THE EFFECTS OF GROUP SIZE, FISH SIZE, AND AVAILABLE SPACE ON AGONISTIC BEHAVIOR DURING GROUP ESTABLISHMENT IN THE ORANGE-SPOTTED SUNFISH, *LEPOMIS HUMILIS* (GIRARD)

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Bachelor of Arts

Southwestern College

Winfield, Kansas

1965

Submitted to the Faculty of the Graduate College
of the Oklahoma State University
in partial fulfillment of the requirements
for the Degree of
MASTER OF SCIENCE
May, 1970

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ACKNOWLEDGEMENT

Thanks are due Drs. R. J. Miller, L. H. Bruneau, and W. A. Drew who served on my committee. I would also like to express my thanks to Dr. J. L. Folks and Mr. B. M. Brandt who helped with the statistical analysis and Mr. D. F. Frey and Mr. H. W. Robison who helped in the procurement of fish.

My special thanks go to Mr. L. E. Powell who assisted in all phases of the study, and without whom this study could not have been accomplished.

Finally, I am grateful to Miss M. O. Matthews who transcribed most of the data and typed the rough draft and Mrs. T. A. Heist who typed the manuscript.

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CHAPTER I

INTRODUCTION

This investigation was conducted to determine the effects of group size, fish size, and available space on the agonistic behavior of the Centrarchid fish, Lepomis humilis (Girard) during the first hour of social interaction.

Collias (1944) has suggested that social rank is determined very early in the interaction of a group of fish by fighting, bluffing, or passive submission at the initial encounter between individuals or during an early series of encounters. If this is in fact true, then most of the work on social organization in fishes has come after the social rankings have been determined.

Many factors contribute to the establishment of social organization in fishes. Braddock (1945), Greenberg (1947), Huck and Gunning (1967), and Hadley (1969) have found that size is a determining factor, the larger fish usually assuming the dominant role. Braddock (1945), Greenberg (1947), Allee et al. (1948), Erickson (1967), and Hadley (1969) have found that sex is also important, males usually dominating females.

Many workers have been concerned with the relationship between complexity of the habitat and the size and number of territories in a given space. Greenberg (1947), Fabricius (1951), Fabricius and Gustafson (1954), van Iersel (1958), Barlow (1962), Miller (1964a, 1964b), van den Assem (1967), and many others have shown how important cover or environmental complexity are for establishing territories in many fishes.

Similarly, numerous investigators like Allee et al. (1948), Fabricius and Gustafson (1954), Forselius (1957), Miller (1964), Erickson (1967), Huck and Gunning (1967), van den Assem (1967), Gibson (1968), Hadley (1969), Miller and Miller (in press), and others have shown that total available space can influence social organization.

The effect of the number of individuals in a group on social organization has been investigated by Hixson (1946), Miller (1964a), Borkhuis (1965), Myrberg (1965), Pfeiffer (1965), van den Assem (1967), Gibson (1968), Hadley (1969), and Miller and Miller (in press).

Before any model can be proposed for agonistic behavior or social hierarchy in fishes, it seems paramount that a framework be established on which different studies of agonistic behavior can be compared. This involves the use of comparable experimental conditions. This study was conducted to further the knowledge of some of the factors that contribute to agonistic behavior and to the type of social organization formed.

The author selected group size, fish size, and available space as the most relevant factors to investigate in this study.

The effects of size and sex are known and appreciated and an attempt was made to hold them constant in this investigation. Because only males were to be used the sexually dimorphic Orange-spotted sunfish was selected for the study.

Individual fish size was fairly constant within each fish size although some variation was unavoidable. This study was aimed at determining if fish with a mean standard length of 66 mm behaved differently than fish with a mean standard length of 76 mm.

Another factor which is often present, Braddock (1949), Hadley (1969), and Miller and Miller (in press), but rarely considered, is the length of pretest isolation. Although Borkhuis (1965) found a significant increase in frequency of attacks of green sunfish isolated for 10 days compared to those isolated for 3 days, most authors seem to select arbitrarily the pretest isolation period. This author selected 3 days as the pretest isolation period.

CHAPTER II

MATERIALS AND METHODS

The research was conducted in the Animal Behavior Laboratory of the Oklahoma State University Zoology Department from July 1969 to November 1969.

Physical Conditions: All experiments were conducted in 12 tanks 81 cm long, 56 cm wide, and 38 cm deep with a capacity of approximately 173 liters. Six tanks were made of enameled steel and six of marine plywood. All had white interiors and each had an end made of plate glass. Moveable transverse opaque partitions of plexiglass or plate glass 56 cm wide and 38 cm tall were used in the tanks randomly selected as small tanks. The bottoms of all tanks were covered with sand to a depth of about 4 cm. Tanks were supplied with air from a central compressor via airstones. No plants or artificial cover was supplied. The tanks were cleaned and refilled with dechlorinated water before each experiment. Water temperatures were maintained at 21 ± 2 C. Illumination was provided by overhead banks of fluorescent bulbs.

Feeding: Fish were fed *Daphnia* sp., *Chironomus* sp. larvae, and Tetra Min Staple Food during the pretest period.

<u>Collections and Handling</u>: The fish used were collected using seines and electro-fishing gear from Boomer Lake and its tributaries in Stillwater, Payne County, Oklahoma. They were kept in stock tanks in the laboratory under the same conditions of lighting, temperature, and feeding as in the experimental tanks for a minimum of one month previous to each experiment.

<u>Pretest Treatment</u>: Prior to each experiment the fish to be used were isolated for 3 days in plastic containers with approximately 9 liters of aerated water. Immediately prior to isolation the fish were weighed to the nearest .1 gram on a pan balance and their standard length measured to the nearest millimeter. Identification of individuals was accomplished by clipping a small portion of the soft dorsal, soft anal, upper caudal lobe, lower caudal lobe, or combinations of these fins.

