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Social interaction in juvenile channel catfish

Lynda Lee Roys

To the Graduate Council:

I am submitting herewith a thesis written by Lynda Lee Roys entitled "Social interaction in juvenile channel catfish." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Wildlife and Fisheries Science.

Larry Wilson, Major Professor

We have read this thesis and recommend its acceptance:

Richard Strange, Gordon Burghardt

Accepted for the Council:
Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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L. Evans Roth

Vice Chancellor
Graduate Studies and Research

SOCIAL INTERACTIONS IN JUVENILE CHANNEL CATFISH

A Thesis
Presented for the
Master of Science
Degree
The University of Tennessee, Knoxville

Lynda Lee Roys

December 1978

DEDICATION

To my husband, Larry.

ACKNOWLEDGMENTS

I wish to thank Dr. Larry Wilson, my major professor, for his guidance and support during the course of my graduate study. His resourcefulness, patience and compassion are sincerely appreciated. I also want to thank my committee members, Dr. Richard Strange and Dr. Gordon Burghardt, for the time and effort they spent in contributing to my thesis. I am very grateful for the laboratory work Dr. Strange introduced me to and assisted me in. Recognition is also due to Dr. William L. Sanders for his help in the statistical analysis of my data.

Special thanks is given to my parents, Mr. and Mrs. Roger E. Roys. Without their financial and loving support my education would not have been possible.

ABSTRACT

Social interactions between 11 pairs of channel catfish (Ictalurus punctatus) were observed and discrete behavioral units were described and analyzed. Dominant fish engaged regularly in aggressive activities and never in submissive activities, whereas subordinate fish were observed in submissive activities on a regular basis and rarely in those that were aggressive. Activity levels were significantly higher in dominant fish. There was no significant difference in activity levels between pairs equal and unequal in size. A factor analysis indicated three motivational systems underlying the social behavior in juveniles and two behaviors, which appeared as displacement activities, were functioning in agonistic encounters. Plasma cortisol concentrations measured in singletons, pairs, and individuals from a control tank suggested that the least amount of stress occurred in fish that were not interacting with any other individuals. Cortisol levels, however, were below those associated with stress in all the test fish.

TABLE OF CONTENTS

INTRODUCTION

The behavior of fish has received limited attention, with most studies being viewed separately from other components of fish biology, such as anatomy, physiology, and ecology. However, in reality, behavior is the expression of all these components as they interact. There have been a number of studies dealing with the ethological description and analysis of dominant - subordinate relationships and territoriality (Greenberg 1947, Newman 1956, Iersel 1958, Erickson 1967, Farwell and Green 1973, Cole 1976).

Of the 31 families in the order Siluriformes, only one species, the yellow bullhead (Ictalurus natalis), has been subjected to a thorough ethological examination (Todd 1968). The channel catfish (Ictalurus punctatus) is quite important as a commercial and game species throughout the United States and its reproductive and feeding habits have been well documented. However, while it has been shown that feeding efficiency is directly related to social structures and agonistic activities of channel catfish in culture operations (Konikoff and Lewis 1974, Randolph and Clemens 1976a, Randolph and Clemens 1976b), only fragments of its social behavior have been described.

The objective of this research was to describe the aspects of social behavior in channel catfish which support its territoriality, hierarchical patterns, and agonistic activities. The existence of this behavior and the strength of its survival value should not be neglected.

Of this subject Lorenz (1966) wrote,

> . . . This territorial aggression, really a very simple mechanism of behavior-physiology, gives an ideal solution to the problem of the distribution of animals of any one species over the available area in such a way that it is favorable to the species as a whole. Even the weaker specimens can exist and reproduce, if only in a very small place. . . .

Thus, from observed interactions between juvenile pairs, nonreproductive behavior was described and analyzed with some related aspects and ramifications. Since aggression levels are closely tied with the difference in rank between individuals, the pairs observed in this study differed in weight in varying amounts. Differences in the quality and quantity of their aggressive bouts may prove useful in stocking procedures. Also, physiological stress, as a result of agonistic interactions, was investigated through measuring levels of a stress-indicator hormone in blood samples.

CHAPTER I

LITERATURE REVIEW

A survey of the literature indicates that there has been no research to date which deals directly with channel catfish social behavior. Several studies, however, have rendered general information about the subject.

In a study of factors influencing feeding behavior in culture ponds, hierarchies were described which were based on the size of fish and population densities (Randolph and Clemens 1976a). Channel catfish were marked and followed during their daily trip to a feeding station throughout an entire growing season. A feeding pattern for each size fish was established. Large fish played a dominant role in the feeding behavior whereby smaller, subdominant fish had to wait. Aggressive activity was observed in the formation and maintenance of these hierarchies. In one instance four large fish chased a similar size fish away from the feeder on 50 out of 60 occasions. The authors concluded that the fifth fish was not aggressive enough to compete since the feeder could have accommodated all five. Small fish were chased from the feeder on a routine basis. Furthermore, when larger, dominant fish were removed, the hierarchy was sustained through the remaining individuals which moved up in the hierarchical pattern.

Strong schooling and shelter-seeking tendencies were observed in fingerling channel catfish by Brown et al. (1970). Experiments showed the "hiding" behavior to occur in groups of fish rather than individuals. (Groups of fish were made up of densities ranging from 50 to 60 and held in circular pools 3 m in diameter.) It was felt that the groups were true aggregations and that the aggregating tendency was intense enough to cause the fingerlings to seek shelter only when that shelter was large enough to accommodate the whole group. The fish were not observed to split up when a smaller shelter was offered.

Randolph and Clemens (1976b) also found that in channel catfish the establishment of territories or home areas and swimways in ponds reflected aggregations or schooling behavior. The size of the aggregations and the number of home areas and swimways appeared to be dependent on the degree to which different sized fish made up the population. Fewer, but larger, home areas and swimways were established in ponds checked with similar sizes compared to ponds stocked with mixed sizes.

The existence of hierarchies and agonistic behavior between channel catfish was suggested in an investigation of the variation in weight of cage-reared animals (Konikoff and Lewis 1974). Two environmental variables, variation in water depth and "escape" or "rest" areas, were introduced to study the possible behavioral effects which produce differential growth. Neither factor was found to affect the normality of the weight-frequency distributions. However, there were definite indications that hierarchical activities occurred. Populations held in shallow areas exhibited more evidence of fighting and had higher rates of mortality than those held in deeper water. A higher degree of aggressive behavior was thought to be caused by insufficient vertical space for hierarchical formation. Furthermore, a few disproportionately large individuals developed in cages which were held in deeper areas. According to the authors, "In populations of only 100 or 200 fish, it is not unreasonable to expect 1 or 2 large fish to be able to dominate the rest of the population." It is interesting that when the density of fish was increased in cages in shallow water, damage from fighting and mortality were both reduced. In an earlier study, they found fighting to occur frequently at densities less than 60 fish per m^3 and infrequently at densities above 125 fish per m^3.

