THE ONTOGENY OF AGONISTIC BEHAVIOR IN THE BLUE GOURAMI, *TRICHOGASTER TRICHOPTERUS*

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PREFACE

The objectives of this study on the ontogeny of agonistic behavior in the blue gourami, Trichogaster trichopterus, were: 1) to describe the appearance and development of post-hatching larval motor patterns and sensory capabilities, and the subsequent development of early intraspecific social interactions during the first 30 days of life; 2) to describe the ontogenetic appearance of agonistic behavior patterns from hatching to 136 days of age; and 3) to study some of the factors which effect the development of agonistic behavior in the blue gourami.

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CHAPTER I

INTRODUCTION

The science of ethology, which G. P. Baerends (1971, p. 279) describes as "...the study of all aspects of behavior using biological methods" has grown out of the concept of species-typical behaviors as component elements of evolutionary phylogeny (Lehrman, 1970). This concept was originally formulated as a result of studies by Spalding (1873), Heinroth (1911), and Whitman (1919), and was later expanded by Lorenz (1935, 1937, 1950) and Tinbergen (1951) to form the basis of all ethological studies (Eibl-Eibesfeldt, 1970). As a result of this background, the European school of ethology has continued to stress the importance of the "innateness" or genetic basis of behavior. This philosophy has been continuously criticized by American psychologists schooled in the tenets of behaviorism, placing primary importance on the experiential effect of the environment on the development of behavior (Lehrman, 1953; Hebb, 1953). More recently Lehrman (1970) has pointed out the value of a synthesis of the two views, whose product would be a more balanced and dynamic approach to the analysis of behavioral systems. In his discussion of the weakness of the "learning/instinct" dichotomy in behavioral studies Hinde (1970, p. 427) states that

> ...dichotomies between learnt and innate behavior involve the assignment of units of behavior into one or the other category, rather than an analysis of factors and processes

> involved in their development...in practice the processes concerned constitute an interacting and reacting system.

Schneirla (1957, p. 105) made a similar criticism much earlier.

> The traditional heredity-environment dilemma stands out more and more clearly as a pseudo-problem as further evidence indicates that in all animals intrinsic and extrinsic factors are closely related throughout ontoteny.

Although spokesmen for both schools have paid lip service to such criticisms (Lorenz, 1965; Lehrman, 1970), the philosophies which form the basis for their respective approaches to the study of behavioral mechanisms remain largely unchanged.

The persistance of the European philosophy has had a great influence on the further development of ethological concepts and research; unitl recently the bulk of ethological studies have dealt with the behavior patterns of adult animals as representative of the species under consideration, and have disregarded the developmental aspects of such behaviors. Of the five aspects of behavior which Baerends (1971) describes as relevant to ethological studies, one has remained conspicuously absent, until recently, from the ethological literature: description, function, causation, and evolution are all common subjects of ethological studies. However, the ontogeny of behavior has been relatively neglected. The description and analysis of behavioral ontogenies can provide additional insight into the dynamic nature of behavioral systems.

To function successfully as reproductive adults, the usual criterion for species adaptedness, species representatives must also be successful as young; it appears logical to assume, then, that adaptive elements of behavior in both of these stages of ontogeny are interrelated, for the success of either depends on the other, and both together form an adaptive whole. The validity of this hypothesis has been well illustrated by Kruijt (1964) in his study of the ontogeny of social behavior in the red junglefowl, Gallus gallus spadiceus; and by Harlow (1963) in his studies of the determinants of affectional systems in the rhesus monkey, Mocaca mulatta.

Due to the wide-spread evolution of complex social behavior patterns among vertebrate animals, the function of which has been the issue of much discussion (Wynne-Edwards, 1962; Wilson, 1975) social behavior has served as a focal point for the majority of ethological studies over the last forty years (Collias, 1944; Etkin, 1964; Lorenz, 1935, 1966; Marler and Hamilton, 1967; Baerends, 1971; Eibl-Eibesfeldt, 1970). The abundant literature on the subject of social behavior suggests that it serves a multitude of very diverse functions; most of these functions, however, are associated with reproduction, population regulation and resource use, and protection from predators and other harmful elements of the environment.

One behavioral complex underlying vertebrate social systems is termed "agonistic behavior", which Hinde (1970) describes as a complex system composed of attack, threat, submissive and fleeing behavior. Collias (1944, p.118) suggests that

> The general advantage of groups over individuals as competing units has led to the selection of individuals in terms of social values. Furthermore, competition at one functional level of social organization may be considered as co-operation at a higher level, and vice versa.

In a review of studies concerning the agonistic behavior of rats and mice Scott (1966) describes a complex behavioral system which appears to be composed of a multitude of different elements: developmental processes, hormonal systems, neurophysiological mechanisms, and past social experiences, as well as the immediate social stimuli. All of these factors interact to produce a functional agonistic system. Although the behavioral systems of the lower vertebrates are assumed to be simpler in organization and function than those of mammals, they do appear to follow the same general principles which Scott (1966) describes for rats and mice.

Ethological studies concerning the social behavior of fish have dealt mainly with the reproductive aspects of social behavior due to the elaborate signalling mechanisms which have evolved in many species. Reviews of the extensive literature on the subject are given by Aronson (1957), Liley (1969), and Baerends (1971). It is evident from these reviews that agonistic behavior plays a major role in both the reproductive and non-reproductive aspects of social behavior in fish. In general, agonistic behaviors appear to be part of a system which is temporally integrated into other more limited adaptive behavioral systems and operates as a "tool" in the functioning of these behavioral systems.

A number of studies have dealt with the non-reproductive aspects of agonistic behavior in fish. Factors affecting the initiation, organization and maintenance of dominance hierarchies among adult fishes have been investigated: group size has been studied in Lepomis cyanellus (Hixon, 1946), Trichogaster trichopterus (Miller, 1964; Miller and Miller, 1970), Macropodus opercularis and Colisa lalia (Miller and Miller, 1970), and Lepomis humilis (Dennis, 1970; Powell, 1972); relative size of fish within a group has also been studies in Lepomis megalotis (Huck and Gunning, 1967) and Mollienesia latipinna (Baird, 1968); Miller (1964) noted that in _T. trichopterus_ the length of a fight between two fish appeared to be longest when the size difference is minimal.

Prior residency effects have been shown in both _L. cyanellus_ (Greenburg, 1947) and _T. trichopterus_ (Frey and Miller, 1972). The effects of previous experience on the outcome of agonistic encounters have been studied in _L. cyanellus_ (McDonald, Heimstra, and Damkot, 1968), and _P. maculatus_ (Braddock, 1945).

Miller and Miller (1970) related shifts in social order to changes in the occurrence and frequency of agonistic behavior patterns in three anabantoid species.

Frey and Miller (1972) used a dyadic encounter technique to study the effects of all of the above-mentioned factors, except group size, and their interrelationships in the establishment of dominance hierarchies in _T. trichopterus_. They also attempted to develop methods of quantitative analysis of these factors and the behaviors observed during dominance encounters.

Hale (1956) studied the effects of forebrain lesions on the aggressive behavior of the green sunfish, _L. cyanellus_, and Hart (1973) has investigated the effects of brain lesions on the agonistic behavior of _T. trichopterus_.

With few exceptions the studies which have dealt with the relationship between the endocrine system and agonistic behavior in fishes have concerned themselves with mature fish, using hypophysectomy, gonadectomy, and hormone therapy treatments in various combinations (van Tienhoven, 1968; Aronson, 1957; Liley, 1969; Hoar, 1962). The findings have revealed that the effects of gonadal hormones are variable from species to species (Liley, 1969; Tavolga, 1955). It appears that for the majority of species studied gonadal hormones function as co-ordinators of agonistic behavior during reproductive periods; during non-reproductive periods, however, it appears that pituitary hormones may act directly to co-ordinate agonistic behavior, and that gonadal hormones are not involved (Johns and Liley, 1970). The role which gonadal hormones play in the organization of agonistic behavior during ontogeny has been conspicuously neglected in the behavioral studies of fish: both Aronson (1957) and Liley (1969) point out the possibility of such as organizational role in fishes as has been repeatedly shown for mammals (Young, 1961; van Tienhoven, 1968).

Most of the early works dealing with the development of behavior in fish were directed toward the determination of neurological development during the embryological period, and for only a limited period after hatching; in these studies simple motor patterns were used as indicators of neurological development (Tracy, 1926). Abu Gideiri (1966, 1969) used this same principle in his investigation of the development of early behavior patterns in eight different fish species: the four-beared rockling (*Motella cimbria*), the herring (*Clupea harengus*), the lesser weever (*Trachinus vipera*), the lumpsucker (*Cyclopterus lumpus*), the salmon (*Salmo salar*), the brown trout (*Salmo trutta*), the blue gourami (*Trichogaster trichopterus sumatranus*), the Mozambique mouth brooder (*Tilapia mossambica*). He found a distinct relationship between the stage of development of the nervous structures and the appearance of simple independent, and later fully co-ordinated, motor patterns; four stages in early ontogeny were distinguished: 1) myogenic, 2) neurogenic, 3) reflexogenic, and 4) swimming. Abu Gideiri also pointed out large differences in the developmental rates of the fish species studied, reflecting the ecological conditions of the respective species' eggs and fry.

Studies of the lateral line development in larval marine schooling fishes (Menidia menidia and M. beryllina) by Cahn, Shaw, and Atz (1968) revealed a direct relationship between the appearance of the behavioral elements involved in schooling and the progressive development of the lateral line system. In his studies of lateral line development and behavior of a number of fish species, Disler (1960) focused on the interrelationship of ecological and developmental factors. He was able to correlate behavioral changes with progressive changes in body shape and neurological growth, and was also able to show that, in some species, the use of specific sensory-motor systems changed progressively during development, often in relation to changing ecological conditions.

Bergmann (1971) has studied the behavioral development of the angel fish, Pterophyllum scalare, including the appearance and elaboration of agonistic behavior patterns in the young fish. His findings concerning the emergence of motor patterns suggest a correspondence with somatic development as proposed by Abu Gideiri (1966); first breathing and stretching movements are observed, then locomotion and feeding behavior, followed by comfort movements, and finally agonistic behavior.

Ohm (1964) studied the ontogenetic development of agonistic behavior patterns in Aequidens portaligrensis and A. latifrons. Significant time differences in the development of agonistic behavior repertoires in the two species were found, as well as some quantitative differences in behavior pattern frequencies. Compound behavior patterns were found to develop gradually through superposition of simpler behavior elements, and the most complicated activities appeared later in ontogeny.

The ontogeny of behavior in the convict cichlid, Cichlasoma nigrofasciatum, has been studied by Williams (1972). The sequence of motor pattern appearances and their functional organization was determined, and it was shown that early in ontogeny new behavioral elements arise by a combining of other elements, some of whose components are incompatible and so are modified or left out in the combination. The causal structure of the behavioral system was examined at four stages during development corresponding to important morphological or behavioral changes, and a motivational model was presented to provide a plausible explanation for the behaviors observed. The ontogenetic sequence of behavioral development was also related to the biology and group behavior of the species.

In the study of the development of behavior in the cichlid fish Etroplus maculatus Wyman and Ward (1973) also stated that the agonistic behavior of the young fish develops in a sequential manner from less complex to more complex motor patterns.

The ontogeny of aggressive behavior in Badis badis is described by Barlow (1962) as consisting of the insertion of ever more elements between the initial approach and the final ram and bite; he states that the increasing complexity may stem from steadily greater conflicts between behavioral elements. He asserts that aggressive behavior reverts to simple attack when fright stimuli are not presented by other fish; whereas the larger the opponent, the more hesitation and use of different and more complicated displays.

The effects of raising in isolation on the development of social behavior in fishes have been variable, and do not support a simple explanation attributing the observed behaviors to any specific causal mode (learned vs. innate). The disparity of the results may, at least in part, be due to the varied techniques used in the respective experiments, the different species that were being studied, and the specific behaviors which were being monitored in each experiment. In some cases fish reared in isolation have developed normal aggressive and reproductive behavior patterns (*Gasterosteus aculeatus* males, Cullen, 1961; *Astatotilapia strigigena* males, Seitz, 1940; *Tilapia mossambica*, Neil, 1964; *Betta splendens*, Braddock and Braddock, 1958, 1959; Laudien, 1965). Goude and Edlund (1972) studied the development of approach and withdrawal behaviors in young *Tilapia mossambica* as a function of age and social experience; the results of their isolation and group rearing experiments indicated that the development of such behaviors is related to a critical period during development. Shaw (1961) found that fry (*Menidia*) raised in isolation joined a school of equal-aged socially-reared fish, and that when a number of isolation-reared fish were brought together they also formed a school; however, it took more time to do so. The length of the delay was inversely proportional to the length of the isolation period. This same relationship was pointed out by Goude and Edlund (1972) with respect to performance frequency of approach and withdrawal behaviors in young *T. mossambica*. Breder and Halpern (1946) found that although *Brachydanio rerio* reared in isolation from the egg schooled when confronted with an aggregation, those that had spent some time in a group before isolation showed considerable hesitancy in joining a school. The latter three studies suggest that there are experiential factors which do affect the development of early social behavior patterns in some fishes. During early associations a certain inhibition of approach may be built up, and is then modified by subsequent experiences. In many instances the behavior patterns of isolates, although complete when exposed to socially-raised fish, are extreme or unco-ordinated with the actions of the other fish (Miller, personal communication). Kruijt (1964) has pointed out the same phenomenon in the red junglefowl.

Evidence available concerning the visual imprinting of young fish on adults or other juveniles indicates much variability in development of this phenomenon from species to species. In some species a specific color is responded to regardless of ontogenetic experiences (Cullen, 1961), while in other species responsiveness to colors or color patterns is highly modified by experience (Kuhme, 1962). A number of studies have been concerned with the possibility of parental imprinting as a factor in the discrimination and care of the young by some cichlid fishes; the results have been controversial on both sides of the issue (Noble and Curtis, 1939; Greenberg, 1963; Myrberg, 1964), however, there are indications that chemical stimuli from the young may be significant (Kuhme, 1963; Myrberg, 1966). Many of the temporal and experiential parameters involved in the process of preference development from one species to another are often at variance with a strict interpretation of the term "imprinting" as described by Hess (1958); rather, a large spectrum of different "imprinting" processes exists within the species that have been studied (Baerends, 1971).

The effects of population density and absolute living space on the growth and development of fishes have proved to be very complex. Both Brown (1957) and Chen, et al. (1964) have described the "hierarchy effect" characteristic of fish raised in high population densities. As a result of agonistic interactions between fish living in high density populations, and the effects of their metabolic byproducts, the size distribution of the population is attenuated, and individual growth rates are greatly reduced except for a few individuals forming the upper end of the dominance hierarchy. Absolute living space has also been shown by Chen, et al. (1964) to have an effect on growth and development--fish (T. mossambica) living at equal population densities grew larger in larger ponds.

In a review of the relationship between maturation, size and age in fishes, Alm (1959) concluded that within a certain year class and in specimens of the same age, maturity is reached earlier by larger than by smaller fish; the better growth rate of the larger fish applies also to the inner organs, including the pituitary and gonads. Shaw (1961) found that the appearance of schooling behavior in Menidia was primarily determined by size and not age. Fish raised under crowded conditions grew more slowly and did not exhibit schooling behavior until they had attained sizes equal to those of control fish which had been raised under less crowded conditions and had schooled much earlier (two weeks).

Barlow (1962) observed that the emergence of fighting behavior is delayed by group raising of the cichlid fish Etroplus, and this same delay has been observed in high density populations of young blue gouramis (T. trichopterus).

CHAPTER II

METHODS AND MATERIALS

The blue gourami was chosen as the subject for the proposed study for a number of reasons:

(1) The blue gourami's repertoire of agonistic behavior patterns is easily observable under laboratory conditions, and it has been described in the adult (Miller, 1964); hierarchical relationships are normally established soon after a group is formed and a characteristic set of agonistic behavior patterns occurs during social interactions (Miller and Miller, 1970). The temporal pattering of these behaviors and factors relevant to their expression have also been investigated (Frey and Miller, 1972).

(2) Adult fish are easily maintained and spawned under laboratory conditions, and it was determined during the pilot study that the young can be raised easily in sufficient numbers in the laboratory to provide a dependable supply for the necessary observations and experiments.

(3) The period of development required for the study, determined to be approximately 4 months, made the study feasible.

(4) The blue gourami is one of a number of anabantoid species whose reproductive and non-reproductive social behavior have been studied in order to gain a better understanding of the

phylogenetic relationships within the family Belontiidae, and to formulate a model for the behavioral complex characteristic of that family (Miller, 1964; Miller and Hall, 1968; Hall, 1965; Rainwater and Miller, 1968; Miller and Miller, 1970; Wimmer, 1970; Robison, 1971; Hopkins, 1971; Frey and Miller, 1972; Frey, Dunn, and Line, 1972; Hart, 1973).

Because of the abundant information available on the adult behavior of the blue gourami and related species, an understanding of the ontogenetic development and causal relationships of the agonistic behavior system would be helpful in attaining a better understanding of the anabantoid behavioral complex. The need for such additional information is stated by Miller and Miller (1970, p.61)

> 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.

A further benefit of studies dealing with the agonistic behavior of the blue gourami during the pre-adult stage is that problems stemming from the interaction of reproductive and non-reproductive elements of the behavioral system may be eliminated (Miller and Miller, 1970; Johns and Liley, 1970).

The study was carried out in the Animal Behavior Laboratory of the School of Biological Sciences at Oklahoma State University from January, 1973 to April, 1975.

The adult fish used for spawning were obtained from local aquarium dealers and were maintained in the laboratory in 173-liter tanks in groups of five to ten. Spawning pairs were placed in a 40-liter aquarium (50 x 27 x 30 cm) with a gravel bottom and four aquatic plants (Vallisneria sp.). The female was removed soon after spawning was completed and the male was removed three days later.

In all of the aquaria used in this study the water temperature was maintained at 23 to 28 C, and the pH ranged from 7.0 to 7.6. All aquaria were airated with airstones and 80% of the water was replaced weekly with fresh water. Two 25 watt incondescent light bulbs illuminated each aquarium on a 14 hr photoperiod.

The study consisted of two phases: 1) the first phase involved the qualitative description of behavior from hatching to 30 days of age in groups of 20 fish, and from 33 to 77 days of age in groups of six fish. The description of behavior from hatching to 30 days of age was based on three spawnings from different spawning pairs. The description of behavior from 33 to 77 days was based on three groups of six fish all from one spawning. In each of the spawnings the newly hatched larvae remained in the spawning aquarium in a group of 500 to 1000 individuals for the first two days; some fry were then transferred in groups of 20 to three 60-liter aquaria (60 x 27 x 35 cm) for the remaining 28 days of observation. During the first week the fry were fed with cultured infusoria water (mostly Paramecium sp.), diluted boiled egg yolk, and powdered commercial flake food (Tetramin). At two weeks the infusoria water was replaced by ground-up frozen brine shrimp (Artemia), which became the primary food source from three weeks on.

From hatching to seven days of age the fry were observed twice daily for 15 minutes both in the spawning tank (500 to 1000 fry) and in the three aquaria containing 20 fry each. During this same period five fry were removed from the spawning tank twice daily and observed in a watch glass under a disecting microscope. After the first week aquarium observations were made every other day for the remaining 23 days on the three groups of 20 fish each.

At 30 days of age 18 fish ranging in size from 9 to 15 mm standard length, were removed from the three groups of 20 fish each, and six fish were placed in each of three 60-liter aquaria (60 x 27 x 35 cm). From day 33 to day 77 the fish in each of the three aquaria were observed once every two to three days, for 10 minutes before feeding and for 10 minutes immediately after ground-up frozen brine shrimp was added to the aquarium.

The second phase of the study involved the quantitative description of nine agonistic behaviors exhibited during 15-minute dyadic encounters by group-raised fish from day 26 to day 136, and by fish raised under three different conditions of social isolation when tested between 113 and 136 days of age. During this phase of the study two-day-old fry were removed from the spawning tank and 20 were placed in each of fourteen 137 liter group-raising tanks (81 x 56 x 38 cm) containing gravel bottoms planted with six to nine aquatic plants (<u>Vallisneria</u> sp.). Thirty-two fry were also removed from the spawning tank at two days of age and placed individually in one-gallon jars with gravel bottoms and one aquatic plant (<u>Vallisneria</u> sp.). At 30 and 60 days of age 16 fish of various sizes were removed from two of the group-raising tanks and placed in similar one-gallon jars. In all three of the isolated groups of fish the jars had one side painted white, and were placed together in groups of 16 in a long water bath (180 x 40 x 28 cm) with white dividers between pairs of bottles so that all of the fish could see people walking by but could not see the other fish. The bottles were illuminated by overhead fluorescent ceiling lights on a 14 hr photoperiod. The water bath was continuously circulating and maintained at 23 to 28 C. The water in the bottles ranged from 7.0 to 7.6 in pH, and it was changed weekly. All of the fish isolated were fed the same food as the fish raised under group conditions. The fry isolated at two days of age experienced a 50% mortality during the first two weeks, compared to a 20% mortality in the group-raising tanks with 20 fish per tank. The mortality in the other two isolation groups was negligible, with only one fish lost in the 30-day group.

Description of Dyadic Encounter Chambers and Data Recording Methods

A long narrow aquarium (57 x 16 x 30 cm) was subdivided into three encounter chambers (18 x 14 x 26 cm) by lining the sides and back of the aquarium with green plexiglass and installing two permanent green plexiglass dividers. Each chamber was water tight and was subdivided by a removeable divider of green plexiglass. The chambers contained gravel bottoms and were uniformly illuminated by an overhead fluorescent lamp.

Before dyadic encounters were begun, aged water maintained at 23 to 28 C was added to the encounter chambers to a depth of 14 cm, and a temporary divider was placed in each. Two size-matched fish (within 1 mm sl) from different raising tanks were then placed on opposite sides of the temporary divider in the left chamber; 15 minutes after that two fish were placed in the right chamber. After each pair of fish had been in their chamber for at least 30 minutes the divider between the two fish was removed and the following 15 minutes of interaction between the two fish was observed from a sitting position 120 cm in front of the encounter chambers. The frequency, latency and duration of nine agonistic behaviors was recorded for each of the two fish separately on a 20 pen Esterline-Angus event recorder with two 10-key keyboards, at a speed of 7.62 cm/min. All fish were fed regularly twice a day at least one hour before testing. At the end of the three encounters all fish were returned to their home tanks and fish of their size (large, medium, or small) were not used from that tank again for at least six days. The water in the encounter chambers was then replaced with more aged water before another set of encounters was observed. In this manner three encounters were observed in the morning and three in the afternoon on each observation day. On each observation day two small, two medium, and two large pairs of fish were selected for testing from the available sizes in the raising tanks.