<u>Experimental Variables</u>:

A. <u>Fish Size</u>: Two sizes of fish, 66 and 76 mm average standard length, were used in this experiment. In the 66 mm average size, hereafter referred to as small size, fish ranged in size from 60 to 72 mm. In the 76 mm average size, fish ranged in size from 74 to 82 mm. Fish within each size group were assigned to a treatment at random and treatments were randomly assigned to each of the 12 tanks.

B. <u>Group Size</u>: Three group sizes were used in this experiment, either two, four, or six fish per group.

C. <u>Tank Size</u>: Two sizes of available space were used in this experiment, 86 liters, hereafter referred to as half tank, and

172 liters, hereafter referred to as whole tank. After randomly selecting which tanks would contain which treatment, the partitions were placed in the six half tanks.

Observations: All observations were made between 11:00 A.M. and 4:00 P.M. and lasted for exactly one hour from the time that the fish were introduced into the tank. All observations were made by two experimenters simultaneously seated directly in front of the tank at a distance of about 1 meter. The observers were relatively motionless and their presence did not seem to affect the fish's behavior.

A pilot study permitted both observers to agree on the identification of the behavior patterns that were recorded. All observations were recorded using a Wollensak tape recorder and were later transcribed in a notebook. Although the fish could be disturbed by sudden movement or vibrations set up by kicking the floor or tank, no amount of normal vocalization seemed to affect the fish.

Subjective Measurements:

A. Color Patterns: At the beginning and end of each observation and at any other time when a significant change occurred, the color patterns of the fish were noted and recorded. Although the recording of color patterns is very subjective, it is a valuable tool in predicting a fish's general behavior. All color patterns were recorded by one observer.

B. Territory: The presence of any territory was recorded as it became apparent. A territory is defined as an area into which no other fish enters or an area which is defended by an individual and in which he defeats all other group members in all or nearly all definitive bouts.

In most cases there was no apparent territory after one hour, but many times it could be predicted that a territory was about to be established. This was later confirmed by Mr. L. E. Powell as he continued to observe the fish for a subsequent 3 week period.

C. Ranking: This was a third subjective measurement that was taken at the end of each observation. Fish were assigned a rank of 1, 2, etc., or were said to be evenly matched. This ranking was accomplished by noting which fish appeared more aggressive and seemed to win most often. There were instances in which ranking was impossible to determine.

For this study a factorial experiment in a randomized block design was selected in which group size was studied at three levels (two, four, and six fish), fish size at two levels (60 to 72 mm and 74 to 82 mm), and available space at two levels (86 liters and 172 liters). Two replicates were observed, each replicate included 12 different treatments or factor combinations.

CHAPTER III

BEHAVIOR PATTERNS

Miller (1963) described the non-reproductive social behavior of *Lepomis humilis*. Except as noted, the form of the behavior patterns recorded in this study do not differ significantly from those described by Miller (1963).

Approach: An approach was recorded whenever one fish swam into the vicinity of another and displayed or elicted a response from that fish.

Fin Erection: A fin erection was recorded when all median fins were erected and the fish was usually stationary in the water. As mentioned by Miller (1963) the pelvic fins were usually not erected, but were pressed against the ventral surface.

Although fin erection was sometimes seen in a head-on encounter, one fish was usually perpendicular to the body axis of the other or fish were oriented parallel, either head-to-tail or head-to-head.

Bite: A bite was recorded whenever mouth contact was made with the opponent. Most bites were directed at the caudal region of the opponent.

Chase: A chase was recorded whenever one fish was in direct pursuit of another.

Opercle Spread: The opercle spread was made by opening the opercles and was nearly always performed as one fish was directly facing another. Mutual opercle spreads by two fish were recorded by Miller and Miller (in press) on the territory borders and were referred to as pendulum movements. Although each opening of the opercle was of short duration it was counted as a separate act in this study.

Tail Beating: Tail beating usually occurred mutually when two fish were parallel, either head-to-head or head-to-tail. The caudal peduncle was swung strongly to one side, pushing water against the body of the other fish. These beats of the tail usually occurred one after the other in rapid succession in a burst of tail beating called a session, and each tail beating session was counted as one tail beat.

CHAPTER IV

COLOR PATTERNS

Color patterns, although exhibiting a great deal of variation, are of some predictive value in subjectively determining which fish in a group are dominant and which are more subordinate. The following components of the various color patterns were observed:

Opercle Flap: Coloration of the opercle flap varied from black to grey to nearly pale. Darker color was usually indicative of a dominant fish, and lighter of a more subordinate fish.

Iris Color: The color displayed was related to rank and varied from bright orange to red to black. The bright orange eye was usually an indication of dominance and the black eye a sign of subordination. Iris color changed rapidly and, in some cases, a visible change was apparent within 15 seconds after initiation of an encounter with another fish.

Banding: Fish varied from entirely pale to dark banded. The dark banded fish possessed five vertical dark bands approximately 1 cm in width and was usually the most subordinate fish in a tank. Other fish usually ranged from light to moderately banded, the most dominant fish being most lightly banded. Pale coloration was only observed when the fish were first placed in the tank and may be attributable to either fear or the fact that the plastic pretest isolation containers were white in color.

Fin and Belly Color: In the more dominant fish there was orange coloration in the fins and the abdominal area. The pelvic and anal fins were often bordered in black.

Table I is a summary of the various components of the color patterns as they are usually found in fish of different hierarchial ranks.

TABLE I

A COMPARISON OF SOCIAL RANK AND COLOR PATTERNS OBSERVED

Rank	Opercle Flap	Iris Color	Banding	Fin Color
Subordinate	light	black	dark	none
Intermediate	grey	red	moderate	none
Dominant	dark	bright orange	light	orange

The above table is not intended to imply that there was always only one subordinate or one dominant, but the above gradients of coloration apply to the relative positions within a given group.

The above color patterns agree well with those described by Hadley (1969) for the longear sunfish (L. megalotis).

