FACTORS AFFECTING AGGRESSIVE BEHAVIOR AND SOCIAL HIERARCHY IN THE LONGEAR SUNFISH, *LEPOMIS MEGALOTIS* (RAFINESQUE)

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PREFACE

The objectives of the study were: (1) to describe the agonistic behaviors and associated color patterns of longear sunfish; (2) to evaluate the influence of turbidity on the consequences of aggressive behavior; (3) to determine the effects of various spatial levels, change of spatial level, and average size of group members on aggressive and social behaviors of groups of four longear; (4) to define and evaluate the factors effective in social ranking; and (5) to integrate the results of the study of these parameters into a general statement of their relationships.

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CHAPTER I

INTRODUCTION

This study of aggressive behavior and social hierarchy of the longear sunfish, Lepomis megalotis, deals with the influences of available space, change of available space, average size of group members, and turbidity on the behavior of groups of four fish in the laboratory. The effect of these variables on color pattern display, freedom of movement of subordinates, number of agonistic bouts, territoriality, and ranking were investigated.

The work was prompted by my previous study on aggressive behavior and social hierarchy in pinfish, Lagodon rhomboides, (Hadley, 1967) which raised some questions concerning the present status of knowledge of this area. While many studies of social groups of fish were available and a variety of social classifications had been erected, there seemed to be a dearth of information dealing with the influence of experimental conditions on the results obtained. It appeared that if variation in technique could affect the experimental results, a major reevaluation of conclusions regarding social behavior of fishes might be necessary. Comparisons of the results of work done under different experimental conditions would have to be made with care and the applicability of conclusions drawn under a particular set of circumstances would be greatly reduced. Further, the use of such conclusions in more general works attempting synthesis among various animal groups would be severely limited. Of particular relevance to the present investigation are the works of Braddock (1945), Greenberg (1947), Miller (1963), Huck and Gunning (1967), and Erickson (1967).

Braddock (1945) showed that size and sex were important factors in the the determination of dominance in Platypoecilus maculatus. Some evidence for the ability of fishes to recognize others as individuals was presented.

Greenberg's 1947 work perhaps represents the single most important contribution to knowledge of aggressive behavior and social hierarchy in fish. Using immature green sunfish, Lepomis cyanellus, he found that maleness and larger size were important in determining dominance. He noted the function of subordinates in lessening tension among territory holders. By increasing the complexity of the habitat he was able to increase the number of successfully defended territories.

Miller (1963) studied the qualitative aspects of the behavior of species of Lepomis and Elassoma evergladei. The majority of the Lepomis observations were of L. gibbosus but L. humilis, L. auritus, L. megalotis and L. cyanellus were also studied. Her work dealt with basic description of color patterns, general behavior, and reproductive behaviors.

Huck and Gunning (1967) investigated some facets of the behavior of Lepomis megalotis. They observed longear in nature and commented upon territoriality, nest construction, spawning behavior, and other aspects of longear ecology. Using pairs of longear in aquaria they also studied aggressive behavior and its relationship to tank size. They concluded that size was important in ranking but that sex had no influence.

Erickson (1967) investigated relationships between social hierarchy, territoriality, and stress reactions in *Lepomis gibbosus*. He found maleness to be effective in rank determination. He contended that hierarchical behavior was an artifact of confinement. Interrenal tissue weights were negatively correlated with the number of attacks initiated by the fish, leading him to suggest that stress was most severe for least aggressive fish.

Papers dealing with social hierarchy in various fishes are numerous. Among them are observations on *Xiphophorus helleri* (Noble and Borne, 1938), *Hemichromus bimaculatus* (Noble and Curtis, 1939), *Platypoecilus maculatus* (Braddock, 1945 and 1949), *Lepomis cyanellus* (Hixson, 1946; Greenberg, 1947; Allee et al., 1948; and McDonald and Kessel, 1967), *Mustelus canis* (Allee and Dickinson, 1954), *Salmo gairdneri* (Stringer and Hoar, 1955 and Newman, 1956), *Betta splendens* (Braddock and Braddock, 1955), *Salvelinus fontinalis* (Newman, 1956), *Colisa lalia* (Forselius, 1957), *Stephanolepis cirrhifer* (Okaichi et al., 1958), *Danio malabaricus* (Haas, 1959), *Gambusia hurtadoi* (McAlister, 1958), *Gambusia affinis* (Caldwell and Caldwell, 1962), *Oryzias latipes* (Magnuson, 1962), *Lepomis gibbosus* (Miller, 1963; Erickson, 1967), *Lepomis humilis* (Miller, 1963), *Trichogaster trichopterus* (Miller, 1964), *Ptychoceilus oregonense* (Pfeiffer, 1965), *Mollienesia latipinna* (Baird, 1965), *Lepomis macrochirus* (Borkhuis, 1965), and *Lagodon rhomboides* (Hadley, 1967).

Various aspects of longear behavior and ecology have been studied by a number of workers. Gerking (1953), Gunning (1959), and Gunning and Shoop (1963) have studied home range and homing mechanisms of longear. Reproductive behavior has been investigated by Witt and

Marzolf (1954), Miller (1963), Huck and Gunning (1967), and Boyer (1969). In addition to reproductive behavior, Boyer described feeding, sleeping, and agonistic behaviors. Keenleyside (1967) described reactions of male longear to females of three species in laboratory tests which indicated that specific distinctions were made.

Since considerable information relative to aggression and social hierarchy was available and few attempts had been made to clarify the effect of various aspects of the experimental regime on these phenomena, it seemed desirable to investigate the relationships among a few variables and the commonly studied behavioral correlates. Fish size and available space were considered likely to influence experimental results and to be of opposite valence. That is, the results would be altered in the same fashion if fish size were increased or spatial level decreased. Accordingly tests were designed to subject groups of three average sizes of longear to various spaces. In other tests the available space was changed at five day intervals to determine the influences of such change. Turbidity experiments were conducted to assess the effect of reduced visibility on aggressive behavior.

CHAPTER II

MATERIALS AND METHODS

The research was conducted in the Aquatic Biology Laboratory of the Oklahoma State University Zoology Department from 14 November 1966 to 17 August 1968. Dates for all tests are shown in Table I.

Physical Conditions: All experiments were conducted in 12 tanks 81 cm long, 56 cm wide, and 38 cm deep with a capacity of approximately 173 liters. Six tanks were made from enameled steel and six from marine plywood. All had white interiors and each had one end made of plate glass. Moveable, transverse, transparent partitions of plexiglas or plate glass 56 cm wide and 38 cm tall were used in all tanks. The length of the tank could be varied by moving the partition. The bottoms of the tanks were covered with sand to a depth of about 3 cm. Tap water was conditioned by aeration in a large, wooden reservoir tank before use. In the experimental tanks aeration was provided by airstones. No plants or artificial cover was supplied. The tanks were cleaned and the water changed before each experiment. Illumination was provided by overhead banks of fluorescent bulbs 24 hours daily. Water temperatures were maintained at 22 to 25°C.

Feeding: Fish were fed *Daphnia* and *Chironomus* larvae to repletion after each daily observation period.

TABLE I

INCLUSIVE DATES OF ALL TESTS

Fish Size	Test: 43L	86L	172L	><	<>
Small					
Group A	20 January – 13 February 1968	24 July – 17 August 1968	24 July – 17 August 1968	23 October – 16 November 1967	28 June – 22 July 1967
Group B	(Same)	(Same)	(Same)	(Same)	(Same)
Group C	(Same)	(Same)	(Same)	(Same)	(Same)
Group D	(Same)	(Same)	(Same)	(Same)	(Same)
Medium					
Group A	20 January – 13 February 1968	20 January – 13 February 1968	24 July – 17 August 1968	11 September – 5 October 1967	14 November – 8 December 1966
Group B	(Same)	(Same)	(Same)	(Same)	31 January – 24 February 1967
Group C	(Same)	(Same)	(Same)	(Same)	31 January – 24 February 1967
Group D	(Same)	(Same)	(Same)	(Same)	21 March – 14 April 1967
Large					
Group A	21 June – 15 July 1968	21 June – 15 July 1968	21 June – 15 July 1968	11 September – 5 October 1967	2 May – 26 May 1967
Group B	(Same)	(Same)	(Same)	(Same)	(Same)
Group C	(Same)	(Same)	(Same)	(Same)	(Same)
Group D	(Same)	(Same)	(Same)	(Same)	(Same)

Collections and Handling: The fish used were collected by seines, funnel traps, and electro-fishing gear from Salt Creek and its tributaries in Osage County, Oklahoma. They were kept in stock tanks in the laboratory under the same conditions of lighting, temperature, and feeding as in the experimental tanks for a minimum of two weeks.

Pretest Treatment: Prior to each experiment, the fish to be used were isolated for 14 days in plastic containers with approximately 9 liters of aerated water. The day before an experiment was begun, and at the termination of each experiment, the fish were weighed to .1 gram on a pan balance and their standard lengths measured to the nearest mm. Identification of individuals was accomplished by clipping a small portion of the soft dorsal, soft anal, upper caudal lobe, or lower caudal lobe. At the end of a test the fish were individually tagged, preserved in 10% formalin, and sex determined by examination of the gonads. These fish were assigned catalog number 6443 in the Oklahoma State University Museum.

Aging: Scale samples were taken from an area postero-dorsad from the left pectoral fin. Plastic slide scale impressions were made and the year class determined by employees of the Oklahoma Department of Wildlife Conservation at the Oklahoma Fishery Research Laboratory in Norman, Oklahoma.

Fish Size: Three sizes of fish, 4.0, 5.5, and 7.0 cm average standard length, were used in each experiment except the turbidity tests where only 8.5 cm average standard length fish were used. In the 4.0 cm groups, fish ranged in size from 3.5 to 4.5 cm, in the 5.5 cm groups they ranged from 5.0 to 6.0 cm, and in the 7.0 cm groups from 6.5 to 7.5 cm. In all tests, groups of four fish were used. The individuals in a group were selected to maximize the range of sizes represented (within the 1.0 cm variation allowed) and the difference in size among group members. In the turbidity experiments, standard lengths varied from 7.5 to 10.2 cm.

Observations: Tests were 25 days long and each group of fish was observed 10 minutes daily. Observations were made between 11:30 AM and 1:30 PM. All observations were made with the experimenter seated directly in front of the tank at a distance of about 1 meter. The observer was relatively motionless and his presence did not seem to affect the fish's behavior.

Agonistic bouts: During an observation period the results of all definitive aggressive encounters were recorded on a standard win-lose grid. An aggressive bout was considered to have been definitive if a clear-cut winner and loser could be distinguished (flight or submissive posturing by the defeated fish). Encounters were not recorded if (1) the loser was attacked from behind; (2) the loser had been defeated by another fish immediately before the bout in question; (3) the winner was in his own territory (when both fish involved held territories); and (4) the bout was terminated by mutual withdrawal or cessation of display.

Color Patterns: At the end of an observation period the color patterns of the fish were recorded. Changes in color patterns sometimes occurred during agonistic encounters but these were usually of short duration and the pattern recorded for a fish was that which seemed to be displayed for the greater part of the period. It must be noted that, while efforts were made to eliminate bias, this was a subjective measure.

Movement: The extent of movement by fish other than territory holders was recorded as having been of one of four categories. Instances in which subordinate fish were able to move freely throughout the tank except in the immediate vicinity of the dominant(s) were termed Little Restricted. When non-territory holders were allowed frequent access to the substrate it was called Somewhat Restricted. Those cases where relatively unmolested movement of subordinates occurred only in the upper areas of the tank were classified as Restricted, and when subordinates moved only to escape a territory holder, the condition was referred to as Completely Restricted.

