FACTORS INFLUENCING AGONISTIC BEHAVIOR AND SOCIAL ORGANIZATION IN THE ORANGESPOTTED SUNFISH, *LEPOMIS HUMILIS* (GIRARD)

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PREFACE

The objectives of this study were: 1) to determine the influence of three experimental parameters on the frequency and sequencing of agonistic behavior and social organization of groups of male orange-spotted sunfish, Lepomis humilis (Girard); 2) to determine to what extent frequency and sequencing of agonistic behavior was influenced by the formation of dominance relationships; 3) to determine if the frequency and/or sequencing of agonistic behavior differed between groups of these fish which exhibited particular types of social organization; and 4) to formulate a general statement concerning the relationships among the experimental parameters of this study, agonistic behavior, and social organization in the groups of L. humilis observed.

Dr. R. J. Miller served as major advisor and provided valuable suggestions throughout the study. Drs. T. C. Dorris, W. A. Drew, and L. H. Bruneau served on the advisory committee and reviewed the manuscript. Dr. R. W. Jones served on the advisory committee prior to his retirement. Drs. L. Folks, R. Morrison, and L. Claypool of the Oklahoma State University Statistical Laboratory assisted with the statistical analyses and computer programming. Drs. D. F. Frey and H. W. Robison and Mr. G. P. Dennis assisted in collecting the fish. Mr. Dennis and Miss S. Andrews provided invaluable assistance in recording and transcribing data. Mrs. Lisa Thompson typed the manuscript. The aid of all of these people is appreciated. The encouragement and understanding of my wife and children throughout this study is greatly appreciated.

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CHAPTER I

INTRODUCTION

The social structure of a group of vertebrates is a dynamic system of the interactions of many factors. Among these factors are: 1) the behavioral processes involved in establishing, maintaining, and/or changing the social structure; and 2) the various physical and environmental parameters which influence the behavior of individual animals or the behavior of the group as a whole (Crook, 1970). During the past 30 years many studies have demonstrated that various physical and environmental parameters influence the level of agonistic behavior of fishes in group situations (cited below). Some of these studies have pointed out the propensity of groups of fish to form a particular type of social organization under a given set of environmental conditions. While it is generally accepted that agonistic behavior is somehow related to the establishment and maintenance of dominance relationships and consequently to the type of social structure exhibited by a group of fish, the possibility that the kinds, numbers, and/or patterning of agonistic behaviors have a definitive effect on the type of social structure developed has not been investigated. The major objective of this study was to investigate this possibility. To accomplish this objective the study was conducted in the following manner:

1. Groups of male orangespotted sunfish, Lepomis humilis (Girard),

were established under different environmental conditions to evaluate the effects of these conditions on the level of agonistic activity of these fish. The orangespotted sunfish was selected as the experimental subject because the species is sexually dimorphic, permitting sex to be eliminated as a variable; and because groups of male L. humilis show much easily recognizable agonistic behavior and establish and maintain various types of social organization in captivity.

2. The influence of selected environmental parameters on measures relating to the type of social organization formed and maintained was examined.

3. Analyses were then performed to determine whether correlations existed between various measures of social organization and (a) the levels of agonistic activity of individual fish or of the group, (b) the patterning of agonistic activity, and (c) measures of environmental parameters themselves.

4. The results of the study were then used to formulate a general statement concerning the relationships among the experimental parameters, agonistic behavior, and social organization in the groups of L. humilis observed.

Studies by Hazlett and Bossert (1965), Delius (1968), Gibson (1968), Hadley (1969), Dingle (1969), Black-Cleworth (1970), Dennis (1970), and Frey (1970) were especially helpful in providing experimental or analytical methods used in this study.

Prominent among early studies of social behavior in fishes are the works of Noble and Borne (1938), Noble and Curtis (1939), Breder (1936, 1945, 1959, and 1965), Braddock (1945 and 1949), and Greenberg (1947). These studies, along with the work of Schjelderup-Ebbe (1935) and Allee

(1938 and 1942), form the basis for the study of social organization in animals.

Studies dealing with the behavior of members of the genus *Lepomis* that are particularly relevant to the present work include investigations on *L. gibbosus*, *L. humilis*, *L. auritus*, *L. megalotis*, and *L. cyanellus* (Miller, 1963), *L. cyanellus* (Hixson, 1946; Greenberg, 1947; and Borkhuis, 1965), *L. macrochirus* (Borkhuis, 1965), *L. gibbosus* (Erickson, 1967), *L. megalotis* (Hadley, 1969; and Keeleyside, 1971), and *L. humilis* (Dennis, 1970).

Other studies dealing with the behavior of various species of *Lepomis* are observations on *L. auritus* (Breder and Nigrelli, 1935), *L. cyanellus* (Allee et al., 1948; McDonald and Kessel, 1967; and McDonald, Heimstra, and Damkot, 1968), *L. gibbosus* (Ingram and Odum, 1941; and Smith, 1969), and *L. megalotis* (Witt and Marzolf, 1945; Huck and Gunning, 1967; Keenleyside, 1967; Boyer, 1969; and Smith, 1969).

Among the many social, physical, temporal, and environmental parameters that have been demonstrated to have some effect on the social organization of groups of fishes, perhaps none is characterized by such a wide diversity of expeirmental results as is group size. Hixson (1946) reported that a minimum population density of *L. cyanellus* (three fish) was necessary for the establishment of territories and that the number of territories increased with increasing population density (up to eight fish) in a constant space. She also reported that large groups of these fish tended to exhibit territorial behavior. Fabricius and Gustafson (1954) found territorial dominance at low density in groups of *Salmo alpinus* which shifted to hierarchical dominance at high density. Black-Cleworth (1970) found that dominance hierarchies occurred in *Gymnotus carapo* when four of fewer fish were kept together, yet territories were established with five and six fish. Braddock (1942) found that groups of three *Platypoecilus maculatus* could usually maintain a stable straight-line hierarchy, but groups of four could not. He also reported (1945) that groups of *P. maculatus* (four or ten fish) did not exhibit territorial behavior. Noble and Borne (1940) found that groups of four *Xiphophorus helleri* could maintain stable hierarchies for months. Pfeiffer (1965) reported that groups of two to eight young *Ptychocheilus oregonense* establish a linear rank order and that high ranking members of the group establish territories. Miller and Miller (1970) found that three species of anabantoids exhibited territorial behavior more commonly in groups of six fish than in groups of two or four fish.

The level of agonistic activity that occurs within a group of fish has been linked to the density of the group in several studies. Forselius (1957) suggested that maintaining goups of anabantoids at high densities would reduce aggression. Jenkins (1969) made the same suggestion for two trout species. Borkhuis (1965) found that the frequency of attack behavior increased in *L. cyanellus* as group size increased under one pretest condition but did not increase under another pretest condition. She also found that increased group size did not result in increased attack frequency in *L. macrochirus* under either pretest condition. Pfeiffer (1965) found that fighting decreased or stopped with 20 *Ptychocheilus oregonense* per tank but resumed when all but four had been removed. Erickson (1967) reported that increased crowding in *L. gibbosus* resulted in increased aggressiveness. Gibson (1968) found no significant difference in the level of agonistic behavior between groups of two and five juvenile Blennius pholis in three experimental situations. Miller and Miller (1970) found that more absolute agonistic activity occurred in larger groups (six fish) of anabantoids, yet the net activity per fish tended to decrease with increasing group size. Dennis (1970) found that increasing group size in L. humilis (from two to six fish) resulted in a significant increase in the total frequency of agonistic behaviors and the frequency of agonistic behaviors per fish but he did not find a significant increase in the frequency of agonistic behaviors on a per opponent basis. Van den Assem (1967) found that the initial density of rivals (Gasterosteus aculeatus) was an important factor governing nesting success. He also pointed out the necessity of considering the effects of density in experimental situations depending upon whether fish were introduced simulataneously or successively.

A systematic attempt is made in the present study to examine the effects of group size on the level of agonistic behavior in groups of male L. humilis and to show how this might in turn relate to the establishment of particular types of social structures.

Fish size and available space can hardley be separated from group size. It would seem that if spatial relationships were to have some effect on agonistic behavior and/or social organization one should be aware of the possible common effects of these two parameters. Hadley (1969) found that the number of territories present in groups of four L. megalotis tended to increase with increased available space, with small fish having the fewest number of territories, medium-sized fish the greatest number of territories, and large-sized fish having an intermediate number of territories. Greenberg (1947) reported that in

24 groups of four L. cyanellus kept in three different sized tanks maximum territory development and minimum hierarchy development occurred in tanks of intermediate size. Hixson (1946) reported that tanks in which territoriality was most likely to occur were those with the least space per individual. If group size, fish size, and available space have common effects on agonistic behavior and/or social organization, then measures of agonistic activity should correlate among various combinations of these factors (e.g. between groups of four large fish in a small space and six small fish in a large space). An attempt is made in this study to identify common patterns of agonistic behavior among several combinations of group size, fish size, and available space.

The effect of fish size on social behavior has been investigated in several studies. The general tendency for large fish to dominate smaller ones was found in various sunfish (Miller, 1963), Salmo gairdneri and Salvelinus fontinalis (Newman, 1956), Platypoecilus maculatus (Braddock, 1945), L. megalotis (Huck and Gunning, 1967; and Hadley, 1969), L. cyanellus (Hixson, 1946; and Greenberg, 1947), Oryzias latipes (Magnuson, 1962), and L. gibbosus (Erickson, 1967). The relative size of fish in group situations has been shown to affect the hierarchical rank of Xiphophorus helleri (Noble, 1938), Platypoecilus maculatus (Braddock, 1945), L. megalotis (Huck and Gunning, 1967; and Hadley, 1969), Blennius pholis (Gibson, 1968), and Mollienesia latipinna (Baird, 1968). Jenkins (1969) found size (especially weight) to be the primary correlate of success in agonistic encounters in groups of Salmo trutta and S. gardneri. Lack of uniform size between group members was also mentioned by Jenkins as one of the three factors promoting hierarchical social order in salmonids. Miller (1964) found that when the relative size difference between pairs of *Trichogaster trichopterus* was minimal fights were of longer duration than when the size differerence was large. Frey and Miller (1968) suggested that relative size differences in *T. trichopterus* and *Macropodus opercularis* were more important in the maintenance of dominance relationships than in determination of the initial dominant. Barlow (1968a) found that smaller males of *Etroplus maculatus* attack larger females more than they attack smaller females. Frey (1970) found that the relative size of opponents was of primary importance in determining the outcome of agonistic encounters between pairs of *T. trichopterus* while absolute size was not correlated with measures of dominance. Dennis (1970) did not find significant differences in the frequency of occurrence of agonistic behaviors within groups of small versus groups of large *L. humilis*. The effect of fish size, however, was involved significantly with the effects of group size and available space. Myrberg (1965) found that the larger males of the African cichlid fish, *Pelmatochromis guentheri*, were the first to establish territories followed by less stronger (and presumably smaller) males and then females.

Many other factors have been shown to influence the behavior of groups of fishes. Greenberg (1947), Braddock (1949), and Baird (1968) found that prior residency was an important determinant of the outcome of dominance encounters in *L. cyanellus*, *Platypoecilus maculatus*, and *Mollinensia latipinna*, respectively. The influence of sex in determining dominance relationships has been shown in *Xiphophorus helleri* (Noble and Borne, 1940), *Platypoecilus maculatus* (Braddock, 1945), *L. cyanellus* (Greenberg, 1947; and Allee et al., 1948), *Trichogaster trichopterus* (Miller, 1964), *Mollinenesia latipinna* (Baird, 1958), *L. gibbosus* (Erickson, 1967), and *L. megalotis* (Hadley, 1969). The general conclusion of these studies is that males tend to dominate females.

Several studies have demonstrated a relationship between the complexity of the habitat and the size and number of territories established in a given space. Among these are studies by Greenberg (1947), Fabricius (1951), Fabricius and Gustafson (1954), van Iersel (1958), Barlow (1962), Miller (1964), and van den Assem (1967).

Agonistic behavior has been related to the availability of food in groups of medaka, *Oryzias latipes* (Magnuson, 1962), and *Salmo salar* (Symons, 1968), in which the level of agonistic behavior increased following food deprivation. Chapman (1966) suggested that the interaction of food supply and minimal space requirements of salmonoids regulates their density in summer.

Social conditioning and the influence of pretest conditions have been investigated by Braddock (1945), Borkhuis (1965), and McDonald, Heimstra, and Damkot (1968).

Other factors that influence social behavior of fishes are age (Hadley, 1969), injections of hormones or gonadectomy (Noble and Borne, 1940 and 1941; Baenninger, 1968a; and Smith, 1969), brain lesions (Noble, 1936 and 1939; and Hale, 1956), general aggressiveness (Braddock, 1945), prior experience as a dominant or subordinate individual (McDonald, Heimstra, and Damkot, 1968; Jenkins, 1969; and Frey, 1970), and physical condition of the fish (Jenkins, 1969).

Studies of the causation and motivation of agonistic behavior include investigations by Hale (1956), Heiligenberg (1965), Baenninger

(1966, 1968a, and 1968b), Ward (1966), Clayton and Hinde (1968), Dunham, Kortmulder, and van Iersel (1968), Gibson (1968), Miller and Hall (1968), Southwick and Ward (1968), and McKenzie (1969).

The perciform fish Lepomis humilis is a member of the sunfish family, Centrarchidae, and is midwestern in distribution, being found in the Mississippi River drainage west through Texas and the eastern Dakotas (Miller, 1963:90). Bailey (1938), Branson and Moore (1962), and Moore (1968) describe the proposed phylogenetic relationships of the 11 genera and 30 species of the family Centrarchidae. Miller (1963), Cross (1967), and Trautman (1957) present descriptions and taxonomic characters of Lepomis humilis. Barney and Anson (1923) described the life history and ecology of the orangespotted sunfish. Miller (1963) described various aspects of orangespot behavior (sleep, comfort movements, feeding behavior, agonistic behavior, reproductive and social behavior) and compared this species with other members of the same genus.

CHAPTER II

MATERIALS AND METHODS

The study was conducted in the Ethology Research Laboratory of Oklahoma State University from 25 July 1969 to 3 July 1970.

Fish Collection and Laboratory Maintenance

Male orangespotted sunfish were collected from Boomer Lake in Payne County, Oklahoma, be means of seines and electro-fishing gear and acclimated to laboratory conditions in two large stock tanks for a minimum of one week. They were fed dried commercial flake food (Tetramin), Daphnia sp., Chironomus sp. larvae, and earthworms once or twice daily. Water temperature in the stock tanks ranged from 20°C to 26°C and room temperature varied from 21°C to 26°C during the study. Stock tanks were supplied with air from a central compressor via air stones. Illumination was provided by overhead banks of fluorescent lights and automatic switches maintained a 12 hour photoperiod.

Experimental Conditions

Physical Conditions

Fish were observed in 12 tanks 81x56x38 cm in size with a water capacity of 172 liters. Six were constructed of marine plywood and six of enameled steel. Each of the tanks had a white interior and one end of plate glass. In tanks randomly selected as small tanks movable opaque partitions of plexiglass or painted plate glass 56x38 cm were used to reduce their size to 40.5x56x38 cm with a water capacity of 68 liters. Each tank was equipped with an air stone and approximately 3 cm of bottom gravel. No plants or artificial cover were present. Water temperature in the experimental tanks ranged from 20°C to 23°C. The same conditions of lighting and photoperiod existed in the experimental tanks as in the stock tanks. Fish were fed the same foods in the experimental tanks as in the stock tanks but they were fed only once daily at the conclusion of all observations on each day of the experiment. The experimental tanks were cleaned and painted (if necessary) after each replicate of the experiment.

Pretest Conditions

Prior to each replicate the fish to be used were isolated for 3 days in plastic containers with approximately 9 liters of aerated water. On the day before each replicate was begun and at the end of each replicate the fish were weighed to 0.1 gram on a pan balance and their standard lengths measured to the nearest millimeter. At the same time individual fins or combinations of fins were clipped to facilitate recognition of individuals once the fish were put into groups. This was accomplished by clipping a small portion of the soft dorsal, soft anal, upper or lower caudal lobe, or a combination of two of these fins. At the end of each replicate a confirmation of sex was obtained by examination of the gonads.

Experimental Parameters

Three experimental variables or parameters were included in this study.

1. Group Size: Three levels of group size included two, four, and six fish per group.

2. Fish Size: Standard lengths of fish included in field collections ranged from less than 55 mm to over 80 mm with most falling between 60 and 80 mm. These individuals were separated into two populations: those having standard lengths from 60 to 72 mm and those from 74 to 80 mm. The purpose of this procedure was to determine if agonistic behavior of groups of small fish differed from that of larger fish. An attempt was made to establish in the experimental situation groups of fish with average standard lengths of 66 and 76 mm for small-sized groups and large-sized groups, respectively.

3. Available Space: To determine the extent to which available space or tank size influenced agonistic behavior groups of fish were placed in tanks of two sizes; 172 liters and 86 liters.

Individual fish were placed in a population of large or small-sized fish, then randomly placed in isolation containers, and then weighed and measured. These fish were then randomly assigned to groups, but adjustments were made, if necessary, to keep the average within-group fish size difference at or near the 66 or 76 mm standard. Fish assigned to groups were fin clipped for identification. At this point each experimental tank was randomly assigned a treatment number and set up (cleaned, supplied with an air stone and gravel, and partitions placed to create small tanks). Immediately prior to the first observation period all members of a given treatment were removed from their separate isolation containers and simultaneously introduced into the proper tank. The first observations were made at this time.

Experimental Design

A factorial experimental design was used to investigate the relative influence of the three experimental parameters on the behaviors associated with agonistic encounters and subsequent dominance relationships. The 3x2x2 factorial experiment (Table I) was in a complete block design. The three factors were tested at the following levels:

1. Group Size: A_o = two fish per group; A_1 = four fish per group; A_2 = six fish per group.
2. Fish Size: B_o = small fish (66 mm average S.L.); B_1 = large fish (76 mm average S.L.).
3. Available Space: C_o = small tank (86 liters); C_1 = large tank (172 liters).

The experiment was replicated three times.

Observations

All observations were made by two people seated directly in front of the experimental tank at a distance of approximately one meter. As long as the observers remained relatively motionless their presence did not seem to affect the behavior of the fish. The occurrence of six behavioral acts were recorded in the order in which they occurred as was the identity of fish which performed the behavior and the identity of the fish toward which the behavior was directed. These data were spoken into a Wollensak tape recorder and later transcribed into

TABLE I

DESIGN LAYOUT FOR THE 3x2x2 FACTORIAL EXPERIMENT*

Treatment No.	Code	Description Group Size	Fish Size	Tank Size
1	200	2	small	small
2	201	2	small	large
3	210	2	large	small
4	211	2	large	large
5	400	4	small	small
6	401	4	small	large
7	410	4	large	small
8	411	4	large	large
9	600	6	small	small
10	601	6	small	large
11	610	6	large	small
12	611	6	large	large

*Three replicates were performed

notebooks. Preliminary observations and practice sessions enabled the observers to agree on the fine points of identifying and recording each behavioral act.

The first observation period extended for one hour from the time the fish in a particular group were simultaneously placed together. Daily 10-min. observations were made on each group from 24 hours after the first observation period through 20 days to give a total observation time for each tank of 4 hours and 10 minutes (60 minutes on day 1, and 10 minutes each day for the succeeding 19 days). Total observation time for all tanks and all replicates was 150 hours less the amount of time lost when fish died during the experiment. Observation of a group ceased when a fish died or was injured to such an extent that it could not respond to the other fish in the group.

The color patterns of each fish in the group were recorded at the beginning and end of each observation period and at any time when a significant change occurred. Miller (1963), Hadley (1969), and Dennis (1970) all reported that color patterns give a good indication of the degree of dominance or subordination in groups of sunfish. Three components of color patterns were recorded:

1. Color of the opercle flap - dark, medium, or light.
2. Iris color - red or orange, dark orange, black or clear.
3. Appearance of lateral bands on the body - no bands or only light banded, moderately banded, or dark banded.

The order in which the components of each color pattern is given is from dominant coloration to subordinate coloration.

The degree of restriction of movement of each fish in the group was recorded as one of four categories:

1. Not restricted - an individual (usually a dominant) moved throughout the tank and at any level of the water column without being prevented from doing so.

2. Little restricted - a fish, even though a subordinate, had access to some part of the bottom of the tank, yet was kept from moving freely throughout the tank by one or more of the other group members.

