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SPECIES AND MATE DISCRIMINATION IN THE
BLUEGILL SUNFISH, LEPOMIS MACROCHIRUS
(PISCES: CENTRARCHIDAE).

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THE UNIVERSITY OF OKLAHOMA
GRADUATE COLLEGE

SPECIES AND MATE DISCRIMINATION IN THE BLUEGILL SUNFISH,
LEPOMIS MACROCHIRUS (PISCES: CENTRARCHIDAE)

A DISSERTATION
SUBMITTED TO THE GRADUATE FACULTY
in partial fulfillment of the requirements for the
degree of
DOCTOR OF PHILOSOPHY

BY
HERBERT JAMES GRIMSHAW
Norman, Oklahoma

1978

SPECIES AND MATE DISCRIMINATION IN THE BLUEGILL SUNFISH,
LEPOMIS MACROCHIRUS (PISCES: CENTRARCHIDAE)

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SPECIES AND MATE DISCRIMINATION IN THE BLUEGILL SUNFISH,
LEPOMIS MACROCHIRUS (PISCES: CENTRARCHIDAE)

CHAPTER I

INTRODUCTION

Early in this century, field observations of fishes during spawning raised questions concerning the mechanism of sex discrimination. Reeves (1907) working with two darters, Reighard (1913) working with the logperch, and Lissman (1932) working with the Siamese fighting fish, all emphasized the importance of movement in sex discrimination.

In 1934, G. K. Noble conducted a series of field experiments using models to delineate the sex discrimination mechanism of the pumpkinseed sunfish, Lepomis gibbosus. Based on experiments using recently stunned and formalin preserved males manipulated on strings, nest guarding males responding to their image in a mirror, lacquer painted plasticine models, and leaves, he concluded: (1) ". . . the male sunfish . . . is unable to distinguish the sex of a quiescent adult of his own species by appearance alone"; (2) ". . . male movements, chiefly the display of opercula and fins . . . call forth . . . an attack by the guarding male"; (3) ". . . smell does not enter at all into the problem of sex recognition"; (4) "tactile stimulation, supplemented probably by stimulations of the lateral line organs, were directly responsible for the circling movements practiced by the male during oviposition"; (5) ". . . it is probable that the brighter males, because

(they are) more conspicuous, would be visited more often by females;
. . ."

The validity of conclusions based upon an experimental design of this type, however, rests upon the ability of the observer to accurately determine normal courtship behavior. Furthermore, Noble did not provide any quantifiable data in support of his conclusions. In spite of these reservations, Breder (1936), Miller (1963), Huck and Gunning (1967), and Avila (1976) working with L. auritus and L. gibbosus, L. gibbosus, L. megalotis, and L. macrochirus, respectively, have all reaffirmed the validity of his work.

Subsequently, the following field and laboratory studies have either primarily focused on or have made inferences concerning sunfish behavioral mechanisms: (1) mechanisms used by nesting males to attract females (Noble, 1938; Gerald, 1971; Stacey and Chiszar, 1975; Avila, 1976); (2) mechanisms of species (Witt and Marzolf, 1954; Childers, 1967; Clark and Keenleyside, 1967; Gerald, 1971; Keenleyside, 1971), mate (Clark and Keenleyside, 1967; Steele and Keenleyside, 1971), sexual (Huck and Gunning, 1967; Gerald, 1971; Stacey and Chiszar, 1975), individual (Erickson, 1967), status (Miller, 1963; McDonald, et. al., 1968), and nest discrimination (Miller, 1963; Hunter, 1963); (3) the sensory modality mediating homing (Gunning, 1959); (4) the mechanism of colony formation and the function of the colony (Hunter, 1963; Gerald, 1971); (5) on the mechanism of breeding synchronization (Hunter, 1963).

To date, however, the specific cues and sensory modalities utilized by sunfishes in species discrimination are unknown (Childers, 1967; Gerald, 1971; Keenleyside, 1971). This study, therefore, attempts to determine if the visual sensory modality can exclusively mediate

species and mate discrimination in the bluegill sunfish, L. macrochirus and if so, to identify stimulus components which are critical to this discrimination.

CHAPTER II

MATERIALS AND METHODS

The bluegill, *L. macrochirus*, and longear, *L. megalotis*, sunfishes utilized in this study were seined from a local farm pond near Norman, Oklahoma on February 13, 1977 and were housed in a 1000-liter concrete tank (7 x 7 x 26 dm deep) supplied with heaters, well water and aerated via airstones. Water temperature in the tank varied between 18 and 21°C over the annual cycle, since a continuous flow of water was maintained through the tank. Illumination was provided by two 200-W tungsten filament bulbs with reflectors, set on a 16L:8D h photoperiod, suspended 6 dm above the waters surface and positioned 9 dm from each end of the tank. The fishes were fed a diet of Purina Catfish Chow ground to a suitable size for ingestion.

All specimens were acclimatized for three months prior to their experimental use. Most individuals exhibited growth and developed "breeding coloration" while resident within the tank. In addition, individuals destined for use as "stimulus fishes" were resident for two weeks within individual 20-liter glass aquaria. The linear array of these twelve aquaria was illuminated by four 200-W tungsten filament lamps, set on a 16L:8D h photoperiod, suspended 3 dm above the water's surface and evenly distributed above the tanks.