Territory: The presence of any territory was recorded at each observation. Territory here means an area defended by an individual in which he defeats all other group members in almost all definitive bouts. Partial territories, i.e., areas successfully defended against most but not all other individuals, were not recorded. The presence of multiple territories was easily determined, but a single territory could not be distinguished since no boundary displays occurred. Rather than assume that no territory existed unless two or more were present, and thereby forfeit some valuable comparisons, groups in which a single dominant fish confined the movement of the subordinates at the Restricted or Completely Restricted level were recorded as having a single territory present.

<u>Ranking</u>: After each observation period, the group members were assigned hierarchical ranks on the basis of the outcomes of aggressive bouts. A fish that defeated another fish three or more times (or by a margin of three of more if both won bouts) during an observation period was considered dominant in that pair relationship for that observation. An individual dominating the other three group members was ranked number 1; a fish dominating two others was ranked number 2; a fish dominating a single individual was ranked number 3; and the number 4 ranked fish did not dominate any other. When too few encounters occurred to determine the relationship of a pair of fish, their ranks from the preceding observation period were assigned. If bouts between a pair of fish were frequent but were not definitive or neither fish won by a margin of three bouts, the fish were considered to be equally ranked.

<u>Space Tests</u>: Five experimental conditions were imposed on three average sizes of fish in tests evaluating the influences of space and fish size on aggressive behavior and group social structure. Four similar groups of four fish each of each size tested were used in these experimental regimes. Each experiment was of 25-day duration. In three of the five tests of spatial effects, the partitions were left in position for the entire experiment (static space tests). The dividers were positioned as follows:

20 X 56 X 38 cm	43L Test
40 X 56 X 38 cm	86L Test
80 X 56 X 38 cm	172L Test

In the other two tests, the amount of available space was changed at 5-day intervals during the 25-day test period as follows:

Day	1-5	6-10	11-15	16-20	21-25	
	43L	86L	172L	86L	43L	Test
	172L	86L	43L	86L	172L	Test

Turbidity Tests: The effects of turbidity were tested by the use of four similar groups (about 8.5 cm in average standard length) of four fish each at three different turbidity levels in 172 liters of water. Turbidity was achieved and maintained by the addition of India ink to conditioned tap water. Turbidity was measured with a Bausch and Lomb Spectronic 20 spectrophotometer using 2.54 cm diameter tubes at 450 millimicrons. Turbidity levels were maintained at 45-50% transmittance (High Turbidity), 75-80% transmittance (Moderate Turbidity), and 95-100% transmittance (Low Turbidity). Since observations were precluded in these tests, deaths resulting from aggression were used in the analysis. Dead fish were removed, identified, preserved in 10% formalin, and the day of death recorded.

CHAPTER III

COLORATION AND COLOR PATTERNS

The following description of coloration deals with the basic elements of color display of longear in agonistic encounters. The combination of these components into the various color patterns is described and discussed subsequently.

Coloration

Opercle Flap - Coloration of the opercle flap varied from black through shades of dark grey to an iridescent pale green, with the contrast between flap and body color decreasing similarly. In fish engaged in aggressive display, the flaps, with the exception of the silvery-white margins, were an intense black. Black opercle flaps were typical of the highest ranking fish in a group, territory holders, and subordinate fish engaged in aggressive displays. Fish with lower social rank typically displayed less intense coloration of the flaps, although the degree seemed to vary with size of fish and available space. Color changed rapidly and flaps of the loser of a mutual agonistic bout became pale within seconds.

Iris Color - The color displayed was related to rank and the behavior performed. Dominant fish showed relatively large amounts of red in the iris. The extent of red color decreased with rank; low ranking fish had dark brown or black irises with no red visible. Iris color changed rapidly but appeared to require more time than changes in opercle flap coloration.

Fin Color - The fins of longear, except the pectorals, which remained translucent at all times, were subject to some variation in color. In some instances, the median and pelvic fin colors were pale and flesh-toned like the pectorals. However, in dominant individuals, particularly in the larger fish, the fins became suffused with orange. The intensity and extent of orange pigmentation varied among group members and tended to decrease with rank. Change in fin color was slow and seemed to be mediated differently than color changes in the other structures.

Body Color - In general, the basic body color of all fish was similar and agreed with the description by Miller (1963), but was less intense in lower ranked fish. In dominant individuals, some increase in the extent of orange pigmentation was noted. The most striking variation, however, was in the intensity of the lateral bands. The sides of fish were marked by eight to twelve lateral bands which varied greatly in intensity. Typically, the highest ranking fish in a group showed no banding. Subordinate members were often identifiable with regard to rank on the basis of intensity of lateral banding; higher rank - lighter bands, lower rank - darker bands.

Color Patterns

Differences in the expression of the various markings described above were observed, associations between changes in color of the various body areas were noted, and descriptive terminology applied to these combinations of color components. While the patterns described here are relatively distinct, they are selected portions of a continuum.

Pale - The Pale color pattern occurred when the lateral bands were not expressed. Typically, the opercle flaps were black or very dark, the irises were red, and the fins showed some orange. However, variation in color of these areas was extreme. A fish might show the Pale color pattern with the opercle flaps green, the irises dark brown and no red visible, and the fins entirely translucent.

Banded - When the dark lateral bands were visible, the condition was termed Banded. A wide range of band intensities was observed, and three levels of band expression were distinguished and recorded.

Light Banded - Fish were said to be Light Banded when the lateral bands were visible but of low intensity. Iris color, amount of orange in the fins, and darkness of the opercle flaps were variable. In general, however, the Light Banded pattern was accompanied by some red in the iris, a darkened but not black opercle flaps, and a small amount of orange in the fins.

Moderately Banded - When the intensity of the lateral bands was at a level approximately midway between Light Banded and Dark Banded, the fish was considered to be Moderately Banded. This pattern is typically displayed with little or no red in the iris, light opercle flaps, and pale, translucent fins; but exceptions were common.

Dark Banded - A fish with the lateral bands maximally pigmented, or nearly so, was Dark Banded. This condition was accompanied by some blanching of the basic body coloration so that the lateral bands were emphasized and their visibility enhanced. Iris color was dark, opercle flaps pale and fins translucent when this pattern was shown.

CHAPTER IV

BEHAVIOR PATTERNS

Miller (1963) described the non-reproductive social behavior of Lepomis species, deriving most data from L. gibbosus, L. humilis, and L. macrochirus. In the main, her observations of the general forms of agonistic displays are in accord with those made here on L. megalotis. In the discussion below, the more discrete agonistic behaviors are briefly described, the associated color patterns noted, and their occurrence relative to the experimental regime mentioned. No quantification of individual behaviors was attempted, hence all statements are of a qualitative nature.

Lateral Display - A fish in Lateral Display was oriented so that the lateral body aspect was toward the other individual involved. Median fins were typically erected, and the pelvics extended ventrally. Usually the Pale color pattern was manifest, but occasionally fish with a Banded pattern engaged in this display. Body and fin color were extremely varied, but some red in the iris was normally present and the opercle flaps were always black. Lateral display occurred most frequently in the first day of a group's existence, before hierarchical relationships were established. It was common at territorial boundaries later in the test period but otherwise declined in frequency with time. The form of this behavior was modified with time from test inception. On the first day of observation, Lateral Display appeared to be of high intensity with maximal fin erection. Later, However, fin erection in most instances decreased in magnitude, and ultimately it became impossible to distinguish between fish engaged in Lateral Display and a fish that was fortuitously oriented broadside to another. The significance and causation of this change were not investigated in this study, but habituation, learning, and motivational changes may have been operative. Miller (1963) termed analogous behavior Lateral Threat Display.

Frontal Display - The Frontal Display postures, color patterns, and fin positions were similar to those of Lateral Display, the primary distinction being orientation. In Frontal Display the fish was positioned facing the opponent. This behavior in its most distinctive form, like Lateral Display, decreased in frequency with time from group formation. However, the occurrence of Frontal Display seemed to wane more slowly than that of Lateral Display. The form of the behavior followed a pattern of modification in time similar to Lateral Display.

Opercle Spreading - Longear in Frontal Display postures occasionally spread the opercles laterally with concomitant erection of the opercle flaps. This behavior was rarely observed. It was most often observed on the first day of a test but occurred later in a few mutual display contexts. Opercle Spreading was displayed only by fish in a Frontal Display posture, and then only when the rank of the opponents was undecided and mutual display was occurring.

Biting - The term Biting was applied to cases where the jaws of a fish contacted the body of another. Median fins were most frequently bitten, but other body parts also received bites. Biting increased in frequency with time, and hemorrhage resulting from damage to median fins by biting was the apparent cause of death of many fish. Fish were seen to engage in Biting while displaying all of the color patterns described, although Pale was by far the most common. Miller (1963) described Biting movements in which no contact between the jaws and the opponent occurred. In this study such behavior could not have been distinguished from Biting, as here defined, owing to the rapidity of the movement. The Biting by dominants of thoroughly defeated subordinates was slow enough to be readily observed. Huck and Gunning (1967) observed similar behavior in captive groups of longear.

Tail Beating - Tail Beating involved lateral flexure of the caudal peduncle and caudal fin so that a flow of water was directed toward the opponent. With a few exceptions, Tail Beating was mutual; the two fish were side by side with head opposite the opponent's tail. This orientation was not invariable, and longear were seen Tail Beating from a number of other positions. This behavior frequently occurred in the initial stages of hierarchy formation, more rarely in boundary disputes between adjacent territory holders, and was occasionally engaged in by dominants attacking thoroughly subjugated subordinates. Any color pattern might be displayed while Tail Beating, but Pale and Light Banded were most common.

Subordinate Postures - Subordinate fish subject to approach or display by a dominant frequently behaved in a manner similar to that described as "appeasement" by other authors. Since the function and causation of the behaviors described here have not been studied, the less interpretive term Subordinate Postures has been applied. A variety of behaviors were included in this category, perhaps related only by context although they may represent selected parts of a continuum. Subordinate Posture involved a shift of the longitudinal body axis away from the horizontal (head up or head down in response to a dominant's approach from below or above respectively) or inclining the vertical axis away from a laterally approaching superior. The extent of the inclination from the horizontal or vertical varied widely, from an almost imperceptible shift to a full 90 degree movement. Although no quantitative data are available to support the contention, it appeared that the extent of the movement was related to the following factors: (1) distance of closest approach by the dominant; (2) behavior of dominant subsequent to closest approach; (3) speed of dominant's approach; (4) course of previous encounters of the pair (both recent and long-term); and (5) status of subordinate relative to other group members. In cases of extreme domination, the head up or head down postures were maintained at all times, and these postures were typical of fish just prior to death from Biting by a dominant. Median fins were depressed in all Subordinate Postures. A rarely seen behavior similar in form to the latter was displayed in response to a laterally approaching dominant. The vertical body axis was inclined toward the dominant and a variable amount of dorsal spine erection occurred. A head down posture termed Head Standing occasionally occurred. It differed from the more common head down movement previously described in that it was displayed without apparent regard for the angle of approach of the dominant and involved a more complex motor element. In this behavior the subordinant fish assumed a nearly vertical, head down position but moved rather freely in a horizontal plane by use of the pectorals and possibly the caudal. Subjectively, it seemed that this behavior was performed in a somewhat different context than the other head down display. The Banded color patterns were displayed by fish engaged in Subordinate Postures.

Combat - If an agonistic encounter was not resolved by other less damaging behaviors, a pair of longear might engage in a mutual behavior termed Combat. The opponents would orient head to tail and, maintaining this position, whirl rapidly through the water. Little could be determined regarding the elements of this pattern owing to its speed. It appeared that Biting, directed at the soft dorsal rays of the opponent, occurred simultaneously with movements of the caudal away from him. Median fins were spread at the outset of this behavior, but their position during actual Combat could not be determined. A Combat encounter was usually terminated by Flight (see below) of one fish, but at territorial boundaries the opponents simply ceased spinning and retreated tail first into their respective territories. The Pale color pattern was displayed at the outset with large amounts of red in the irises and black opercle flaps. During Combat the Light Banded pattern seemed to appear. If the bout terminated with definite winner and loser, their patterns were Pale and Moderately or Dark Banded, respectively, within seconds. In Combats which terminated without resolution, both fish showed a Banded pattern.