3. Somewhat restricted - both movement and position were restricted; the individual was not allowed access to the bottom of the tank and was limited to certain areas in mid or top-water.

4. Completely restricted - these individuals did not have access to the bottom, were restricted to top-water (generally in one corner of the tank), and moved only when forced to do so by one of the other group members.

Dominance hierarchies and territoriality (Collias, 1944) were the predominant social orders formed. Dominance hierarchies were determined on the basis of color patterns, degree of restriction of movement and position, and type and amount of behavioral acts initiated and performed. High ranking members of the group tended to be more brightly colored, initiate and perform more acts than lower ranking members, and were seldom restricted in movement and position. Lower ranking members of the same group tended to have little eye or body color (orange or red), initiated few behaviors, assumed submissive postures when approached or attacked by dominant fish, and were restricted in both movement and position.

A territory was considered to be present when a fish restricted its movement to a certain bottom area of the tank, defeated all other group members that entered this area, or prevented other fish from entering the area. Little difficulty existed in the identification of a territory, especially in groups of four and six fish where multiple territories were often present. Incipient territories were often difficult to identify but they were noted and confirmed or rejected by subsequent observations.

Social organization in groups of two fish was a rather unique situation which requires some clarification of the dominance hierarchy and territoriality paradigms. For the most part, all 12 groups of two fish showed clear-cut dominance-subordination relationships in which the fish were ranked 1,2; this was considered a hierarchical arrangement. In some of the two-fish groups, however, the dominant fish behaved in a manner similar to territorial fish in the larger group sizes, i.e. they restricted the position and movement of the subordinate fish, assumed color patterns associated with territory holders, and even dug and defended nests. Under these conditions the dominant fish in a two-fish group was considered territorial with the extent of his territory being most or all of the tank.

At the end of each observation period the location of each fish was plotted on a prepared diagram of a top and front view of the tank. These diagrams indicated where each fish spent the majority of the observation period (vertical and horizontal spacing) and the limits of its territory, if the fish were a territory holder. These diagrams show when a fish began to be restricted or began to restrict its own activity in the establishment of a territory.

Water temperatures were also recorded at the end of each observation period.

Statistical and Computing Services

The data of the factorial experiment were analyzed using the Statistical Analysis System Program of the Oklahoma State University Computer Center Library. Entropy values were calculated using a species diversity program provided by Dr. J. Wilhm of the Oklahoma State University Department of Zoology.

CHAPTER III

BEHAVIORAL UNITS AND MEASURES

A quantitative record of behavior is a necessity in order to determine how agonistic activity is related to the establishment and maintenance of various types of social organization in a group of animals. This record should include the units of behavior which occur in agonistic contexts and which, according to Barlow (1968b) are ". . . repeatedly recognizable events." The term behavioral act (or simply, act) is used in this study to designate distinct categories of behavior which occurred between two individual orangespotted sunfish, although some of these acts can and do occur in individual fish. The term act agrees with the definition proposed by Russell, Mead, and Hayes (1954:200), i.e. ". . . a simple unit of overt behavior . . .", although no unit mechanism of co-ordination in the central nervous system is implied in its use in the present study. An act sequence refers to a series of acts either performed by the same individual (an intra-individual act sequence) or by two different individuals (an inter-individual act sequence). The term bout refers to a complete act sequence from the initial approach until the agonistic interaction between the two fish ceased.

Behavioral Acts

Miller (1963) described the agonistic behavior patterns of several species of Lepomis including L. humilis. Many other studies describe agonistic behavior patterns in sunfish (Huck and Gunning, 1967; Hadley, 1969; Smith, 1969; Dennis, 1970; and Keenleyside, 1971) or other species (Baerends and Baerends Van-Roon, 1950; Forselius, 1957; Miller, 1964; Gibson, 1968; Southwick and Ward, 1968; McKenzie, 1969; Frey, 1970; and Miller and Miller, 1970) which appear to be fairly common patterns of behavior in a wide variety of fishes. In this study eight distinctive behavioral acts which occurred in agonistic contexts were recorded. A brief description of these acts follows.

Approach

An approach consists of one fish swimming directly toward another. Approach speed was highly variable as was the behavior following an approach. Since only one approach was recorded for a given interaction between two fish, a record of the number of approaches is also a record of the number of bouts (a complete sequence of behavior between two given fish) occurring during an observation period. Approach also gives an indication of which individual initiated an agonistic interaction since most bouts began with one fish approaching another. Infrequently, one fish would display a fin erection toward another fish and then approach.

Fin Erection

Another easily recognized unit of behavior in agonistic contexts is the erection of the dorsal fin. Miller (1964) and others describe motor patterns called lateral spread which involve, in addition to the erection of the dorsal fin, the erection of the anal fins and the spreading of the caudal fin rays. Miller (1963) describes dorsal fin erection as a component of the lateral threat display and the frontal threat display. In the present study fin erection was recorded as a separate unit of behavior regardless of the positioning of the fish involved. The extent and duration of the fin erection display was highly variable. The dorsal fin in many cases was extended maximally and held while the fish performed one or more of the other agonistic acts. In other cases, the dorsal fin was extended then lowered quickly or the fin was extended slowly and lowered slowly. Elevation of the dorsal fin by L. humilis also occurs in a variety of contexts other than in agonistic behavior such as during yawning, fin flickering, fin quivering, caughing, and locomotion (Miller, 1963). Fin erection occurring in these situations was not recorded.

Opercle Spread

This act in L. humilis involves the opening of the opercula to varying degrees and then folding them back to their normal position. This behavioral act was always given as a frontal display toward another fish. Each time the opercula were opened then folded back to normal an opercle spread was recorded. Opercle spreads occurred in a variety of situations, in response to an approach, fin erection, or another opercle spread, but most commonly as a mutual display between two fish facing each other.

Tail Beating

Tail beating consists of one fish moving its tail and caudal peduncle toward another fish while they are in parallel orientation near each other. In most instances the tail beating movements were delivered by both fish. In some cases tail beating was accompanied by fin erection and sessions of tail beating were usually followed by one of the two fish being bitten or chased. A tail beating session which could consist of from one to several thrusts of the tail and caudal peduncle was recorded as one tail beat. The degree of thrust with which the tail beat was delivered was variable and no attempt was made to differentiate between the strength of tail beating thrusts.

Biting

A bite was recorded whenever mouth contact was made with an opponent. Cases where one fish attempted to bite another but did not made actual contact were not scored as a bite. Usually a bite was severe enough to leave no doubt as to its occurrence. In a few instances, however, one or both observers were not sure actual contact had been made. A bite was not recorded when this happened. Although most bites were directed at the ventral caudal region of another fish, some were directed to the lower jaw and head. In many cases bites were delivered frequently and severely enough to cause damage to the caudal and anal fins. Fin damage and hemmorrage were common results of severe biting and this was the apparent cause of death in several fish. Miller (1963), Huck and Gunning (1967), Hadley (1969), and Dennis (1970) have observed biting in captive groups of sunfish.

Chasing

Behavior in which one fish pursued another was considered a chase. If one fish approached another and the second fish moved away but was not pursued a chase was not recorded. The intensity and duration of chases were highly variable. While chasing, a fish could deliver one or more bites, opercle spreads, or dorsal fin erections; however, unless the pursuing fish stopped and approached again, only one chase was recorded.

Avoid

An avoid consists of one fish (usually a subordinate fish being approached by a dominant) moving slowly away from another without being pursued. The distance the avoiding fish moved was variable. An avoiding fish on some occasions would assume a posture which indicated subordination either by tipping its head up or down, or with head down, slightly rolling the body with its ventral surface directed toward the approaching fish. Miller (1963) described this posturing as an attitude of inferiority, Hadley (1969) as subordinate posture, and several others (Miller, 1964; Frey, 1970; and Miller and Miller, 1970) have termed this behavior as appeasement in accordance with its presumed function. Gibson (1968) termed similar behavior as submission and also considered it as functioning in preventing further attack when displayed by a subordinate fish. The avoid behavior or the avoid with the submit component did function, to a great extent, in preventing further attack by a dominant fish, and its occurrence often resulted in the shutting off of ongoing agonistic behavior.

Do Nothing

This behavioral act means that no response was given by one fish when it was approached or attacked by another fish. "No response" means that none of the other seven behavioral acts were performed by one fish in response to the approach or display of another fish. This act was included in only the analysis of inter-individual sequencing of behavior.

A summary of the eight behavioral acts is given in Table II.

Behavior Measures

A considerable number of studies of the agonistic behavior of fishes have used only a single quantitative measure of aggressive behavior. These measures include the number of definitive fights won (Hadley, 1969), the number of nips (Braddock, 1945), number of attacks (Borkhuis, 1965; and McDonald, Heimstra, and Damkot, 1968), or the number of drives (Greenberg, 1947) to name but a few. These single quantitative measures of agonistic behavior along with qualitative data on color patterns, degree of restriction, and so on, yield a descriptive account of dominance-subordination in pairs of fish which rests almost entirely upon subjective data. It is doubtful if any single measure of dominance exists; surely no universal measure of dominance has been adopted in fish studies to date.

The dominance ranking of individuals in groups of more than two fish can become difficult if only one dominance measure is used since all members may not be engaged in this behavior. For example, not all fish in a group may bite all other fish or even be bitten by them especially if the group is allowed to remain together for any length of time. It seems then that a study of dominance-subordination relationships should be based on several measures of the behaviors which produce these relationships.

The measures of agonistic behavior included in the analysis of

TABLE II

BEHAVIORAL ACTS AND THEIR CODING

Act	Symbol	Principle Components or Posturing
Approach	AP	Direct movement of one fish toward another
Fin Erection	FE	Erection of the dorsal fin
Opercle Spread	OP	Opening of the opercula with the head directed toward the opponent
Tail Beat	TB	Movement of the tail and caudal peduncle toward another fish; parallel orientation
Bite	BT	Mouth contact made with an opponent
Chase	CH	Pursuit of one fish by another
Avoid	AV	Contains two components: 1) avoid - the approached fish moves or turns slowly away from another fish, and/or 2) submit - approached fish tips head up or down or while tipping the head gives a slight ventral roll of the body
Do Nothing	DN	A fish does not respond with one of the recorded acts to an approach or display of another fish

variance of the factorial experiment are listed in Table III. The first six of these variables represent the frequency of each of the first six acts described previously. Variable seven is the total frequency of all six of these acts (AP + FE + OP + TB + BT + CH). These seven variables were then divided by the number of fish in each group (2, 4, or 6) to determine if any significant effects occur when these variables are calculated on a per fish basis. This procedure has been followed by Dennis (1970) and Miller and Miller (1970). These values represent variables 8 through 14. One further adjustment was made to obtain variables 15 through 21. The first 7 variables were divided by the number of possible opponents in each group (1 for the two-fish groups, 3 for the four-fish groups, and 5 for the six-fish groups) to obtain a measure of agonistic activity on a per opponent basis. The variables 8 through 14 and 15 through 21 were included in the analysis to determine if increased group size resulted in a disproportionately large increase in the level of agonistic activity.

Variables 22 through 27 were used to determine the effects of the experimental variables on the total number of acts per bout and the mean number of acts per bout. Variable 22 was obtained by dividing the number of total acts (TOTAL) by the number of approaches or bouts (AP), the resulting value being the mean number of acts per bout. Since approach frequency (AP) is synonymous with bout frequency, the remaining five original variables (FE, OP, TB, BT, and CH) were each divided by AP to obtain the mean number of each of these acts per bout.

Variables 28 through 33 are measures associated with the intra- and inter-individual sequencing of behavioral acts. Variable 28 is the entropy or uncertainty associated with the intra-individual two-act

TABLE III

VARIABLES MEASURED DURING THE FIRST HOUR OF GROUP INTERACTION

Number	Variable	Abbreviation
1.	Approach Frequency (Same as Bout Frequency	AP
2.	Fin Erection Frequency	FE
3.	Opercle Spread Frequency	OP
4.	Tail Beat Frequency	TB
5.	Bite Frequency	BT
6.	Chase Frequency	CH
7.	Total of these 6 acts	TOTAL
8.	Approach Frequency per Fish	AP/F
9.	Fin Erection per Fish	FE/F
10.	Opercle Spread Frequency per Fish	OP/F
11.	Tail Beat Frequency per Fish	TB/F
12.	Bite Frequency per Fish	BT/F
13.	Chase Frequency per Fish	CH/F
14.	Total of these 6 Measures per Fish	TOTAL/F
15.	Approach Frequency per Opponent	AP/O
16.	Fin Erection Frequency per Opponent	FE/O
17.	Opercle Spread Frequency per Opponent	OP/O
18.	Tail Beat Frequency per Opponent	TB/O
19.	Bite Frequency per Opponent	BT/O
20.	Chase Frequency per Opponent	CH/O
21.	Total of these 6 Measures per Opponent	TOTAL/O
22.	Mean Number of Acts per Bout	TOTAL/AP

TABLE III

(Continued)

Number	Variable	Abbreviation
23.	Mean Number of Fin Erection per Bout	FE/BOUT
24.	Mean Number of Opercle Spreads per Bout	OP/BOUT
25.	Mean Number of Tail Beats per Bout	TB/BOUT
26.	Mean Number of Bites per Bout	BT/BOUT
27.	Mean Number of Chases per Bout	CH/BOUT
28.	Entropy for the 5 Behaviors: (FE, OP, TB, BT, CH) in Intra-Individual Two-Act Sequences	H(INTRA)
29.	Total Number of Intra-Individual Two-Act Sequences	INTRA
30.	Mean Number of Intra-Individual Two-Act Sequences per Bout	INTRA/BOUT
31.	Entropy for the 7 Behaviors: (FE, OP, TB, BT, CH, AV, DN) in Inter-Individual Two-Act Sequences	H(INTER)
32.	Total Number of Inter-Individual Two-Act Sequences	INTER
33.	Mean Number of Inter-Individual Two-Act Sequences per Bout	INTER/BOUT

sequencing of behavior while variable 29 represents the total number of these two-act sequences. Variable 30 is the mean number of these sequences per bout. For example, in a sequence of acts (a bout) between two fish the following acts might occur: [1 AP-FE-OP-BT 2-2AV]. This bout indicates that fish number 1 approached, fin erected, opercle spread, and then bit fish number 2; the only act performed by fish number 2 following the sequence of acts of fish number 1 was an avoid. To determine the number of intra-individual two-act sequences that occurred in this bout only the acts performed in succession by one fish were considered. The bout described above would yield three intra-individual two-act sequences: AP-FE, FE-OP, OP-BT. The behavior of fish number 2 is ignored. The procedure used is similar to that employed by Dingle (1969) in his study of the sequencing of behavior in the mantis shrimp, *Gonodactylus bredini*.

Variable 29 represents the number of two-act sequences which occurred during the first hour observation period of each group. Variable 28 was calculated using the following equation of Shannon and Weaver (1948): $H(X) = -\sum p(i) \log_2 p(i)$ where p(i) is the probability of occurrence of a given act. The logarithm was taken to the base 2 with the result that H(X), the information present, is expressed in bits (Quastler, 1958; Dingle, 1969; and Frey, 1970). As Peilou (1966) and others have pointed out, H is an estimate rather than an exact measure of uncertainty or information.

Variables 31 through 33 are measures associated with the inter-individual two-act sequencing of behavioral acts. Inter-individual two-act sequencing of behavior considers the act performed by one fish following an act performed by another fish. For example, in the bout

[1 AP 2-2 FE-OP 1-1 OP 2], the following inter-individual two-act sequences would be recorded: AP-FE, OP-OP. The sequence FE-OP is an intra-individual two-act sequence. Variable 31 is the entropy or uncertainty associated with these sequences and was calculated using the same formula as the intra-individual entropy values. Variable 32 is the total number of inter-individual sequences which occurred during the first hour observation period while variable 33 is the mean number of these sequences per bout.

Analysis of variance was also performed on nine measures pertaining to social structures established and maintained in the 36 groups of L. humilis (Table IV).

The type of social organization exhibited was recorded either as a dominance hierarchy or territoriality. Since these were mutually exclusive categories the interpretation of results of a factorial analysis of variance for the two measures of social organization (IO-type of initial social organization formed and FO-type of final social organization exhibited) requires some caution. These variables were included, however, to determine the effects of the three experimental variables on the type of social organization initially or ultimately formed. Variable 35 is a measure of the length of time required for one of the two types of social organization to become established in each group while variable 36 represents the number of days the initial social order lasted. Variable 37 is a measure of the number of changes in social structure which took place in each group over the duration of the experiment. The day upon which the final social order was formed is represented by variable 39. Variables 41 and 42 were included as measures of the prevailing type of social organization in each group for

TABLE IV

VARIABLES ASSOCIATED WITH SOCIAL ORGANIZATION OF 36 GROUPS OF MALE <u>LEPOMIS HUMILIS</u>

Number	Variable	Abbreviation	Unit
34.	Type of Initial Social Order Formed	IO	1,2
35.	Time of Formation of Initial Social Order	TIO	Min.
36.	Duration of the Initial Social Order	DIO	Days
37.	Number of Changes in the Social Order During the Experiment	CIO	#
38.	Type of Final Social Order Exhibited	FO	1,2
39.	Time of Formation of the Final Social Order	TFO	Days
40.	Duration of the Final Social Order	DFO	Days
41.	Total Number of Days Dominance Hierarchies were Exhibited	HD	#
42.	Total Number of Days Territorial Dominance was Exhibited	TD	#

the entire experiment. Analysis of these two variables gives an indication of the effects of the experimental parameters on the overall type of social organization.

CHAPTER IV

THE RELATIVE INFLUENCE OF EXPERIMENTAL PARAMETERS ON SOCIAL ORGANIZATION AND AGONISTIC ACTIVITY

A factorial experiment was conducted in order to evaluate systematically the relative influence of the three experimental parameters (independent variables) on various measures of agonistic behavior and social organization (dependent variables). The independent variables are:

1. Group Size - 2, 4, or 6 fish per group (Factor A).
2. Fish Size - small or large fish (Factor B).
3. Tank Size - small or large tank (Factor C).

Main effects and first- and second-order interactions were computed using the Statistical Analysis System Program and the IBM System/360 computer facilities of the Oklahoma State University Computer Center. The following statistical model was used:

$$Y = R + A + B + C + AB + AC + BC + ABC + ERROR$$

where the error term was a combination of the replicate (R) components. Probability levels for the calculated F-Statistics and coefficients of variation for all dependent variables are presented in Appendix A. Two-way tables for interactions exceeding the .05 level of significance are presented in Appendix B.

Results

A separate analysis of variance was performed on each of three sets of data: 1) 27 variables relating to the frequency of occurrence of behavioral acts; 2) 6 variables pertaining to the sequencing of these acts; and 3) 9 variables pertaining to social organization of 36 groups of L. humilis. The 33 variables pertaining to frequency or sequencing of behavioral acts include only data for the first hour of group interaction. Although some of these variables were derived from others (e.g. AP/F and AP/O were derived from the values for AP) and are not independent of the parent value, each variable was treated as an independent measure of either the level of agonistic behavior or of the sequencing of agonistic acts. The nine variables for social organization include some data from the entire 20 days of the experiment.

The Influence of Group Size

Significant ($P < .05$) main effects of group size were present for 17 of the 42 dependent variables (Table V). Included in these variables are 10 measures of the frequency of agonistic acts, two measures of act sequencing, and five measures pertaining to social organization.

A summary of the 21,764 individual behavioral acts recorded for all groups during the 36 hour observation periods is given in Table VI. These data represent the agonistic activities of three replicates of the treatment combinations (see Table I) of three groups sizes, two fish sizes, and two tank sizes.

