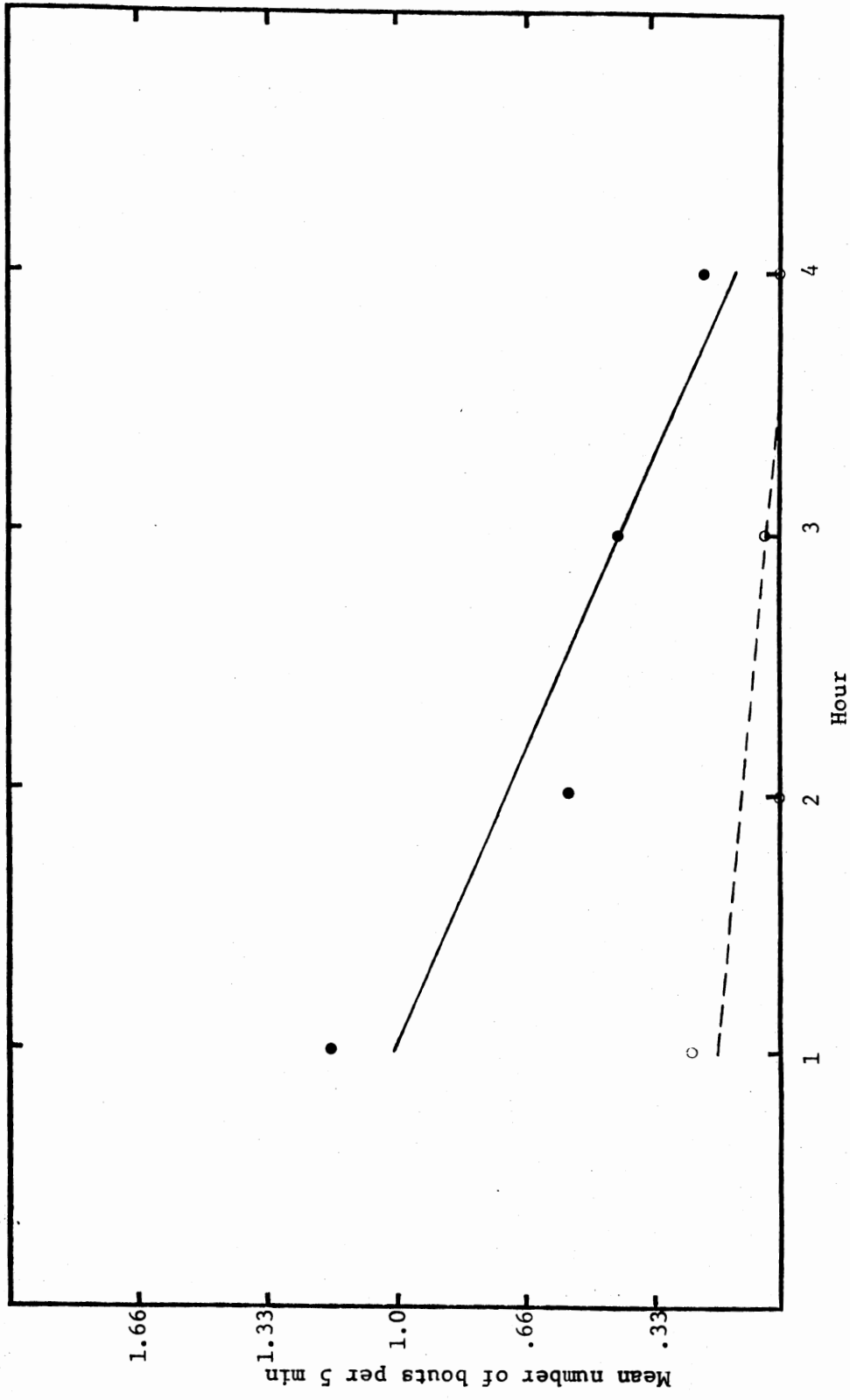


Figure 9. Plot of regression of TBC (solid line) and TBH (dashed line) on hour for deolfacted fish. Circles are observed hourly means (solid=TBC, clear=TBH).

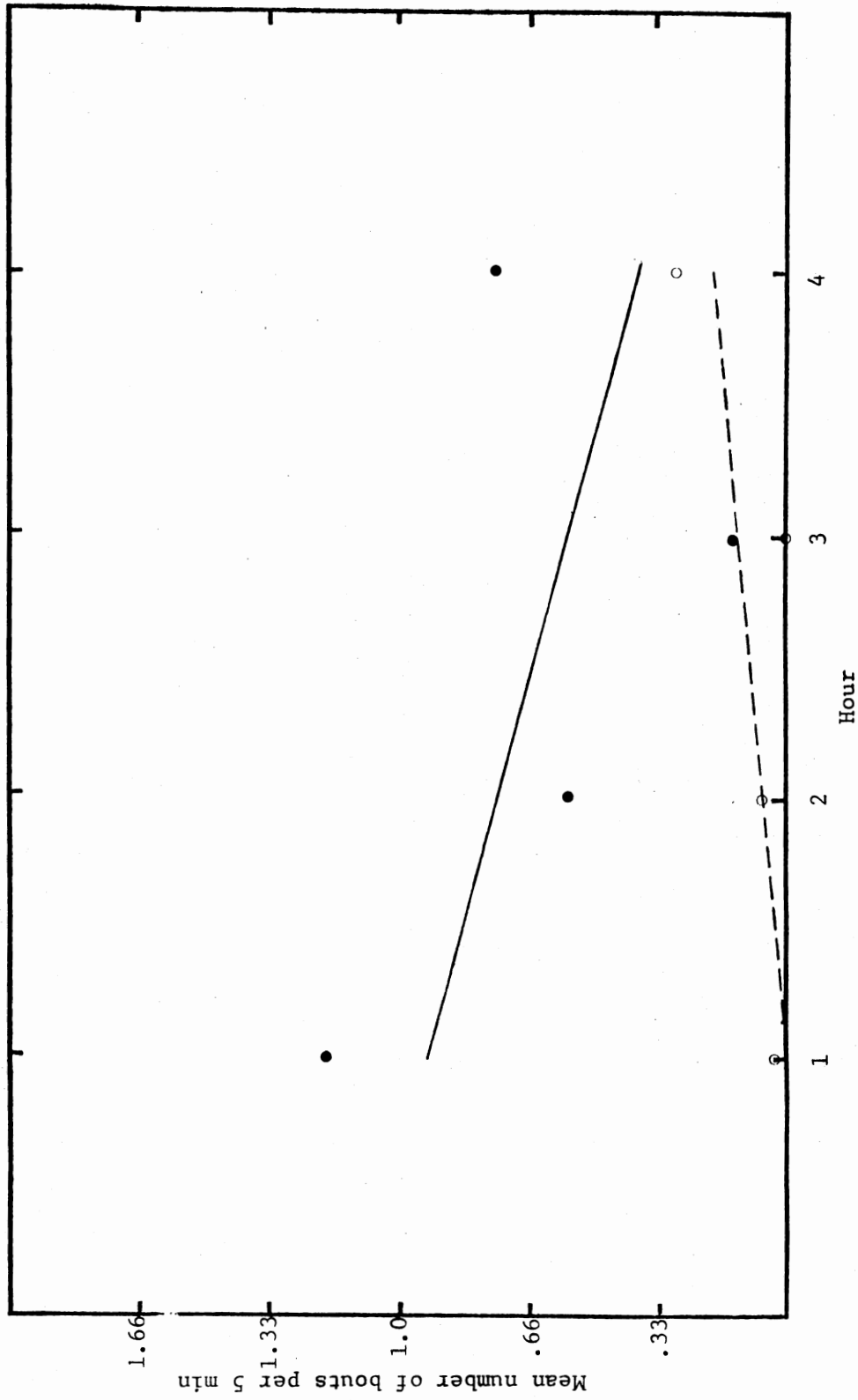


Figure 10. Plot of regression of TBC (solid line) and TBH (dashed line) on hour for lateral line-enuvated fish. Circles are observed hourly means (solid=TBC, clear=TBH).

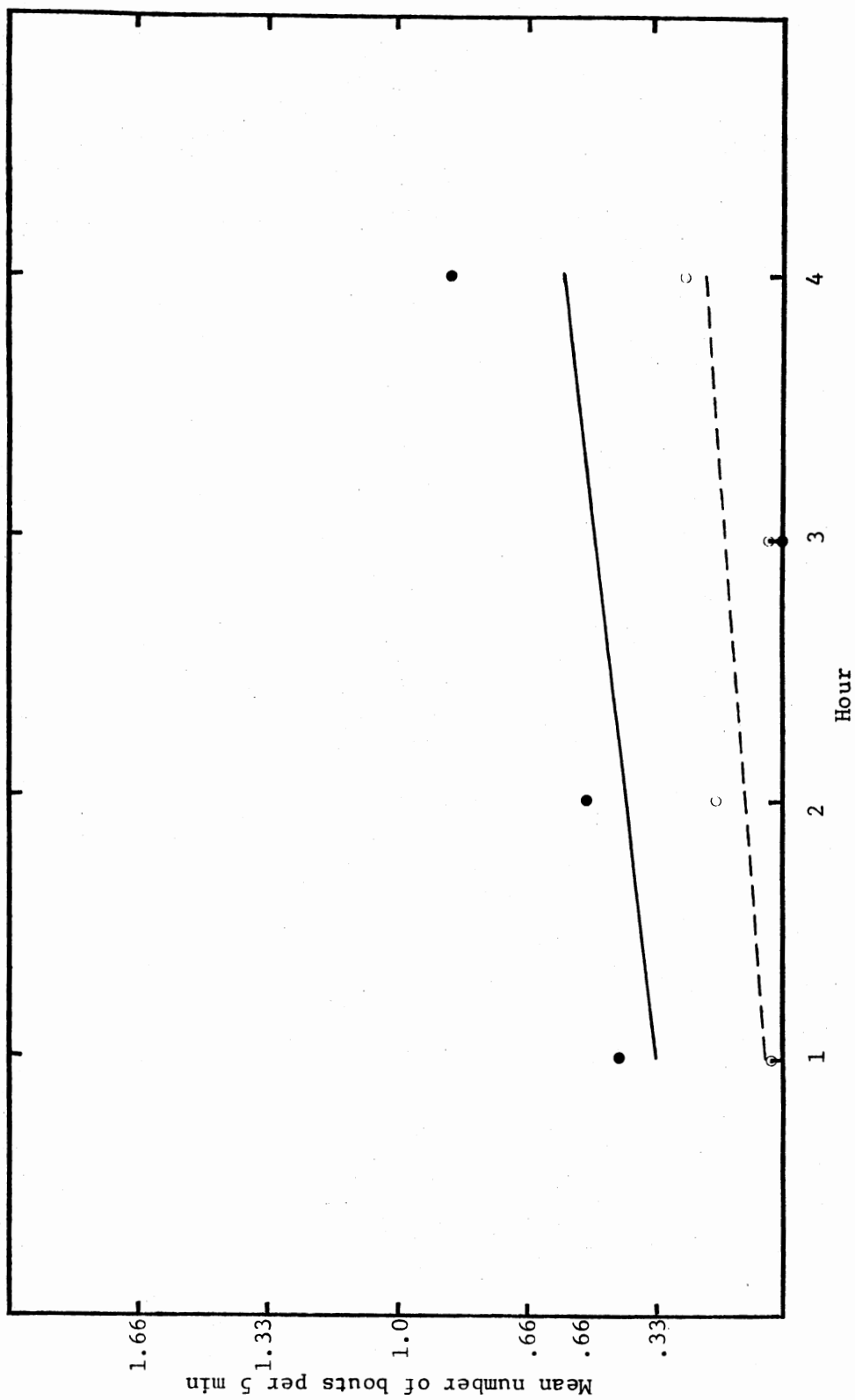
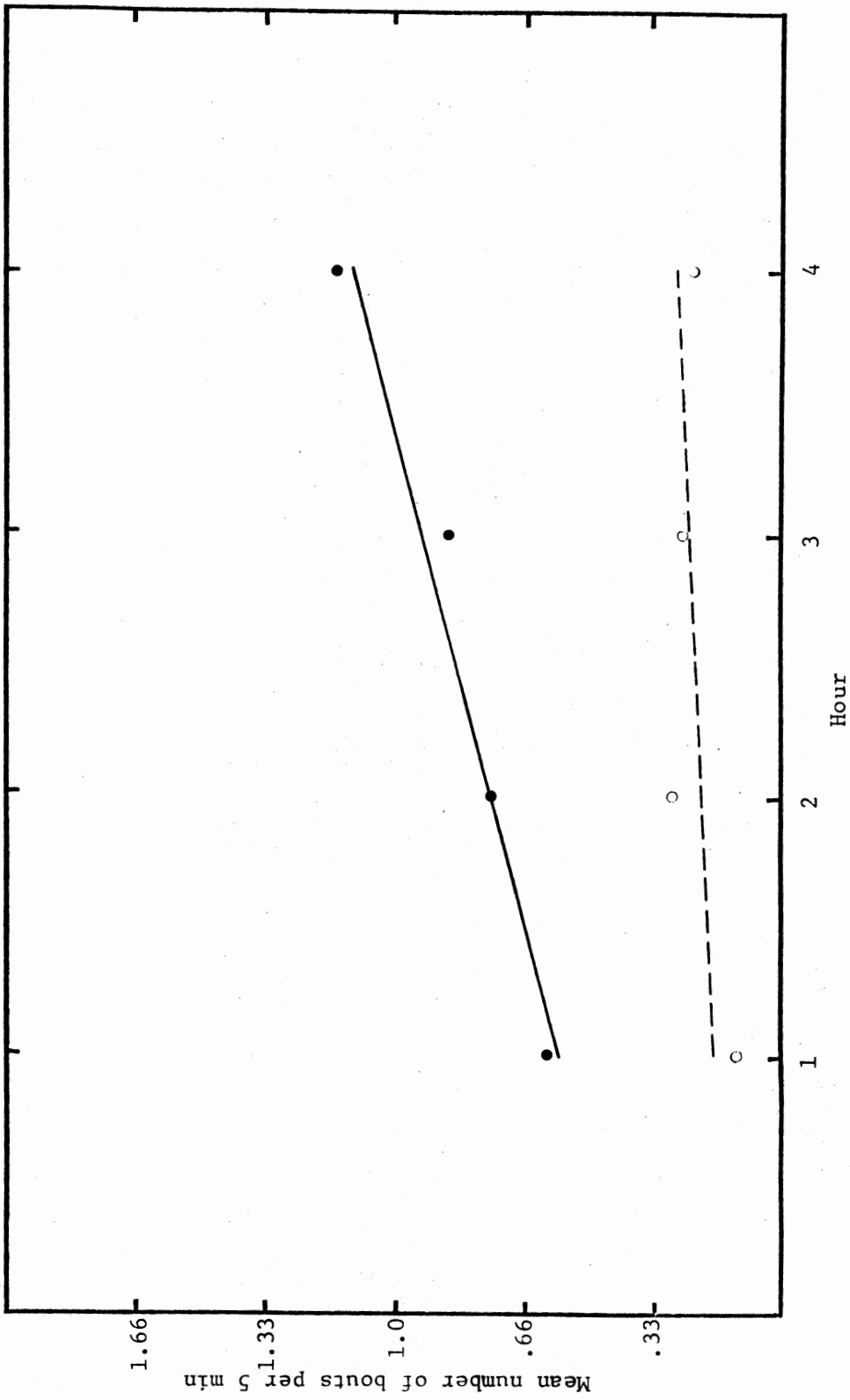