CHAPTER V

THE EFFECTS OF GROUP SIZE

Group size was found to have a significant effect on the total number of behaviors performed in the three levels of group size. (See Table II for the levels of significance of each factor for each behavior recorded). The greatest difference in frequency of bites, chases, opercle spreads, and tail beats occurred between the group of two and the group of four fish. The average difference between group sizes can be seen in Figure 1. The shape of the curve for approach and fin erection suggest that their frequency would tend to increase with further increase in group size. However, the shapes of the curves for bites, chases, opercle spreads, and tail beats suggest that they are approaching an asymptote and might remain constant with increasing group size or perhaps decline as suggested by Pfeiffer (1965) and Greenberg (1947).

Of all the behaviors recorded in this experiment, approach and fin erection seem to be the least aggressively motivated behaviors since they often occur in the absence of overt behaviors such as biting and chasing. Fin erection may be a defensive or flight posture, as suggested by Miller (1963). In many cases after one fish approached another, a fin erection was the only behavior that occurred.

An analysis of variance was also performed on the number of agonistic behaviors of the group divided by the number of fish in the

TABLE II

SIGNIFICANCE LEVELS OF THE TOTAL FREQUENCY OF AGONISTIC BEHAVIORS FROM THE F TEST PERFORMED ON THE MEAN SQUARES OF THE ANALYSIS OF VARIANCE

Factor	Approach	Bite	Chase	Fin Erection	Opercle Spread	Tail Beat
Group Size	.01	.10	.05	.01	.05	.05
Fish Size	NS	NS	NS	NS	NS	NS
Group Size - Fish Size Interaction	NS	.10	NS	NS	NS	NS
Tank Size	.05	.10	.10	.05	NS	NS
Group Size - Tank Size Interaction	NS	NS	NS	NS	NS	NS
Fish Size - Tank Size Interaction	NS	NS	NS	.10	NS	NS
Group Size - Fish Size - Tank Size Interaction	NS	NS	NS	NS	NS	NS

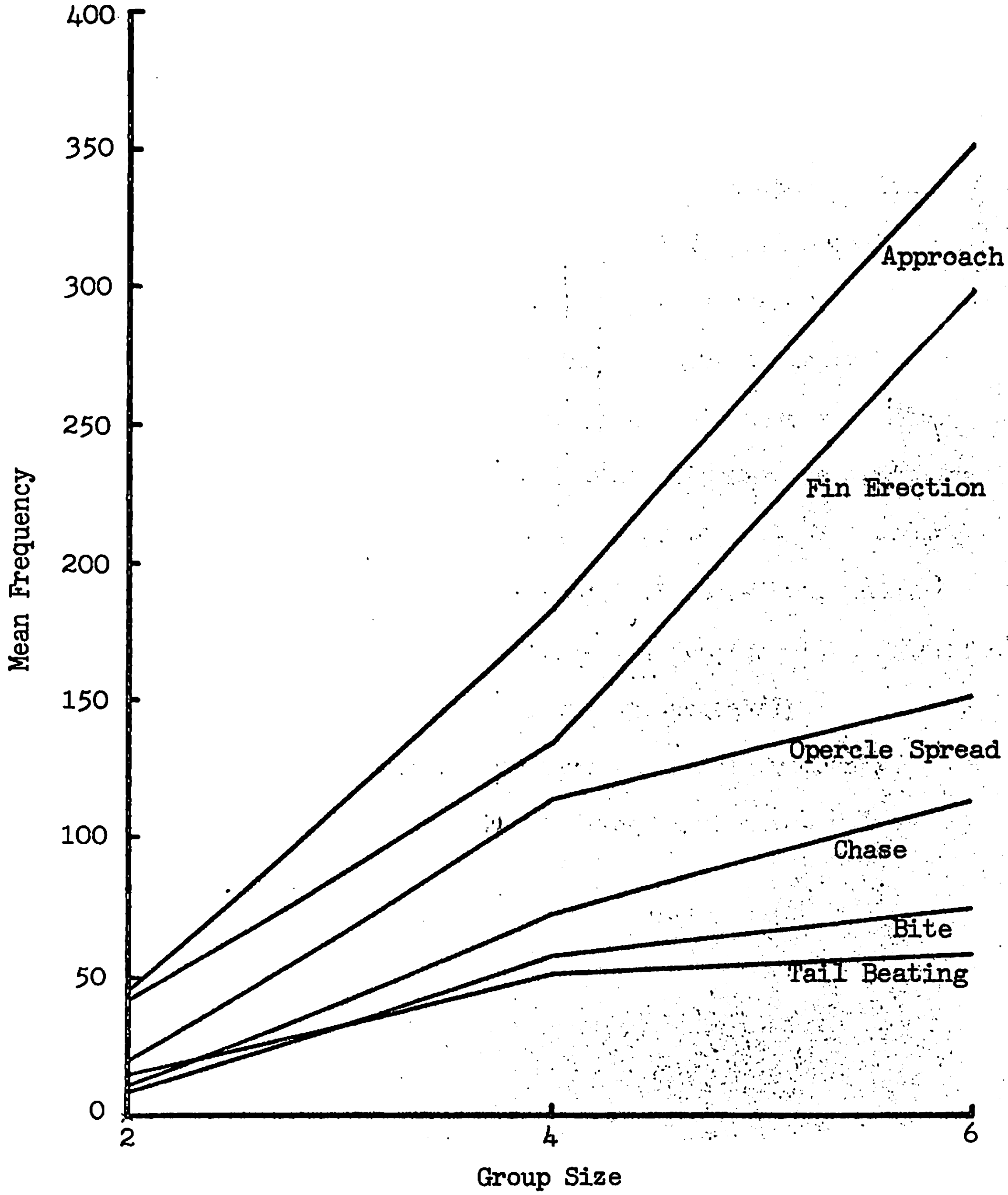

Figure 1. Mean Frequency of Agonistic Behavior for Each Level of Group Size During the First Hour of Observation.

group. The results of this test give approximately the same result as the test of total frequency of each behavior (Table III). A graphical presentation is presented as Figure 2 to aid in visualizing the results.

Dividing the frequency of each behavior by the number of fish seems to be an accepted procedure (Miller and Miller, in press), but another procedure seems to be more relevant to this author. This procedure involves dividing the total frequency of each behavior by the number of possible opponents that any one fish could have at a given time. Thus, in a group of two fish, each fish only has one other fish with which to interact. This procedure seems as logical as assuming that both fish each performed the same number of behaviors; thus, the total frequency of each behavior was divided by one, three, or five in each of the group sizes, two, four, and six, respectively.