The experimental apparatus consisted of three separate aquaria, positioned as shown in Fig. 1. One large plat glass aquarium, hereafter called the experimental tank (5 x 3 x 12 dm long) was individually sup-

ported by a metal stand, while two smaller aquaria, hereafter called stimulus tanks, were positioned at opposite ends of a second metal stand. Three electrodes, connected in parallel, were fastened evenly across both ends of the experimental tank, reaching to within 2 cm of the bottom of the tank, and an acetate aquarium liner was inserted which covered the bottom, one side and both ends of the tank, giving it effective inner dimensions of 5 x 3 x 11.5 dm long. Identical patterns of small holes were drilled in the bottom of each end liner covering an area of approximately 4 dm². The water level in the experimental tank was maintained at a depth of 13 cm, which was sufficient to cover the pattern of holes in both end liners.

Two experimental units were constructed. While both contained identical experimental tanks, the stimulus tanks differed. Three different types of stimulus tanks were used in this study. Two types were constructed of 6 mm plexiglas. One set measured 5 x 2.3 x 3.7 dm long, while a second narrow set measured 50 x 5 x 38 cm long. The third type was simply a standard grey slate-bottomed, 20-liter, glass aquarium measuring 2.4 x 2 x 3.5 dm long. The back and bottom of the plexiglas tanks were painted flat black as was the chrome frame and moveable acetate liner fitted to the back of the 20-liter aquaria. Flat black paint was applied to the back, bottom and ends of both experimental tanks, rendering them opaque, and to all four metal aquarium stands.

Electrodes were constructed of silver wire electroplated for five minutes in the dark in normal hydrochloric acid, producing a silver-silver chloride interface. The electroplated wires were inserted and lowered to within 5 cm of the end of individual 6 mm glass tubes. A preheated solution of 3 molar potassium chloride and 5 percent by weight

agar was then poured into each of the tubes, which were then immersed in a water bath to hasten the solidification of the agar. Each experimental tank contained 6 electrodes in banks of 3, supplied from a 45V, 60 cycle a.c. source. Initially lamp switches were used to open and close the circuit; however, subsequent experience indicated spring return switches were more suitable and were employed during most of the study.

A light source consisting of a bank of 4, 61 cm, 20-W Sylvania F20T12-DSGN DE SIGN WHITE and 5, 122 cm, 40-W Sylvania F 40 DSGN DE SIGN WHITE Bulbs, contained within a common housing, passed through a grey plexiglas filter, suspended 3.8 dm above the surface of the water in both experimental and stimulus tanks, and set on a 16L:8D h photoperiod, provided illumination. It was possible to position this source approximately equally over both the experimental and stimulus tanks, due to its filter width of 20 cm and length of 122 cm. Two identical light sources were constructed, each of which was supplied with identical series of plexiglas filters.

Both experimental units were positioned as shown in Fig. 2 and a platform (2.1 x 2.4 m), from which sections were removed to permit the observation of both experimental tanks, was constructed 1.8 m above them. Grey cloth hung from its four sides reaching to ground level, covered the bottom of the platform and concrete floor beneath it, and separated the two experimental units. An opaque curtain, which could be lowered and raised, was suspended between the experimental and stimulus tanks in both experimental units. Fishes within these units were fed Lumbricus sp. and all aquaria were aerated by airstones.

An aversive, instrumental conditioning paradigm, utilizing discrete trials, was employed in this study. Sexually mature male blue-

gill sunfish, hereafter referred to as experimental fish, were placed in individual experimental tanks and remained there throughout training and testing. A bluegill sunfish, hereafter referred to as the S+, occupied one of the stimulus tanks, while the other tank contained a longear sunfish, hereafter referred to as the S-. Two different longears, one with a longer and one with a shorter total length than the S+, were alternately employed as the S-. A random number table alternating with a coin toss, determined which stimulus tank was occupied by the S+. Training commenced upon a lowering of the curtain which visually separated the two stimulus tanks from the experimental tank. When the curtain was lowered the experimental fish was negatively reinforced (shocked) if it did not assume a position in front of the stimulus tank occupied by the S+ ($1/3$ of the experimental tank area), within 1 minute. The experimental fish was also required to remain in front of the S+ for 4 additional minutes during the training process, and would be negatively reinforced if it failed to do so. Since the experimental fish could move freely within the experimental tank, a positive response consisted of either swimming the length of the experimental tank if it was positioned in front of the S- when the curtain was lowered, or of remaining in place if it happened to be in front of the S+.

With few exceptions, training was conducted daily, always beginning at 1315h and ending at 1700h. Training and testing trials were conducted once every half hour in each experimental unit. Since two units were employed, one unit was operated from 1315h to 1645h, while the other was operated from 1330h to 1700h. Training began June 8, 1977 and was completed June 30, 1978. Records were taken of the position of the fish within the experimental tank prior to lowering the curtain

(precurtain position) and 1 minute afterwards (postcurtain position). just prior to any negative reinforcement. These data were analyzed in groups of 20. The precurtain positions provided an expected frequency to which postcurtain positions could be compared statistically, using a chi-square goodness of fit test.