Figure 11. Plot of regression of TBC (solid line) and TBH (dashed line) on hour for deolfacted-lateral line-
enervated fish. Circles are observed hourly means (solid=TBC, clear=TBH).



Regression analysis of TBH data demonstrate that slopes do not differ significantly among groups. In general, these data indicate that all test fish groups had a consistently low tendency to engage in tailbeating bouts with bluegill.

Comparison of TBC and TBH regression lines within test fish groups indicates that control, deolfacted, and deolfacted-lateral line-ennervated fish tended to carry on more bouts with bass than with bluegill over the whole 4 hours of observation. Lateral line-ennervated test fish, however, treated bass and bluegill similarly over time.

Chase

Contrary to expectations, chasing appears to be a relatively uncommon behavior under these experimental conditions. All test fish performed chases infrequently. Consequently, though statistical significance ($p=.032$) was achieved for the CHC main effect of operation, real differences are extremely small and probably biologically insignificant. Likewise, the CHH main effect, "presentation order of stimulus fish", is significant ($p=.007$), but the differences seem too small to be meaningful (Tables 5 and 6).

Time Spent Together

TMC and TMH data are presented in Figure 12. Fish were arbitrarily considered to be "together" when they were within 30 cm of one another since observations indicated this was approximately the distance within which fish would begin to interact. TMC and TMH values represent mean number of minutes spent together per 5-min observation.

When TBC means are compared, test fish appear to fall into two

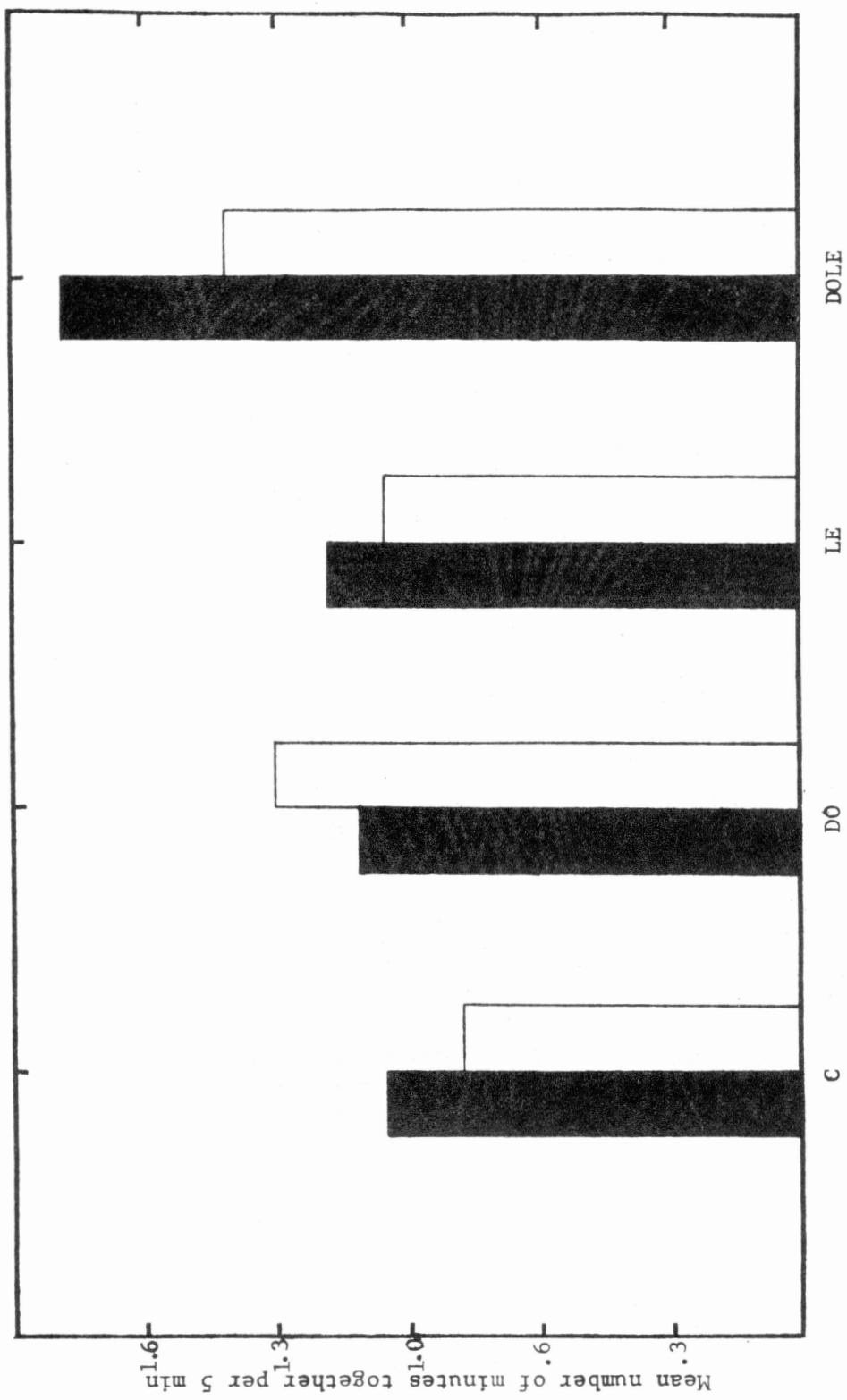
Table 5. CHC and CHH means for all test fish groups.

Group	N	CHC	CHH
Control	12	.2708	.2917
Deolfacted	11	.3409	.3106
Lateral line enervated	12	.1389	.1667
Deolfacted-lateral line enervated	12	.5764	.4375

Table 6. CHC and CHH means for presentation orders.

Group	df	CHC	CHH
Bass first	29	.2701	.1695
Bluegill first	18	.4306	.5139

Figure 12. Bar graph of TMC and TMH means for the 4-hour observation period (C=control, DO=deolfacted, LE=lateral line-enervated, DOLE=deolfacted-lateral line-enervated).



categories. Control ($\bar{X}=1.04$), deolfacted ($\bar{X}=1.14$), and lateral line-
enervated ($\bar{X}=1.31$) are inclined to spend less time with other bass,
while deolfacted-lateral line-enervated fish ($\bar{X}=1.90$) spend more time
with other bass (Figure 12). However, since control and deolfacted
fish interacted more with bass per unit TMC than deolfacted-lateral
line-enervated fish did, greater time spent together is not necessarily
a correlate of recognition of a conspecific.

TMH means exhibit another pattern of similarity among operation
groups. Now, control and lateral line-enervated test fish form one
similar pair ($\bar{X}=.85$ and $.93$, respectively), while deolfacted and
deolfacted-lateral line-enervated fish, which tend to spend more time
with bluegill ($\bar{X}=1.42$ and 1.46 , respectively) form a second pair.

Comparison of TMC and TMH means within operation groups by means
of T tests reveals no statistically significant differences. However,
with the exception of deolfacted test fish, which spent a greater mean
number of minutes with bluegills, test fish spent more time with bass.

Analyses of regression of TMC and TMH data on hour of observation
were completed and slopes were compared among groups on the basis of
F test (Figures 13-16).

TMC slopes indicate that control, deolfacted, and lateral line-
enervated test fish spent less time with other bass as time progressed
($r=-.792$, $-.957$, $-.836$; $b=-11.086s$, $-13.27s$, $-14.61s$, respectively).
Deolfacted-lateral line-enervated fish alone exhibited an increase in
TMC over the 4 hours ($r=.767$; $b=7.204s$).

Regression lines for TMH data present a similar pattern of rela-
tionship. Again, control, deolfacted, and lateral line-enervated fish
exhibited a decrease in TMH over 4 hours ($r=-.779$, $-.676$, $-.608$;

Figure 13. Plot of regression of TMC (solid line) and TMH (dashed line) on hour for control fish. Circles are observed hourly means (solid=TMC, clear=TMH).

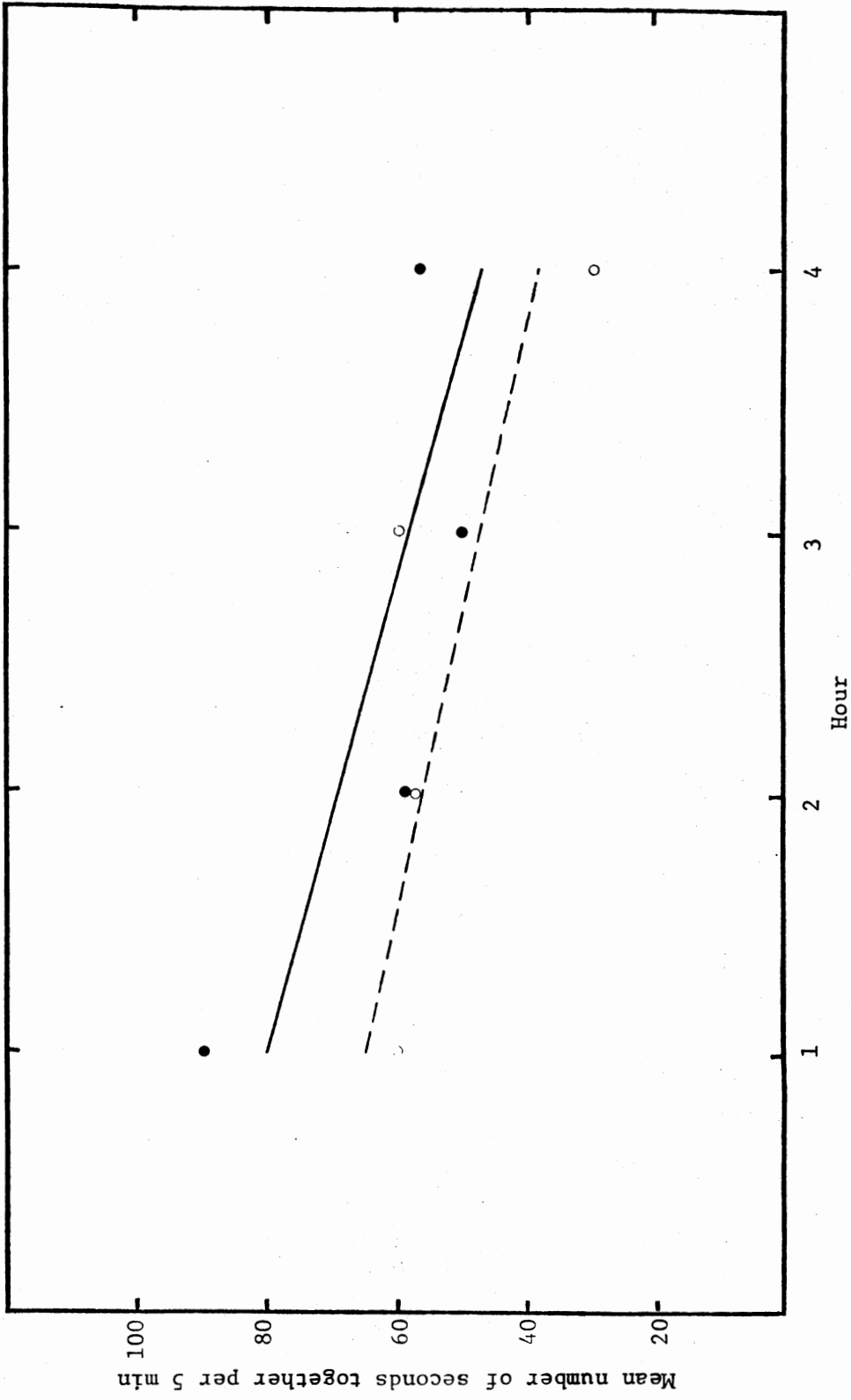


Figure 14. Plot of regression of TMC (solid line) and TMH (dashed line) on hour for deoifacted fish. Circles are observed hourly means (solid=TMC, clear=TMH).

