Studies on the Agonistic Behavior of Anabantoid Fishes

RUDOLPH J. MILLER and HELEN C. MILLER[1],

Oklahoma State University, Stillwater

INTRODUCTION

The Anabantoidei are a large, diverse suborder of perciform fishes containing about 15 genera and 53 species (Liem, 1963; Forselius, 1957). Distributed throughout much of southern Asia and Africa, they are characterized primarily by the presence of a suprabranchial accessory respiratory apparatus and several associated behavior patterns. Use of atmospheric oxygen for respiration has enabled many of these fishes to penetrate submarginal or even anoxic waters, and the concomitant development of mouthbrooding or nest-building behavior permits much of the life cycle to be carried out in adverse habitats. Most of the intensively studied species are bubble nest builders and have evolved elaborate courtship and spawning rituals centered about the male-constructed nest. Forselius (1957) and Miller (1964) described the complex prespawning actions and pointed out the significant role played by aggressive activities in defending the nest area and courting the female.

In captivity, small social groups of the common gourami species exhibit both territorial and hierarchical organization and often show combinations of both. In general, smaller groups have a territorial organization, though a hierarchical structure may be superimposed on it. Dense populations may show decreased agonistic activity, but this is not always true (Miller, 1964).

Hierarchical relationships are generally determined within a few days after the establishment of a group. Nonreproductive territoriality often is more sporadic in occurrence and less permanent. In both cases a fairly characteristic set of agonistic behavior occurs during social interaction. Although there is much overlap in the kinds of patterns used in fighting, previous studies have shown that there is also a moderate amount of species specificity in both the kind and frequency of action exhibited. Because many of the agonistic patterns are used in both sexual and nonsexual social contexts, the motivational substrates underlying these activities may perhaps become better understood as a result of a thorough analysis of this activity complex.

The causal organization of courtship and fighting behavior has been discussed by numerous authors (Baerends, 1958; Barlow, 1962; Brown and Hunsperger, 1963; Hinde, 1966; Morris, 1958a, 1958b; Tinbergen, 1964) and critically reviewed by Miller and Hall (1968) in a paper on the court-

---

[1] Department of Zoology, Oklahoma State University, Stillwater, 74074. Contribution Number 459.

ship and reproductive behavior of *Trichogaster leeri*. In that species, the generally accepted conflict theory of agonistic and courtship display motivation ("attack-escape" theory) is shown to be just one model for describing the occurrence of these behaviors in the pearl gourami. With alternate possibilities available for describing the causal organization of agonistic activity, it should be worthwhile to acquire as much information as possible on such behavior in many different contexts in order to select the most accurate model.

This work was prompted in part by the observation that strikingly different use was made of overt aggressive patterns such as butting and biting in the courtship patterns of several different anabantoid species. For example, courtship butting is one of the most distinctive preclasp actions in *T. leeri*, but generally is limited to fewer than five butts in the closely related *T. trichopterus* (Miller, 1964; Miller & Hall, 1968), and often is absent in other forms such as *M. opercularis* (Hall, 1965) and typically is absent in *Betta splendens* (Rainwater and Miller, 1968). Likewise, *T. microlepis* exhibits much less biting and other presumably aggressive actions in its courtship behavior than is found in its congeners, although *Trichogaster* as a group appears to utilize such actions in courtship more prominently than some other genera observed.

This paper is a progress report on observations and experiments on social groups of different size in three anabantoid species, *Trichogaster trichopterus, Macropodus opercularis,* and *Colisa lalia*. Most of the behaviors used by anabantoid fishes in agonistic encounters and the relative frequency of such occurrence of these patterns in the three species are described. Some tentative hypotheses about the relationships between agonistic behaviors and several aspects of the social environment which may influence such behavior are proposed.

MATERIAL AND METHODS

At least 20 fish of each of the three species were used in these experiments. Similar-sized adult fish of the same sex and species were taken from holding tanks and placed in 10-gallon aquaria (50 × 30 × 24 cm) in groups of 2, 4, and 6. In all cases except the 6-♂ *Colisa lalia* group, fish were placed in social groups with strangers. An attempt was made to keep size variation within a group at a minimum (6 mm or less in most groups). The aquaria had gravel bottoms, sparse aquatic vegetation, fluorescent lighting, and thermostatically controlled heaters. Although water temperature varied between 22 and 28 C, the usual range was between 25 and 27 C. Lights were automatically controlled to provide a 12-hr photoperiod.

Ten-min observation periods were conducted in the morning and afternoon for 15 days. In most cases the observation days were nearly, but not completely, consecutive. Because we have found distinct daily rhythms in general activities (Hopkins, pers. comm.) and spawning activity (Miller, 1964; Hall, 1966) all observations were randomized so that one tank would not be observed at the same time throughout the study. The occurrence of each behavior pattern was recorded on a multichannel lab tally or directly on a specially prepared observation sheet. Observations on the nature of the social structure and types of social interactions occurring in each tank were also recorded on the sheet for that tank. Thus, summary sheets for each individual observation period contain data on the type and frequency of occurrence of agonistic actions, the general type of social structure prevailing, the number of individuals contributing to the bulk of activity, water temperature, time, and general comments on the qualitative nature of social activities occurring during the 10-min period.

A second series of observations was made under conditions identical to those described above, except that fish of both sexes were used in one-and two-pair groups. Three-pair groups were not used because of the known inhibitory effect of crowding on sexual behavior. These observations were conducted in order to determine whether or not any gross differences in agonistic patterns existed between one- and two-sex groups.

MOTOR PATTERNS

We have categorized 11 fairly distinctive motor patterns which occur in agonistic contexts. While all appear to have some communicatory function, some appear to be more specialized as displays than others, and one, appeasement, is actually highly variable in a motor sense, though fairly constant in a functional and apparently causal sense. We make no claims about the equivalency among these units, either in their causation or their motor coordination. They are simply easily recognized units, occurring frequently in threat and fighting behavior and courtship, and appear to be the principal actions used in the determination of social relationships. A brief description of these patterns follows.

Approach — Any movement by one fish toward another, in the absence of any immediate previous interaction, was considered an approach. Movement toward another fish during the subsequent course of a social encounter was not counted as an approach, though concomitant postural factors such as fin or opercle spreading were counted. Most variations in the type of approach are described in Miller (1964:471), except for the increased prominence of opercle spreading and sigmoid body orientation in **Macropodus** and the darting movments often present in C. **lalia**.

Opercle Spread — Described by Forselius (1957:170) as Gill-cover erection, this pattern involves movement of the operculum forward to produce an enlarged visual projection frontally. In M. **opercularis** the opercular flap extends out from the head at a sharp, nearly perpendicular angle, while in C. **lalia** and T. **trichopterus** the opercle is barely moved. Although an associated branchiostegal membrane erection is described for both M. **opercularis** and C. **lalia** by Forselius (1957:171) and for M. **opercularis** by Southwick and Ward (1968:58), this element of display was rarely observed outside of the full frontal display complex in M. **opercularis** and was not recorded as a separate unit. The difficulty of even identifying it in C. **lalia** and T. **trichopterus** (where we believe it is absent) precluded recording its use in those species.

Lateral Spread (LD) — Comprehensively described by Miller (1964), this pattern involves varying degrees of erection of the dorsal fin and anal fins and spreading of the caudal fin rays. Although intensity varied from very slight fin erection to maximal spread (other motor elements sometimes accompany the latter), no attempt was made to differentiate between spreads of different intensity for the purposes of our quantitative records. High intensity spreading was noted qualitatively on our summary sheets when it occurred prominently during an observation period.

Sigmoid Posture — A lateral curving of the body into an S-shaped posture occurs during social encounters in all of the anabantoid fishes we have studied. It characteristically accompanies the higher intensity lateral spreads but is most prominent in **Macropodus**, where it appears to be a more regular component of the lateral display complex. This seemingly highly ritualized display of **Macropodus** is well illustrated in Southwick and Ward (1968).

Tail-beating — Occurs primarily during lateral display and consists of generally slow, powerful thrusts of the tail and caudal peduncle toward the other fish, while reverse beats of the pectoral fin prevent forward movement (Miller, 1964:472). This pattern appears to be a "swimming in place" and occurs in all anabantoids we have studied. It occurs in what are apparently more intense conflict situations than most other responses.

Quivering — According to Forselius (1957:176), **vibrating** is a "spasmodic vibration that pervades the whole fish body from head to caudal fin, apparently in a caudal direction." He feels that this pattern represents the highest intensity of undulating movements, a response Miller (1964:472) termed tail beating. **Quivering** appears to be equivalent to **vibrating**, but we have some doubts about the relationship to true tail-beating, because of the high frequency and low amplitude of the lateral movements and the apparent absence of any true locomotory components; i.e., it does not appear to be derived from "swimming in place." It is found most commonly in the high-intensity, lateral-threat displays of **Macropodus** and only rarely in **Colisa** and **Trichogaster**. The frequency of vibration appears to resemble closely that of quivering movements that occur during the spawning clasp of all anabantoids.

Butting and biting — In biting, often a more violent or intense action, the attacker grasps the body or fin with its teeth and sometimes shakes its head while doing so. Butting is a thrust with the lips against the opponent's body without the grasping attempts of biting. Because it is not always possible to determine whether grasping movements are being made with the mouth, all contacts were counted as butts unless they were seen clearly as bites.