The results of the analysis of variance of total frequency divided by the number of opponents shows fewer significant values for F tests (Table IV, Fig. 3).

TABLE III

SIGNIFICANCE LEVELS OF THE FREQUENCY PER FISH OF AGONISTIC BEHAVIORS FROM THE F TEST PERFORMED ON THE MEAN SQUARES OF THE ANALYSIS OF VARIANCE

Factor	Approach	Bite	Chase	Fin Erection	Opercle Spread	Tail Beat
Group Size	.01	NS	NS	.01	.10	NS
Fish Size	NS	NS	NS	NS	NS	NS
Group Size - Fish Size Interaction	NS	.05	NS	NS	NS	NS
Tank Size	.05	.10	NS	.05	NS	NS
Group Size - Tank Size Interaction	NS	NS	NS	NS	NS	NS
Fish Size - Tank Size Interaction	NS	NS	NS	.05	NS	NS
Group Size - Fish Size - Tank Size Interaction	NS	NS	NS	NS	NS	NS

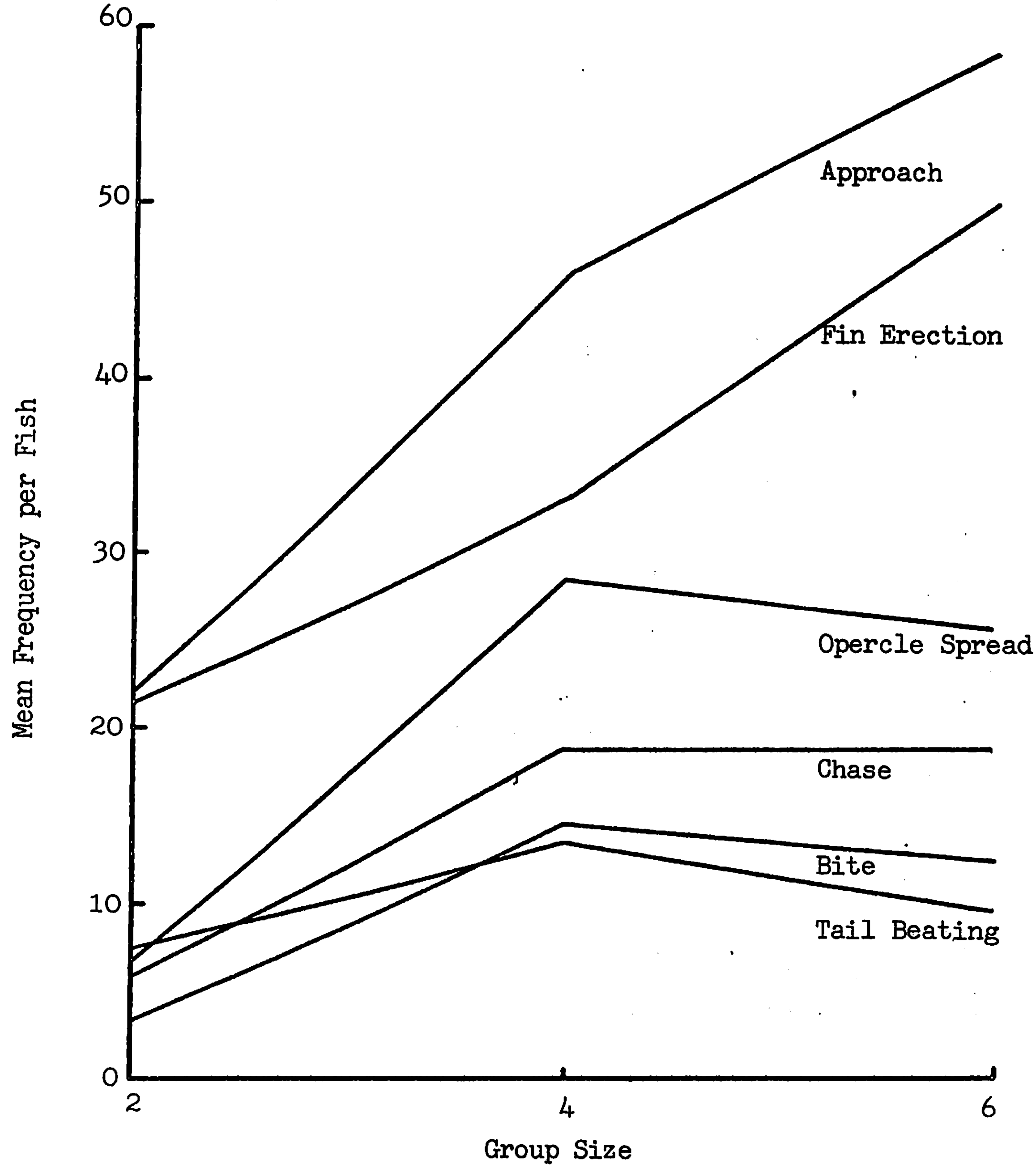

Figure 2. Mean Frequency per Fish of Each Agonistic Behavior for Each Level of Group Size During the First Hour of Observation.