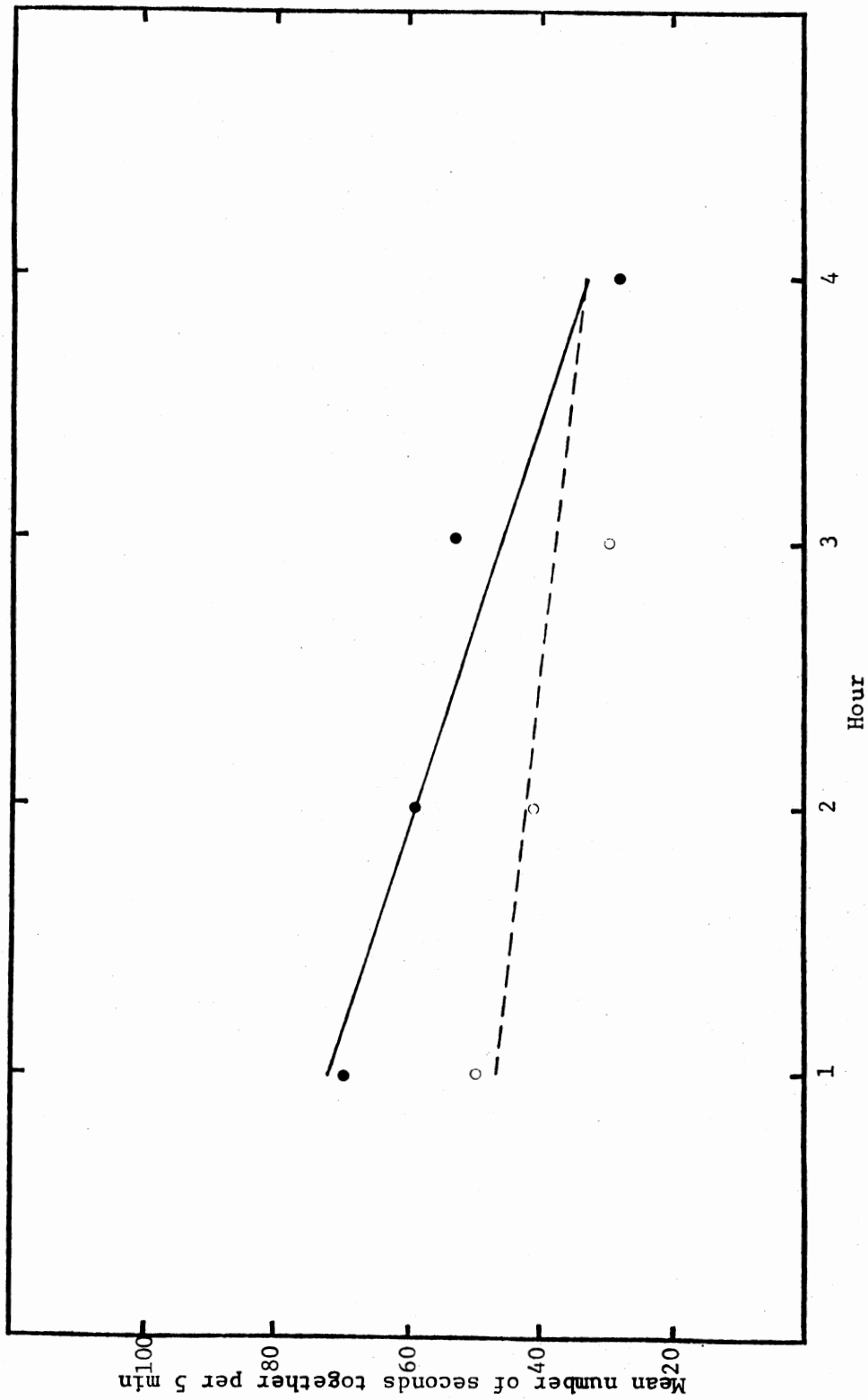


Figure 15. Plot of regression of TMC (solid line) and TMH (dashed line) on hour for lateral line-enervated fish. Circles are observed hourly means (solid=TMC, clear=TMH).

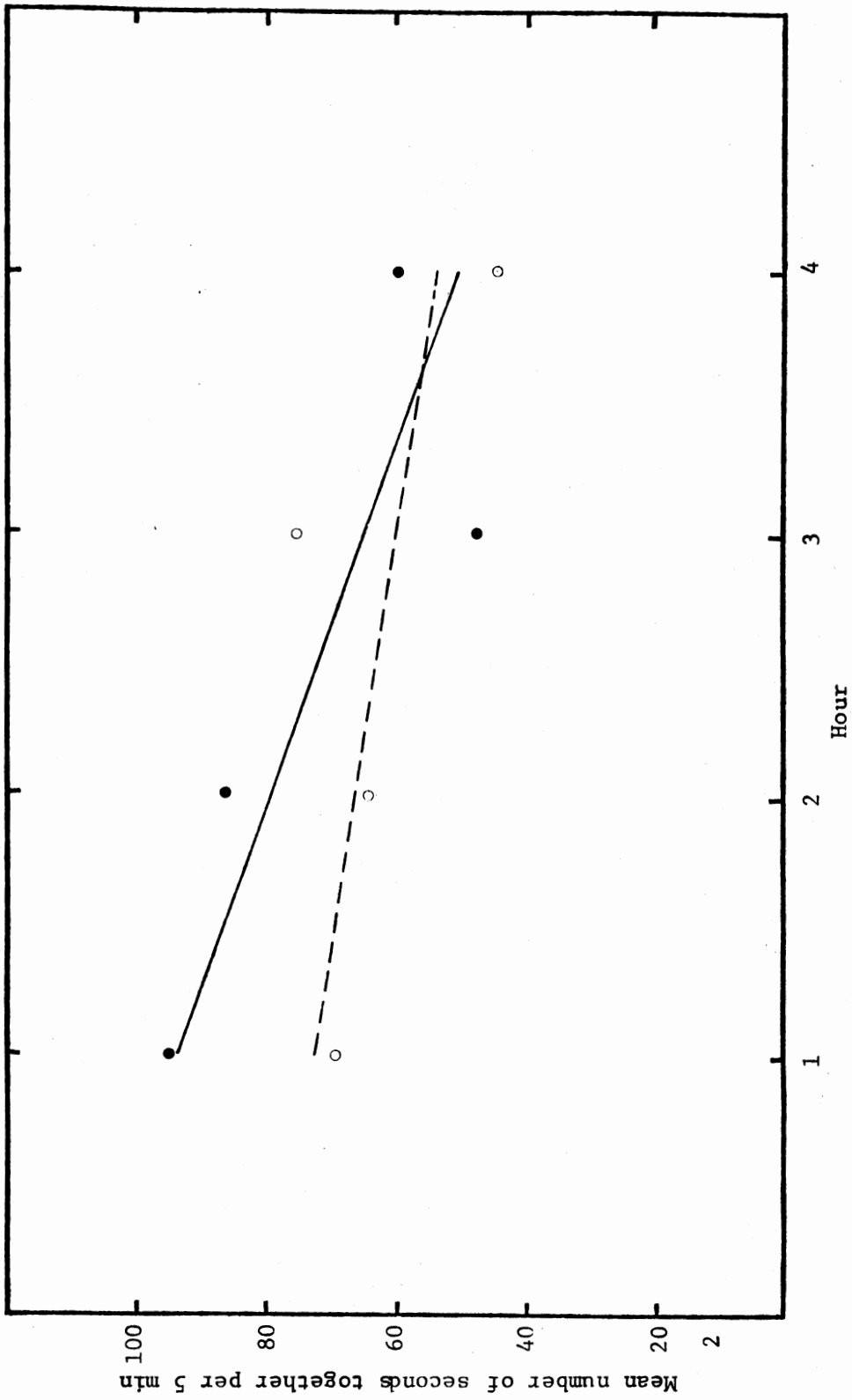
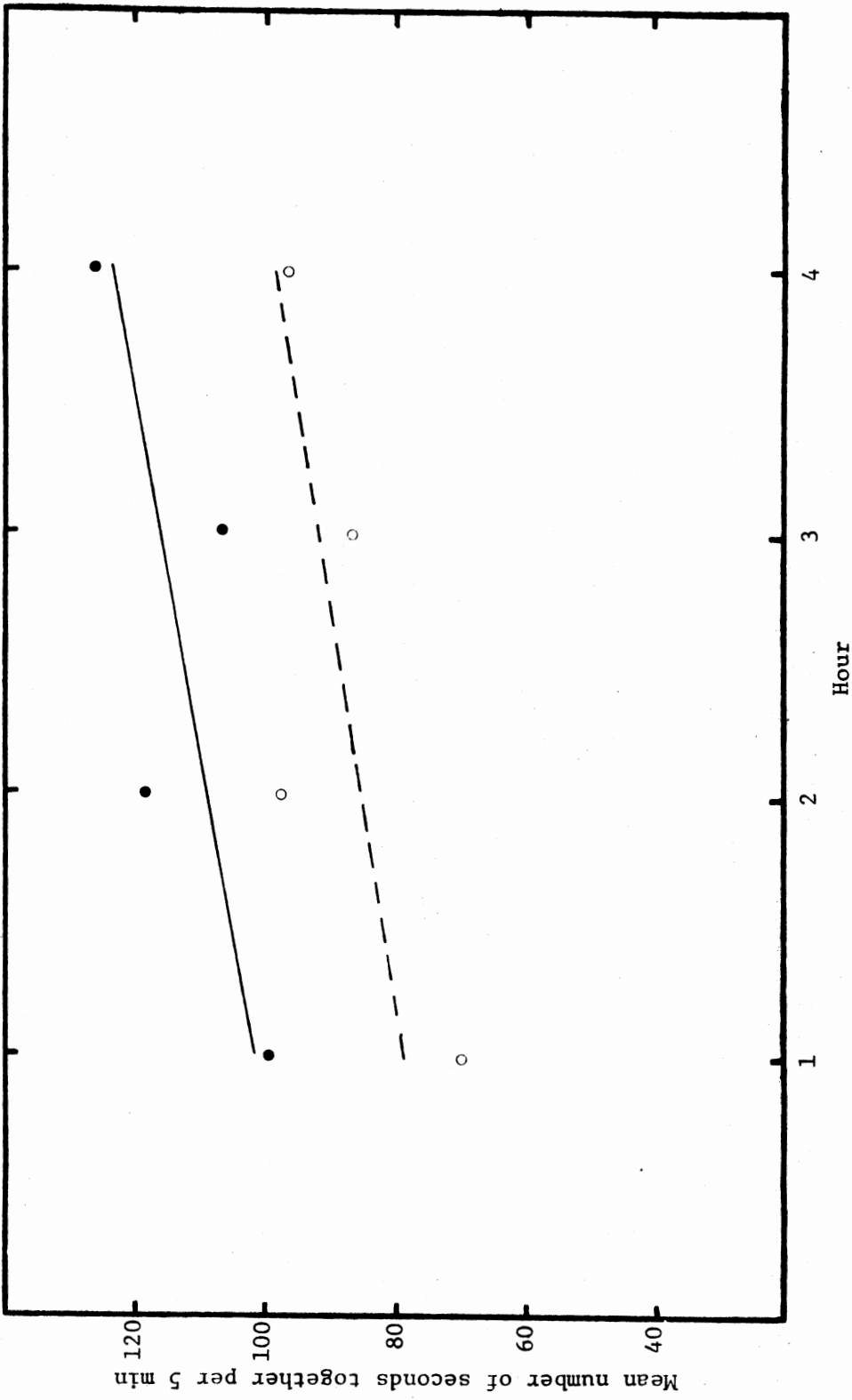


Figure 16. Plot of regression of TMC (solid line) and TMH (dashed line) on hour for deolfacted-lateral line-ennervated fish. Circles are observed hourly means (solid=TMC, clear-TMH).



b=-8.995, -4.393, -6.345, respectively), while deolfacted-lateral line-
enervated fish displayed an increase in TMH over time ($r=.696$; $b=6.948$).

Qualitative comparison of TMC and TMH regression lines within
groups shows only deolfacted-lateral line-enervated test fish spent
more minutes with bass than with bluegill over the total 4 hours. Com-
parison of observed values for this group suggests a rhythmical pattern
of time spent with both types of stimulus fish, indicating some internal
rhythm may be at work. Deolfacted fish also tended to spend more time
with bass, but began to do so at hour 2.

CHAPTER VI

QUALITATIVE DESCRIPTION OF EXPERIMENT

II RESULTS

In experiment II, pairs of fish subjected to identical treatments were observed in dyadic encounters for the first hour of interaction. Qualitative analysis of these data consists of descriptions of typical sequences of motor patterns comprising these interactions and descriptions of spatial, temporal, and intensity differences between motor patterns exhibited by normal and treatment fish.

In addition, all pairs were observed at intervals during several hours following the first hour and at the beginning of the second day. Again, qualitative descriptions of motor patterns, interactions, and hierarchy stability as measured by occurrences of subordinate approaches, tailbeats, and butts/bites were made. Particular emphasis was placed on observing pairs which had not established hierarchies during first hour observations.