With the lone exception of OP, the total frequency of acts (TOTAL)

TABLE V

VARIABLES FOR WHICH SIGNIFICANT ($P < .05$) MAIN EFFECTS OF THE GROUP SIZE PARAMETER WERE PRESENT

Variable (Abbreviation)	$P <$
Approach Frequency (AP)	.0001
Approach Frequency per Fish (AP/F)	.0006
Fin Erection Frequency (FE)	.0001
Fin Erection Frequency per Fish (FE/F)	.0205
Opercle Spread Frequency (OP)	.0136
Tail Beat Frequency (TB)	.0011
Mean Number of Tail Beats per Bout (TB/BOUT)	.0469
Chase Frequency (CH)	.0122
Total Act Frequency (TOTAL)	.0001
Total Act Frequency per Fish (TOTAL/F)	.0109
Total Number of Intra-Individual Sequences (INTRA)	.0022
Total Number of Inter-Individual Sequences (INTER)	.0001
Duration of the Initial Social Organization (DIO)	.0366
Number of Changes in the Social Order (CIO)	.0004
Number of Dominance Hierarchy Days (HD)	.0022
Number of Territory Days (TD)	.0063
Time of Formation of the Final Social Order (TFO)	.0211

TABLE VI

THE TOTAL NUMBER OF AGONISTIC RESPONSES OCCURRING FOR THREE GROUP SIZES OF *L. HUMILIS* DURING 36 ONE-HOUR OBSERVATIONS

Act	Group Size			
	2	4	6	Total
AP	619	2440	3935	6994
FE	700	2248	3659	6607
OP	253	1486	1401	3140
TB	202	586	654	1442
BT	163	567	700	1430
CH	201	823	1127	2151
TOTAL	2138	8150	11476	21764

and all of the original six acts (variables 1 through 6) increased in frequency of occurrence as group size increased. These data suggest that group size did have some effect on the level of agonistic activity. This was verified by the fact that significant main effects of group size (F-tests, $P < .05$) were present for all but BT. Bite frequency did, however, approach the .05 level of significance ($P < .08$) for main effects of group size. These results indicate that the number of fish in the group influenced the absolute frequency of occurrence of AP, FE, OP, TB, CH, and TOTAL.

When the frequency of the first seven variables was adjusted to a per fish basis only the variables AP/F, FE/F, and TOTAL/F still exhibited significant main effects of group size. The variable OP/F approached the .05 significance level ($P < .0512$) so closely that it requires inclusion in the further analysis of these data. Thus, the significant effects of group size for TB and CH were reflected in only the absolute frequency of occurrence of these acts. Group size influenced AP, FE, TOTAL, and OP frequency more than could be expected from the effects of additional group members alone.

Reduction of the original data to a per possible opponent basis revealed the absence of any significant main effects of group size. Thus, a grossly disproportionate difference in frequency of the agonistic acts measured relative to group size was not exhibited.

The mean number of tail beats per bout was also influenced by the number of fish in the group. This was the only act-per-bout variable which reflected such an influence at the .05 level, although FE/BOUT approached this level of significance ($P < .09$).

The number of intra-individual act sequences and the number of inter-individual act sequences both exhibited significant main effects of group size. Neither the frequency of these sequences per bout nor the entropy associated with these variables was significantly influenced by the group size parameter.

All but four of the dependent measures of social organization were significantly affected by the number of fish in the group. Significant main effects of group size were found for DIO, TFO, CIO, HD, and TD. The variable DFO approached the .05 significance level for group size ($P < .0591$).

Group size had some influence on several variables, but since this parameter was at three levels the results do not reveal the location of the main effects. To determine if the effects of group size were due to differences among all three group sizes or only to certain combinations of them, Newman-Keuls tests (Snedecor and Cochran, 1967:273) were performed on the mean frequencies of the variables which exhibited significant main effects of group size. The results of these tests are given in Table VII.

The mean number of AP, FE, TOTAL, and INTER were found to differ significantly ($P < .05$) for all group sizes. In all four cases, the lowest mean frequency was for groups of only two fish, followed by the four-fish groups, with groups of six fish exhibiting the highest mean frequencies for these variables. In other words, as the number of fish in the group changed from two to four to six fish a corresponding linear increase in the mean number of AP, FE, TOTAL, and INTER took place.

For seven of the frequency or sequencing variables the significant differences were between groups of two fish and four fish, and two fish

TABLE VII

LOCATION OF THE MAIN EFFECTS OF GROUP SIZE

Variable	Group Size 2	 4	 6
AP	51.6	203.3	327.9
AP/F	25.8	50.8	54.7*
FE	58.3	187.3	304.9
FE/F	29.2	46.8	50.8
OP	21.1	123.8	116.8
OP/F	10.5	31.0	19.5
TB	16.8	48.8	54.5
TB/BOUT	0.3	0.2	0.1
CH	16.8	68.6	93.9
TOTAL	178.2	679.2	956.3
TOTAL/F	89.1	169.8	159.4
INTRA	90.9	326.2	428.3
INTER	64.3	248.7	376.3
DIO	6.8	3.5	0.7
CIO	0.8	1.5	3.3
HD	8.9	12.7	1.3
TD	6.9	6.9	16.6
TFO	3.1	7.2	10.9
DFO	13.3	13.5	8.0

*Means underscored by the same line are not significantly different from each other at the .05 ~~level of~~ probability. Newman-Keuls Test (Snedecor and Cochran, 1967:273) and six fish, but not between groups of four and six fish. For all of these variables (AP/F, FE/F, OP, TB, CH, TOTAL/F, and INTRA) groups of two fish performed a significantly lower mean frequency than did groups of four or six fish. The adjustment of three of the significant frequency variables to a per fish basis had the effect of eliminating a significant difference between the two larger group sizes, while significant differences between these two group sizes were not present to begin with for OP, TB, CH, and INTRA.

Groups of two fish were found to perform a significantly greater mean number of TB/BOUT than did groups of six fish, but groups of two and four fish and four and six fish did not exhibit significantly different mean numbers of TB/BOUT.

The Newman-Keuls test revealed that groups of two fish exhibited a lower mean frequency of OP/F than did groups of four fish. Neither the mean frequency of OP or OP/F differed between groups of four and six fish, which could possibly have been anticipated from examination of the raw frequency data (Table VI). The mean frequency of OP, however, did differ between groups of two and six fish. Adjustment of the raw data to a per fish basis eliminated the significant difference in mean OP frequency between groups of two and six fish.

Main effects of group size were not present for either IO or FO. Since these two variables represent discrete categories which were coded as either 1 or 2, caution is required when applying a factorial analysis of variance to these data. For this reason, Fisher's exact probability tests (Siegel, 1956:96) were performed to determine if the proportion of the two types of social orders initially or eventually formed differed among group sizes. The initial social organization established in 29 of the 36 groups was a hierarchical arrangement of some sort, whereas two or three territories were initially established in the remaining seven groups (Table VIII). The proportion of hierarchies (or territories) formed as the first social organization was found to differ significantly between groups of two and six fish. Groups of six fish were not equally likely to establish either type of social organization (Table VIII), and it should be emphasized that the results of these tests do not reveal which type of social order is likely to occur within a particular group size, but only that in a sample of an equal number of groups of two and six fish, the proportion of initial social orders differs significantly. Since the two types of social orders were considered to be mutually exclusive categories, it is evident that groups of six fish were more likely to show territory defense initially than groups of two fish.

The proportion of the two types of social organization which existed as the final social order differed significantly between groups of four and six fish (Table IX). The type of final social order formed by groups of four fish consisted of proportionately more hierarchies than did the type of final social organization in groups of six fish. Groups of six fish were more likely to exhibit territorial behavior as a type of social organization than were groups of four fish at the end of the experiment.

None of the significant differences for the measures of social organization were found to exist between groups of two and four fish, although significant differences between groups of two and six fish were found for all five variables. These results are especially interesting since all behavioral measures but TB/BOUT (for frequency and sequencing

TABLE VIII

GROUP SIZE AND THE TYPE OF INITIAL SOCIAL ORGANIZATION FORMED IN 36 GROUPS OF L. HUMILIS

Group Size	Type of Initial Order Hierarchy	Territory	Comparison	P*
2	12	0	2-4	$>.05$
4	9	3	2-6	$=.047$
6	8	4	4-6	$>.05$

*Fisher's exact probability test (Siegel, 1956:96)

TABLE IX

GROUP SIZE AND THE TYPE OF FINAL SOCIAL ORGANIZATION FORMED IN 36 GROUPS OF L. HUMILIS

Group Size	Type of Final Order Hierarchy	Territory	Comparison	P*
2	4	8	2-4	$>.05$
4	6	6	2-6	$>.05$
6	1	11	4-6	$=.03$

*Fisher's exact probability test (Siegel, 1956:96) variables) showed significant differences between groups of two and four fish. This indicates that groups of two and four fish behaved quite differently in the performance of individual behavioral acts (more accurately, in measures of these acts), yet exhibited no significant differences for the measures of social organization.

The Newman-Keuls tests for social organization variables indicated that the initial social organization formed in groups of two fish lasted for a significantly greater period of time than it did in groups of six fish. Groups of two and four fish exhibited fewer changes in social structure for the duration of the experiment than did groups of six fish. For the comparison between the two and six-fish groups these results are consistent; the initial social organization formed in groups of two fish lasted longer with fewer changes than it did in groups of six fish. Groups of two fish also formed the eventual or final social order significantly earlier in the existence of the group than did groups of six fish. Newman-Keuls tests for the variables TD and HD shows that groups of two and four fish were less territorial than were groups of six fish, consequently the opposite results were found for HD, i.e. groups of six fish exhibited a hierarchical arrangement as the predominant social order less than did groups of two and four fish. The duration of the final social order, which only approached the .05 significance level for main effects of group size, differed significantly between groups of two and six fish with the final social order existing for a longer period of time in the two-fish groups than in the six-fish groups. Very little difference exists between the means for DFO in the two- and four-fish groups; however, this was just enough difference to prevent the finding of a significant effect for group size between groups of four and six fish.

The Influence of Fish Size

Fish size did not significantly affect either the frequency or sequencing of behavioral acts or any of the measures of social organization. Only the variables OP/O ($P < .08$), OP/BOUT ($P < .10$), and H(INTER) ($P < .09$) had a probability level of .10 or less. There were no significant differences between the agonistic behavior or social organization of groups of small and large fish used in this study. It should be emphasized that the comparison being made is between entire groups of small fish and entire groups of large fish and not between small and large fish within the same group.

The Influence of Tank Size

Only three measures of agonistic activity resulted in signigicant main effects of the tank size parameter. These were the related measures AP, AP/F, and AP/O (Table X). Also included in Table X is the variable INTER which approahced the .05 level of significance for main effects of tank size.

In each case, groups of fish in the smaller space exhibited a higher mean frequency of the variable than did groups in the larger tanks. Fish in the smaller tanks approach more frequently or have more bouts of agonistic behavior (since AP is synonymous with bout frequency) than do groups of fish with more space per fish. The effects of tank size were also significant when AP was measured on a per fish and per opponent basis. This means that a reduction in available space (or an increase in available space) had a significant influence on approach

TABLE X

VARIABLES FOR WHICH SIGNIFICANT ($P < .05$) OR NEAR SIGNIFICANT MAIN EFFECTS OF THE TANK SIZE PARAMETER WERE PRESENT

Variable (Abbreviation)	$P <$	Means	
		Small Tank	Large Tank
Approach Frequency (AP)	.0276	223.3	165.2
Approach Frequency per Fish (AP/F)	.0303	49.9	37.7
Approach Frequency per Opponent (AP/O)	.0373	70.0	53.3
Total Number of Inter-Individual Sequences (INTER)	.0567	258.8	200.7

or bout frequency even after adjustments to a per fish or per opponent basis were made. Reduction in space increased the likelihood that group members would come into contact with each other more frequently, but the absence of any other significant main effects of tank size indicates that an increased contact rate does not necessarily result in a significant increase in agonistic behavior.

The near-significant main effect of tank size on INTER reveals a strong tendency for a difference in the sequencing of agonistic bouts since the variable INTRA did not approach significance. The ability of a given fish to perform a series of agonistic acts which are uninterrupted by responses of another fish is reflected by INTRA, while INTER indicates just the opposite. Consequently, tank size appears to affect not only the frequency of approaches or bouts, but also the way in which individual acts within these bouts are patterned. Fish in the smaller tanks exhibited a greater number of inter-individual two-act sequences of behavior than did fish in the larger tanks.

None of the measures of social organization exhibited significant main effects for tank size.

The Influence of Interactions Between Experimental Parameters

The five two-factor interactions present in this study are presented in Table XI, which also includes two variables which approached the .05 level of significance for a given interaction.

Bite frequency only approached the .05 significance level for main effects of group size and was not significantly influenced by fish size, yet this was the only frequency or sequencing variable which exhibited a significant interaction between these two parameters. A

TABLE XI

VARIABLES WHICH APPROACHED OR EXCEEDED THE .05 LEVEL FOR SIGNIFICANT FIRST-ORDER INTERACTIONS

Interaction	Variable (Abbreviation)	P<
Group Size x Fish Size	Bite Frequency (BT)	.0430
	Bite Frequency per Fish (BT/F)	.0746
	Duration of the Final Social Organization (DFO)	.0224
Group Size x Tank Size	Tail Beat Frequency per Opponent (TB/O)	.0229
	Mean Number of Tail Beats per Bout (TB/BOUT)	.0170
	Tail Beat Frequency per Fish (TB/F)	.0666
Fish Size x Tank Size	Mean Number of Fin Erections per Bout (FE/BOUT)	.0457

plot of the interaction means for the three levels of group size and the two levels of fish size is presented in Figure 1. The interaction of group size and fish size involves not only a change in the magnitude of the BT response, but also a change in the direction of the response. Groups of two fish, whether small or large, differ only slightly in mean bite frequency, but groups of four small fish exhibited a lower mean bite frequency than did groups of four large fish. Groups of six small fish showed a higher mean bite frequency than did groups of six large fish. The real interaction between these two parameters for BT appears to be between groups of four and six fish of the two sizes; at the group size of four fish, the mean number of bites increased from small to large fish while the opposite results occurred for groups of six fish. The mean bite frequency for groups of small fish increased slowly from group size two to four then increased rapidly from four to six. Mean bite frequency for large fish increased rapidly from groups of two fish to groups of four fish then decreased sharply from groups of four to six fish. It seems that within the group sizes and fish sizes used in this study, bite frequency of small fish was affected very little as the group size increased; however, there appeared to be some inhibition of biting as group size was increased for the larger fish. The interaction of group size and fish size for the variable BT/F exhibited the same type of interaction as did BT.

The interaction means for the group size x fish size interaction of DFO are plotted in Figure 2. Groups of four small fish exhibited the greatest degree of stability of social organization, i.e. the final social order had a mean duration of 18.2 days. Five of the six groups of four small fish initially established a dominance hierarchy and four

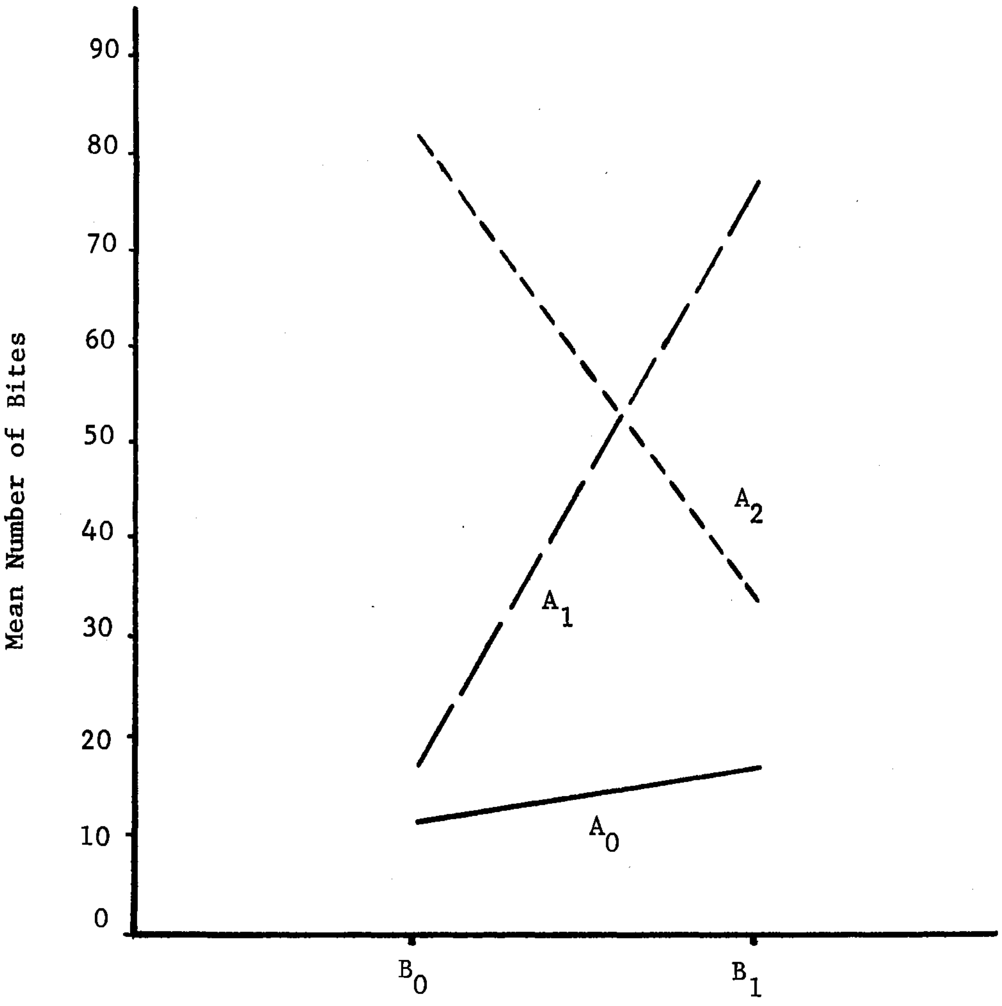


Figure 1. Group Size and Fish Size interaction for bite frequency (BT) during the first hour observations on 36 groups of L. humilis (B_0 = small fish; B_1 = large fish; A_0 = groups of 2 fish; A_1 = groups of 4 fish; A_2 = groups of 6 fish)

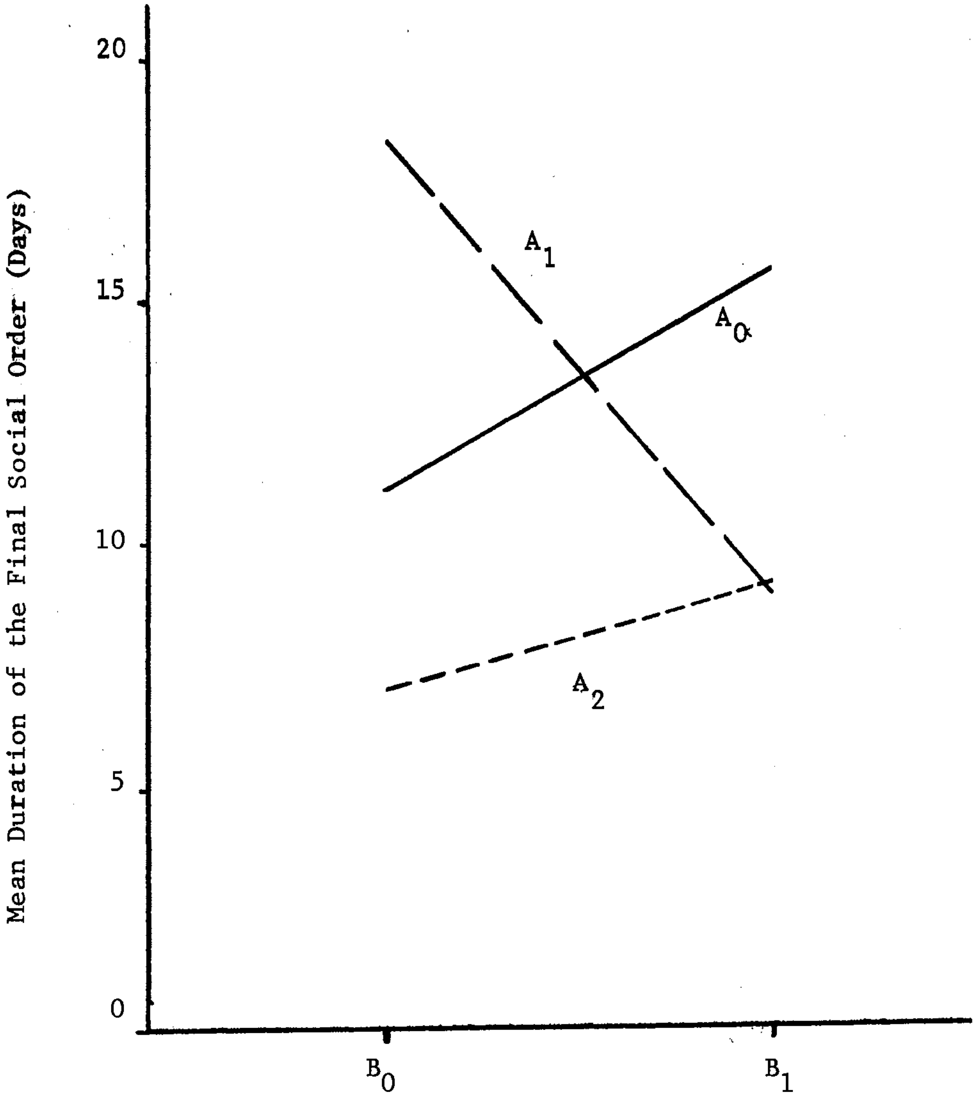


Figure 2. Group Size and Fish Size interaction for mean duration of the final social order (DFO) for the 20 day experiment on groups of L. humilis (B_0 = small fish; B_1 = large fish; A_0 = groups of 2 fish; A_1 = groups of 4 fish; A_2 = groups of 6 fish)

of these groups did not show any territorial behavior during the entire 20 days of the experiment. None of these six groups had more than one change in the type of social organization initially formed. Groups of two and six large fish had a greater mean duration of the final social order than their corresponding small fish groups. Overall, groups of six fish showed the lowest mean duration of the final social order, which is an indication that social organization in these groups was rather unstable.