In addition to feeding behavior, dominance and aggressive interactions appear to be related to reproductive behavior. During the breeding season the male channel catfish selects and prepares the nest site, cares for the eggs, and defends the area from intruders, including the female (Davis 1965, Calhoun 1966, Huet 1970). According to Huet, the male becomes aggressive after spawning and "reacts sharply when disturbed." There is no indication in the literature that the female participates in any territorial behavior. She is, in fact, chased off by the male since there is a chance she will devour the eggs if they are not protected from her.

Another factor related to the phenomena of social dominance and structured communities is the varying physical conditions associated with different individuals within the hierarchy. Specifically, it has been postulated that animals of a subordinate status exist under physiological stress (Sassenrath 1970, Noakes and Leatherland 1977).

Sassenrath (1970) found that in caged groups of rhesus monkeys

(*Macaca mulatta*) the production of corticosteroids in response to the amount of ACTH (adrenocorticotrophic hormone) in the blood was directly related to the amount of avoidance behavior in which the individuals engaged. The lowest levels occurred in alpha, or dominant, animals.

Noakes and Leatherland (1977) reported a clear relationship between interrenal cell activity, indicative of corticosteroid production, and dominance status in rainbow trout (*Salmo gairdneri*). Interrenal activity correlated inversely with dominance rank. The one exception to this was the highest ranking individual which had more interrenal activity than was expected. The authors felt that this could be explained by the higher general activity and/or greater involvement in agonistic encounters. They also suggested that increased subordination, as an individual ranks lower and lower in the observed linear hierarchy, accounted for the physiological repercussions of "social stress."

Social behavior in yellow bullheads (*Ictalurus natalis*) has been well documented. Todd et al. (1967) first demonstrated the recognition between individuals of this species and its importance in their social interactions. Information was found to be transferred through the water and chemically communicated in the form of pheromones. Immature fish were blinded and then successfully conditioned by reward (food) and punishment (electrical shock) to discriminate between 50 ml of tank water from two different donor fish when it was poured through the filtering device of their aquariums. The test fish responded to the positive stimulus by rising rapidly to the surface at the front of the aquarium and gulping, as if in search of food. The negative stimulus caused them to flee to their shelter where they were safe from shock. The bullheads lost their ability to distinguish between donor fish when they were deprived of their sense of smell by destruction of the olfactory epithelia. The percentage of correct responses for blinded bullheads was 96 compared to 43 for the fish deprived of their olfactory sense. An observed change in status, chemically communicated to other bullheads, indicated to the authors that stress influenced chemosensory recognition. Several pairs of bullheads, a dominant and a submissive, were forced to share 190 l aquaria. When the dominant was removed and isolated for one night, the submissive was not observed to react with any aggression upon its return. When the dominant fish was returned to the aquaria after losing an encounter with another dominant bullhead, the submissive fish immediately attacked it. In addition, test fish recognized in the same manner without fail, fish subjected to stress from mild electrical shocks at regular intervals.

Todd (1971) pursued the investigation of pheromones to the communities or aggregations where hierarchies and territories were absent. A large number of newly trapped bullheads coexisted peacefully without any aggressive activity. It was only when individuals were removed from the group, isolated, and then introduced into a low-density situation that aggression and territorial behavior emerged. By exposing a territorial pair to water from the tank of the communal group for an extended period of time, aggressive behavior was replaced by behavior of the nonaggressive bullheads. When the communal water was suspended, high levels of aggression were restored within 24 hours. It was concluded that a pheromone concentration was produced in dense aggregations which inhibited aggression. It was thought that possibly the state of stress of an individual might signal whether it was a dominant or subordinate and that this was indicated through certain products carried in the urine and/or mucous.

Standard differences have been established in the agonistic behavior patterns between unacquainted fish, between acquainted dominants and submissives, and between acquainted fish of comparable status (Bardach and Todd 1970). In an experiment devised to test these patterns, pairs of bullheads were observed in 200 l aquaria. Strangers engaged in biting, mouth fighting, and quivering; these behavioral actions were only observed in conflicts between strangers. Lower-keyed patterns like displays, circling, and nipping occurred between acquaintances with the submissive bullhead clearly avoiding the fish of higher status. There was a balance between approaching and fleeing activities with an absence of behavioral units leading to physical injury between pairs of equal status. It was found that after the bullheads interacted, a small amount of water from the tank of one pair member elicited the same responses as observed previously from the other. When the water from the dominant's tank was added to the subordinate's, the subordinate fled or avoided water from the area where the water had been introduced. When the dominant had water from the subordinate's tank introduced, it swam rapidly to the point of inflow and in some cases "attacked" the area.

Todd (1968) described 70 individual behavioral units in the bullhead repertoire. This was the first ethological investigation and description of any species of catfish. The behavior was recorded in spatial and temporal sequences and evaluated in terms of social significance. He discovered that test fish required shelters before establishing territories and hierarchies and that shelters were the center of most dominant bullhead territories. He, too, found that once bullheads established a community their conflicts were low-keyed and stylized, but that strangers often fought violently. The detailed behavioral "pathways" of aggressive interactions were described and illustrated. Todd also found that at certain high densities bullheads do not establish territories or behave aggressively. Instead, groups of eight in 200 l aquaria were observed to swim throughout the tanks continuously seeking contact with each other. These aggregations remained cohesive during feeding. During the reproductive season, March through May, this behavior was gradually replaced with vicious aggression. By the end of May only one fish survived the others. He suggested that changes in the behavior of the aggregations may have been due to hormonal changes since temperature, light intensity, and day length in the laboratory had not been altered. The majority of animals in his experiment were immatures; those that matured were females.

Establishing a territory was not found to be an instinct limited to sex and reproduction. Extremely small fish (7 cm) occupied shelters and defended them against other bullheads of similar size. Sex did not appear to influence dominance apart from the breeding season. Females as well as immature animals achieved a dominant status in the community. Todd showed that territoriality and dominance were related. Territories which were meekly guarded against a dominant tankmate were strongly defended against intruding subordinates or strangers by the same individual. It was also noted that the borders of the territories were not fixed and continual interactions between tank members were necessary for community stability.

Todd (1968) was also able to observe and describe "cooperative" behavior which was based on recognition of individuals. Mutually beneficial activities were investigated by studying three bullheads held together in a large aquarium for several months. The dominant fish was the largest and the fish at the bottom of the hierarchy was the smallest. Each bullhead resided in its own territory in or around a clay tile. When water from tanks of previous antagonists was introduced, the subordinates fled from their territories to the dominant's territory and rested on the dominant's back. The dominant clearly was able to distinguish between strangers and its subordinates. If a stranger was placed in the tank, the subordinates remained in the dominant's shelter until the stranger was defeated. After a period of time, the dominant would evict them from its territory. Todd postulated that the submissive fish were provided with protection while the dominant "enjoyed" the advantages of dominance, the best territories, access to food and females, etc., with little threat from community neighbors. He concluded that possibly this behavior might contribute to observed community stability which, once established, exists with limited aggression.