Application of eyecaps resulted in some damage to the tissue of the orbit, but caused no observable injury to the eye. Presence of eyecaps did, however, result initially in some fish attempting to dislodge them. Within several minutes after application of eyecaps, a few fish periodically shook the head from side to side and/or opened the mouth widely, apparently trying to displace eyecaps from the orbit. In several instances when fish successfully removed eyecaps in this

manner, behavior of these individuals became qualitatively similar to behavior of normal fish. Several minutes after application of eyecaps, fish no longer exhibited gaping or head shaking, and appeared to become acclimated to eyecaps.

Subsequently fish were tested by exposure to quick movements of the hand and to tapping on the tank's front glass to determine the effects of eyecaps on their general awareness of external stimuli. Normal fish and fish with transparent eyecaps responded immediately to movement by swimming in a startled manner away from the glass. In addition, these fish reacted to movement of the observer at distances of approximately 3 m, indicating they were visually aware of their surroundings.

All fish equipped with translucent eyecaps appeared to be unable to perceive movement of the observer. Although they moved about in response to tapping on the glass, quick hand movements caused no startle reaction. However, when a shadow was passed across their heads, these fish slowly moved away, suggesting they were capable of perceiving differences in light intensity. They also exhibited movement and color changes when overhead lights were turned on or flash assisted photographs were taken.

Another distinct characteristic common to all fish wearing translucent eyecaps was their tendency to swim near or in contact with the bottom. They would traverse the tank by swimming slowly with the pelvic fins just above or gliding across the substrate. In contrast, fish which were normal or fitted with transparent eyecaps tended to swim at approximately middle depth in the tank.

To provide an opportunity to observe responses of bass in each

group to prey, golden shiners, Notemigonus crysoleucas (6-5 cm TL), were provided to each test fish several hours after being placed in observation tanks. Normal fish oriented to and ingested minnows almost immediately. Fish fitted with transparent eyecaps and those with translucent eyecaps but otherwise untreated also reacted quickly to presence of prey, but differed in their ability to capture prey. Bass with transparent eyecaps oriented quickly, pursued, and engulfed prey; those with translucent eyecaps approached the general position of moving prey, did not begin pursuit until within several centimeters of the minnows, and required more capture attempts before ingestion occurred. Bass with translucent eyecaps and severed lateralis nerves also responded to prey, but usually did so less quickly and often only after minnows had moved close to or actually made contact with them. These fish were, however, also successful in ingesting prey after several capture attempts.

In the account below, all fish except "normal" and "transparent" eyecap groups were fitted with translucent eyecaps.

Normal Fish Encounters

All encounters between normal fish were not resolved in the first hour. Three pairs established hierarchies, while two remained unresolved until later. One of these unresolved pairs established a hierarchy near the end of their second hour together; the other pair did so by the beginning of the second day.

Qualitative observations made on the second day of interaction within normal pairs revealed hierarchies remained stable over time. No reversals in hierarchical position occurred in any pair, and no

subordinate fish ever directed an overtly aggressive act toward a dominant fish.

Encounters between normal fish were characterized by relatively high activity levels. Fish tended to begin interacting a few seconds after withdrawal of the partition and continued to interact for most of the hour. At withdrawal of the partition, both fish typically responded to this disturbance of the water by orienting to the center of the tank. Then, as they saw one another, one of both individuals approached and the pair usually commenced tailbeating. In contrast, one resolved pair began parallel swimming for several minutes. In the two pairs which failed to establish a hierarchy within the first hour, parallel swimming continued for as long as 45 min.

Generally, the sequence of tailbeating bouts continued for at least several minutes and increased in intensity. Fish started tailbeating with one to four relatively small amplitude undulations of the peduncle. This would elicit corresponding tailbeats from the recipient fish as the initiator continued to deliver simultaneous or alternate tailbeats of increasing force. Although fish sometimes continued to parallel swim while tailbeating, they began to localize their interactions at one end of the tank toward the end of the tailbeating period.

In unresolved pairs, two extremes of tailbeating were observed. One pair did no tailbeating; the other engaged almost exclusively in tailbeating. The first pair eventually began tailbeating during the second hour and established a hierarchy, while the second did not achieve resolution of their encounter until the second day.

As tailbeating progressed, bouts began to be interspersed with opercle displays, butts, and bites. These butts and bites characteris-

tically were sharp, forceful strikes occurring in groups of one to four, though in all but one pair, initial biting sequences sometimes took place as rapid, reciprocal biting while the two fish swam quickly in a small circular path. During these flurries of activity, actual enumeration of butts and bites was virtually impossible.

The increasing localization of agonistic activities at one end of the tank and the appearance of butting and biting were harbingers of resolution of an encounter. Soon after fish began reciprocal butting and biting, one fish would begin to perform fewer approaches, tailbeats, butts, and bites and finally assume an appeasement posture.

Appeasing normal fish assumed a posture in which the tail and peduncle were raised approximately 3 cm above the head, and the body listed 5 to 10° away from the dominant, while ascending toward the surface. Later, in response to butts and bites, this posture often was intensified with subordinates sometimes in an almost vertical tail-up position or listing so greatly that they rolled over. Typical subordinate coloration was exhibited.

After resolution, subordinate fish moved little at all; thus, interaction within a pair was due primarily to the repeated approaching of dominant fish. Dominants usually approached, delivered several tailbeats and butts or bites, then withdrew following the subordinate's intensification of appeasement. Such short sequences of motor patterns were repeated many times during the remainder of the observation hour.

Tailbeats performed by dominants after the hierarchy was well established often were delivered from positions other than parallel head-to-head. These bouts occurred while dominants were at an angle in front of or several centimeters beneath the subordinate, a change

dictated by the subordinate's maintenance of a position near the surface.

Encounters of Pairs Fitted With Transparent Eyecaps

Four of five pairs in this group formed hierarchies within the observation hour. Three resolved pairs were very active and resolution occurred within several minutes; the remainder of interactions were maintenance and reinforcement of hierarchical relationships. In contrast, the unresolved pair exhibited long intervals of inactivity and appeared less aggressive. Bass in the unresolved pair approached more slowly and, though they engaged in several low intensity tailbeating bouts, spent most of the hour parallel swimming. By the second day this pair also had established a hierarchy.

Motor patterns of bass in this group were qualitatively similar to those of normal bass. Transparent eyecaps did not seem to hinder activity of these fish; swimming motions and agonistic activities were like those of normal fish. Additional evidence that transparent eyecaps had little inhibitive effect on fish is the domination of a normal fish by a fish with transparent eyecaps during preliminary studies.

Transparent eyecaps, however, did seem to have an incremental effect on the intensity of interaction between fish. Butts, bites, and tailbeats appeared more forceful than in normal fish interactions, indicating these fish were somewhat hyperaggressive.

Temporal patterning of encounters in these pairs generally was similar to patterning of interactions in normal pairs. Fish usually oriented to and approached opponents within several seconds after

removal of the divider. However, initial approaches were followed more frequently by a series of reciprocal approaches, withdrawals, and follows than by tailbeating bouts. Sessions of parallel swimming also occurred after initial approaches.

Subsequently, three pairs progressed to butting and biting, while two pairs performed tailbeating bouts. As bouts proceeded, butts, bites, which sometimes developed into rapid circling and reciprocal biting, and shambites began to interlace bouts. As in normal fish encounters, the appearance of biting closely preceded appeasement.

First appeasement in these pairs was not a clear indicator of resolution as it was in normal bass. After appeasing, one subordinate engaged in tailbeating, opercle spreading, and biting until performing a second appeasement. Furthermore, another subordinate interspersed appeasements with occasional approaches, shambites, bites, and chases until finally reversing the hierarchy at the end of the observation.

Later observations on the first day and early on the second day indicated hierarchies had stabilized. Activity levels remained relatively high due primarily to approach-butt/bite-tailbeat sequences by dominant fish.

Encounters of Fish Fitted With Translucent Eyecaps

Bass fitted with translucent eyecaps differed from normal bass in several ways. These fish were slower to orient to opponents, assumed typical positions in the water, and were less active than normal bass. In addition, qualitative differences in motor pattern performance and temporal patterning were exhibited by these bass.

Unlike normal fish and fish with transparent eyecaps, all pairs with translucent eyecaps established hierarchies within the observation hour. Later observations revealed no changes in hierarchical status of any fish and indicated temporal patterns of interactions were similar to first hour post-resolution behavior sequences.

Encounters of pairs in this group typically began when fish swam about in response to removal of the partition. However, fish did not orient directly to one another, but moved through the water until passing within 5-10 cm of one another. At this point, both fish usually stopped, one or both approached, and observable interactions began.

In contrast to approaches by normal fish, approaches by these bass often were slow and meandering. In addition, as individuals swam toward an opponent, they sometimes oriented the body at an oblique angle and completed the approach in a sideways manner. In one encounter, an individual performed several short, threat-like approaches which consisted of moving forward several centimeters, halting, and then swimming backwards to the original position.

In response to approach, recipient fish usually withdrew or the pair began parallel swimming. When fish withdrew, approaching fish usually followed at variable distances, sometimes making the distinction between parallel swimming and following difficult. As parallel swimming continued, fish began periodically to tailbeat until parallel swimming developed into a series of tailbeating bouts. These bouts were performed primarily in a head-to-head position but, more often than in normal pairs, took place at variable positions and angles. Although bouts typically consisted of reciprocal tailbeats by both fish, in one pair only the eventual dominant performed tailbeats.

In contrast to the general pattern, one pair did not enter a period of tailbeating after initial approaches occurred. Following the approach, the recipient fish withdrew and a 5-min period of no observable interaction occurred. The initially approaching fish then reapproached and the recipient fish exhibited an appeasement posture.

Tailbeating bouts initially tended to cluster as in encounters between normal fish. However, as tailbeating continued, opercle spreads, butts, and bites began to occur between bouts. Butts and bites were not as forceful as in normal fish and tended to be performed by only one fish rather than reciprocally. Furthermore, no pairs engaged in reciprocal biting while rapidly circling.

Appeasement generally occurred after one to several butts and bites by the eventual dominant. When approached and subjected to butts or bites, recipient fish tended to withdraw rather than to respond with aggressive motor patterns; thus, initiating butting and biting was a characteristic of eventual dominants.

Behavior of subordinates differed in several ways from behavior of normal subordinates. Subordinate color patterns appeared later and were neither as distinctive, nor as consistently maintained as in normal fish. During lulls in interaction, several subordinate individuals exhibited less intense lateral bands and mottling but these were intensified again when dominant fish initiated subsequent interactions. In addition, during relatively long intervals of quiescence, subordinate fish tended to return to a horizontal position and to descend from near the surface.

As in encounters between normal fish, post resolution interactions were very consistent in temporal pattern. A typical sequence of

approach, butts or bites, and then performance of several tailbeats was repeated many times by dominant fish during this period.

Encounters Between Deolfacted Fish

Four of five pairs in this group established hierarchies within the first hour of observation. Three resolved pairs were similar to normal fish in activity levels; one pair was relatively inactive following an initial approach, but began to interact during the last 4 min of the hour. The unresolved pair was very inactive and seldom moved subsequent to initial reciprocal approaches.

Although motor patterns performed by these fish were usually qualitatively similar to those exhibited by normal fish, several differences were apparent. Initial approaches were similar to approaches by fish in the translucent eyecap treatment group, i.e., slow and often at an oblique angle. In addition, some approaches appeared to occur accidentally as fish moved about the tank. In one pair, the dominant sometimes ended post resolution approaches 10-15 cm short of the subordinate and then swam slowly backwards to its original position or occasionally reinitiated the approach.

Temporal patterning of encounters in this group was generally similar to patterning in encounters of fish in the translucent eyecap group. An initial approach was typically followed by a series of consecutive tailbeating bouts comprised of 2-3 tail beats per fish. Subsequently, fish began to intersperse tailbeating bouts with butts, bites, chases, opercle spreads, and quivers. No one of these motor patterns was more likely than another to initially intersperse tailbeats; however, once tailbeating was interrupted butts and bites

usually occurred more often than other motor patterns. In two pairs, initial butts and bites developed into rapid circling and biting.

After several bites, butts, and/or opercle spreads, one interactant usually appeased by exhibiting a typical tail-up, listing posture while ascending in the water. However, in this group resolution was not as easily recognized as it was in normal pairs. In two pairs, fish which adopted appeasement postures immediately returned to performing approaches, tailbeats, opercle spreads, butts, and bites. Another fish followed appeasement with an approach to its withdrawing opponent. In each of these pairs, however, initially appeasing fish later exhibited a second appeasement which was followed by typical subordinate behavior.

Subordinate fish in this group also tended to terminate appeasement postures when dominant fish withdrew. In addition, the development of subordinate color patterns was not as predictable as in normal fish; the appearance of mottling and the lateral band sometimes did not occur until well after an appeasement posture was performed.

Post resolution interactions were similar to those occurring in normal fish. Subordinate fish remained practically motionless for most of this period, while dominant fish repeated approach-butt/bite-tailbeat-withdraw sequences for the remainder of the hour.

Observations later on the first day and early on the second day indicated this sequential pattern was maintained over time and that hierarchies stabilized.

Encounters Between Lateral Line

Enervated Fish

Four of five lateral line enervated pairs resolved encounters within the first hour of activity. The unresolved pair interacted minimally until the last 8 min of the observation hour, but then established a hierarchy during the second hour.

Motor patterns performed by these fish were generally less stereotyped and not as well-defined in form as in normal fish. At the beginning of interaction, approaches were slow and usually occurred as fish drifted in an undirected manner into proximity of each other. Approaches were highly variable in form; fish approached head-on, sideways, and even backwards.