Experiment 1. Species Discrimination

One sexually mature male bluegill sunfish (the experimental fish) was placed within the experimental tank, and a second sexually mature, male bluegill (S+) was placed within one of the stimulus tanks. The other stimulus tank contained one of two sexually mature male longear sunfish (S-). The two longears, as described above, were chosen to have longer and shorter total lengths than the S+. The aversive paradigm was begun and continued until the experimental fish was responding significantly to the S+. Once a consistent response pattern had been established, the S+ and S- within the stimulus tanks were manipulated in one of the following ways:

- (1) One from a series of four broad band plexiglas filters was placed over the light source restricting the range of wavelengths illuminating the S+ and S-. The filters were assigned the subjective designations blue, green, yellow and red.
- (2) Acetate sheets, painted flat black, were positioned diagonally within both stimulus tanks restricting the movement of the S+ and S- and confining them to a lateral posture with respect to the experimental fish.

- (3) Different individuals of the same respective species and maintaining the same length relationship as the S+ and S-s, were substituted for the S+ and S-.

Experiment 2, Mate Discrimination

The procedure employed in this experiment is the same as that employed in experiment 1, with the exception that in this case, the S+ was a sexually mature female bluegill sunfish.

CHAPTER III

RESULTS

In the initial phase of each of these experiments, i.e., prior to the administration of negative reinforcement, lowering the curtain which separated the experimental from the stimulus tanks never resulted in locomotor behavior on the part of the experimental fish. This is reflected in the control values shown in Figures 4 through 7 and demonstrates that the behavior observed in this study does not occur spontaneously prior to training. Figures 3 through 7 illustrate, quantitatively, individual temporal changes which occurred in the behavior of five sexually mature male bluegill sunfish when they were exposed to the aversive discriminatory paradigm described above. In all five of these individuals, significant discriminatory behavior developed, typically after from 80 to 300 trials. Once developed, this behavior continued at significant levels for some time in the absence of negative reinforcement. While individual variation was observed in the behavioral responses exhibited by fish undergoing training, a "typical" temporal behavioral response sequence was observed. Initially in the early stages of training the experimental fish would remain motionless when the curtain was lowered and continued to do so until it was subsequently shocked, while later in the training process, the experimental fish would back to the rear of the tank using its pectoral fins and would assume a 45 degree angle there with respect to the sides of the tank, in response to curtain lowering. Positioned in such a manner,

the experimental fish was presumably better able to simultaneously view both stimulus fishes. The fish's eyes would then shift, first to one stimulus fish, then to the other, and so on, apparently actively comparing them. Occasionally eye movement was accompanied by vacillatory locomotor behavior. In such cases, the experimental fish would begin to advance toward either the S+ or S-, then stop, back up with its pectoral fins and advance toward the other stimulus, only to stop again short of its presumed goal. Such behavior was often repeated several times during a single trial. Still later in training, when discriminatory behavior was occurring at statistically significant levels, the experimental fish would often view the S+ or S- from a position immediately in front of it and as circumstances demanded, either remain in the immediate vicinity, or swim to the opposite end of the tank. A simultaneous visual comparison was seemingly no longer required by the experimental fish to discriminate successfully between the S+ and S-. Figures 3, 5 and 6 demonstrate the ability of male bluegill sunfish to discriminate between heterospecific, congeneric forms solely on the basis of species criteria. These results constitute, to my knowledge, the first demonstration of species discrimination utilizing training techniques.

Figure 5 illustrates the ability of male bluegills to discriminate between heterospecific, congeneric forms when both species and sexual cues are available, a situation presumably more similar to biologically relevant discriminations made during courtship. Figures 3 through 7 all demonstrate the crucial importance which free movement on the part of the stimulus fishes plays in both species and mate discrimination. During experimental manipulation of the stimulus fishes, it was discovered that a statistically significant nonreinforced discrim-

inatory behavior would become nonsignificant if the free movement of the stimulus fishes was restricted as described above and, additionally, that significant behavior would reappear when the stimulus fishes were again permitted unrestricted movement. Figure 5 demonstrates the occurrence of this same phenomenon in mate discrimination. In addition, Fig. 4 illustrates that the effect of movement restriction was also manifest on the development as well as the maintenance of species discrimination. Figures 5, 6 and 7 illustrate the fact that the placing of broad band plexiglas filters of several different restricted wavelength ranges (blue bandwidth = 400-525 nm, dominant wavelength = 475; green bandwidth = 500-575 nm, dominant wavelength = 550; yellow bandwidth = 550-750 nm, dominant wavelength = 600; red bandwidth = 600-750 nm, dominant wavelength = 650; grey bandwidth = 400-750 nm, dominant wavelength = 550) over the light source had no effect upon the statistical significance of either species or mate discrimination.