Driving - The activity of a fish that pursued another was termed Driving. Driving differed little from normal swimming movement; the principal distinguishing factor was orientation toward the subordinate fish. Dorsal and anal fin erection was greater than in simple locomotion, but this was not invariable. A fish engaged in Driving might display any color pattern, but Pale and Light Banded were the more common. Driving behavior appeared to increase in frequency early in a test period and then decrease somewhat in later days.

Flight - A fish retreating from another was said to be Fleeing. Median fins were usually folded during Flight and the color pattern displayed was typically Banded. An increase in the darkness of the lateral bands from their condition prior to Flight was frequently noted, e.g., Light Banded changed to Moderately Banded. Driving behavior was obviously associated with Flight, but the latter could occur in response to other behaviors such as Lateral Display, Frontal Display, etc.

As discussed above, many of the behaviors described were observed only early in the test period. Tail Beating, Opercle Spreading and Combat were uncommon after the first or second day of a test except in cases where two territories were present or where two or more subordinates were of equal rank. The bulk of the definitive agonistic bouts recorded consisted of rather modified Frontal Display, Lateral Display, Biting, or Driving by the winner and Subordinate Posturing or Flight by the loser. The display of a dominant was rarely returned by a subordinate in the later days of a test.

CHAPTER V

OCCURRENCE OF COLOR PATTERNS

The occurrences of the four color patterns, Pale, Light Banded, Moderately Banded, and Dark Banded, recorded in this study are interpreted as indicators of experimental treatment. While the color pattern displayed by a fish was found to be related to rank, the particular color pattern was not constant for all fish with that rank. For example, a fish ranked number 2 in one experimental regime might show the Pale color pattern, while the number 2 fish in another test might show the Moderately Banded color pattern. The occurrence of color patterns appeared to be a rather accurate reflection of test effects.

The classification of fishes into size groups and the discussion of results from different sizes are not meant to imply that size was the only difference among the three sizes observed. Obviously, other factors differed among fish sizes and could not be controlled when wild caught fish were employed. While size appeared to play a central role in the differences among sizes, acknowledgement of the possible influences of uncontrolled factors is necessary.

The percent occurrence of each color pattern for each 5-day period and the entire 25 days from all experimental treatments is shown in Table II. The total number of occurrences of a pattern in each 5-day period is expressed as a percent of the total number of all color

TABLE II

PERCENTILE OCCURRENCE OF FOUR AGONISTIC COLOR PATTERNS IN FOUR SIMILAR GROUPS OF FOUR LONGEAR SUNFISH

Total number of occurrences of a pattern in each 5-day interval expressed as a percent of total number displayed by all groups and percent of 25-day total. Data for large fish in 43L test from four groups on days 1-5, three groups on days 6-10, two groups on days 11-15, and one group subsequently. Data for large fish in 86L test from three groups on days 1-5 and from two groups subsequently. All data from three groups in the 172L and large to small to large tests of large fish. Data for small to large to small tests of large fish from two groups on days 1-5 and from one group subsequently.

Test				Small					Medium						Large					
Fish Size																				
43L	Days 1-5	6-10	11-15	16-20	21-25	Avg.	1-5	6-10	11-15	16-20	21-25	Avg.	1-5	6-10	11-15	16-20	21-25	Avg.		
Pale	29	96	100	100	100	85	25	25	26	25	25	25	31	18	17	25	25	23		
Light Banded	59	4	0	0	0	13	9	5	20	24	44	20	14	3	2	0	0	4		
Moderately Banded	12	0	0	0	0	2	17	26	39	46	27	31	29	2	26	0	0	11		
Dark Banded	0	0	0	0	0	0	49	44	15	5	4	24	26	77	55	75	75	62		
86L																				
Pale	89	98	100	100	100	97	47	47	66	66	50	55	32	25	27	25	27	27		
Light Banded	9	1	0	0	0	2	26	35	25	33	41	32	17	25	23	25	25	23		
Moderately Banded	2	1	0	0	0	1	18	13	5	1	8	9	46	30	27	27	28	32		
Dark Banded	0	0	0	0	0	0	9	5	4	0	1	4	5	20	23	23	20	18		
172L																				
Pale	100	100	100	100	100	100	34	49	65	71	64	57	35	42	42	42	35	39		
Light Banded	0	0	0	0	0	0	25	41	34	29	36	33	22	38	35	32	33	32		
Moderately Banded	0	0	0	0	0	0	40	10	1	0	0	10	33	17	15	18	20	21		
Dark Banded	0	0	0	0	0	0	1	0	0	0	0	0	10	3	8	8	12	8		
><																				
Pale	92	96	96	100	100	97	60	52	64	74	100	70	42	37	33	80	94	57		
Light Banded	8	4	4	0	0	3	20	29	19	17	0	17	25	17	15	15	3	15		
Moderately Banded	0	0	0	0	0	0	20	14	12	9	0	11	26	15	28	2	3	15		
Dark Banded	0	0	0	0	0	0	0	5	5	0	0	2	7	31	24	3	0	13		
<>																				
Pale	66	80	91	89	73	80	49	70	93	85	75	74	35	25	50	50	40	40		
Light Banded	29	19	9	11	25	18	15	11	3	5	1	7	10	20	50	50	60	38		
Moderately Banded	5	1	0	0	2	2	20	5	2	6	10	9	22	30	0	0	0	10		
Dark Banded	0	0	0	0	0	0	16	14	2	4	14	10	33	25	0	0	0	12		

patterns displayed in that period. Data for all four groups of a particular size in each test have been combined. A number of fatalities occurred in the large fish groups. Groups with deaths are not included after the last 5-day period in which all members were alive. Hence, in Table II values for large fish in the 43 liter test are from four groups in the 1-5 day period, three groups in the 5-10 day period, two groups in the 11-15 day period, and one group in the 16-20 day and 21-25 day periods. The data for large fish in the 86 liter test are from three groups in the 1-5 day period and two groups in all subsequent periods. The 172 liter test data from large fish were all taken from three groups. In the large to small to large tests of large fish all data were from three groups. Large fish data from the small to large to small test are from two groups in the 1-5 day period and one group in subsequent periods.

The relationship between time and social structure must be considered before analysis of experimental treatments is attempted. Color pattern frequencies, in general, changed with time in static space tests. Typically, the more subordinate patterns decreased in frequency and the less subordinate patterns increased. This change with time may have resulted from increased stability of relationships between group members and a consequent decrease in social stress. It may also have reflected a reduction in aggressive behaviors by the highest ranked fish and a subsequent lessening of social stress.

In any single experimental design, differences in frequencies of color pattern display among the three sizes of fish were observed. In all cases the more subordinate color patterns, Moderately Banded and Dark Banded, were expressed with increased frequency in larger sized fish. The less subordinate patterns, Pale and Light Banded, were more common among smaller fish groups. Larger sized fish were apparently subject to greater social stress, at a given spatial level, than were smaller fish.

For any size fish, less available space resulted in greater numbers of the more subordinate color patterns. Tests with more space had fewer of the more subordinate patterns. Hence, the amount of space available to a group of fish was effective in determining the color patterns displayed.

The data from the two experimental treatments in which spatial parameters were changed during the course of the tests present some difficulty in interpretation. To analyze the results in terms of a single influencing factor is impossible. In both the treatments the possible influences of three factors must be considered. (1) The average amount of space available throughout the test period. (2) Time related alteration of the social environment. (3) Change in spatial parameters.

The average amount of space available to a group during the entire course of a test seems likely, on the basis of the static space test results, to have affected social parameters. The large to small to large design made available an average of 111.8 liters per day. The small to large to small tests averaged 86 liters. Presumably, if the average space were of prime import, results from the small to large to small design, for a given size of fish, should have closely resembled those from the 86 liter static space tests and those of the large to small to large tests should have been intermediate between the 86 liter and 172 liter test results. The data in Table II do not show the predicted relationship. Therefore, it appears that while the average available space may have had some influence on the display of color patterns its effects were outweighed by those of other factors.

Since time related change in color pattern display was shown to occur in the static space tests, its effects must be considered in the changing space tests. If time related change had not functioned, the data gathered from a given size fish in the first two 5-day periods of a changing space test should have closely resembled that recorded during the last two 5-day periods. Examination of Table II shows that all fish sizes in both changing space tests had fewer of the Moderately and Dark Banded patterns in the 16-20 and 21-25 day periods than in the 1-5 and 6-10 day periods. Thus, time was effective in reducing the numbers of the more subordinate patterns in both changing space designs.

The effects of change of available space were of primary interest in the changing space tests. The manipulation of this parameter may have affected social phenomena in a number of interrelated ways. It was assumed that change of spatial regime would result in modification of the social milieu in accordance with the absolute amount of space made available. It was also hypothesized that the direction of the change, increase or decrease, would affect the social group. Further, it was anticipated that the space available during the first few days of a test might have important consequences in subsequent days.

In the large to small to large space design with small fish, relatively little change in color pattern frequencies was recorded. The distribution of color pattern occurrences in this test resembled those of the 86 liter static space test. However, the difference between the large to small to large design results and those of the

172 liter static space test are so small that distinction seems unwise. Time related change seems to have effected color pattern expression under this regime. It is notable, though hardly conclusive, that the time related decrease in the Light Banded color pattern extended over a longer period in these tests than in the 86 or 172 liter static space tests; presumably the effect of decreasing space and resultant continued social stress.

The data from the small to large to small tests of small fish contrast rather sharply with all other small fish test results. These data seem to indicate that stress under this regime was greater than in any other design. The frequency of display of the color patterns varied in conjunction with spatial change. Increasing space resulted in fewer of the more subordinate patterns, while decrease in space resulted in greater frequency of display of these patterns. The converse held for the less subordinate patterns. Time related change in pattern display may have been responsible for the failure of the frequencies of the more subordinate patterns in the last ten days of the tests to reach levels equal to those of the first ten days.

Comparison of the results from the two changing space tests with small fish showed indication of a mirror-image relationship modified by time. On a five day basis, the data from large to small to large tests seemed to indicate increasing and then decreasing stress. The small to large to small tests resulted in decreases and then increases in social tension. In both cases there appeared to be a direct relationship between spatial change and its direction and the color patterns observed.

Medium sized fish groups displayed color patterns in the changing space tests in similar fashion to small fish groups except that the medium fish showed more Banded and fewer Pale patterns than small fish in a particular test. Stress, as measured by color pattern display, varied similarly in both sizes but was apparently greater proportionally in medium sized fish.

The data for large fish in Table II was compiled only for groups with no mortality at the end of any 5-day period. Groups in which one or more individuals were killed were not included. Thus, color pattern data for some designs were taken from less than four groups as previously indicated. Large sized fish reacted to the large to small to large tests much like small and medium fish, although stress at any point in the test was apparently greater for large fish. So little data was available for the small to large to small tests with large fish that no conclusions were possible. However, the information collected did show tendencies much like the other fish sizes.

The frequency of color pattern display was influenced by spatial level, the average size of group members, and time. Changing the available space had a definite effect on the frequency of color patterns. Change in spatial level seemed to be more important in influencing color pattern display than did the average space available throughout the entire test period.

CHAPTER VI

EXTENT OF MOVEMENT

The extent of movement of the subordinate fish in a group was utilized as a means of assessing the rigors of the social situation. It appeared that the amount of movement by subordinate fish was a function of several variables. The dominant fish seemed to regulate subordinates' movements by attacking them and subordinates appeared to learn that in some regions of the tank they were less subject to attack. A similar phenomenon may have influenced the dominant's behavior. That is, the dominant seemed to become habituated to the presence of subordinate fish in a particular area and directed attacks at them less frequently as long as they remained in that area. Hence, with time, mutual learning seemed to serve to restrict the subordinates' movements and concomittantly reduced overt aggression by the highest ranked individual.