Using group-raised fish, six dyadic encounters between size-matched fish from different raising tanks were observed every three days from day 26 to day 110, and on days 116, 123, 128, 134, and 136. Qualitative notes describing the general nature of the interactions occurring during each encounter were also taken on a tape recorder at the conclusion of each encounter.

Utilizing the same encounter chambers, similar observations were made on the fish raised under the three conditions of social isolation. For each of the three isolation groups the following pairings were observed between 113 and 136 days of age: 1) isolates paired with isolates as a first experience; 2) isolates paired with group-raised fish as a first experience; 3) isolates from (1) paired with group-raised fish as a second experience; 4) isolates from (2) paired with each other as a second experience. Group-raised fish tested during this same period were used as controls.

Behavioral Units, Measures, and Terminology

During the first two weeks after hatching fry exhibit some behaviors which later develop into more complex forms or are incorporated into more complex behavior groupings. A brief operational description of some of these early behaviors follows:

Arcing. A lateral bending of the body seen in a number of different contexts. Fry maintaining a stationary position in a water current, or investigating a large, active prey may arc their bodies and hold the position for 2 to 5 seconds or more. Two fish coming into close proximity may also arc their godies for short periods when they notice each other.

Darting. A straight line forward movement of from 1 to 5 cm resulting from a brief burst of high frequency undulations of the tail. This is the first form of directed movement which the fry exhibit.

Nipping at the Surface. As labyrinth fish, adult *T. trichopterus* rise periodically to the surface to gulp air, an act described by Forselius (1957) as surfacing. Nipping at the surface is an early form of surfacing in which fry positioned at the water surface bite repeatedly at the surface film, sometimes creating a bubble at the surface.

Spiking at the Surface. A later form of surfacing which incorporates a diagonal charge at the surface (45^o) from 1 to 2 cm below it, with a single, rapid nipping at the surface. This is followed immediately by a diagonal descent of 1 to 2 cm.

Comprehensive descriptions of some of the nine agonistic behaviors used in this study, as seen in adult fish, have been made by Forselius (1957), Miller (1964), Hall (1965), and Miller and Miller (1970). Although these agonistic behavior patterns have been designated as "repeatedly recognizeable events which represent states of the behavioral system" in adult fish (Frey and Miller, 1972, p. 13), many of these behaviors undergo changes in both form and context during ontogeny. With this in mind, brief operational descriptions of the behavior patterns used in this study follow:

Approach. An approach is defined as a direct movement toward another fish when previously separated by more than two body lengths.

Chase. A chase occurs each time one fish swims vigorously after another, and its occurrance implies the fleeing of one fish from the other.

Bite. Although biting and butting have been differentiated on the basis of whether a fish actually attempts to grasp the opponent with its teeth (Miller, 1964; Miller and Miller, 1970) the quickness of the movement and actual contact prevented any discrimination of the two acts in this study and both are recorded as biting. Biting occurs when one fish lunges toward and makes body contact with its mouth on another fish; biting is usually limited to the caudal peduncle, tail fin, anal fin and lower flank region. From my observations I expect that actual butting appears quite late in development as a more formalized and restricted form of biting.

Raised Dorsal Fin. The raised dorsal fin response occurs when the dorsal fin is expanded from 70 to 100% of its maximum size with the anal fin retracted. No body curvature accompanies the raised dorsal response. In interactions between two or more fish the raised dorsal response indicates the relative level of responsiveness of one fish to the presence of another fish.

Lateral Display. A lateral display is exhibited by the maximal spreading of the dorsal and anal fins, and is sometimes accompanied by body curving components. It usually occurs in a lateral orientation to a facing fish, a parallel or an anti-parallel position. When the motor pattern is exhibited by a single fish which is not aligned with or close to another fish, it will be called median fin spreading.

Tail Beat. Tail beats are exhibited by a high amplitude lateral undulating of the caudal peduncle and tail of a fish exhibiting a lateral display.

Fin Tug. A fin tug occurs when one fish bites the fin (usually the anal fin) of another fish, and hangs on for one to several seconds; the fish may actually pull the fin by undulating tugging movements.

Carousel. A carousel occurs when two fish which are aligned and exhibiting lateral displays in an anti-parallel position each approach the tail of the other fish simultaneously, creating a circular movement of one to many revolutions.

Appease. Appeasement occurs when the losing fish in a dominance fight tilts away from the winner along the median axis of the body and folds its dorsal fin at the same time. Appeasement is usually accompanied by the fish becoming inactive and remaining stationary in a corner near the surface or at the bottom.

When observing the dyadic encounters in this study, approaches and bites were recorded as having a maximum duration of 2 seconds, representing the smallest time unit on the recording chart; therefore, the durations of approach and bite approximate twice the frequency values for those behaviors. All other behavior duration values represent the total time in seconds spent by each fish exhibiting the respective behaviors during the 15 minutes of observation.

Each encounter was defined as resolved or unresolved by the presence or absence of appeasement. In resolved encounters the fish exhibiting appeasement was designated as the subordinate and the opponent was designated as the dominant. In unresolved encounters the fish were classified as "greater" or "lesser" representing the differences in the approach frequencies of the two fish. In unresolved encounters, which occurred primarily during the first half of the study period, the fish exhibiting the greatest approach frequency also usually exhibited virtually all of the chasing and biting, indicating a similarity to later dominant fish.

After summarizing the data for each fish on computer cards the average values for behavior frequencies, latencies, and durations for group-raised fish were calculated and plotted against age and size. Intra-individual entropy values, using the frequencies of the nine behaviors recorded for each fish, were also calculated for each fish and the average values were plotted against age and size. Average values for all of the behavior parameters measured were also plotted against age and size for each of the four categories of individuals in an encounter (dominant, subordinate, "greater", "lesser").

When evaluating the data on the fish raised under different social conditions, average values for all of the above behavior parameters were calculated for dominant and for subordinate fish, and mean comparisons were made between control fish (group-raised), the three groups of isolated fish, and the group-raised fish which were paired with the isolated fish in dyadic encounters.

CHAPTER III

QUALITATIVE DESCRIPTION OF BEHAVIORAL DEVELOPMENT IN GROUPS

Development of Behavior in Groups of 20 Fish From Hatching to 30 Days of Age

Day 1

During the first 24 hours after spawning the male spent most of his time patroling the nest area and gathering stray eggs which he then deposited in the bubbel nest along with more bubble. In this manner the bubble nest was maintained and the eggs were kept in or under the bubble nest at the water surface. After 24-30 hours the eggs began to hatch and the bubble blowing and tending of the eggs and young fry by the male began to decrease. This resulted in the breakup of the bubble nest and dispersal of the young fry by about 24 hours after hatching. Although the fry dispersed from the immediate nest area during the first day after hatching they remained at or very near the water surface, floating free of "moored" to leaf surfaces or the sides of the aquarium at the air-water interface.

At hatching the yolk sacs of the fry were very large and the fry remained upsidedown at the water surface. High frequency undulations of the rear body and tail fin primordium produced periodic circular or figure-eight movements from 1 to 2 cm in diameter, during which the fry turned right-side-up. The intensity and duration of these body movements determined the nature of the spinning movements. The movements ranged from brief movement of the pectoral fin primordia, which were limited by the presence of a large yolk sac, to a 3 to 4 second continuous undulation of the rear body and movement of the pectoral fin primordia together. The spinning movements were closely grouped, whereas the short movements of the pectoral fin primordia or rear body separately were evenly spread throughout the observation period. When congregated under the bubble nest, the spinning movements of one fry often initiated variable spinning movements in the fry located nearby as a result of collisions.

At 3 to 5 hours after hatching the eyes were not yet completely formed, and there was no eye movement or response to light source movement; there was no movement of the mouth parts, and the fry still remained up-side-down at the water surface. Tapping on the side of the aquarium with the fingernails produced no noticeable response in the fry although it did disturb the adult male. Rocking the aquarium, which caused a disturbance of the water surface, created a wave of spinning movements by the fry; if the rocking persisted for 3 to 5 seconds or more the spinning movements of the fry increased in intensity and duration and assumed a straight line, downward direction, causing the fry to move directly to the bottom (20 to 25 cm) and remain there until the rocking stopped, at which time they would float slowly back to the surface. Less intense or prolonged rocking resulted in horizontal or low angle spinning movements, with only a few fry descending 2 to 5 cm from the surface.

During the first 24 hours after hatching the activity level of the fry continued to increase, resulting in the spreading of the fry into all areas of the aquarium at or near the water surface. By the end of this period the fry had begun to move down 5 to 8 cm from the water surface, and their spinning movements had begun to change to short, quick darting movements with no consistant orientation from one darting movement to the next. The fry still did not react visually to nearby movement, and they sometimes collided with each other during their darting movements. These collisions often resulted in brief flight responses.

Day 2

The fry had turned right-side-up and occupied the top 10 to 12 cm of the aquarium. Movements of the pectoral fin primordia were continuous, and regular rhythmic movements of the opercles occurred. Erratic movements of the mouth parts occurred, but were not coordinated with the rhythmic movements of the opercles. The eyes were completely formed, and coordinated and independent eye movements occurred. The fry reacted visually to other fry, but only at close range (3 to 5 mm), by a brief orientation of the eyes; collisions with each other resulted in immediate flight. The fry were very active and exhibited short rapid darting movements in random directions, but no feeding occurred. Rocking the aquarium or tapping on the side of it had the same effects as on day 1.

Day 3

The fry exhibited a much greater degree of coordination in their activities. Coordinated mouth and opercle movements occurred regularly;

the darting movements had increased in length and were followed by coordinated eye rotation and body reorientation in response to near-field visual stimulation. Collisions occurred very seldom and the fry were spread throughout all parts of the aquarium. The fry began orienting on small objects at close range (3 to 5 mm) and would approach and consume <u>Paramecium</u> sp. and other protozoa and small invertebrates which were available. At this stage only about one half of the feeding attempts on moving prey were successful. Approaches between fry began to appear as general stimulus responses to the large head with dark eyes, but did not result often in close proximity. If two fry came into close proximity before noticing each other, immediate flight occurred. A positive phototaxis was exhibited by the fry, and if one of the two overhead lights was turned off the fry would slowly congregate under the remaining light. Placement of the light source along the side of the tank also attracted the fry, and some continued to bump into the glass wall in approaching the light source. Tapping now produced a general darting response which was greatest near the tapping point, and directed away from it. Rocking caused only horizontal or low angle darting movements.

<u>Day 4</u>

During their searching activities fry oriented on and approached a wide variety of objects including other fry, drifting organic matter, or protozoans and small invertebrates. Most searching activity involved close inspection of leaf surfaces, the gravel bottom, the aquarium walls, and head-to-head approaches to other fry. The head-to-head approaches usually resulted in turning away at a distance of 7 to 10 mm, and flight reactions to other fry were more intense than in younger fry. When approaching prey organisms the movement and large size of some prey produced an arcing of the body while the fish held its position and inspected the prey; the fry then formed a snake-like sigmoid posture before springing on and consuming the prey by sucking it into the large mouth. Arcing of the body was also exhibited by fry when in a water current or sometimes by an approached or approaching fry in close proximity. The utilization of the arcing and sigmoid motor patterns in feeding was quite variable, and depended on the proximity of the prey and its position in relation to the head of the fry. A prey organism which moved diagonally by the head of a fry from the rear or front was often snapped up with a rapid flexing of the head to the side and gaping of the mouth as the prey organism was sucked in. Tapping and rocking of the tank produced very similar darting responses throughout the aquarium, and both stimuli were subject to rapid habitation.

Day 5

Fry fed on a variety of food items, including powdered flake food (Tetramin), dissolved boiled egg yolk, protozoans, small invertebrates, and algae. The movements of the fry during their searching and feeding activities were more varied; they searched for 2 to 3 minutes at one depth and then moved diagonally about 8 to 10 cm to another depth before resuming their searching activities. The response of the fry to movement of the light source was now less pronounced. The fry reacted to each other with only brief visual orientations, and only a few head-to-head approaches occurred. In chance meetings with other fry or large invertebrates (Cladocerans) the fry responded with an arcing of the body and subsequent flight or reorientation of the body away from the source of stimulation. At this stage of development the largest fry were only 3 to 4 mm long and their median fins had not yet formed, appearing only as narrow fin primordia along the dorsal and ventral aspect of the body. For this reason, although arcing of the body later contained some elements of fin spreading, it was not yet descernable.

Days 6-9

There was an increasing frequency of diagonal darting movements exhibited by the fry during this period, between the top, middle and bottom areas of the aquarium; some fry moved all the way from the bottom to near the surface in a continuous directed series of long darts (4 to 6 cm) before resuming searching activities near the surface. These directed diagonal movements, which were exhibited first at 5 days of age, appeared to be the initial elements of surfacing to take air into the suprapharyengeal organ, which is done regularly by adult fish. Adding food to the aquarium disturbed the regularity of these diagonal movements, and the fry became less responsive to outside disturbances. The largest fry (5 to 6 mm) now had a black caudal pigment spot and a silvery patch on the mid-body; these were the only distinctive body markings other than the large dark eyes. When two fry were paired in a small observation chamber (18 x 14 x 26 cm) at this age only intermittent orientations and partial approaches were made during the first few minutes, after which the fry continued their searching activities independently.

Days 10-13

Diagonal movements were longer and occurred regularly, and the larger fry (7 to 8 mm) were observed nipping at the surface or near it as if feeding on some material there, although none was seen by the observer. Some of the large fry were also observed spiking at the surface, which involved a rapid diagonal charge (45°) at the water surface layer from about 1 to 2 cm below the surface, accompanied by nipping at the surface. The charge was followed immediately by a diagonal movement away from the water surface to a depth of 1 to 2 cm. Both nipping at the surface and spiking resulted in a bubble being formed at the point of surface contact, indicating a breaking of the water surface film. By day 13 all of the larger fry were spiking at the surface and the smaller fish were nipping at the surface regularly. By day 13 the larger fry also began orienting on and approaching the tail spots of other fry. These approaches were from the rear or side, and after coming within 8 to 10 mm the approached fish usually moved away.

Days 15-18

The larger fry (10 to 11 mm) approached the tail spot of other fry to within 1 to 3 mm and some nibbling on or near the tail spot was observed, causing a flight response in the fish being nibbled if contact was made. The approaching fish did not turn away from the tail spot before inspecting it closely unless the other fish moved away. Some fish were observed to approach the tail spot of other fish repeatedly. Chance meetings of two fry in a head-to-head or head-to-side position sometimes resulted in both fish "freezing" and arcing the body with the median fins spread; this was usually followed by one or both fish rotating their bodies slowly using only their pectoral fins before moving slowly away. During these "freezing" periods both fish appeared very tense and as if in a state of conflict.

Days 19-22

The frequency of tail approaches continued to increase and a wide variety of involvement was observed. Some fish approached and turned away, some approached and investigated the tail spot before turning away, and some fish approached and nibbled at or on the tail spot causing the other fish to flee if contact was made; some fish were observed to approach, nibble and follow for a short distance as the other fish moved off. During these interactions neither of the fish seemed to exhibit any conflict in their body posturing or overall attitude, unless the approached fish turned back on the approaching fish, resulting in a head-to-head or head-to-side position. The attitude of both fish then changed to one of conflict; the body was arced and the median fins were spread until one or both of the fish moved away. This conflict situation sometimes resulted in the approaching fish exhibiting a very rapid bite to the caudal spot of the other fish, resulting in the rapid flight of both fish.

On day 22 when ground-up brine shrimp of large particle size was added to the aquarium 3 or 4 fights were observed involving brief body arcing with median fins spread and a short exchange of bites before one or both of the fish fled. During these conflicts fish ranging from 10 mm to 14 mm were involved; some fights were between equal-sized fish and some between large and small fish. Previous to adding the food the interaction between the fish was minimal, and it appeared that the large size of the food particles contributed to the occurrence of overt fighting, since two or more fish were often attracted to the same food particle. When fed with food of smaller particle size such as commercial flake food (Tetramin) no fights were observed.

Days 25-30

The larger fish (14 to 17 mm) exhibited an increased responsiveness to disturbances in and outside the aquarium, as well as to other fish moving near them; their movements were quick and jumpy. The characteristic response to other fish moving near by was a raised dorsal fin for a period of 1 to 3 seconds, and occurred at variable distances depending on the activities of the two fish involved, as well as their orientations toward each other. The general responsiveness of fish to each other was increased by the addition of food, and this increase occurred after the first 2 to 3 minutes of frenzied feeding; during this period the fish were very unresponsive to each other and often bumped into each other with only a minimal flight response resulting.

The larger fish (14 to 17 mm) often approached and followed smaller fish (9 to 12 mm), and this often resulted in the active fleeing of the smaller fish. Head-to-head, head-to-tail and head-to-side approaches sometimes resulted in close proximity stationary positions with median fins spread. If not already aligned in a parallel or anti-parallel position, the two fish turned slowly by the use of their pectoral fins to assume an anti-parallel position. The parallel position produced a less stable interaction between the two fish and did not often occur. A subsequent rapid circling or carouselling of both fish for one or two cycles then usually occurred before the interaction was terminated with one fish biting the tail or caudle peduncle of the other, causing it to flee, and sometimes chasing it off for a short distance. This mutual median fin spreading and carouselling was sometimes accompanied or followed by non-contact nibbling or yawning, and sigmoid was usually exhibited by the approaching fish.

Fish placed together in small encounter chambers (18 x 14 x 26 cm) at this age (10 to 17 mm) showed a marked increase in sensitivity to outside disturbances. Approach and following was seen initially in the smaller fish (9-12 mm) followed by general searching behavior. In the medium or large sized fish (14 to 17 mm) initial approach and following was followed by nibbling (contact or non-contact) and/or biting of the caudal spot, as well as short mutual lateral displays with brief carousels concluded by biting and chase. The interest between the two fish was usually shown only during the first 2 to 4 minutes of a 10 to 15 minute observation period, and was then replaced by searching activities. During the first 30 days of development the larger fish in a group appeared to exhibit new behaviors and general changes in motivational states before the smaller fish.

Development of Behavior in Groups of Six Fish From 33 to 77 Days of Age

The following description has been presented in three consecutive age phases; these phases do not represent actual groupings, rather they provide a simplified format for description of behavioral development.

Days 33-44

During pre-feeding periods all of the fish were actively searching for food in all parts of the aquarium. Fish in the same area of the aquarium intermittently exhibited raised dorsal fin responses for 1 to 4 seconds when other fish moved around nearby, and fish which crossed paths usually skirted around each other with a brief mutual median fin spread and some body curving while passing each other. The larger fish intermittently approached smaller fish from the rear and followed them for a short distance, sometimes closely investigating their black tail spots before moving away. These interactions did not result in any chasing or fleeing. During the latter part of this phase the frequency of following by the larger fish increased and following was often concluded with brief chases after the smaller fish. This activity began to attract other fish which followed one of the original fish. Approaches from the rear (head-to-tail approaches) sometimes resulted in the stationary positioning or "freezing" of both fish while exhibiting unaligned median fin spreads. After alignment was accomplished, nibbling on the tail spot of one fish, with or without actual contact, sometimes occurred; in some instances the nibbling changed to a few short and powerful bites which usually caused the other fish to flee. By the end of this phase all of the fish were conditioned to my approach and all moved immediately to the surface areas of the aquarium where the food was usually added. When food was not added, after about 1 minute the fish dispersed throughout the aquarium and resumed their searching activities.

When brine shrimp was added to the aquarium the fish began a 2 to

3 minute feeding frenzy. During this period little or no interaction between fish occurred other than brief raised dorsal fin responses; in some instances one fish approached and nibbled at the tail spot of another fish in the midst of its feeding activities. These interactions did not appear to be aggressive, but rather appeared to be part of normal feeding activity. As the food became more scarce and settled to the bottom, the frequency of interactions between fish increased and their character became increasingly more aggressive. Chance meetings of two fish were sometimes followed by biting. If a specific food item was approached by two fish at the same time, or one fish approached another fish which was actively feeding on a large food item, mutual lateral displays, carouselling, biting and chasing, as well as mutual tugging on the food item often resulted. Larger fish observing other fish feeding on a food item sometimes approached and bit the fish directly without displaying or hesitating, and would then chase the fish away before returning to feed on the food item. Either fish involved in these various interactions often moved off, and then chased and bit other fish in a different part of the aquarium.

During the middle and latter parts of this phase the large fish in the aquarium began to approach and chase other smaller fish out of specific areas along the bottom after the 2 to 3 minute feeding frenzy. When two of these large fish which were defending adjacent areas confronted each other, mutual lateral displays and carouselling resulted before one fish, which was usually the "resident", bit, and chased the other fish out of the area. These agonistic encounters appeared to increase both the readiness of the fish involved, as well as the readiness of the other fish in the aquarium to enter into agonistic interactions with fish of all sizes. The three or four fish which were not defending bottom areas were usually involved in only brief interactions, including approach, follow, bite, brief unaligned median fin spreads and chasing. During these hightened periods of interaction the most aggressive fish became noticeably darker in color. The behavioral content and duration of the interactions was highly variable and seemed to be dependent on a number of factors, including the relative size of the fish involved, their individual status in the aquarium, their immediate past interactions with other fish, and the distribution and abundance of food in the aquarium. The interactions of longest duration, and including the greatest variety of behaviors, occurred characteristically between the large fish that were defending specific bottom areas. Near the end of this phase these large fish began to exhibit tail beating during their mutual lateral displays.

By the end of this phase the smaller fish remained on the edges of defended areas, or in the upper parts of the aquarium, and were usually much more active than the larger fish in continuously moving about. In a few instances a small fish was observed successfully defending a small bottom area in a corner of the aquarium against fish of much larger size.

By 10 to 12 minutes after the food was added it had all been eaten and the large fish no longer remained in one area to defend it, but moved around the tank randomly, and the frequency of agonistic interactions decreased to a pre-feeding level.

Days 45-54

During pre-feeding periods interactions between fish continued to include brief raised dorsal responses to the movement of other fish.

Approaches by large fish to smaller ones often resulted in nibbling and biting of the tail spot, or following, biting and chasing. Interactions between the larger fish increased during this phase, and usually involved stationary mutual lateral displays followed by brief carouselling and/or biting and chasing. These were the fish which defended bottom areas during the post-feeding periods.