CHAPTER IV

DISCUSSION

Many authors have made suppositions concerning the mechanism or mechanisms utilized by sunfishes in species discrimination. Childer (1967) suggested that the coloration of the opercular flap was possibly an important stimulus component critical to species discrimination in sunfishes, based on pond hybridization experiments using opercular flap ablated and non-ablated redear (L. microlophus) males and bluegill females. Clark and Keenleyside (1967) suggested that male bluegill and pumpkin-seed (L. gibbosus) sunfishes can visually discriminate conspecific from heterospecific females on the basis of differential behavior. Keenleyside (1967) demonstrated that when male bluegill sunfish are presented with both conspecific and heterospecific female sunfishes simultaneously, they will bite at, display toward, courtship circle and spend more time near the conspecific female regardless of whether the females are enclosed in jars or are free swimming. Gerald (1971) demonstrated sound production during courtship in the bluegill and five other sunfish species. He believed, however, that the cues utilized by sunfishes in species discrimination also contained visual and olfactory components. Avila (1976), on the basis of field observations, suggested that tail sweeping and rim circling behaviors served as visual signals utilized in species discrimination, mate attraction and courtship.

Results obtained in these experiments demonstrate that sexually mature, male bluegill sunfish can discriminate bluegill from longear

sunfishes when size, sex and individual variation are eliminated as possible cues, i.e., the discrimination is based on species differences. Additionally, due to the nature of the apparatus, these results also demonstrate that species and mate discrimination can occur prior to the arrival of the approaching fish upon the nest, and in the absence of olfactory and auditory cues.

The inability of the experimental fish to successfully perform the discrimination when the movement of the stimulus fishes is restricted demonstrates (1) that the visual modality can exclusively transduce information necessary for both species and mate discrimination; and (2) that the critical cue or cues utilized in species and mate discriminations is not or are not a morphological, colorational or coloration pattern component on the lateral surface of the fish's head, body, or tail, i.e., that body shape, the pattern of lateral bars on the flanks, the opercular flap, and/or its coloration, ventral head and body coloration, etc., are not functioning as sufficient cues for species and mate discrimination. These results do not exclude the possibility, although it seems unlikely due to the bilaterally compressed nature of the fish's body, that some morphological, colorational or color pattern feature, only visible when the stimulus fish is viewed frontally, is functioning as the critical cue.

These data do strongly suggest that the coding of information necessary for species and mate discrimination in the bluegill sunfish is behaviorally mediated in the form of body and/or fin movements. Although the specific nature of these movements is presently unknown, two morphological features, (1) the perioral area including the lips, maxillary, premaxillary and dentary bones, and (2) the dark black pelvic

fins bordered anteriorly by their bright white pelvic spines, suggest themselves as likely candidates in light of results discussed above.

Of these two possibilities, the pelvic or ventral fins seems the most likely morphological component to convey movement stimuli due to their relatively large size, the length of their high contrast border, their ventral position, their apparent freedom from primary locomotor functions during courtship, and lastly their capacity for producing modulated signals.

Several additional observations also support the supposition, discussed above, that sunfishes utilize behavioral signals to convey species information to congeneric forms. These are:

- (1) experimental fish, recently introduced into the experimental tank, and prior to experiencing any training, oriented toward, maintained an interactive distance with an occasionally threatened the nearest stimulus fish;
- (2) circling, tail sweeping and threat behaviors increased in their frequency of occurrence as training progressed;
- (3) the experimental fish exhibited a rather long response latency, which although decreasing slightly as training progressed suggests that the experimental fish were actively waiting for a behavioral response from the stimulus fish prior to performing the discrimination and engaging in any locomotor behavior;
- (4) on rare occasions when the stimulus fish was not oriented toward the experimental fish after the curtain was lowered, the experimental fish would threaten the stimulus fish as if to elicit the behavioral response which was necessary for it to satisfactorily perform the discrimination.

In conclusion, therefore, it appears that the bluegill sunfish conveys species information behaviorally utilizing species specific body or fin movements and in doing so avoids the problems which a coloration or coloration pattern cue would encounter in the aquatic environment.