McLarney et al. (1974) examined the effects of the breakdown of social behavior in bullheads with changes in water temperature. Their work reinforces the importance of the social organization in communities.

Groups of two bullheads of approximately the same size were observed 15 minutes after feeding for a duration of 30 minutes. Their behavior was recorded into discrete units in temporal sequence. When the group was judged as having reached a social equilibrium with regards to aggressive and submissive interactions and size and location of territories, they were subjected to a series of 1 C temperature increments. Each time the temperature was raised, the fish were allowed to acclimate for one day before observation. The level of activity increased with temperature with the exception of the range between 30-31 C, during which activity levels dropped below that recorded at the lowest temperatures studied. In looking at the incidence of aggressive behavior, it appeared that the frequency of aggression was a function of the increased frequency of interaction from contact between individuals, which was, of course, dependent on the degree of activity. When, however, the authors subdivided the aggressive units into levels of intensity, warning and damaging, they found a marked increase in the occurrence of damaging behavior above 30 C, without a corresponding increase in the occurrence of warning displays. This increased aggression and breakdown of natural bullhead social behavior indicated the significance of normal activities which were based on the ability of the fish to recognize individuals in the community and to react in an appropriate manner by displays of varying intensities.

The role of chemosensory perception in channel catfish has been investigated in a study of the locomotor responses of males to a pheromone released by a ripe female of the species by Timms and Kleerekoper (1972). Sexually mature channel catfish approached the point source of the pheromone and oriented themselves in a tropotactic manner. When the concentration of the stimulus was lowered, restricted movements were replaced by more loosely organized locomotion patterns described by the authors as "searching" or a type of alarm response. No further behavioral descriptions were offered.

The existing literature dealing with channel catfish behavior shows definite evidence that hierarchical formations and agonistic activities occur in both culture ponds and cage-rearing operations. There appears to be a discrepency between researchers, however, as to what age and density of fish facilitates aggregations or territorial activities. Bullhead social behavior has been subjected to detailed description and analysis. It has been established that the formation of territories and hierarchies, their maintenance, and the agonistic behavior which supports these activities is based on chemosensory perception. Evidence of chemoperception has only been reported in male channel catfish during reproductive behavior. Social behavior in bullheads promotes successful reproduction and aids in the maintenance of the social group. In addition, there may be negative aspects of dominant-subordinate relationships as demonstrated by increased corticosteroid activity in rainbow trout. It appears that further research is needed to fully understand the behavioral interactions which underlie hierarchies in channel catfish.

CHAPTER II

METHODOLOGY

Procedure

Thirty-eight channel catfish, weighing 8 to 45 g and measuring 10 to 15 cm, were obtained from commercial outlets and maintained on floating commercial trout ration. Juveniles were chosen for the study in order to avoid reproductive behavior. Sex was not determined in any of the fish. The 22 individuals undergoing behavioral observation were held in 57 l aquaria equipped with a piece of broken clay pipe which served as a shelter. There were three sets of observations in this study. Information regarding the observations and the animals involved with each observation is presented in Table 1. In all three, the fish were grouped into 11 pairs of equal and unequal size and behaviors were recorded during a 30-minute observation period which began 15 minutes after feeding. The feeding process facilitated agonistic interactions. Since territorial borders were not respected while the fish fed, dominant individuals reestablished boundaries shortly afterwards which manifested the status and territory of each pair member. All individual, mutually exclusive, agonistic and nonagonistic behaviors which were significant in a feeding and/or social context were identified and registered. The catalogue of units was constructed on the basis of Todd's (1968) list of behaviors, but has been condensed (see Appendix). Most of the deletions were due to morphological differences between the species or

TABLE 1. Initial weights and pair identification of channel catfish in three sets of behavioral observations.

Fish No.	Weight (grams)	Observation Set[a]	Pair No.	Δ Size[b]	Fish No.	Weight (grams)	Observation Set	Pair No.	Δ Size
1	--	1,3	9	0	12	8	2,3	1	+
2	--	1,3	9	0	13	35	2,3	4	+
3	--	1,3	10	0	14	14	2,3	4	+
4	--	1,3	10	0	15	26	2,3	8	0
5	--	1,3	11	+	16	26	2,3	8	0
6	--	1,3	11	+	17	12	2(repl.)	6	0
7	45	1,2,3	3	+	18	8	2(repl.)	7	0
8	15	1,2,3	3	+	19	12	2(repl.)	7	0
9	24	1,2,3	3	+	20	16	2(repl.)	7	0
10	26	1,2,3	5	0	21	21	2(repl.)	2	+
11	28	2,3	1	+	22	10	2(repl.)	2	+

[a]Dates and temperature ranges for observation:
1. July-Sept., 1977, 24-27 C.
2. Dec., 1977-Feb., 1978, April-May, 1978, 16-19 C.
2(replicated). Sept.-Oct., 1978, 13-26 C.
3. Feb.-May, 1978, 16-19 C.

[b]0 indicates pairs considered equal in size. + indicates pairs considered unequal in size.

because certain behavioral units listed by Todd, although exhibited by the channel catfish, were not judged to be mutually exclusive. Specific methods varied according to the aspect of behavioral information sought.

The first set of observations that were taken focused on only one pair member at a time and the behaviors were recorded by hand. Two observations were made for every individual after social equilibrium had been established between the pair. Social equilibrium was considered established when a stable, stylized, daily routine of interactions was judged to be functioning. The building that contained the tanks was exposed to natural environmental conditions so that temperature and lighting were held constant while behavior was being recorded. Four pairs were grouped so that two were less than 4 g difference in weight and two were greater than 9 g difference in weight. Behavior was recorded until social equilibrium had been established for every pair (11 consecutive days). Territories and their day-to-day changes were drawn and described. Five consecutive observations were also recorded three weeks later to insure that stability had been reached. These observations were replicated, taped, and transcribed at a later time.

In the third set of observations, the ordering of behavioral events was recorded in two observations from eight pairs (four equal and four unequal in size) for sequential analysis.

From blood samples of the remaining 16 catfish, approximately equal in size, plasma cortisol concentrations were measured to investigate whether stress levels varied in (1) individuals kept in a large holding tank, (2) single individuals after two days in the 57 l aquaria, and

(3) paired individuals after two days of interaction in the aquaria. The cortisol concentrations for each sample was determined using a competitive binding assay as described by Strange and Schreck (1978a). Four singletons and four pairs were netted from the holding tank and placed in the eight aquaria where they were maintained in the previously described manner for two days. On the afternoon of the third day (18 October 1978) these 12 fish and the four control fish from the holding tank were quickly netted and sacrificed by a sharp blow to the head. Cortisol response to this procedure was not considered significant as long as it was carried out in less than two minutes (Strange pers. comm.). Water temperature was recorded at 10.5 C. Blood samples were collected into heparnized capillary tubes by severing the caudal peduncle.