Aggressive encounters between subordinates may also have had some bearing on the extent of movement, but this factor was of much lesser magnitude than the relationship with the highest ranked fish.

Time was a factor in the subordinates' freedom of movement. This influence seems likely to have been at least a partial function of learned restriction of movement with time. However, Table III shows that gradual increases in subordinate movement occurred through time in many groups. This change with time was paralleled in most instances

TABLE III

EXTENT OF MOVEMENT OF SUBORDINATE MEMBERS OF FOUR SIMILAR GROUPS OF FOUR LONGEAR SUNFISH

Total number of observations of a particular movement level in each 5-day interval expressed as a percent of the total of all categories in that period and percent of 25-day total. Data for large fish in 43L test from four groups on days 1-5, three groups on days 6-10, two groups on days 11-15, and one group subsequently. Data for large fish in 86L test from three groups on days 1-5 and from two groups subsequently. All data from three groups in the 172L and large to small to large tests of large fish. Data for small to large to small tests of large fish from two groups on days 1-5 and from one group subsequently.

Test	Small						Medium						Large					
Days	1-5	6-10	11-15	16-20	21-25	Avg.	1-5	6-10	11-15	16-20	21-25	Avg.	1-5	6-10	11-15	16-20	21-25	Avg.
43L																		
Little Restricted	20	60	100	75	65	65	5	0	0	0	5	2	0	0	0	0	0	0
Somewhat Restricted	45	40	0	25	30	27	5	0	5	5	35	10	0	0	0	0	0	0
Restricted	35	0	0	0	5	8	25	50	80	95	60	62	70	47	47	0	0	33
Completely Restricted	0	0	0	0	0	0	65	50	15	0	0	26	30	53	53	100	100	67
86L																		
Little Restricted	40	40	50	70	70	54	20	20	30	30	25	25	0	0	0	0	0	0
Somewhat Restricted	55	60	50	30	30	45	40	10	10	30	25	23	40	40	10	0	0	18
Restricted	5	0	0	0	0	1	25	60	60	40	50	47	47	50	90	100	100	77
Completely Restricted	0	0	0	0	0	0	15	10	0	0	0	5	13	10	0	0	0	5
172L																		
Little Restricted	100	100	100	100	100	100	0	0	0	5	15	4	0	46	34	40	20	28
Somewhat Restricted	0	0	0	0	0	0	15	25	15	20	35	22	40	34	33	20	46	35
Restricted	0	0	0	0	0	0	75	70	85	75	50	71	46	20	33	40	27	33
Completely Restricted	0	0	0	0	0	0	10	5	0	0	0	3	14	0	0	0	7	4
><																		
Little Restricted	100	10	45	95	100	70	10	10	10	35	60	25	0	0	0	26	34	12
Somewhat Restricted	0	90	55	1	0	30	45	60	65	35	20	45	26	7	20	53	40	29
Restricted	0	0	0	0	0	0	30	30	25	30	20	27	60	40	46	21	26	39
Completely Restricted	0	0	0	0	0	0	15	0	0	0	0	3	14	53	34	0	0	20
<>																		
Little Restricted	45	60	65	90	75	67	0	0	5	0	0	1	0	0	0	0	0	0
Somewhat Restricted	40	30	35	10	25	28	0	10	45	30	5	18	0	0	80	40	0	24
Restricted	15	10	0	0	0	5	60	90	50	70	85	71	50	60	20	60	100	58
Completely Restricted	0	0	0	0	0	0	40	0	0	0	10	10	50	40	0	0	0	18

by the changes in color pattern frequencies (see Table II); both seemingly indicative of decreased social stress through time. If the extent to which movement of subordinates was restricted varied inversely with social stress, then the changes observed seem to support the hypothesis that time factors served to lessen the level of stress.

The extent of subordinate movement in any single experimental regime differed among fish sizes. At a given spatial level, the subordinate members of small fish groups had greater freedom of movement than subordinate medium fish and they, in turn, moved more freely than subordinate large fish. It must be noted that many mortalities occurred in large fish groups, necessitating exclusion of the observations from those groups from Table III, and as a result the data presented were recorded from groups which presumably were subject to the least social stress and, hence, likely to have had less restriction of movement than those groups in which mortalities occurred. Comparisons of the data from large fish groups in Table III must be evaluated in this light.

The influence of space on extent of subordinate movement appeared to be similar to the effect of space on color pattern frequency. In tests with greater available space, all subordinates typically had more freedom of movement than in experiments with less space. The only major deviation from this relationship was in the 86 and 172 liter tests with medium fish. Movement was generally more restricted in the 172 liter tests and less restricted in 86 liter experiments. The summary nature of Table III obscures the explanation; one group at 86 liters was consistently Little or Somewhat Restricted throughout the test, and one group in the 172 liter test was always Restricted or Completely Restricted. With the exception of these groups, the data fits with the predicted results.

Subordinate movement data from the two changing space tests were much like those on color pattern frequency. The large to small to large tests resulted in less restriction of movement than comparable small to large to small tests. In all tests the extent of movement of subordinates tended to increase or decrease with increase or decrease in available space.

Small fish groups showed rather small differences in response to the two changing space experiments. The differences between the corresponding 5-day averages were, however, of the nature expected. The small to large to small tests resulted in less restricted movement than did the 86 liter static space experiments; a rather surprising situation. However, the 86 liter test groups showed somewhat more restriction than might have been expected from comparison of the 43 and 172 liter test data and the differences between 86 liter and large to small to large tests may represent rather unusual circumstances in the 86 liter test groups. The large to small to large test fish behaved as expected with regard to subordinate movement when compared to 86 and 172 liter test groups.

Medium sized fish in the changing space regimes had subordinates' movements restricted in generally inverse manners. The large to small to large test fish were somewhat less restricted than the small to large to small test groups. Subordinate fish in the large to small to large tests moved somewhat more extensively than the 86 or 172 liter groups. Although this is rather surprising, it is in harmony with the previous observation that the data from the 86 and 172 liter tests may have been somewhat distorted by a single rather atypical group in each design.

Large sized fish in the changing space tests reacted much like medium fish, but in all cases large fish moved less than medium fish. So few groups were available in these tests that little else may be inferred.

CHAPTER VII

TERRITORIALITY

Territoriality, as here defined, was observed in most groups, as shown in Table IV. Of the 60 groups tested, six had no territorial behavior, 46 had a single territorial individual, four had two fish with territories, four had three territories, and no instance of a group with four territories was observed. Small sized fish groups were least likely to have territories, only 15 fish displaying territorial behavior. Medium sized fish engaged in territorial behavior most frequently, 29 instances. The large sized fish had 22 territorial individuals, intermediate between the numbers of small and medium territory holders. Groups with more than one territory occurred in all size categories, but both large and small fish each had only a single instance, while six groups of medium fish had two or more territories. Before an attempt is made to clarify these data, some consideration of the factors influencing territoriality is in order.

TABLE IV

NUMBER OF TERRITORIES

Fish Size	Small					Medium					Large				
Group	A	B	C	D	Total	A	B	C	D	Total	A	B	C	D	Total
Test															
43L	2	1	1	1	5	1	1	1	1	4	3	1	1	1	6
86L	1	1	0	0	2	1	1	1	3	6	1	1	1	1	4
172L	0	0	0	0	0	2	1	1	3	7	1	1	1	1	4
><	1	1	1	1	4	1	1	1	3	6	1	1	1	1	4
<>	1	1	1	1	4	2	1	2	1	6	1	1	1	1	4

Single territories provided little insight into factors affecting their establishment as a result of difficulty in definition, as previously discussed and as Greenberg (1947) has described. Those groups in which two or more territories were maintained were much more productive. In these groups originally a single territory was defended and the others(s) were defined later in the test period. Several factors appeared to influence the establishment of second and third territories. The following enumeration of potentially operative factors is not intended as a description of discrete, non-interacting variables; they should be interpreted as interrelated functions distinguished here for reasons of clarity and convenience.

1. Equality of Aggressive Ability. This factor is a composite of influences including sex, size, age, reproductive state, etc., which result in the potential equality in fighting ability of two individuals.
2. Available Space. The finite space available appears to be of importance in determining the likelihood of second territory formation. Increased space seems to enhance this probability. Van den Assem's 1967 model has some relevance here.
3. Environmental Configuration. Complexity of the physical environment has been shown to affect territory numbers by many authors working with fish (Miller, 1964; Greenberg, 1947: van den Assem, 1967; and others).
4. Presence of Subordinates. Greenberg (1947) hypothesized that the diversion of the first territory owner's aggression by the other members of a group reduced the frequency of attacks on a prospective territory holder and thereby enhanced the

probability of second territory formation. Subjective appraisal of the fish in the present study seemed to support this contention.

5. Freedom from Attack. A fish subject to large numbers of aggressive actions by a dominant seemed to be less likely to engage in territorial defense than an individual receiving fewer attacks. The impression was received that decreased aggression by the first territory holder tended to favor establishment of a second territory.

6. Restricted Movement. The limits placed on the mobility of subordinate fish by the territory holder were thought by Greenberg (1947) to have a positive influence on the acquisition of territory by a subordinate. A factor of this nature appeared to be operable in the present study. It seemed that fish allowed to occupy a particular area for an extended period tended to center subsequent territorial behavior in that area and that occupancy was a part of the complex leading to territoriality.

7. Presence of More Than One Territory. In instances where two territories were already extant, the definition of a third territory was apparently facilitated. Obviously, there were multiple influences within this classification, but of prime import was the reaction of the two territory holders to the presence of a rival of equal aggressive ability. The driving of subordinate fish from their territories resulted in ultimate positioning of the subordinates at the mutual boundary of the already present territories. On several occasions a third

territory was defined and ultimately expanded from this area. Some evidence to support this contention can be drawn from the fact that as many groups had three territories as had two territories. Most factors, with the exception of the phenomenon under discussion, served to make establishment of territories beyond the first one progressively more difficult. Therefore, the number of groups with two territories should have exceeded the number with three. Van den Assem (1967) observed that male sticklebacks introduced into a tank already containing territorial males took up territories at the boundaries of the pre-existing territories, and attributed this to the distance-aggression relationship. Certainly this is an important element but the fact that territorial males were accustomed to the presence of a rival of equal aggressive ability at that place may also have favored that site for establishment of a third territory. Myrberg (1965) made similar observations on territory formation of Pelmatochromus guentheri.

The highest incidence of territoriality in small fish was in the 43 liter test, suggesting the hypothesis that non-breeding territoriality may be space-related for a given fish size with a particular combination of population size and available space tending to enhance its expression. If this is true, then the occurrence of territoriality would be less frequent with more available space. Small fish did, in fact, show less tendency to defend an area in tests with greater space. It is necessary to use such information with some caution since the means of assessing territorial behavior employed here may be prone to error as previously discussed.

Medium fish defended territories more frequently than any other size. This differs from the results that would have been predicted on the basis of a strict fish size-available space relationship hypothesis. However, the possibility that differences in the likelihood of territorial behavior among fish sizes existed cannot be dismissed. If the hypothesis that territoriality reaches maximum expression at a particular level of space relative to fish size holds, then the increase in numbers of territories observed in tests with greater space may be interpreted to mean that space was critical at all levels used. Presumably, still larger spatial levels would have been necessary to implement the decrease in territoriality in medium fish that was observed in small fish groups.

Large size fish defended similar numbers of territories in all test regimes. With one exception, a single fish held a territory in each group. Only one group had more than one territory. It seems reasonable to conclude that spatial influences were critically low in all tests and that larger amounts of available space might have resulted in more instances of multiple territories, particularly in view of the greater numbers of multiple territories in the medium fish groups at the same spatial regime.