The first-order interaction group size x tank size was significant for two related variables, TB/O and TB/BOUT (Figure 3 and 4). Figure 3 shows that fish in the smaller space exhibited a lower mean frequency of TB/O as the number of fish in the group was increased, while groups of fish in the larger tanks performed less TB/O in groups of two and six fish but more in groups of four fish. There again appears to be some inhibition of behavior in the largest groups.

There also appears to be some inhibition of the behavior of fish in the six-fish groups for TB/BOUT (Figure 4). Groups of fish in the small tanks exhibited a sharp decrease in TB/BOUT as group size decreased from two to four to six fish per group. On the other hand, fish in large tanks exhibited an increase in BT/BOUT as the number of fish in the group was increased from two to four fish and a decrease between four and six fish groups. Considerable similarity exists in the interaction effects of group size and tank size for the two variables TB/O and TB/BOUT (Figure 3 and 4) doubtless due to the close relationship between these variables since they were derived from the same original TB values. The variable TB/F approached the .05 level of significance for the group size x tank size interaction and a plot of

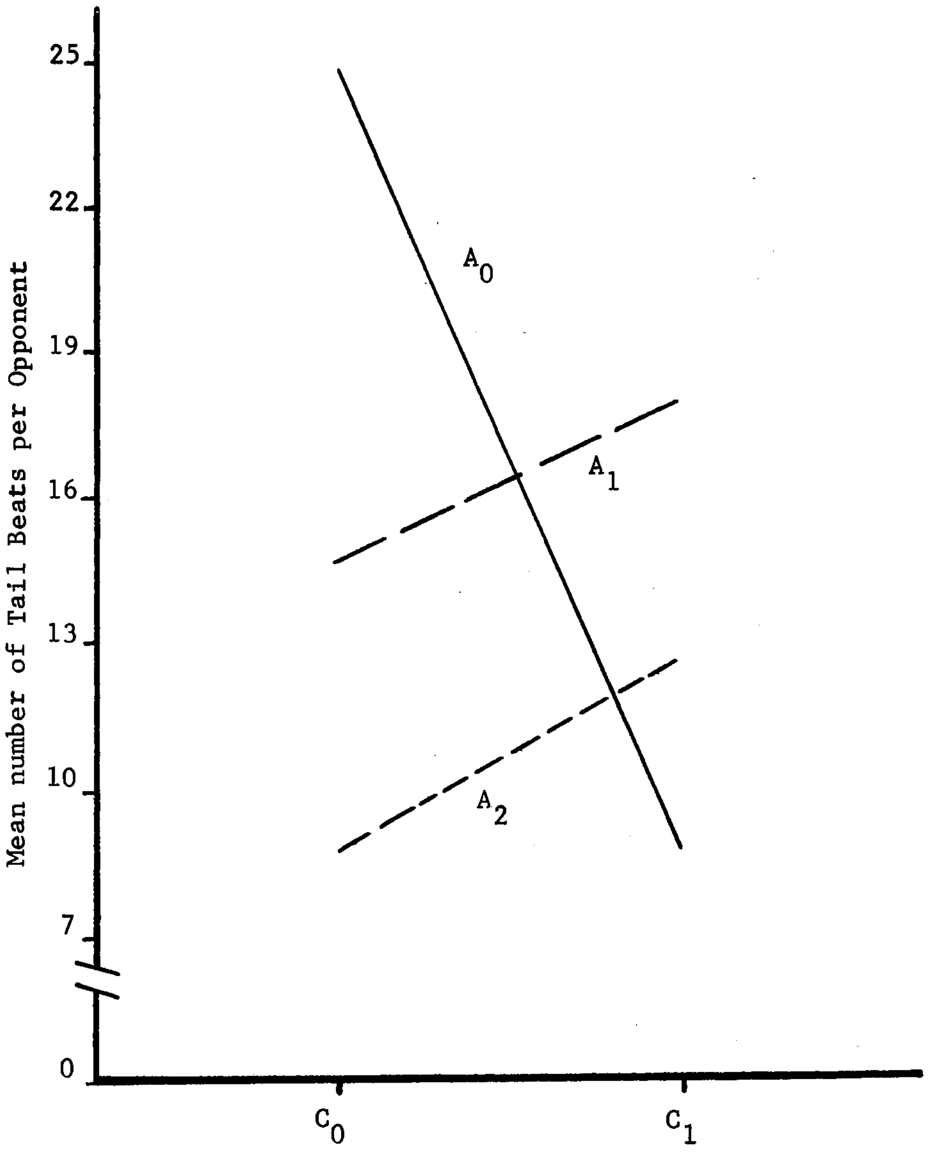


Figure 3. Group Size and Tank Size interaction for tail beat frequency per opponent (TB/O) during the first hour observations on 36 groups of L. humilis (C_0 = small tank; C_1 = large tank; A_0 = groups of 2 fish; A_1 = groups of 4 fish; A_2 = groups of 6 fish)

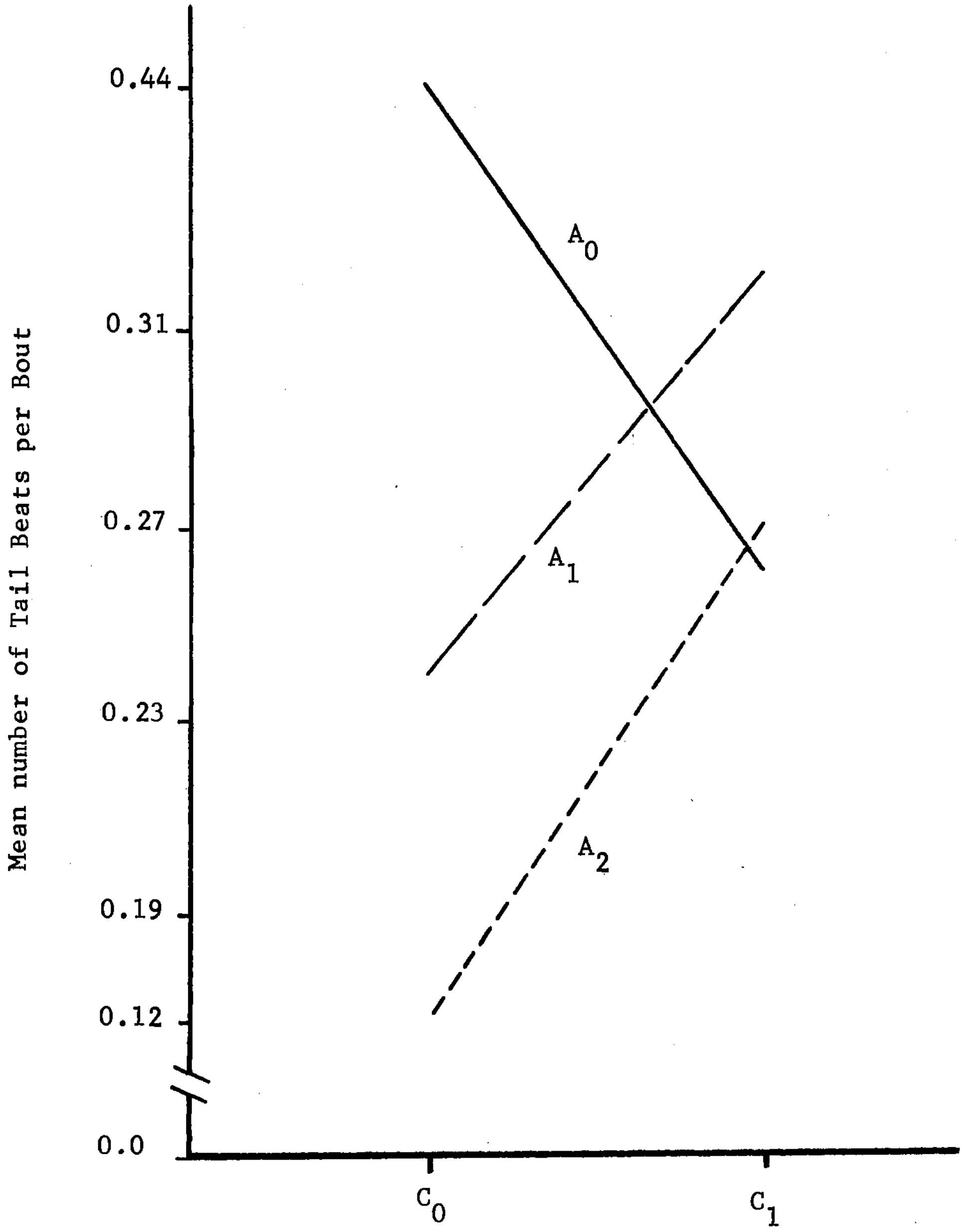


Figure 4. Group Size and Tank Size interaction for mean number of tail beats per bout (TB/BOUT) during the first hour observations on 36 groups of <u>L. humilis</u> (C_0 = small tank; C_1 = large tank; A_0 = groups of 2 fish; A_1 = groups of 4 fish; A_2 = groups of 6 fish)

the interaction means showed the same trend as for TB/O and TB/BOUT.

The only fish size x tank size interaction that was significant involved FE/BOUT (Figure 5). The mean frequency of FE/BOUT decreased slightly for small fish as the tank size changed from small to large, while there was an increase in mean FE/BOUT for large fish as the space changed from a small tank to a large tank. The interaction for FE/BOUT, then, affected both the level of the FE/BOUT response as well as the direction of the response.

The second-order interaction of group size x fish size x tank size did not approach the level of significance for any of the 42 dependent variables.

Coefficients of Variation

The coefficients of variation (C.V. = $S/\bar{X}$) for the 42 variables are presented in Appendix A. The C.V.'s ranged from 10.85% for INTER/BOUT to 129.59% for BT/O. Such high variation is often associated with behavioral studies. The C.V.'s for associated variables such as AP, AP/F, and AP/O differed only slightly since per fish and per opponent values were derived from the original frequency data and would as a result, reflect the variation therein. Approach frequency and its related measures exhibited lower C.V.'s than did any other group of frequency measures followed by FE, TB, OP, CH, and finally BT and their related measures. Per bout variables for frequency measures generally had lower C.V.'s than their respective related variables.

Coefficients of variation for measures of total agonistic activity (TOTAL, TOTAL/F, TOTAL/O, and TOTAL/AP) as a group were lower than all other frequency measures except AP. Since these variables are

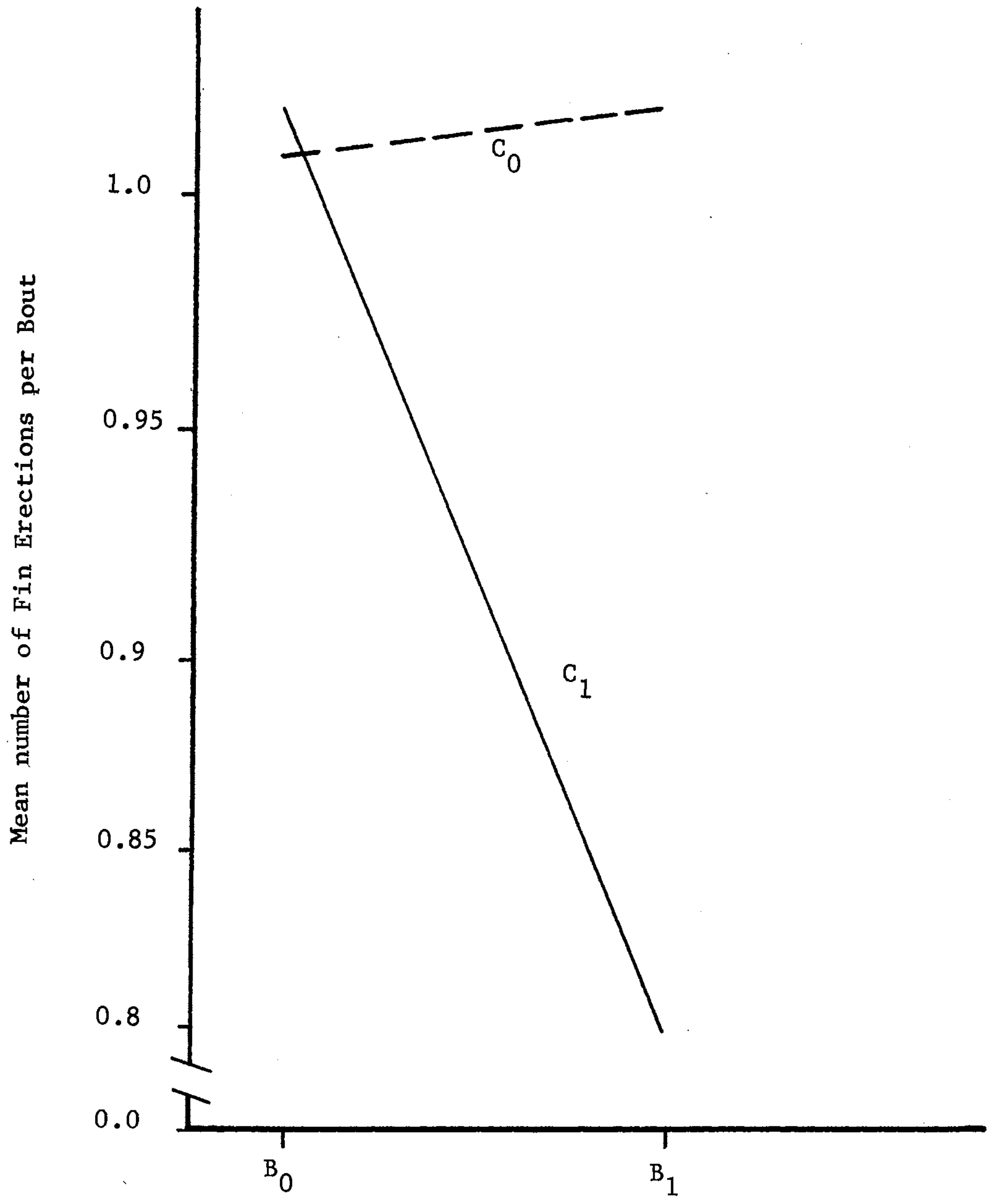


Figure 5. Fish Size and Tank Size interaction for mean number of fin erections per bout (FE/BOUT) during the first hour observations on 36 groups of _L. humilis_ (B_0 = small fish; B_1 = large fish; C_0 = small tank; C_1 = large tank)

combinations of all acts, their variation tends to be reduced with the result that they are better estimates of behavior than individual acts.

Coefficients of variation for the six act-sequence variables were low with the exception of INTRA. This exception was probably due to the extended intra-individual two-act sequences which frequently occurred in the two-fish groups.

A wide range of C.V.'s occurred for the nine variables associated with social organization. The low C.V.'s for IO and FO can partially be attributed to the fact that measures of these variables were discrete values. Measures dealing with the initial social organization (IO, TIO, and DIO) had much lower C.V.'s than did measures pertaining to the final social organization (FO, TFO, and DFO). This was no doubt due to the fact that the initial observation period was one hour in length and most of the groups formed the initial social order during this period.

Discussion

Each of the significant effects of a factor or interaction obtained in the factorial experiment reflects the degree to which the particular factor or interaction influenced the general phenomenon of crowding. Individual fish were crowded by three processes: 1) increasing the number of fish in the group, 2) decreasing the amount of space available to these fish, and 3) increasing the overall size of the fish. Twenty of the 42 dependent variables were significantly affected by one of these processes, while only five of these variables were influenced by a combination or interaction of two of these processes.

The most obvious effect of crowding pertained to changes in the general overall frequency or sequencing of agonistic activity as opposed to changes in the frequency of specific behavioral acts. The variables AP, AP/F, AP/O, TOTAL, TOTAL/F, TOTAL/O, INTRA, and INTER, and to some extent, FE, FE/F, and FE/O, reflect the level of agonistic activity that occurred in the 36 groups. As mentioned previously, AP is synonymous with bout frequency, and as such, is a measure of the number of two-fish interactions that occurred during the first hour of group existence. The variable TOTAL is a measure of the frequency of all behavioral acts which occurred during this same time period. Both INTRA and INTER are measures of the total number of times two-act sequences took place in all bouts, and give not only an indication of the level of agonistic activity taking place, but also indicate the pattern of this activity. Since FE was a very frequent act (Table VI) and was often the only act performed in conjunction with an approach, it too gives some indication of the overall level of activity that occurred in groups of these fish. The variables mentioned here include 11 of the 15 significant main effects of group size and tank size (no main effects of fish size were present) for frequency or sequencing variables which resulted from the factorial analysis of variance. The predominant effects of crowding, then, appear to pertain to measures of general agonistic activity. It is interesting to note, however, that of the five variables which exhibited significant first-order interaction effects none were measures of general agonistic activity (Table XI).

From preliminary observations and the reports of others (Borkhuis, 1965; Erickson, 1967; Dennis, 1970; and Miller and Miller, 1970) it was expected that more absolute agonistic activity would occur as the number of fish per group was increased. The variables AP and TOTAL both indicated that the level of absolute activity was significantly different for all group sizes (Table VII). These variables measured on a per fish basis revealed that the significant effects of group size still prevailed, but no significant effects existed between groups of four and six fish. None of the per possible opponent measures for these variables exhibited significant main effects for group size. The variables AP, AP/F, and AP/O were all significantly influenced by tank size. These results, when combined, suggest the following effects of crowding: differences in AP and TOTAL can be attributed to the effects of crowding due either to increasing the number of fish per group or decreasing the amount of available space; AP exhibited significant effects of both of these processes while TOTAL was only influenced by the group size parameter. Bout frequency per fish and total activity per fish showed no significant difference between the two larger group sizes, although the means for these acts showed opposite effects for groups of four and six fish. The mean frequency of AP increased (nonsignificantly) from four to six fish per group while there was actually a decrease in mean TOTAL/F for these same group sizes (Table VII).

Measures of the level of overall frequency of agonistic activity (AP and TOTAL) with significant main effects of group size or tank size exhibited no significant interaction effects for these two parameters. These results suggest that either group size or tank size influenced the level of agonistic activity, but combinations of various levels of these two parameters may result in fairly similar frequencies of these two variables. This was especially apparent in the interaction of these two parameters at the four and six-fish group sizes where groups of four fish in the small tanks exhibited almost the same level of AP and TOTAL as did groups of six fish in the larger tanks (mean AP for four fish in the small tanks was 225.5 compared to a mean of 268.7 for six fish in the large tanks; mean TOTAL for four fish in the small tanks was 708.6 compared to 774.5 for six fish in the larger tanks).

It is difficult to generalize about the effects of crowding on the frequency of occurrence of specific behavioral acts. All acts except OP increased in frequency as group size increased (Table VI), and all but one of these acts, BT, was significantly affected by the group size parameter. With the exception of AP and FE which have been mentioned previously in connection with measures of overall agonistic activity, the acts which exhibited significant main effects of group size, OP, TB, and CH, did not do so for the two larger group sizes (Table VII). This suggests that the effects of crowding brought about by an increase in the number of group members were absent after group size reached the level of four fish per group. These same effects of crowding were found for the per fish measures AP/F and FE/F.

None of the specific behavioral acts exhibited significant effects of crowding due to fish size, and the effects of crowding brought about by decreasing the amount of available space were present only for AP. This further supports the generalization made earlier that the level of overall agonistic activity was affected more by crowding than was the frequency of occurrence of specific behavioral acts. In addition, it can be concluded that the effects of crowding brought about by an increase in group size were almost entirely due to differences in the absolute level of behavior rather than to differences in the amount of behavior per fish or per possible opponent.