Data Analysis

Frequency distributions were graphed for 38 behaviors observed in pair members of five tanks to delineate the behavioral characteristics of dominant and subordinate roles. Total frequencies for each behavior were summed separately for the dominant and subordinate individuals. The pairs consisted of both equal and unequal-sized fish and were judged as having a clearly defined dominant-subordinate relationship.

Data from eight pairs observed during the establishment of social equilibrium were analyzed to determine the change in the behavioral composition over time and to view quantitative and qualitative differences between pairs. Activity levels, the total of all behavioral units recorded in one observation, were established for each pair member and each pair. The Chi-square test was used to determine whether the average activity levels of the dominant fish differed significantly from that of the subordinate fish. The Mann-Whitney U test was used to test whether there was a significant difference between the average activity levels of equal and unequal-sized pairs. Also, weight difference and average activity of each pair were tested for positive correlation using the Spearman rank correlation coefficient. Frequencies of aggressive and submissive behaviors were calculated for both pair members on each of the 16 observations. Aggressive behaviors were defined as those that were threatening in nature, those that indicated the animal was highly agitated, and those that included actual contact with another fish and caused physical injury. Submissive behaviors were defined as those defensive in nature or behavior that displayed an animal's attempt to retreat. The frequencies for the groups of equal-sized and unequal-sized fish (both consisting of four pairs) were averaged and graphed. A one-sample Runs test was used to determine whether there was a random order of events or if there were any significant trends.

A factor analysis was developed by Wiepkema (1961) to investigate quantitatively the causation of behavior in the bitterling (Rhodeus amarus). To explore possible factors thought to control the occurrence of a number of common behaviors, the correlations among these were grouped on the basis of temporal association. This same method was applied to the sequential data recorded from the third set of observations. Specifically, Spearman's rho was calculated from ratios which were derived from observed and expected frequencies. Correlations that were obtained between pairs of events (each behavior and its preceding and following behavior) were factor analyzed using the principal axes method rotated by Varimax.

After cortisol levels were determined for each fish, the Mann-Whitney U test was used to test for significant differences between the control group, the singletons, and the pairs.

CHAPTER III

RESULTS AND DISCUSSION

The qualitative differences in behavior between dominant and subordinate pair members which are characteristic of each role are illustrated in Figure 1. The greater amount of activity in dominant fish can be seen. The dominant individuals accounted for 71 percent of all the behaviors observed, whereas the subordinates accounted for 29 percent. Feeding behaviors (barbel feel, barbel touch surface, dig, explore, head stand, ingest, search, spit, and surface creep) had low frequencies for both pair members since observations were purposely taken 15 minutes after feeding when agonistic behavior was at a peak. The agonistic behaviors were categorized as either aggressive or submissive. Dominant fish were never observed to flee, quiver, window creep, or window push. The subordinates had their highest frequencies in these units, but never engaged in biting, bottom bouncing, bottom creeping, butting, chasing, head thrusts, head wags, nips, pushes, or tail thrusts. There were, however, several aggressive activities the subordinates were observed doing; approaches, mouth flaps, mouth displays, push thrusts, and tail beats occurred occasionally in subordinate fish when they were highly agitated.

In general, aggressive behaviors were observed in dominant animals. Those individuals also utilized the shelter exclusively and were usually successful in getting most of the food. Due to

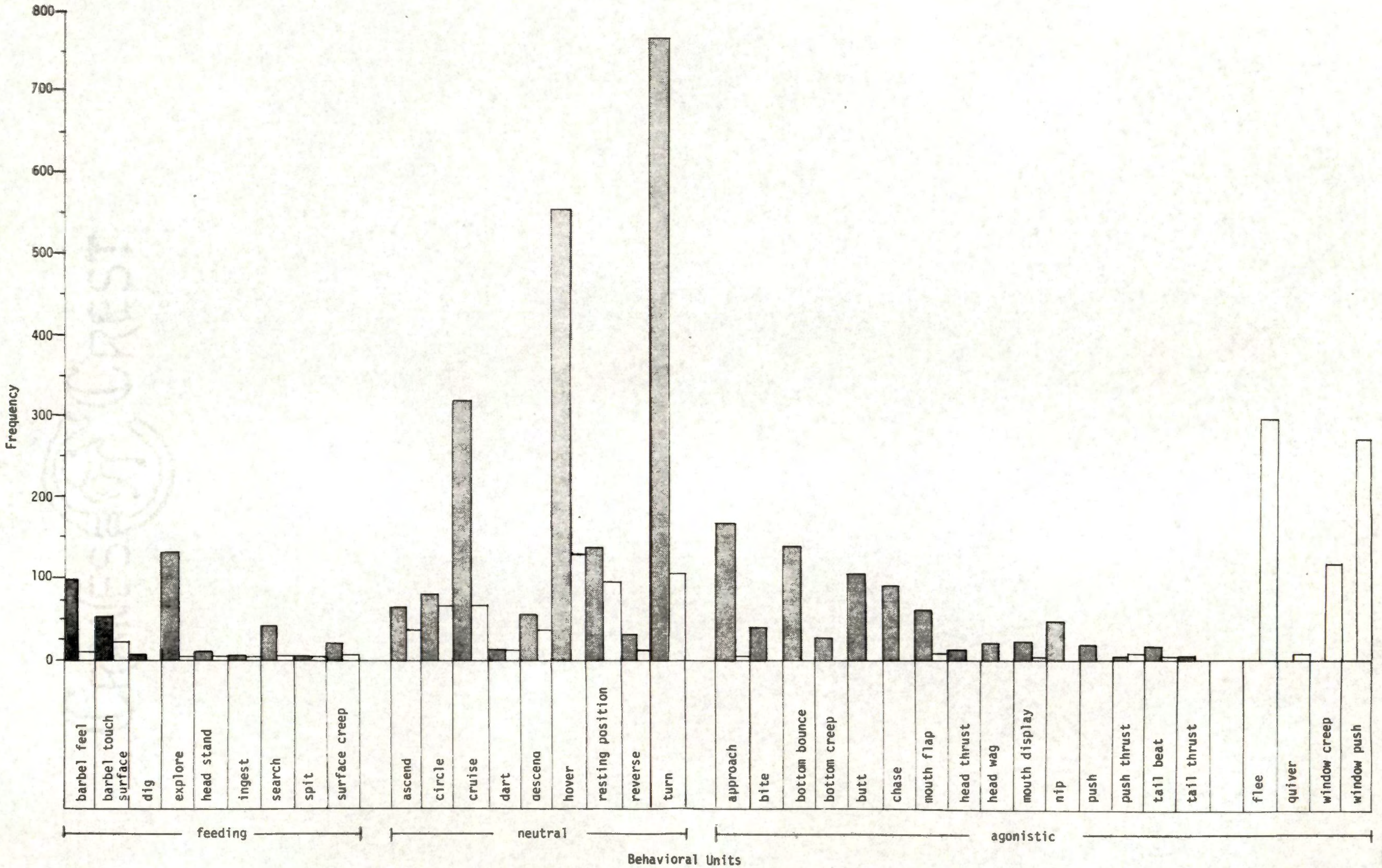

Figure 1. The frequency distribution of behavioral units observed in dominant (gray bar) and subordinate fish (clear bar) during two 30-minute observations for five pairs of channel catfish.