The adding of food to the aquarium still created an initial feeding frenzy of 2 to 3 minutes, during which little interaction occurred. After the food became more scarce and settled to the bottom the agonistic interactions of the large fish increased both in duration and behavioral content, and these interactions were centered on specific defended areas along the bottom. Tail beating appeared as a regular part of interactions between large fish and often resulted in one fish pushing the other fish out of its area with broad, slow tail beats. Consecutive bouts of activity involving lateral displays, biting, tail beating, carouselling and chasing occurred between the same two "territory" holders; these bouts were often separated by short periods during which one or both of the large fish chased away smaller fish which had been attracted by the interactions of the two large fish. These chases often resulted in a random series of interactions between fish of all different sizes; these interactions involved brief lateral displays, and/or chasing and biting. The frequency and duration of raised dorsal responses during this active period also increased. The large fish in the aquarium now defended territories for 15 to 20 minutes, which included a span of 8 to 10 minutes after all of the food had been eaten.

Days 55-77

During pre-feeding periods agonistic interactions were common among all of the fish and were more frequent than in younger fish. The larger fish were defending territories along the bottom during these pre-feeding periods, and most interactions in the aquarium occurred between the large fish. Interactions between territorial and non-territorial fish were usually brief and consisted mainly of the territorial fish chasing and biting the smaller, non-territorial fish away. Interactions between non-territorial fish consisted of brief median fin spreads or raised dorsal responses, with a minimum amount of chasing and biting. Chasing and biting usually was exhibited by these smaller fish only after they had been chased by the larger territorial fish.

After food was added and it settled to the bottom the frequency of interactions increased, and the large territorial fish would often approach and enter into an ongoing encounter between two smaller fish. This interference would often result in the involvement of 3 to 6 fish in a drawn out series of interactions of increasing intensity in which size and status made little difference; there was no consistant pairing of fish, but rather a random progression of brief interactions.

During the latter part of this phase the addition of food effected an increase in the frequency of interactions in the aquarium but caused no visible qualitative changes in the interactions of the group of fish. Also, during the latter part of this phase interactions involving a third fish interrupting an ongoing encounter occurred regularly before feeding, and the general arousal level of the fish in the aquarium was highly variable. The largest single fish in the aquarium now assumed a position of dominance over all of the other fish in the aquarium, and other large fish were able to defend areas against this dominant fish only during periods when recently added brine shrimp was spread along the bottom of the aquarium. During these periods the dominant fish would, itself, defend a limited area along the bottom.

CHAPTER IV

QUALITATIVE DESCRIPTION OF BEHAVIORAL DEVELOPMENT IN DYADIC ENCOUNTERS

The following qualitative descriptions are based on observations made on 15-minute dyadic encounters between equal-sized fish (within 1 mm SL) from 26 to 136 days of age.

Days 26-38

During this phase of development there was a qualitative difference in the behavior of different sized fish. The smallest fish exhibited initial orientations, approaches and some short following before losing interest early in the encounter. The medium sized fish exhibited approach, following and nibbling on the tail spot, and during the latter part of this period these sequences sometimes led to brief chasing and biting. The large fish appeared very nervous and exhibited more raised dorsal responses to the movement of the other fish. The large fish were also less active in their general searching activities, and they sometimes exhibited "freezing" in stationary positions when near each other; they would then move apart slowly or one fish would give a few quick bites before the other fish fled. The content of the encounters between the large fish at this time was quite variable, but usually involved an initial brief period of interest or confrontation followed by a long period of disinterest. In all of the encounters observed during this period one fish was usually much more active in approaching and/or following then the other fish.

Days 41-59

During this phase the smallest fish still showed only initial brief interest in each other. There was an increasing amount of variation in the behavioral content of dyadic encounters during this period, and the medium and large sized fish were less distinctive in their behavioral interactions. Some fish exhibited a lot of raised dorsal fin but were generally inactive, while others interacted soon after the encounter began. Some large fish remained cautious and inactive without exhibiting lateral displays or chasing and biting, which was often exhibited by the medium sized fish. Large fish which did enter into agonistic confrontations exhibited more agonistic behaviors than medium fish usually did in the same situation. Tail beating appeared along with lateral display in the large fish during this period. The chasing fish often exhibited a sigmoid body posture briefly in its initial approaches before mutual displaying occurred, and later during pauses between chasing and biting sequences. Agonistic activity now commonly occurred in bouts when exhibited by the medium and large fish, beginning with approaches and brief displays and building to a chasing and biting sequence.

Some fish began to exhibit brief appeasement tilts of the body at about the middle of this phase while actively fleeing from the other fish. These early appeasements were very short, and were not extreme in form or held for long periods as in adult fish. In these early appeasements the dorsal fin was raised and the fish did not remain stationary or inactive. These early appeasements had little effect on reducing the chasing and biting of the dominant fish.

Days 62-83

During this phase the number of resolved encounters increased and the appeasement tilt of subordinates, though not extreme, was held for short periods after the dominant fish had moved away. Some encounters, however, were still characterized by high levels of chasing and biting by one fish but with no appeasement by the other fish. Some fish appeased in an extreme fashion with the dorsal fin collapsed, and assumed stationary positions near the bottom or up near the surface. This more formal appeasement soon deteriorated into a simple avoidance and fleeing pattern as the dominant fish continued to approach, chase and bite. Some of the subordinate fish which exhibited longer periods of appeasement tilting and inactivity also jerked their heads sideways two or three times in succession when the dominant fish approached. Some fish appeased before any interaction (approach, lateral display, etc.) had occurred between the two fish, yet other fish appeased only after a series of mutual lateral displays, and some tail beating. Some subordinates now spent less time fleeing and initiated new bouts of chasing and biting by approaching the dominant fish during pauses in activity. At this age appeasement by the subordinate appeared to have only a minimal effect on reducing the aggressive activities of the dominant fish.

During the latter part of this phase the dominant fish often attempted to localize the subordinate and get in front of it to exhibit a lateral display and sometimes tail beating. As these localization and display attempts increased in intensity the raised dorsal fin response of the dominant fish often shifted to median fin spreading even when not near to or aligned with the subordinate fish.

When overt agonistic interactions occurred between the larger fish during the latter part of this phase the interactions began to take on a more formalized and slow-motion character, indicating an increase in the coordination of activities between the two fish. This formalization of interactions continued to increase in later phases of development; in adult fish there may be a long series of mutual exchanges of lateral displays, tail beating, and fin tugging in a well coordinated slow-motion fashion before one fish appeases. In fish of this age, however, this initial period of coordinated mutual exchanges was soon followed by chasing and biting which was not significantly reduced by the appeasement of the subordinate. The progression of an encounter from initial approaches to exchanges of lateral displays and tail beating, appeasement, and subsequent chasing and biting usually resulted in both fish appearing very nervous and jumpy. Outside disturbances during the chasing and biting sequences often caused both fish to revert back to a more formal interaction involving lateral displays before the dominant again resumed chasing and biting, and the subordinate again appeased.

Days 86-107

Many subordinate fish of large size now exhibited body tilting for long periods; appeasement was also indicated by stationary positioning near the surface or at the bottom without maintaining body tilting, and subordinates exhibited less fleeing after appeasement began. Collapsing of the dorsal fin during these periods of inactivity was highly variable. Many subordinates approached the dominant after appeasement began and resumed or increased their tilting as they approached, sometimes with the head jerking. Some subordinates were observed to challange the dominant in a bout of lateral displaying and tail beating; in most cases this ended with the subordinate appeasing again, but in one case the dominant-subordinate relationship was reversed.

During initial approaches some fish would rub their pelvic threads across the head or sides of each other; sometimes only one fish, which was usually the dominant, would do this. More time was now spent in formalized mutual lateral displays and tail beating, and fin tugging was sometimes exhibited, most often by the dominant fish. The raised dorsal fin response often graded quickly into a median fin spread which was exhibited by both dominant and subordinate fish when close together or far apart.

Dominant fish now appeared less aggressive after an agonistic bout in which they exhibited lateral displays, tail beating and fin tugging; and the subordinates usually appeased in a stationary position. In encounters where the subordinate was less cooperative both during the sequence of mutual displays and during appeasement, the dominant exhibited more chasing and biting while trying to localize and display to the subordinate.

Days 110-136

The large and medium sized fish now typically exhibited loose, wide circling of each other with the median fins spread during the initial approaches; this was commonly accompanied by extending the pelvic threads forward or to the side and then rubbing them over the head and/or flank of the other fish. During this phase some of the fish continued to exhibit median fin spreading for long periods interspersed between raised dorsal responses, but did not enter into mutual displays, tail beating or fin tugging, and no chasing, biting or appeasement occurred. In resolved encounters, the initial period of loose circling was followed by mutual displays, tail beating and fin tugging. This sequence of displays was sometimes repeated two or three times, but was usually terminated when one fish appeased. The dominant fish would remain relatively unaggressive as long as the subordinate maintained a stationary position, but if the subordinate continued to move around the chamber, the dominant fish initiated a sequence of chasing and biting interspersed with attempts at displaying to and tail beating the subordinate fish.

The smaller fish paired during this phase were cooperative in their agonistic interactions. The subordinates appeased less formally and exhibited more fleeing; the dominants exhibited more chasing and biting, accompained by localizing and displaying attempts. By the end of the study period large variations in the levels of agonistic interactions were still common between fish of all sizes.

CHAPTER V

QUANTITATIVE DESCRIPTION OF AGONISTIC BEHAVIOR DEVELOPMENT

The dyadic encounters observed during this portion of the study between 26 and 136 days of age were defined as resolved or unresolved by the presence or absence of appeasement. This definition has been used often in the study of agonistic interactions in adult anabantids, including the blue gourami (Miller, 1964; Miller and Miller, 1970; Frey and Miller, 1972). Resolution first occurred on day 50 in one encounter, after which the percentage of encounters resolved increased to a peak of 100% between days 83 and 100 (Figure 1). From day 104 to day 136 the number of encounters resolved was variable.

The fish involved in resolved encounters were designated as subordinates if exhibiting appeasement and dominant if not exhibiting appeasement. The fish in the unresolved encounters were designated as "greater" or "lesser", indicating the relative approach frequencies of the two fish.

Where fish of the four social classifications of dominant, subordinate, "greater," and "lesser" exhibited consistant differences in the behavior parameters measured these differences will be illustrated and discussed. If no apparent differences between these groups occur, the trends in the average behavior parameter values for all fish will be used to describe quantitative changes that occur during development.

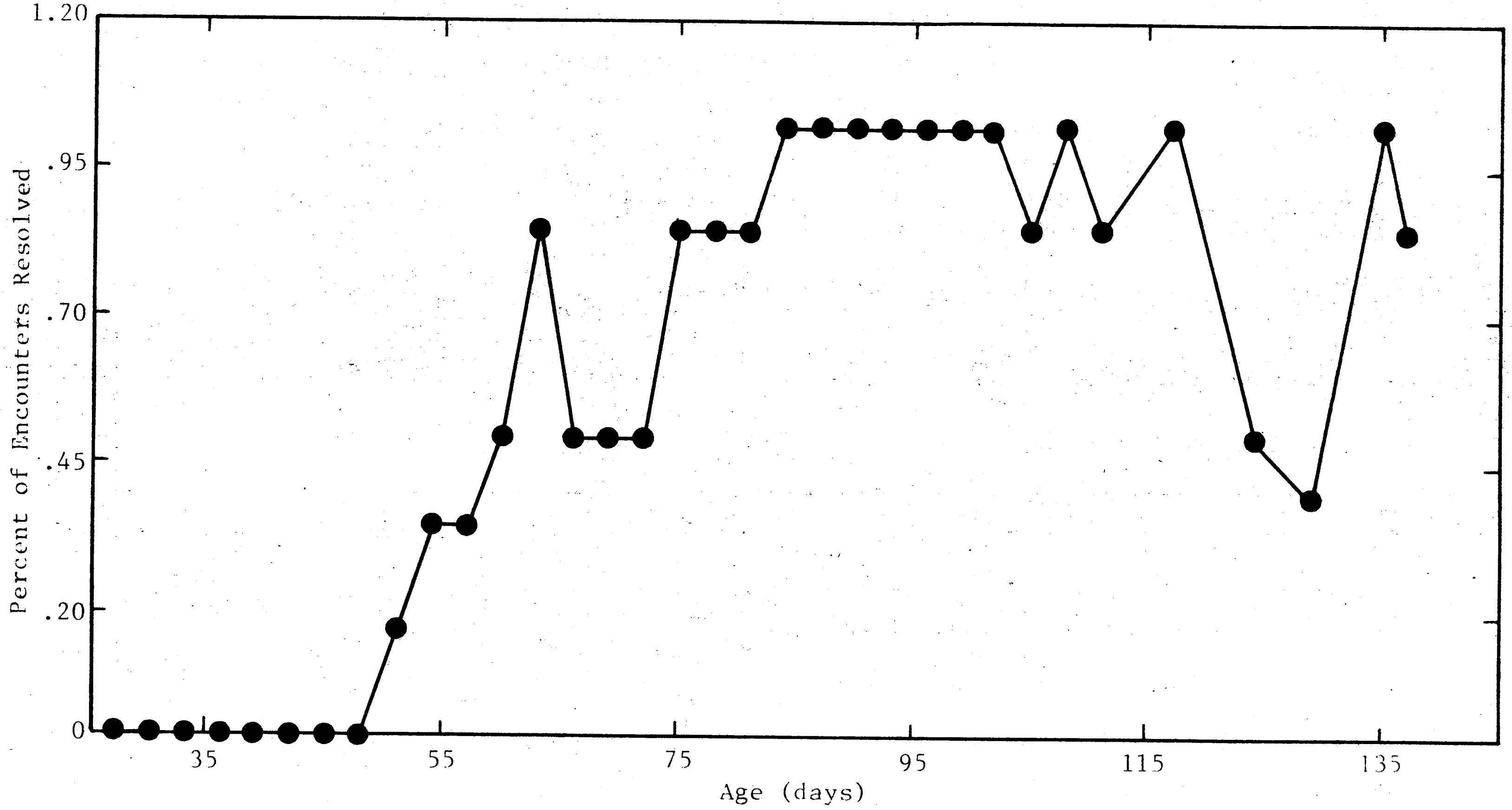

Figure 1. Plot of percentage of dyadic encounters resolved by age.

Where the frequency and duration of a behavior indicate a similar trend only the frequency will be discussed.

Approach

Approach behaviors were the first of the nine agonistic behaviors measured to occur during development. The relative approach frequencies of the two fish in an encounter served as an indicator of overall behavior differences between the fish from day 26 on. The approach frequency of the "greater" fish in unresolved encounters increased to a peak between days 56 and 74 (Figure 2). This peak coincided with the general approach frequency of the dominant fish which first appeared on day 50. The "lesser" fish exhibited a much lower approach frequency which was similar to that exhibited by subordinates. Between days 83 and 101 no unresolved encounters occurred. Between days 104 and 136 the approach frequencies of the "greater" fish were consistantly less than those of dominant fish, and were more similar to those of the "lesser" fish. The approach latency of all fish decreased during the 15 weeks of the study (Figure 3).

Chase

Chase behaviors were exhibited exclusively by the "greater" and the dominant fish in encounters. As with approach frequencies, the frequency of chase behaviors of the "greater" fish increased to a peak between days 65 and 71 which approached the level of chase exhibited by the dominant fish. Between days 74 and 80, and from day 104 to day 136 no chases were exhibited by the "greater" fish (Figure 4). Chase behaviors were first exhibited by dominant fish on day 50, increased

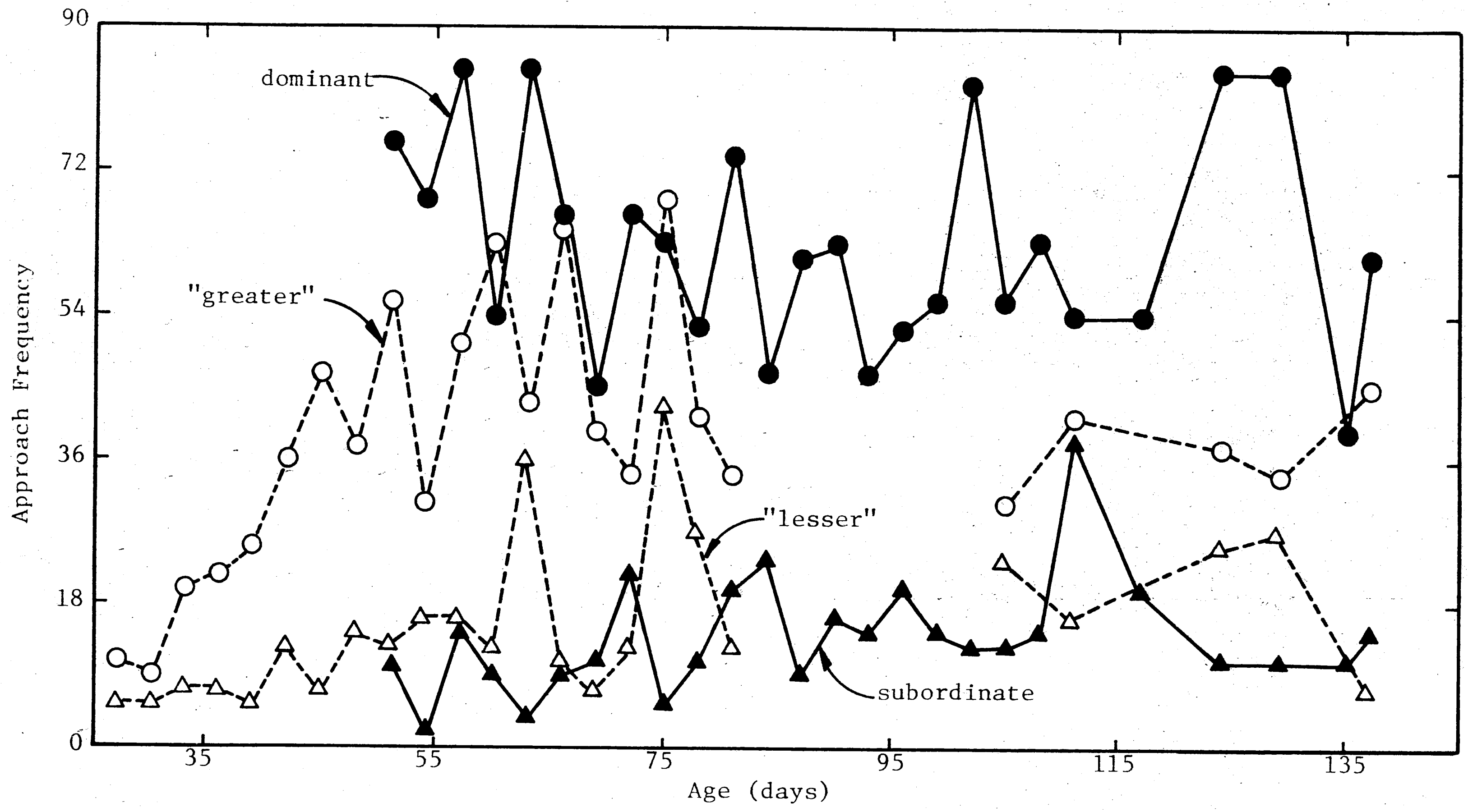

Figure 2. Plot of average approach frequency by age for dominant, subordinate, "greater" and "lesser" fish.

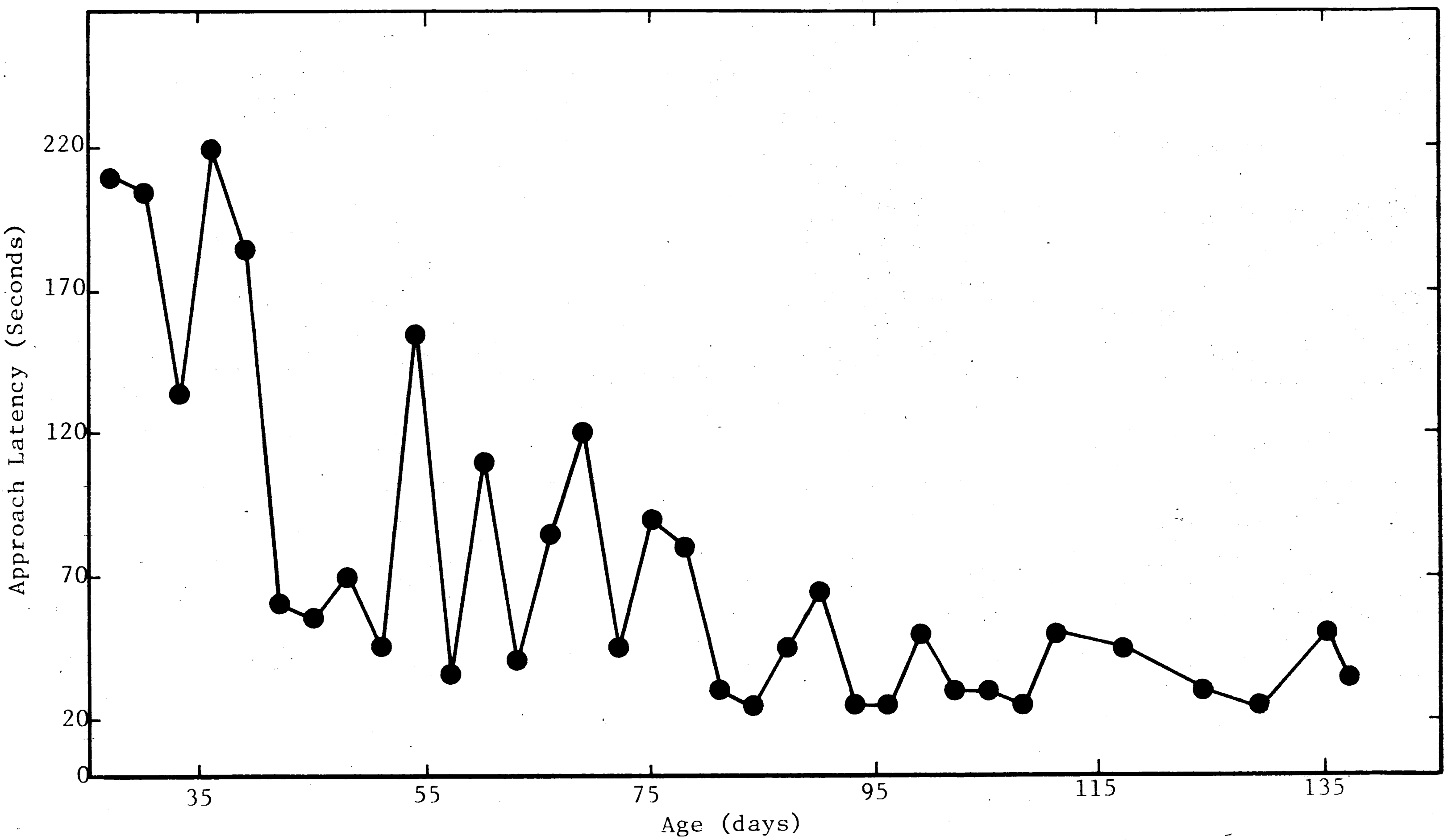

Figure 3. Plot of average approach latency by age for all fish.