The single multiple territory group of large fish may be considered somewhat atypical since it occurred in the 43 liter test. It should be noted that this group had three territories rather than two, a fact which lends credance to the contention that the occurrence of two territories expedites the third.

It appears that by manipulation of numbers of individuals, selection of sexes, and size differences among group members, it may be possible to have large numbers of territory holders in quite restricted areas, i.e., much smaller territories than would at first seem possible. It is possible that non-reproductive territories may have lower size limits approaching in diameter the body length of the defenders. Further, minimum territory size may be found to be more a measure of equality of aggressive ability than of finite available space.

Non-reproductive territoriality has received very little attention in studies of fish behavior. Further study seems most desirable since some freedom from the influences of reproductive factors and consequent simplification of the variables involved could yield valuable behavioral and ecological insights. A tentative hypothesis is proffered here in the hope that it may stimulate more rigorous investigation of non-reproductive territoriality. The model described below is, in large measure, speculative and should not be interpreted as more than one of a number of possibilities that should be tested.

The number of territories established by longear in a captive group may be a function of a number of interacting factors and, other factors being equal, the number of territories established will increase as available space is increased. Beyond a certain spatial level the number will decrease. Inherent in this is the assumption that an optimum level of space should exist relative to number of fish in the group, average size of fish, distribution of fish sizes within the range used, and sex of individuals such that maximum numbers of territories will be established. Hence, spatial level either lesser or greater than the optimum will result in fewer territories.

A similar representation could be expected if space were constant but different fish sizes were employed. At a given spatial level the largest fish would presumably display an intermediate number of territories, medium fish the most, and small fish the least. This presumes, of course, that the spatial regime selected is optimum for inducing this relationship or that fish sizes employed vary greatly. The observations made here seem to have followed a pattern consistant with this model.

CHAPTER VIII

AGONISTIC BOUTS

Data on numbers of definitive aggressive bouts are summarized in Figures 1 through 4. In Figures 1 and 2 are shown the total number of definitive agonistic bouts recorded for each group at 5-day intervals during the 25-day observation period. The points in Figures 3 and 4 are the means of the four points plotted in Figures 1 and 2. Figures 3 and 4 are intended to clarify the data for comparison of different test regimes and fish sizes, while Figures 1 and 2 are included to avoid oversimplification. Figures 1 and 2 emphasize the variation between groups in the numbers of bouts recorded and it is apparent that generalization and reference to Figures 3 and 4 must be tempered with due regard for the complexity of the data. Conclusions drawn must, of necessity, be tentative.

Small sized fish showed little difference between 43 and 86 liter regimes. The major variation was recorded in the 1-5 day period where 86 liter fish had more encounters than 43 liter groups. Both tests had peak levels of agonistic bouts in the 6-10 day period and subsequent general declines in bout frequency. The 172 liter test had more variation between groups, but all showed decreased numbers of interactions in the 21-25 day period.

Medium fish groups in the static space designs engaged in agonistic encounters in frequency and time much as did small fish. Typically, in

Figure 1. Number of Definitive Agonistic Bouts/5-Days/Group of Four Longear Sunfish in Static Space Tests.

∘∘∘ = Group A. ---- = Group B. -∘- = Group C. —— = Group D.

Data from large fish groups omitted after death of one or more subordinates.

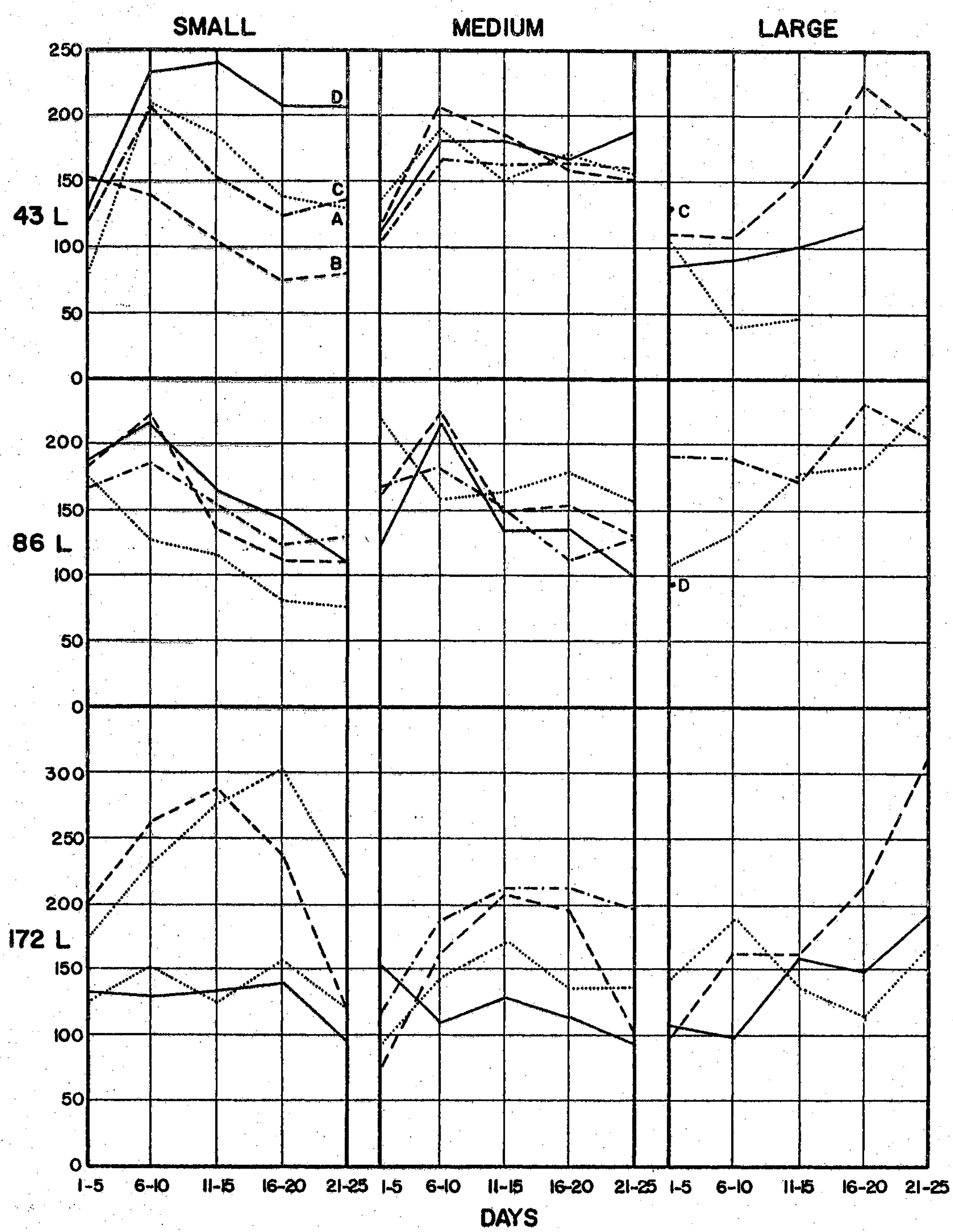

SMALL
MEDIUM
LARGE
43 L
86 L
172 L
A
B
C
D
0
50
100
150
200
250
300
1-5
6-10
11-15
16-20
21-25
DAYS

Figure 2. Number of Definitive Agonistic Bouts/5-Days/Group of Four Longear Sunfish in Changing Space Tests.

Data from large fish groups omitted after death of one or more subordinates.

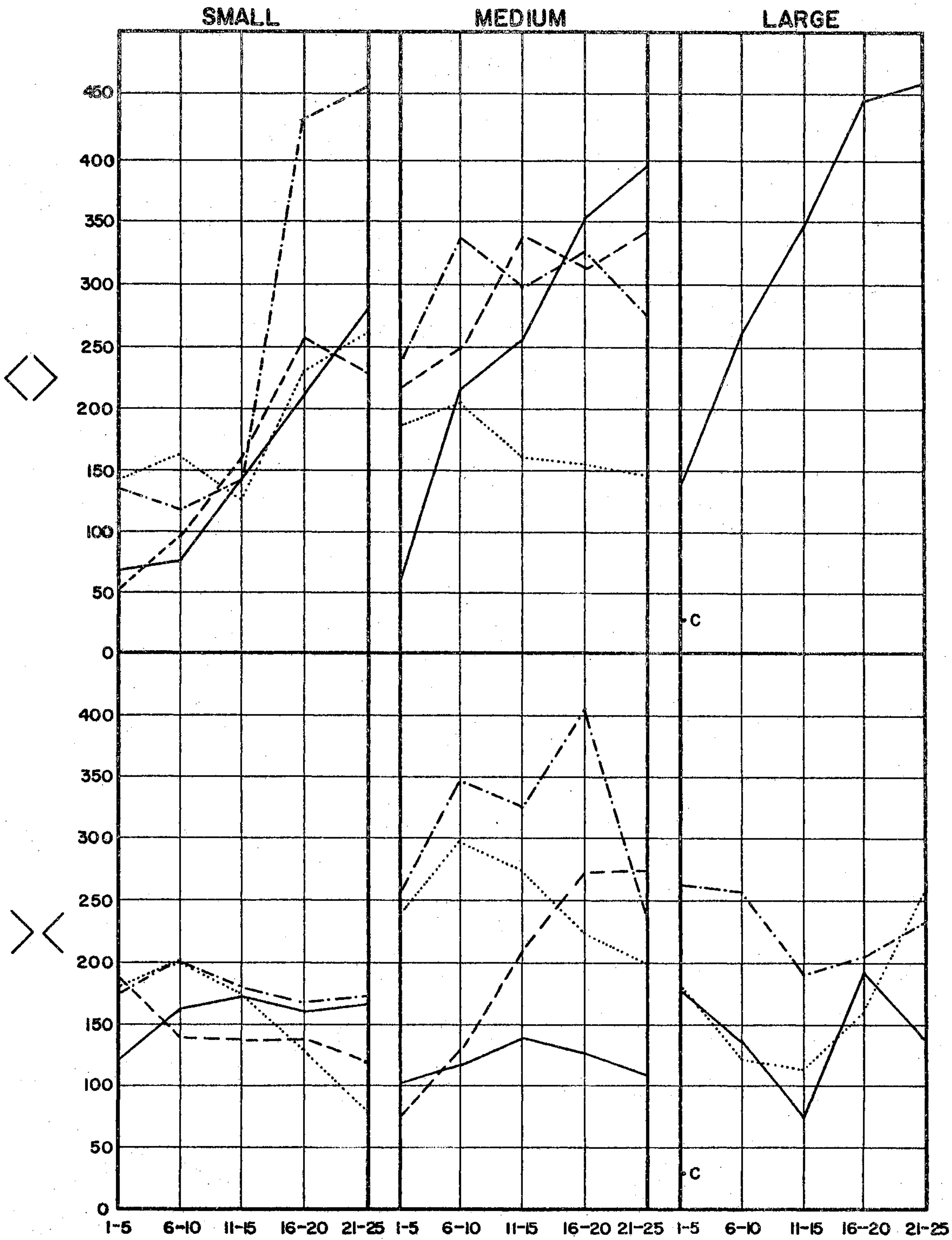

SMALL
MEDIUM
LARGE
450
400
350
300
250
200
150
100
50
0
c
1-5
6-10
11-15
16-20
21-25

Figure 3. Average Number of Definitive Agonistic Bouts/5-Days for Four Similar Groups of Four Longear Sunfish in Static Space Tests.

Data for large fish in 43L test from four groups on days 1-5, three groups on days 6-10, two groups on days 11-15, and one group subsequently. Data for large fish in 86L test from three groups on days 1-5 and from two groups subsequently. All data from three groups in the 172L and large to small to large tests of large fish. Data for small to large to small tests of large fish from two groups on days 1-5 and from one group subsequently.