overall greater activity levels, frequencies were higher in the neutral behaviors for the dominant fish, but these units appeared to be behaviors that both fish engaged in regularly.

During the establishment of social equilibrium, activity levels differed between dominant and submissive fish and between animals of the same status. The differences are presented in Table 2. Subordinate fish were found to be significantly less active than the dominants at the .01 level. Individual variability was, however, high and relatively consistent for each animal. Neither fish of pair eight ever manifested itself as the dominant individual, nor ever behaved in a submissive manner. Each continually struggled against the other within the shelter. The only time the pair was observed outside the shelter was during feeding.

One would expect to find higher activity levels due to higher frequencies of interaction between two fish of comparable size. Dominance is usually established through a series of agonistic bouts when the outcome is not dictated by a particular advantage of either individual. In pairs where one animal has a size advantage, it is theoretically unnecessary and adaptively inefficient to waste energy and risk injury in aggressive encounters when the outcome of such a contest is obvious. As Hinde (1974) said, "In other words, the more uncertain the rank, the greater the need to confirm it." Although the results of these data indicated that larger individuals in pairs always assume the dominant role, there was not a significant difference in activity levels between pairs of equal and unequal size. In addition, there was no

TABLE 2. Number of activities observed for each pair member during the establishment of social equilibrium. The top figure represents activity levels of the dominant and the bottom figure represents activity levels of the subordinate.

Pair	1	2	3	4	5	6	7	8	9	10	11	22	23	24	25	26	Fish avg.	Pair avg.	Δ Wt. (grams)
	Observation Day																		
1	284	213	154	230	175	223	243	193	290	319	217	201	184	247	194	308	230	272	20.3
	5	1	23	135	22	107	13	16	14	139	58	34	27	42	10	37	40		
2	428	441	404	161	223	276	336	352	304	366	408	225	417	407	422	394	294	527	10.6
	285	222	108	232	233	298	166	225	168	212	353	173	12	75	28	72	143		
3	224	159	160	424	222	385	517	216	398	610	615	---[a]	---	---	---	---	357	575	30.0
	53	50	71	325	140	309	405	173	228	352	290						218		
4	14	18	11	12	72	20	46	36	57	36	89	62	125	110	81	240	64	98	21.3
	1	13	24	32	55	23	20	29	49	29	54	15	62	11	22	99	34		
5	99	122	110	87	100	215	218	381	366	202	210	410	419	488	484	369	267	439	2.4
	1	61	160	170	94	116	331	264	187	110	284	98	267	341	186	78	171		
6	448	685	426	305	306	501	304	327	685	412	475	225	297	273	342	284	393	506	3.8
	186	56	36	108	160	216	168	156	215	165	124	27	24	45	81	32	112		
7	55	205	514	383	228	463	558	248	410	360	535	333	263	193	212	197	322	571	3.6
	66	150	349	277	348	368	433	202	429	445	586	23	99	13	46	21	241		
8	65	84	52	50	187	6	26	143	137	210	125	112	98	187	143	292	120	240	0.1
	199	13	132	67	87	93	148	94	175	125	195	79	26	122	106	220	117		

[a] Subordinate fish killed by its dominant tank mate.

positive correlation between the average amount of activity in pairs and the difference in weight between pair members. The lack of statistical difference between the groups was due in part to pair three. Even though the subordinate fish (30 g less in weight) never displayed aggressive or threatening behavior, it was viciously attacked and and harassed by the dominant until it was mutilated and killed even before observations could be completed. The dominant individual was found to be a precocious female, but it is not known whether or not its abnormal behavior could be attributed to its reproductive condition.

The change in aggressive and submissive activities of dominant and subordinate fish in the group of unequal-sized pairs is illustrated in Figure 2. The dominant individuals never engaged in any submissive behavior. Submissive activity in the subordinates and aggressive activity in both the dominants and subordinates over time occurred randomly when tested at the .05 level of significance. There was, however, a high degree of association between the submissive behavior of the subordinates and the aggressive behavior of the dominants. The peaks and valleys which appear might represent periodic "testing" of subordinate fish and the reestablishment of status from the dominant fish. The low levels of agonistic behavior during the last five observations (after 22 days of pair interaction) might indicate that, at this point, roles between the pairs had become more stable and fewer agonistic interactions were necessary to maintain the hierarchical pattern.