TABLE V

SIGNIFICANCE LEVELS OF THE FREQUENCY PER OPPONENT OF AGONISTIC BEHAVIORS FROM THE F TEST PERFORMED ON THE MEAN SQUARES OF THE ANALYSIS OF VARIANCE

Factor	Approach	Bite	Chase	Fin Erection	Opercle Spread	Tail Beat
Group Size	NS	NS	NS	NS	NS	NS
Fish Size	NS	NS	NS	NS	NS	NS
Group Size - Fish Size Interaction	NS	.05	NS	NS	NS	NS
Tank Size	.05	.10	NS	.10	NS	NS
Group Size - Tank Size Interaction	NS	NS	NS	NS	NS	NS
Fish Size - Tank Size Interaction	NS	NS	NS	.01	NS	NS
Group Size - Fish Size - Tank Size Interaction	NS	NS	NS	NS	NS	NS

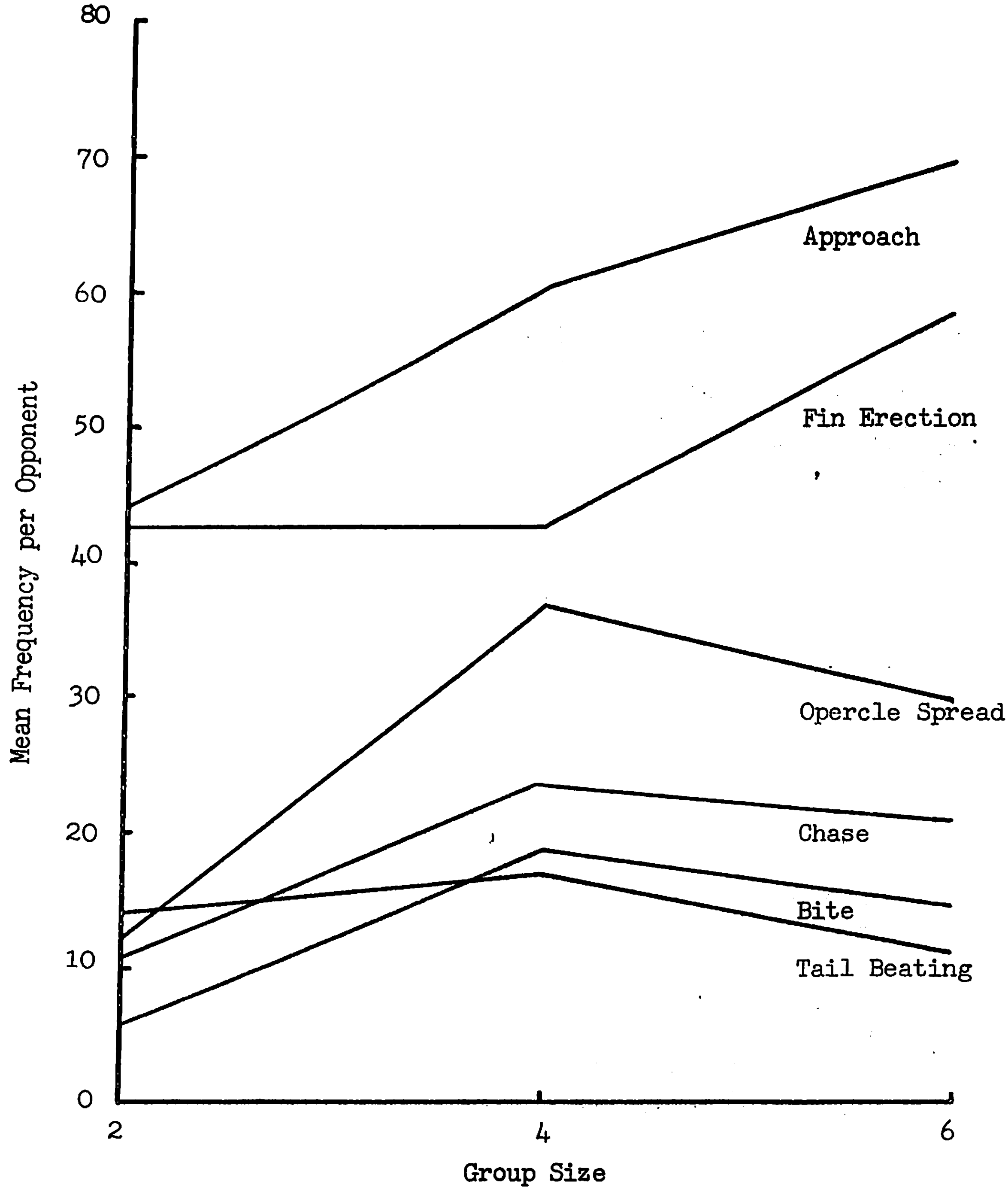

Figure 3. Mean Frequency per Opponent of Each Agonistic Behavior for Each Level of Group Size During the First Hour of Observation.

CHAPTER VI

THE EFFECTS OF FISH SIZE

The analysis of variance for fish size revealed no significant difference in the frequency of any of the behaviors recorded between the two sizes of fish (Tables II, III, and IV). These results do not agree with those obtained by Hadley (1969) for L. megalotis but may be due to a species difference or the fact that there was only a 10 mm difference in the average standard length of the two sizes of fish. Hadley (1969) maintained an average difference of 15 mm between his three sizes of fish. Table V presents the total frequency, frequency per fish, and frequency per opponent of each behavior in the two size groups. Although the results are not statistically significant, the trend of increasing frequency of behavior with increasing fish size is readily apparent.

There were two cases in which an interaction involving fish size was significant. The frequency of bites, the frequency of bites per fish, and the frequency of bites per opponent were significant for the group size-fish size interaction. The frequency of fin erection, the frequency of fin erections per fish, and the frequency of fin erections per opponent were significant for the fish size-tank size interaction.

In the case of the significant group size-fish size interaction the frequency of bites per fish and the frequency of bites per opponent were greatest in the group of six for small fish, and in the group of four for large fish. The frequency of bites per fish and the frequency of bites per opponent were minimum for the group of four for small fish, and the group of two for large fish. In other words, with increasing group size in small fish the result was a hyperbola; with large fish, the result was a parabola.

TABLE V

MEAN FREQUENCIES OF EACH AGONISTIC BEHAVIOR FOR EACH LEVEL OF FISH SIZE

Agonistic Behavior	Mean Frequency		Mean Frequency per Fish		Mean Frequency per Opponent	
	Small	Large	Small	Large	Small	Large
Approach	187.4	199.2	40.5	44.0	56.1	61.2
Bite	46.1	46.7	9.6	10.5	13.4	13.9
Chase	63.1	68.8	13.6	14.8	18.6	19.9
Fin Erection	140.6	175.9	32.1	37.4	46.2	51.3
Opercle Spread	86.0	101.0	17.7	22.5	23.4	30.7
Tail Beat	35.3	48.6	8.4	11.7	12.3	16.9

In the case of the significant fish size-tank size interaction, the frequency of fin erections per fish and the frequency of fin erections per opponent were greatest for the small tank with small fish, but were greater in the large tank with large fish.