Fin tugging — Fin tugging was described in T. trichopterus (Miller, 1964:473) as a movement in which a fish grasps the soft rays of the median fin (usually the anal) and violently jerks its head in a tugging motion. It appears to be a high-intensity biting movement but is categorized separately because it appears to have some function in providing a test of strength during the terminal portions of hierarchical encounters in T. trichopterus, where two fish often alternate fin tugs until one finally submits, thus ending the bout. It gives the appearance, in this species, of being at least partly ritualized.

Chasing — Any pattern in which one fish pursues another attempting withdrawal, is considered chasing.

Appeasement — Because of the wide variety of potential postures, this category is named in accordance with its presumed function rather than its form, as is customary. In most cases, the median fins are folded, the caudal fin sometimes droops, and the fish may tilt to one side. The long axis of the body may tilt upward or downward. It often appears as if the appeasing fish is presenting flanks or abdomen to the attacker.

SOCIAL ORGANIZATION

Our observations were made on a total of 24 unisexual and 6 bisexual groups. A unique social situation prevailed in each tank, and one of the most striking features in many cases was the speed with which a given group would suddenly undergo major reorganization. Individual variation was so great that relatively little generalization is possible about the nature of the factors controlling social relationships in these fishes. In the discussion below, our data will be organized within the general categories of hierarchical and territorial relationships. By doing this we do not wish necessarily to imply any clear-cut dichotomy; rather, these two types of social groupings may be extreme representatives from alternate ends of a spectrum of possible relationships occurring in anabantoid fishes. In sunfish, Greenberg (1947:297) found ". . . that the principles of hierarchy and territory are not sharply separate but interplay in a variety of ways to shape the form of sunfish organization. It is highly probable that hierarchical relationships of some sort exist in every instance of territory. . ." Although our experience with these and other fishes in both natural and artificial environments argue that hierarchical relationships are often artifacts of captivity in fishes, they are inescapably significant in aquaria and must be dealt with if laboratory studies on fishes are to be interpreted correctly.

Hierarchical relationships were interpreted on the basis of one fish giving way before another in feeding or locomotory situations and the consistent flight or submissive posturing of one fish before the approach of another nonterritorial fish. A territory was judged present whenever a fish drove another from a restricted part of the tank. The dominant member of a 2-fish group might be considered to have the entire tank as his territory, but the fact that some of these fish built nests and defended the area near the nest more vigorously than other areas suggests a difference between the ability of a dominant fish to overcome another anywhere in the tank and the spatially oriented aggressive activity of a true territory holder. In the present study, therefore, territoriality is indicated only when a fish can drive all others from a limited portion of the total habitat.

Hierarchical relationships — Of the 24 unisexual groups, 15 exhibited relatively clear hierarchies, while 4 (groups with question marks) showed only some indication of dominance relationships (Table Ia). Hierarchies occurred in all 6 two-sex groups (Table Ib). In no case did we find a permanent straight-line hierarchy of the sort described by Noble and Borne (1938) in *Xiphophorus helleri* and by Hixson (1964) in *Lepomis cyanellus* and sometimes in other vertebrates. Even in groups of two, t was not always possible to determine which fish was dominant on any given day. Furthermore, in the larger groups, dominance relationships did not achieve stability during the 15-day observation period. Although t is possible that a longer period of time is required for the establishment of a stable hierarchy, fish in two tanks, tested for an additional 15 days, did not demonstrate any increased stability. Previous long-term observations suggest that, while stability may come to groups kept unchanged, periodic "tests" of dominants by subordinates occur and may effect change in the ranking (Miller, 1964). The present observations do not contradict this view. This contrasts with the situation we have found in sunfish *(Lepomis)* where hierarchies often form quickly and are more stable.

In all cases (Table I a & b), hierarchies initially were formed within six days of the establishment of a group, and the majority (18) were formed within three days. Despite the fact that all of the hierarchies showed some changes during the observation period, the determination of social relationships begins early in the history of a group. Groups with little or no indication of a rank order were those in which one or more fish were strongly territorial or those in which little interaction of any sort occurred. In the former, territory holders were preeminent within their boundaries, highly competitive with other territory holders, and highly aggressive toward nonterritorial fish. This typically produced a system of approximate equality among propertyholders and complete submission of others. Examples of those exhibiting little interaction were two groups of *Trichogaster* (6 ♀, 4 ♂) and one *Colisa* group (6 ♀) which spent most of their time hiding in vegetation or the corners of the tank.

TABLE I (A). INITIAL OCCURRENCE OF HIERARCHY, TERRITORY DEFENSE, AND NESTS IN SINGLE-SEX GROUPS OF ANABANTOID FISHES

	First day on which phenomenon appeared		
Group	Territory	Hierarchy	Nest
2 Blue G. ♀	—	6	—
4 Blue G. ♀	—	1	—
4 Blue G. ♀*	—	?	—
6 Blue G. ♀	6	6	—
6 Blue G. ♀*	—	—	—
2 Blue G. ♂	14	—	—
4 Blue G. ♂	2	2	—
4 Blue G. ♂*	—	—	—
6 Blue G. ♂	7	—	10
2 Par. ♀	5	5?	—
4 Par. ♀*	—	1	—
4 Par. ♀*	—	1	—
4 Par. ♀	—	5	—
6 Par. ♀	4	3	—
2 Par. ♂	—	1	—
4 Par. ♂	5	2	5
6 Par. ♂	5	?	—
2 Dwarf G. ♀	—	3	—
4 Dwarf G. ♀	—	2	—
6 Dwarf G. ♀	—	3?	—
6 Dwarf G.♀*	—	—	—
2 Dwarf G. ♂	6	2	6
4 Dwarf G. ♂	—	3	—
6 Dwarf G. ♂	1	1	1

* Replicate groups not included in Table II.

Table I (B). INITIAL OCCURRENCE OF HIERARCHY, TERRITORY DEFENSE, NESTS, AND SPAWNING IN PAIRED GROUPS OF ANABANTOID FISHES.

Group	First day on which phenomenon appeared Territory	Hierarchy	Nest	Spawning
1 pr. Blue G.	1	1	1	2
2 pr. Blue G.	2	6	5	7
1 pr. Paradise	5	1	5	—
2 pr. Paradise	3	1	3	—
1 pr. Dwarf G.	2	2	2	2
2 pr. Dwarf G.	3	3	3	—

A single fish was dominant in most groups, but in three tanks it was difficult to determine which of two top-ranking fish was dominant. Considerable shifting of ranks and the formation of dominance triangles produced social groupings which were often difficult to characterize. In many tanks, one or more fish quickly dropped to the bottom of the social order and did little but appease or flee from attacking dominants. Such "omega" fish (Greenberg, 1947:272) received apparently redirected attacks by intermediate group members as well as attacks of top dominants.

Figures 1-4 show total daily values (AM plus PM observations) of butting and chasing for 6 groups in which normal interaction occurred and a hierarchy was clearly established, but with no indications of territory development.

In terms of demonstrating a decrease in frequency or intensity of agonistic behavior with time, our observations are equivocal. If daily values are averaged for the 5 groups containing 4 fish (Fig. 5), butting and chasing frequency both show a tendency to decrease later in the 15-day period. However, Figures 1-4 show that in 2 groups (4 ♂ dwarf, 4 ♀ blue) butting peaked during the last 7 days, long after the hierarchies were originally established. Except for the 4-♂ dwarf-group, chasing seems to decrease steadily toward the end of the 15 days.

Braddock's (1945) suggestion, that familiarity between individuals leads to an increased ease of activity and decreased frequency and intensity of aggressive interaction, does not appear to hold completely true for anabantoids. If hierarchy formation led to stable social relationships, we would expect rather marked differences in frequency of aggressive behavior before and after the initial day of hierarchy formation. Figures 1-4 show no such relationship except in tank 5 (4-♀ paradise), where butting and chasing increases until the hierarchy is formed on day 5, then fluctuates downward. The initial formation of a hierarchy, however, clearly does *not* have a direct effect on the rate of performance of aggressive behavior in most of our groups. When lower-ranking fish periodically attempt to improve their stations, random fluctuations in frequency of aggression should be expected and do appear. The overall tendency for decreasing aggressiveness, especially in chasing frequency, might be dealt with by using some kind of "familiarity" construct, but then it is hard to explain why the 4-♂ dwarf group showed a consistent increase in aggressive actions with time. Factors other than familiarity with other individuals and their relative rank in the society seem to be at play in producing the kinds of variations we observed.

Finally, there appeared to be no appreciable qualitative or quantitative uniqueness in responses occurring during the formation of a hierarchy.

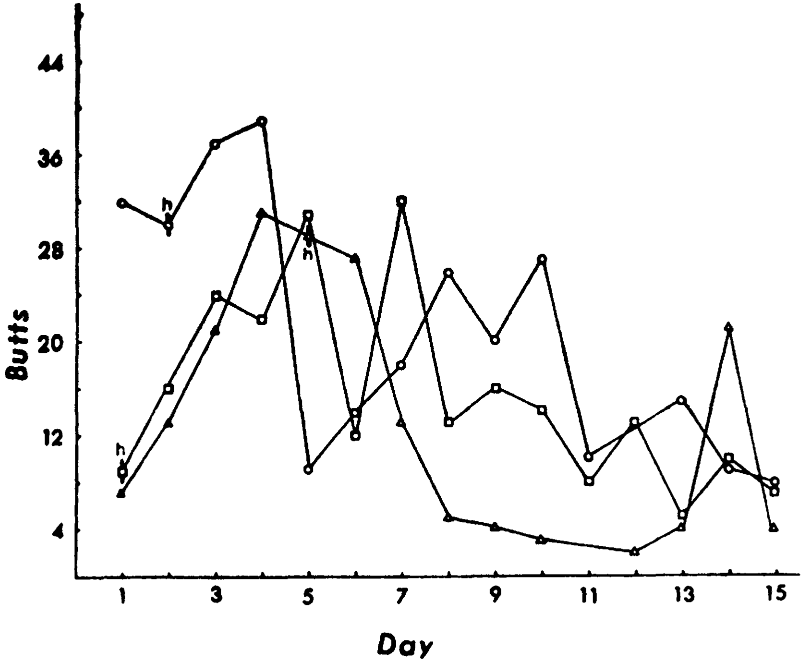

Fig. 1. The letters "h" or "t" represent day on which hierarchy or territory first appeared. Ordinate = no. of actions; abscissa = day. Total number of butts occurring during two ten-minute observation periods (a.m. and p.m.) per day over a 15-day period in three hierarchically organized groups of anabantoid fishes. Open circles = 4 female dwarf; Squares = 4 female paradise (T8); Triangles = 4 female paradise.