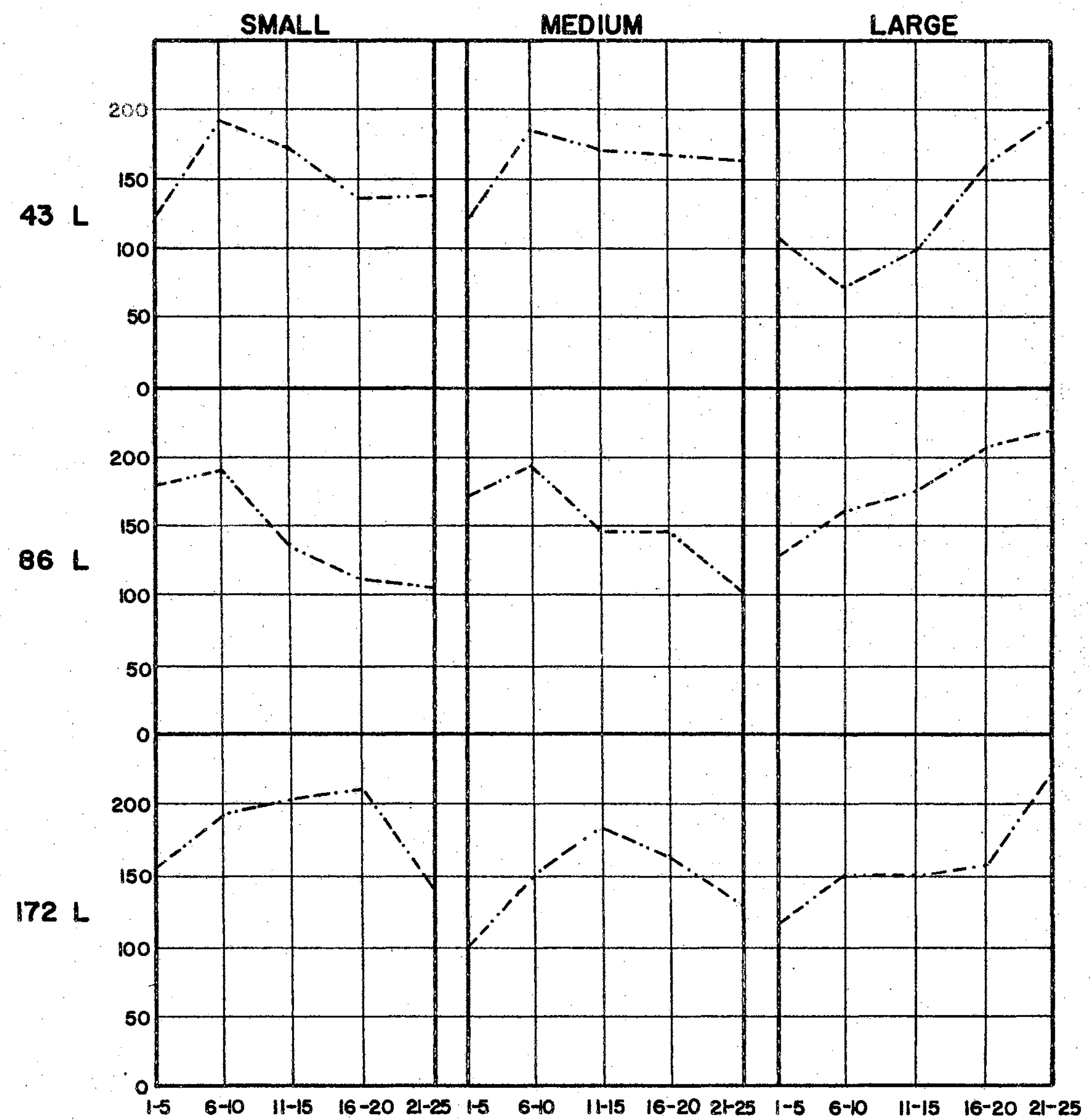
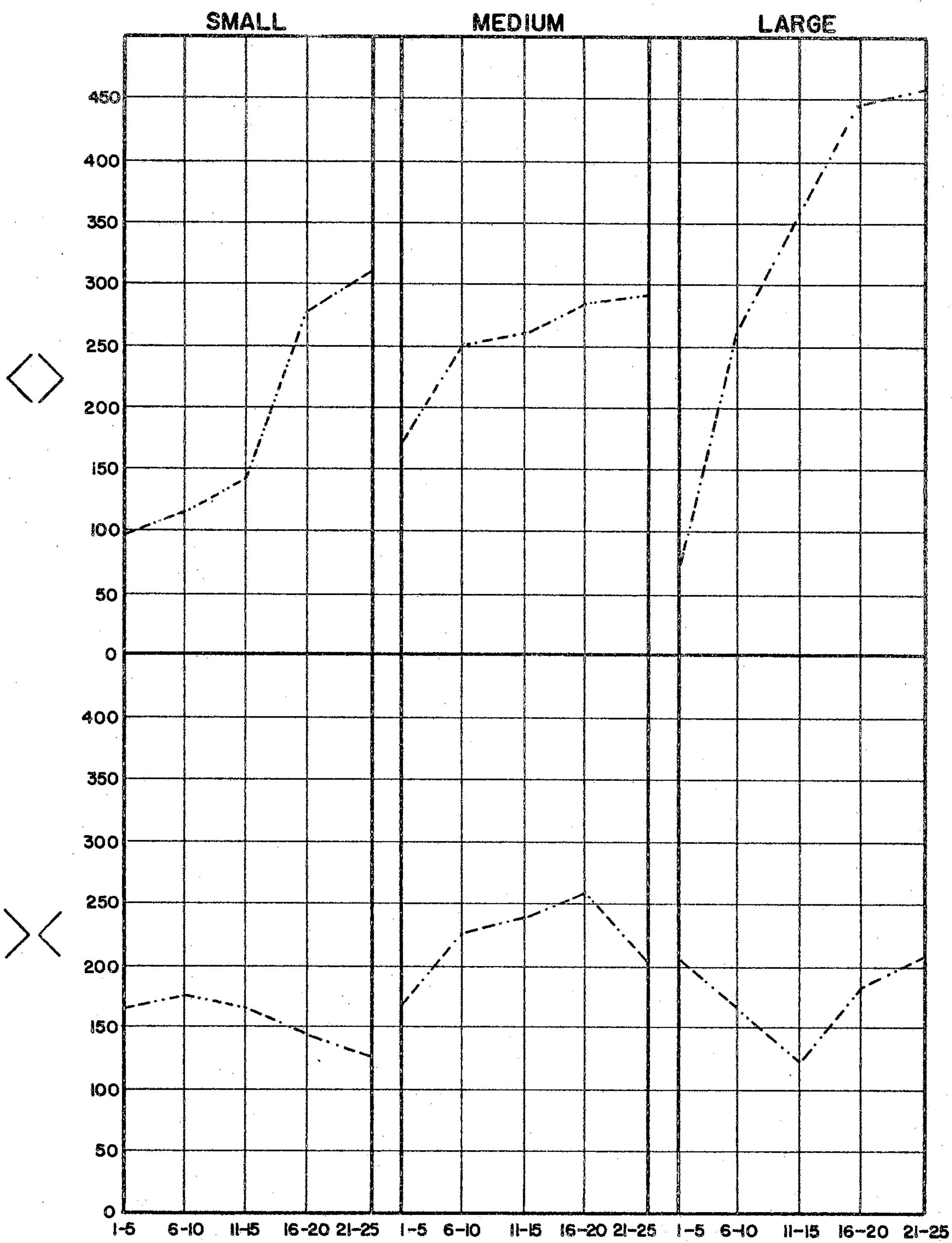

SMALL
MEDIUM
LARGE
43 L
86 L
172 L
200
150
100
50
0
1-5
6-10
11-15
16-20
21-25

Figure 4. Average Number of Definitive Agonistic Bouts/5-Days for Four Similar Groups of Four Longear Sunfish in Changing Space Tests.

Data for large fish in 43L test from four groups on days 1-5, three groups on days 6-10, two groups on days 11-15, and one group subsequently. Data for large fish in 86L test from three groups on days 1-5 and from two groups subsequently. All data from three groups in the 172L and large to small to large tests of large fish. Data for small to large to small tests of large fish from two groups on days 1-5 and from one group subsequently.


SMALL
MEDIUM
LARGE
450
400
350
300
250
200
150
100
50
0
400
350
300
250
200
150
100
50
0
1-5
6-10
11-15
16-20
21-25
1-5
6-10
11-15
16-20
21-25
1-5
6-10
11-15
16-20
21-25

the 43 and 86 liter tests, numbers of bouts were greater in the 6-10 day period than in the 1-5 day period. The peak levels in the 6-10 day period were followed by a gradual decline in frequency. The 172 liter data compares to the 43 and 86 liter results much as did that for small fish groups. The 172 liter groups displayed higher frequencies later in the test than did 43 and 86 liter groups and then declined.

The information gathered from large fish groups was limited by the mortalities that occurred in those groups. Groups were not included in the summary after a death had occurred. The information available shows little difference between any of the static space tests of large fish. Generally, it appears that the number of bouts increased throughout the test period.

Comparison of the three fish sizes in the static space tests shows some tendency toward divergence between large fish and the small and medium groups. Although little data is available, large fish groups had increasing numbers of interactions for the entire test periods, while small and medium fish groups reached peak levels of interaction frequency rather early in the tests and subsequently declined. No distinction of bout frequencies between small and medium fish groups seems warranted.

The two changing space tests with small fish groups appeared to result in rather different bout frequencies. The small to large to small test groups engaged in agonistic bouts with increasing frequency throughout the test periods. Change in interaction frequency during the first 15 days (5 days at 43 liters, 5 days at 86 liters, and 5 days at 172 liters) was rather minor; in marked contrast to the data from the three static space designs where general increases and then decreases in bout numbers occurred in the same period. In the last 10 days of the tests (5 days at 86 liters and 5 days at 43 liters) numbers of bouts increased sharply, particularly in the 86 liter period. Static space groups in the same time span typically had decreased bout frequencies.

Small fish in the large to small to large design differed sharply from the small to large to small test with the same size fish in frequencies of definitive agonistic bouts. In general, large to small to large groups had fairly constant bout numbers throughout the 25-day test period, although some tendency was evident for interactions to decrease during the last 15 days. The data for this design show considerable resemblance to those from 86 liter tests of small fish.

Medium fish groups in the two changing space designs were perhaps most notable for the extreme variation in bout frequencies between groups in the same test. Differences among similarly treated groups of medium fish in these designs were greater than those for any other design or fish size.

Large size fish in the changing space tests showed quite different bout numbers, but data from only one group of small to large to small test could be employed. The large to small to large test groups for which data was recorded had reasonably similar patterns of agonistic interactions. In all three groups numbers of bouts declined in the 6-10 and 11-15 day periods and subsequently increased. These groups compare in almost totally inverse relationships with small and medium fish groups in the same spatial regime.

The comparison of results from changing space tests among fish sizes is hampered by lack of data for large fish and the extreme variations among the medium fish groups. In general, small to large to small test groups of all sizes showed increasing numbers of bouts with time in contrast to static space treatments where numbers of interactions typically decreased later in the tests. Thus, it seems that the increase in frequency of agonistic bouts during the last 10 days of the small to large to small tests may have been related to the decrease in available space.

Generalization regarding the large to small to large tests with respect to all fish sizes is still more difficult. Each fish size seemed to be differentially affected by this regime. In large fish groups the number of interactions appeared to be positively related to spatial level; increasing bout numbers with increasing space and vice versa.