Appeasement postures also were less stereotyped than in normal subordinates. Lateral line enervated subordinates sometimes performed only slight "tail up" movements or did not list to one side. In addition, they sometimes held a position on or near the bottom rather than near the surface.

Tailbeating was qualitatively similar in form to tailbeating by normal fish. However, intensity of tailbeating sometimes seemed increased.

Color patterns also were not typical in lateral line-enervated fish. One dominant maintained a dark lateral band and some mottling well after resolution had occurred.

Temporal patterning in encounters of these fish was generally similar to patterning described for deolfacted fish. At the onset of interaction, fish approached and began a series of reciprocal tailbeating bouts. However, bouts tended to be more temporally separated

and were interspersed more frequently with withdrawals by one fish. Like patterning of encounters in other groups, tailbeating bouts soon began to be interrupted with butts, bites, and occasional shambites or opercle spreads. Eventually, this led to appeasement by one fish.

In general, patterning of postresolution interaction was qualitatively similar to postresolution activity in normal pairs. However, on several occasions subordinates approached dominants but did so apparently accidentally while drifting in the water.

Deolfacted-Lateral Line-Enervated

Group Encounters

Three of five pairs in this group resolved encounters before the end of the observation hour. Unresolved pairs were considerably less active than unresolved normal pairs; in one pair no interaction occurred, in the other pair several approaches and withdrawals by one fish were the only activity. Unresolved pairs did not establish hierarchies by the second day.

Several qualitative differences in motor patterns existed between normal fish and deolfacted-lateral line-enervated fish. Initial approaches were similar to those of lateral line-enervated fish, i.e., slow and undirected. Fish seemed unaware of each other and would drift about, apparently in response to water displacements caused by pulling the divider. After drifting brought individuals together, fish remained inactive several centimeters apart, followed one another about the tank, or performed low amplitude tailbeats.

In addition, appeasement postures exhibited by subordinates in this group were like those of lateral line-enervated subordinates: less

well defined and sometimes incomplete. Initial appeasements usually consisted of only slight "tail-up" movements and often were not accompanied by ascent to the surface. In part, these less intense appeasements seemed to be due to the rapid quality of the dominants early approaches, butts, and bites of the dominants. Fish in this group appeared least aware of their surroundings.

Temporal patterning of encounters between these bass deviated somewhat from patterning characteristics of normal fish. Initial approaches in these pairs was not as closely followed by tailbeating as in normal fish. Instead, fish more often withdrew and reapproached or moved about near one another as though exploring one another. In only one pair did tailbeating immediately follow approach.

Subsequently, however, all eventually resolved pairs began tailbeating reciprocally until bites, quivers and opercle spreads occurred between bouts. As in other treatment groups, appeasement typically followed biting.

Post resolution patterning of interactions suggests that resolution in these pairs was not clear cut. One subordinate approached the dominant several times well after resolution; another initiated a number of post resolution tailbeating bouts. In addition, the dominant partner of this second subordinate appeased once in response to tailbeating.

Another subordinate in this group displayed post resolution patterning different from all other subordinates. Rather than appeasing to an approaching and biting dominant, this fish responded with quivers.

CHAPTER VII

QUANTITATIVE ANALYSIS OF EXPERIMENT II

Twenty-four behavioral variables were quantitatively analyzed to evaluate the effects of treatments on hierarchy establishment in the six treatment groups used in this experiment (Table 7). Motor pattern data were recorded as frequencies for each variable. In addition, when the same motor pattern occurred in an uninterrupted sequence (e.g., BIBIBI), it was recorded as a bout; bout frequencies and rates were calculated. Latency variables were measured from start of an observation to initiation of a particular activity.

Various measures of establishment of a dominance hierarchy have been used to assess dominance relationships. Measures ranging from summing relative frequencies of aggressive motor patterns exhibited by individuals (Gorlick 1976) to first appearance of appeasement (Tooker 1976) have been used. Preliminary observations in this study revealed subordinate normal bass seldom direct aggressive motor patterns at dominant fish; thus, resolution of an encounter (=hierarchy establishment) is defined here as first occurrence of appeasement.

For analysis, resolved and unresolved pairs were treated separately. In addition, dominant and subordinate bass were considered separately in comparisons among treatment groups.

Dominance relationships are known to consist of two distinct phases, establishment and maintenance (Frey and Miller 1972). Con-

Table 7. Abbreviations used for the twenty-four behavioral variables recorded during observations.

Abbreviation	Variable
AP	Appeasement
AB	Alternate biting while circling
AR	Approach
BI	Bite
BIB	Bite bout
(BI/BIB)	Bites per bout
BU	Butt
BUB	Butt bout
(BU/BUB)	Butts per bout
CH	Chase
CO	Cough
FL	Flee
FO	Follow
LAP	Latency to approach
LRS	Latency to resolution
OP	Opercle spread
PA	Pass
QV	Quiver
SB	Shambite
SBB	Shambite bout
(SB/SBB)	Shambites per bout
TB	Tailbeat
TBB	Tailbeating bout
(TB/TBB)	Tailbeats per bout
TOT	Total activity

sequently, data from resolved pairs was divided into prerelution and postresolution activity for analysis.

Statistical comparison of treatment group means for the twenty-four variables was accomplished using one-way analyses of variance. Comparison of dominant and subordinate bass within treatment groups was done with t tests. Significance levels less than 0.1 are reported.

Latency to Approach and Resolution

Latency to first approach was analyzed without regard to presence or absence of resolution. Subsequently, approach latencies of resolved and unresolved pairs were considered separately. Results are presented in Tables 8 and 9.

When considering all pairs, control, transparent eyecap, and lateral line groups exhibit relatively low approach latencies, while remaining treatment groups exhibit very high approach latencies. In almost every case, these high mean latencies are due to single pairs which were unresolved, suggesting unresolved pairs had lower tendencies to interact with one another.

Inspection of the means of only resolved pairs shows that now the translucent eyecap group alone has a high approach latency. This was due to one pair of bass which did not begin to interact until several minutes after the observation began. Examination of mean latencies of unresolved pairs reveals that fish in deolfacted and deolfacted-lateral line-ennervated groups approached much later than fish in other groups.

Latency to resolution results are displayed in Table 10. Control pairs required the least time to resolve encounters. Pairs equipped

Table 8. Mean latency to approach and standard deviations by treatment group (all pairs).

Treatment group	n	\bar{X}	SD
Control	5	40.02	29.64
Transparent eyecap	5	57.44	66.65
Translucent eyecap	5	428.58	767.11
Deolfacted	5	593.58	1295.50
Lateral line enervated	5	26.96	12.84
Deolfacted + lateral line enervated	5	928.64	1549.55

Table 9. Mean latency to approach and standard deviations by treatment group (resolved pairs only).

Treatment group	n	\bar{X}	SD
Control	3	38.40	40.28
Transparent eyecap	4	22.00	12.01
Translucent eyecap	5	428.58	767.11
Deolfacted	4	14.23	9.10
Lateral line enervated	4	26.90	14.83
Deolfacted + lateral line enervated	3	22.23	24.93

Table 10. Mean latency to resolution and standard deviations by treatment group.

Treatment group	n	\bar{X}	SD
Control	3	325.73	156.26
Transparent eyecaps	4	585.30	432.34
Translucent eyecaps	5	1095.52	1186.24
Deolfacted	4	1110.70	1656.32
Lateral line enervated	4	513.00	307.19
Deolfacted + lateral line enervated	3	409.43	199.49

with translucent eyecaps and deolfacted pairs took longer to resolve encounters; however, the extended latency for deolfacted pairs was due to a single pair which did not establish a hierarchy until the end of the hour (latency = 3590.6).

Preresolution Results - Dominants

Results for preresolution interaction were highly variable within treatment groups. In part, this is due to the wide range of latencies to resolution since early appeasement meant fewer motor pattern sequences could develop. Thus, some motor patterns were absent or of very low frequency in pairs having subordinates which appeased early.

Means and standard deviations for all preresolution results are presented in Table 11. The variable TOT is the sum of all other variable frequencies, and was included to assess activity levels.

Only AB frequency differed enough across groups to approach the .05 level of significance ($F=2.344$; $df=5, 17$; $p=.0857$). Examination of the data shows only control group pairs were inclined to engage in rapid circling and alternate biting, an interaction which requires quick assessment of an opponent's position and movement.

Differences among treatment groups for other variables failed to reach an acceptable level of statistical significance. However, several differences warrant mention as behavioral trends. The low approach frequency of control and deolfacted-lateral line-ennervated dominants is attributable to their tendency to remain with opponents following initial approach. Fish in other groups withdrew more often after approaching. Lower bite frequencies for control, transparent eyecap, and later line-ennervated eventual dominants seem to be due to different

Table 11. Preresolution mean frequencies, mean rates,
and standard deviations () for dominant fish.

	Control	Transparent eyecap	Translucent eyecap	Deofactored	Lateral line enervated	Deofactored lateral line enervated
AB	1.00 (1.00)	0.25 (0.50)	0.00	0.25 (0.50)	0.00	0.00
AR	1.33 (0.58)	3.50 (4.36)	4.00 (2.45)	2.25 (2.22)	4.00 (3.16)	1.33 (1.16)
BB	1.33 (1.53)	2.00 (2.71)	6.20 (5.22)	4.75 (3.10)	2.25 (2.22)	5.00 (7.00)
BBPS	1.33 (1.53)	1.75 (2.22)	5.00 (3.81)	3.75 (2.22)	1.75 (1.71)	2.67 (3.79)
BI	1.33 (1.53)	1.00 (0.82)	5.20 (4.44)	3.75 (1.71)	1.00 (0.82)	4.67 (6.43)
BIS	1.33 (1.53)	0.75 (0.50)	4.00 (3.08)	2.75 (0.26)	0.75 (0.50)	2.33 (3.22)
BI/BIS	1.00 (0.00)	1.33 (0.58)	1.33 (0.25)	1.50 (0.58)	1.33 (0.58)	2.00 (6.00)
BU	0.00	1.00 (2.00)	1.00 (1.00)	1.00 (1.41)	1.25 (1.90)	0.33 (0.58)
BUS	0.00	1.00 (2.00)	1.00 (1.00)	1.00 (1.41)	1.00 (1.41)	0.33 (0.58)
BU/BUS	0.00	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	1.17 (0.24)	1.00 (0.00)
CH	0.00	0.25 (0.50)	0.60 (0.89)	0.50 (0.58)	0.00	0.33 (0.58)
CO	0.33 (0.58)	0.00	0.60 (0.89)	0.00	0.00	0.00
FL	0.00	0.00	0.00	0.25 (0.50)	0.00	0.00
FO	0.00	1.00 (2.00)	1.00 (1.00)	1.00 (1.41)	1.25 (1.90)	0.33 (0.58)
OP	2.33 (2.52)	0.00	0.60 (0.55)	0.75 (1.50)	0.25 (0.50)	0.33 (0.58)
PA	0.33 (6.58)	0.25 (0.50)	0.00	0.00	0.00	0.00
PS	0.00	1.25 (1.89)	0.00	0.00	1.00 (1.41)	0.00
QV	0.00	0.00	0.60 (1.34)	0.50 (1.00)	0.00	0.00
TB	37.00 (53.41)	8.00 (10.30)	41.00 (39.96)	29.75 (17.91)	20.75 (12.18)	44.67 (50.89)
TBT	15.00 (12.29)	3.25 (3.40)	17.80 (20.86)	9.50 (3.27)	9.00 (5.72)	15.00 (16.37)
TB/TBT	1.98 (0.91)	2.13 (0.69)	2.70 (0.56)	2.93 (0.84)	2.49 (0.45)	2.63 (0.56)
TOT	44.00 (35.37)	21.00 (20.69)	55.00 (46.49)	40.25 (12.15)	34.50 (23.67)	52.00 (51.57)
WI	0.33 (0.58)	4.50 (6.67)	0.40 (0.55)	0.25 (0.50)	5.00 (6.38)	0.00

factors. When comparing these groups, a greater proportion of bites by control fish were contained within AB sequences; thus, BI frequency is somewhat obscured for controls.

The lower TB frequency for transparent eyecap group reflects the tendency of fish in these pairs to reduce or eliminate the tailbeating phase from preresolution activity. Compared to other groups, these fish more frequently followed approaches with butting and biting instead of tailbeating. In part, this may be indicative of the apparently hyperaggressive state of fish wearing transparent eyecaps.

Rates of biting, butting, and tailbeating (number/bout) were very similar across all treatment groups. This suggests sensory deficit may have less effect on mechanisms controlling consecutive performance of the same motor pattern than it does on overall frequency of that pattern.

Preresolution Results - Subordinates

Table 12 contains preresolution treatment group means and standard deviations for all behavioral variables of subordinate fish. TOT and rate variables were calculated as described for dominant fish.

Like preresolution results for dominant fish, only AB frequency differences approached the .05 significance level ($F=2.344$; $df=5, 17$; $p=.0857$). This similarity between dominants and subordinates with reference to AB frequency is attributable to the fact that alternate biting while circling is mutually performed by both fish in a pair.

Examination of preresolution means reveals eventual subordinates in the transparent eyecap group exhibited the highest frequencies for the following behavioral variables: AR, BI, BU, BUS, SB. This

Table 12. Preresolution mean frequencies, mean rates,
and standard deviations () for subordinate fish.