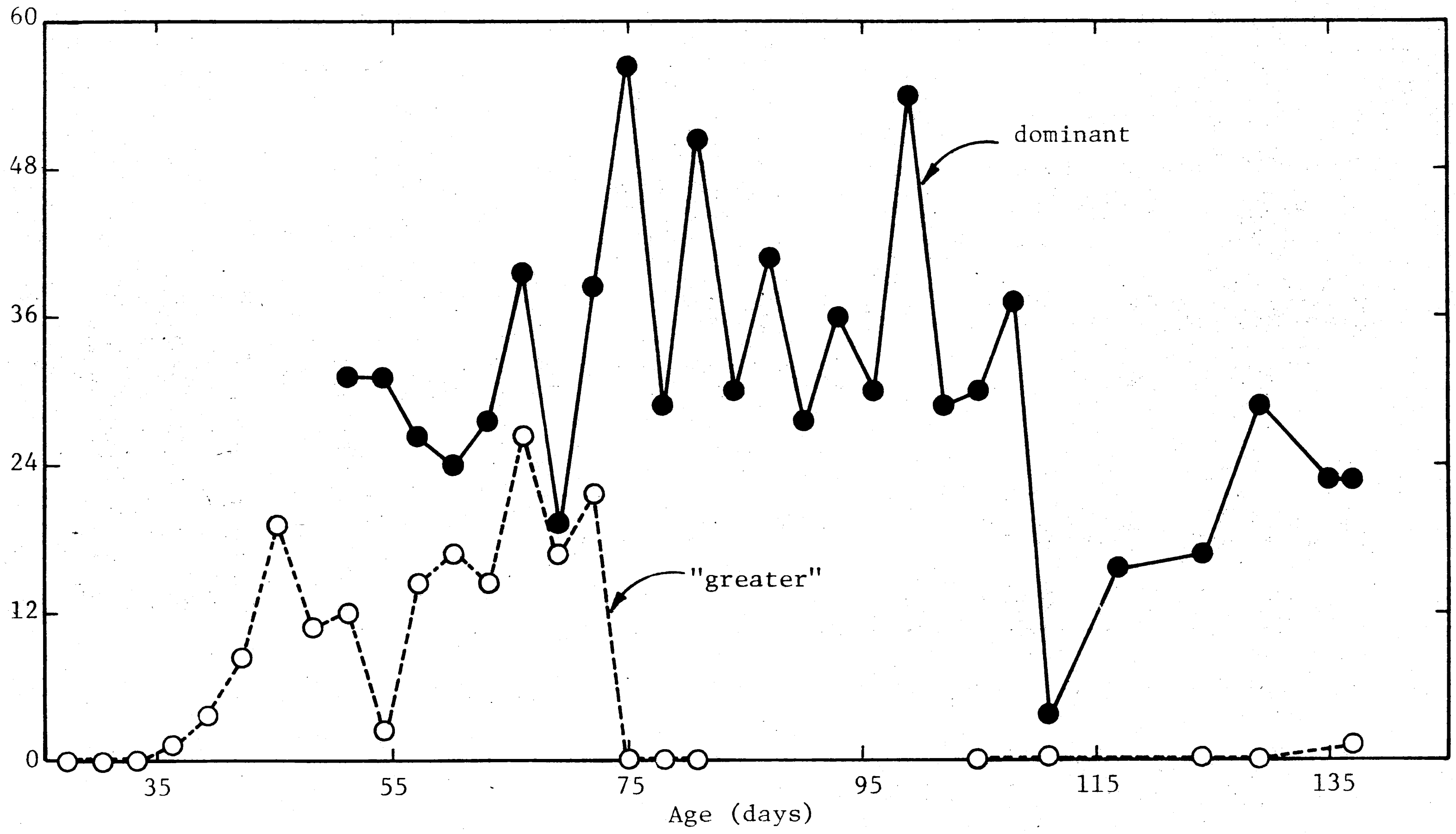

Figure 4. Plot of average chase frequency by age for dominant and "greater" fish.

to a peak between days 74 and 95, and then decreased between day 98 and 136. The average latency to chase was least variable from 80 to 104 days of age (Figure 5), which coincided generally with the period of peak chase frequencies of dominant fish.

Bite

Bites were exhibited more frequently by the "greater" and dominant fish (Figure 6). The frequency of bites exhibited by the "greater" fish increased to a peak on day 71, approaching the level of biting exhibited by the dominant fish. From day 77 to day 136 the frequency of biting in the "greater" fish remained at a very low level. A consistantly low level of bites was exhibited by the "lesser" fish during the entire study period, and the general level of biting by subordinates was also consistantly low. Between days 83 and 101, which was the peak period of chasing by dominant fish, no bites were exhibited by the subordinate fish. The average frequency of biting exhibited by dominant fish remained at a relatively constant level from day 50 to day 107, but between days 110 and 136 the frequency of biting became quite variable. The average latency to biting was highly variable from day 26 to day 38, and thereafter decreased to a relatively constant level (Figure 7).

Raised Dorsal Fin

The raised dorsal fin frequency was similar in all four categories of fish. It reached a peak between days 74 and 98, and then decreased from day 101 to day 136 (Figure 8). Although the frequency of raised dorsal fin decreased after day 98 the duration of the behavior continued to increase to a peak near the end of the study period (Figure 9).

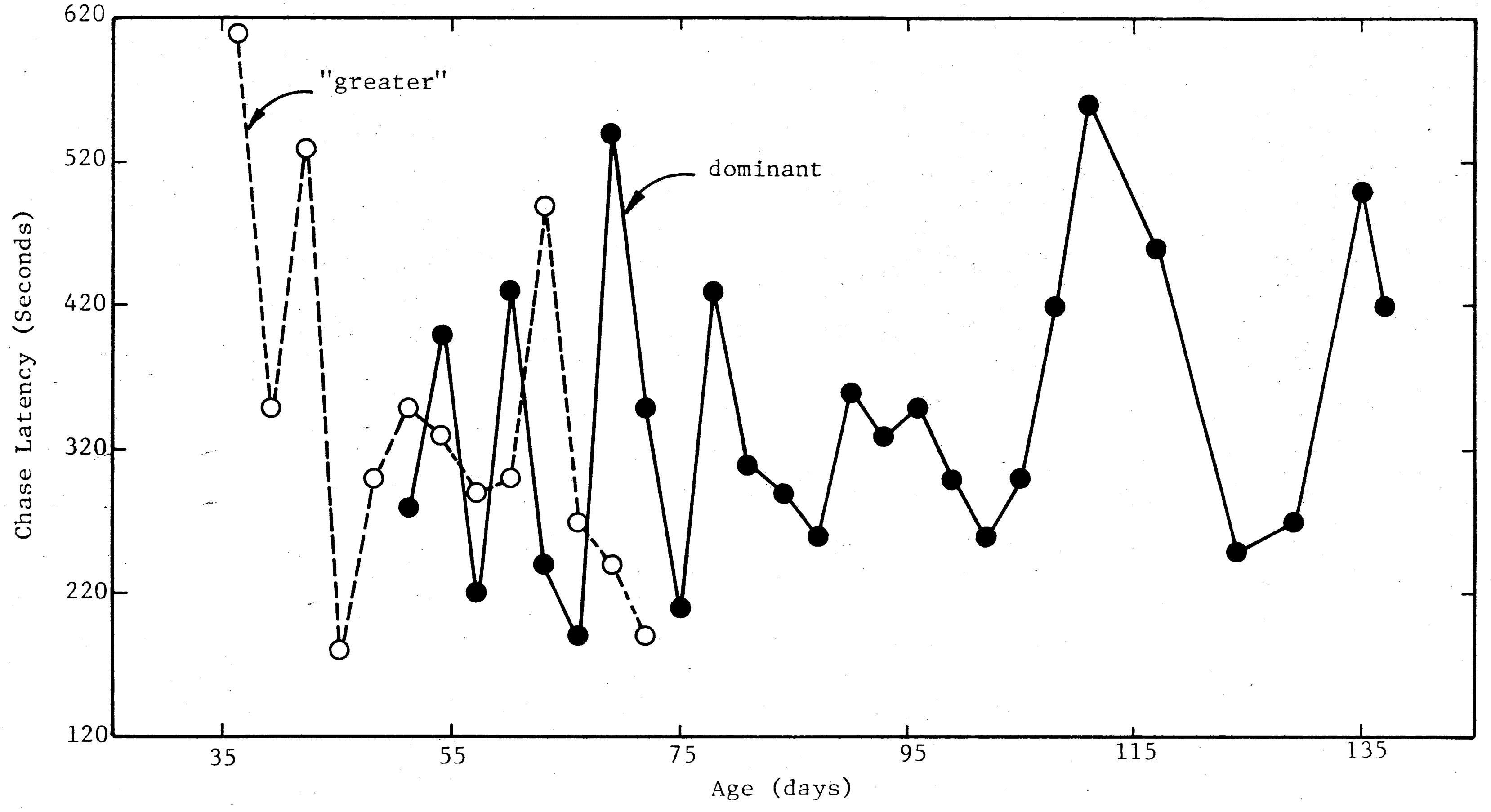

Figure 5. Plot of average chase latency by age for dominant and "greater" fish.

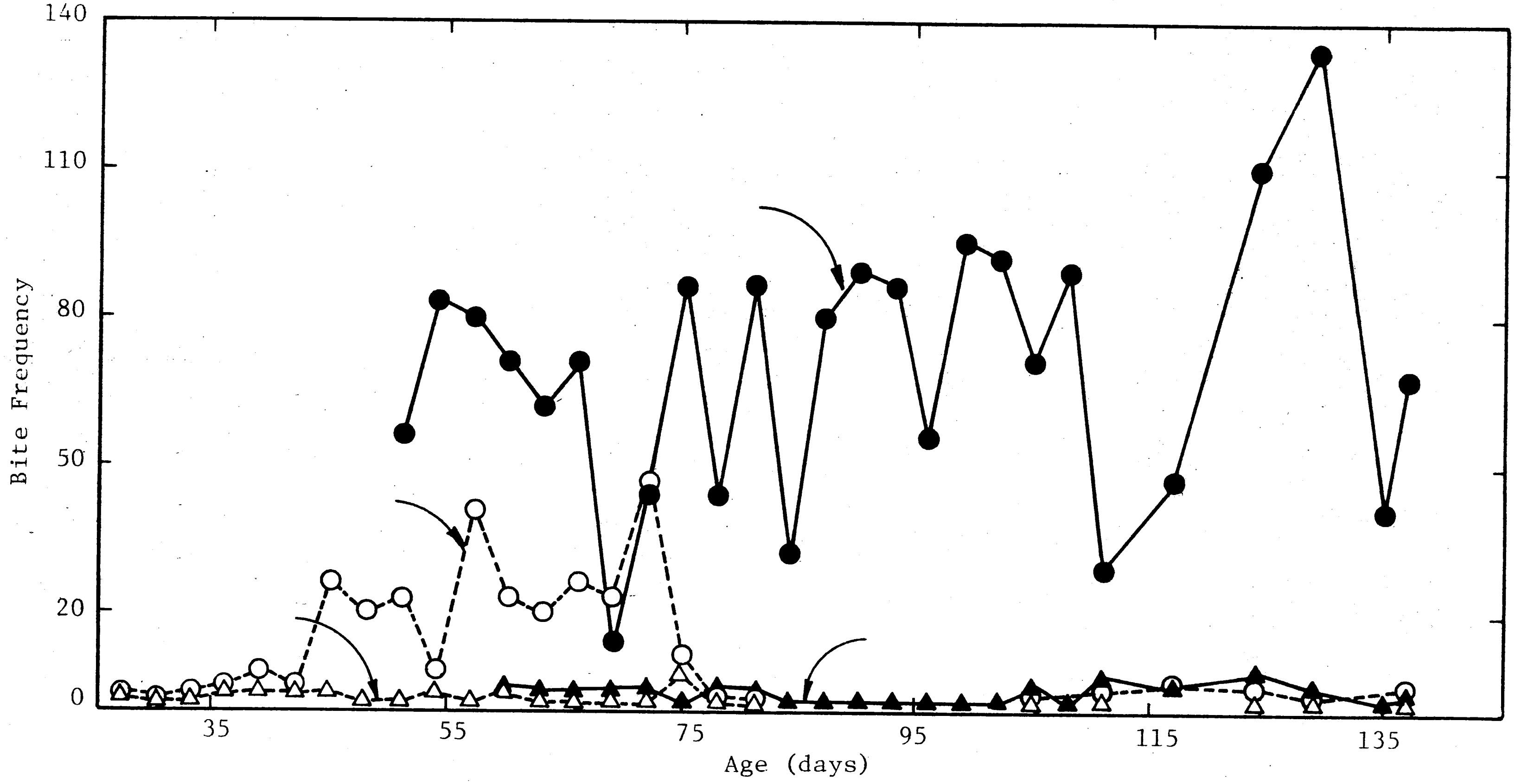

Figure 6. Plot of average bite frequency by age for dominant, subordinate, "greater" and "lesser" fish.

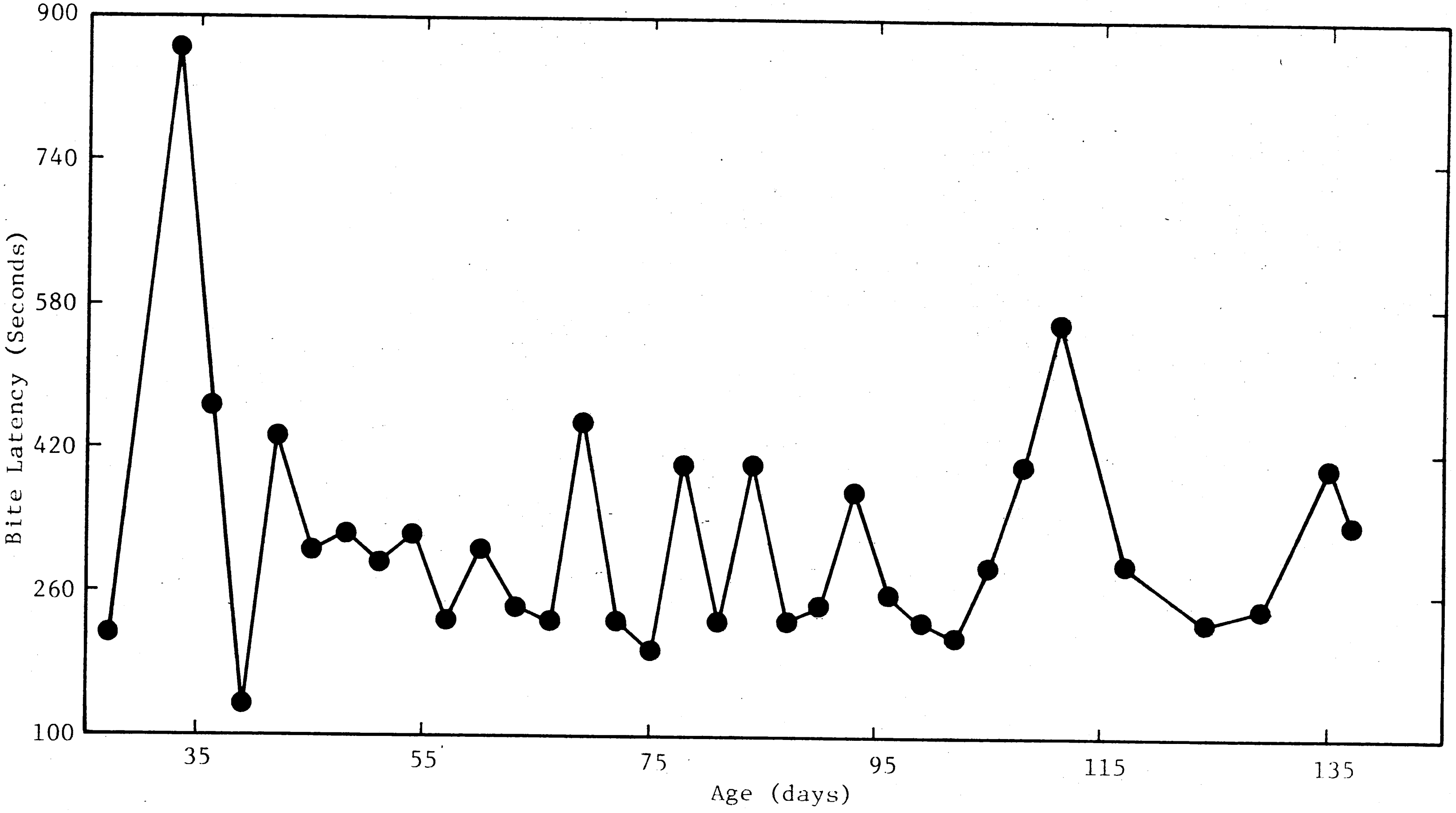

Figure 7. Plot of average bite latency by age for all fish.

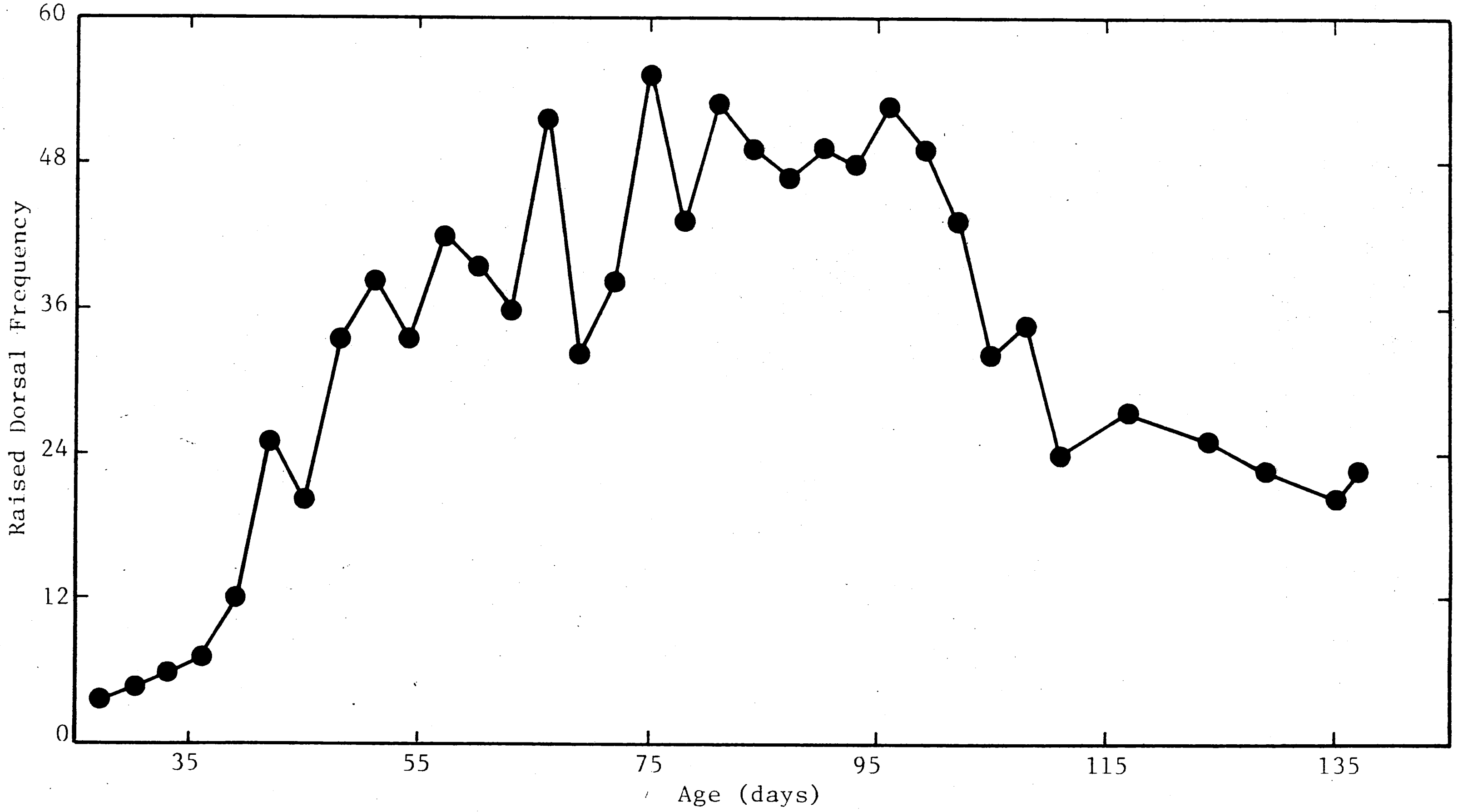

Figure 8. Plot of average raised dorsal frequency by age for all fish.

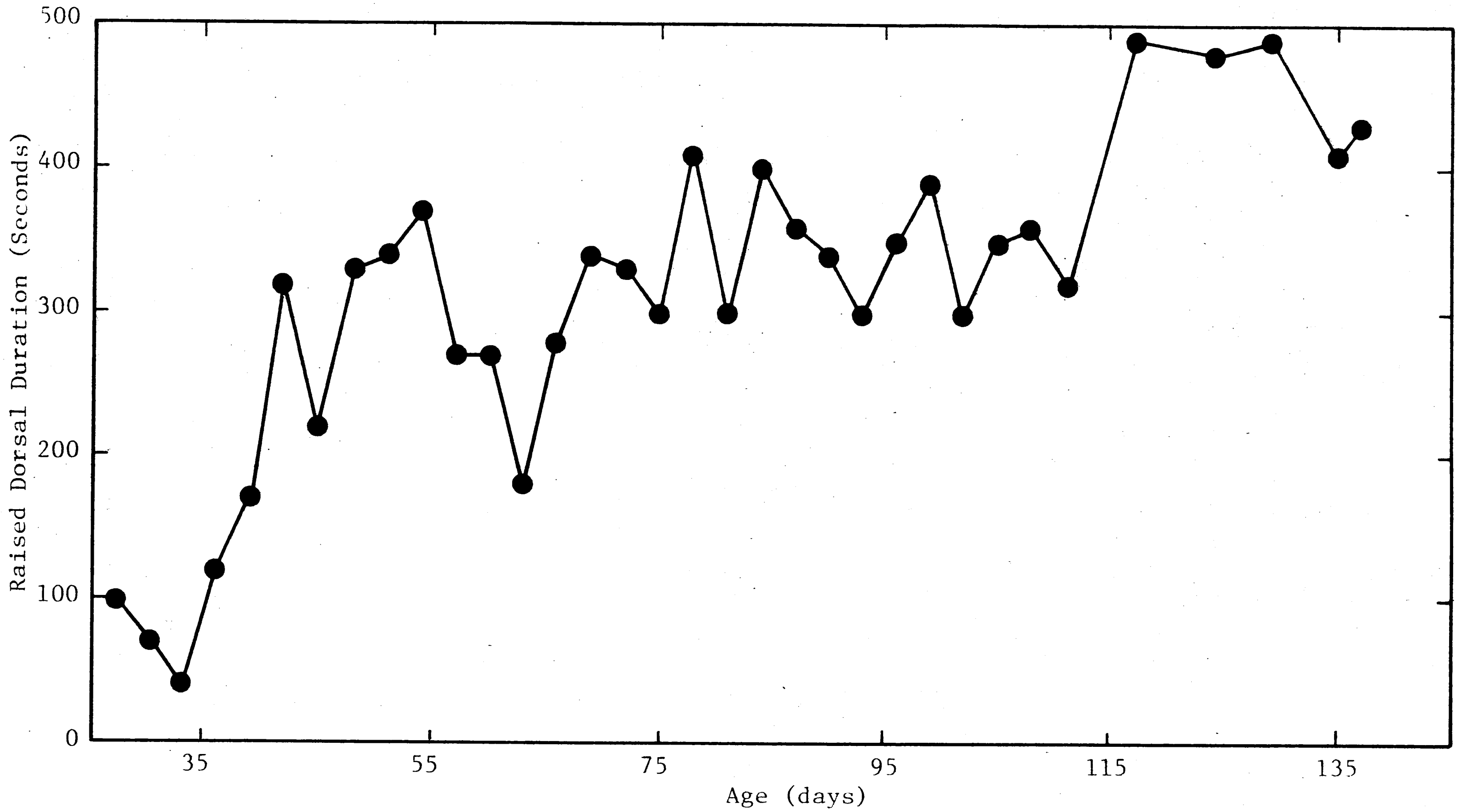

Figure 9. Plot of average raised dorsal duration by age for all fish.