The behavioral changes over time for the fish of equal sizes are

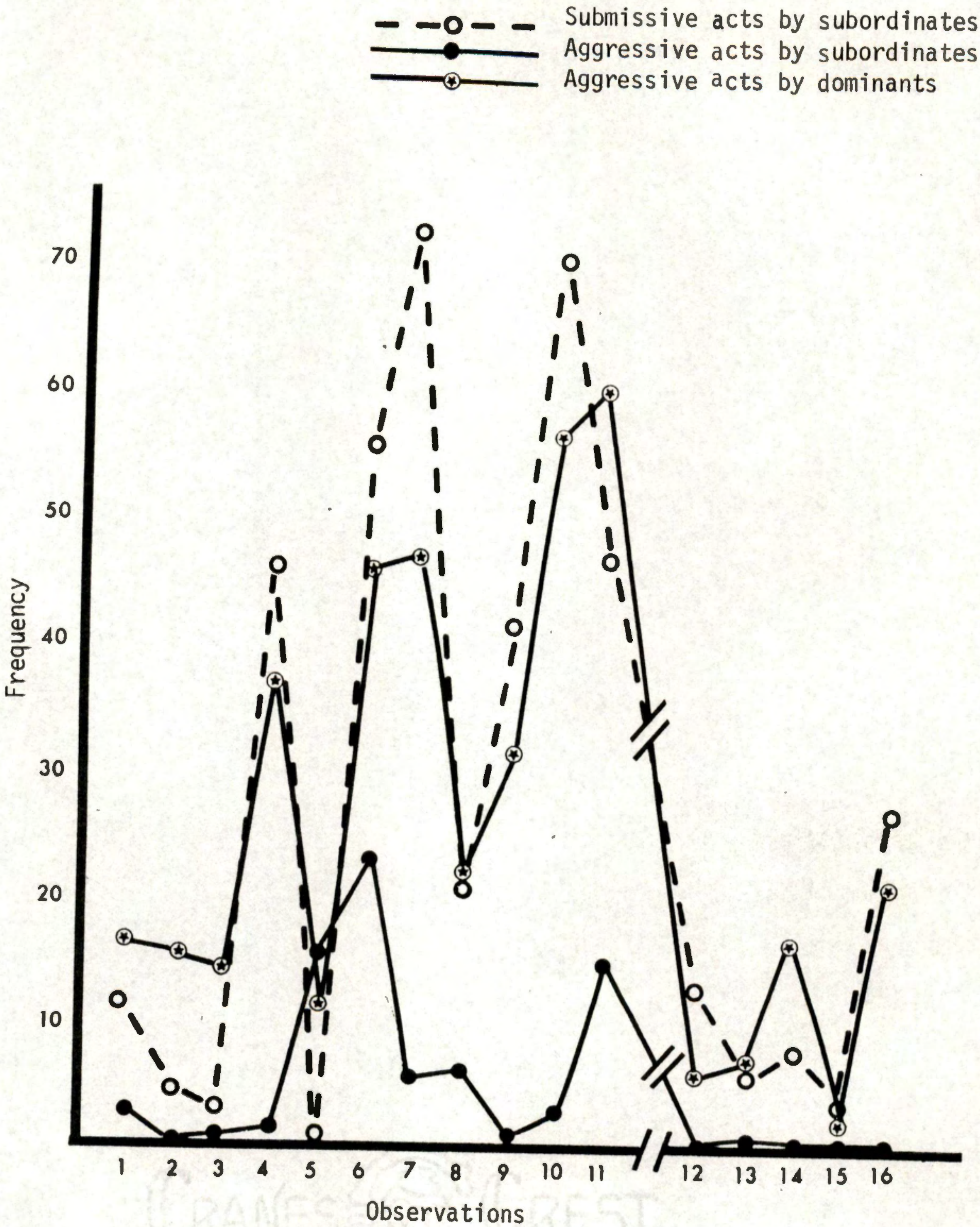

Figure 2. Average number of aggressive and submissive activities observed in dominant and subordinate fish of unequal size.

shown in Figure 3. Although there was an increase in submissive activities and a decrease in aggressive activities as dominance was established, this trend was not significant at the .05 level. Submissive behavior was never observed in the fish which eventually manifested themselves as dominant and their aggressive activities were consistently high (no significant trend was determined when tested at the .05 level).

The existence of underlying motivational systems in juvenile channel catfish behavior was investigated through factor analysis. According to Wiepkema (1961), those activities which have high temporal association or have positively correlated frequencies can be arranged into groups of activities which are characterized by common causal factors. Four factors were retained which accounted for 52 percent of the variance. The behaviors and their factor loadings are presented in Table 3. Since three feeding activites (barbel touch surface, surface creep, and search) and two neutral activities which were often used during feeding (ascend and descend) loaded highly on factor 1, it was referred to as the feeding factor. High loadings of neutral behaviors on factor 1 may have been due to the use of the floating ration. Aggressive activities loaded highly on both the second and third factor; head thrust, push, push thrust, tail beat, and tail thrust had high loadings on factor 2, and bite, butt, chase, and nip had high loadings on factor 3. Factors 2 and 3, therefore, were referred to as the aggressive factors. The behaviors which had high loadings on factor 4 (head wag and hover) did not appear to have a common causal factor.

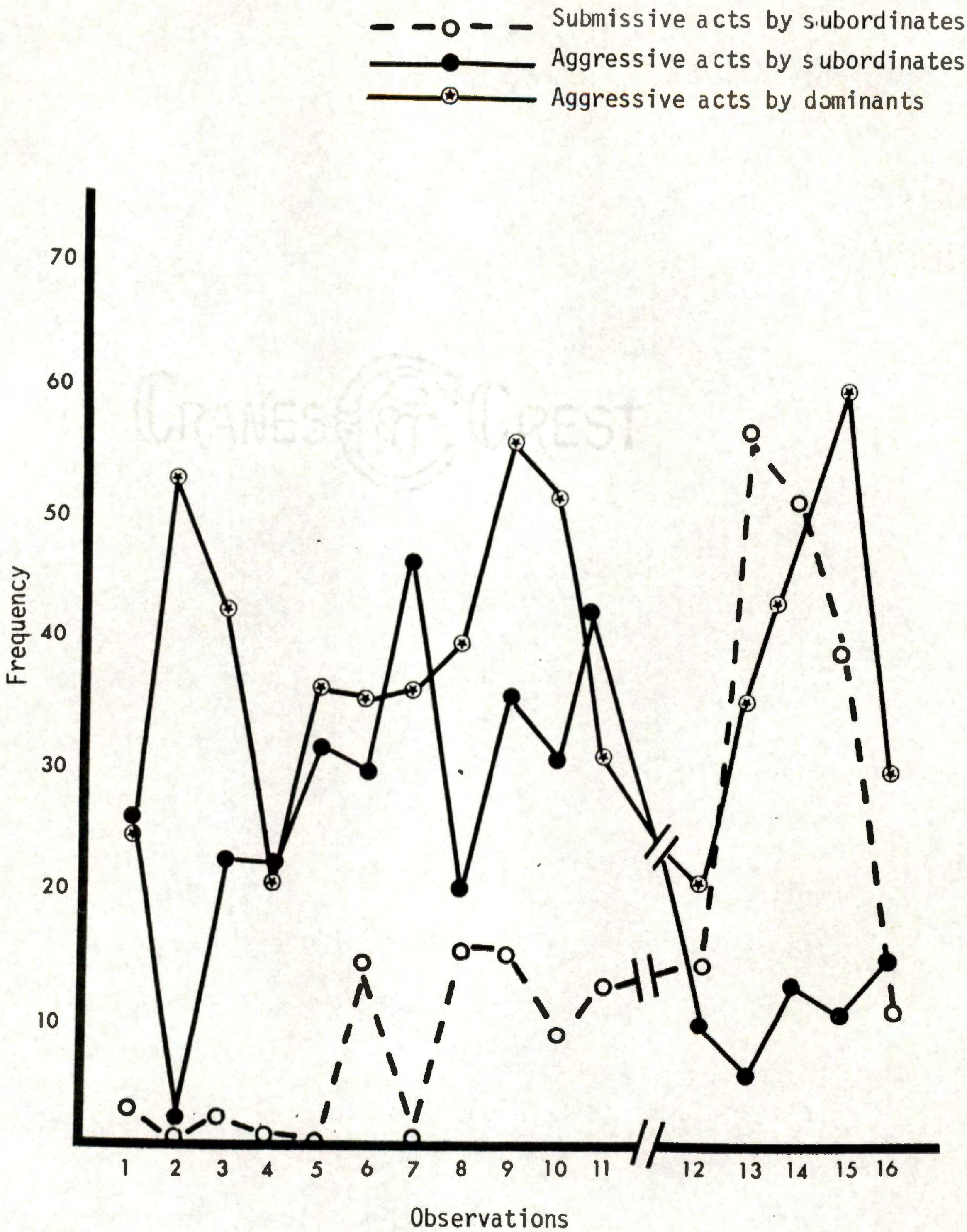

Figure 3. Average number of aggressive and submissive activities observed in dominant and subordinate fish of equal size.