CHAPTER IX

MORTALITY

Aggressive behavior by dominant fish resulted in the deaths of 25 subordinates in large fish groups. No mortalities occurred in small or medium fish groups. Typically, situations which led to the deaths of subordinates began with complete restriction of subordinate movement. Under these circumstances the dominant individual bit the three subordinates repeatedly. In most cases, a single subordinate received the majority of the attacks. Bites appeared to be most frequently directed at the caudal, soft dorsal, and soft anal, although any body area might be bitten on occasion. Repeated bites gradually removed the soft fin rays until only stumps projected from the body. Hemorrhage appeared to be extensive when fin destruction was nearly complete. At this stage, attacked fish lost ability to equilibrate, sank to the bottom, floundered without control and died. The dominant individual continued to bite the afflicted subordinate throughout this period. Dominants were seen to bite dead subordinates, and one instance of a dominant Tail Beating the body of a dead subordinate was observed. Similar observations of aggressive behavior and subordinate deaths were made by Huck and Gunning (1967).

Table V shows the distribution of deaths by group for all tests of large fish. In the static space designs the number of groups suffering mortalities was greatest with the least space, three of four groups in the 43 liter test, intermediate with medium space, two of four 86 liter groups, and least with the greatest space, one of four 172 liter groups. In the changing space tests, one group had deaths due to aggressive behavior in the large to small to large tests while in the small to large to small design three groups had mortalities.

TABLE V

NUMBER OF SUBORDINATES KILLED IN LARGE FISH GROUPS

	Deaths/Group				
Test	A	B	C	D	Total
43L	1	0	3	1	5
86L	0	3	0	3	6
172L	0	0	3	0	3
><	0	3	0	0	3
<>	3	2	3	0	8

Spatial level appeared to be directly related to the incidence of mortality due to aggressive behavior in both the static space designs and the changing space tests. The number of groups with deaths due to aggressive behavior in the large to small to large test (approximately 111 liters average space) was less than that of the 86 liter static space tests. The small to large to small tests, however, had more groups with deaths than would be expected on the basis of average available space. Space available during this test averaged 86 liters but three groups suffered subordinate mortalities, while two of the 86 liter groups had deaths. It is possible that the average space available was less important than the initial space. The number of groups with mortality in the small to large to small tests was the same as that recorded for the 43 liter static space groups, lending some credance to this assertion. Presumably, spatial regime during the first few days of the test may have had long-term effects on learning and behavioral responses.

CHAPTER X

DOMINANCE

In this study a fish was considered to have defeated another when it was able to elicit flight or subordinate posturing by the opponent. If, during a single observation period, a fish won encounters with another by a margin of three or more, he was termed the dominant member of that pair for that observation. For summary purposes, the number of observations in which one fish dominated another was compared with the sum of periods in which the other fish was ranked as dominant. The individual that dominated in the majority of observations was ranked as dominant for the test as a whole. In the vast majority of pair relationships, one of the individuals was dominant in most or all observations. In Table VI rank for the entire 25-day test period was assigned in this manner. Included in the table are the sexes of the group members, their ages as determined by scale reading, and their relative sizes at the beginning of the test period.

Size, sex, and age were hypothesized to be effective in determination of rank on the basis of previous studies reported in the literature. Other factors may affect ranking, but no data relative to them are available from this investigation. In the following discussion, size, sex, and age are considered separately; however, it is obvious that they are not always mutually exclusive categories and interaction is probably typical.

TABLE VI

RELATIVE SIZE, AGE, SEX, AND RANK
OF LONGEAR SUNFISH IN EACH TEST

Age in years. Size relative to other group members: 1 = largest, 2 = second largest, 3 = second smallest, 4 = smallest. Rank in social hierarchy: 1 = highest, 2 = second highest, 3 = second lowest, 4 = lowest. Same rank number indicates equally ranked fish. D indicates death.

							Test									
Fish Size		43L			86L			172L			><			<>		
SMALL																
Group A	Size	Age	Sex	Rank	Age	Sex	Rank	Age	Sex	Rank	Age	Sex	Rank	Age	Sex	Rank
	1	2	♀	1	2	♂	1	2	♂	1	2	♀	1	1	♂	1
	2	2	♀	2	2	♂	2	1	♂	2	2	♀	2	2	♀	2
	3	2	♂	3	1	♂	2	2	♂	4	1	♂	3	1	♂	3
	4	2	♀	4	1	♂	2	2	♂	3	1	♀	4	1	♂	4
Group B																
	1	2	♀	1	1	♀	1	2	♀	1	2	♂	1	2	♂	1
	2	2	♀	2	2	♂	2	2	♂	2	1	♂	2	1	♀	3
	3	2	♀	2	2	♂	3	2	♀	4	1	♀	3	1	♀	2
	4	1	♀	4	1	♂	4	1	♂	3	1	♀	4	1	♂	4
Group C																
	1	2	♀	1	2	♂	1	3	♀	1	3	♂	1	3	♂	2
	2	2	♀	2	2	♀	2	2	♂	2	2	♀	2	2	♂	1
	3	2	♂	3	2	♀	3	2	♂	2	2	♀	3	2	♂	3
	4	2	♂	4	1	♂	4	2	♀	4	1	♂	4	1	♂	4
Group D																
	1	2	♂	1	2	♀	1	2	♀	1	2	♀	1	2	♂	1
	2	1	♀	3	2	♂	4	2	♂	2	2	♀	2	1	♀	2
	3	2	♀	2	2	♂	2	2	♂	2	2	♂	3	2	♀	3
	4	1	♂	4	1	♂	4	2	♀	4	2	♂	3	2	♀	4
MEDIUM																
Group A	1	3	♂	1	3	♀	1	3	♀	1	3	♂	1	3	♂	1
	2	2	♀	3	3	♀	3	3	♂	1	2	♂	2	2	♀	4
	3	2	♀	4	3	♂	2	3	♀	3	3	♀	3	2	♀	3
	4	3	♂	2	2	♀	4	2	♀	4	3	♀	4	3	♂	2
Group B																
	1	3	♀	1	4	♀	1	2	♀	1	3	♂	3	3	♂	1
	2	3	♂	2	3	♀	2	3	♀	2	3	♀	2	2	♀	3
	3	2	♀	4	2	♀	2	2	♂	3	3	♂	1	2	♀	2
	4	3	♀	2	3	♀	4	2	♂	4	3	♂	4	3	♀	4
Group C																
	1	3	♂	1	2	♂	1	3	♀	1	3	♂	1	2	♂	1
	2	3	♂	2	2	♀	4	2	♀	2	3	♀	2	3	♀	1
	3	3	♀	3	2	♂	2	1	♂	2	3	♀	3	2	♀	4
	4	3	♀	4	2	♀	2	3	♀	4	3	♀	4	2	♂	3
Group D																
	1	3	♂	1	3	♀	3	2	♀	1	2	♀	3	2	♂	2
	2	3	♀	2	3	♀	1	3	♀	1	2	♀	1	2	♂	1
	3	3	♂	3	3	♀	1	3	♂	4	2	♀	1	2	♀	3
	4	2	♀	4	2	♀	4	2	♀	1	2	♂	4	2	♀	4
LARGE																
Group A	1	4	♀	D	3	♂	1	4	♂	1	3	♀	1	3	♀	D
	2	3	♂	1	3	♂	3	3	♀	3	3	♀	4	4	♂	D
	3	3	♂	1	3	♂	2	3	♂	2	2	♀	3	2	♂	1
	4	3	♀	1	3	♂	4	3	♂	4	4	♂	2	3	♂	D
Group B																
	1	3	♂	4	3	♂	1	4	♀	1	3	♂	1	3	♂	1
	2	4	♂	1	2	♀	D	3	♂	3	3	♀	D	2	♂	D
	3	3	♂	4	2	♂	D	4	♂	4	3	♂	D	3	♀	D
	4	3	♀	4	3	♀	D	3	♂	2	2	♂	D	3	♂	D
Group C																
	1	3	♂	D	3	♂	1	5	♂	1	3	♂	1	3	♂	1
	2	3	♂	1	3	♂	2	3	♀	D	5	♂	2	3	♀	D
	3	4	♀	D	2	♂	3	3	♀	D	2	♂	3	3	♂	D
	4	4	♂	D	2	♀	4	3	♂	D	2	♀	4	3	♀	D
Group D																
	1	5	♂	1	3	♂	1	4	♀	2	4	♂	1	2	♂	1
	2	5	♀	D	3	♂	D	3	♂	1	2	♀	2	3	♂	2
	3	4	♀	4	3	♂	D	3	♀	4	2	♀	2	3	♀	3
	4	4	♀	4	3	♂	D	3	♀	3	3	♀	4	3	♀	4

Relative size seemed to be of paramount importance in determining dominance in a fish pair. Many authors have observed that larger fish tend to dominate smaller ones (Miller, 1963; Hixson, 1946; Huck and Gunning, 1967; Newman, 1956; Erickson, 1967; Greenberg, 1946; Magnuson, 1962; Braddock, 1945; and others). Analysis of the data from this investigation supports this conclusion, although the mode of operation of size effects remains unclear. During these experiments, 360 pair relationships were established. Of these, 26 pair relationships are unavailable for analysis due to fish death. An additional 27 pairs were equally ranked and cannot be utilized for clarification of dominant-subordinate relationships. The remaining 307 pairs established definite rank orders and form the basis for this discussion. Since sex and age have been found to be effective in dominance relationships, the analysis of size influences must be made as independently of these as possible. Therefore, the following data were taken from unisexual pairs in which both fish were of the same age. Seventy-five unisexual pairs of equal age formed definite dominance relationships. Of these, 59 pairs were dominated by the larger fish. Chi-square analysis showed this to differ from a random pattern at the .005 level. Thus size is effective in rank determination, the larger of a pair being much more likely to dominate.

Sex has been shown to be a factor in ranking by several authors (Braddock, 1945; Miller, 1964; Greenberg, 1946; Erickson, 1967; Hixson, 1946; and others). However, Huck and Gunning (1967) studied longear in aquaria and on the basis of observations of dominance relationships between pairs of fish concluded that "sex plays no role in the determination of dominance." Apparently, this statement was based on the relationships established between 21 heterosexual pairs of longear. They made no attempt to differentiate between the influences of sex and size. Ages were apparently not determined. From the data they present, it is possible to determine the number of heterosexual pairs in which the larger dominated the smaller, and in 19 of the 21 pairs the larger dominated the smaller. In two pairs lengths were equal. If it is assumed that size and sex are equally effective in determining rank, then their conclusions may have some credibility despite the small number of pairs used. Alternatively, there seems to be little justification for accepting such a thesis since no evidence has been proffered to support it. Perhaps more persuasive is the assumption that the variables involved need not be of equal effect; that is, the influence of a particular variable may mask the effect of another. In such a situation the hypothesis may be advanced that size differences obscure the effect of sex. Subject to this, the only valid test of the effect of sex on ranking would by the use of heterosexual pairs of equal size or cases in which the smaller fish of a pair dominated the larger.

In the present study, 153 heterosexual pairs were ranked. Of these, 97 were dominated by males and 56 by females. If this data is analyzed without regard for the other factors involved, it might be concluded that males tended to dominate females. However, as discussed above, most pairs must be excluded because of size or age differences. Since no equally sized pairs were included in these experiments, only cases where a smaller fish dominated a larger are available. With regard to age, only those pairs of equal age or pairs in which the younger dominated the older may be used. Twelve heterosexual pairs in which the larger, older, or equal age fish was dominated by the smaller, younger, or equal age individual may be analyzed. Of the 12, two pairs were dominated by females and 10 pairs by males. Chi-square analysis showed this ratio to differ from 1:1, the expected if sex were not influencing dominance, with $.025 > p > .005$. Hence, sex affected ranking. Under the conditions described above, the male of a heterosexual pair was likely to dominate the female.