Territoriality — Territory defense occurred in 10 unisexual groups and in all 6 two-sex groups (Tables Ia and b). In all cases but one, territories were initially established within 7 days, but their appearance in time seems to be distinctive from that of the hierarchy groups. While most hierarchies were established within the first 3 days, most territories were first defended after day 3 (8 or 10 unisexual groups, Table Ia).

Eight of the 10 unisexual groups containing territorial fish also had hierarchies present. Of this group, four exhibited hierarchies prior to territoriality, whereas four initially showed the two relationships on the same day (Table Ia). The fact that hierarchies often precede territoriality or are absent in territorial groups, argues against the possibility that establishment of a territory facilitates imposition of a measure of hierarchical structure on a group.

Figures 6-10 suggest a general, though not universal trend toward increased frequency of agonistic responses later in the 15-day observation period. The upper curve in Fig. 10 strongly indicates that above-average performance of agonistic activities does tend to occur most commonly later in the 15-day period.

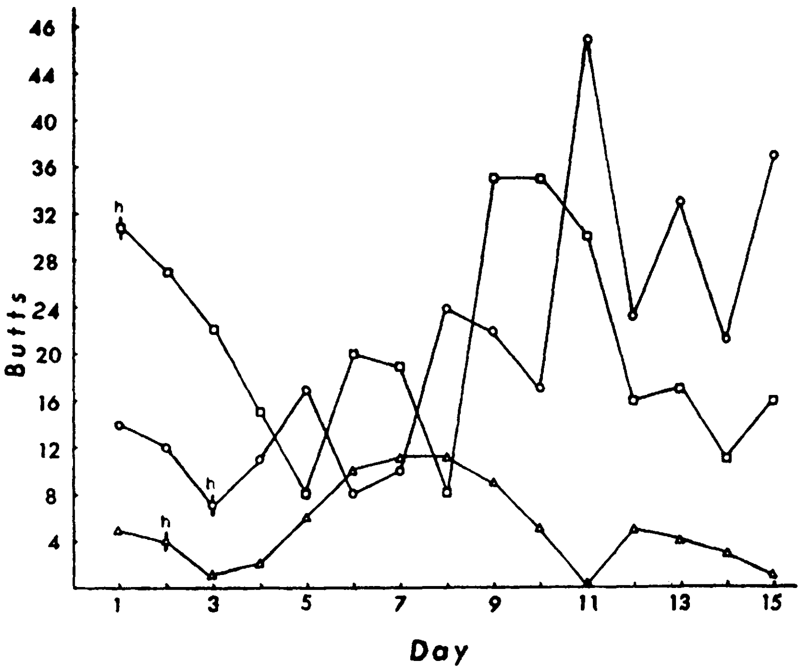

Fig. 2. As in Fig. 1, Open circles = 4 male dwarf; Squares = 4 female blue; Triangles = 2 female paradise.

One factor that seems to influence the appearance of territoriality is the number of fish in the group. Territories developed in 5 of the 6 normal tanks containing 6 fish (two other 6-fish groups showed no normal social interaction) while only 5 of 16 groups of 2 or 4 developed territoriality. The difference is significant at 0.05 (chi-square = 4.77 with one *df*) and clearly suggests that large groups, within the range studied, tend to exhibit territorial responses. This suggestion agrees with Hixson (1946) but is contrary to our previous experience (Miller, 1964) and that of Forselius (1957:197), who suggested: "By keeping a fairly big number of males together, aggressiveness and nest-building can be almost completely inhibited for several months." Since we also often have observed this phenomenon, we conclude that the mechanism(s) regulating agonistic responses and producing social organization responds to population density in such a way that "territorial tendencies" appear to peak at intermediate densities. Perhaps 6 fish is near the optimum for producing territoriality in aquaria of the size we used. A remarkably similar, but obverse, observation was made by Greenberg (1947:294) in 24 groups of 4 green sunfish kept in containers of three different sizes. He found that maximum territory development and minimum hierarchy development occurred in tanks of intermediate size.

Fabricius and Gustafson (1954), Miller (1964), Forselius (1957), Huck and Gunning (1967), and others have suggested that a certain amount of living space is required for the establishment of territories in captivity. It is difficult to reconcile these observations with our present data and those of Hixson (1946), which seem to show that the tanks in which territoriality is most likely to occur are those with least space per individual.

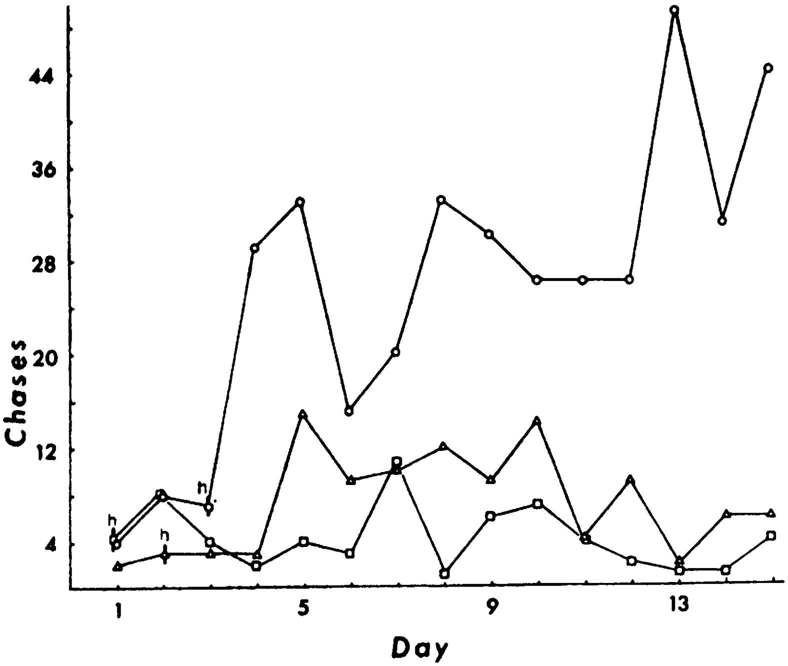

Fig. 3. Total number of chases occurring during two ten-minute observation periods per day over a 15-day period in three hierarchically organized groups of anabantoid fishes. Open circles = 4 male dwarf; Squares = 4 female blue; Triangles = 2 female paradise.

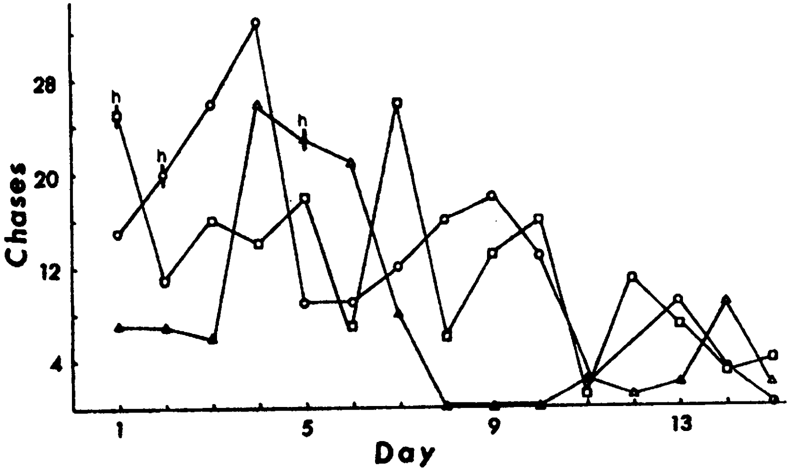

Fig. 4. As in Fig. 3. Open circles = 4 female dwarf; Squares = 4 female paradise (T8); Triangles = 4 female paradise.