CHAPTER VII

THE EFFECTS OF TANK SIZE

Tank size or available space has the effect of causing increased frequency of each behavior with smaller available space. An analysis of variance revealed a significant difference at the .05 level in the frequency of approach, fin erection, approach per number of fish, and approach per number of opponents. At the .10 level, bites, chases, and bites per fish were also significant. See Tables II, III, and IV for the significance levels of the results obtained.

Figure 4 is a graphical representation of the trend of increased frequency of behavior with smaller available space. Again, as in Figure 1, approach and fin erection have a greater slope than any of the other behaviors. Figures 5 and 6 represent the frequency of each behavior per fish and the frequency of each behavior per opponent, respectively.

The agreement between the effects of increasing group size and decreasing available space suggest that a change in either of these factors will produce the same effect.

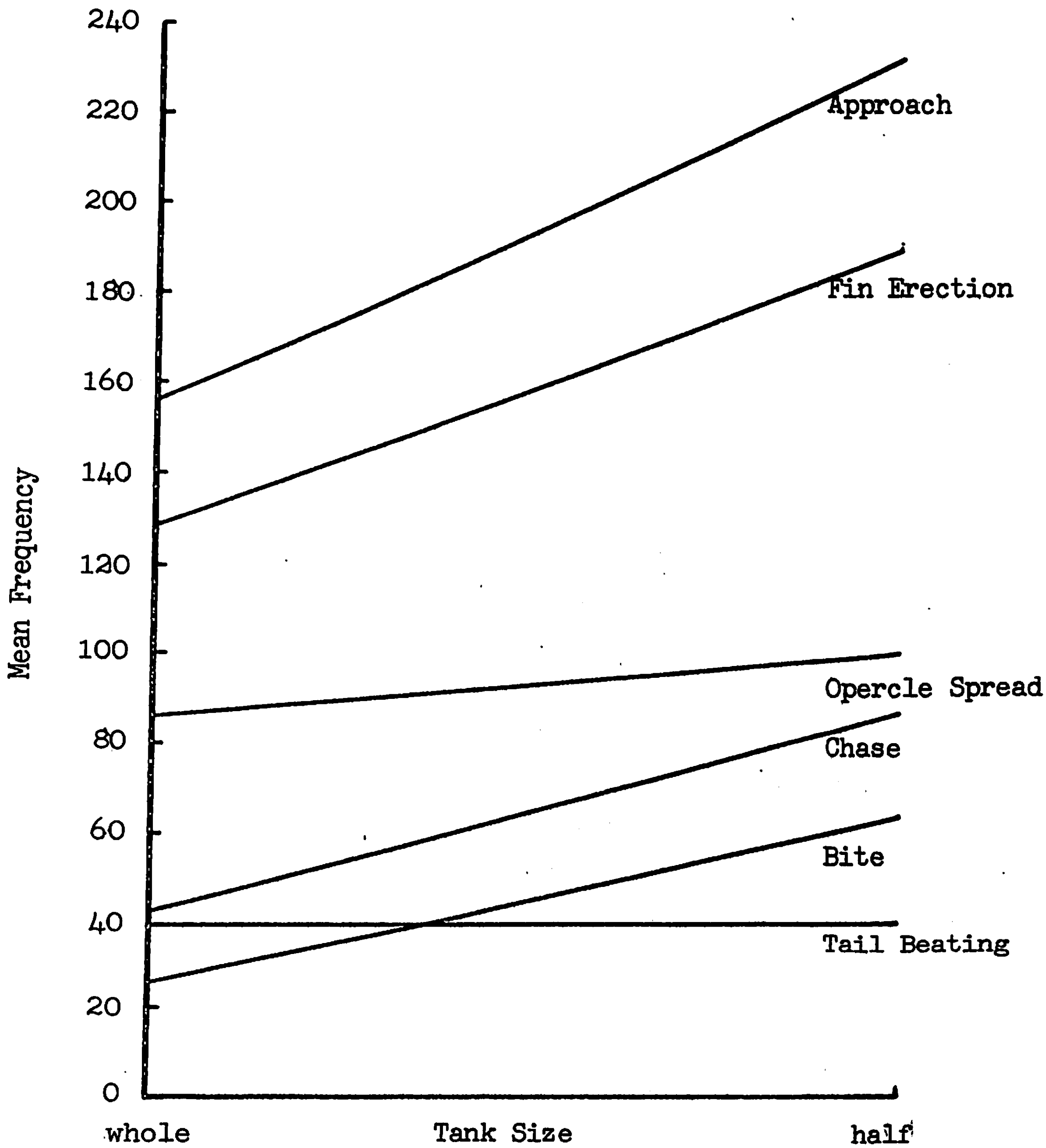

Figure 4. Mean Frequency of Each Agonistic Behavior for Each Level of Tank Size During the First Hour of Observation.