The generalization that measures of overall activity were affected more by crowding than were measures of specific behavior appears at first to lack support since only measures of specific behavioral acts (BT, TB/O, TB/BOUT, and FE/BOUT) exhibited significant interaction effects of crowding (Table XI). Since no significant main effects of the three parameters were found for the four variables which exhibited these interaction effects one is tempted to attribute the occurrence of these effects to chance. Dr. Larry Claypool, of the Oklahoma State University Statistics department, (personal communication) has pointed out, however, that specific interaction effects are present as a result of particular combinations of factors and as a result their presence (especially in the light of the absence of main effects) can be especially meaningful. In other words, it is only the combination of effects of crowding that results in significant effects for BT, TB/O, TB/BOUT, and FE/BOUT. There appears to be more of a tendency for measures of overall activity or absolute agonistic activity to be affected by an individual parameter than for measures of specific behavioral acts to be affected thus. On the other hand, measures of specific acts which were not significantly affected by single parameters of crowding were affected by combinations of these parameters.

Neither entropy variable, H(INTRA) or H(INTER), was found to be affected significantly by the three processes of crowding. These results indicate that the amount of information (or uncertainty) present in the average distribution of acts was unaffected by the experimental parameters of this study. Thus, neither H(INTRA) nor H(INTER) was affected by the various levels of the experimental parameters of group size, fish size, or tank size. These results are not surprising since the entropy values for each group were calculated from data for the first hour of group existence during which time the initial social organization in 32 of the 36 groups was established and it has been shown (Dingle, 1969) that the formation of social orders affects entropy measures. It is interesting to note, however, that the total number of intra- and inter-individual two-act sequences were significantly affected by the group size parameter (Table V). Inspection of the means for these variables (Table VII) reveals that they were not affected in the same manner, i.e. the mean number of INTER increased significantly across all group sizes but no significant increase in INTRA was present as group size changes from four to six fish per group. The per bout variables, INTRA/BOUT and INTER/BOUT did not exhibit significant main effects of group size, consequently it is only at the level of absolute frequency that crowding affected the sequencing of behavioral acts.

The effects of crowding on measures of social organization should be viewed with some caution since they may agree less with the assumptions of the parametric analysis of variance than do the sequencing or frequency variables. Their inclusion in this analysis did indicate, however, the tendency for crowding (especially an increase in group size) to affect significantly the stability of social organization. Groups of six fish exhibited more changes in social organization, a greater likelihood of establishing and maintaining territorial behavior, and formed the final or eventual social order at a later time than did groups of two or four fish. The most revealing outcome of the analysis of the measures of social organization relative to group size, however, lies in the comparison of the location of main effects for frequency and sequencing measures and measures of social organization. There was a tendency for significant main effects of group size for measures of social organization to be present between groups of four and six fish while differences between two and four fish were present for the frequency and sequencing variables (Table VII). If group size were the only factor being considered one would be tempted to conclude that very little connection exists between the frequency of occurrence of agonistic behavior and measures pertaining to the type and stability of social organization. This possibility will be further investigated in the next section.

CHAPTER V

SOCIAL ORGANIZATION AND AGONISTIC BEHAVIOR

The purpose of this chapter is to identify the relationships which existed between social organization and agonistic behavior in the groups of L. humilis observed. Specifically, an attempt is made to determine if 1) the establishment of a social order of some kind was associated with significant changes in the frequency or sequencing of agonistic behavior and 2) whether particular types of social organization were correlated with certain frequencies or patterns of behavioral acts. If it could be shown that act frequency or patterning differed significantly before and after social relationships were established then the results of the factorial analysis would require a reassessment. It would also promote a better understanding of the functional significance of individual agonistic acts and social organization in these fish.

Effects of Social Organization on Agonistic Behavior

To determine if the establishment of social organization affected the frequency of occurrence and/or sequencing of agonistic behavior only data from groups which met two criteria were used. First, the initial social order must have been established during the one hour observation period since a complete record of agonistic behavior was available for these observations. Second, once the initial social order was established it must have remained unchanged during the rest of the observation period since shifts in dominance relationships could possibly affect the level of agonistic behavior. Ten groups each of the two- and four-fish group sizes met these criteria while only two of the six-fish groups did so. The two and four-fish groups were analyzed separately and the six-fish groups were eliminated. Frequency data were calculated on an act per minute basis so that differences in act frequencies due to differences in time periods before and after dominance establishment could be taken into account. Where applicable, data pertaining to other aspects of social organization and agonistic behavior have been included to make the analysis as complete as possible.

Groups of Two Fish

A clear-cut dominance-subordination relationship existed in the 10 groups of two fish included in this analysis. Obvious differences occurred in the distribution of act frequencies before and after these dominance relationships were estalished (Table XII). For acts AP, OP, BT, and CH as well as TOTAL, an increase in frequency and frequency per minute took place after dominance was established; FE, FE/min., TB, and TB/min. exhibited the opposite pattern. The differences in act frequencies per minute, however, were not statistically significant at the .05 level (Wilcoxon's rank-sum test; Bradley, 1968:105). These results indicate that the establishment of dominance relationships did not significantly affect the frequency per minute occurrence of either the total agonistic behavior or the individual acts measured. In fact,

TABLE XII

ACT FREQUENCY AND ACT FREQUENCY PER MINUTE BEFORE AND AFTER DOMINANCE ESTABLISHMENT IN TEN GROUPS OF TWO *L. HUMILIS*

Act	Before Dominance Establishment f	f/min.	After Dominance Establishment f	f/min.
AP	250	.81	315	1.09
FE	346	1.12	284	.98
OP	80	.26	155	.53
TB	120	.39	69	.24
BT	39	.12	110	.38
CH	53	.17	135	.47
TOTAL	888	2.86	1068	3.68

rather than dominance establishment functioning to reduce the level of agonistic activity as has been suggested by Etkin (1964:15) the frequency of all but two acts increased after dominance establishment. These results can be better understood by examining the changes in agonistic activity of dominant and subordinate fish. Included in Table XIII are the act frequencies and act frequencies per minute for the eventual dominant and subordinate individual of all 10 groups. In no instance did an eventual subordinate individual perform a greater frequency of agonistic behavior than did the eventual dominant prior to dominance establishment. After dominance was established subordinate individuals performed relatively little agonistic behavior and did not OP, TB, or CH at all. For the eventual dominant individuals only BT and TB/min. decreased from one period to the next. This agrees well with the observation made by Miller (1963) that tail beating was a common behavior in groups of _L. gibbosus_ and _L. humilis_ when dominance-determining encounters were occurring. These data further suggest that dominant individuals were responsible for performing the large majority (94%) of all agonistic behavior which took place after they had attained dominance.

No significant differences were found for any of the act frequency per minute data or the total agonistic behavior per minute of dominant individuals before and after dominance establishment ($P > .05$, Wilcoxon's rank-sum tests). Statistical tests could not be performed on the corresponding data for subordinate individuals due to the low frequency of acts following dominance establishment, however, the decrease in individual act frequency and the decrease in total activity relative to dominance establishment indicates that considerable constraint was

TABLE XIII

ACT FREQUENCY AND ACT FREQUENCY PER MINUTE FOR THE EVENTUAL DOMINANT AND SUBORDINATE FISH BEFORE AND AFTER DOMINANCE ESTABLISHMENT IN TEN GROUPS OF TWO *L. HUMILIS*

	Eventual Dominant		Eventual Subordinant	
Act	Before	After	Before	After
AP	162 (.52)*	290 (1.00)	88 (.28)	25 (.09)
FE	198 (.64)	253 (.87)	148 (.48)	31 (.11)
OP	75 (.24)	155 (.53)	5 (.02)	0 (.00)
TB	82 (.26)	64 (.22)	38 (.12)	5 (.02)
BT	35 (.11)	110 (.38)	4 (.01)	0 (.00)
CH	51 (.16)	135 (.47)	2 (.006)	0 (.00)
TOTAL	603 (1.94)	1007 (3.47)	285 (.92)	61 (.21)

*Frequency per minute

placed on their behavior by the dominant member of each group. Collias (1944:83) defined social dominance as being ". . . the determination of behavior of given individuals by other individuals . . ." and it is evident that this was what occurred in these groups of L. humilis.

The possible effects of dominance establishment on the sequencing of behavioral acts was accomplished by examining intra- and inter-individual two-act sequencing data for these same 10 groups of two fish. Tables XIV and XV contain the matrices for the frequency distribution of intra-individual two-act sequences of behavior before and after dominance establishment. The unbracketed values represent the number of times one of the five acts (AP does not occur as a following act) followed another act with both acts being performed by the same individual. The bracketed numbers represent the expected values which were calculated using the distribution of following acts (row totals) in the same manner described by Dingle (1969:564).

The distribution of all following acts (row totals) for Tables XIV and XV were found to differ significantly (chi-square = 28.28, $P < .001$). This indicates that the distribution of act sequences performed by an individual differed significantly before and after dominance establishment.

Differences in specific two-act sequences before and after dominance establishment can be identified by comparing the observed and expected values of Tables XIV and XV, for these comparisons provide an estimate of the deviation from randomness of any two-act sequence (Frey, 1970). Sequences which occurred more frequently than expected can be described as "directive" while those which showed the opposite trend can be described as "inhibitive" (Hazlett and Bossert, 1965).

TABLE XIV

OBSERVED AND EXPECTED FREQUENCY DISTRIBUTION OF 338 INTRA-INDIVIDUAL TWO-ACT SEQUENCES IN TEN GROUPS OF TWO FISH BEFORE DOMINANCE ESTABLISHMENT

Initial Act	Following Act					
	FE	OP	TB	BT	CH	Total
Approach	107	15	6	1	4	133
(AP)	(46)	(31)	(24)	(13)	(19)	
Fin Erection	0	27	39	10	19	95
(FE)	(33)	(22)	(17)	(9)	(14)	
Opercle Spread	4	15	7	6	18	50
(OP)	(17)	(11)	(9)	(5)	(7)	
Tail Beat	5	5	7	1	3	21
(TB)	(7)	(5)	(4)	(2)	(3)	
Bite	0	2	1	10	5	18
(BT)	(6)	(4)	(3)	(2)	(3)	
Chase	2	14	1	4	0	21
(CH)	(7)	(5)	(4)	(2)	(3)	
TOTAL	118	78	61	32	49	338

TABLE XV

OBSERVED AND EXPECTED FREQUENCY DISTRIBUTION OF 680 INTRA-INDIVIDUAL TWO-ACT SEQUENCES IN TEN GROUPS OF TWO FISH AFTER DOMINANCE ESTABLISHMENT

	Following Act					
Initial Act	FE	OP	TB	BT	CH	Total
Approach	222	18	4	1	10	255
(AP)	(89)	(56)	(21)	(40)	(48)	
Fin Erection	1	52	39	30	56	178
(FE)	(62)	(39)	(15)	(28)	(34)	
Opercle Spread	2	34	5	20	34	95
(OP)	(32)	(21)	(8)	(15)	(18)	
Tail Beat	2	6	8	3	0	19
(TB)	(7)	(4)	(2)	(3)	(4)	
Bite	2	8	0	28	28	66
(BT)	(23)	(15)	(5)	(10)	(12)	
Chase	9	32	0	26	0	67
(CH)	(23)	(15)	(6)	(11)	(13)	
TOTAL	238	150	56	108	128	680

These terms are used in a statistical sense and in the analysis which follows a sequence was considered to be "directive" or "inhibitive" if the chi-square value for that sequence exceeded the .05 significance level (1 d.f.). These terms do not necessarily imply causation, however, Dingle (1969:565) has pointed out that since an intra-individual sequence of acts is performed by the same individual there is good reason to believe that they are behaviorally linked. A list of the "directive" and "inhibitive" act sequences before and after dominance establishment for the 10 groups of two fish is given in Table XVI.

Similar patterns of intra-individual act sequencing occurred for acts following an AP for both time periods, which indicates that the sequence AP - FE was much more common than would be expected by chance. Although these fish did perform other acts immediately following an AP (Tables XIV and XV) they did so much less frequently than expected if all following acts were distributed randomly.

A fin erection performed immediately after the other five acts tended to shift from the "directive" category prior to dominance establishment to the "inhibitive" category after dominance establishment. This was accompanied by the addition of several acts to the "directive" category (chiefly OP, BT, and CH), an indication that the sequencing after dominance establishment changed from the performance of the display, FE, to the more overt agonistic acts.

Since subordinate individuals did not perform OP, BT, or CH after dominance establishment (Table XIII) these results can be interpreted in terms of the behavior of dominant individuals. The three acts appear to be behaviorally linked, i.e. the performance of one of these acts

TABLE XVI

ANALYSIS OF INTRA-INDIVIDUAL TWO-ACT SEQUENCES BEFORE AND AFTER DOMINANCE ESTABLISHMENT IN TEN GROUPS OF TWO *L. HUMILIS*

Act	Time of Dominance Establishment	Category	
		Directive	Inhibitive
AP	Before	FE	OP, TB, BT, CH
	After	FE	OP, TB, BT, CH
FE	Before	TB	FE
	After	TB, CH	FE
OP	Before	CH	FE
	After	CH, OP	FE
TB	Before		
	After	TB, CH	
BT	Before	BT	FE
	After	BT, CH	FE, TB
CH	Before	OP	
	After	OP, BT	FE, TB

reinforced the performance of one of the others. It is not surprising to find the act OP connected with the overt acts BT and CH since Miller (1963:102) considered OP to ". . . occur at higher levels of aggressiveness than did biting movements . . ." The possible link between these three acts may also explain their rather large increase in frequency of occurrence following dominance establishment (Table XIII). This relationship after dominance establishment appears to be as follows: after displaying an OP, a dominant individual chased the subordinate and then bit the subordinate or performed another OP; a BT led to a CH, which again was followed by another OP or BT.

The fact that TB was the only act to decrease in frequency after dominance establishment (Table XIII) is reflected in the addition of TB to the "inhibitive" category following BT and CH, although when a TB did occur it was likely to be followed by another TB.

The matrices for the frequency distribution of the inter-individual two-act sequences of acts before and after dominance establishment are given in Tables XVII and XVIII, respectively. In these tables the unbracketed values represent the number of times a particular act was performed by one individual in response to a given act performed by a different individual. As before, the values in brackets are the calculated expected values for a given two-act sequence.

The distribution of all following acts before dominance establishment differed significantly (chi-square = 134.77, $P < .001$) from the distribution of all following acts after dominance establishment. This means that sequences of behavior performed by one fish in response to the behavior of another fish were different relative to the

TABLE XVII

OBSERVED AND EXPECTED FREQUENCY DISTRIBUTION OF 366 INTER-INDIVIDUAL TWO-ACT SEQUENCES IN TEN GROUPS OF TWO FISH BEFORE DOMINANCE ESTABLISHMENT

Initial Act	Following Act							
	FE	OP	TB	BT	CH	AV	DN	Total
Approach	92	0	1	0	0	0	3	96
(AP)	(51)	(.8)	(13)	(1)	(.5)	(4)	(26)	
Fin Erection	75	3	19	4	2	3	21	127
(FE)	(67)	(1)	(17)	(2)	(.7)	(6)	(34)	
Opercle Spread	5	0	1	0	0	8	17	31
(OP)	(16)	(.2)	(4)	(.4)	(.2)	(1)	(8)	
Tail Beat	17	0	28	0	0	5	17	67
(TB)	(35)	(.5)	(9)	(.9)	(.3)	(3)	(18)	
Bite	1	0	0	1	0	0	12	14
(BT)	(7)	(.1)	(2)	(.2)	(.1)	(.6)	(4)	
Chase	3	0	0	0	0	0	28	31
(CH)	(16)	(.3)	(4)	(.4)	(.2)	(1)	(8)	
TOTAL	193	3	49	5	2	16	98	366

TABLE XVIII

OBSERVED AND EXPECTED FREQUENCY DISTRIBUTION OF 358 INTER-INDIVIDUAL TWO-ACT SEQUENCES IN TEN GROUPS OF TWO FISH AFTER DOMINANCE ESTABLISHMENT

	Following Act							
Initial Act	FE	OP	TB	BT	CH	AV	DN	Total
Approach	28	0	0	0	0	6	8	42
(AP)	(9)	(.4)	(1)	(.4)	(.4)	(5)	(26)	
Fin Erection	32	3	8	3	3	17	43	109
(FE)	(23)	(.9)	(3)	(.9)	(.9)	(12)	(68)	
Opercle Spread	4	0	0	0	0	4	43	51
(OP)	(10)	(.4)	(1)	(.4)	(.4)	(6)	(32)	
Tail Beat	9	0	1	0	0	11	18	39
(TB)	(8)	(.3)	(1)	(.3)	(.3)	(4)	(28)	
Bite	1	0	0	0	0	2	43	46
(BT)	(10)	(.4)	(1)	(.4)	(.4)	(5)	(29)	
Chase	2	0	0	0	0	0	69	71
(CH)	(15)	(.6)	(2)	(.6)	(.6)	(8)	(44)	
TOTAL	76	3	9	3	3	40	224	358

time of dominance establishment.

As with the intra-individual sequences, differences in observed and expected values are estimates of which acts occurred more or less frequently than expected, however, since the sequences which are involved were between two different fish it would perhaps be more meaningful to determine the categories "directive" and "inhibitive" relative to the rank (or eventual rank) or the fish which performed the following acts. The .05 level was used to justify inclusion of a given sequence in the list of "directive" and "inhibitive" acts for inter-sequencing which appear in Table XIX.

The list of "directive" and "inhibitive" acts in Table XIX reflects to a great degree the level of performance of acts by subordinate or eventual subordinate individuals, consequently, very few of these acts were recorded for dominant or eventual dominant individuals. For example, dominant individuals could not respond to OP, BT, or CH performed by subordinate individuals after dominance establishment since subordinates did not perform these acts (Table VIII).

Two significant shifts in the responses of subordinates relative to dominance establishment took place; the first of these was the addition of the AV response following an AP by a dominant after dominance establishment while the second was the change in "directive" response to a TB. To the approach of a dominant individual after dominance establishment, subordinate individuals exhibited the submit or avoid (AV) response more than expected by chance if the possible responses were distributed randomly. The AV response was also given following a TB after dominance establishment when prior to this time the subordinate was more likely to respond to a TB by the dominant with

TABLE XIX

ANALYSIS OF INTER-INDIVIDUAL TWO-ACT SEQUENCES FOR DOMINANTS AND SUBORDINATES BEFORE AND AFTER DOMINANCE ESTABLISHMENT IN TEN GROUPS OF TWO *L. HUMILIS*

		Category	
Act	Time of Dominance Establishment	Directive	Inhibitive
AP	Before	[FE]*, *FE	[TB] , TB, DN
	After	[FE], FE, AV	
FE	Before	FE	DN
	After	[FE]	TB
OP	Before	AV, DN	FE
	After	DN	
TB	Before	[TB], TB	[FE]
	After	AV	
BT	Before	DN	FE
	After		
CH	Before	DN	FE
	After	DN	AV

*Acts within brackets represent directive and inhibitive responses of dominants to acts performed by subordinates; unbracketed acts represent directive and inhibitive responses of subordinates to acts performed by dominants.

a TB. McKenzie (1969) reported that tail beating in Culaea inconstans appeared to indicate a state of balance between the tendency to attack and flee, and Miller (1963) reported tail beating as occurring early in dominance encounters in sunfish. These ideas, coupled with the finding that TB was the only act to decrease in frequency for dominants in the two-fish groups after dominance establishment, indicates that tail beating may serve as a test of strength between two L. humilis as fin tugging does in Trichogaster trichopterus (Frey, 1970; Miller and Miller, 1970). If this were the case, the shift from TB being a "directive" response by subordinates before dominance establishment to AV after dominance establishment would be expected.

Groups of Four Fish

The initial type of social organization formed in eight of the 10 groups of four fish used for the analysis of the effects of social organization on the frequency and sequencing of agonistic behavior was a dominance hierarchy of some sort, while two of the groups exhibited territorial defense. One of the hierarchy groups formed a linear straight-line hierarchy of the type described by Noble and Borne (1938) and Hixson (1964). In the remaining seven hierarchy groups a single fish dominanted the other group members and it was not possible to rank the three subordinate members of these groups. Two territories were defended in the territorial groups with the two subordinate members of each of these groups being equally ranked.