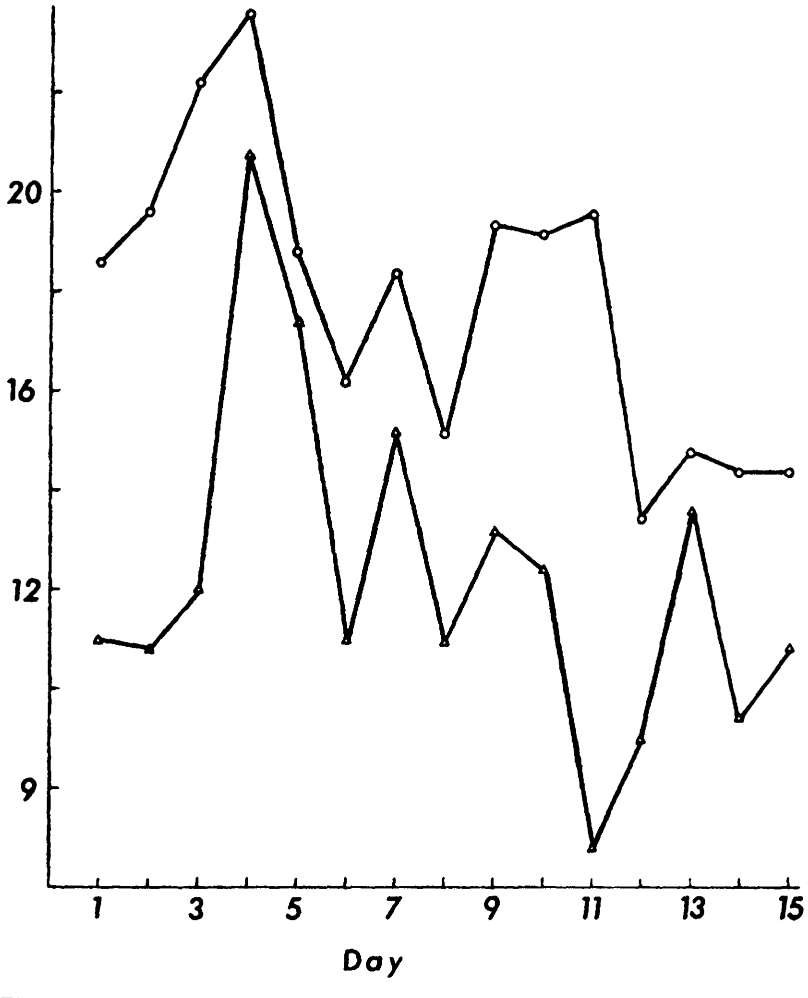

Fig. 5. Mean number of butts (circles) and bites (triangles) occurring during two 10-minute observation periods in five hierarchical groups of four fish over a fifteen-day period. Ordinate = mean no. of actions; abscissa = day.

Many authors suggest that increased crowding produces enhanced aggressiveness in fishes, and experimental support for this view is provided by Erickson (1967) and Borkhuis (1965; in green sunfish). However, Borkhuis did not find this to be true in bluegills or in green sunfish that had limited experience with high density populations. While our data (Table II) seem to indicate a fairly consistent trend toward increased agonistic activity in larger groups, consideration only of groups showing territoriality may provide more information about the relationship between frequency of aggression and the appearance of territorial behavior. If crowding induces an enhanced aggressive state, leading to the appearance of territory defense, we would expect the daily values for agonistic responses to be consistently greater in groups of six than in smaller groups. Figures 6 to 10, while not unequivocal, appear to show a trend toward increased aggression in groups of six, especially after initial establishment of a territory. Perhaps all that can be said at present is that increased population density leads to increased frequency of aggressive activities and greater likelihood of the establishment of territories, up to a given density, beyond which formal group organization involving all members of the group breaks down. This critical density probably will be different in different species and ontogenetic stages.

Another factor complicates the determination of causal factors leading to definitive social organization in these fishes. While previous studies such as those of Greenberg and Hixson dealt primarily with immature fish, thereby excluding the possibility that territory defense was mediated via sexual mechanisms involving endocrines associated with reproduction, this study used mature, sexually responsive fish. The fact that all 6 tanks with fish of both sexes contained nests and territorial males within 5 days of initial grouping, argues for a link between sexual stimuli (presence of female), territoriality, and nest-building. Although spawning occurred in only 3 of the 6 tanks, typical nest-building and courtship responses occurred in all. Since nests also occurred in 4 of the single-sex groups (Table

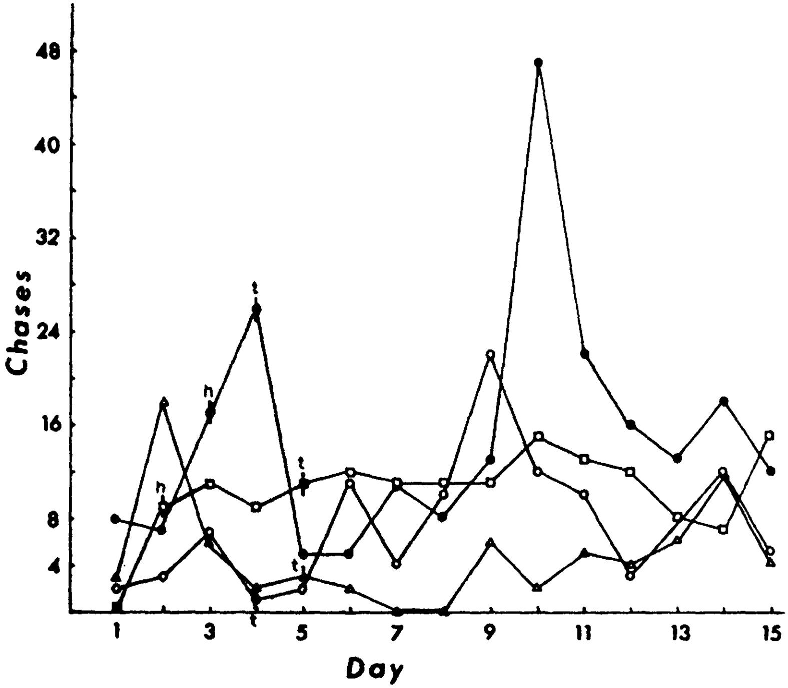

Fig. 6. Total number of chases occurring during two ten-minute observation periods per day over a 15-day period in four territorial groups of anabantoid fishes. Closed circles = 6 female paradise; Open circles = 6 male paradise; Squares = 4 male paradise (T7); Triangles = 2 female paradise.

TABLE II. TOTAL NUMBER OF AGONISTIC RESPONSES OCCURRING OVER A 15-DAY PERIOD IN 18 GROUPS OF ANABANTOID FISHES (see text).

Behavior				Species					
	Blue G.			Paradise			Dwarf G.		
No. of fish	2	4	6	2	4	6	2	4	6
Female groups									
Approach	28	156	1036	203	144	930	85	193	427
Chase	6	66	328	73	177	241	47	190	110
Opercle spread	—	—	—	181	81	351	—	—	4
Lateral spread	20	126	791	160	60	421	90	74	99
Sigmoid posture	—	—	14	40	16	211	2	3	—
Quivering	—	—	—	2	2	56	—	—	—
Tail-beat	—	37	193	6	9	12	2	8	18
Butt	52	310	1187	82	222	295	60	294	199
Bite	1	12	30	—	8	—	—	11	2
Fin Tugging	4	24	70	—	—	—	—	—	—
Appeasement	—	8	7	2	34	26	—	17	1
Male groups									
Approach	9	53	537	172	370	386	243	601	1560
Chase	—	12	97	120	155	104	232	377	376
Opercle spread	—	—	—	38	430	171	—	1	—
Lateral spread	27	149	471	38	233	144	46	538	1713
Sigmoid posture	—	—	3	52	220	159	1	3	9
Quivering	—	—	—	28	7	19	—	—	8
Tail-beat	3	5	31	4	5	4	9	16	65
Butt	13	85	537	76	70	100	299	303	868
Bite	2	6	7	—	2	—	1	1	41
Fin-tugging	1	8	3	—	—	—	—	—	15
Appeasement	—	—	4	103	74	3	11	18	50

Ia), the possibility exists that sexual mechanisms contribute to the appearance of territoriality even in the absence of obvious sexual stimuli. The fact that territories developed in 7 of 10 ♂ groups, but in only 3 of 14 ♀ groups (two in paradise fish groups; ♀ paradise fish sometimes construct and defend their own nests in breeding tanks; Hall, 1965) further suggests that this factor may be of significance in studies on adult fish. Conversely, however, there is little indication that frequency of aggression and persistence or intensity of territory defense were any greater in those tanks containing nests than in others. Thus, there appears to be a clear relationship between sex-related factors and territoriality in the 2-sex groups, but a much more ambiguous connection between such factors and territoriality in single-sex groups.

Evaluation of all qualitative and quantitative data suggests the following scheme. Any factor that tends to produce increased contact between individuals within a restricted area will lead to increased frequency and intensity of agonistic behavior and the subsequent development of a structured social order. In small groups factors such as increased locomotion, "searching" for nest sites, mates, etc., and competition for food might be expected to increase contact frequency. In groups of six, the density of the population alone would be enough to produce a much higher rate of contact. Once agonistic interaction is occurring at a high rate, the relative significance of size, physical condition, hormone state, previous experience, and other factors may begin to be reflected in the out-