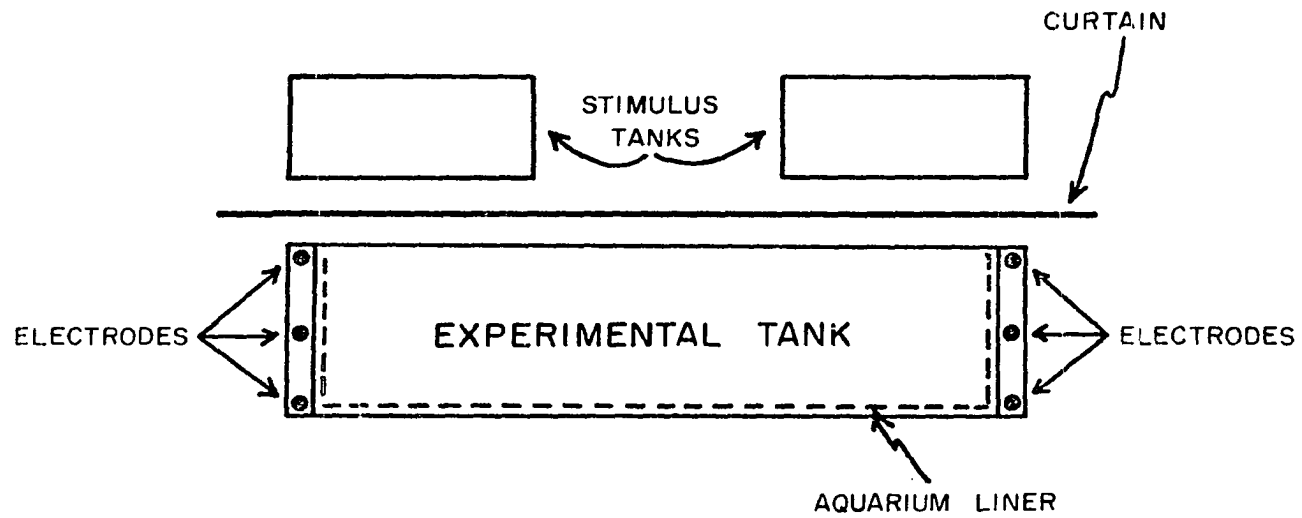
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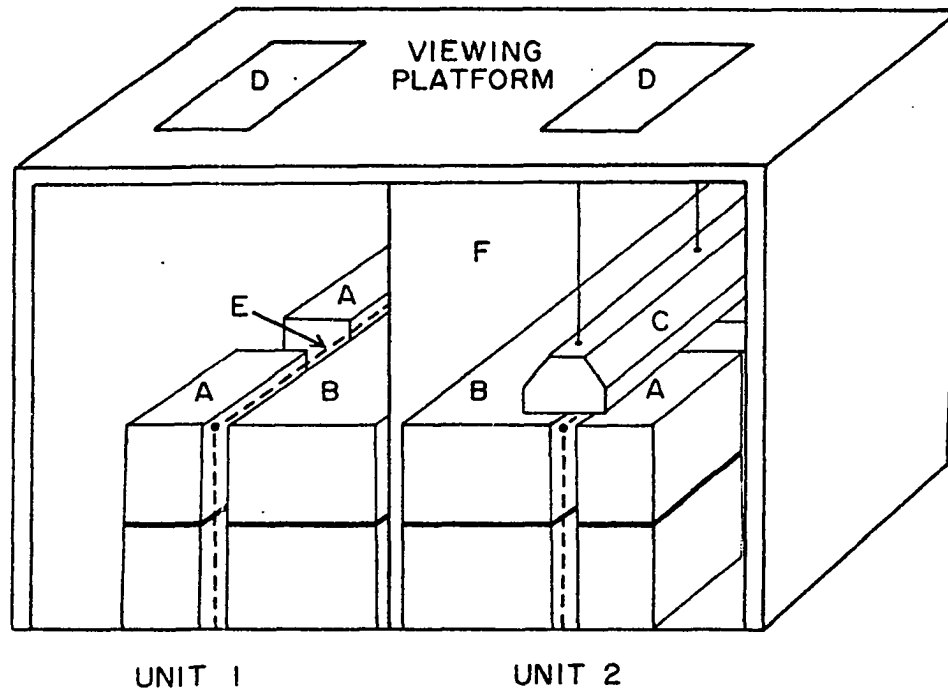
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Fig. 1. Diagram of the experimental apparatus.

EXPERIMENTAL APPARATUS
(polar view)