	Control (3)	Transparent eyecap (4)	Translucent eyecap (5)	Deofactored (4)	Lateral line enervated (4)	Deofactored lateral line enervated (3)
AB	1.00 (1.00)	0.25 (0.50)	0.00	0.50 (0.58)	0.00	0.00
AR	0.33 (0.58)	4.25 (8.50)	2.20 (1.64)	0.50 (0.58)	2.50 (3.00)	0.67 (0.58)
BI	0.67 (1.16)	1.50 (2.38)	0.60 (0.89)	1.25 (0.96)	0.50 (0.58)	0.67 (1.16)
BIB	0.67 (1.16)	1.25 (2.50)	0.60 (0.89)	1.25 (0.96)	0.50 (0.58)	0.67 (1.16)
BI/BIB	1.00 (0.00)	1.50 (1.73)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)
RU	0.00	1.25 (2.50)	0.20 (0.45)	1.00 (2.00)	0.75 (1.50)	0.00
BUB	0.00	1.25 (2.50)	0.20 (0.45)	1.00 (2.00)	0.50 (1.00)	0.00
BU/BUB	0.00	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	1.50 (0.00)	0.00
FI	0.00	0.50 (1.00)	0.60 (0.89)	1.25 (1.26)	0.25 (0.50)	1.00 (1.73)
FO	0.00	3.00 (3.83)	0.20 (0.45)	0.00	2.00 (3.37)	0.00
OP	1.33 (1.53)	0.00	0.60 (0.89)	0.00	0.00	0.33 (0.58)
PA	0.00	0.25 (0.50)	0.40 (0.89)	0.00	0.00	0.00
PS	0.00	1.50 (1.73)	0.20 (0.45)	0.00	1.00 (1.41)	0.00
QV	0.00	0.00	0.00	0.00	0.00	0.67
SB	0.00	0.75 (1.50)	0.00	0.00	0.50 (1.00)	0.00
SBB	0.00	0.50 (1.00)	0.00	0.00	0.50 (1.00)	0.00
SB/SBB	0.00	1.50 (0.00)	0.00	0.00	1.00 (0.00)	0.00
TB	26.33 (22.86)	3.25 (6.50)	48.80 (68.83)	52.25 (48.23)	24.75 (16.64)	31.67 (34.82)
TBB	11.33 (9.82)	1.75 (3.50)	18.40 (24.28)	16.00 (13.29)	11.00 (7.87)	12.00 (14.18)
TB/TBB	2.32 (0.13)	1.86 (0.00)	2.56 (0.48)	3.07 (0.56)	2.33 (0.52)	2.60 (0.65)
WI	0.33 (0.58)	4.75 (6.19)	2.00 (2.55)	0.75 (0.96)	1.25 (2.50)	0.00
TOT	31.00	22.25	56.80	59.50	34.50	36.00

suggests further the qualitative observation that transparent eyecaps apparently had an incremental effect on aggression levels.

Deolfacted eventual subordinates were second only to transparent eyecap fish in types and frequency of aggressive motor patterns performed. Anosmia may eliminate perception of cues which normally suppress aggression in fish which ultimately become subordinate.

When compared to other groups, eventual subordinates wearing transparent eyecaps clearly tailbeat less often. Since tailbeating by one fish is usually directive of tailbeating in a pair mate, the low frequency of this motor pattern is a correlate of the low number of tailbeats delivered by eventual dominants in this group.

Postresolution Results - Dominants

Mean frequencies and standard deviations for postresolution dominant behavior are found in Table 13.

Several differences among treatment group means exist. BI frequency ($F=2.4275$; $df=5, 17$; $p=.0776$) and BIS frequency exceeded the 0.1 significance level. Examination of the means shows that control and transparent eyecaps groups performed more postresolution bites and bite sessions than other groups did. Translucent eyecap fish exhibited the lowest mean bite frequency.

Differences among AP frequencies were statistically significant ($F=4.14$; $df=5, 17$; $p=0.0122$). This was due primarily to the occurrence of appeasement in three transparent eyecap dominants. One deolfacted-lateral line enervated dominant also displayed a postresolution appeasement posture.

Differences in TB frequencies ($F=2.2941$; $df=5, 17$; $p=.0910$) and

Table 13. Postresolution mean frequencies, mean rates,
and standard deviations () for dominant fish.

	Control	Transparent eyecap	Translucent eyecap	Deolfacted	Lateral line enervated	Deolfacted lateral line enervated
AP	0.00	1.00 (0.82)	0.00	0.00	0.33 (0.58)	0.33 (0.58)
AR	43.33 (36.30)	87.75 (62.88)	43.20 (31.46)	29.50 (28.35)	16.33 (5.13)	16.33 (5.13)
BT	34.67 (26.10)	35.75 (24.64)	6.60 (6.66)	10.50 (12.23)	10.33 (12.70)	10.33 (12.70)
BIB	28.67 (20.60)	30.50 (23.10)	6.20 (6.38)	7.50 (7.59)	10.33 (12.70)	10.33 (12.70)
BI/BTB	1.25 (0.20)	1.17 (0.21)	1.04 (0.10)	1.28 (0.28)	1.00 (0.00)	1.00 (0.00)
BU	71.67 (16.62)	69.75 (46.62)	44.80 (54.23)	34.50 (39.67)	33.67 (48.87)	33.67 (48.81)
BUB	59.00 (15.13)	61.00 (44.05)	39.20 (47.48)	30.25 (32.94)	29.00 (41.58)	29.00 (41.58)
BU/BUB	1.22 (0.07)	1.16 (0.18)	1.11 (0.07)	1.09 (0.15)	1.11 (0.10)	1.11 (0.10)
CH	1.67 (1.53)	6.50 (9.15)	0.80 (1.10)	0.75 (0.96)	0.67 (1.16)	0.67 (1.16)
CO	1.33 (0.58)	0.25 (0.50)	2.80 (4.21)	0.25 (0.50)	3.33 (4.93)	3.33 (4.93)
FL	0.00	1.75 (2.36)	0.00	0.00	0.00	0.00
FO	3.67 (1.53)	6.25 (5.56)	0.20 (0.45)	4.25 (7.23)	1.25 (0.96)	3.00 (3.46)
OP	2.33 (4.04)	0.25 (0.50)	3.20 (3.27)	6.00 (6.93)	1.50 (3.00)	4.33 (5.86)
PA	1.33 (2.31)	0.25 (0.50)	1.00 (1.41)	0.25 (0.50)	0.75 (1.50)	0.00
QV	0.00	0.00	0.00	5.25 (10.50)	0.00	2.00 (2.00)
SB	3.00 (1.00)	4.00 (6.16)	1.40 (0.55)	3.00 (3.56)	4.50 (6.61)	2.67 (2.52)
SBB	3.00 (1.00)	4.00 (6.16)	1.40 (0.55)	3.00 (3.56)	4.50 (6.61)	2.33 (2.08)
SB/SBB	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	1.13 (0.18)
TB	185.00 (131.76)	87.00 (64.73)	17.60 (11.15)	94.75 (112.25)	21.25 (18.46)	89.33 (80.03)
TBB	78.67 (58.56)	34.25 (25.32)	8.60 (5.27)	36.25 (38.54)	8.50 (6.46)	44.33 (46.37)
TB/TBB	2.47 (0.25)	2.64 (0.25)	2.03 (0.11)	2.34 (0.36)	2.44 (0.76)	2.16 (0.49)
WI	11.00 (18.19)	20.75 (21.93)	19.00 (22.97)	9.25 (11.53)	16.00 (17.17)	3.67 (6.35)
TOT	359.00 (125.37)	321.25 (168.80)	140.60 (92.84)	198.25 (139.84)	199.25 (226.65)	169.67 (144.54)

TBT frequencies ($F=2.3006$; $df=5, 17$; $p=.0903$) also exceeded the 0.1 level of significance. Control fish performed considerably higher numbers of tailbeats and bouts than other groups did. In contrast, the translucent eyecap and lateral line-enervated groups executed low numbers of tailbeats and bouts.

As in prerelution activity, biting (BI/BIB), butting (BU/BUB), and tailbeating (TB/TBB), rates are very similar across groups. Again, sensory deficit seems to effect total frequencies of individual motor patterns without altering the way in which these activities clump during interaction.

Comparison of total activity means (TOT) indicates that control and transparent eyecap groups performed the largest number of individual motor patterns.

Though not statistically significant, the occurrence of postrelution alternate biting (AB) in the transparent eyecap and deolfacted groups indicates relution was equivocal in these fish.

Comparison of total activity means (TOT) indicates that control and transparent eyecap groups performed the largest number of individual motor patterns. Thus presence of translucent eyecaps appears to reduce activity levels.

Postrelution Results - Subordinates

Table 14 presents postrelution means and standard deviations for subordinate bass.

Only differences among BI frequencies and BIS frequencies ($F=2.4827$; $df=5, 17$; $p=.0727$ for both) were statistically significant at the 0.1 significance level. This effect is the consequence of two

Table 14. Postresolution mean frequencies, mean rates, and standard deviations () for subordinate fish.

	Control	Transparent eyecap	Translucent eyecap	Deaffacted	Lateral line enervated	Deaffacted Lateral line enervated
AB	0.00	0.50 (1.00)	0.00	0.25	0.00	0.00
AI	79.33 (3.06)	122.75 (103.21)	51.60 (63.32)	35.50 (29.96)	134.50 (156.27)	20.00 (11.53)
AR	0.00	3.25 (5.85)	1.20 (1.30)	2.00 (4.00)	1.00 (1.41)	1.00 (1.73)
BI	0.00	1.50 (1.73)	0.00	0.25 (0.50)	0.00	0.00
BIB	0.00	1.50 (1.73)	0.00	0.25 (0.50)	0.00	0.00
BI/BIB	0.00	1.00 (0.00)	0.00	1.00 (0.00)	0.00	0.00
BI	0.00	0.25 (0.50)	0.00	1.00 (2.00)	0.00	0.00
BUB	0.00	0.25 (0.50)	0.00	1.00 (2.00)	0.00	0.00
BU/BUB	0.00	1.00 (0.00)	0.00	1.00 (0.00)	0.00	0.00
CH	0.00	1.25	0.00	0.25	0.00	0.00
FI	4.00 (2.65)	10.25 (12.61)	1.40 (1.95)	3.00 (4.08)	11.50 (14.85)	2.00 (2.65)
FO	0.00	0.50 (0.58)	0.40 (0.89)	0.00	0.00	0.00
OP	0.00	0.50 (1.00)	0.00	0.75 (1.50)	0.00	0.00
PA	0.00	0.25 (0.50)	0.20 (0.45)	0.00	0.00	0.00
QV	6.33 (10.97)	0.00	1.00 (2.24)	0.00	0.00	14.67 (25.40)
SB	0.00	0.50 (1.00)	0.00	0.00	0.00	0.00
SBB	0.00	0.50 (1.00)	0.00	0.00	0.00	0.00
SB/SBB	0.00	1.00 (0.00)	0.00	0.00	0.00	0.00
TB	0.00	5.50 (7.14)	0.00	20.50 (33.48)	2.00 (2.83)	7.00 (12.12)
TBB	0.00	3.25 (4.27)	0.00	7.25 (10.87)	0.50 (0.71)	3.00 (5.20)
TB/TBB	0.00	1.71 (0.06)	0.00	2.52 (0.74)	4.00 (0.00)	2.33 (0.00)
WI	3.00 (1.00)	8.50 (4.45)	3.00 (2.55)	3.75 (5.19)	5.00 (1.41)	6.00 (3.46)
TOT	93.00 (6.56)	155.50 (111.58)	58.80 (65.51)	67.25 (49.16)	91.00 (124.97)	50.67 (23.86)

subordinates in the transparent eyecap group which bit dominant pair mates. In addition, one deolfacted subordinate administered a bite to its dominant partner.

Bass equipped with transparent eyecaps also chased and withdrew more frequently than other treatment bass, and were the only subordinates to shambite dominant fish.

Deolfacted subordinates are distinguished particularly by their high tailbeating frequency (TB). Two individuals in this group reinitiated tailbeating subsequent to resolution, indicating resolution was equivocal. Furthermore, one subordinate performed a single butt.

Variation in approach frequencies represents, for the most part, the aggressive behavior of dominants.

Overall Results - Unresolved Pairs

Since fish in these pairs could not be classified as dominant or subordinate, results were summed over individuals within treatment groups for comparison (Table 15).

Bass in control, transparent eyecap, and lateral line-enuvated groups approached (AR) more frequently than fish in other groups. However, control fish pairs had approximately equal approach frequencies, while one bass tended to perform most of the approaches in transparent eyecap and lateral line-enuvated pairs.

Only tailbeat frequency (TB) differed significantly among treatment groups ($F=3.3228$; $df=4, 9$; $p=.0621$). Examination of the means reveals that control and lateral line-enuvated pairs performed considerably more tailbeats than did pairs in remaining groups.

Table 15. Mean frequencies, mean rates, and standard deviations () for unresolved pairs.