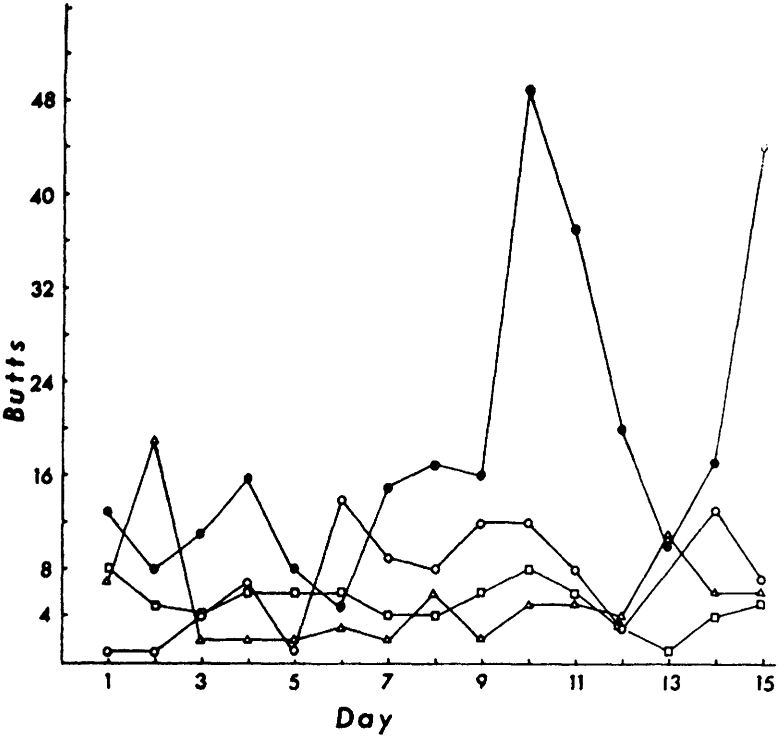

Fig. 7. Total number of butts occurring in same groups as in Fig. 6.

comes of such interactions. Initial relationships between individuals will usually be determined within the first 3 or 4 days and take the form of a social hierarchy. Where appropriate gaps exist between the success rates of the individuals of a group, the hierarchy will tend to maintain itself, with some modification, to the end of the period. In at least some cases, formation of a stable hierarchy will permit a decrease in overt aggressive interaction (Figs. 1 to 5). In cases where the rate of success in agonistic encounters does not show individual distinctiveness, where sexual mechanisms may be highly active, or where several individuals retain high competitive response rates for food, space, etc., the most dominant individuals will begin to defend restricted areas of the tank. Once this occurs, success in territory defense becomes self-reinforcing, and the frequency and intensity of aggressive behavior increases (Figs. 6 to 10). Aggressive encounters at this stage may also produce higher response totals through mimetic effects and redirected aggression by subordinate fish.

While we do not wish to contradict our introductory statement concerning the continuity between hierarchical and territorial organization, there appear to be not only distinctive patterns of activity for the 2 types of social groupings but also an indication of dissimilarity in the causal factors producing them.

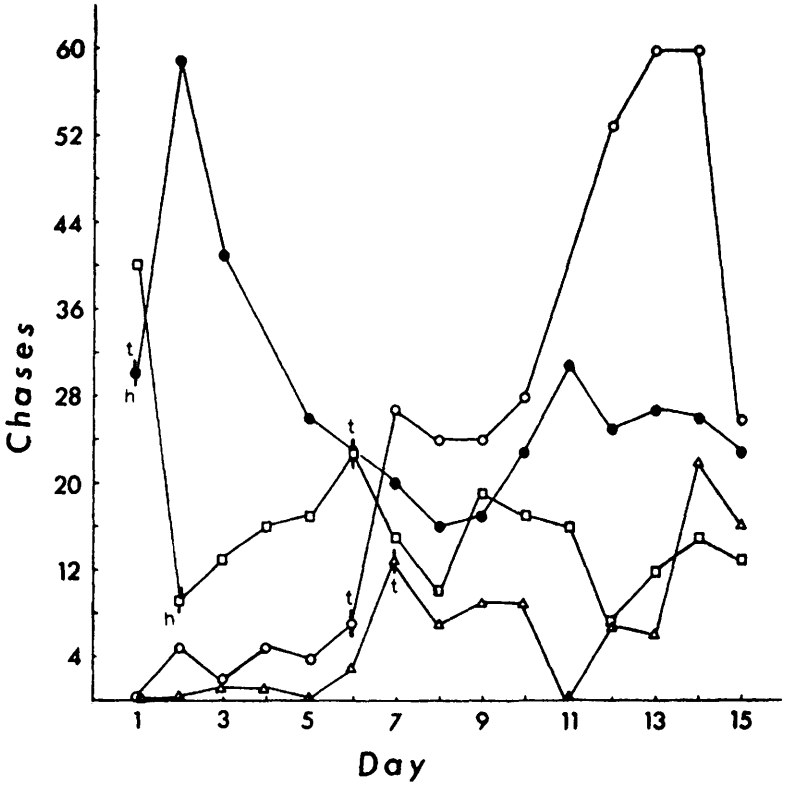

Fig. 8. As in Fig. 6. Closed circles = 6 male dwarf; Open circles = 6 female blue; Squares = 2 male dwarf; Triangles = 6 male blue.

QUALITATIVE DIFFERENCES IN BEHAVIOR

General Patterns — Although the 3 species studied share a majority of behavioral traits, qualitative differences are evident. In some cases these distinctive qualities seem to be associated with certain morphological specializations imposing a form or rhythm to movement and producing a recognizably unique pattern. In others, it is possible that behavioral adaptations may have occurred independently of structurally imposed restrictions, and in some cases, may actually have led to morphological change.

The behavior of *Colisa lalia* is an example of the first possibility. Most *Colisa* movements have a fluttery or jerky coordination. The fish go forward or backward in swift, darting moves. Although they can use the pectoral fins to make slow, smooth movements, much of their behavior during social interaction is characterized by less graceful darting approaches associated with body propulsion. This is most striking in their attack and chasing patterns. We believe that this qualitative trait is associated with the relatively deep, short body and caudal peduncle, which do not permit body undulation to produce the more sinuous movements found in more elongated species. This locomotory constraint may have produced some degree of behavioral specialization in which many approaches during social interactions involve a fast charge, often eliciting a brief dodging movement and subsequent chase. Table II shows that ♂ dwarf gouramis tend to approach and chase more frequently than males of the other two species. A tendency toward increased butting (associated with direct frontal attack) also seems to exist in ♂ *C. lalia*.

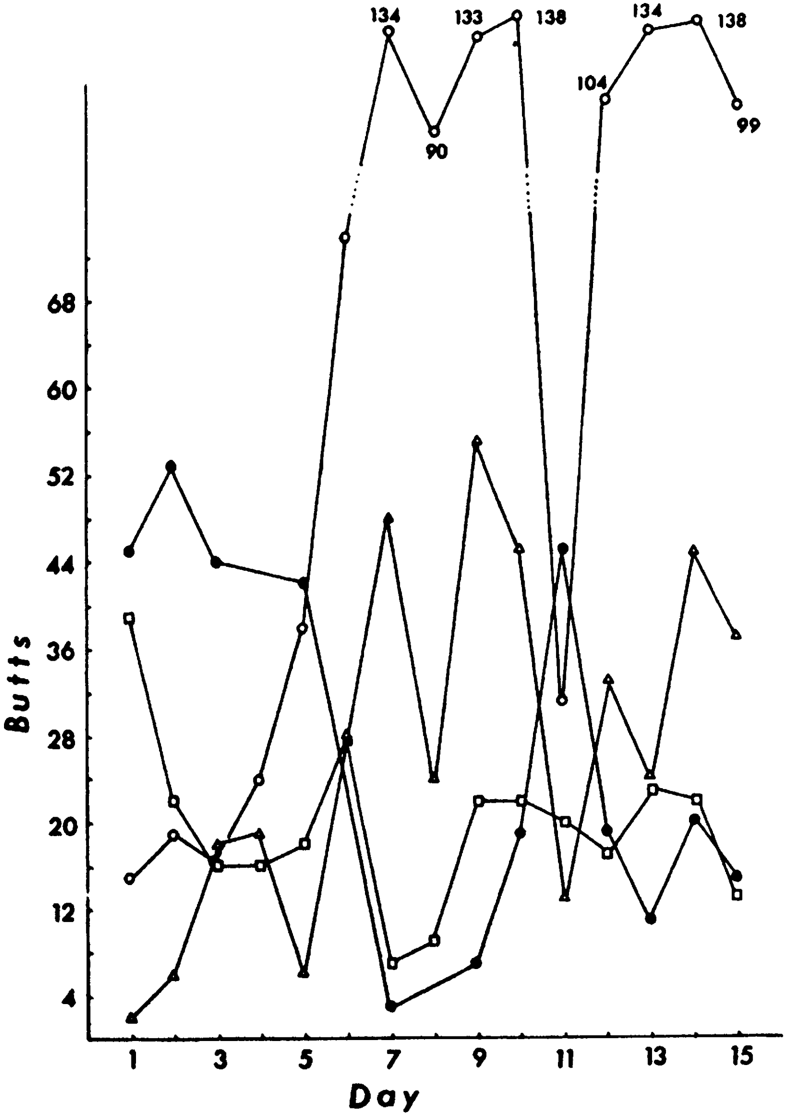

Fig. 9. Total number of butts occurring in same groups as in Fig. 8.