As with the two-fish groups, differences in the distribution of act frequencies relative to dominance establishment or the establishment of social organization took place in the four-fish groups (Table XX);

TABLE XX

ACT FREQUENCY AND ACT FREQUENCY PER MINUTE BEFORE AND AFTER DOMINANCE ESTABLISHMENT IN TEN GROUPS OF FOUR <u>L. HUMILIS</u>

Act	Before Dominance Establishment f	Before Dominance Establishment f/min.	After Dominance Establishment f	After Dominance Establishment f/min.
AP	1130	3.42	1052	3.90
FE	1112	3.37	752	2.78
OP	616	1.87	870	3.22
TB	346	1.05	225	0.83
BT	251	0.76	316	1.17
CH	333	1.01	490	1.81
TOTAL	3788	11.48	3705	13.72

however, the pattern of these changes was more diverse, which should be expected from the increased number of group members. Approach frequency (or bout frequency) and TOTAL frequency both decreased after the establishment of social organization, however, the frequency per minute increased. Fin erection frequency and TB frequency as well as FE/min. and TB/min. decreased after dominance establishment while OP, OP/min., BT, BT/min., CH, and CH/min. all increased after the social structure was formed during the hour. The only one of the frequency per minute changes which was statistically significant was that of TB/min. (Wilcoxon's rank-sum test, $P < .05$). Significantly fewer TB/min. occurred after the establishment of social organization. This is in agreement with the proposed functional significance of tail beating discussed earlier.

These results indicate that the formation of a social structure did not result in significant increases or decreases in the level of agonistic behavior with the lone exception of TB/min. Simple effects of the formation of social organization were present, however, with most acts being performed more frequently after the establishment of a social order than prior to this time. These increases in agonistic behavior were due to the dominant member or members of each group, for the single dominant individual in seven of the hierarchy groups performed from 61% to 96% of the total agonistic activity that occurred after the formation of the dominance hierarchy, and the top dominant member of the straight-line hierarchy groups performed 82% of all agonistic activity while the territory holders in the remaining two groups performed a combined 96% of all activity.

The matrices for the frequency distribution of intra-individual two-act sequences of behavioral acts before and after the establishment of a social organization are presented in Table XXI and XXII respectively. The distribution of all following acts was found to differ significantly (chi-square = 89.08, $P < .001$) between these two time periods, suggesting that the sequencing of acts performed by the same individual was affected by the establishment of a social structure of some kind.

Following acts which are considered "directive" or "inhibitive" are listed in Table XXIII. Since the intra-individual sequencing of acts for the four-fish groups represents all two-act sequences regardless of the rank of the fish performing them, the interpretation of the significance of which acts were "directive" or "inhibitive" must be made relative to the general sequencing of acts of all group members rather than the sequencing of acts for dominants and subordinates. Table XXIII illustrates that similar patterns of sequencing of following acts before and after the formation of a social structure occurred following AP and CH, i.e. if one of these acts was "directive" or "inhibitive" toward a given following act before social organization it exhibited the same pattern after the establishment of a social structure. The likelihood that certain acts would follow a FE, OP, TB, or BT, however, changed with the formation of dominance relationships in the groups of four fish.

Table XXIII provides a further indication that the acts OP, BT, and CH are behaviorally linked as they were in the two-fish groups. Again, this may account for the increase in the frequency of occurrence for these three acts following the formation of a social structure of some kind.

TABLE XXI

OBSERVED AND EXPECTED FREQUENCY DISTRIBUTION OF 1733 INTRA-INDIVIDUAL TWO-ACT SEQUENCES IN TEN GROUPS OF FOUR FISH BEFORE DOMINANCE ESTABLISHMENT

	Following Act					
Initial Act	FE	OP	TB	BT	CH	Total
Approach (AP)	469 (191)	63 (183)	26 (74)	26 (64)	42 (113)	626
Fin Erection (FE)	2 (137)	236 (131)	125 (53)	22 (46)	62 (81)	447
Opercle Spread (OP)	27 (102)	84 (97)	26 (39)	38 (34)	157 (60)	332
Tail Beat (TB)	14 (23)	23 (22)	13 (9)	10 (8)	16 (14)	76
Bite (BT)	4 (36)	24 (35)	4 (14)	50 (12)	36 (21)	118
Chase (CH)	14 (41)	78 (39)	11 (16)	31 (14)	0 (24)	134
TOTAL	530	508	205	177	313	1733

TABLE XXII

OBSERVED AND EXPECTED FREQUENCY DISTRIBUTION OF 2115 INTRA-INDIVIDUAL TWO-ACT SEQUENCES IN TEN GROUPS OF FOUR FISH AFTER DOMINANCE ESTABLISMENT

	Following Act					
Initial Act	FE	OP	TB	BT	CH	Total
Approach	416	179	26	42	140	803
(AP)	(184)	(287)	(47)	(105)	(179)	
Fin Erection	3	189	37	38	95	362
(FE)	(83)	(130)	(21)	(47)	(81)	
Opercle Spread	31	175	33	58	172	469
(OP)	(108)	(168)	(27)	(61)	(105)	
Tail Beat	14	19	12	9	23	77
(TB)	(18)	(28)	(4)	(10)	(17)	
Bite	5	42	6	82	42	177
(BT)	(41)	(63)	(10)	(23)	(40)	
Chase	16	153	9	49	0	227
(CH)	(52)	(81)	(13)	(30)	(51)	
TOTAL	485	757	123	278	472	2115

TABLE XXIII

ANALYSIS OF INTRA-INDIVIDUAL TWO-ACT SEQUENCES BEFORE AND AFTER DOMINANCE ESTABLISHMENT IN TEN GROUPS OF FOUR *L. HUMILIS*

Act	Time of Dominance Establishment	Category Directive	Inhibitive
AP	Before	FE	OP, TB, BT, CH
	After	FE	OP, TB, BT, CH
FE	Before	OP, TB	FE, BT, CH
	After	OP, TB	FE
OP	Before	CH	FE, TB
	After	CH	FE
TB	Before		
	After	TB	
BT	Before	BT, CH	FE, TB
	After	BT	FE, OP
CH	Before	OP, BT	FE
	After	OP, BT	FE

Since AP was "directive" toward a FE in the four-fish groups as it was in the two-fish groups (Table XVI), the decrease in AP frequency after dominance relationships were established in the four-fish groups (Table XX) probably accounts for the decrease in FE frequency as well. Also note that all acts except AP and TB were "inhibitive" toward FE (Table XXIII) in the four-fish groups which may account for some of the decrease in FE frequency in these groups.

Tables XXIV and XXV contain the matrices for the inter-individual two-act sequencing of behavior in the four-fish groups before and after dominance establishment. As with the intra-individual matrices, the distribution of all following acts before the establishment of a social structure differed significantly (chi-square = 178.06, $P < .001$) from the distribution of all following acts after dominance establishment. The distribution of acts given in response to acts performed by a different fish, then differed significantly relative to the formation of a social organization of some kind.

The categories "directive" and "inhibitive" (Table XXVI) for inter-sequencing of acts for the four-fish groups must be interpretated in terms of the sequencing of acts between different fish regardless of the rank of the individual involved; however, comparison of the acts listed under these categories for the four-fish groups with those of subordinate individuals in the two-fish groups (Table XIX) indicates that the responses AV and DN were probably made by lower ranking members of the group. This possibility was checked for one of the four-fish groups with the result that the dominant or highest ranking member of the group performed no AV and only one DN out of 59 AV and DN responses which occurred in this group during the entire hour.

TABLE XXIV

OBSERVED AND EXPECTED FREQUENCY DISTRIBUTION OF 1356 INTER-INDIVIDUAL TWO-ACT SEQUENCES IN TEN GROUPS OF FOUR FISH BEFORE DOMINANCE ESTABLISHMENT

	Following Act							
Initial Act	FE	OP	TB	BT	CH	AV	DN	Total
Approach	311	7	16	0	0	17	29	380
(AP)	(160)	(12)	(31)	(12)	(2)	(18)	(146)	
Fin Erection	147	8	29	6	3	13	99	305
(FE)	(127)	(10)	(25)	(10)	(2)	(14)	(117)	
Opercle Spread	43	17	8	4	1	17	150	240
(OP)	(100)	(8)	(19)	(8)	(1)	(11)	(92)	
Tail Beat	56	4	51	10	2	2	57	182
(TB)	(76)	(6)	(15)	(6)	(1)	(9)	(70)	
Bite	4	7	5	23	2	4	63	108
(BT)	(45)	(3)	(9)	(3)	(.6)	(5)	(42)	
Chase	6	0	1	0	0	11	123	141
(CH)	(59)	(4)	(11)	(4)	(.8)	(7)	(54)	
TOTAL	567	43	110	43	8	64	521	1356

TABLE XXV

OBSERVED AND EXPECTED FREQUENCY DISTRIBUTION OF 1310 INTER-INDIVIDUAL TWO-ACT SEQUENCES IN TEN GROUPS OF FOUR FISH AFTER DOMINANCE ESTABLISHMENT

	Following Act							
Initial Act	FE	OP	TB	BT	CH	AV	DN	Total
Approach	134	16	5	0	3	32	24	214
(AP)	(44)	(15)	(18)	(7)	(3)	(16)	(110)	
Fin Erection	74	17	15	2	15	40	108	271
(FE)	(56)	(19)	(23)	(8)	(5)	(20)	(7)	
Opercle Spread	32	48	19	1	1	17	215	333
(OP)	(69)	(23)	(28)	(1)	(6)	(25)	(171)	
Tail Beat	19	9	63	9	3	1	18	122
(TB)	(25)	(9)	(10)	(4)	(2)	(9)	(63)	
Bite	3	2	7	29	1	4	84	130
(BT)	(27)	(9)	(11)	(4)	(2)	(10)	(67)	
Chase	9	0	3	0	0	3	225	240
(CH)	(50)	(17)	(21)	(8)	(4)	(18)	(123)	
TOTAL	271	92	112	41	23	97	674	1310

TABLE XXVI

ANALYSIS OF INTER-INDIVIDUAL TWO-ACT SEQUENCES BEFORE AND AFTER DOMINANCE ESTABLISHMENT IN TEN GROUPS OF FOUR *L. HUMILIS*

Act	Time of Dominance Establishment	Category Directive	 Inhibitive
AP	Before	FE	TB, BT, DN
	After	FE, AV	TB, BT, DN
FE	Before		
	After	FE, CH, AV	BT, DN
OP	Before	OP, DN	FE, TB
	After	OP, DN	FE, CH, BT
TB	Before	TB	FE, AV
	After	TB, BT	AV, DN
BT	Before	BT, DN	FE
	After	BT, DN	FE, OP
CH	Before	DN	FE, TB, OP, BT
	After	DN	FE, OP, TB, BT, CH, AV

"Directive" responses to AP or CH by another individual were similar for groups of two and four fish (Table XIX and XXVI), but a similar pattern between the two group sizes for "inhibitive" responses to a given initial act did not occur. This undoubtedly was due to the increased complexity of dominance relationships as group size increased.

One interesting result of the inter-sequencing analysis of the four-fish groups was the fact that the performance of an OP, TB, or BT by one individual was "directive" toward the performance of the same act by the other interacting group member, and that this tendency did not differ relative to the formation of dominance relationships. This would imply that pairs of fairly equally ranked individuals are present which produce inter-individual sequences not characteristic of groups of only two fish in which dominance relationships were more stable.

Effects of the Type of Social Organization on Agonistic Behavior

To determine if any relationships existed between the frequency of occurrence or sequencing of agonistic behavior and the type of social organization formed, only groups which exhibited either territoriality or a hierarchical social order by the end of the first hour of group existence were used. Six groups exhibited territoriality as the primary type of social organization and the frequency of behavioral acts performed during the hour for these groups was compared to that of six groups which formed dominance hierarchies during the first hour. The groups were selected in such a way that paired observations occurred, i.e. each territorial group was paired with a hierarchical group from the same treatment combination so that differences in experimental parameters would not affect the results of the analysis. Frequency measures were calculated on an act per fish basis since groups from both the four and six-fish group sizes were used and no significant main effects of group size were found between these two group sizes for acts per fish measures (Table VII). Also, since most significant effects of experimental parameters were on the absolute measures of agonistic behavior, the use of per fish measures should result in more meaningful differences in agonistic behavior relative to the type of social organization formed.

Analysis of the possible relationships between the sequencing of agonistic behavior and the type of social organization exhibited were accomplished by constructing matrices of intra-individual and inter-individual two-act sequences of behavior as before.

Differences in Agonistic Acts Relative to the Type of Social Organization

The number of acts per fish which occurred in the six pairs of observations are included in Table XXVII. Wilcoxon's signed-rank tests (Bradley, 1968:96) were performed on the data for each act as well as the total acts/fish values. No signficant differences were found between hierarchy groups and territorial groups for the measures AP/F, BT/F, CH/F, and TOTAL/F. The number of FE/F was significantly greater for the hierarchy groups than for the territorial groups (P = .0313, one-tailed) which is an indication that groups of these fish exhibited more FE/F when the social order established during the first hour was a dominance hierarchy rather than a dominance order in which two or more

TABLE XXVII

ACT FREQUENCY PER FISH FOR SIX TERRITORY AND SIX HIERARCY GROUPS OF *L. HUMILIS*

Treatment	Rep	Social Order	Number of Acts per Fish						
			AP	FE	OP	TB	BT	CH	Total
410	1	Territory	67.2	7.0	66.5	22.3	27.3	16.5	206.8
	2	Hierarchy	56.0	43.8	23.3	9.7	46.0	39.5	218.3
411	1	Territory	42.5	33.0	45.7	25.7	16.3	13.0	176.0
	2	Hierarchy	47.5	58.3	5.5	6.7	3.7	9.7	131.5
600	1	Territory	86.8	44.5	46.8	12.8	43.8	41.7	276.5
	2	Hierarchy	63.5	71.5	1.8	4.0	10.8	19.8	171.5
601	1	Territory	49.8	3.8	55.8	11.0	14.0	10.8	145.3
	3	Hierarchy	54.2	70.0	12.5	11.7	3.7	13.3	165.3
610	1	Territory	51.3	41.5	20.0	7.5	5.7	15.3	141.3
	3	Hierarchy	41.7	40.8	2.8	6.2	4.0	11.8	107.3
611	1	Territory	58.7	36.8	29.3	15.5	10.5	24.5	175.3
	2	Hierarchy	45.7	61.7	7.2	9.0	0.3	4.0	127.8

fish established territories. Analysis of OP/F and TB/F revealed the opposite trend; groups of fish in the territorial situation exhibited a significantly greater number of OP/F (P = 0.0156, one-tailed) and TB/F (P = .0313, one-tailed) than did fish which established dominance hierarchies. These results show that the type of social organization formed during the first hour of group existence significantly affected the level of occurrence of three acts, even when these acts were measured on a per fish basis.

Observed and expected values for the intra-individual two-act sequencing of behavior of the six hierarchical and six territorial groups are given in Table XXVIII and XXIX, respectively. The total number of sequences for the two types of social organization was fairly similar although the distribution of acts was not. The distribution of all following acts (row totals) for Tables XXVIII and XXIX was found to differ significantly (chi-square = 447.29; $P < .001$) and examination of the contributions made to chi-square by FE or OP as following acts reveals that either one by itself was sufficiently large to result in a significant difference at the .001 level. Thus the major difference in the intra-individual sequencing of behavioral acts between hierarchical and territorial groups was primarily due to the distribution of FE and/or OP as following acts. Differences between observed and expected values (Table XXX) indicate that several differences in the distribution of these two acts occurred. For example, an AP was "directive" toward an OP in the territorial groups but was "inhibitive" toward an OP in the hierarchical groups. This means that in the territorial situation there was a frequent occurrence of the intra-sequence AP → OP performed by the same fish while the performance of an

TABLE XXVIII

OBSERVED AND EXPECTED FREQUENCY DISTRIBUTION OF 2110 INTRA-INDIVIDUAL TWO-ACT SEQUENCES IN SIX DOMINANCE HIERARCHY GROUPS OF *L. HUMILIS*

	Following Act					
Initial Act	FE	OP	TB	BT	CH	Total
Approach	819	14	10	56	100	999
(AP)	(352)	(119)	(85)	(142)	(223)	
Fin Erection	2	175	139	84	208	608
(FE)	(261)	(73)	(52)	(86)	(136)	
Opercle Spread	11	8	17	22	67	125
(OP)	(54)	(15)	(11)	(18)	(28)	
Tail Beat	17	16	5	7	27	72
(TB)	(31)	(9)	(6)	(10)	(16)	
Bite	22	10	2	65	69	168
(BT)	(72)	(20)	(14)	(24)	(38)	
Chase	37	29	7	65	0	138
(CH)	(59)	(16)	(12)	(20)	(31)	
TOTAL	908	252	180	299	471	2110

TABLE XXIX

OBSERVED AND EXPECTED FREQUENCY DISTRIBUTION OF 2891 INTRA-INDIVIDUAL TWO-ACT SEQUENCES IN SIX TERRITORIAL GROUPS OF <u>L</u>. <u>HUMILIS</u>

Initial Act	Following Act FE	 OP	 TB	 BT	 CH	Total
Approach (AP)	218 (223)	588 (455)	97 (117)	125 (212)	226 (247)	1254
Fin Erection (FE)	2 (50)	105 (101)	79 (26)	44 (47)	49 (55)	279
Opercle Spread (OP)	179 (116)	130 (237)	48 (61)	102 (110)	193 (128)	652
Tail Beat (TB)	55 (30)	28 (62)	19 (16)	35 (29)	33 (33)	170
Bite (BT)	17 (46)	66 (94)	14 (24)	93 (44)	68 (51)	258
Chase (CH)	44 (50)	133 (101)	12 (26)	89 (47)	0 (55)	278
TOTAL	515	1050	269	488	569	2891

TABLE XXX

ANALYSIS OF INTRA-INDIVIDUAL TWO-ACT SEQUENCES FOR TWO TYPES OF SOCIAL ORGANIZATION

Act	Type of Social Order	Category	
		Directive	Inhibitive
AP	Territory	OP	BT
	Hierarchy	FE	OP, TB, BT, CH
FE	Territory	TB	FE
	Hierarchy	OP, TB, CH	FE
OP	Territory	FE, CH	OP
	Hierarchy	CH	FE
TB	Territory	FE	OP
	Hierarchy	OP, CH	FE
BT	Territory	BT, CH	FE, OP, TB
	Hierarchy	BT, CH	FE, OP, TB
CH	Territory	OP, BT	TB
	Hierarchy	OP, BT	FE

AP by a fish in the hierarchical situation would not likely be followed by an OP (out of 999 acts which immediately followed an AP in the hierarchical groups, the sequence AP - OP was only recorded 14 times). This does not imply that the sequence AP - FE did not occur often in the territorial groups but only that its occurrence was close to that expected if the sequencing of behavioral acts were determined by chance alone.

In the light of the findings of differences for FE, OP, and TB between the two types of social organization it was not surprising to find that the sequencing of these acts was responsible for most of the differences in "directive" and "inhibitive" acts. Notice in Table XXX that fairly similar patterns occur for BT and CH as following acts regardless of the social order, while most of the differences involve OP, TB, and FE. The likelihood of an OP following a TB was opposite for territorial groups and hierarchy groups as was the sequence TB - FE. The intra-sequencing of OP, BT, and CH for both territorial and hierarchical groups appeared to follow a pattern similar to that found for groups of two and four fish discussed earlier.