	AR	BU	BUB	BU/BUB		FO	LAP	SB	SBB	SB/SBB	TB	TBB	TB/TBB	WI
Control	10.50 (11.62)	0.50 (0.58)	0.50 (0.58)	1.00 (0.00)	0	6.00 (7.79)	42.45 (15.77)	0.50 (1.00)	0.50 (1.00)	1.00 (0.00)	40.25 (47.12)	14.25 (16.58)	2.82 (0.12)	14.25 (16.85)
Transparent eyecaps	8.50 (6.36)	0	0	0	0	3.00 (0.00)	169.20 (0.00)	0	0	0	4.50 (2.12)	2.00 (1.41)	2.50 (0.71)	9.50 (3.54)
Deolfacted	1.00 (0.0)	0	0	0	0	2911.00 (0.0)	0	0	0	0	0	0	0	0
Lateral line enervated	9.00 (8.49)	1.00 (0.00)	1.00 (0.00)	1.00 (0.0)	0	0.50 (0.71)	27.20 (0.0)	0	0	0	72.0 (1.4142)	24.50 (2.12)	2.95 (0.31)	9.00 (7.07)
Deolfacted- lateral line enervated	4.00 (7.35)	0	0	0	0	0	2288.25 1855.09	0	0	0	0	0	0	3.50 (7.00)

Comparison of Dominants and Subordinates

Within Groups

In normal pairs, eventual dominants and subordinates do not appear to differ behaviorally until resolution. Both fish in a pair exhibit similar motor pattern repertoires and frequencies until resolution suddenly occurs.

T tests were used to identify any treatment effects causing dominants and subordinates to behave differently during the preresolution period. Comparisons of mean frequencies of motor patterns, rates per bout, and total activity were made and revealed that dominant and subordinate fish within groups differ little until resolution of an encounter. Only in pairs belonging to the translucent eyecap and deofactored groups were some differences statistically significant. Eventual dominant and subordinate bass wearing translucent eyecaps exhibit significantly different bite (BI) frequencies ($t=2.2718$; $df=8$; $p=.0527$) and bite bout (BIB) frequencies ($t=2.3689$; $df=8$; $p=.0453$). Eventual deofactored dominants and subordinates also performed significantly different numbers of bites (BI) in preresolution activity ($t=2.5538$; $df=6$; $p=.0433$). No other differences between dominants and subordinates in any group were significant.

CHAPTER VIII

SUMMARY AND CONCLUSIONS

Captive largemouth bass exhibit agonistic motor patterns similar to those described for several Lepomis species (Greenberg 1945; Miller 1963; Hadley 1969; Powell 1972). However, in dyadic encounters they also perform spits, shambites, and quivers, none of which have been reported for centrarchids.

Spitting and shambiting, although very different, are consistently performed with the snout several centimeters from an opponent's mid-trunk lateral line organs, suggesting both behaviors may be providing lateral line stimuli. Since spitting may rock an opponent's body, a water displacement which could affect cupulae presumably occurs.

The snapping jaw movements associated with shambiting appear to be very similar to jaw movements reported by Gerald (1970) to be highly correlated with a popping sound produced by interacting Lepomis microlophus. Whether a similar association between jaw movements and sound production occurs in M. salmoides is purely speculative, but the fact that shambites are directed at the lateral line is suggestive of such a possibility. Further study is needed to determine whether sounds are produced by M. salmoides in this context.

Quivering or extremely rapid vibration of the body by subordinates was associated with very aggressive attacks by dominants. Quivering may provide a tactile stimulus since quivering fish often descend onto

the dorsum of a dominant fish.

Color patterns in bass, though not as striking as coloration in some Lepomis species, are distinctive and consistently associated with particular behavioral states. Signal properties seem to be associated mainly with subordinate color changes since both fish generally begin with the silvery color retained by dominant fish. Interestingly, subordinate color patterns described here are extremely similar to those which occur in gravid female M. dolomieu (Schneider 1971) and M. punctulatus (L. E. Vogel, pers. comm.) attempting to enter a nesting male's territory. In both contexts this color pattern is associated with proximity to a highly aggressive bass. The red eye coloration of dominant bass in this study is also similar to the iris of nesting male M. dolomieu (Schneider 1971).

Experiment I - Species Recognition

The use of species-specific visual cues is well documented in fish (Tinbergen 1948; Keenleyside 1971; Steele and Keenleyside 1971; Miller 1963; Thresher 1976). The existence of a variety of visual displays, distinct color patterns, and large eyes in largemouth bass indicates that they are also primarily dependent on vision to recognize conspecifics and carry on social interactions. Yet bass successfully inhabit periodically or permanently turbid waters.

Results of this experiment, though somewhat ambiguous due to the lack of strict control groups, indicate that the lateral line becomes the most important sense when vision is limited in bass. Control and deolfacted test bass consistently interacted more with bass than with bluegill, suggesting they could discriminate between the two stimulus

fish types. In contrast, lateral line-enuvated test bass appeared unable to discriminate between conspecifics and heterospecifics since they exhibited similar approach and tailbeating frequencies with both stimulus fish groups.

Two factors may contribute to these results. First, enervation of the trunk lateral line may significantly hamper reception of key stimuli (shape, vortices, fin movement) necessary for identification of conspecific fish. This is suggested by the similarity of the lateral line-enuvated group's approach and tailbeating frequencies with bass and bluegill, and the similarity of these frequencies to frequency of approach and tailbeating with bluegill for control and deolfacted groups. Thus the lateral line enuvated group results cannot be explained simply by their somewhat lower activity level.

Second, enervation of the trunk lateral line may have a decremental effect on the responsiveness of a bass. Prior to the addition of stimulus fish, swimming movements and general activity levels of control, deolfacted, and lateral line enuvated test bass appeared qualitatively similar. However, after release of stimulus fish, the consistently lower approach and tailbeating frequencies of enuvated bass (see regression lines, Figures 3-6 and 8-11) with both stimulus fish and the undirected quality of most of their approaches seemed to indicate they were less aware of the presence of stimulus fish. This is further supported by the fact that lateral line-enuvated bass eventually located floundering minnows which produced constant water displacements, but had difficulty locating minnows and stimulus fish which were relatively inactive.

The deolfacted-lateral line-enuvated group was distinctly dif-

ferent from other treatment groups. Their incessant traversing behavior may represent an anxiety response to extreme sensory deprivation. Since their vision was hampered but not completely obstructed, they may have been constantly swimming to obtain environmental information through visual and cephalic lateral line stimuli.

Although this experiment does not eliminate the possibility that olfaction plays a role in species recognition in bass, the constraints of the aquatic medium and physical qualities of chemical signals suggest why olfactory cues would be an inefficient means of identifying distant conspecific animals. Under field conditions, species recognition often must be accomplished quickly and while animals are at some distance. In the lentic habitats characteristic of bass, olfactory cues are neither highly directional nor readily dispersed. Thus olfaction seems more likely to be important in initial recognition of conspecifics than vision and the lateral line which can perceive and localize stimuli at some distance.

Several factors in this experiment may limit the generality of our conclusions, however. First, although their vision was severely limited, test bass probably obtained some visual cues when within 2-3 cm of stimulus fish. Second, the form of the experimental tanks (long, narrow, and shallow) undoubtedly causes water displacement patterns to differ from the way in which they occur in natural habitats characterized by wave action.

Experiment II - Dominance Hierarchies

Dominance relationships in bass appear to be similar to those described for Lepomine centrarchids (Greenberg 1945; Hadley 1969;

Powell 1972) and other fish (Frey 1970). Bass dominance encounters are characterized by the two distinct phases described by Frey and Miller (1972) for Trichogaster trichopterus: a relatively brief establishment phase and an extended maintenance phase. Operationally, the two phases are divided into (1) a preresolution phase consisting of an approach and tailbeating period, and a biting and appeasement period, and (2) a postresolution phase in which dominants repeatedly approach, butt, bite, and tailbeat subordinates.

The preresolution periods in an encounter are not clearly separated from one another, but are linked by a gradual transition from reciprocal tailbeating to reciprocal biting. But, separation of preresolution and postresolution periods is marked by a well-defined behavioral boundary since resolution is typically very abrupt. Few behavioral differences were apparent between eventual dominants and subordinates until one suddenly appeased, bringing on the distinct post resolution period.

Under these experimental conditions, dominance relationships in normal bass remained stable over several days (up to 4 days in preliminary observations). In addition, unlike some other fish (Gorlick 1976) subordinate bass seldom if ever direct aggressive acts at dominant bass.

As expected, results from experiment II verify that vision is the critical sense used by bass to coordinate agonistic activities. Normal and transparent eyecap bass oriented rapidly to opponents, and performed coordinated, well-defined motor patterns. In contrast, all fish equipped with translucent eyecaps swam more slowly and along the sides and bottom of tanks, a behavioral change similar to the effect of blinding on Carassius auratus (Timms 1976).

Obstruction of vision also caused bass to perform less stereotyped and often disoriented agonistic motor patterns. Approaches, tailbeats, bites, and appeasements were not as complete or well-defined as in normal and transparent eyecap bass. Thus vision provides information which permits a fish to control the orientation of agonistic displays and make rapid adjustments of position during interaction.

Comparison of groups in which vision was blocked reveals that olfactory cues are important to the development of stable dominance relationships in the largemouth bass. Unlike normal pairs, deolfacted and deolfacted lateral line enervated pairs did not unequivocally resolve encounters. Instead, subordinates in these groups engaged in postresolution reciprocal biting while circling, butting, tailbeating, opercle spreading, and even chasing of dominants. In addition, deolfacted and deolfacted-lateral line-enervated dominants occasionally exhibited appeasement, and those in the latter group quivered during postresolution activity. Furthermore, though all pairs in other treatment groups eventually resolved encounters, some unresolved deolfacted and deolfacted-lateral line-enervated pairs remained unresolved through second day observations. Clearly, olfaction is providing some type of cue which aids in the stabilization of dominance relationships in bass.

Several other treatment effects are of interest. The presence of transparent eyecaps apparently had an incremental effect on aggression levels. Bass in this group attacked more vigorously than controls, and tended to eliminate or reduce the tailbeating phase of prerelution activity. They typically went from initial approaching to biting and butting, indicating they were somewhat hyperaggressive. Further evidence of hyperaggressiveness was the tendency of subordinates in

this group to perform aggressive motor patterns, and the fact that a transparent eyecap subordinate was the only submissive fish to eventually overthrow a dominant.

Comparison of experiment I deolfacted-lateral line-enervated bass with deolfacted-lateral line-enervated bass wearing translucent eyecaps reveals another interesting result. The first group was hyperactive, while the second was very inactive. The added stress of the eyecaps and the complete obstruction of vision combined with anosmia and lack of the trunk lateral line obviously produces a significantly more altered animal than in the first experiment. This seems to support the idea that deolfacted-lateral line-enervated bass in experiment I may have been traversing to obtain any visual cues available under the turbid conditions existing in their tanks.

A Note on Feeding Behavior

Although observations of feeding behavior were only a small part of this study, they provided some insight into the sensory world of bass. Results tentatively indicate that when vision is very limited, bass can effectively locate and capture prey using only the cephalic portion of the lateral line. Although deolfacted-lateral line-enervated bass in experiment I may have used some visual cues to make final orientations in capturing minnows struggling on the surface, deolfacted-lateral line-enervated fish fitted with translucent eyecaps followed and ingested intact minnows swimming beneath the surface. This suggests strongly that under conditions of low visibility, such as nocturnal feeding or high turbidity, bass can use the lateral line system as the primary sense in feeding. The capture of blinded fish

which have survived in natural habitats seems to corroborate this conclusion (A. K. Andrews, pers. Comm.).

General Discussion

Thresher (1976) concluded that a bimodal system exists for species recognition and intraspecific social interaction in Eupomacentrus planifrons. By manipulating stimuli associated with conspecifics and heterospecifics he showed that species recognition in damselfish is based on discrimination of general form, while intraspecific interactions depend on finer details of form and color.

This study indicates a similar system probably exists in the large-mouth bass. In bass, vision and the lateral line appear to be the primary senses involved in discriminating between conspecifics and heterospecifics, while vision and olfaction are important in organizing intraspecific interactions.

The nature of these sensory systems and the environmental constraints placed on fish make such a bimodal system functional. Vision and the lateral line can function as distance senses providing information about spatial relationships and form. Thus they are well adapted for providing information to bass which must decide whether to expend energy approaching and interacting with another fish.

Once species recognition has occurred and two fish are in close proximity, vision undoubtedly is important in recognition of complex color patterns and other visual displays. In addition, the proximity of fish in intraspecific interactions also makes olfactory cues useful. Biting, butting, and shambiting bring the nares near or in contact with a conspecific, providing the opportunity for detection of chemical cues.

Thus, a bimodal system operating with reference to species recognition and intraspecific agonistic activity seems biologically functional for this species.