The latency to raised dorsal fin decreased rapidly from day 26 to day 44 and thereafter maintained a low level (Figure 10).

Lateral Display

The dominant fish exhibited the highest frequencies of lateral display throughout the study period (Figure 11). Between days 35 and 53 the lateral display frequencies exhibited in unresolved encounters were very low and similar in both fish. Between days 56 and 74 the frequency of lateral display in "greater" fish increased. "Lesser" fish maintained a relatively low frequency of lateral display with the exception of day 74. The frequency of lateral display in unresolved encounters dropped to a low level again on day 77 and did not increase again until near the end of the study period. Subordinates exhibited low, but gradually increasing frequencies as the study progressed. All fish exhibited a similar increase in lateral display frequencies between days 123 and 136. The latency to lateral display generally decreased during the study period (Figure 12).

Tail Beat

Between day 50 and day 80 the frequency of tail beating exhibited by fish in unresolved encounters was very low and similar to the frequency of behaviors exhibited by subordinates; however, between days 104 and 136 the subordinate fish exhibited consistantly higher levels of tail beating (Figure 13). The dominant fish usually exhibited more tail beating than the other fish but not consistantly, and the frequency of tail beating in the older dominant fish was highly variable. No trend appeared in the latency to tail beating during the study period.

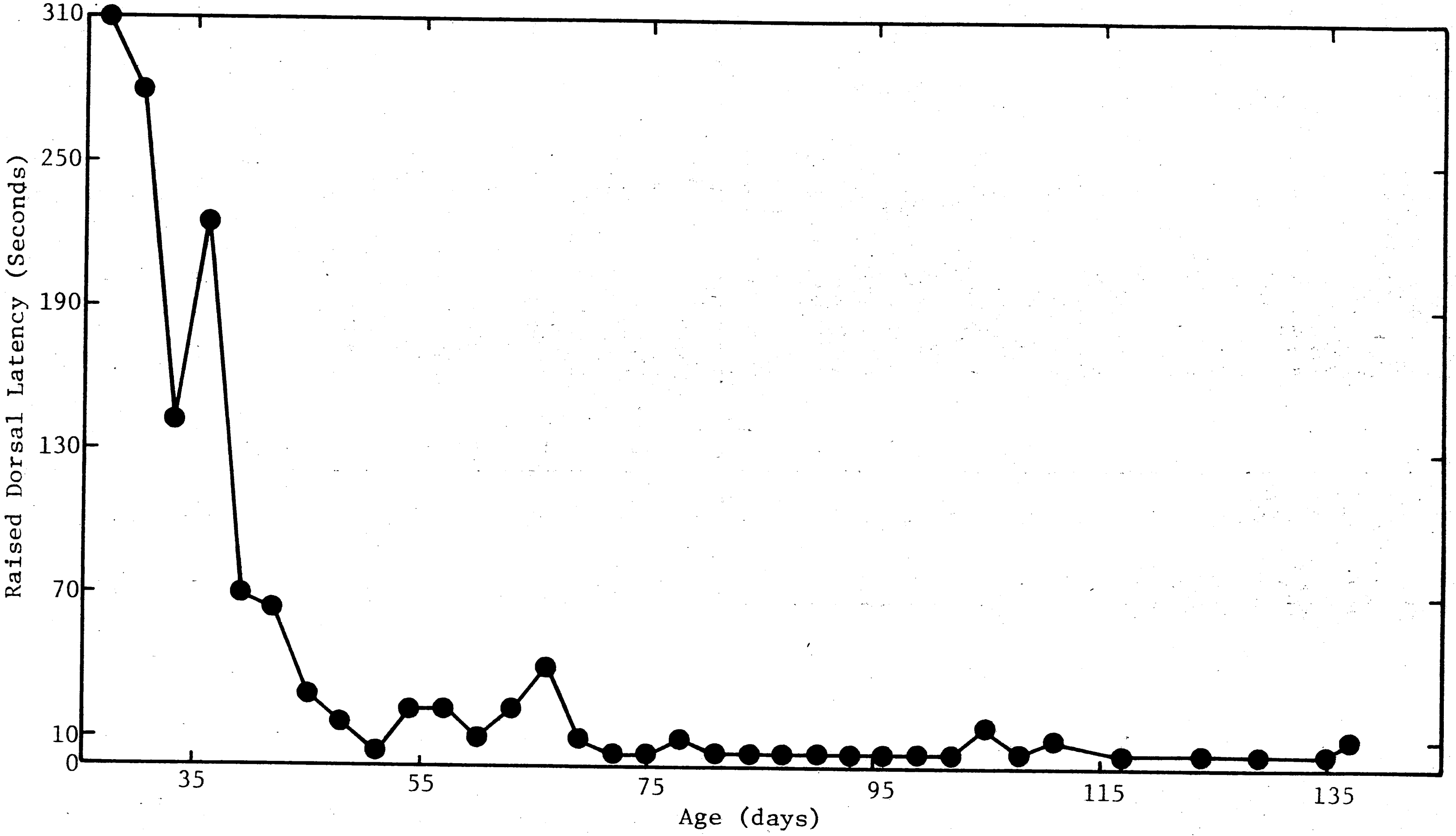

Figure 10. Plot of average raised dorsal latency by age for all fish.

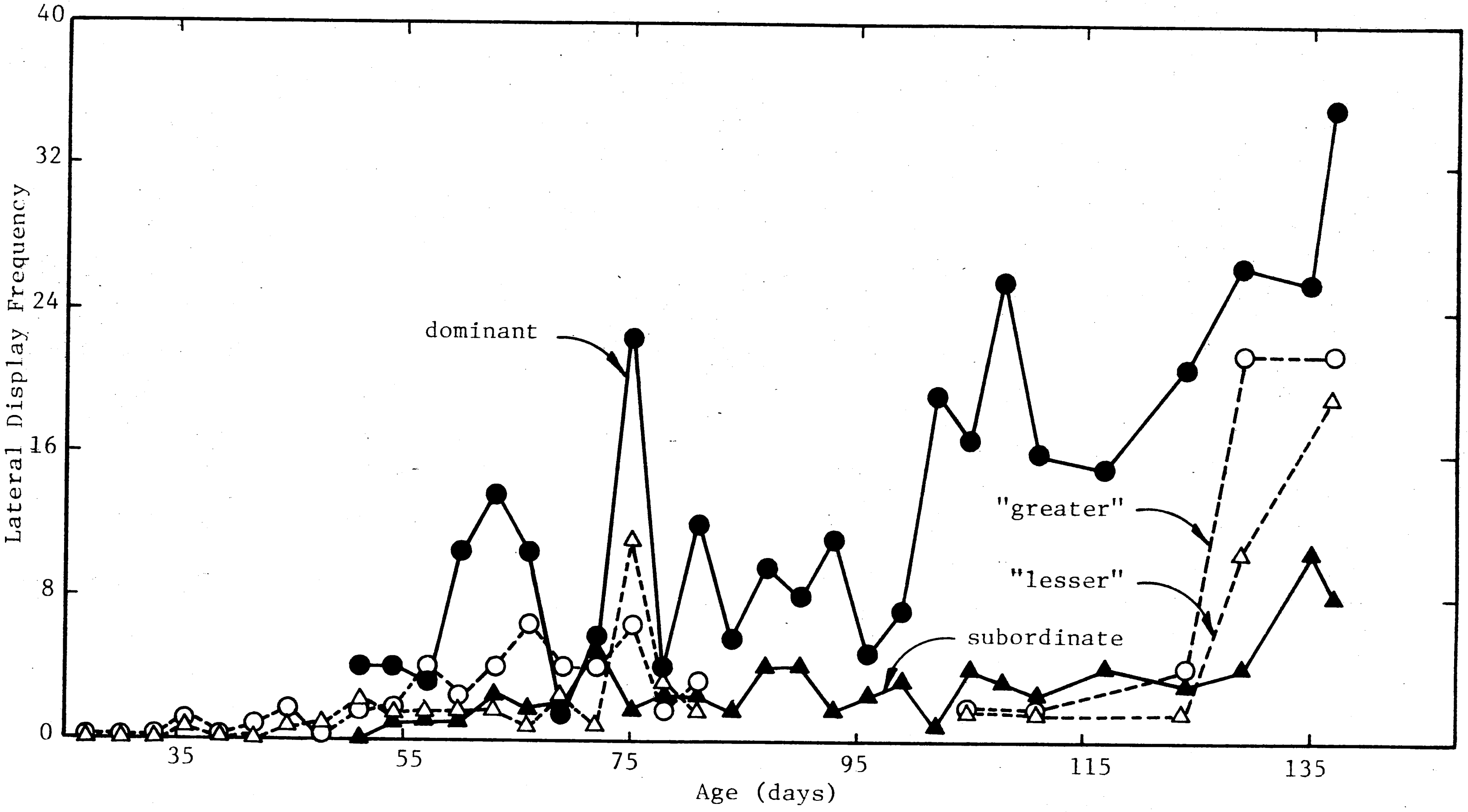

Figure 11. Plot of average lateral display frequency by age for dominant, subordinate, "greater" and "lesser" fish.

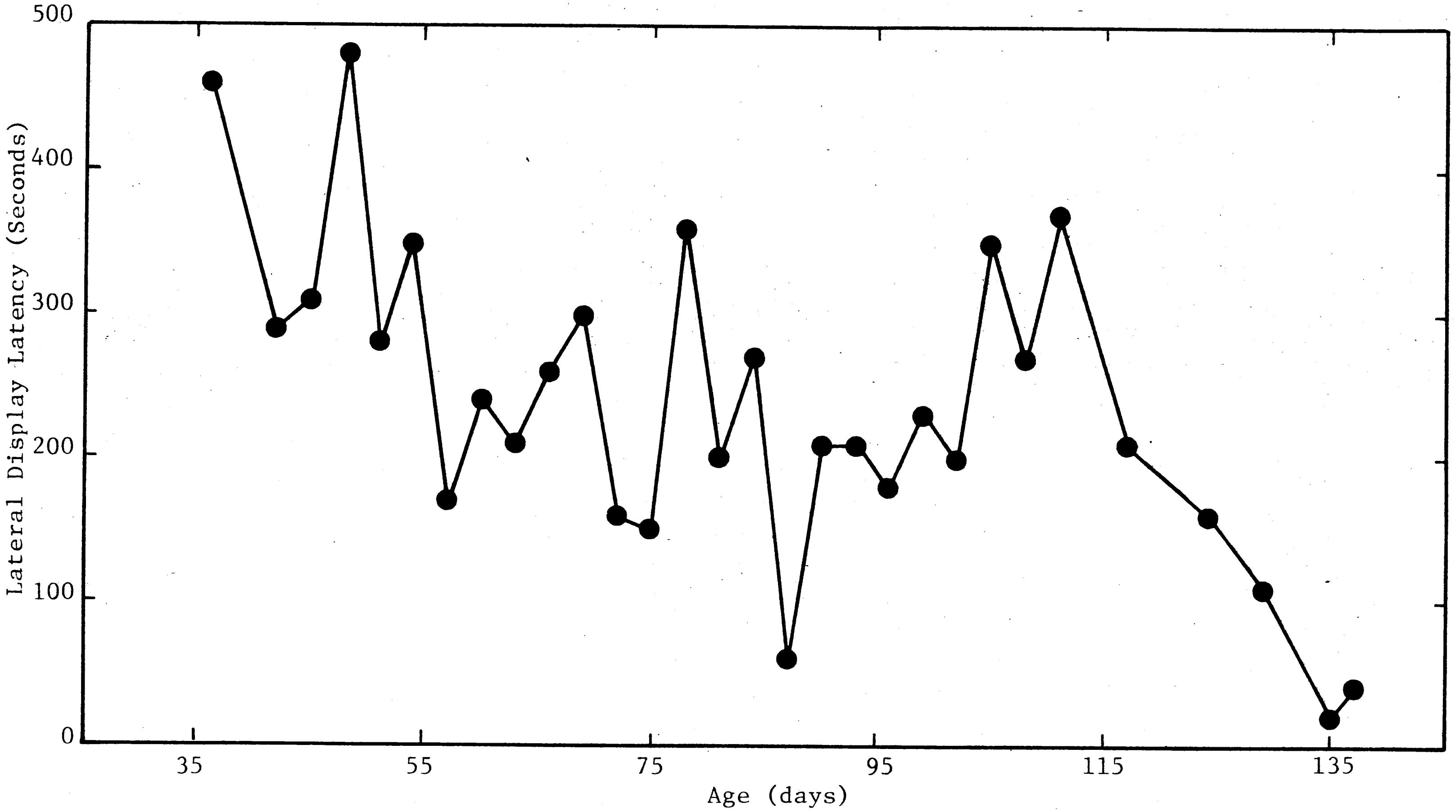

Figure 12. Plot of average lateral display latency by age for all fish.

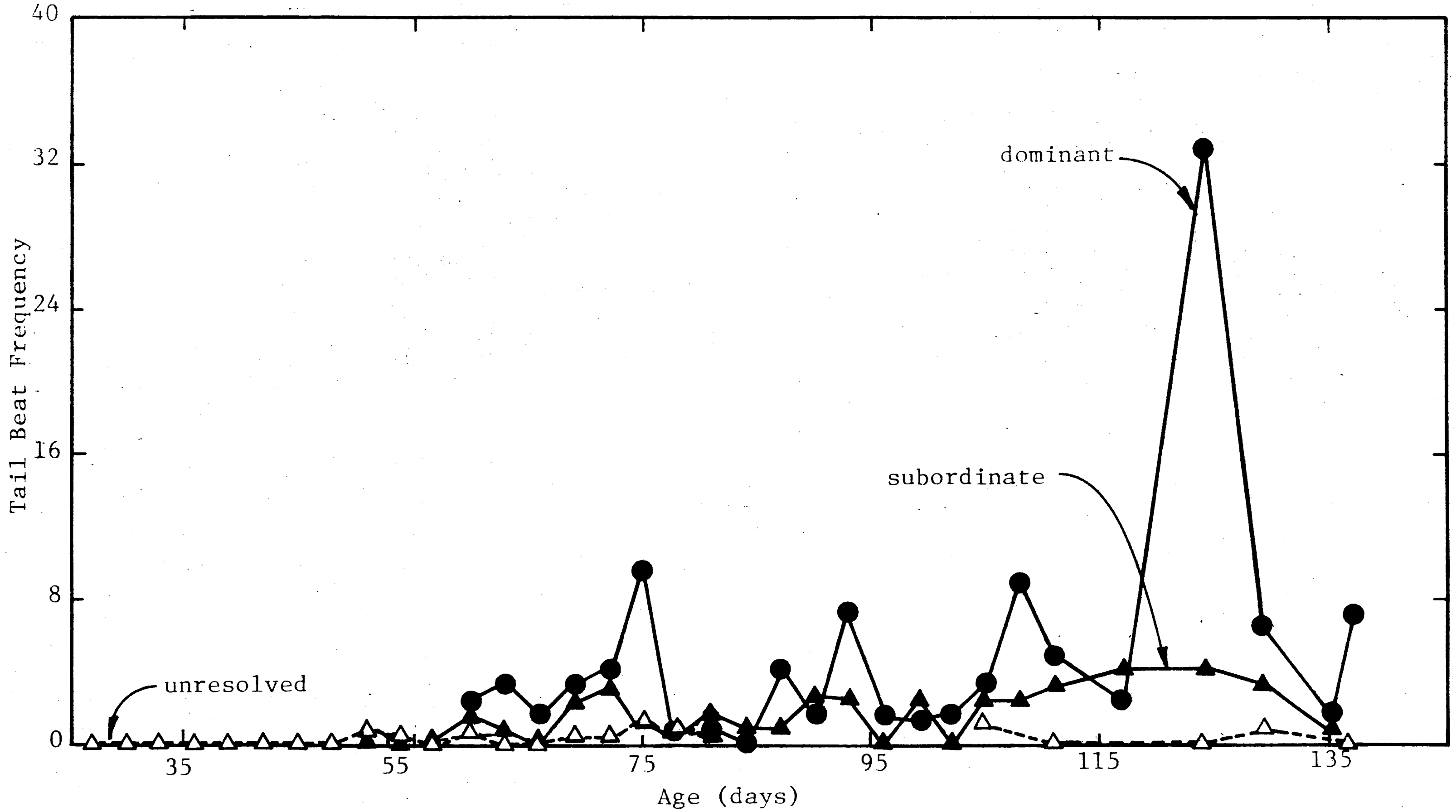

Figure 13. Plot of average tail beat frequency by age for dominant, subordinate, and combined "greater" and "lesser" fish.

Fin Tug

Fin tugging was exhibited only by fish in resolved encounters; first, briefly on day 68 and then from day 86 to day 136. Fin tugging was exhibited more frequently by dominants than subordinates on any given day; and dominant fish exhibited fin tugging on 12 of the 13 encounter days between day 86 and day 136; whereas subordinates exhibited fin tugging on only 5 out of the 13 encounter days (Figure 14).

Carousel

Carouselling first appeared on day 59, and occurred as mutual carouselling between dominant and subordinate fish from day 59 to day 89. On day 107 and from day 123 to day 136 after initial sequences of mutual carouselling and subsequent chasing and biting, the dominant fish usually attempted to circle and display to the subordinate. This circling by the dominant was recorded as non-mutual carouselling, and is indicated by a difference in carousel frequencies for dominant and subordinate fish during the latter part of the study period (Figure 15).

Appease

When appeasement first appeared on day 50 it was in the form of brief tilts of the body without the folding of the dorsal fin, and it was accompanied by fleeing. Between day 50 and day 83 the frequency of appeasement was highly variable and did not include dorsal fin folding, but the duration of appeasement increased during this period (Figures 16 and 17). From day 86 to 136 the frequency of appeasement was con-

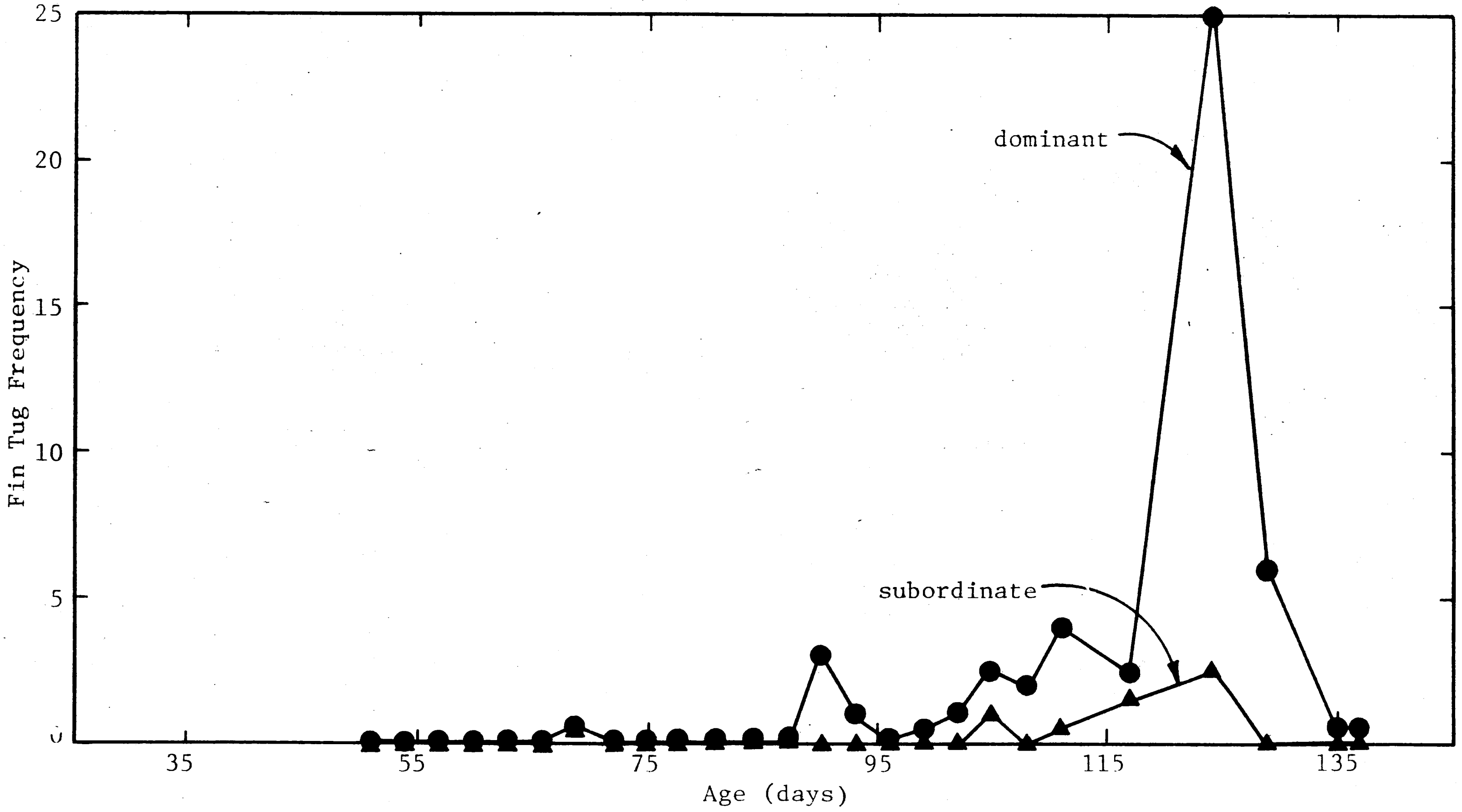

Figure 14. Plot of average fin tug frequency by age for dominant and subordinate fish.