The frequency distributions of inter-individual two-act sequences for hierarchical and territorial groups are recorded in Table XXXI and XXXII, respectively. As with intra-individual sequencing, the average distribution of all following acts differed significantly (chi-square = 970.77; $P < .001$) between the two types of social organization. Inspection of the contributions made to chi-square by the following acts reveals, however, that the distribution of any act as a following act was more than sufficient to result in a significant difference between the two types of social organization. This means that the

TABLE XXXI

OBSERVED AND EXPECTED FREQUENCY DISTRIBUTION OF 1901 INTER-INDIVIDUAL TWO-ACT SEQUENCES IN SIX DOMINANCE HIERARCHY GROUPS OF *L. HUMILIS*

	Following Act							
Initial Act	FE	OP	TB	BT	CH	AV	DN	Total
Approach	565	1	5	0	4	32	10	617
(AP)	(305	(3)	(23)	(3)	(5)	(52)	(227)	
Fin Erection	278	5	29	4	8	103	213	640
(FE)	(316)	(3)	(24)	(3)	(5)	(54)	(236)	
Opercle Spread	41	1	1	0	1	8	64	116
(OP)	(57)	(.5)	(4)	(.5)	(.9)	(10)	(43)	
Tail Beat	45	2	32	1	1	11	28	120
(TB)	(59)	(.6)	(4)	(.5)	(.9)	(10)	(44)	
Bite	3	0	3	3	0	3	120	132
(BT)	(65)	(.6)	(5)	(.5)	(1)	(11)	(49)	
Chase	8	0	0	0	0	2	266	276
(CH)	(136)	(1)	(10)	(1)	(2)	(23)	(102)	
TOTAL	940	9	70	8	14	159	701	1901

TABLE XXXII

OBSERVED AND EXPECTED FREQUENCY DISTRIBUTION OF 2290 INTER-INDIVIDUAL TWO-ACT SEQUENCES IN SIX TERRITORIAL GROUPS OF *L. HUMILIS*

	Following Act							
Initial Act	FE	OP	TB	BT	CH	AV	DN	Total
Approach	177	83	22	7	43	15	124	471
(AP)	(82)	(53)	(42)	(22)	(15)	(8)	(249)	
Fin Erection	112	32	31	15	8	10	184	392
(FE)	(68)	(44)	(35)	(18)	(13)	(7)	(207)	
Opercle Spread	47	109	31	5	10	7	365	574
(OP)	(100)	(64)	(51)	(27)	(19)	(10)	(303)	
Tail Beat	43	20	96	16	6	2	72	255
(TB)	(46)	(29)	(22)	(12)	(8)	(4)	(135)	
Bite	8	11	17	62	7	5	180	290
(BT)	(51)	(33)	(26)	(14)	(9)	(5)	(153)	
Chase	13	2	5	2	0	0	286	308
(CH)	(54)	(35)	(27)	(14)	(10)	(5)	(163)	
TOTAL	400	257	202	107	74	39	1211	2290

responses given by one fish to the behavior of another differed considerably between the two types of social organization. This is reflected in the occurrence of the "directive" and "inhibitive" responses made by fish in the different social orders (Table XXXIII). An interesting result of this analysis occurred for "directive" responses in the territorial groups. The abundance of "directive" acts which occurred after an AP was not found in any of the previously examined inter-individual sequencing (Tables XIX and XXVI), nor was it found in the responses made by fish in the hierarchical situations. This is probably a direct result of interactions between territory holders in these groups; subordinate individuals would not likely CH after being approached by another fish, yet the AP or intrusion of a fish into another's territory would probably result in an immediate CH by the territorial fish. Also, the intrusion of one fish into another's territory would probably lead to an OP or FE.

The measures INTRA/F and INTER/F were used to determine if the type of social organization formed during the first hour of group existence affected the number of the two types of sequences which occurred. Also, the entropy measures, H(INTRA) and H(INTER), were used for the same purpose.

The results of this analysis indicated that neither H(INTRA) nor H(INTER) differed significantly between groups of hierarchical or territorial fish. Likewise, INTRA/F did not differ between the two types of social organization formed. However, the number of INTER/F differed significantly between the two types of social organization formed. Groups which established territorial dominance during the first hour of group existence exhibited a significantly greater number of

TABLE XXXIII

ANALYSIS OF INTER-INDIVIDUAL TWO-ACT SEQUENCES FOR TWO TYPES OF SOCIAL ORGANIZATION

Act	Type of Social Order	Category	
		Directive	Inhibitive
AP	Territory	FE, OP, CH, AV	TB, BT, DN
	Hierarchy	FE	TB, AV, DN
FE	Territory	FE	
	Hierarchy	AV	FE
OP	Territory	OP, DN	FE, TB, BT, CH
	Hierarchy	DN	FE
TB	Territory	TB	DN
	Hierarchy	TB	DN
BT	Territory	BT, DN	FE, OP
	Hierarchy	DN	FE, AV
CH	Territory	DN	FE, OP, TB, CH, AV
	Hierarchy	DN	FE, TB, AV

inter-individual sequences per fish than did groups of fish in the hierarchical dominance type of social organization (Wilcoxon's signed-rank test, one-tailed; $P < .0469$). This means that the overall patterning of behavioral acts for territorial groups consisted of significantly more sequences which were interrupted by responses to acts initiated by a different individual than were the hierarchical groups. This also suggests that the behavior of fish in the hierarchical dominance groups tended more toward intra-sequencing than toward inter-sequencing of acts. Data for hierarchical groups in Table XXXIII also gives this same impression as does that from column totals in Table XXXI.

CHAPTER VI

DISCUSSION

To some degree, three relationships have been shown to exist in the present study:

1. The experimental parameters influenced the frequency of occurrence of agonistic acts, the sequencing of these acts, and the type and stability of social organization formed and maintained by groups of *L. humilis*;

2. The establishment of dominance relationships influenced the frequency of occurrence of certain behavioral acts as well as the sequencing of these acts;

3. The type of initial social organization formed influenced both the frequency of occurrence of certain acts and the sequencing of behavioral acts.

In the discussion which follows, an attempt is made to evaluate the interdependence of the three relationships listed above. This is accomplished by identifying common patterns of behavior which occurred in the groups of *L. humilis* analyzed, and relating these patterns to the effects of the experimental parameters and social organization.

Patterns of Behavior

In order to identify common patterns of behavior in the groups of *L. humilis* studied, each of the six original behavioral acts (AP, FE, OP, TB, BT, and CH) has been separately listed in Tables XXXIV through XXXIX, respectively. Each table includes a summary of the effects of the experimental parameters and social organization on the frequency of occurrence of these acts as well as significant "directive" and "inhibitive" intra- and inter-sequences involving each act.

Tables XXXIV through XXXIX show that certain patterns or sequences of behavioral acts are common in the groups examined regardless of which experimental conditions prevailed. The common patterns for "directive" intra- and inter-individual two-act sequences of agonistic acts are summarized in Figures 6 and 7, respectively. From these two illustrations some of the possible relationships between act frequency and act sequencing may be inferred. An AP was directive toward a FE in both the intra- and inter-sequencing of behavior. This would suggest that FE frequency should be of approximately the same magnitude as AP frequency, and that the effects of the experimental parameters conducive to crowding should be similar for these two acts.. Inspection of Table VI shows that FE frequency and AP frequency did exhibit similar levels of occurrence, with groups of two fish actually performing more FE than AP while the reverse was true for the four- and six-fish groups. Since intra-sequencing for territorial groups did not exhibit the "directive" sequence AP - FE, and since groups of six fish had a tendency to initially form territories (Table VIII) this may partially explain the reduction in FE frequency for the six-fish group size and to a lesser extent, for the four-fish groups as well. Both AP and FE were significantly affected by the group size parameter (Table V) and in the same manner (Table VII). The measures AP/F and FE/F were also affected by the group size parameter in the same way

TABLE XXXIV

A SUMMARY OF SIGNIFICANT EFFECTS OF EXPERIMENTAL PARAMETERS AND SOCIAL ORGANIZATION ON AP

Experimental Parameters

Group Size: AP $2 < 4 < 6$
AP/F $2 < 4$; $2 < 6$

Tank Size: AP small > large
AP/F small > large
AP/O small > large

Group Characteristics	Sequencing			
	Intra-sequencing		Inter-sequencing	
	Directive	Inhibitive	Directive	Inhibitive
Two Fish Before Dominance Establishment	AP → FE	AP → OP AP → TB AP → BT AP → CH	AP → FE	AP → TB AP → DN
Two Fish After Dominance Establishment	AP → FE	AP → OP AP → TB AP → BT AP → CH	AP → FE AP → AV	
Four Fish Before Dominance Establishment	AP → FE	AP → OP AP → TB AP → BT AP → CH	AP → FE	AP → TB AP → BT AP → DN
Four Fish After Dominance Establishment	AP → FE	AP → OP AP → TB AP → BT AP → CH	AP → FE AP → AV	AP → TB AP → BT AP → DN
Hierarchy Groups	AP → FE	AP → OP AP → TB AP → BT AP → CH	AP → FE	AP → TB AP → AV AP → DN
Territory Groups	AP → OP	AP → BT	AP → FE AP → OP AP → CH AP → AP	AP → TB AP → BT AP → DN

TABLE XXXV

A SUMMARY OF SIGNIFICANT EFFECTS OF EXPERIMENTAL PARAMETERS AND SOCIAL ORGANIZATION ON FE

Experimental Parameters

Group Size: FE $2 < 4 < 6$ Fish Size x Tank Size: FE/BOUT
FE/F $2 < 4$; $2 < 6$
Social Structure: FE/F greater for hierarchy groups than territory groups.

	Sequencing			
	Intra-sequencing		Inter-sequencing	
Group Characteristics	Directive	Inhibitive	Directive	Inhibitive
Two Fish Before Dominance Establishment	FE → TB	FE → FE	FE ↔ FE	FE → DN
Two Fish After Dominance Establishment	FE → TB	FE → FE	FE ↔ FE	FE → TB
Four Fish Before Dominance Establishment	FE → TB	↗ FE FE ↔ BT ⤡ CH		
Four Fish After Dominance Establishment	FE → TB	FE → FE	⤢ FE FE → AV ↘ CH	⤢ BT FE ↘ DN
Hierarchy Groups	FE → TB	FE → FE	FE → AV	FE ↔ FE
Territory Groups	FE ↔ TB	FE → FE	FE ↔ FE	FE ↔ OP

TABLE XXXVI

A SUMMARY OF SIGNIFICANT EFFECTS OF EXPERIMENTAL PARAMETERS AND SOCIAL ORGANIZATION ON OP

Experimental Parameters

Group Size: OP $2<4$; $2<6$
OP/F $2<4$
Social Structure: OP/F greater in Territory Groups than in Hierarchy groups

Group Characteristics	Sequencing Intra-sequencing Directive	 Inhibitive	 Inter-sequencing Directive	 Inhibitive
Two Fish Before Dominance Establishment	OP ↔ CH	OP → FE	OP ↗ AV OP ↘ DN	OP → FE
Two Fish After Dominance Establishment	OP ⤢ OP OP ⤡ CH	OP → FE	OP → DN	
Four Fish Before Dominance Establishment	OP ↔ CH	OP ↗ FE OP ↘ TB	OP ⤢ OP OP ↘ DN	OP ↗ FE OP ↘ TB
Four Fish After Dominance Establishment	OP ↔ CH	OP → FE	OP ⤢ OP OP ↘ DN	OP ↗ FE OP → CH OP ⤡ BT
Hierarchy Groups	OP ↔ CH	OP → FE	OP → DN	OP → FE
Territory Groups	OP ⤢ CH OP ↘ FE	OP → OP	OP ⤢ OP OP ↘ DN	OP ⤢ FE OP ↗ TB OP ⤡ BT OP ↘ CH

TABLE XXXVII

A SUMMARY OF SIGNIFICANT EFFECTS OF EXPERIMENTAL PARAMETERS AND SOCIAL ORGANIZATION ON TB

Experimental Parameters

Group Size: TB $2 < 4$; $2 < 6$
Group Size x Tank Size: TB/O and TB/BOUT

Social Structure: TB/F greater for territory groups than for hierarchy groups.
TB/min. in four-fish groups decreased after dominance establishment.

Group Characteristics	Sequencing			
	Intra-sequencing		Inter-sequencing	
	Directive	Inhibitive	Directive	Inhibitive
Two Fish Before Dominance Establishment			TB↔TB	TB→FE
Two Fish After Dominance Establishment	⤢TB TB ↘CH	TB→FE	TB→AV	
Four Fish Before Dominance Establishment			TB↔TB	TB→FE
Four Fish After Dominance Establishment	TB↔TB		⤢TB TB ↘BT	TB→DN
Hierarchy Groups	↗OP TB ↘CH	TB→FE	TB↔TB	TB→DN
Territory Groups	TB↔FE	TB→DN	TB↔TB	TB→DN

TABLE XXXVIII

A SUMMARY OF SIGNIFICANT EFFECTS OF EXPERIMENTAL PARAMETERS AND SOCIAL ORGANIZATION ON BT

Experimental Parameters

Group Size x Fish Size: BT

Group Characteristics	Sequencing			
	Intra-sequencing		Inter-sequencing	
	Directive	Inhibitive	Directive	Inhibitive
Two Fish Before Dominance Establishment	BT↔BT	BT→FE	BT→DN	BT→FE
Two Fish After Dominance Establishment	BT⤢BT BT⤡CH	BT→FE		
Four Fish Before Dominance Establishment	BT⤢BT BT⤡CH	BT⤢FE BT↘TB	BT⤢BT BT↘DN	BT→FE
Four Fish After Dominance Establishment	BT↔BT	BT↗FE BT↘OP	BT⤢BT BT↘DN	BT⤢FE BT⤡OP
Hierarchy Groups	BT⤢BT BT⤡CH	BT↗FE BT→OP BT↘TB	BT→DN	BT↗AV BT↘FE
Territory Groups	BT⤢BT BT⤡CH	BT↗FE BT→TB BT↘OP	BT⤢BT BT↘DN	BT↗FE BT↘OP

TABLE XXXIX

A SUMMARY OF SIGNIFICANT EFFECTS OF EXPERIMENTAL PARAMETERS AND SOCIAL ORGANIZATION ON CH

Experimental Parameters

Group Size: CH $2<4$; $2<6$

	Sequencing			
	Intra-sequencing		Inter-sequencing	
Group Characteristics	Directive	Inhibitive	Directive	Inhibitive
Two Fish Before Dominance Establishment	CH↔OP		CH→DN	CH→FE
Two Fish After Dominance Establishment	CH↔OP CH↔BT	CH→FE CH→TB	CH→DN	CH→AV
Four Fish Before Dominance Establishment	CH↔OP CH↔BT	CH↔FE	CH→DN	CH→FE CH→OP CH→TB CH→BT
Four Fish After Dominance Establishment	CH↔OP CH→BT	CH→FE	CH→DN	CH→FE CH→OP CH→TB CH→BT CH→AV CH↔CH
Hierarchy Groups	CH↔OP CH↔BT	CH→FE	CH→DN	CH→FE CH→TB CH→AV
Territory Groups	CH↔OP CH↔BT	CH→TB	CH→DN	CH→FE CH→OP CH→TB CH→AV CH↔CH

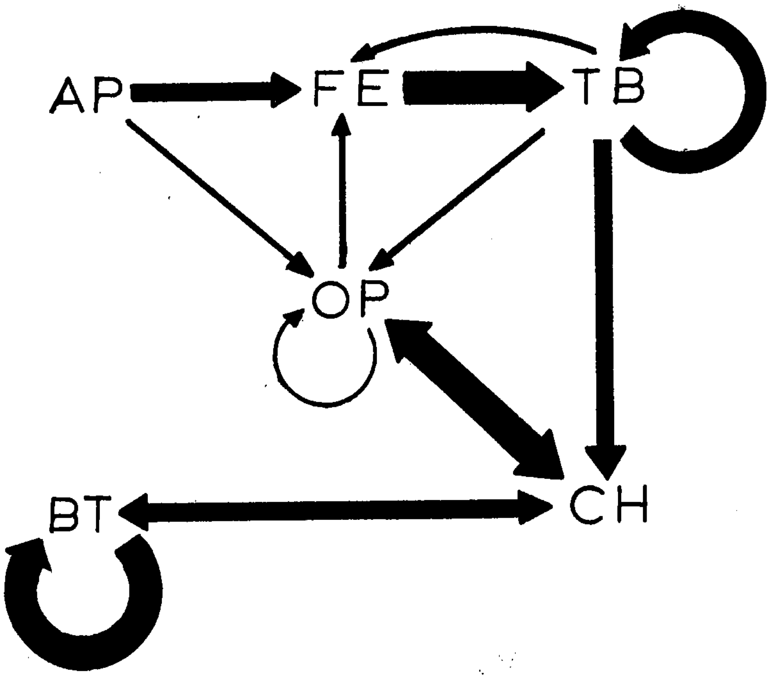


Figure 6. "Directive" intra-individual two-act sequences (widest lines represent intra-sequences common to all groups tested; medium-width lines represent sequences common to more than one group; narrowest lines represent a sequence which occurred in only one group)

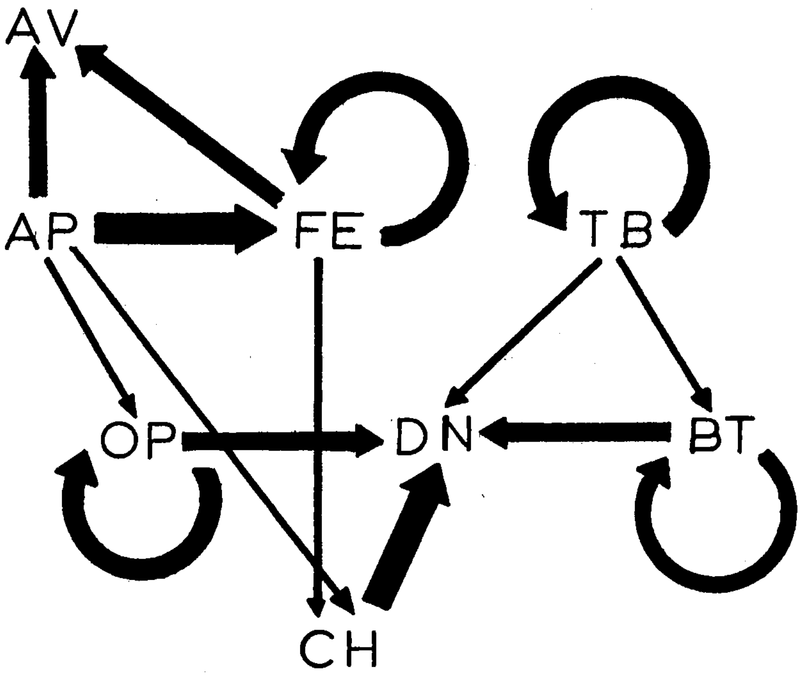


Figure 7. "Directive" inter-individual two-act sequences (widest lines represent inter-sequences common to all groups tested; medium-width lines represent sequences common to more than one group; narrowest lines represent a sequence which occurred in only one group)

(Table VII).

The effects of tank size were significant for AP, AP/F, and AP/O while main effects of tank size were not present for any of the FE variables (Table X). Groups of fish in small tanks did perform more FE (3742) than did groups in the large tanks (2865), however, the difference was not statistically significant.

Relationships between OP frequency and sequencing and the effects of crowding are more difficult to define. Opercle Spread was the only act to decrease in frequency as group size increased (Table VI), yet territorial groups which consisted of larger group sizes performed more OP/F than did the hierarchy groups. Opercle Spread was also found to be behaviorally linked with CH in the "directive" intra-sequencing of behavior of all groups tested (Table XXXVI). These two results indicate that the level of occurrence of OP was related to the type of social organization initially formed and to the level of occurrence of another act. Opercle Spread exhibited the same main effects of group size as CH although the means for these two acts differed in direction relative to groups of four and six fish (Table VII). The several "directive" intra-sequences involving OP also indicate the effects of dominance formation or social organization formation on the frequency of occurrence of this act.

Tail beating frequency might be expected to be much higher than it was (Table VI) since FE was "directive" toward TB in all groups (intra-sequencing, Fig. 6); however, TB was affected by the establishment of dominance relationships in the four-fish groups and by the formation of territorial dominance in four- and six-fish groups (Table XXXVII). Also, TB was the only act performed by dominant members of the two-fish groups which decreased in frequency after dominance establishment (Table XIII). As mentioned in Chapter V, TB may very well function as a test of strength between two fish in which dominance relationships are being decided. These results indicate that TB is closely associated with dominance formation; consequently, the significant effects of the experimental parameters on this act (Tables V and XI) may be confounded to such an extent to make them less meaningful than some of the other variables measured (e.g. AP or FE). This confounding may also be greatly responsible for the significant interaction effects of TB/O and TB/BOUT (Table XI and Figures 3 and 4) for the group size x tank size first-order interaction. In fact, both of these interactions were mainly due to the direction of the TB act in the two-fish group size where TB/O and TB/BOUT decreased in frequency with an increase in tank size. This could possibly be due to the fact that fish in the smaller tanks took longer to establish dominance relationships which would tend to increase TB frequency. Actually, dominance relationships were formed earlier in the small tanks than in the large tanks ($\bar{X}$ = 23.3 min. for small tanks; $\bar{X}$ = 40.0 min. for large tanks), but more TB occurred in the small tanks prior to dominance establishment than in the large tanks ($\bar{X}$ = 15.0 for small tanks; $\bar{X}$ = 7.5 for large tanks). Another possible reason for the higher levels of TB for fish in the smaller tanks is that the establishment of dominance relationships in these groups was more intense (more TB) than in the larger tanks. Miller and Miller (1970:62) reported that tail beating ". . . occurs in what are apparently more intense conflict situations than most responses" which would agree with the idea of an increased level of TB in groups of L. humilis in the crowded situation.