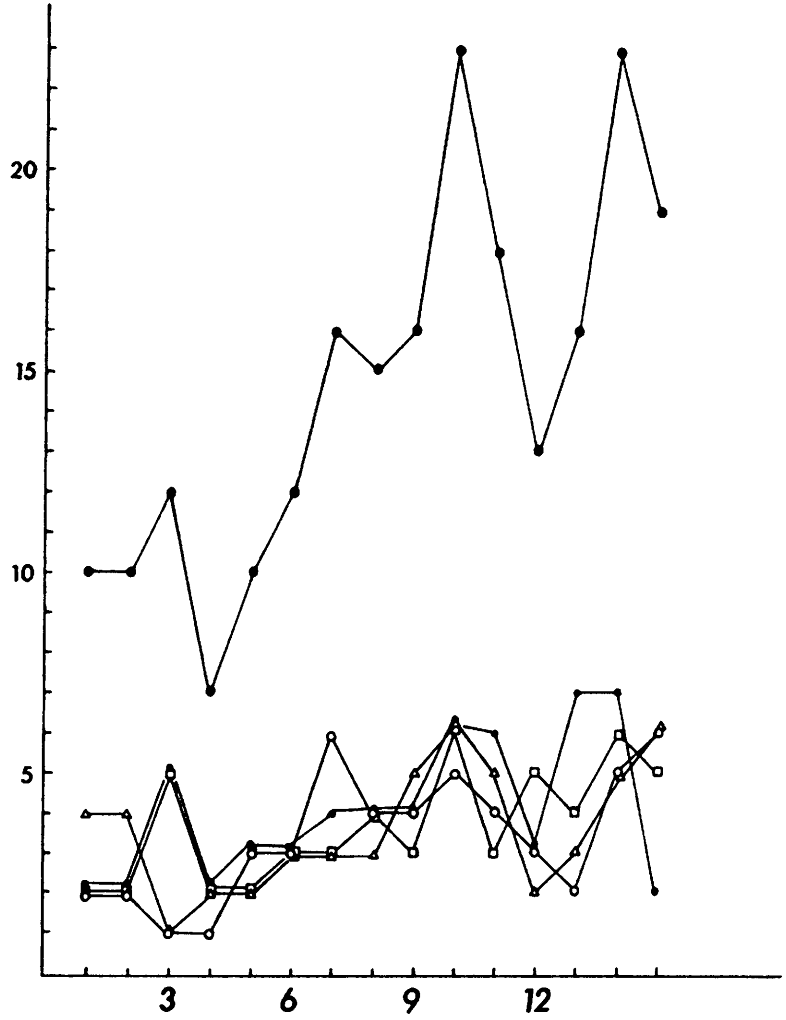

Fig. 10. Lower curves represent the total number of groups (of the eight described in Figs. 6-9) showing above-average response rates in 4 activities on each day of the 15-day period. Triangle = butting; Closed circle = chase; Square = LD; Open circle = approach.

Upper curve is a simple summation of the lower curves.

Ordinate = number of groups above average for each response on a given day. Abscissa = day number.

Behavior patterns such as chasing and butting are often considered to be the best indicators of aggressive motivation. If our hypothesis about a morphologically influenced locomotory pattern is correct, it is possible that a behavioral adaptation fitting preferred agonistic response patterns to optimal locomotory functions might actually be interpreted, on the basis of unqualified quantitative data, as an indication of a characteristically high aggressive motivation in the species. Qualitative considerations would argue otherwise, however. Although *C. lalia* shows much chasing and butting, the chases are often very brief; furthermore, the strong biting and tugging movements so often seen in the more violent struggles of *T. trichopterus* are generally absent. Thus, while overt aggressive movements are a more prominent part of ♂ *C. lalia* interaction in terms of frequency, they appear to be less violent than those of some other species, and seem to have more signal value than equivalent actions of contraspecifics. Therefore, any attempt to categorize *C. lalia* as being a "more aggressive" species because it chases and butts more frequently than other species would be most arbitrary and probably meaningless in a causal sense.

Another example of the interaction between structural and behavioral specialization occurs in *Macropodus opercularis* and also to some extent in *Macropodus cupanus, Betta splendens,* and probably other congeners. These species are among the most elongate, serpentine forms of the suborder and tend to have long, flowing caudal fins. Their typically graceful, fluid movements are in marked contrast to those of *C. lalia*. Although they rely heavily on frontal confrontation during agonistic encounters; the elements utilized in frontal threat are different from the darting rushes of *C. lalia*. In *M. opercularis* the frontal display appears to be highly ritualized and is typically performed in a relatively slow or stationary locomotory context (see p. 5).

Possibly the more elongate body and caudal fin are related to a more undulatory locomotory pattern and greater use of display patterns most effective in relatively stationary mutual display situations (opercle spreading, branchiostegal erection, median fin erection in lateral displays, and quivering). This cannot be true for all of the patterns because lateral spreading occurs in all anabantoids, regardless of body form, in stationary or slow-moving contexts. Nonetheless, the difference between the rushing attack of *C. lalia* and the deliberate posturing approach of *Macropodus* might well be dependent on the way they move which, in turn, may be dependent on a particular body form that evolved under the influence of nonsocial factors.

Conversely, at least one morphological element of the frontal display complex seems to have evolved after the development of opercle spreading as a social signal. Forselius (1957:171-3) pointed out that while many species exhibit gill-cover erection, only those with an exaggerated movement also have well-developed opercular color markings. This suggests the more recent acquisition of a morphological change contingent on prior behavioral specialization.

Our observations suggest that many of the qualitative differences between species may be directly due to certain structural modifications which can constrain behavior and which may have originally evolved under the control of nonsocial selective mechanisms. Since the faster or slower performance of an activity may lead to changes in the total number of such activities performed in a given time unit, the quantitative divergences discussed below may owe some of their distinctiveness to these morphological limitations and influences rather than to divergent motivational mechanisms, per se. Information on the nature of interactions between independent variables of this sort is nonexistent, and we can only provide the suggestion that such factors perhaps should be considered in causal analyses of the behavior of species groups. An experimental verification of the reality of this distinction, however, does not seem possible without mutilating the fish.

Specific Differences — Despite their differences, each species appears to have the structural capacity to perform all behaviors monitored in this study. The fact that they do not perform these behaviors in quite the same way or with the same relative frequency may be due to one or more of the following factors: (1) An action may be difficult or uncomfortable to perform, given a certain morphological configuration. (2) Social organization may be distinctive enough in the different species that one group of actions may be predominantly dictated by circumstances in one species, a different group in another. (3) Each behavior may be associated with a characteristic motivational state; occurrence of this state may not be uniform in the different species.[3] (4) Although a complex of individual actions may occur as a mosaic during a given motivational state, various factors operating during the ritualization process may produce a *characteristic mosaic* for each species; thus, while motivational state may be identical in a given situation in different species, the behaviors observed at that time may not be the same in all species. For example, during a conflict state involving simultaneous tendencies to approach and avoid another fish, frontal approach (including at least some special display elements) at the outset of an agonistic encounter is often transformed gradually into a lateral display which, in turn, is often terminated by either full approach or avoidance (attack or fleeing) and their concomitant signal elements. The threshold for shifting from frontal threat to lateral threat might gradually change in one species so that, at a given conflict state, one form might still be exhibiting frontal threat while the other might be showing lateral threat. Thus, *M. opercularis* might be in a motivational state relatively identical to that of *T. trichopterus*, yet still be performing a frontal threat while the latter has already shifted to lateral threat. By "pushing forward" the threshold level for transition from one pattern to the next, it may be possible to almost eliminate appearance of the former response because of the transitory nature of its causal state. In grouped animals with relatively high environmental stimulation, a conflict state may be nearly always present. Other factors may enter into determining which patterns are utilized and how they are performed, but the above seem to be the most likely possibilities.

Clues as to which factors are significant in the occurrence of or nature of any given response pattern are limited, but the four following examples illustrate the usefulness of the concept in describing relationships among some of the behavior patterns investigated.

Opercle spreading and other elements of frontal threat display play a significant role in social interaction only in *M. opercularis,* of the 3 species discussed here.

This behavior appears to be fairly highly ritualized in *Macropodus. T. trichopterus* rarely shows opercle spreading (not recorded in the present study) and *C. lalia* exhibited it only 6 times in this study. Because the amplitude of the movement is so low in the two latter species, especially in *T. trichopterus,* it is possible that a few occurrences were missed by the observers. Nonetheless, it is clearly not a significant component of frontal threat or fighting in either form. Opercle spreading in the latter 2 species seems to be associated with a high attack tendency which is at least partly inhibited. Since there are no nonsignal attributes which might provide a functional link with the context in which opercle spreading occurs, it is likely that fixing of the behavior in the repertoire is based primarily on its communication value. If the response evolved primarily

---

[3] Both (3) and (4) are based on tentative acceptance of an attack-escape model of the sort proposed by Morris (1958a) to account for motivation during threat and fighting.

as a signal, it is unlikely that discomfort or motor difficulty associated with its execution could be a strong factor in limiting its performance. Factor 2 (above) seems of little value here since there appear to be no significant differences in the social orders formed by the 3 species. Factors 3 and 4 thus seem most likely to provide an answer to the question of causal organization, but there is little evidence as to which, if either, is the more likely. In favor of factor 4, it seems unlikely that the motivational organization of threat and fighting could be very different among these species.

Sigmoid display occurs mainly in what qualitatively appear to be extremely intense conflict situations in all 3 species. Quantitatively, this pattern occurs mainly in the larger groupings (Table II) where rather high numbers of agonistic actions occur and where presumably there exists a fairly high background level of agonistic motivation. A shift in the threshold for appearance of the response could easily account for the interspecific variations.

Quivering has never been seen in *T. trichopterus*, is rare in *C. lalia*, and fairly common in *M. opercularis*. In the latter, it typically accompanies strong sigmoid flexure. Since quivering occurs during strong body flexure in spawning of all species, it is possible that its appearance in the display context originated as a mechanical concomitant of an extremely high muscle tension occurring during sigmoid flexure. It appears to have achieved a signal function which may be distinctive from that generated by sigmoid flexure alone. This would agree well with the observation that sigmoid flexure is a much more conspicuous and exaggerated movement in *M. opercularis* than in the other 2 species. In this case, motor exaggeration of one signal movement (sigmoid flexure) may have led to the psychologically passive appearance of another which then developed its own signal function.