TABLE 3. The results of behavior correlations observed in eight pairs of juvenile channel catfish subjected to factor analysis.

Behavior	Rotated Factor Pattern			
	Factor 1	Factor 2	Factor 3	Factor 4
Approach	0.65874	-0.28730	0.44967	0.18347
Ascend	0.74918	-0.17794	0.31688	-0.01310
Barbel feel	0.35255	0.16361	0.10606	0.49562
Barbel touch surface	0.75059	0.06643	0.15731	-0.10471
Bite	0.08212	-0.02668	0.75656	-0.02038
Bottom bounce	0.49360	-0.07128	0.58829	0.27696
Butt	-0.12737	0.12303	0.77452	-0.14913
Chase	0.06912	0.06593	0.83323	0.19298
Circle	0.20676	-0.03419	0.77985	-0.16311
Cruise	0.13877	-0.37158	0.22031	0.48115
Dart	0.28507	0.05201	0.21124	0.19323
Descend	0.80328	-0.18745	-0.04711	-0.00691
Dig	0.43277	0.14641	-0.02812	-0.00851
Explore	0.26345	-0.27680	0.47414	0.35503
Flee	0.03329	0.36175	0.36417	-0.51673
Head stand	0.44492	0.21202	0.02537	0.06668
Head thrust	0.14037	0.82516	0.18914	-0.04237
Head wag	-0.10505	0.16617	-0.04610	0.51235
Hover	0.02111	0.13065	0.02343	0.73103
Mouth display	0.24712	0.61376	0.16050	0.07700
Mouth flap	0.29581	0.23020	-0.01358	0.44244
Nip	0.16397	0.10647	0.80009	-0.23971
Push	-0.06608	0.82283	0.10986	-0.06080
Push thrust	-0.25167	0.80381	-0.13809	0.12661
Quiver	0.00213	0.57986	-0.08715	0.35103
Resting position	0.06892	0.54876	-0.24460	0.32555
Reverse	0.55481	0.50463	0.18342	0.24715
Search	0.59263	-0.17514	0.41537	0.24191
Surface creep	0.80128	0.07876	0.01434	-0.18732
Tail beat	0.29878	0.75579	0.04673	0.23560
Tail thrust	-0.21413	0.67114	-0.00646	0.11165
Turn	0.17565	0.16216	0.07801	0.39785
Window creep	0.23587	0.02063	0.59446	-0.39330
Window push	0.53167	-0.41243	0.42647	-0.01880

[a]Behaviors which had high positive loadings on factor 1 (feeding).

[b]Behaviors which had high positive loadings on factor 2 (aggressive).

[c]Behaviors which had high positive loadings on factor 3 (aggressive).

[d]Behaviors which had high positive loadings on factor 4.

The aggressive behaviors of factor 3 are of a slightly greater intensity. It was difficult to say whether they were actually more dangerous, but this distinction was the only apparent explanation for the split of aggressive behaviors on two different factors. It seems reasonable to postulate that different motivational systems may underlie different intensities of aggression. Of special interest were the two behaviors, mouth display and bottom bounce, which had high loadings on factors 2 and 3, respectively. The function of these activities was questionable, but the results of the factor analysis indicated that they were only related to agonistic interactions. Theoretically, displaced activites may evolve into effective warning or threat displays. The mouth display gave the image of increased size as did the finspreading Wiepkema (1961) observed in agonistic encounters. Although the author never observed a "scratch" behavior in channel catfish, Todd (1968) stated that the bottom bounce, which was observed during agonistic bouts, appeared to be a rapid version of the scratch. Todd felt the motor patterns were extremely similar and viewed the bottom bounce as a displacement activity since it seemed irrelevant in the context of combat. Wiepkema (1961) also found the "chafing" behavior, which was described as very similar to the scratch, to be one of the comfort movements which showed some positive correlation with agonistic behaviors in the bitterling. Since mouth displays and bottom bouncing apparently served no other purpose and predominantly occurred during agonistic interactions, it was concluded they were at least evolving towards some form of aggressive communication.

As compared to the results of Wiepkema's factor analysis, these results were not nearly so well-defined. The discrepancy, however, can be partly attributed to the fact that all the behaviors observed in the data taken for this investigation (34 out of 38) were subjected to factor analysis. Wiepkema selected and used only 12 behaviors that he considered ". . . were easily measurable, not too rare in occurrence, biologically meaningful, and not entirely correlated with any other chosen variable." Still, since he accounted for 90 percent of the variance with three clear and biologically meaningful factors and because his non-factoral evidence backs up his factoral results, this method of determining common causal factors has merit.

The results from the investigation of stress as a possible ramification of behavioral interactions and/or acclimation to the aquaria are presented in Table 4. The singletons had significantly lower levels of cortisol than the controls at the .05 level, but there were no significant differences between the singletons and the pairs or between the pairs and the controls. For all three groups, plasma cortisol concentrations were comparable to non-stress levels found in salmonids, approximately 0-50 ng/ml (Strange and Schreck 1978b). Furthermore, these levels were below the cortisol concentrations found in channel catfish subjected to severe confinement stress, about 200 ng/ml, and the control fish of that experiment, about 100 ng/ml (Strange unpub. data). The lowest cortisol concentrations which occurred in the singleton group indicated that the least stressful conditions may exist where there were no interactions of any kind between other fish. Noakes and Leatherland (1977) also found that isolated fish had

TABLE 4. Plasma cortisol concentrations (ng cortisol/ml plasma) in three groups of channel catfish.

Group	Sample 1	Sample 2	Sample 3	Sample 4
Controls	40	35	30	30
Singletons	0	10	20	0
Pairs[a]	43	38	23	13

[a]Values represent averages between pair members.

significantly lower levels of interrenal cell activity than fish from "crowded" holding tanks. The relevance of this interpretation was questionable, however, in view of the fact the cortisol levels were below those associated with stress in all the test fish.