The effect of age on dominance relationships is difficult to determine on the basis of the data available. The foremost source of error was probably in the aging technique. Considerable variation in annulus formation occurs at this latitude and the effect of laboratory holding periods on growth was unknown. It is likely that errors were made due to these influences and analysis of age effects must be tempered in this light. Further, if the influences of size and sex are minimized by excluding heterosexual pairs and those in which the larger fish was dominant, only nine pairs are subject to analysis. Of the nine, three were dominated by the older fish and six by the younger (Chi-square: $.500 > p > .250$). Since the number of pairs suitable for analysis was so limited and some questions exist as to the reliability of the aging technique, little may be said about the influence of age alone on rank.

Investigation of the factors subject to analysis in these tests showed that both maleness and larger relative size were associated with dominance. Size differential seemed to mask the effect of sex and, therefore, larger relative size is presumed to have been of greater valence than sex in rank determination.

CHAPTER XI

TURBIDITY

The results of the turbidity tests are presented in Table VII. The low turbidity groups all had deaths resulting from aggressive behavior. In three of the four test groups all subordinates were killed and in the other group all but one subordinate died. The number of fatalities in the low turbidity test contrasts sharply with those in the moderate and high turbidity groups. At the moderate turbidity level only one group suffered deaths due to aggressive behavior; two subordinates killed. The high turbidity tests had a single group which had a fatality; all other subordinates survived. Thus, of 12 subordinates in each turbidity level, one was killed at high turbidity, two were killed at moderate turbidity, and 11 were killed at low turbidity.

TABLE VII

NUMBERS OF SUBORDINATES KILLED
IN TURBIDITY TESTS

	Turbidity Level		
	Low	Moderate	High
Group A	3	0	1
Group B	2	2	0
Group C	3	0	0
Group D	3	0	0
Total	11	2	1

Some qualitative observations were made of the behavior of groups in this series of experiments despite the limited visibility in the moderate and high turbidity tests. In the low turbidity groups the subordinates were typically Dark Banded and their movement was completely restricted throughout the test period. Mortalities occurred in the same manner as described previously.

Behavior at moderate turbidity was difficult to observe but it appeared that aggressive activity by the dominant served to keep subordinates at the Restricted or Completely Restricted level of movement in most cases. When observations could be made, color patterns of subordinates seemed to be Moderately or Dark Banded.

The subordinates in the high turbidity tests were occasionally observed to be motionless near the surface, apparently driven there by the dominant. While observations were seldom possible, it is noteworthy that even at this level of turbidity aggressive behavior was of such a nature that subordinate movement was at least at times Restricted or Completely Restricted.

It seems evident from the numbers of subordinate deaths that occurred in the different turbidities that the effects of aggressive behavior were diminished at higher turbidities. Qualitative observations support this conclusion although it appeared that aggressive behaviors in the greatest turbidity were still important social determinants. More intensive and sophisticated investigation of the relationship between agonistic behaviors and turbidity is most desirable. If visual stimuli at high turbidities were as limited as they seemed, then some other sensory system(s) must have functioned as primary mechanisms for the orientation of agonistic behaviors. The role of these mechanisms should be most revealing and could give valuable insight into the possible mechanism and function of agonistic behavior in turbid environments. It should also be pointed out that agonistic behaviors may be important in a number of ecological situations and that turbidity may influence this relationship.

CHAPTER XII

SOCIAL STRUCTURE

Longear in this study formed a variety of social structures. In the majority of groups, the society formed could not be assigned with confidence to any of the accepted classifications. Most were of an intermediate nature, with elements of territoriality, hierarchy, and monarchistic dominance present. Hence, no quantification of the occurrence of the various social types was possible. Greenberg (1947) noted similar intergradation of social types in green sunfish.

Social orders may be ranked according to degree of restriction and severity of the consequences for subordinates. Monarchistic dominance is the most rigorous type. Social hierarchy includes a range of conditions from instances in which the highest ranked fish engages in the vast majority of encounters and bouts between subordinates are few to types in which all group members interact rather freely and the total number of agonistic bouts is small. For the purposes of this discussion, monarchistic dominance and those hierarchies in which subordinates are greatly repressed by the dominant are considered to have more rigorous consequences for subordinates than those hierarchies in which the dominant's influence was of lesser magnitude.

It was observed that the type of social structure formed by longear seemed to be influenced by the amount of space present, the size of group members, and the time that the group had been in existence. For a given fish size, groups in lower spatial levels typically had more restrictive social types at a given time than did fish in greater space. Similarly, in a given space and at the same date from test inception, larger size fish had more restrictive social groups than did small fish. The effect of time was a gradual decrease in the severity of the social structure. For example, with time a monarchistic dominance pattern might change to a drive right hierarchy. Social groupings appear to reflect, at least to some degree, the spatial regime under which fish are held, the average size of the individuals comprising the group, and the length of time the group has existed. It appears that the form of social groups from drive dominance, drive right hierarchy, to monarchistic dominance was an expression of a complex of interacting factors including space, fish size, and time, which described points of a continuum. Evidence to support this contention is available from the changing space tests. In these, type of social condition varied as space was changed; decreased space resulted in more restrictive social types, while increased space was followed by less severe social conditions. Type of society might change from monarchistic dominance to drive right hierarchy after an increase in space and then be reversed when space was lessened once more. While distinction between these types of social organization may be valuable in some cases, it should be made only with appropriate regard for their relative natures and only with detailed description of experimental conditions.

CHAPTER XIII

DISCUSSION

Three primary responses were measured in this study. Color pattern expression, extent of subordinate movement, and numbers of definitive agonistic bouts were recorded and utilized in assessing the effects of amount of available space, fish size, and time on social conditions.

The numbers of agonistic bouts observed are difficult to interpret. Variation in the values recorded for equal size fish in the same spatial regime was extreme. It appeared that the number of bouts engaged in by a group of longear was subject to at least two major influences only partially associated with spatial level, time, and fish size. The source of contribution to the total number of bouts recorded for a group was frequently the total of bouts won by the highest ranked individual while interactions between the 2, 3, and 4 ranked fish were almost non-existent. This situation was typical of groups in which movement was confined to the Completely Restricted level, and was more common at lower levels of space and with larger size fish. When fish size was reduced or space increased, the number of encounters engaged in by the highest ranked fish often declined; but this was masked in the group total by a corresponding increase in bouts between subordinates. Thus the alternative sources of bout totals served to buffer changes in group totals recorded. Due to this effect, total definitive agonistic bouts appeared to be less useful than color pattern frequencies or extent of subordinate movement in assessing response to experimental manipulation. Recording of distinct patterns of agonistic behaviors might be more fruitful in this regard.

Comparison of extent of movement and color pattern frequency shows that at lower spatial levels the number of subordinate color patterns increased and the extent of subordinate movement was reduced. In larger space fewer subordinate patterns were displayed and extent of movement increased. In the changing space tests, greater available space resulted in a reduction in numbers of subordinate color patterns and more subordinate movement while lessening the spatial level was followed by more frequent display of subordinate color patterns and reduced subordinate movement. Thus, it appears that a causative relationship existed between spatial level and extent of subordinate movement and color pattern display.

The relationships between fish size and color pattern expression and extent of subordinate movement were relatively clear-cut. Smaller fish typically showed fewer of the subordinate color patterns and greater subordinate movement than did larger fish at a similar level of space and time. Size of fish employed in a test bore a direct relationship with the frequency of display of subordinate color patterns and the extent of subordinate movement.

Time related change in frequency of display of color patterns and extent of subordinate movement was recorded. In general, as time from group inception increased, fewer of the subordinate color patterns were recorded and greater extent of subordinate movement occurred. Time then served to lessen the severity of the results of aggressive behaviors.

In the foregoing paragraphs, three factors found to affect the responses measured were discussed and the direction of the response changes resulting from their manipulation indicated. If decrease in the number of subordinate color patterns displayed and greater freedom of subordinate movement may be considered to have been indicative of reduced social stress, it is possible to construct a simple model describing these relationships. Since so few replicate groups were employed in these experiments, the following model should be regarded as tentative.

Social stress is a positive function of fish size and a negative function of available space and the length of time from group formation. The properties of the model would indicate that stress would be greater with larger fish, smaller space, or earlier in a group's existence. Reduced stress would be predicted if smaller fish were used, space were increased or assessment were made later in a group's history. It should be noted that additional variables, untested in this study, such as pretest treatment, and sex, number, and relative size of group members may apply and the model expanded to include them.

The model proposed and the data from which it was derived have important implications for students of aggressive and social behavior of fishes. Study of these behaviors should be made only with detailed description of experimental conditions, particularly of those factors discussed above. Precise evaluation of experimental results is possible only where adequate description of those variables is available. The literature on aggression and social behavior of fishes contains numerous, and otherwise praiseworthy, works in which the lack of the requisite information on technique renders interpretation of the conclusions difficult at best and at the worst, impossible. The integration of these studies into synthetic works of a more general nature and the application of their results to other animal groups seems fraught with pitfalls.

CHAPTER XIV

SUMMARY

Seventy-two groups of four longear sunfish in aquaria formed dominance hierarchies based on agonistic behavior. Hierarchies were typically stable; few rank reversals were observed after the first few days.

Color patterns were found to vary in accordance with rank and fish could frequently be assigned to positions in the hierarchies on the basis of the color pattern displayed. Color patterns were presumed to be indicative of motivational state and those patterns typical of lower ranked fish were thought to be associated with greater levels of social stress than those commonly displayed by higher ranked fish. The frequencies of occurrence of the four color patterns recorded were utilized as indices of space - fish size relationships on motivational state. Tests with less available space had greater numbers of the more subordinate patterns and vice versa. Treatments with changing available space influenced the expression of color patterns in a rather direct manner but the influence was modified by other factors so that results were somewhat confused. The size of fish was effective in determining the expression of color patterns. At a given spatial level the frequency of the more subordinate patterns increased with larger fish size.

The extent of movement of subordinate fish appeared to be largely

determined by the dominant group member. Smaller size fish moved more freely than larger fish at a given spatial level. For any size of fish, greater available space resulted in greater extent of movement. In general, in the changing space tests the extent of movement increased or decreased in accordance with the change in available space.

Territoriality, as defined in this study, was observed in most groups. Small fish groups had the fewest territories, medium fish the most and large fish an intermediate number. Greater available space, within limits, appeared to be effective in increasing the number of territories. Factors thought to influence the formation of second and third territories in a group were: equality of aggressive ability; amount of available space; environmental configuration; presence of subordinates; freedom from attack; restricted movement; and the presence of more than one territory.

The numbers of agonistic bouts recorded at each observation period showed some differences to occur in different available space tests. In static space tests a decrease in numbers of bouts occurred in both small and medium fish groups later in the tests. Large fish had increasing numbers of bouts throughout the test period. The various fish sizes had relatively similar numbers of bouts at any given spatial level. The changing space tests had rather wide variations among groups of a similar size in the same design. There appeared to be a general increase in agonistic encounters with decreased space. Presumably greater space reduced the extent of the dominant fish's inhibitory influence on subordinates' interactions.

Deaths due to aggressive interactions occurred only in large size fish. Death of subordinates were more common with less space and less numerous in the larger spaces. Changing space tests had more mortalities in the small to large to small tests. It seems that the difference in numbers of aggression caused mortalities between the changing space designs was largely due to the initial low space in the small to large to small tests.

Three factors, age, sex, and size, were analyzed to determine their effect on ranking. Age was difficult to investigate due to the small number of pair relationships with the requisite size and sexual characteristics and no conclusions were possible with respect to age. Sex was found to function in ranking; males being likely to dominate females, although size differences could obscure this relationship. Size was found to be the most important of the factors studied. Larger fish typically dominated smaller fish.

The influence of turbidity was shown to be of considerable importance in lessening the severity of aggressive interactions. The number of deaths of subordinate fish was greatest at the lowest turbidities tested and least in the most turbid conditions. It was noted, however, that even at the greatest turbidities aggressive behavior continued to be an important factor in social behavior.

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VITA 2

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Doctor of Philosophy

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