Fin tugging is the other pattern showing major qualitative differences among the 3 species. It tends to occur at the end of intense agonistic bouts in *T. trichopterus*. It has been seen ocassionally in some *C. lalia* and *M. opercularis* encounters, where the behavior is variable and has forms different from the deliberate, formalized tugging of *T. trichopterus*. There is no evidence identifying factors which might account for interspecific variations in the occurrence of this pattern.

These comments on possible origins and causal relationships of these agonistic behaviors are clearly conjectural, but we feel that such suggestions have value if they encourage discussion and experimentation.

QUANTITATIVE DIFFERENCES IN BEHAVIOR

A summary of the total frequency of agonistic actions occurring in groups over a 15-day period is presented in Table II. Difficulties are encountered in interpreting these data for several reasons. Probably the most significant problem is that of replication. Because of limitations on time and space, it was impossible to replicate all of the original groups. Furthermore, while most replicated groups were very similar, groups that showed little or no normal social interaction were strikingly different from normally interacting groups. Thus, while several apparently significant patterns can be observed in those groups judged to contain normal interaction, there remains some question about the meaning of the nonreactive groups. We have some apprehension about generalizing too broadly on the basis of quantitative data of this sort. Accordingly, some of the suggestions presented below are tentative, requiring future work for confirmation.

In evaluating these data it would be desirable to have a value representing all interactions occurring during observation periods; this would permit determination of how often the fish acted in a certain way while in a situation conducive to social activity. Although we initially attempted to record such circumstances under the term "encounter" we abandoned this measure because of the difficulty of determining when one encounter ended and another began, especially in the crowded, highly interactive groups. The best substitute, as a baseline measure for comparative purposes, is approach frequency, though it must be remembered that an initial approach sometimes may be followed by a series of bouts of interactions not involving appreciable separation of the fish, and any approaching movements occurring therein were not scored. Nonetheless, it is possible to get a rough idea of how often a particular response pattern appeared when two fish were in position to interact.

Group Size — Table II shows that, with few exceptions, the total number of approaches per single-sex group increased with increased number of fish. This suggests there is no major inhibition of activity due to increasing numbers in the group (within these limits) but tells little about the nature of interactions in the groupings. If these values are transformed to *total number of approaches per fish,* the same general pattern is observed, though two of the paradise fish groups do not conform precisely. It seems clear that where interaction is not grossly inhibited by unknown factors, as in several nonreactive groups, increasing the number of fish in a group produces a disproportionately large increase in the number of approaches (and probably total interactions) occurring in that tank.[3] When we consider the fact that in most of the 4- and 6-fish groups 1 or 2 fish remained in permanent submission, we are led to suggest that increased crowding has a stimulatory effect on group interaction. The form that this may take is not constant, inasmuch as most of the increased interaction may be due to intense activity of 1 or 2 fish, or to repetitive challenging of as many as 4 fish, as in the 6-female paradise group. As might be expected, there is a trend for the higher numbers of interactions to occur in those tanks in which more than one fish dominated or possessed a territory, but here too there is some variation and the shifting nature of the relationships from day to day makes precise analysis impossible.

Such a finding is not surprising when one considers the nature of the habitats used. While it is possible for a fish to achieve visual isolation from a single tankmate in the sparse vegetation present, it is impossible to do so in groups of four, and it is almost impossible for a member of a group of six to avoid *intimate* sensory contact with several others when moving about the tank for any purpose. Under such conditions heightened sensory input alone might be adequate to produce the increase in responses.

Although it seems that social interaction is increased by crowding, we must try to determine whether or not agonistic response patterns show similar relationships with group size. If approach frequency is used as an estimate of the total number of times 2 fish were in a position permitting performance of agonistic actions, it is clear from Table II that the relative frequency of overt aggressive responses *per fish* (chasing and butting) generally drops sharply with increased group size. This is especially true for chasing frequency, but is also true for butting, except in the blue gourami groups. The apparent close correlation between butting and approach frequency in blue gouramis probably is spurious, be-

---

[3] It could be argued that in the 4- and 6-fish groups, the total number of pair combinations jumps to 6 and 15, respectively, and that these figures should be used to calculate expected frequency of contact rates for larger groups. This would be correct if all fish in the groups had an equal chance to contact or react to all others. Since this was not the case in any of the groups, a simple arithmetic relationship based on increase in number of individuals was used as the best estimate of increased likelihood of contact. Probably some value between the two sets discussed here would be most accurate in reflecting increases due primarily to increased probability of contact.

cause of the very high incidence of repetitive butting in that species. Thus a substantial proportion of the approaches are not followed by butting in this species. Although *LD* frequency shows a slightly better correlation with approach frequency, the data are equivocal on this point. The conclusion that seems to derive from these observations is that, while increasing the number of fish in a tank promotes a disproportionately large increase in social encounters, many of these encounters are relatively mild, with little or no overt aggression. Here, then, may lie some support for the contention that frequent contact may promote familiarity leading to increased tolerance of tankmates. Alternatively, this could also mean that in larger groups approached fish learn to withdraw more rapidly and effectively without eliciting chasing or butting. Since we showed earlier that daily values for aggressive actions often tended to rise on successive days in territorial groups and drop in hierarchical groups, the effects of total number of fish in a group are probably so intertwined with effects of the nature of the social organization as to defy elucidation with the present data. We can point out, however, that all but one of the 6-fish groups exhibited well-defined territoriality, whereas hierarchical tendencies were often poorly defined or ephemeral in the same groups.

Effects of Species and Sex — If approach frequency is used as a baseline, it is possible to calculate the relative frequency of certain agonistic responses in male and female groups of the 3 species. Table III shows the mean rate of chasing, butting, and *LD* responses per approach in 3 groups (2, 4, 6 fish) of each sex in the 3 species.

An unexpected observation derived from this table is that females show more overt aggressive responses per approach than do males. Response rates for chasing and butting were significantly higher (0.05 or better) in ♀ groups than in ♂ groups, except in the paradise fish chasing rate, whereas the converse was true for *LD* rate, again with paradise fish being the exception. The reasons for this are not immediately apparent,

TABLE III. AVERAGE NUMBER OF CHASES, BUTTS AND LATERAL SPREADS OCCURRING PER APPROACH IN THREE GROUPS (2, 4, 6 FISH) OF EACH SEX IN THREE SPECIES OF ANABANTOID FISH.

		Species	
	Blue Gourami	**Paradise**	**Dwarf Gourami**
No. of chases per approach			
Males	.18	.40	.40
Females	.32	.38	.49
No. of butts per approach			
Males	1.06	.26	.40
Females	1.26	.46	.78
No. of *LD* per approach			
Males	1.08	.44	.95
Females	.76	.50	.37

but may be related to the fact that social patterns are quite distinctive sexually in blue and dwarf gouramis in mixed groups and breeding contexts. The absence of inhibitions normally provided by dominant or territorial males may produce a "rebound effect" of heightened aggressive responses in females. Paradise fish, which show a divergent pattern in chasing and *LD* rates, do not exhibit such prominent sexual dimorphism in agonistic responses: both males and females defend nests and territories, and the intensity of aggressive behaviors is lower in this species than in the others, especially in males. Acceptance of the "rebound effect" hypothesis requires that the fish have had previous contact with males in mixed groups, a situation that did prevail in most of our fish.

The high butting rate in blue gouramis reflects the greater incidence of repetitive butting in that species, while we believe the relatively high chasing rate in dwarf gouramis is associated with the darting approach, brief display, and short chase described earlier as a possible concomitant of their specialized body form. Paradise fish exhibit a rather high chase rate but the lowest butting rate, a factor which may contribute to the general impression we have of these fish being less "violent" in their social interactions. Perhaps noteworthy is the fact that relative butting rates here are in agreement with courtship butting rates observed in spawning females, where the courtship butt apparently serves as a sexual signal as well as a means for inhibiting male aggression (Miller, 1964; Miller and Hall, 1968). Female blue gouramis generally butt the male 1-10 times after approaching him, while dwarf gouramis butt at a lower rate (1-4) and paradise fish often do not butt. Whether this similarity is merely a coincidence or is another indication of a kind of species-typical channeling of responses in agonistic situations cannot as yet be determined. The latter possibility, however, would fit in well with the hypothesis that the effects of one major adaptive modification may permeate a wide variety of response modes dependent on the modified structure or mechanism.

Paired Groups — Table IV presents the total number of agonistic responses occurring in 1- and 2-pair groups over a 15-day observation period. While they are obviously not in complete agreement with the results obtained from single-sex groups, these data will not support any strong divergence from the generalizations described above, but usually

TABLE IV. TOTAL NUMBER OF AGONISTIC RESPONSES OCCURRING OVER A 15-DAY PERIOD IN 6 PAIRED GROUPS OF ANABANTOID FISHES (see text).