CHAPTER IV

SUMMARY

1. Social behavior in juvenile pairs of channel catfish (Ictalurus punctatus) was observed and discrete behavioral units were recorded for description and analysis.
2. In all but one pair, a social equilibrium was established in which a clear, dominant-subordinate relationship was functioning. Dominant pair members resided exclusively in the single shelter provided in each aquarium and defended their territories on a routine basis.
3. There were qualitative differences in observed behavior between dominant and subordinate pair members. Dominant fish engaged regularly in aggressive activities and never in submissive activities, whereas subordinate fish were observed in submissive activities on a regular basis and rarely in those that were aggressive. The difference in these frequencies indicated the behaviors characteristic of each role.
4. Activity levels, the total number of behaviors recorded during one observation, were significantly higher in the dominant than in the subordinate individuals at the .01 level.
5. There was no significant difference in activity levels between pairs equal or unequal in size, nor was there a positive correlation between size difference and activity levels in the pairs. It

was concluded that the abnormally aggressive behavior of a precocious, dominant female in one of the unequal-sized pairs may have confounded the statistical findings.

6. The change in the behavioral composition over time during the establishment of social equilibrium differed between pairs equal and unequal in size. In the former, aggressive activities decreased and submissive activities increased in subordinate fish when dominance was established. In the latter, aggressive activities were relatively low and submissive activities high in subordinate fish throughout the observation period. In both groups, the dominants never displayed any submissive behavior.
7. Factor analysis indicated that there were underlying motivational systems or common causal factors in juvenile channel catfish behavior. The analysis also revealed two seemingly unrelated behaviors to be functioning in agonistic interactions.
8. Plasma cortisol concentrations measured in singletons, pairs, and individuals from a control tank suggested that the least amount of stress occurred in fish that were not interacting with any other individuals. Cortisol levels, however, were below those associated with stress in all the test fish.

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APPENDIX

CATALOGUE OF BEHAVIORAL UNITS FOR THE CHANNEL CATFISH

1. approach Approach is slow speed swimming directly towards another fish.

2. ascend Ascend is swimming upward, away from the bottom, usually to locate some gustatory stimulus on the surface.

3. barbel feel Barbel feel denotes the tactile or gustatory investigation of the tank, objects in the tank, or other fish with the ventral and/or lateral barbels while the fish is relatively stationary.

4. barbel touch surface Barbel touch surface is the forward extension of the lateral barbels making contact with the surface film.

5. bite Bite is contact made with the jaws widely open. Penetration into the flesh of the opponent may or may not occur. In either event, the bite indicates a high level of aggression.

6. border turn Border turns are abrupt avoidances, while swimming, of a neighboring territory. This behavior is rarely observed.

7. bottom bounce Bottom bounce is a nose dive towards the bottom, followed by the fish rolling over on its side and bouncing off the bottom. This indicates an agitated state perhaps due to an unresolved conflict.

8. bottom creep Bottom creeping is the slow, hesitating approach of one fish towards another along the floor of the tank.

9. butt A butt is a head ram made with the mouth closed.

10. chase Chasing is a high speed pursuit. Chasing is a daily ritualized activity of dominant fish and also functions to drive intruders from a resident's territory.

11. circle A circle is a circular swimming pathway. It may occur when two fish in combat are pursuing one another.

12. cruise Cruising is undirectional swimming throughout the tank and also directional swimming to and from the shelters.

13. dart A dart is an erratic, high speed swim and its direction is unpredictable. According to Todd (1968), darting allows a fish to move from a dangerous area with minimized chances of being followed.

14. Descend Descend is the downward swimming from the surface or near it.

15. dig Dig is a part of feeding behavior. It occurs when the fish in in a head stand and is sampling the substrate. The open mouth is pushed downward and filled with debris and substrate material such as gravel.

16. explore Exploring is slow speed, investigatory swimming characterized by intermittent barbel feeling of the tank area or objects. It can be distinguished from searching by the lack of continual barbel feeling.

17. flee Fleeing is the retreat of a subordinate fish. It can be slow and ritualized or a rapid, intense flight.

18. head stand Head stands occur as the fish feed and search over the tank bottom.

19. head thrust The head thrust is an aggressive displacement activity. The head is abruptly swung laterally against another fish.

20. head wag Head wagging is a series of head thrusts; side-to-side displacement movements of the head region during conflict.

21. hover Hovering is a stationary position maintained by undulating pectoral and pelvic fin movements and slow tail wagging. Hovering occurs in almost every context.

22. ingest Ingest is taking food or material in through the mouth.

23. mouth display Mouth displays occur when a fish is agitated or involved in an active conflict. The mouth is opened wide and the opercules are extended.

24. mouth flap The mouth flap is a rapid succession of the mouth opening and closing. It often occurs during agonistic interactions.

25. nip Nipping is contact made with a less opened mouth than the bite. It also may or may not actually be damaging.

26. push Pushing is a thrust made towards another fish with the aggressor's entire body. It is effective in displacing an intruder out of a resident's territory or shelter.

27. push thrust The push thrust occurs when the two fish are laterally aligned. One fish will thrust its head against the side of the other and then displace it by moving forward.

28. quiver Quivers are vibrating movements occurring when aggressive interaction is extremely intense.

29. resting position Resting positions occur in four fashions and are indicated by the number of fins which actually come into contact with the floor of the tank. RP1 stands for only the caudal fin resting on the bottom. RP2 is when the anal and caudal fins are resting on the bottom. In RP3 the pelvic, anal and caudal fins are in contact with the bottom. In RP4 the entire ventral surface and the ventral barbels are resting on the tank floor. These positions do not seem to have much social significance.

30. reverse Reverse is the backward swimming of a fish accomplished by the undulation of the pelvic and pectoral fins in a circular manner.

31. search Searching is slow speed investigatory swimming along the walls and floor of the tank with continual aid of the barbels. Searching is intermittently interrupted by head stands and digging behavior when a food stimulus is encountered.

32. spit Spits are the expulsion of the material that is not digestible after sampling the substrate during digging.

33. surface creep Surface creeps are used to scan the water surface for food with the lateral and dorsal barbels.

34. tail beat The tail beat is a series of tail thrusts used as a means of displacing another individual.

35. tail thrust The tail thrust is an abrupt and powerful lateral swing of the tail against another fish. It also is a displacement act.

36. turn Turns are considered when the fish changes its direction less than 360°.

37. window creep Window creeping is the swimming along the walls of the tank in a somewhat circular fashion. The barbels may come into contact, but the function of window creeping does not seem to be searching. More likely, it may be a behavior subordinates assume when they are harassed and not permitted a territory to rest in.

38. window push Window pushing is pushing of the snout against the walls of the tank while remaining relatively stationary and is maintained by vigorous tail wags. The subordinate fish are the only ones observed in this behavior. It seems to act as a refuge as dominant fish will usually harass a submissive fish much less when they are window pushing.

VITA

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