The acts BT and CH were shown to be behaviorally linked (intra-sequencing, Fig. 6); however, they did not exhibit similar effects of crowding. Biting increased with increasing group size (Table VI) but not significantly (Table V). A significant interaction effect for BT was present for the group size x fish size interaction (Table XI), however, which probably is sufficient to explain the nonsignificant main effects for BT since BT was so closely related to fish size. Chase frequency exhibited main effects of group size, but no significant difference occurred between the two larger group sizes (Table VIII).

Neither BT or CH frequency was shown to be significantly affected by the formation of dominance relationships or by the establishment of a particular type of social structure; however, the frequency of each act increased after dominance establishment in groups of two and four fish (Tables XII and XX). It was also found that subordinate individuals in the two-fish groups size performed no biting or chasing after they became subordinate (Table XII). That subordinate members of the group tended to exhibit little if any biting behavior was probably responsible for the fact that BT had the lowest frequency of occurrence of the acts recorded (Table VI). Also contributing to the low frequency of biting was the fact that only one act, CH was "directive" toward a BT (except BT itself) when intra-sequencing was considered (Table XLIV and Fig. 6).

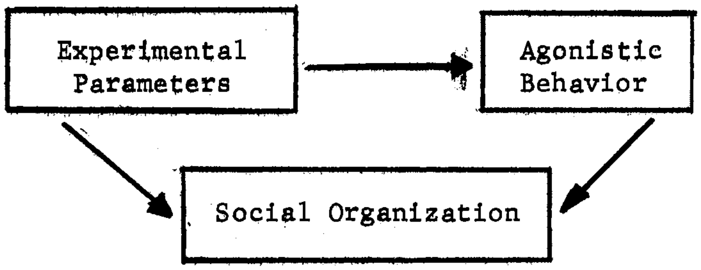
An opercle spread was "directive" toward CH in all groups examined (Fig. 6) and TB was "directive" toward a CH in two groups (Table XXXVII) which probably contributed to the fact that after AP, FE, and OP, CH was the most frequently recorded act during the first hour of group existence.

Very little can be said concerning the significance of "directive" inter-sequencing of behavior and the relationships between these sequences and act frequencies since the acts which form these sequences are performed by different fish. The "directive" inter-sequence AP - FE was found to be "directive" in all groups tested regardless of the experimental conditions involved (Fig. 7). Undoubtedly this sequence contributed to the high level of FE observed in all groups, but especially in the two-fish groups where even after dominance relationships were formed it was by far the most frequent act performed by subordinate individuals (Table XIII).

Changes in inter-sequencing were shown to occur relative to dominance establishment (Chapter V) which would likely affect the frequency of occurrence of some acts. For example, the shift from TB as a "directive" response given to a TB, to AV as the "directive" response following dominance establishment in groups of two fish (Table XIX) would likely contribute to the observed reduction in TB frequency in these groups (Table XII).

A Proposed Model of Social Behavior

Most of the studies of fish behavior mentioned in Chapter I fall into three categories: 1) those which demonstrate that certain relationships exist between experimental (or environmental) parameters and social organization; 2) those which relate various aspects of agonistic behavior to social organization; and 3) those which relate social or environmental conditions of some sort to agonistic behavior. These three relationships can be illustrated by a simple descriptive model such as the following:

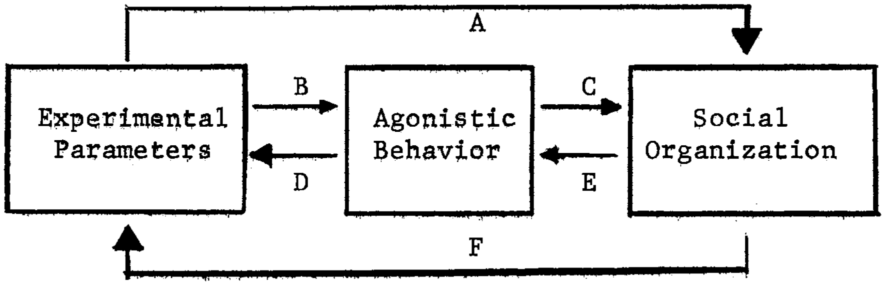


where the arrows represent effects or influences of one component of the model on another component. However, the implication is often made that these effects are direct and unitary, i.e. a certain parameter (such as available space) directly affects the type of social organization formed by a group of fish, and that perhaps this is the only factor responsible for such an effect. Admittedly, this implication is usually present due to the limited scope of a given study. For example, if the only objective of a particular study is to determine whether group size affects the type of social organization formed by a group of fish, and significant results to this effect are found, the implication is often given that group size is the only parameter (or at least the main parameter) which affects social organization and that this effect is direct.

The above model is simplistic and as such fails to take into account at least four important possibilities: 1) the effects of the three components of the model may not be direct effects; 2) the effects may change in time; 3) other relationships or effects are possible, especially reciprocal effects; and 4) the effects of one component may not be the same (either in direction or magnitude) on all other aspects of another component.

It has been demonstrated in the present study that some interdependence is present among the three components of the preceding model.

This interdependence can be considered to be operating in what Crook (1970) refers to as a dynamic social system, i.e. a set of units or components with relationships among the components. This social system for groups of L. humilis is envisioned as having three major components: 1) environmental or experimental parameters; 2) agonistic behavior; and 3) social organization. The following possible relationships exist:



where the arrows represent effects or relationships which are described below in their simplest form.

1. Experimental parameters may have a direct effect on the type of social organization formed (A), or they may exert their effects indirectly through various aspects of agonistic behavior (B) + (C);

2. Agonistic behavior may directly affect the form of social structure exhibited by the group (C);

3. Ongoing agonistic behavior may reduce or increase the effects of various experimental parameters (D);

4. Social organization may directly affect various aspects of agonistic behavior (E); and

5. Social organization may reduce or increase the effects of a given set of experimental parameters either directly (F) or indirectly (E) + (D).

Results of the present study revealed the propensity of groups of L. humilis to establish and defend territories under certain sets of experimental conditions. It was found that group size significantly influenced the type of social organization initially formed (Table VIII) or finally exhibited by these fish (Table IX). Groups of six fish were significantly more territorial throughout the entire study than were groups of two or four fish (Table VII).

The results support the possibility that experimental parameters have an effect on the type of social organization exhibited in these groups, however, they do not reveal whether this effect operates in a direct (A) or indirect way (B) + (C).

The experimental parameters were shown to influence measures of act frequency and act sequencing (Table VII), and significant differences in act frequency of FE/F, OP/F, and TB/F were found between groups which initially established dominance hierarchies versus territorial defense (Chapter V). Significant differences in the intra- and inter-individual sequencing of behavioral acts relative to the type of social organization initially formed were also found (Chapter V). These results indicate that agonistic behavior of groups of these fish differs with the type of social organization they form. It was beyond the scope of this study to determine the trajectory of the causal relationships between these two components of the model, although they are certainly related in some manner.

Changes in act frequency and sequencing also occurred between the time dominance relationships were being established and after they had been established (Chapter V). Whether these changes were responsible for the formation of these relationships or a consequence of this formation was not determined.

The various experimental parameters of this study, or combinations of these parameters, were also found to significantly affect measures of act frequency and act sequencing (Table VII).

In addition, similar patterns of behavior existed in these groups regardless of the experimental parameters involved or the type of social organization formed (Chapter VI). This implies that a certain degree of stability of behavior is present in the agonistic patterns of behavior of these fish. It is not difficult to conceive of these patterns becoming fixed in the behavioral repertoire in the course of the evolution of the species.

CHAPTER VII

SUMMARY

Groups of male orangespotted sunfish (Lepomis humilis) were placed together under 12 different experimental conditions and observed for 20 days. From records of agonistic behavior and social organization the relative effects of group size, fish size, and available space on measures of social organization and agonistic behavior were examined. The results of this investigation are summarized below.

1. Group size significantly influenced 17 of the 42 dependent variables. Ten of these variables were measures of agonistic act frequency, two were measures of act sequencing, and five measures pertained to social organization.

2. No significant main effects of fish size were present in the comparison between entire groups of small fish (66 mm average S.L.) versus entire groups of large fish (76 mm average S.L.).

3. The amount of space available to groups of male L. humilis significantly influenced measures of approach frequency, approach frequency per fish, and approach frequency per opponent.

4. Five significant first-order interactions occurred. Two were for the group size x fish size interaction of bite frequency and duration of the final social order, two for the group size x tank size interaction of tail beat frequency per opponent and mean number of tail beats per bout, and one was the fish size x tank size interaction for

mean number of fin erections per bout.

5. Significant effects of parameters were considered as operating under the general phenomonon of crowding. Increased effects of crowding were brought about by increasing the number of fish per group, increasing the overall size of group members, and by reducing the amount of available space. Most main effects of crowding on frequency measures were reflected by measures of general overall frequency of agonistic activity rather than measures of specific agonistic acts, while interaction effects were present only for measures pertaining to the frequency of specific agonistic acts. Sequencing of agonistic behavior was only affected by crowding at the level of absolute frequency of sequencing variables. Crowding influenced the stability of social organization. Territorial defense prevailed as the fish became more crowded due to an increase in group size, and the social structures of these groups were less stable over time than were social organizations in the smaller group sizes.

6. During the first hour of group existence a clear-cut dominance-subordination relationship existed in 10 of the two-fish groups. Act frequencies per minute did not differ significantly before and after these dominance relationships were established; however, the distribution of acts relative to the rank of the individuals involved changed considerably. Subordinate fish in these groups did not perform any opercle spreads, bites, or chases after dominance-subordination relationships were established. The overall distribution of intra- and inter-individual two-act sequencing of behavior before and after dominance establishment differed significantly. Differences in responses to individual agonistic acts not only changed relative to the

time of dominance establishment, but also changed relative to the rank of the individual involved.

7. After the establishment of some kind of dominance relationships in 10 of the four-fish groups frequency of tail beating per minute decreased significantly. The distribution of intra- and inter-individual two-act sequences of behavior before and after dominance establishment differed significantly in these groups of four fish.

8. Significant differences in fin erections per fish, opercle spreads per fish, and tail beats per fish found between groups which established dominance hierarchies during the first hour and those which exhibited territoriality. Hierarchical and territorial groups also differed significantly in the average distribution of intra- and inter-individual two-act sequences of behavioral acts.

9. The possible relationships among experimental parameters, establishment of dominance relationships, and the establishment of dominance hierarchies or territories were examined. Frequency and sequencing of agonistic behavior were found to be influenced by experimental parameters and also by the formation of social organizations. Regardless of the experimental conditions, or formation of social structures, certain common patterns of act sequencing occurred.

10. The interdependence of aspects of social organization, agonistic behavior, and experimental parameters was considered to represent a social system and a model was presented to describe this interdependence.

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APPENDIXES

APPENDIX A

PROBABILITY LEVELS OF THE F-STATISTICS FOR MEASURES OF AGONISTIC BEHAVIOR AND SOCIAL ORGANIZATION

The 42 measures of agonistic behavior and social organization are described in Chapter III. A list of these variables and their abbreviations is found in Tables III and IV. Appendix A has been arranged so that related variables appear together and includes the following variables:

1. AP
2. AP/F
3. AP/O
4. FE
5. FE/F
6. FE/O
7. FE/BOUT
8. OP
9. OP/F
10. OP/O
11. OP/BOUT
12. TB
13. TB/F
14. TB/O
15. TB/BOUT
16. BT
17. BT/F
18. BT/O
19. BT/BOUT
20. CH
21. CH/F
22. CH/O
23. CH/BOUT
24. TOTAL
25. TOTAL/F
26. TOTAL/O
27. TOTAL/AP
28. INTRA
29. H(INTRA)
30. INTRA/BOUT
31. INTER
32. H(INTER)
33. INTER/BOUT
34. IO
35. FO
36. TIO
37. DIO
38. CIO
39. HD
40. TD
41. TFO
42. DFO

TABLE XL

PROBABILITY LEVELS AND COEFFICIENTS OF VARIATION

Factor or Interaction	Probability Level for Variable:						
	AP	AP/F	AP/O	FE	FE/F	FE/O	FE/BOUT
Group Size	0.0001	0.0006	0.1908	0.0001	0.0205	0.9295	0.0979
Fish Size	0.8471	0.5072	0.0634	0.9203	0.7849	0.7119	0.1836
Tank Size	0.0276	0.0303	0.0373	0.1180	0.1781	0.2802	0.1923
Group x Fish	0.5206	0.5652	0.6029	0.9816	0.9301	0.8775	0.3490
Group x Tank	0.2206	0.5695	0.7988	0.2952	0.3672	0.5789	0.2792
Fish x Tank	0.9271	0.9479	0.8846	0.2625	0.1481	0.1419	0.1457
Group x Fish x Tank	0.8802	0.8895	0.8946	0.6555	0.5584	0.6264	0.5532
C. V.	38.46	36.52	37.00	49.44	43.89	44.14	27.50

TABLE XL

(Continued)

Factor or Interaction	Probability Level for Variable:						
	OP	OP/F	OP/O	OP/BOUT	TB	TB/F	TB/O
Group Size	0.0136	0.0512	0.1778	0.1569	0.0011	0.2428	0.2075
Fish Size	0.3146	0.1184	0.0815	0.1047	0.1904	0.1402	0.1397
Tank Size	0.8089	0.7902	0.8295	0.5695	0.8654	0.5082	0.2198
Group x Fish	0.2692	0.2356	0.2544	0.2398	0.5075	0.5326	0.6034
Group x Tank	0.8249	0.7859	0.8038	0.5488	0.2775	0.0666	0.0229
Fish x Tank	0.5833	0.5535	0.5040	0.5746	0.9517	0.9789	0.8955
Group x Fish x Tank	0.8290	0.8081	0.8310	0.8863	0.7946	0.7575	0.7440
C. V.	99.60	94.90	98.33	85.50	55.77	57.70	59.63

TABLE XL

(Continued)

Factor of Interaction	Probability Level for Variable:						
	TB/BOUT	BT	BT/F	BT/O	BT/BOUT	CH	CH/F
Group Size	0.0469	0.0845	0.5793	0.8538	0.6672	0.0122	0.2509
Fish Size	0.5468	0.7298	0.5689	0.5956	0.6802	0.5574	0.6516
Tank Size	0.6490	0.1412	0.2444	0.6600	0.6660	0.1789	0.2965
Group x Fish	0.5322	0.0430	0.0746	0.1507	0.1091	0.8139	0.7274
Group x Tank	0.0170	0.3649	0.6327	0.7610	0.9511	0.1813	0.5872
Fish x Tank	0.6770	0.8178	0.8227	0.7388	0.5292	0.9563	0.9385
Group x Fish x Tank	0.6353	0.2964	0.3124	0.3493	0.2697	0.7559	0.7420
C. V.	58.63	122.57	122.57	129.59	116.17	98.09	97.70

TABLE XL

(Continued)

Factor or Interaction	Probability Level for Variable:						
	CH/O	CH/BOUT	TOTAL	TOTAL/F	TOTAL/O	TOTAL/AP	INTRA
Group Size	0.7451	0.8338	0.0001	0.0109	0.5340	0.1453	0.0022
Fish Size	0.2693	0.2928	0.5138	0.2373	0.1812	0.3123	0.6283
Tank Size	0.6405	0.5790	0.1282	0.1763	0.2240	0.8663	0.2835
Group x Fish	0.6318	0.8069	0.3315	0.3122	0.3435	0.2320	0.2136
Group x Tank	0.5635	0.5512	0.3070	0.6093	0.7793	0.7751	0.6150
Fish x Tank	0.9820	0.8959	0.8651	0.8383	0.8128	0.3049	0.8672
Group x Fish x Tank	0.7590	0.6676	0.9629	0.9580	0.9487	0.5450	0.8868
C. V.	100.52	86.19	47.60	46.19	48.65	19.40	73.08

TABLE XL

(Continued)

Factor or Interaction	H(INTRA)	INTRA/BOUT	INTER	H(INTER)	INTER/BOUT	IO	FO
	Probability Level for Variable:						
Group Size	0.5069	0.5008	0.0001	0.5554	0.1700	0.0881	0.0652
Fish Size	0.1626	0.1998	0.6993	0.0955	0.9714	0.6572	0.2389
Tank Size	0.5257	0.5126	0.0567	0.1380	0.1810	0.6572	0.2389
Group x Fish	0.3512	0.2232	0.5098	0.6085	0.2647	0.8158	0.6271
Group x Tank	0.9865	0.5567	0.3270	0.5403	0.9724	0.8158	0.2540
Fish x Tank	0.7148	0.5988	0.8063	0.1838	0.5327	0.6572	0.2389
Group x Fish x Tank	0.9179	0.6452	0.9582	0.6430	0.2693	0.8158	0.2540
C. V.	28.28	53.33	38.15	32.49	10.86	30.63	24.45

TABLE XL

(Continued)

Factor or Interaction	Probability Level for Variable:						
	TIO	DIO	CIO	HD	TD	TFO	DFO
Group Size	0.7315	0.0366	0.0004	0.0022	0.0063	0.0211	0.0591
Fish Size	0.0657	0.8983	0.2997	0.7053	0.5166	0.6980	0.6468
Tank Size	0.1744	0.7139	0.5606	0.5760	0.2944	0.6622	0.2237
Group x Fish	0.7569	0.2855	0.3418	0.9488	0.8156	0.1869	0.0224
Group x Tank	0.7406	0.5879	0.2479	0.5494	0.7543	0.9333	0.9181
Fish x Tank	0.1826	0.5639	0.5606	0.3019	0.8065	0.2693	0.8421
Group x Fish x Tank	0.7568	0.3842	0.5434	0.2936	0.1459	0.8738	0.9727
C. V.	28.04	14.49	66.40	90.37	74.95	89.38	51.93

APPENDIX B

TWO-WAY TABLES FOR INTERACTIONS OF THE FACTORIAL EXPERIMENT EXCEEDING THE .05 LEVEL

The following symbols are used in all the tables of Appendix B:

A_0 = Group Size of Two Fish

A_1 = Group Size of Four Fish

A_2 = Group Size of Six Fish

B_0 = Fish Size Small

B_1 = Fish Size Large

C_0 = Tank Size Small

C_1 = Tank Size Large

TABLE XLI

GROUP SIZE AND FISH SIZE INTERACTION FOR BITE FREQUENCY

	A_0	A_1	A_2	$\bar{X}$
B_0	11.12	17.50	82.00	36.89
B_1	16.00	77.00	34.67	42.56
$\bar{X}$	13.59	47.25	58.34	

TABLE XLII

GROUP SIZE AND FISH SIZE INTERACTION FOR DURATION OF THE FINAL SOCIAL ORDER

	A_0	A_1	A_2	$\bar{X}$
B_0	11.0	18.2	7.0	12.07
B_1	15.5	8.8	9.0	11.10
$\bar{X}$	13.25	13.5	8.0	

TABLE XLIII

GROUP SIZE AND TANK SIZE INTERACTION FOR TAIL BEAT FREQUENCY PER OPPONENT

	A_0	A_1	A_2	$\bar{X}$
C_0	24.83	14.94	9.73	16.50
C_1	8.83	17.61	12.07	12.84
$\bar{X}$	16.83	16.28	10.90	

TABLE XLIV

GROUP SIZE AND TANK SIZE INTERACTION FOR MEAN NUMBER OF TAIL BEATS PER BOUT

	A_0	A_1	A_2	$\bar{X}$
C_0	0.44	0.19	0.13	0.25
C_1	0.21	0.26	0.22	0.23
$\bar{X}$	0.33	0.23	0.18	

TABLE XLV

FISH SIZE AND TANK SIZE INTERACTION FOR MEAN NUMBER OF FIN ERECTIONS PER BOUT

	B_0	B_1	$\bar{X}$
C_0	1.15	0.82	0.99
C_1	1.08	1.15	1.12
$\bar{X}$	1.12	0.99	

VITA

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