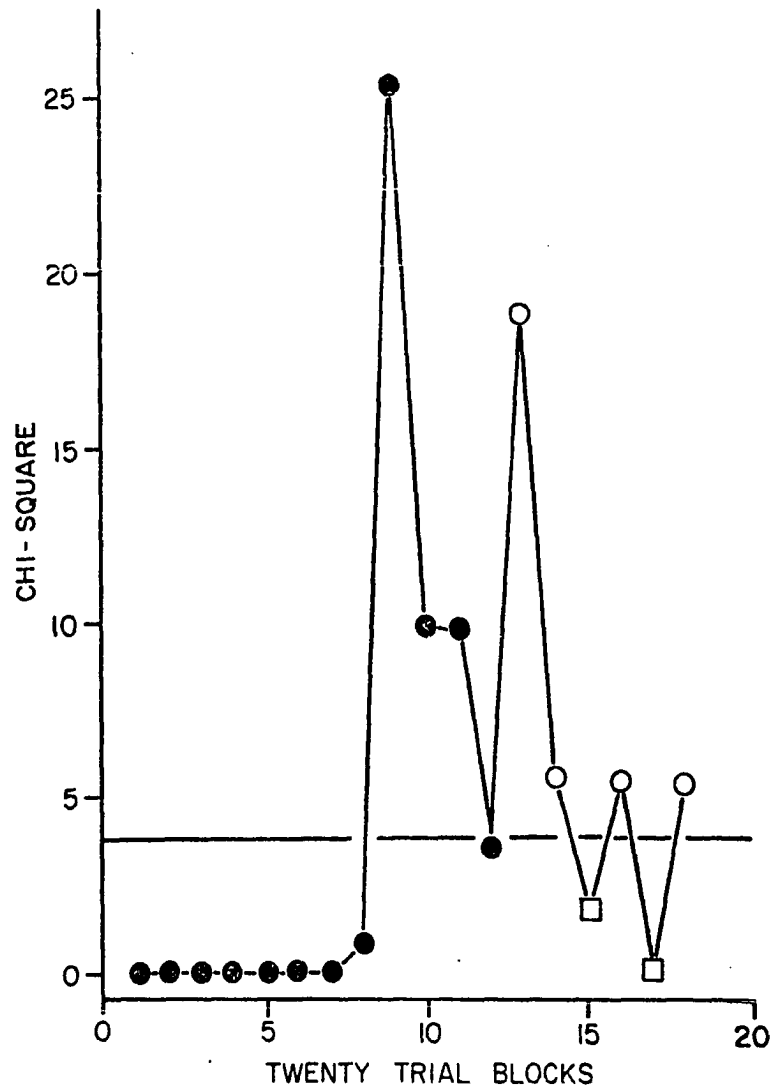


**Fig. 2. Diagram illustrating the relative positions
of both experimental units to each other
and to the viewing platform.**



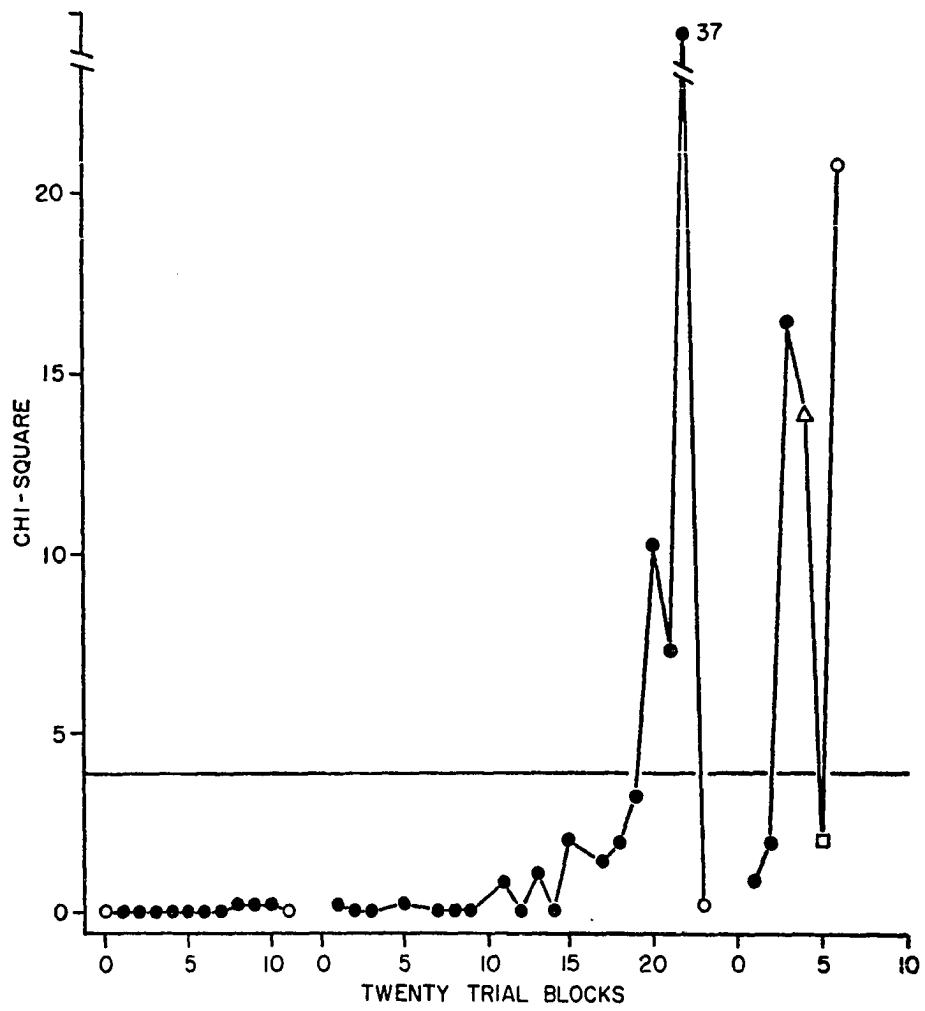
- A- Stimulus Tanks
- B- Experimental Tanks
- C- Light (Omitted from unit 1 for illustrative purposes)
- D- Opening
- E- Movable Opaque Curtain
- F- Stationary Opaque Curtain

Fig. 3. Acquisition of and the effects of experimental manipulation upon species discrimination by a sexually mature, male bluegill sunfish. In this case the S+ was a sexually mature male bluegill sunfish and the S-s were sexually mature male longear sunfish. The open squares depict results obtained without reinforcement, when movement by the stimulus fishes was restricted. The closed and open circles represent results obtained with and without negative reinforcement, respectively. In this and in subsequent figures points above the dark horizontal line represent those twenty trial blocks in which the "postcurtain" frequency was significantly different from the "precurtain" frequency, where a chi-square value of 3.841 was significant at the .05 level, where d.f. = 1. See text for further explanation.