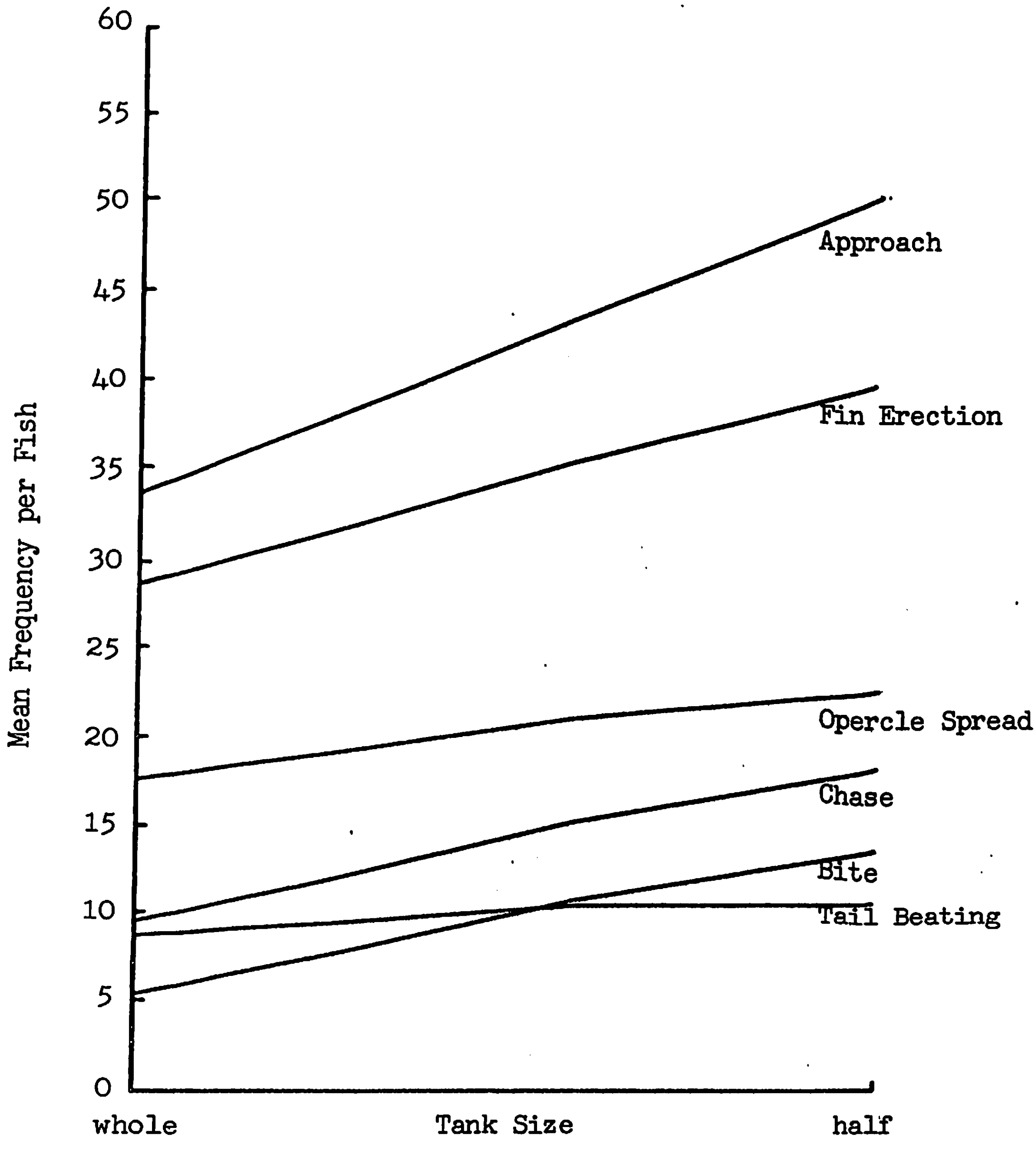

Figure 5. Mean Frequency per Fish of Each Agonistic Behavior for Each Level of Tank Size During the First Hour of Observation.