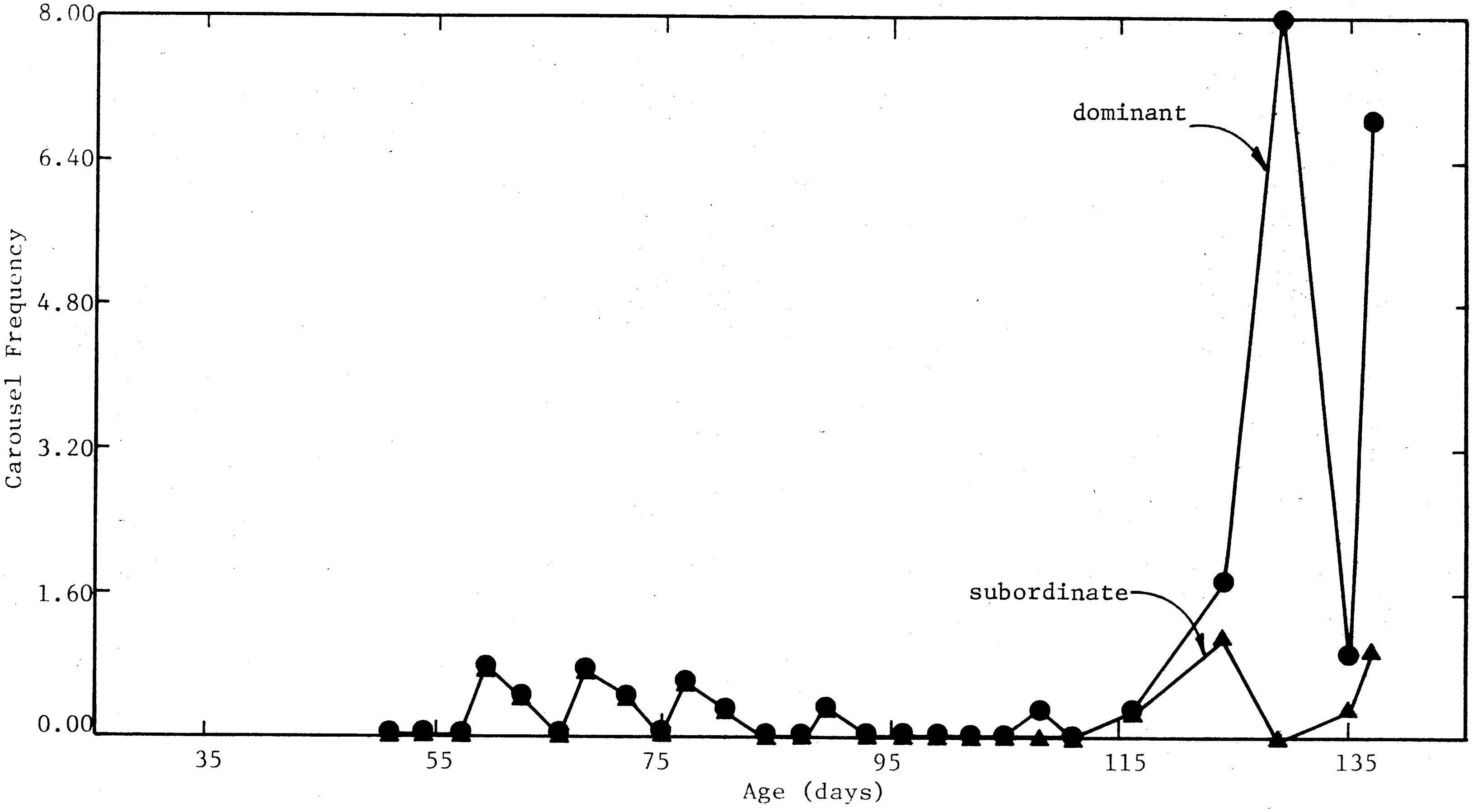

Figure 15. Plot of average carousel frequency by age for dominant and subordinate fish.

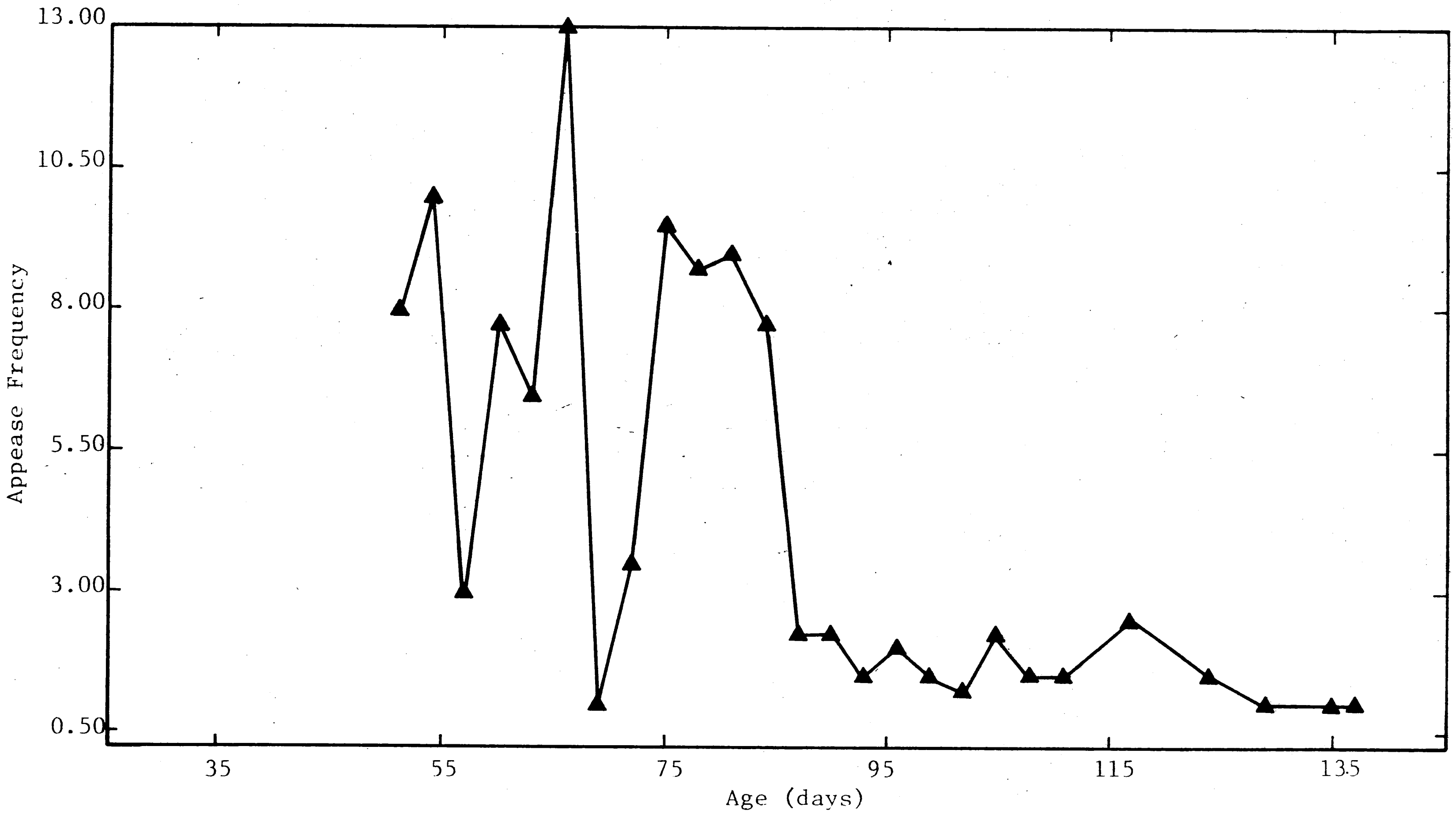

Figure 16. Plot of average appeasement frequency by age for subordinate fish.

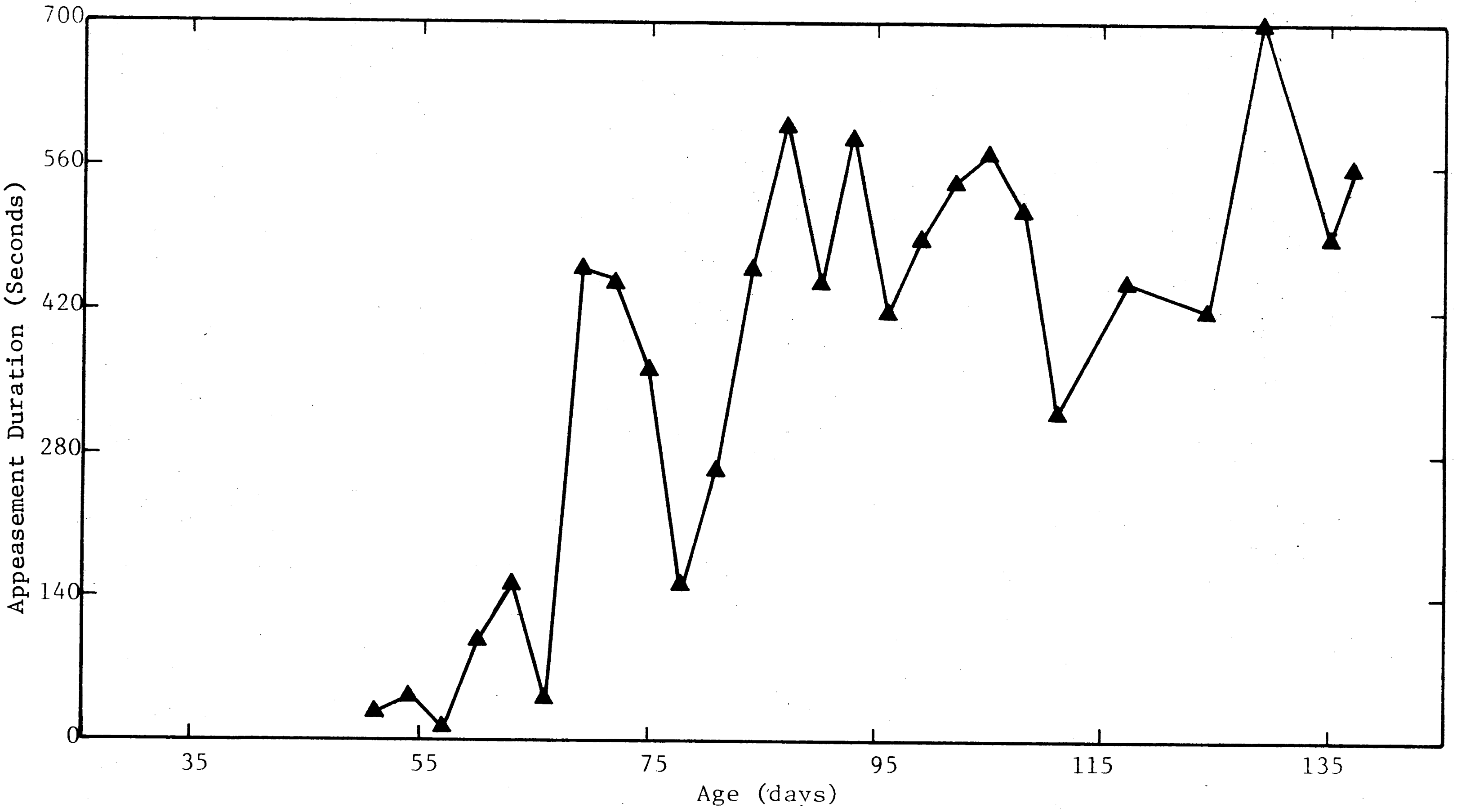

Figure 17. Plot of average appeasement duration for subordinate fish.

sistantly low but the duration of appeasement continued to increase to a peak at the end of the study period. As the duration of appeasement increased during the latter part of the study period it included more dorsal fin folding; it was associated less with fleeing, and more with periods of inactivity. Although the duration increased there was no consistant trend in the latency to appeasement.

Behavior Diversity

An agonistic encounter in this study was considered to be composed of a set of (N) behavioral elements of which (X) were distinct. A maximum of nine distinct behavioral elements were possible within any given encounter. Using Ashby's (1966) definition, the agonistic encounters in this study would have a maximum variety of nine, or more commonly ($\log_2 9$ bits).

A measure of intra-individual variety or diversity of behaviors associated with these encounters was calculated by using the following equation of Shannon and Weaver (1948): $H(X) = -\Sigma p(i)\log_2 p(i)$ where X is a system classification with categories i and associated probabilities p(i). H is an estimate of the entropy or uncertainty at each step of the sequence of behaviors exhibited by an individual fish during an encounter. The logarithm is taken to the base 2 so that the resulting unit of information is the standard "bit". The diversity of behaviors (H) exhibited by each fish was calculated using the frequencies of the nine behaviors measured during the study.

The diversity of behaviors exhibited by "greater" fish increased to a peak on day 62 which was similar to the diversity values for the dominant fish, and then decreased to a low level on days 77 and 80

(Figure 18). The diversity values of the behavior exhibited by "lesser" fish remained low from day 26 to day 71, but increased to the level of the "greater" fish between days 74 and 80. Between days 104 and 136 the diversity values for both fish in the unresolved encounters showed an increase. From day 50 to day 107 the dominant fish exhibited a consistantly high level of behavioral diversity and the subordinates exhibited a consistently lower diversity of behaviors. From day 110 the diversity values exhibited by both fish increased to a similar peak on days 123 and 128.

The frequencies of the nine behaviors measured appear to be the best overall quantitative indicators of the behavioral changes occurring during the first 136 days of life. An exception to this is seen only in the raised dorsal fin response and appeasement, the durations of which provide the best indication as to the function of these two behaviors in the developing agonistic complex.

The trends in the average behavior frequencies for all fish indicate a biphasic process occurring during development (Figure 20). The overtly aggressive behaviors of biting and chasing appear early and their frequencies increase to a peak during the third month of life, after which they decrease. Lateral display, tail beating, carousel, and fin tug appear progressively later in development, increasing gradually during the balance of the study period with the exception of lateral display which increases dramatically in the fourth month of life. Although the frequency of appeasement decreases after its appearance in the second month, its duration continues to increase. The raised dorsal fin frequency increases to a peak during the third month of life and decreases thereafter, although its duration continues

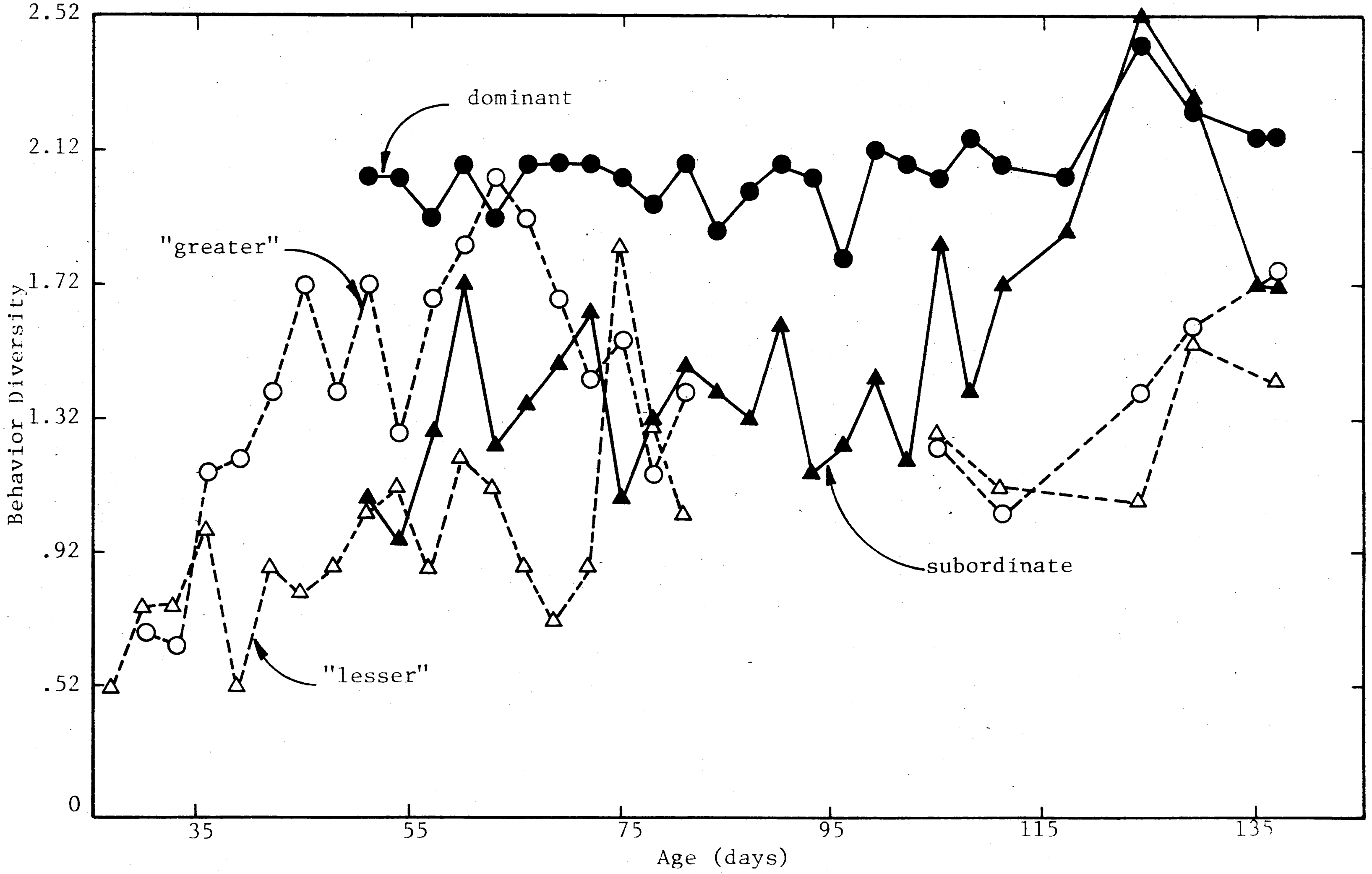

Figure 18. Plot of average behavior diversity by age for dominant, subordinate, "greater" and "lesser" fish.

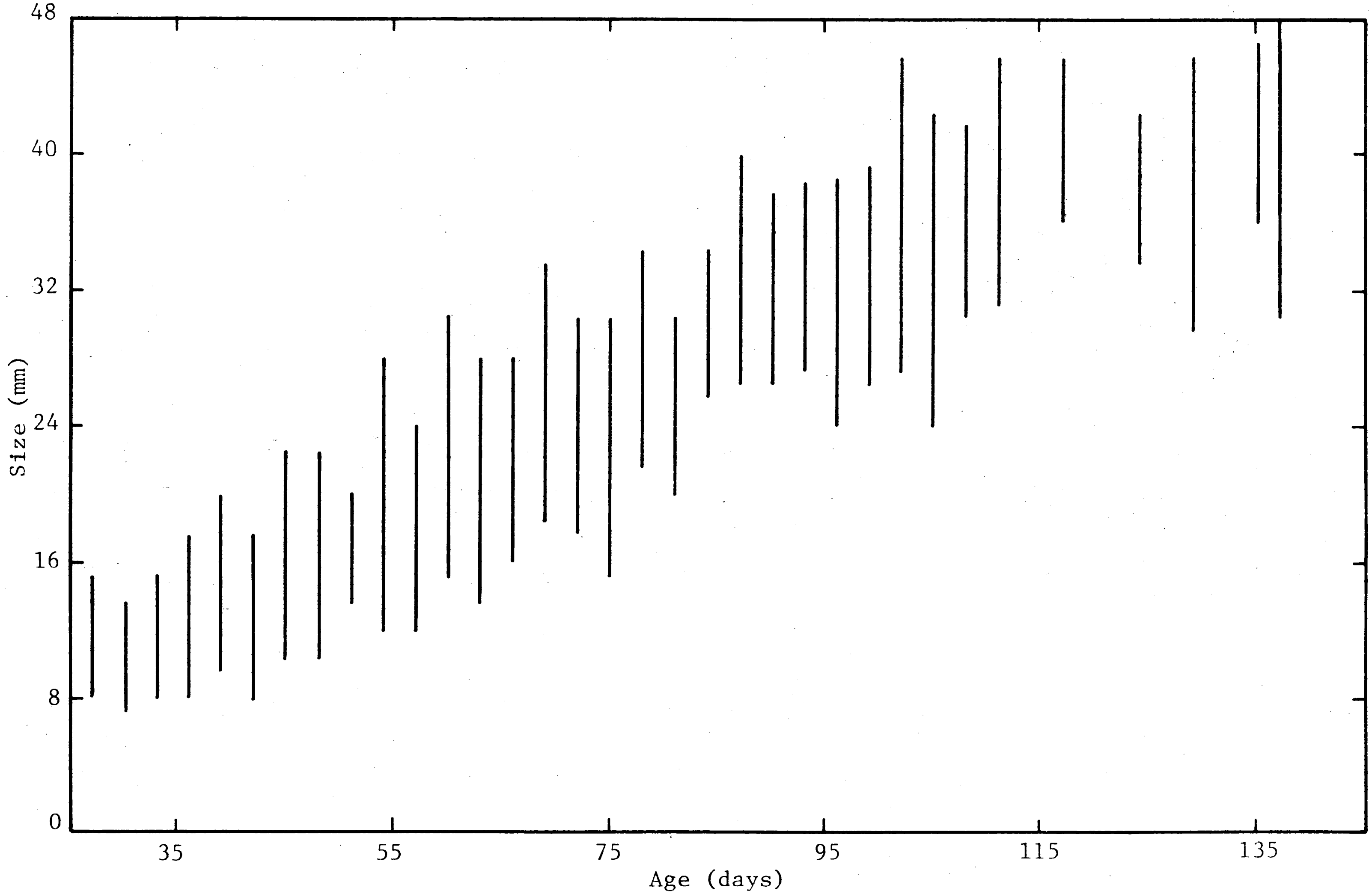

Figure 19. Plot of size ranges of fish sampled by age.

to increase.

Age and Size Relationship

Although it was possible to make a qualitative assessment of differences in the behavior of different sized fish at the same age (Figure 19), due to the design of the study, plots of behavior parameters by size reflected the same trends as those indicated in the plots of behaviors by age. In an attempt to compensate for this, the behavior parameters for three size categories (17-20, 25-28, and 37-40 mm sl) were plotted against age. The trends in the plots for the three size groups showed no differences from those plotted for all sizes by age.