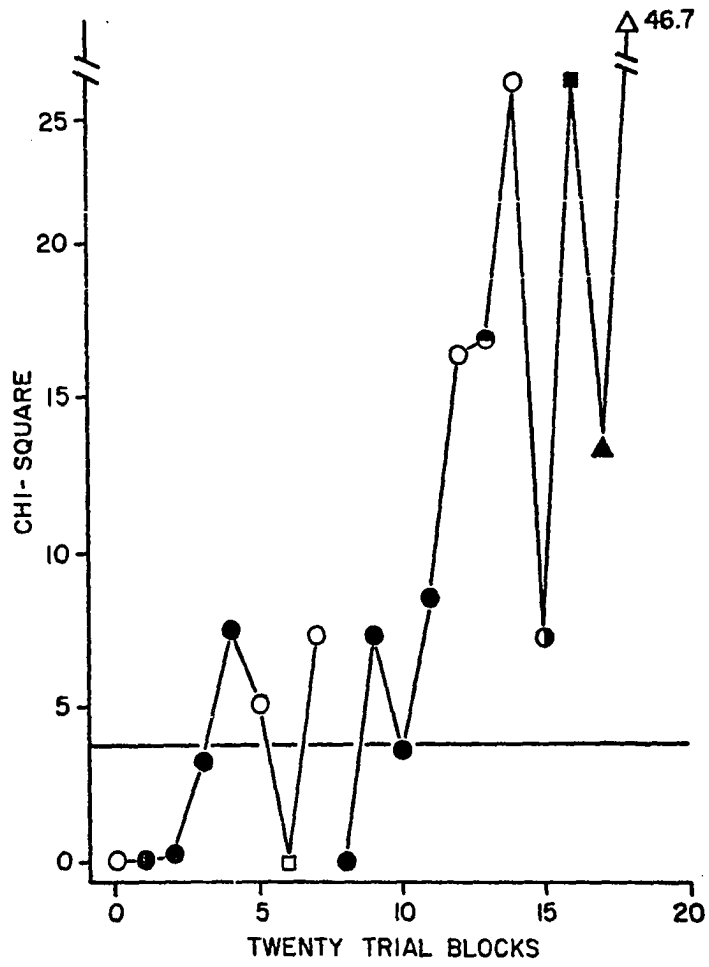
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Fig. 4. Acquisition of and the effects of experimental manipulation upon species discrimination by a sexually mature, male bluegill sunfish. In this case the S+ was a sexually mature, male bluegill sunfish and the S-s were sexually mature male longear sunfish. Three sequential acquisition attempts are shown. The initial acquisition attempt illustrates results obtained when movement by the stimulus fishes was restricted throughout the acquisition process. The second acquisition attempt, the first successful acquisition, demonstrates that significant discriminatory behavior can develop when the stimulus fishes are again permitted free movement. The third acquisition attempt, the second successful acquisition, represents results obtained when movement by the stimulus fishes was again restricted, and when different individuals (S+ = male bluegill, S-s = male longears) are substituted of the S+ and S-s, respectively.



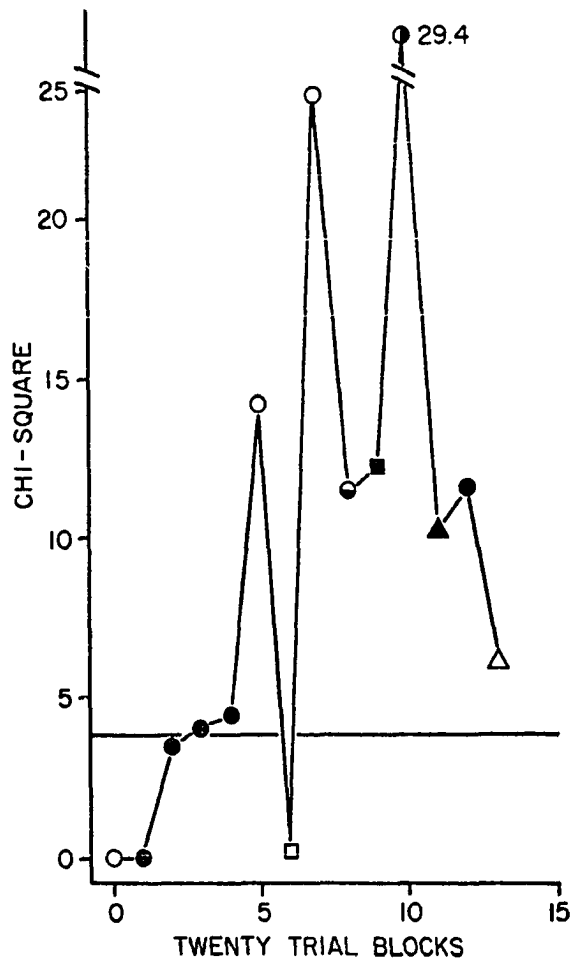
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- △ = DIFFERENT INDIVIDUALS, NOT REINFORCED
- = RESTRICTED MOVEMENT, NOT REINFORCED

Fig. 5. Acquisition of and the effects of experimental manipulation upon mate discrimination by a sexually mature, male bluegill sunfish. In this case the S+ was a gravid, female bluegill and the S-s were sexually mature, male longear sunfish. Two sequential acquisitions are shown. The open triangle represents results obtained when a male bluegill and male longears were substituted for the S+ and S-s, respectively.