LITERATURE CITED

- Andrews, D. W. 1952. Sensitivity of fish to light and the lateral line system. *Physiol. Zool.* 25:240-243.
- Atema, J. 1969. The chemical senses in feeding and social behavior of the catfish, *Ictalurus natalis*. Ph.D. Thesis, Univ. Michigan, Ann Arbor. 147 pp.
- Baerends, G. P., and J. M. Baerends-van Roon. 1950. An introduction to the study of the ethology of cichlid fishes. *Behavior Suppl.* 1:1-242.
- Bardach, J. E., and J. H. Todd. 1970. Chemical communication in fish. Pages 205-240 in J. W. Johnson, D. C. Moulton, and A. Turk, eds. *Advances in chemoreception, Vol. I. Communication by chemical signals.* Appleton-Century-Crofts, New York.
- Barlow, G. W. 1963. Ethology of the Asian teleost *Badis badis*. Motivation and signal value of the color patterns. *Anim. Behav.* 11:97-105.
- Bergeijk, W. A. Van. 1967. Introductory comments on lateral line function. Pages 73-81 in P. H. Cahn, ed. *Lateral line detectors.* Indiana Univ. Press, Bloomington.
- Branson, B. A., and G. A. Moore. 1962. The lateralis components of the acoustico-lateralis system in the sunfish family centrarchidae. *Copeia* 1962(1):1-108.
- Breder, C. M., and F. Halpern. 1946. Innate and acquired behavior

- affecting the aggregation of fishes. *Physiol. Zool.* 19:154-190.
- Breder, C. M., and C. W. Coates. 1935. Sex recognition in the guppy. *Zoologica* 19:187-207.
- Breder, C. G., and R. F. Nigrelli. 1935. The influence of temperature and other factors on the winter aggregations of the sunfish, Lepomis auritus, with critical remarks on the social behavior of fishes. *Ecol.* 16:33-47.
- Brown, F. A. 1937. Response of the largemouth black bass to colors. *Ill. Nat. Hist. Sur. Bull.* 21:33-55.
- Burghardt, G. M. 1970. Defining "communication". Pages 205-240 in J. W. Johnson, D. C. Moulton, and A. Turk, eds. *Advances in chemoreception, Vol. I. Communication by chemical signals.* Appleton-Century-Crofts, New York.
- Cahn, P. H. 1972. Sensory factors in the side-to-side spacing and positional orientation of the tuna, *Euthymus affinis*, during schooling. *NOAA Fish. Bull.* 70(1):197-204.
- Cheal, M., and R. E. Davis. 1974. Sexual behavior: social and ecological influences in the anabantoid fish, Trichogaster trichopterus. *Behav. Biol.* 10:435-445.
- Denny, M. 1937-38. The lateral line system of the teleost, Fundulus heteroclitus. *J. Comp. Neurol.* 68:49-65.
- Dijkgraaf, S. 1967. Biological significance of the lateral line organs. Pages 83-95 in P. Cahn, ed. *Lateral line detectors.* Indiana Univ. Press, Bloomington.
- Disler, N. N. 1960. Lateral line sense organs and their importance in fish behavior. English translation, Israel program for scientific translations, 1971. Keter Press Binding: Weiner Bindery

- Ltd., Jerusalem. 328 pp.
- Eibl-Eibesfeldt, I. 1970. Ethology the biology of behavior. Holt, Rinehart and Winston, New York. 530 pp.
- Fernald, R. D. 1977. Quantitative behavioral observations of Haplochromis burtoni under semi-natural conditions. Anim. Behav. 25(3):643-653.
- Fine, M. L., H. E. Winn, and B. L. Olla. 1977. Communication in fishes. Pages 472-518 in T. A. Sebeok, ed. How animals communicate. Indiana Univ. Press, Bloomington.
- Forselius, S. 1957. Studies of anabantid fishes. I. Zool. Bidrag Fran Uppsala, Bund 32:97-302.
- Freihofer, W. C. 1963. Patterns of the ramus lateralis accessorius and their systematic significance in teleostean fishes. Stanford Ichthy. Bull. 8(2):80-189.
- Frey, D. F. 1970. The establishment of dominance relationships in the blue gourami, Trichogaster trichopterus (Pallas). Ph.D. thesis, Okla. State Univ., Stillwater. 142 pp.
- Frey, D. F., and R. J. Miller. 1972. The establishment of dominance relationships in the blue gourami, Trichogaster trichopterus (Pallas). Behav. 42(1-2):8-62.
- Frings, H., and M. Frings. 1964. Animal communication. Blaisdell Publishing Co., Waltham, Massachusetts. 204 pp.
- Frisch, K. von. 1941. Uber einen Schreckstoff der Fischhaut und seine biologische Bedeutung. J. Vergl. Physiol. 29:46-145.
- Gandolfi, G. 1969. A chemical sex attractant in the guppy, Poecilia reticulata Peters (Pisces, Poeciliidae). Monitore Zool. Ital. (N. S.) 3:89-98.

- Gerald, J. W. 1970. Sound production during courtship in six species of sunfish (Centrarchidae). *Evolution* 25:75-87.
- Gorlick, D. L. 1976. Dominance hierarchies and factors influencing dominance in the guppy, Poecilia reticulata (Peters). *Anim. Behav.* 24:336-346.
- Goz, H. 1941. Uber den art und individual geruch bei fischen. *Zool. Vergl. Physiol.* 29:1-45.
- Greenberg, B. 1947. Some relations between territory, social hierarchy and leadership in the green sunfish (Lepomis cyanellus). *Physiol. Zool.* 20:267-299.
- Gunning, G. E. 1959. The sensory basis for homing in the longear sunfish, Lepomis megalotis megalotis (Rafinesque). *Invest. Indiana Lakes and Streams* 5(3):103-129.
- Hadley, W. F. 1969. Factors affecting aggressive behavior and social hierarchy in the longear sunfish, Lepomis megalotis (Rafinesque). Ph.D. Thesis, Okla. State Univ., Stillwater. 77 pp.
- Hall, D. D. 1966. Reproductive color changes in the pearl gourami, Trichogaster leerii (Bleeker). *Bios* 37(3):104-107.
- Harris, G. G., and W. A. Van Bergeijk. 1962. Evidence that the lateral line organ responds to near-field displacements of sound sources in water. *J. Acoust. Soc. Am.* 34(12):1831-1841.
- Hemmings, C. C. 1966. The mechanism of orientation of roach, Rutilus rutilus L., in an odour gradient. *J. Exp. Biol.* 45:465-474.
- Jearld, A., Jr. 1975. An ethological study of the honey gourami, Colisa chuna, and its congeners. Ph.D. Thesis, Okla. State Univ., Stillwater. 115 pp.
- Keenleyside, M. H. 1971. Aggressive behavior of male longear sunfish

- (Lepomis megalotis). Zeits. fur Tierpsy. 28:227-240.
- Kuhme, W. 1963. Chemisch ausgeloste butflege und Schwarm-reaction bei Hemichromis bimaculatus (Pisces). Zeit. fur Tierpsy. 20: 688-704.
- Kuiper, J. W. 1967. Frequency characteristics and functional significance of the lateral line organ. Pages 105-122 in P. Cahn, ed. Lateral line detectors, Indiana Univ. Press, Bloomington.
- Losey, G. S., Jr. 1969. Sexual pheromone in some fishes of the genus Hypsoblennius Gill. Science 163:181-183.
- Losey, G. S., Jr. 1971. Communication between fishes in cleaning symbiosis. Pages 45-76 in R. C. Chens, ed. Aspects of the biology of symbiosis. University Park Press, Baltimore.
- Lowenstein, O. 1957. The sense organs: The acoustico-lateralis system. Pages 155-186 in M. E. Brown, ed. The physiology of fishes, Vol. II.
- Mainardi, N., and A. C. Rossi. 1968. Chemical communication in reference to construction of the nest in the anabantid fish Colisa lalia. Instituto Lombardo-Accademia di Science e Lettere, Estratto dai Rendiconti, Classe di Science (B) 102:23-28.
- Marler, P. 1967. Animal communication signals. Science 157:769-774.
- McDonald, A. L., and L. A. Kessel. 1967. Relationship between social hierarchy and coloration in green sunfish. Psychol. Repts. 20: 748-750.
- McErlean, D. 1967. Ethyl p-aminobenzoate: an anesthetic for cold-blooded vertebrates. Copeia 1967(1):239-240.
- Miller, H. C. 1963. The behavior of the pumpkinseed sunfish, Lepomis gibbosus (Linnaeus), with notes on the behavior of other species

- of *Lepomis* and the pygmy sunfish, *Elassoma evergladei*. Behav. 22(1-2):88-151.
- Miller, R. J. 1964. Studies on the social behavior of the blue gourami, *Trichogaster trichopterus* (Pisces, Belontiidae). Copeia 1964(3):469-496.
- Morris, D. 1958. The reproductive behavior of the ten-spined stickleback (*Pygosteus pungitius* L.). Behav. Suppl. 61-106.
- Nelissen, M. H. J. 1978. Sound production by some tanganyikan cichlid fishes and a hypothesis for the evolution of the R communication mechanisms. Behav. 64(1-2):137-147.
- Newcombe, C., and G. Hartman. 1973. Some chemical signals in the spawning behavior of rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 30:995-997.
- Noble, G. K., and B. Curtis. 1939. The social behavior of the jewel fish, *Hemichromis bimaculatus* Gill. Bull. Am. Mus. Nat. Hist. 76:1-46.
- Parker, G. H. 1903. Hearing and allied senses in fishes. Bull. U.S. Fish. Comm. 1902:45-64.
- Parker, G. H. 1905. The function of the lateral line organs in fishes. Bull. Bur. Fish. 24(480):185-207.
- Peters, H. M. 1971. Evidence of direct nervous connections between the neuromasts of the lateral-line system of fishes. *Experientia* 27(11):1292-1293.
- Pfeiffer, W. 1960. Über die Schreck-reaktion bei fischen und die herkunft des Schreckstoffes. *Zeit. Vergl. Physiol.* 43:578-614.
- Picciolo, A. R. 1964. Sexual and nest discrimination in anabantid fishes of the genera *Colisa* and *Trichogaster*. Ecol. Monogr. 34:

53-77.

- Powell, L. E. 1972. Factors influencing agonistic behavior and social organization in the orangespotted sunfish, Lepomis humilis (Girard). Ph.D. Thesis, Okla. State Univ., Stillwater. 141 pp.
- Rainwater, F. L., and R. J. Miller. 1966. Courtship and reproductive behavior of the siamese fighting fish, Betta splendens Regan (Pisces, Belontiidae). Proc. Okla. Acad. Sci. 47(1968):98-114.
- Reighard, J. E. 1906. The breeding habits, development, and propagation of the black bass. 16th Bien. Rept. Mich. State Board Fish. Comm. (append.):1-73.
- Reser, J. A. 1969. Courtship and reproductive behavior in the giant gourami, Colisa fasciata (Bloch and Schneider). M.S. Thesis, Okla. State Univ., Stillwater. 43 pp.
- Roberts, B. L., and K. P. Ryan. 1971. The fine structure of the lateral line sense organs of dogfish. Proc. R. Soc. Lond. B. 179:157-169.
- Robison, H. W. 1971. An ethological study of the snakeskin gourami, Trichogaster pectoralis, with comments on phylogenetic relationships among species of Trichogaster. Ph.D. Thesis, Okla. State Univ., Stillwater. 134 pp.
- Rossi, A. C. 1969. Chemical signals and nest-building in two species of Colisa (Pisces, Anabantidae). Monitore Zool. Ital. (N.S.)3: 225-237.
- Schneider, C. P. 1971. SCUBA observations of spawning smallmouth bass. New York Fish Game J. 18(2):113-116.
- Shaw, E. 1969. The duration of schooling among fish separated and those not separated by barriers. Am. Mus. Novitates, 2373. 12 pp.

- Schutz, F. 1956. Über die Schreck-reaktion bei fischen und die herkunft des Schreckstoffes. *Zeit. Vergl. Physiol.* 38:84-135.
- Suckling, J. A. 1967. Trunk lateral line nerves: some anatomical aspects. Pages 45-52 in P. Cahn, ed. *Lateral line receptors.* Indiana Univ. Press, Bloomington.
- Suckling, E. E., and J. A. Suckling. 1964. Lateral line as a vibration receptor. *J. Acoust. Soc. Am.* 36(11):2214-2216.
- Tavolga, W. N. 1954. Reproductive behavior in the gobiid fish, Bathygobius soporator. *Bull. Am. Mus. Nat. Hist.* 103:427-460.
- Tavolga, W. N. 1955. Pre-spawning behavior in the gobiid fish, Bathygobius soporator. *Behav.* 9:53-74.
- Tavolga, W. N. 1956. Visual, chemical, and sound stimuli as cues in the sex discriminatory behavior of the gobiid fish, Bathygobius soporator. *Zoologica* 41(2):49-64.
- Thresher, R. E. 1976. Field experiments on species recognition by the three-spot damsel fish, Eupomacentrus planifrons (Pisces: Pomacentridae). *Anim. Behav.* 24(3):562-569.
- Timms, A. M., and H. Kleerekoper. 1970. Locomotor responses of blinded goldfish (Carassius auratus) to remote perception of barriers. *J. Fish Res. Board Can.* 27:1103-1107.
- Tinbergen, N. 1951. *The study of instinct.* Oxford Press, London. 228 pp.
- Todd, J. H. 1967. The social behavior of the yellow bullhead, Ictalurus natalis. Ph.D. Thesis, Univ. Mich., Ann Arbor. 184 pp.
- Todd, H. H. 1971. The chemical languages of fishes. *Sci. Am.* 98-108.
- Todd, J. H., J. Atema, and J. E. Bardach. 1967. Chemical communica-

- tion in social behavior of a fish, the yellow bullhead (Ictalurus natalis). Science 158:672-673.
- Walker, T. J., and A. D. Hasler. 1949. Detection and discrimination of odors of aquatic plants by the bluntnose minnow (Hyborhynchus notatus). Physiol. Zool. 22:45-63.
- Wells, M. C., and P. N. Lerner. 1978. The relative importance of the distance senses in coyote predatory behavior. Anim. Behav. 26: 251-258.
- Wickler, W. 1962. Zur Stammesgeschichte funktionell korrelierter Organ- und Verhaltensmerkmale: Ei-Attrappen in Maulbrutern bei afrikanischen Cichliden. Zeit. Tierpsychol. 19:129-164.
- Wimmer, R. B. 1970. An ethological study of the moonlight gourami, Trichogaster microlepis (Gunther). Ph.D. Thesis, Okla. State Univ., Stillwater. 153 pp.

VITA 2

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