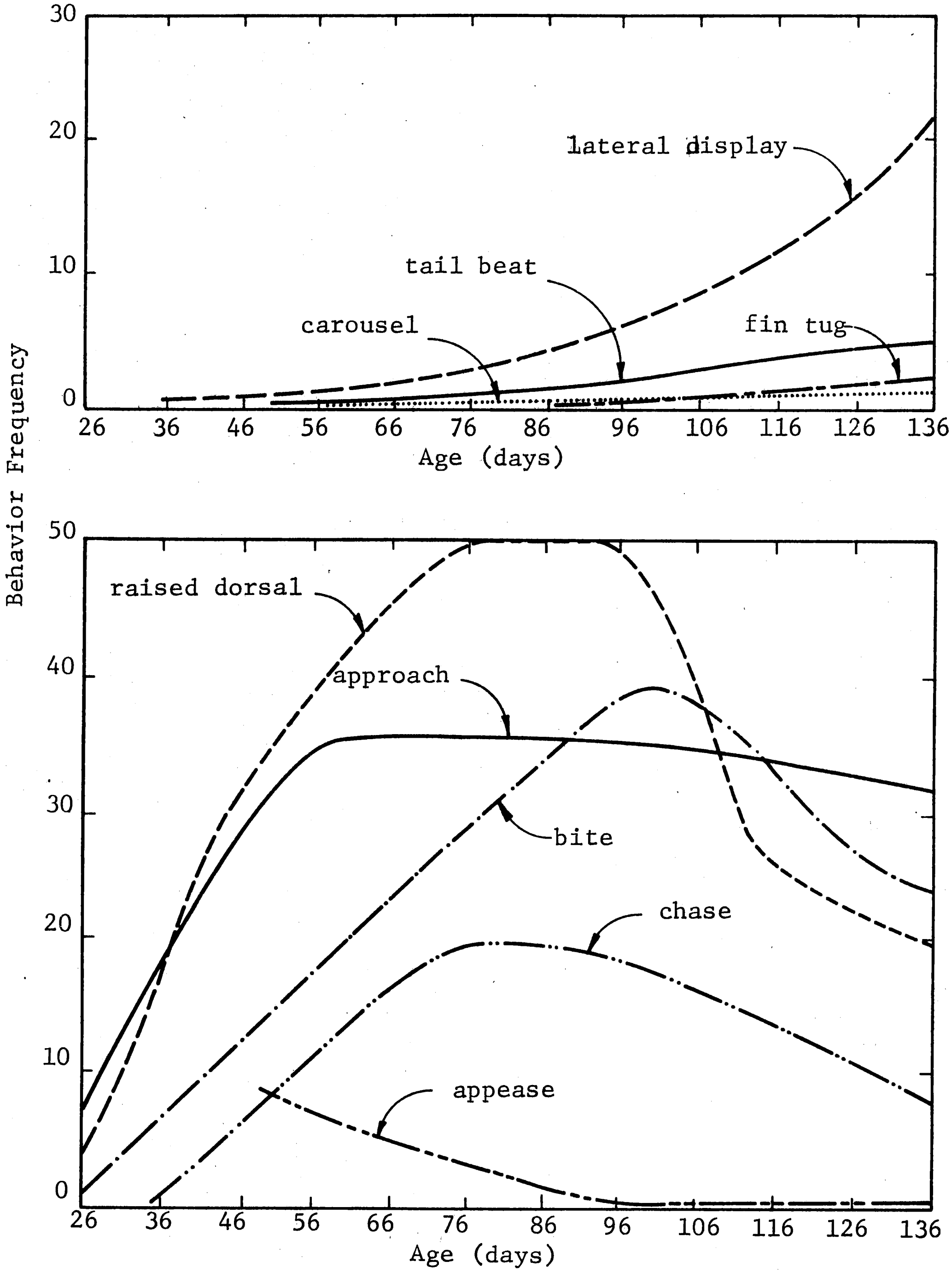

Figure 20. Smooth curve plots of average behavior frequencies for all fish by age.

CHAPTER VI

QUALITATIVE DESCRIPTION OF THE AGONISTIC BEHAVIOR OF FISH RAISED UNDER THREE DIFFERENT CONDITIONS OF SOCIAL ISOLATION

Group 1 - Fish Raised in Isolation From Two Days After Hatching

When paired together with other isolates as a first or second experience between 113 and 136 days of age these isolates usually exhibited typical agonistic behaviors for their age. There was an immediate awareness of each other, as indicated by an extended period of continuous alternation between a raised dorsal fin response and median fin spreading, while making mutual approaches in the form of loose wide circles. The circling observed in these isolate fish appeared less coordinated than the circling which was exhibited by group-raised fish, and contained some elements of tilting away from the opponent. When coming closer together in the circling the two isolates performed pelvic thread manipulation of the opponent. This was followed by a short sequence of mutual lateral display, and only a little tail beating or fin tugging by one or both fish. The isolates spent more time in loose circling, and took longer to interact, and spent less time in mutual displays than group-raised fish. The bout of mutual exchanges was usually terminated when on fish broke away and assumed an extreme stationary appeasement posture with the dorsal fin retracted and the body tilted to the side. This posture was usually maintained for long periods unless the dominant fish was at the other end of the encounter chamber. The dominant did not often approach, display to, or chase and bite the subordinate unless it began to move around. Some subordinates exhibited tilting in an almost horizontal position with the median fins spread when the dominant fish approached.

In one of the four encounters between isolates as a first experience a fish exhibited atypical behaviors which were disoriented and uncoordinated. The fish began a prolonged series of approaches in the form of loose circles soon after the divider was removed, and exhibited slow, rhythmic tilting of the body forward and backward while at the same time rocking on its ventral keel from side to side. During this time the fish was also alternating sporadically between median fin spreads and a retracted dorsal fin. While the fish was performing these odd behaviors its opponent remained inactive, as if confused by the actions of the other fish. The inactive fish eventually appeased without any mutual displaying or tail beating and fin tugging. As the encounter proceeded the dominant fish exhibited less and less of the rocking and tilting and became more aggressive, exhibiting some chasing and biting. During the pairing of isolates as a second experience three of the isolate fish exhibited similar rocking behaviors, but only briefly near the beginning of the encounter, and no forward and back tilting of the body occurred. All of the disoriented and uncoordinated behaviors exhibited by isolates usually occurred during the first two to five minutes of an encounter.

When paired with group-raised fish as a first experience five of the eight isolate fish exhibited the odd combination of rocking, tilting, and fin spreading and retracting; some of these also exhibited head jerking. These behaviors again appeared during an initial long bout of approaches, circling, and moving away, and appeared to confuse the opponent. The intensity of the rocking and tilting usually increased as the isolate moved closer to the group-raised fish, and a lack of consistant orientation of the isolate to its opponent was evident. As the encounter proceeded the rocking and tilting activity decreased. Three of the five rocking isolates became dominant, two became subordinate and one remained unresolved. The three isolates which became dominant became more aggressive as the encounter proceeded, but exhibited only a few lateral displays, tail beats, fin tugs, or chases and bites. The subordinate isolates exhibited extreme appeasement postures in stationary positions. When the group-raised fish appeased during these encounters they did so only with brief side tilting of the body as they moved away from the isolate fish, and did not maintain stationary positions for long if at all. The rocking behavior of isolates occurred only briefly in one encounter when the isolates were paired with group-raised fish as a second experience.

During two encounters with group-raised fish which did not involve rocking, the isolates appeased and turned almost horizontally on their sides as their opponents approached. In one case, as the group-raised fish approached, it exhibited lateral displays and tail beating next to the isolate, and for a short period the extreme lateral display of the dominant wrapped around the subordinate isolate as if executing a spawning clasp. Another subordinate isolate approached its opponent and exhibited a lateral display posture in alignment with the other fish and with the body curved, but the dorsal fin was retracted as in appeasement. A fourth subordinate isolate continued to tilt its body away from the approaching opponent, and as it tilted, it moved away in a slow arc ending up back near the tail of the dominant, accentuating its appeasement tilt with the dorsal fin retracted as it got closer to the dominant fish.

When paired with group-raised fish or other isolate fish, the isolates did not, in general, appear apprehensive, but did have problems with the coordination, orientation and combination of basic motor patterns, especially during the initial phases of the encounters. Although there was much variation in individual behavior and no clear differences between the two types of opponents, the isolate fish did seem to have more problems in coordination and orientation of motor patterns when paired with group-raised fish.

Group 2 - Fish Raised From 30 Days of Age in Isolation

When paired with other group 2 isolates as a first or second experience between 113 and 136 days of age these fish exhibited very formal and discrete behavior patterns. No lack of individual coordination in exhibiting motor patterns was observed. Encounters began with loose circling by both fish which lead to mutual lateral displays, tail beating and fin tugging in variable amounts. The resulting appeasement of one of the fish was usually formal and extreme with the dorsal fin retracted. Dominants exhibited median fin spreading often in place of a raised dorsal fin response, and they sometimes assumed sigmoid postures on approaching the subordinate. In one case, however, as the dominant continued to approach it, the subordinate bent its body into a U shape; the dominant then moved slowly into the U and curved its body into a similar U shape resulting in a brief clasping of the two fish (both males) as seen in spawning sequences.

When paired with group-raised fish as a first or second experience there seemed to be a difference in the response of the isolate fish to their opponents. During first experience encounters with group-raised fish, the isolates appeared somewhat confused, although no irregular behaviors were observed. The actions of the isolates often appeared to cause their opponents to stay away from them during the first part of the encounters. Although the isolates made many approaches they often did not exhibit lateral displays until after their opponents did, and during sequences of mutual displays the isolates seemed to lack the ability to coordinate their actions fully with the group-raised fish, although the behavior patterns which they exhibited appeared normal. One dominant isolate approached and started biting and fin tugging before attempting any lateral display or tail beating which usually was exhibited by group-raised fish before fin tugging. The bites exhibited by the dominant isolate were not very vigorous and did not cause flight in the opponent. Some dominant isolates did exhibit periods of median fin spreading and sigmoids before approaching the subordinate, and this was often followed by localizing attempts by the dominant including backing up to get in front of the subordinate and display to it. The subordinate isolates usually exhibited formal appeasements, although in some cases they began as brief tilting on approach to the opponent and later changed to formal appeasement postures, including head jerking when approaching or being approached by the dominant. The group-raised subordinate fish appeased with only a brief tilting of the body and did not remain stationary.

When paired with group-raised fish as a second experience, the behaviors exhibited by the isolates appeared formal and discrete and did not seem to confuse their opponents. Only one of the eight isolate fish was subordinate and it appeased on the first approach of the opponent. The dominant isolates exhibited normal lateral displaying, tail beating and fin tugging. The group-raised fish appeased with only brief tilts of the body, and did not remain stationary for very long. The dominant isolates spent much time attempting to localize and display to the subordinates with lateral displays, tail beats, and some sigmoids. One dominant isolate arced backward and forward in front of the stationary subordinate with its head down at about a 40° angle for a period of 1 to 2 minutes before observation ended (15 minutes); the dominant then stopped exhibiting lateral displays and went into an extreme appeasement posture accompanied by head jerking as it continued to approach the group-raised fish which was also holding an appeasement posture.

Group 3 - Fish Raised From 60 Days of Age in Isolation

During encounters with other isolates both as a first and as a second experience the fish interacted soon and entered into typical sequences of formal lateral displays, tail beats and fin tugs, and maintained median fin spreads for long periods when not aligned with the opponent. During the initial approaches some isolates exhibited brief tilting, indicating some slight confusion. All of the subordinates appeased in a formal manner, with the dorsal fin retracted and the body tilted sideways in a stationary position. Head jerking was also exhibited by the subordinates when being approached or when approaching the dominant. Some subordinates appeased soon after interactions began while others appeased only after a long series of mutual lateral displays, tail beating and fin tugging. In six of the seven encounters the dominant fish were hyperaggressive after the subordinate appeased, and exhibited long sequences of chasing and intense biting. One of the subordinates was killed and had fresh lesions on the caudal peduncle and head from the repetitive biting of the dominant. The other subordinate fish which were removed from the encounter chamber immediately after the 15 minute observation period was over, also had lesions on the caudle peduncle; two of them vomitted for 1 to 2 minutes while being chased and bitten. The localization attempts by the hyperaggressive dominants were usually followed by biting and fin tugging rather than lateral displaying and tail beating as usually occurred after localizing attempts by group-raised fish. The hyperaggressive dominants all appeared to lack control and became very frenzied in their chasing and biting during the latter part of the encounters.

During encounters with group-raised fish as a first or second experience the isolates behaved generally as they did with other isolated fish. Some tilting was exhibited by a few of the isolates during initial approaches, and in one case even when the group-raised fish was in an appeasement posture, indicating some confusion in communication. Some isolates appeased at or near the beginning of the encounter and others entered into mutual displays, tail beating and fin tugging before appeasing. The dominant isolates were hyperaggressive, exhibiting high levels of chasing, biting and fin tugging accompanied by localization attempts. The appeasements of the group-raised opponents were not formal and stationary; they tilted for only short periods when being chased or bitten, did not retract their dorsal fin, and spent a lot of time fleeing. Both the dominant and subordinate isolates maintained an interest in their opponents after appeasement, whereas the group-raised fish even as dominants tended to avoid the isolate fish.

CHAPTER VII

QUANTITATIVE DESCRIPTION OF THE AGONISTIC BEHAVIOR OF FISH RAISED UNDER THREE DIFFERENT CONDITIONS OF SOCIAL ISOLATION

To assess the quantitative effects of social isolation on the three groups of isolated fish, and their effects on group-raised fish which were paired with them in dyadic encounters, quantitative data for 15 different behavior parameters were used. The following comparisons were made for dominant and for subordinate fish separately for each of the three isolation groups:

- isolates vs. group-raised fish (controls)
- first vs. second experience of isolates
- isolate as first opponent vs. group-raised fish as first opponent
- isolate as opponent vs. group-raised fish as opponent
- group-raised fish paired with isolates vs. control fish.

A standard t-test for differences among several means was used to test for significant differences between means, and pooled variances were used for the classes being compared. Tests of significance of .05 and .1 were used to indicate differences between test groups.

Comparison of Dominant Fish

Isolates vs. Group-Raised Fish (Table 1)

When comparing dominant isolates to group-raised dominants, group 1 and group 3 isolates showed the greatest differences. In group 1 isolates approaching and chasing frequencies were significantly greater ($\alpha \leq .05$), and the duration of raised dorsal fin, and frequency and duration of lateral display were significantly less ($\alpha \leq .05$). The frequency of tail beating was significantly less ($\alpha \leq .1$), and the overall behavioral diversity of dominant isolates was significantly less ($\alpha \leq .05$). Since 8 of the 15 dominant isolates in group 1 exhibited initial rocking and/or tilting, the initial period of disorientation delayed the appearance and decreased the duration of displays and tail beating, as well as generally decreasing the diversity of behaviors exhibited by the isolate fish.

Group 2 dominant isolates were very similar to controls except for a significantly greater approach frequency ($\alpha \leq .05$) and a significantly shorter latency to bite ($\alpha \leq .05$).

The hyperaggressive nature of group 3 dominant isolates was evident from their significantly higher levels of approach, chase, bite, fin tug and carousel frequencies ($\alpha \leq .05$). They spent more time exhibiting lateral displays and spent significantly less time in raised dorsal fin responses than the group-raised fish.

First vs. Second Experience of Isolates (Table 2)

When comparing the first and second experiences of isolates without regard to opponent, only the group 3 dominant isolates appeared to

Table 1. Comparison of mean values for dominant isolates with dominant controls for the frequency, latency or duration of approach, chase, bite, raised dorsal, lateral display, tail beat, fin tug, carousel, appeasement and behavior diversity ($\bar{d}$).

Isolate group	A(F)	C(F)	C(L)	C(D)	B(F)	B(L)	RD(D)	LD(F)	LD(L)	LD(D)	TB(F)	FT(F)	CA(F)	AP(D)	$\bar{d}$
1	92.14 (15)**	42.47 (15)**	378.13 (15)	83.6 (15)	62.33 (15)	261.6 (15)	327.73 (15)**	7.94 (15)**	150.31 (13)**	32.31 (15)**	2.27 (15)*	2.4 (15)	0.20 (15)	14 (1)	1.95 (15)**
2	93.5 (18)**	16 (18)	324.78 (18)	47.89 (18)	75.84 (18)	156.12 (18)**	407.11 (18)	25.5 (18)	48 (17)	362.12 (17)	5.99 (18)	4.34 (18)	3.83 (18)	64 (1)	2.15 (18)
3	93.94 (16)**	37.62 (16)**	291.87 (16)	130.63 (16)**	137.94 (16)**	182.13 (16)	344.38 (16)**	22.56 (16)	42.12 (16)	510.63 (16)	9.75 (16)	15.5 (16)	11.25 (16)**	136 (2)	2.28 (16)
C	59.69 (16)	21.75 (16)	389.73 (15)	68.4 (15)	72.5 (16)	288.27 (15)	490 (16)	27.31 (16)	35 (16)	403.25 (16)	9.31 (16)	5.5 (16)	3.75 (16)	-	2.21 (16)

$*\alpha \leq .1$ $**\alpha \leq .05$ (n) = sample size

Table 2. Comparison of mean values between 1st and 2nd experience dominant isolates for the frequency, latency or duration of approach, chase, bite, raised dorsal, lateral display, tail beat, fin tug, carousel, appeasement and behavior diversity ($\bar{d}$).

Isolate group	Exper.	A(F)	C(F)	C(L)	C(D)	B(F)	B(L)	RD(D)	LD(F)	LD(L)	LD(D)	TB(F)	FT(F)	CA(F)	AP(D)	$\bar{d}$
1	1st	97.86 (7)	33.29 (7)	352 (7)	66 (7)	48.43 (7)	244.29 (7)	316.57 (7)	10.72 (7)	173.67 (6)	45.35 (6)	3.86 (7)	3.57 (7)	0.43 (7)	14 (1)	2.02 (7)
	2nd	87.13 (8)	50.5 (8)	401 (8)	99 (8)	74.5 (8)	276.75 (8)	337.5 (8)	5.5 (8)	130.29 (7)	21.14 (7)	0.88 (8)	1.38 (8)	0.0 (8)	-	1.88 (8)
2	1st	92.0 (7)	17.57 (7)	348.29 (7)	55.43 (7)	74.29 (7)	144.86 (7)	564.86 (7)**	32.71 (7)*	26.29 (7)	182 (7)**	6.14 (7)	5.71 (7)	2.86 (7)	-	2.25 (7)
	2nd	94.45 (11)	15 (11)	309.82 (11)	43.09 (11)	76.82 (11)	163.28 (11)	306.73 (11)	20.91 (11)	63.20 (10)	488.2 (10)	5.9 (11)	3.46 (11)	4.45 (11)	64 (1)	2.08 (11)
3	1st	85.56 (9)	23.44 (9)**	346.22 (9)	76.67 (9)**	99.11 (9)**	205.56 (9)	468.89 (9)**	26.89 (9)	58.22 (9)	376.89 (9)**	8.67 (9)	17.44 (9)	1.89 (9)**	136 (2)	2.34 (9)
	2nd	104.71 (7)	56.86 (7)	222 (7)	200 (7)	187.86 (7)	152 (7)	184.29 (7)	17 (7)	21.43 (7)	682.57 (7)	11.14 (7)	13 (7)	23.29 (7)	-	2.22 (7)

*$\alpha \leq .1$ **$\alpha \leq .05$ (n) = sample size

react differently. On the second experience the dominant isolates approached more often, and exhibited chasing, biting, lateral display and carousel significantly more often ($\alpha \leq .05$) than on the first experience. Chasing, biting and lateral display also occurred sooner, and the average behavior diversity value was less on the second experience.

Isolate as First Opponent vs. Group-Raised Fish as First Opponent (Table 3)

When comparing dominant isolates by category of first opponent only the group 2 isolates indicated consistant differences. For fish seeing another isolate fish first the frequencies of approach ($\alpha \leq .1$), chase, bite ($\alpha \leq .05$), lateral display ($\alpha \leq .05$), tail beat, fin tug, carousel, and the diversity of behaviors were higher. Overall, isolates seeing other isolates first seemed more responsive and more aggressive then those that saw group-raised fish first. The isolates which saw group-raised fish first appeared to be even less responsive than the control fish (group-raised encounters).

Isolate as Opponent vs. Group-Raised Fish as Opponent

No consistant difference were observed in any of the isolation groups when comparisons were made on the basis of opponent type.

Table 3. Comparison of mean values for isolates by type of first opponent (isolate or group-raised) for the frequency, latency or duration of approach, chase, bite, raised dorsal, lateral display, tail beat, fin tug, carousel, appeasement and behavior diversity ($\bar{d}$).

Isolate group	Opponent	A(F)	C(F)	C(L)	C(D)	B(F)	B(L)	RD(D)	LD(F)	LD(L)	LD(D)	TB(F)	FT(F)	CA(F)	AP(D)	$\bar{d}$
1	I	93 (8)	44 (8)	346.5 (8)	86.75 (8)	58.88 (8)	205.25 (8)*	282.75 (8)	8.25 (8)	176.28 (7)	25.72 (7)	2.38 (8)	1.0 (8)	0.13 (8)	-	1.97 (8)
	G-R	91.14 (7)	40.72 (7)	414.29 (7)	80 (7)	66.28 (7)	326 (7)	379.14 (7)	7.57 (7)	120 (6)	40 (6)	2.14 (7)	4.0 (7)	0.29 (7)	14 (1)	1.92 (7)
2	I	101.54 (11)*	20.55 (11)	245.64 (11)*	65.09 (11)	98.18 (11)**	138.73 (11)	356.18 (11)	30.82 (11)**	50.73 (11)	436.91 (11)**	7.72 (11)	5.46 (11)	4.73 (11)	64 (1)	2.22 (11)
	G-R	80.86 (7)	8.86 (7)	449.14 (7)	20.86 (7)	40.71 (7)	183.43 (7)	487.14 (7)	17.14 (7)	43 (6)	225 (6)	3.26 (7)	2.57 (7)	2.43 (7)	-	2.03 (7)
3	I	78.5 (8)**	38.25 (8)	334.75 (8)	142.75 (8)	125.5 (8)	211 (8)	363 (8)	22.25 (8)	38.75 (8)	501.75 (8)	7.38 (8)	15.13 (8)	10.88 (8)	2.0 (1)	2.3 (8)
	G-R	109.38 (8)	37.0 (8)	249 (8)	118.5 (8)	150.38 (8)	153.25 (8)	325.75 (8)	22.88 (8)	45.5 (8)	519.5 (8)	12.13 (8)	15.87 (8)	11.63 (8)	270 (1)	2.27 (8)

*$\alpha \leq .01$ **$\alpha \leq .05$

Group-Raised Fish Paired With Isolates vs. Control Fish (Table 4)

There were some apparent effects of the isolates on the performance of the group-raised fish as opponents. Dominant group-raised fish paired with group 1 isolates exhibited significantly lower frequencies and durations of lateral display ($\alpha \leq .05$), and began displaying significantly later ($\alpha \leq .05$). Dominant group-raised fish paired with group 2 isolates were generally less aggressive, displayed less often, began displaying significantly later ($\alpha \leq .05$) and spent significantly less time displaying ($\alpha \leq .05$) than the control dominants. Group-raised dominant fish paired with group 3 isolate fish showed no significant differences from control dominant fish.