	Species					
	Blue G.		Paradise		Dwarf G.	
Behavior No. of Fish	one pair	two pair	one pair	two pair	one pair	two pair
Approach	16	333	191	347	228	883
Chase	4	51	151	96	175	179
Opercle spread	1	—	50	213	—	—
Lateral spread	20	298	113	205	32	526
Sigmoid posture	2	13	106	228	—	203
Quivering	—	—	—	4	—	—
Tail-beat	6	12	1	1	—	82
Butt	31	257	113	73	205	257
Bite	25	9	—	—	—	—
Fin-tugging	7	3	—	—	—	—
Appeasement	—	7	5	33	—	—

provide support for them. Thus, while approach frequency is much higher in 2-pair groups, relative frequency of agonistic actions (# per fish) drops in 2-pair groups just as in the 1-sex groups. Likewise, the use of particular patterns among the species appears very similar in the paired and single-sex groups. Spawning occurred in both *T. trichopterus* groups and the 1-pair *C. lalia* groups, while only nest building occurred in the others, but there was no indication that this produced any marked difference in agonistic behavior scores in this limited sample. Although it seems reasonable that factors associated with spawning, courtship, and other reproduction-oriented processes should influence agonistic behavior in these fishes, there does not appear to be any appreciable indication of such an influence, aside from a possible slight increase in frequency of approaching in paired groups. Lateral display, the only recorded response which is regularly used in a courtship context, does not appear to be more frequently used in paired groups. Absence of a recognizable sexual effect on agonistic behavior might be due either to reproductive factors having a very limited temporal effectiveness or simply to their effect being masked by rather high response rates induced by the nonsexual social aspects of the stimulus situation.

SUMMARY AND CONCLUSIONS

Agonistic behavior was studied in different groups of 2, 4, and 6 fish of each of 3 anabantoid species (*Trichogaster trichopterus, Colisa lalia,* and *Macropodus opercularis*) confined in 10-gal aquaria for 15 days. Records were made of the frequency of occurrence of 11 agonistic behavior patterns during two 10-min observation periods per day, and additional notes were taken on the physical situation and social relations prevailing in each group during the observations.

Hierarchies were formed in most of the male-only or female-only groups and in all of the paired groups, while territory defense occurred in less than half of the single-sex groups but in all of the paired groups. Most of the hierarchies originally appeared by the third day of the experiment, whereas most of the territories initially appeared between days 4 and 7. Groups exhibiting hierarchical organization alone tended to show decreased overt aggression toward the end of the 15-day period, while territorial groups were more aggressive later in the period.

Several types of hierarchical arrangements occurred in these groups, with individuals often shifting ranks. Territorial relationships tended to be somewhat more stable, but changes sometimes occurred. The effects of space, sex, and number of fish on the type of social organization in a group were briefly considered.

Qualitatively, the 3 species were found to share most of the 11 behavior patterns utilized in agonistic contexts, though the form, amplitude, and temporal organization often was distinctive. Blue and dwarf gouramis rarely, if ever, utilized the opercle spreading, sigmoid posturing, and quivering common in paradise fish, while the fin-tugging typical of blue gouramis almost never appeared in the other two forms.

Quantitative differences also exist in the frequency of use of the agonistic elements of the 3 species. For example, butting appears to be less frequent in paradise fish groups than in the other two forms, whereas appeasement occurs more commonly in paradise fish.

Analysis of the patterning of individual units of behavior showed numerous divergences among species. Several were suggested as related to locomotory specialization and its subsequent effect on facilitating certain types of social responses. A different type of situation, exemplified by butting frequency, involved a possible relationship between frequency of use of a patently agonistic element, butting in the purely social context, and use of an isomorphic element, courtship butting, in the reproductive context. Some other species-typical differences in tendencies to use certain patterns more frequently were ascribed to differences in the threshold for elicitation, and we argued that evolution of unique threshold relationships might be an important factor in the structuring of social activity.

Group size was found to have a complex relationship with frequency of agonistic activity. While more absolute activity occurred in larger groups, the net agonistic activity per fish in a group tended to decrease with increasing group size. Female groups tended to exhibit more overt aggression per approach (number of approaches gives a rough measure of the amount of inter-individual contact) than similar-sized male groups of the same species.

Paired groups generally showed the same quantitative relationships in agonistic activity as single-sex groups, even though spawning occurred in 3 of 6 groups.

Unquestionably, both qualitative and quantitative differences exist in the agonistic patterns shown by the 3 species in single-sex and two-sex groups. Although we have suggested some ways in which these mechanisms may have developed, our data are not strong enough to support definitive statements on causal organization. We cannot now explain why butting plays such a significant communicatory role in the life of the blue and pearl gouramis, but not in those of paradise fish or fighting fish, or why the blue gourami seems to be the only Belontiid to utilize highly formalized fin tugging during tests of dominance. While more finely detailed quantitative studies such as that of Miller and Hall (1968) provide certain insights into such problems, only careful experimental studies like that of Sevenster (1961), coupled with phylogenetic investigation, offer much hope of accurate analysis.

Until such studies have been conducted, we feel that we must also reject the possibility of characterizing the 3 forms studied as being more or less "aggressive" with relation to one another. As Simpson (1968:3) has pointed out, the concept of "aggression" has been used to encompass a variety of behaviors grouped on the basis of similarity of function, consequences, or causes, often with little attempt being made to define operationally the independent variables involved. It seems desirable at present to concentrate efforts on clarifying the relationships between the use of individual response patterns (as measured in various ways) and the complex social phenomena which are dependent on them for their resolution.

ACKNOWLEDGMENTS:

We gratefully acknowledge the support of the National Science Foundation through grants (GB-1989; GB-4711) to the senior author. Miss Cynthia Fite helped obtain the observational data, and she, Mr. Howard Hopkins, and Mr. Robert Wimmer ably assisted us in maintaining the fishes during the period of the study. We wish to thank these individuals, and the staff of the Oklahoma State University Research Foundation for their aid in conducting the research and preparing this report.

LITERATURE CITED

Baerends, G. P. 1958. The contribution of ethology to the study of the causation of behaviour. Acta Physiol. Pharmacol. Neerl. 7:466-499.

Barlow, G. W. 1962. Ethology of the Asian teleost *Badis badis.* III. Aggressive behavior. Z. Tierpsychol. 19 (1):29-55.

Borkhuis, M. L. 1965. Aggression and group size in fish. M.S. thesis, Univ. South Dakota.

Braddock, J. C. 1945. Some aspects of the dominance-subordination relationship in the fish *Platypoecilus maculatus.* Physiol. Zool. 18:176-195.

Brown, J. L. and R. W. Hunsperger. 1963. Neurothology and the motivation of agonistic behavior. Anim. Behav. 11 (4):439-448.

Erickson, J. G. 1967. Social hierarchy, territoriality, and stress reactions in sunfish. Physiol. Zool. 40(1):40-48.

Fabricius, E., and K. J. Gustafson. 1954. Further aquarium observations on the spawning behavior of the char, *Salmo alpinus* L. Ann. Rept. Inst. Freshwater Res. Drottingholm 35:58-104.

Forselius, S. 1957. Studies of anabantoid fishes. Zool. Bidrag Fran Uppsala 32:93-597.

Greenberg, B. 1947. Some relations between territory, social hierarchy and leadership in the green sunfish *(Lepomis cyanellus)*. Physiol. Zool. 20:267-299.

Hall, D. D. 1965. An ethological study of three species of anabantoid fishes (Pisces, Belontiidae). Ph.D. thesis, Okla. State Univ. 77 p.

Hall, D. D. 1966. Physical and physiological factors influencing spawning in two species of anabantoid fishes. (Pisces, Belontiidae). Texas J. Sci. 18 (4):352-360.

Hinde, R. A. 1966. *Animal Behaviour*. McGraw-Hill, N. Y., 534 p.

Hixson, G. A. 1946. The effect of numbers on the establishment of hierarchies and territoriality in the green sunfish, *Lepomis cyanellus*. Ph. D. thesis, Univ. of Chicago. 69 p.

Huck, L. L. and G. E. Gunning. 1967. Behavior of the longear sunfish, *Lepomis megalotis* (Rafinesque). Tulane Stud. Zool. 14(3):121-131.

Liem, K. F. 1963. *The Comparative Osteology and Phylogeny of the Anabantoidei (Teleostei, Pisces)*. Univ. Ill. Press, Urbana. 149 p.

Miller, R. J. 1964. Studies on the social behavior of the blue gourami, *Trichogaster trichopterus* (Pisces, Belontiidae). Copeia (3):469-496.

Miller, R. J. and D. D. Hall. 1968. A quantitative description and analysis of courtship and reproductive behavior in the anabantoid fish *Trichogaster leeri* (Bleeker). Behaviour 32:85-149.

Morris, D. 1958a. The function and causation of courtship ceremonies in animals (with special reference to fish), in *L'Instinct dans le Comportement des Animaux et de l'Homme*. Masson et Cie, Paris p. 261-286.

Morris, D. 1958b. The reproductive behavior of the ten-spined stickleback *(Pygostius pungitius* L.). Behaviour, Suppl. 6:1-154.

Noble, G. K. and R. Borne. 1938. The social hierarchy in *Xiphophorus* and other fishes. Bull. Ecol. Soc. Amer. 19:14. (Abstr.)

Rainwater, F. L. and R. J. Miller. 1968. Courtship and reproductive behavior of the Siamese fighting fish, *Betta splendens* Regan (Pisces, Belontiidae). Proc. Okla. Acad. Sci. 47:98-114.

Sevenster, P. 1961. A causal analysis of a displacement activity (Fanning in *Gasterosteus aculeatus* L.). Behaviour, Suppl. 9:1-170.

Simpson, M. J. A. 1968. The display of the Siamese fighting fish, *Betta splendens*. Anim. Behav. Monogr. 1:1-73.

Southwick, C. H. and R. W. Ward. 1968. Aggressive display in the paradise fish, *Macropodus opercularis* L. Turtox News 46 (2):57-62.

Tinbergen, N. 1964. The evolution of signaling devices, in: *Social Behavior and Organization among Vertebrates,* ed. by Wm. Etkin, Univ. Chicago Press. p. 206-231.