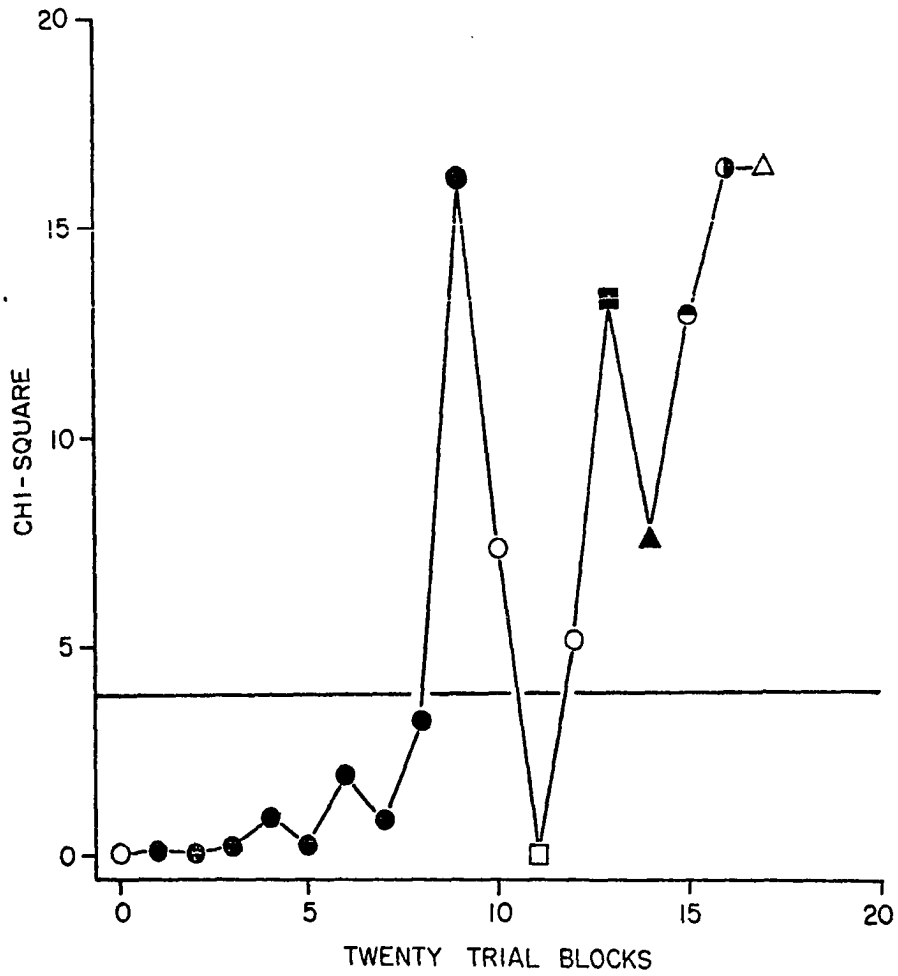
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- = BLUE ILLUMINATION, NOT REINFORCED
- = GREEN ILLUMINATION, NOT REINFORCED
- = YELLOW ILLUMINATION, NOT REINFORCED
- ▲ = RED ILLUMINATION, NOT REINFORCED
- △ = DIFFERENT INDIVIDUALS, NOT REINFORCED

Fig. 6. Acquisition of and the effects of experimental manipulation upon species discrimination by a sexually mature, male bluegill sunfish. In this case the S+ was a gravid, female bluegill. One of the S-s was a ripe male and the other was a gravid female longear. The open triangle represents results obtained when a female bluegill and male and female longears were substituted for the S+ and S-s, respectively.



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- = NOT REINFORCED
- = RESTRICTED MOVEMENT, NOT REINFORCED
- = BLUE ILLUMINATION, REINFORCED
- = YELLOW ILLUMINATION, REINFORCED
- = GREEN ILLUMINATION, REINFORCED
- ▲ = RED ILLUMINATION, REINFORCED
- △ = DIFFERENT INDIVIDUALS, REINFORCED

Fig. 7. Acquisition of and the effects of experimental manipulation upon species discrimination by a sexually mature, male bluegill sunfish. In this case the S+ was a sexually mature, male bluegill sunfish and the S-s were sexually mature, male longear sunfish. The open triangle represents results obtained when a female bluegill and a male and female longear were substituted for the S+ and S-, respectively.



- = REINFORCED
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- = YELLOW ILLUMINATION, REINFORCED
- ▲ = RED ILLUMINATION, REINFORCED
- = BLUE ILLUMINATION, REINFORCED
- = GREEN ILLUMINATION, REINFORCED
- △ = DIFFERENT INDIVIDUALS, REINFORCED