Comparison of Subordinate Fish

Isolates vs. Group-Raised Fish (Table 5)

The greatest differences between subordinate isolate and control fish also appeared in isolate groups 1 and 3. The group 1 subordinate isolates approached significantly more ($\alpha \leq .05$) and exhibited more bites sooner; they started displaying later, spent less time displaying, and spent less time appeasing than control subordinates did although they exhibited a similar behavior diversity.

Although group 2 subordinate isolates were similar to controls, they approached more often, and spent less time displaying or in raised dorsal ($\alpha \leq .05$); they spent significantly more time appeasing ($\alpha \leq .05$) and exhibited a lower diversity of behaviors than the control fish.

Table 4. Comparison of mean values for dominant group-raised fish paired with isolates, and paired with other group-raised fish. Mean values represent the frequency, latency or duration of approach, chase, bit, raised dorsal, lateral display, tail beat, fin tug, carousel, appeasement and behavior diversity ($\bar{d}$).

Isolate group	A(F)	C(F)	C(L)	C(D)	B(F)	B(L)	RD(D)	LD(F)	LD(L)	LD(D)	TB(F)	FT(F)	CA(F)	AP(D)	$\bar{d}$
1	54.83 (6)	28.67 (6)	379.67 (6)	57 (6)	43.83 (6)	264.33 (6)	529.33 (6)	8.5 (6)**	97.33 (6)**	128.33 (6)**	17.67 (6)	6.33 (6)	0.0 (6)	-	2.31 (6)
2	59.8 (5)	9.2 (5)	225.33 (3)	50.67 (3)	52.4 (5)	205.6 (5)	662 (5)	20 (5)	102.4 (5)**	122 (5)**	1.4 (5)	1.8 (5)	0.0 (5)	-	1.97 (5)**
3	48.8 (5)	14 (5)	302 (2)	120 (2)	50.2 (5)	228 (5)	460.8 (5)	26 (5)	46 (5)	270.4 (5)	5.2 (5)	5.8 (5)	2.8 (5)	228 (1)	2.22 (5)
C	59.69 (16)	21.75 (16)	389.73 (15)	68.4 (15)	72.5 (16)	288.27 (15)	490 (16)	27.31 (16)	35 (16)	403.25 (16)	9.31 (16)	5.5 (16)	3.75 (16)	-	2.22 (16)

$^{**}\alpha \leq .05$ (n) = sample size

Table 5. Comparison of mean values for subordinate isolates with subordinate controls for the frequency, latency or duration of approach, chase, bite, raised dorsal, lateral display, tail beat, fin tug, carousel, appeasement and behavior diversity ($\bar{d}$).

Isolate group	A(F)	C(F)	C(L)	C(D)	B(F)	B(L)	RD(D)	LD(F)	LD(L)	LD(D)	TB(F)	FT(F)	CA(F)	AP(D)	$\bar{d}$
1	22.78 (14)**	0.0 (14)	-	-	5.0 (14)	166.25 (8)	190 (14)	5.86 (14)	132.18 (11)**	76.18 (11)	6.64 (14)**	2.21 (14)	0.14 (14)	474.71 (14)	1.97 (14)
2	19.54 (13)	0.0 (13)	-	-	0.77 (13)	185.67 (6)	100.15 (13)**	4.54 (13)	57.33 (9)	70.67 (9)	1.46 (13)	0.31 (13)	1.46 (13)	708.9 (13)**	1.73 (13)
3	19.46 (11)	0.0 (11)	-	-	4.27 (11)	85.33 (6)	60.36 (11)**	2.64 (11)**	75.6 (10)	139 (10)	4.73 (11)	6.09 (11)**	1.27 (11)	722.9 (11)**	1.9 (11)
C	11.13 (16)	0.0 (16)	-	-	1.69 (16)	231.25 (8)	207.87 (16)	7.125 (16)	37.5 (16)	132.63 (16)	1.25 (16)	0.44 (16)	0.56 (16)	520.13 (16)	1.92 (16)

**$\alpha \leq .05$ (n) = sample size

The group 3 subordinate isolates approached more often, and bit sooner and more often than controls; they spent significantly less time exhibiting raised dorsal responses ($\alpha \leq .05$), and exhibited significantly fewer lateral displays ($\alpha \leq .05$), but spent the same amount of time displaying as controls did. The frequencies of tail beating and fin tugging were also significantly greater for the group 3 subordinate isolates ($\alpha \leq .05$), and they spent significantly more time appeasing ($\alpha \leq .05$). The behavior diversity of group 3 subordinate isolates and controls was very similar.

No significant differences were found between subordinate isolates on first and second experiences, or between subordinate isolates compared by first opponent in any of the three groups.

Isolate as Opponent vs. Group-Raised Fish as Opponent (Table 6)

In comparing the responses of subordinate isolates to different opponents, few significant differences appeared, and consistant patterns of differences occurred only in groups 1 and 3. In group 1 it appeared that the subordinate isolates were more responsive to group-raised fish than to other isolate fish. They approached and bit more often, spent more time in raised dorsal ($\alpha \leq .05$), and displayed more often ($\alpha \leq .1$) and longer to group-raised fish. They also exhibited significantly more tail beating ($\alpha \leq .05$) and more fin tugging, and the diversity of behavior exhibited was greater when paired with group-raised fish. Perhaps subordinate isolates interacted less with dominant isolates because of their disoriented and uncoordinated behaviors, or because of the uncertainty of both dominant and subordinate iso-

Table 6. Comparison of mean values for subordinate isolates by type of opponent (isolate or group-raised) for the frequency, latency or duration of approach, chase, bite, raised dorsal, lateral display, tail beat, fin tug, carousel, appeasement and behavior diversity ($\bar{d}$).

Isolate group	Opponent	A(F)	C(F)	C(L)	C(D)	B(F)	B(L)	RD(D)	LD(F)	LD(L)	LD(D)	TB(F)	FT(F)	CA(F)	AP(D)	$\bar{d}$
1	I	21.13 (8)	0.0 (8)	-	-	2.38 (8)	169.33 (3)	142 (8)**	4.25 (8)*	169.2 (5)	28.4 (5)	1.88 (8)**	0.38 (8)	0.125 (8)	469.5 (8)	1.83 (8)
	G-R	25 (6)	0.0 (6)	-	-	8.5 (6)	164.4 (5)	254 (6)	8.0 (6)	101.33 (6)	116 (6)	13 (6)	4.67 (6)	0.167 (6)	481.67 (6)	2.17 (6)
2	I	13 (8)	0.0 (8)	-	-	0.63 (8)	129.33 (3)	128.5 (8)	4.13 (8)	31.2 (5)	46.4 (5)	0.63 (8)	0.0 (8)	1.63 (8)	704.75 (8)	1.74 (8)
	G-R	30 (5)	0.0 (5)	-	-	1.0 (5)	242 (3)	54.8 (5)	5.2 (5)	90 (4)	101 (4)	2.8 (5)	0.8 (5)	1.2 (5)	715.6 (5)	1.70 (5)
3	I	9 (7)**	0.0 (7)	-	-	4.57 (7)	72 (4)	76.28 (7)	2.43 (7)	60.67 (6)	170 (6)	6.29 (7)	8.86 (7)	1.57 (7)	672.28 (7)	2.14 (7)*
	G-R	37.75 (4)	0.0 (4)	-	-	3.75 (4)	112 (2)	32.5 (4)	3.0 (4)	98 (4)	92.5 (4)	2.0 (4)	1.25 (4)	0.75 (4)	811.5 (4)	1.48 (4)

*$\alpha \leq .1$ **$\alpha \leq .05$ (n) = sample size

lates in group 1.

Although the group 3 subordinate isolates approached group-raised fish significantly more often ($\alpha \leq .05$) and appeased longer with them, they spent more time displaying to and exhibited more tail beats and fin tugs to other isolates, as well as exhibiting a greater diversity of behaviors. These differences in activity of the subordinate isolates may be due to the hyperactive nature of the dominant isolates in group 3, which caused a decrease in approach by the subordinate isolates but greater amount of lateral display, tail beating and fin tugging which occurred during mutual exchanges.

CHAPTER VIII

SUMMARY AND CONCLUSIONS

Early post-hatching motor patterns in the blue gourami follow a developmental sequence similar to that described for the embryonic period of development in the species (Guideri, 1966). They appear first as uncoordinated and arhythmic movements, and gradually become regular and well-coordinated. This general sequence applies to mouth movements, opercular movements, pectoral and caudal fin movements, swimming movements and surfacing. These motor patterns, although representing different levels of functional complexity, all proceed through similar stages. Opercular and jaw movements are first irregular and uncoordinated, and subsequently become regular and well-coordinated, accompanying each other in a continuous rhythmic fashion; pectoral and caudal fin movements follow the same sequence of development, and only later appear to function smoothly together in swimming. Swimming, which appears first as short darts in random directions later is accompanied by orientation responses to visual stimuli, adding a directional component to the dart swimming. Surfacing to take in air develops gradually and appears first as short diagonal movements between different depths; this is followed by diagonal movements of greater length, and periods of nipping at or near the surface; spiking at the surface appears next and is the last element to appear before surfacing appears as movement to the surface, nipping at the surface (taking in air), and descending from the surface in one continuous movement.

Gross movements of young fry first appear as random short darting movements before the eyes are fully functional, and are accompained by brief general movement toward large objects (including the heads of other fry) when at very close range. As the eyes and their accompanying muscles become functional, searching activity appears in which darting movements are not random, but are directed by coordinated eye orientation in response to close-field visual stimuli. At this stage the fry initially approach small and large objects but withdraw from large moving objects, whereas they are especially attracted to small moving objects. Soon after this, fry begin snapping up and engulfing small objects, especially moving ones such as protozoans. In the midst of their continuous searching activities fry may arc their bodies and hold a stationary position while investigating small or medium-sized moving objects or leaf surfaces, but may react similarly to large moving objects including invertebrates or other fry, before fleeing or reorienting their bodies in another direction. Thus, arcing of the body which later is accompanied by madian fin spreading as the fins develop, appears initially in a number of different contexts encountered during searching activities, and apparently prepares the fish for staying, fine movement of the body, or fleeing. This hypothesis was stated by Myrberg (1965) and suggests that fin-spreading is primarily a hydrodynamically adaptive response which can be assumed by the fish while awaiting further information from the surroundings, whether the context might be of the possible approach of a predator, a prey item, a conspecific, or just having moved into a water current.

During the period of increasing differentiation in approach to large and small objects, fry make fewer and fewer head approaches to other fry and begin making tail approaches to the black spot on the caudal peduncle which is the first discernable pigment pattern to appear on the fry other than the large dark eyes. These tail approaches are at first incomplete, then complete, and subsequently involve investigating, following and nibbling on the tail spot as if it were a food item. Thus, the first interaction between siblings occurs in a feeding context. During the period of increasing tail approaches, changes in the body orientations of the two fish resulting in a head-to-head or head-to-side relationship often leads to one or both fish arcing the body and spreading the median fins. The approaching fish may continue to maneuver with the pectoral fins toward the tail spot and nibble at it while maintaining a median fin spread and arced body; in some cases when both of the fish appear very nervous, or when disturbances occur near by, the approaching fish may exhibit short quick bites to the tail spot rather than the usual nibbling. These bites initially result in the fleeing of both fish, although later they may lead to brief exchanges of more bites and brief carouselling before fleeing occurs, sometimes accompanied by short chases. The behavioral content of these conspecific interactions is quite variable from one instance to another, and after the appearance of biting and chasing during ontogeny, tail approaches, investigating, nibbling and following still continue to occur; these investigating and/or nibbling and following sequences are usually exhibited by one fish, while the other fish shows no interest and moves off slowly, reorients towards the approaching fish, or flees. Larger fish are usually the ones that show the most interest in approaching and following smaller fish. At this stage the addition of food, which increases the activity level of all the fish in an aquarium may also cause a shift from approach and nibble to approach, chase and bite. Subsequent to this stage the larger fish exhibit an increasing general responsiveness to conspecifics as well as general disturbances inside and outside the aquarium.

All of the agonistic behavior patterns observed during development, with the exception of head-jerking, appeasement and carouselling were first exhibited in non-social contexts. The motor patterns were not consistant in form, orientation or intensity throughout ontogeny, but changed progressively with age, social context and experience. Approaching, biting, chasing, raised dorsal fin, median fin spreading (lateral display), tail beating and fin tugging were all exhibited in early feeding activities; tail beating and fin tugging motor patterns occurred when the young fish were tugging on large pieces of brine shrimp either together or singlely.

The developmental sequence of appearance of agonistic motor patterns in an agonistic context followed generally the same sequence as observed in an individual encounter between two mature fish. Encounters between very young fish began as sequences of approach, bite and chase, all exhibited by one of the two fish; the initial approaches were subsequently separated increasingly during ontogeny from biting and chasing by the appearance of lateral displays, carousels, tail beating, and fin tugging, which were exhibited to different degrees by both fish. Appeasement, which after its ontogenetic appearance at about day 50, was exhibited more and more by the fleeing fish and resulted in the eventual reduction in the level of chasing and biting exhibited by the dominant fish. This developmental sequence is similar to that described for Badis badis (Barlow, 1962) as well as a number of cichlid species (Ohm, 1964; Wyman and Ward, 1973; Williams, 1972).

The large differences in the overtly aggressive behaviors of chasing and biting between the two fish in an encounter continued to increase up through the middle of the study period (third month of life); during the fourth month however, the other agonistic behavior patterns began to increase in frequency and/or duration and appeared to play a greater part in determining social relationships between two fish as dominants and subordinates. Dominants increasingly indicated their status by tail beating and fin tugging while attempting to localize the subordinate, and the subordinates spent increasing amounts of time exhibiting appeasement postures in stationary positions as well as increasing approaches to the dominants while assuming their appeasement postures. The dominant-subordinate relationship between two fish in a dyadic encounter appeared to "evolve" during the course of development as an increasing cooperation between the two fish in the exchanges of signaling behaviors, the outcome of which decided the winner and loser of the "fight". The development of cooperativeness between the two fish also extended more and more into the post-appeasement period of an encounter, as indicated by the increasing effects of appeasement on reducing the aggressiveness of the dominat fish.

The appearance of agonistic behaviors in groups of fish was effected as early as three weeks of age by the relative abundance and distribution of food, and the relative number of fish in a group. The earliest occurrances of overt fighting while feeding appeared at 22 days of age, and territoriality first appeared as a defense of individual areas defined by food distribution during feeding periods; only later at about day 55 were territories maintained in the absence of food. Fish maintained in groups of five exhibited territoriality and the territory holders typically participated in bouts of mutual display, tail beating, biting and carouseling at the territory boundaries. In contrast to this, fish raised in groups of 10 to 12, even though in much larger aquaria, characteristically exhibited much less agonistic behavior and it was confined to chasing, biting and some brief displaying, often involving three to five fish in a continuous series of brief interactions. The characteristically low level of agonistic behavior exhibited in large groups of blue gouramis has also been noted by Forselius (1957) and Miller (1964).

Experiments involving various conditions of social isolation raising do not indicate what is "native" to an animal since the animal is capable of gaining many other types of experience during its development in "isolation" (Schneirla, 195 ; Hinde, 1970). However, if one is interested in asking how behaviors develop during ontogeny rather than classifying the behaviors as "learned" or "innate", isolation studies may indicate some of the factors which are important in the development and/or regulation of agonistic behaviors during ontogeny. The quantitative and qualitative data provided by the three groups of social isolates in this study indicate that social experience at different stages of development may have different effects on the agonistic behaviors exhibited by adult fish. Fish which had had no previous social experiences (group 1) were able to exhibit all of the agonistic behaviors in a stereotyped manner, however, they experienced problems in the proper coordination and orientation of motor patterns. The generally low levels of agonistic behavior exhibited by this group were perhaps due, at least in part, to (1) the inability to interpret the signaling of the opponent, and (2) the inability to coordinate and orient responses. Although overt coordination and orientation problems occurred most during initial experiences, during second experiences these isolates also exhibited generally low levels of agonistic behavior, indicating a continuing problem with the interpretation of opponent signaling, as well as the less obvious difficulties with the coordination and orientation of agonistic behavior patterns.

The fish isolated from 30 days of age exhibited no overt problems with the coordination and orientation of behaviors, and exhibited behaviors in a similar manner to the control fish; however, they did appear to have some problems in interpreting the signaling of group-raised fish.

By contrast to the group 1 fish, the group 3 fish which had been raised in isolation from 60 days of age were generally hyperactive both as dominants and subordinates; they exhibited high levels of stereotyped agonistic behavior patterns and appeared to lack the ability to regulate or control their activities in response to opponent signaling, although they exhibited no orientation or coordination problems.

It is of interest that the group 2 fish which appeared to be most similar to the control fish were isolated before the majority of agonistic behaviors appeared in agonistic contexts (Figure 20), and that the group 3 fish, which were generally hyperactive, were isolated after all of the behaviors except fin tugging had appeared and during a period when the overt aggressive behaviors of bite and chase were still increasing (Figure 20).

Group-raised fish paired with each other, and paired with isolates, were, with few exceptions, very similar in their behavioral characteristics. They also exhibited some consistant differences with all of the isolate fish. Group-raised fish consistantly approached less often in encounters, and as subordinates they exhibited less stereotyped appeasement patterns and exhibited more fleeing than the isolate subordinates. These two factors also indicate that social raising conditions have a significant regulatory effect on both the quantitative and qualitative characteristics of agonistic behaviors exhibited during dyadic encounters.

The early ontogenetic appearance of agonistic interactions in groups of blue gouramis, and the equally early effects of environmental factors (food abundance and group size) on the specific appearance and manifestation of agonistic behavior patterns, indicates that the ontogeny of social relationships in these fishes plays a major functional role in the distribution of fish and their utilization of the available habitat at all stages of development. The development of social relationships in the blue gourami, as well as in most other species exhibiting complex social relationships, must be viewed as a dynamic ontogenetic process, the whole of which is adaptive. This view seems to provide a realistic approach to an understanding of the complex of causal agents underlying the organization and function of social behavior in all animals. This approach has been used productively by Harlow (1965) on the rhesus macaque, Macaca mulatta, by Kruijt (1964) on the Burmese junglefowl, Gallus gallus, and more recently by Williams (1972) on the convict cichlid, Cichlasoma nigrofasciatum.

Most studies of the development of social behavior in fishes, with the exception of Williams (1972), have been concerned with gaining an understanding of the causal basis of adult behaviors; as such they have failed to stress the ecological significance of whole behavioral ontogenies, and the possible changes in the causal organization of behavior at various stages of development. This has usually led to the employment of reductive hypotheses of small numbers of tendencies to explain complex ontogenetic patterns of behavior. This approach is usually based on the assumption that similarity in form or function of behaviors implies common causal agents, an assumption which Hinde (1970) has pointed out as having questionable validity.

In their study of the development of behavior in the orange chromide, Eutroplus maculatus, Wyman and Ward (1973) hypothesize that the two motor patterns of "glancing" and "micronipping" which occur in young fry, develop into 12 more complex agonistic motor patterns in juvenile and adult fish. From this developmental sequence, postulating the development of greater and greater conflicts, they imply a common causal basis for the organization and function of adult social behavior patterns in the orange chromide. However, as has already been pointed out, functional similarity does not indicate causal similarity (Hinde, 1970). Their model incorporates maturational processes (morphological and physiological), the behavioral repertoire, and social experiences, the latter of which is assumed to "mold" "glancing" and "micronipping" into 12 more complex agonistic behaviors. Their observations on fish denied social experiences however, indicate only that the fish had initial problems with the coordination and orientation of behaviors during the first few social encounters, and that subsequent to that they could perform all of the adult behaviors.

In fishes, which exhibit a relatively limited repertoire of motor patterns due to their body form, it is not surprising that common motor patterns and complexes of them may be used in may different contexts. This may be especially true of many of the cichlid species like the orange chromide which have evolved parent-young relationships employing specialized larval motor patterns and stimulus-response relationships (approaching large objects).

Williams' (1972) approach to an understanding of the causal elements underlying the development of social behavior in cichlids is a much more realistic, and I believe, productive one. It assumes that the complex of causal elements underlying behavior changes during the process of development, and that developing behavioral systems (sets of common causal factors) interact with other behavioral systems already present to produce more complex behavioral relationships. These interactions may then result in the shifting of the motivational basis for various behavioral elements. Such shifts in motivational control of behavior have been shown in much of the literature on learning (Sevenster, 1968; Logan, 1972).

At the structural level of motor pattern development Williams describes an increasing combination of orientations and motor elements by superposition and sequential arrangement. He concludes that (1) early in ontogeny new behavioral elements arise by the combination of simpler elements whose components are compatible, and that later in ontogeny new elements arise from the combination of elements whose components are sometimes incompatible; (2) combining of orientations occurs earlier in the ontogeny than the combining of motor patterns; and (3) that the combining of elements sequentially occurs earlier than the combining of elements by superposition.

All of the studies on the development of social behaviors in cichlids describe a progression from simple to more complex motor patterns involving the combination of the early simpler motor patterns into more complex patterns which appear later in development. However, in the blue gourami, the behavioral elements of the agonistic repertoire are much more limited in number, and do not arise as a result of increasingly more complex combinations of simpler motor elements. Rather, the trend in development of agonistic behaviors in the blue gourami is one of encorporating already existing motor patterns used in other contexts into an agonistic role. Subsequent changes occur only in the frequency, duration and intensity of the behavior patterns and their temporal relationships in agonistic encounters. This apparent difference in behavioral ontogenies may be due to the highly specialized nature of parent-young relationships, and early schooling in cichlids, as well as the generally clear water environments they inhabit which may "promote" the use of visual signaling as an adaptive mode. By contrast, anabantoids exhibit little if any parent-young interactions or discernable schooling behavior in the young, and inhabit generally turbid water environments where the value of visual signaling is limited.

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