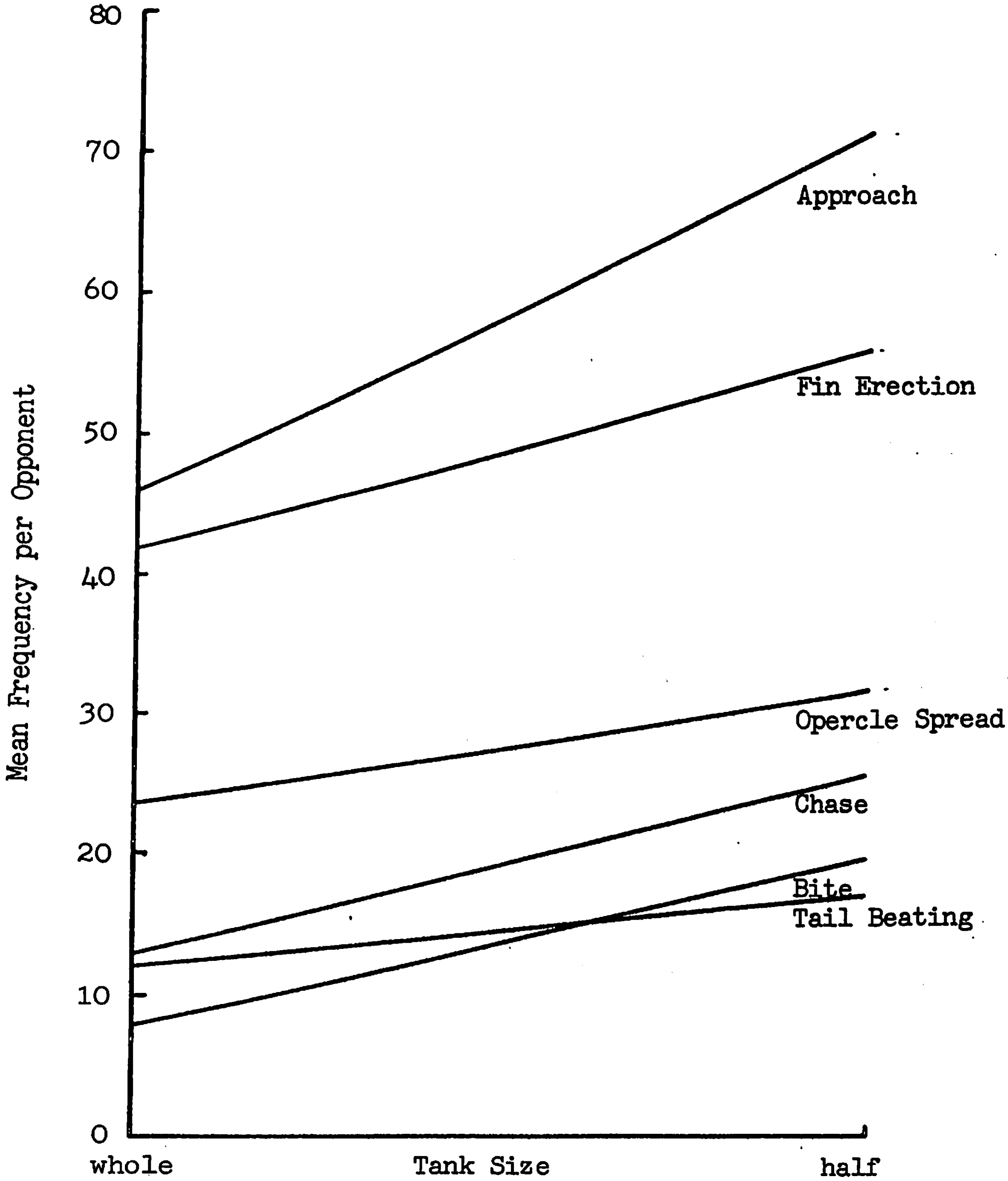

Figure 6. Mean Frequency per Opponent of Each Agonistic Behavior for Each Level of Tank Size During the First Hour of Observation.

CHAPTER VIII

DISCUSSION

Six primary responses were measured in this study. Approach, bite, chase, fin erection, opercle spread, and tail beat frequencies were recorded and used in assessing the effects of group size, fish size, and tank size on agonistic behavior.

In almost all observation periods approach and fin erection were the most common behavior recorded. Tail beating was usually the least frequently observed and showed a definite temporal pattern. Tail beating was usually most frequent at the beginning of the hour and declined throughout the hour.

All encounters were preceded by an approach, and not all encounters included every other behavior; therefore, approach frequency was usually greater than the frequency of any other behavior. The high frequency of fin erections could have been caused by two factors. The most important factor is probably the fact that many fin erections are locomotary in function and aid in stopping or turning. An attempt was made to exclude this type of fin erection from the data, but a distinction is hard to make in some instances. A second factor might be that fin erection is a very low threshold behavior as evidenced by the fact that it is often the terminal behavior in an encounter and by the fact that it often occurs at distances when other behaviors are not possible. In many instances a fish at the rear of the tank was observed apparently displaying fin erection to a fish which was near the front of the tank, a distance of approximately 80 cm.

Tail beating is a behavior which requires a special spatial positioning of two fish. The fish must be alongside one another and usually in a head-to-tail alignment before the behavior occurs. It seems that this complex orientation requirement would be accomplished less often than other orientations and would lead to a reduced frequency of occurrence. When fish are first released in a tank they tend to clump together which could possibly explain the higher rate of tail beating during the first part of the observation period. A second factor that must be considered is the difference in motivational state that may occur with time. The threshold for tail beating may be low before dominance relationships are established and higher after establishment of a rank order between fish. The mean frequency of tail beating across all treatments decreased during the observation periods (18.5 for the first 20 minutes of the hour and 11.2 for the last 20 minutes of the hour).

An analysis of the temporal patterns of each behavior during the observations produced no clear cut results. Within the same treatment combination across the two replicates there was extreme variation in the peaks of each behavior. The only trend that appeared was that the frequency of tail beating was usually high during the first part of the hour and decreased throughout the remainder of the observation periods. An analysis of the temporal patterns of behavior should be undertaken with more replicates.

One of the problems involved in trying to quantify dominance or territorial relationships is the fact that other fish soon avoid a dominant fish or one with a territory. In this study an attempt was made to predict, after one hour of interaction, which fish would become the dominant fish in a tank. Of sixteen observation periods in which a fish could be singled out subjectively as the dominant fish after one hour, that fish performed, during the hour, the greatest number of approaches in fifteen cases, the greatest number of bites in fourteen cases, the greatest number of chases in fifteen cases, the greatest number of fin erections in fourteen cases, the greatest number of opercle spreads in thirteen cases, and the greatest number of tail beats in fourteen cases.

Results of this experiment indicate that increasing group size and decreasing available space cause a significant increase in the frequency of agonistic behaviors, both in total frequency and in frequency per fish and frequency per opponent.

Although not statistically significant the results of small fish compared with large fish also show a tendency for increased frequency of agonistic behavior with increasing fish size.

Observing fish during the first hour of social interation has produced some interesting, if anticipated, results. This type of observation should be extended into a study which would be designed to determine when, during a series of encounters, dominance is determined.

Another factor that deserves more study is the effect of the length of the pretest isolation period.

CHAPTER IX

SUMMARY

Increasing group size, increasing fish size, and decreasing available space were found to cause an increase in the total frequency, frequency per fish, and frequency per opponent of agonistic behaviors in twenty-four groups of male orange-spotted sunfish. The effects of group size were the most pronounced with available space and fish size also important in that order.

Color patterns were found to be correlated with position in a dominance hierarchy. In general lighter fish were more dominant, and darker fish more subordinate.

In almost all cases, the dominant fish in a tank performed more agonistic behaviors than any other fish.

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Candidate for the Degree of

Master of Science

Thesis: THE EFFECTS OF GROUP SIZE, FISH SIZE, AND AVAILABLE SPACE ON AGONISTIC BEHAVIOR DURING GROUP ESTABLISHMENT IN THE ORANGE-SPOTTED SUNFISH, LEPOMIS HUMILIS (GIRARD)

Major Field: Zoology

Biographical:

Personal Data: Born in Ponca City, Oklahoma, July 14, 1942, the son of Glenn P. and Gladys R. Dennis.

Education: Graduated from Medicine Lodge High School, Medicine Lodge, Kansas in 1960; received the Bachelor of Arts degree in Biology and Secondary Education from Southwestern College, Winfield, Kansas in 1965; completed the requirements for the Master of Science degree at Oklahoma State University in May 1970.

Professional Experience: Undergraduate laboratory instructor, Southwestern College, Winfield, Kansas, 1963-1965; Special laboratory assistant, Winfield High School, Winfield, Kansas, 1963-1965; Graduate teaching assistant, Oklahoma State University, Stillwater, Oklahoma, 1968-1970.

Professional Organizations: American Association for the Advancement of Science, American Institute for Biological Sciences, Beta Beta Beta.