THE ESTABLISHMENT OF DOMINANCE RELATIONSHIPS IN THE BLUE GOURAMI TRICHOGASTER TRICHOPTERUS (PALLAS)

By

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THE ESTABLISHMENT OF DOMINANCE RELATIONSHIPS

IN THE BLUE GOURAMI TRICHOGASTER

TRICHOPTERUS (PALLAS)

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PREFACE

The objectives of this study were: 1) to provide a thorough description of the fighting behavior of pairs of male blue gouramis during periods of dominance establishment; 2) to evaluate the influence of environmental, physical, social, and temporal parameters on the outcome of dominance encounters and the attendant agonistic behaviors of these fights; 3) to compare patterns of fighting associated with ultimate winners to those of ultimate losers; 4) to synthesize the results of the study into a general statement concerning the establishment of dominance relationships in this species; and 5) to demonstrate alternate and perhaps more meaningful measures of aggressiveness.

Dr. R. J. Miller served as major advisor and provided valuable suggestions and assistance throughout the study. Drs. W. A. Drew, J. A. Morrison, and J. L. Wilhm served on the advisory committee and reviewed the manuscript. Dr. L. Folks and Mr. B. Brandt of the Oklahoma State University Statistical Laboratory assisted with the statistical analyses. Special gratitude is due to my wife Elouise, who typed the manuscript and provided encouragement and understanding throughout the study.

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CHAPTER I

INTRODUCTION

A phenomenon of social organization in many fishes and probably in numerous vertebrates which seldom has been taken into account is the occurrence of two distinctive temporal phases. The first phase is an initial, often ephemeral, period of dominance establishment, and the second is a period of maintenance or change of that established social order. These two phases are linked by the social order resulting from the outcome of the initial encounters and by certain environmental parameters which remain constant with time. Braddock (1945) pointed out that initial relationships which develop between "contact-pairs" were important in structuring a subsequent social organization; yet, most works on social organization in animals have failed to analyze the dynamics of the period of dominance establishment. This study represents an operational analysis of the quantitative aspects of fighting behavior in the anabantoid fish, Trichogaster trichopterus (Pallas), during dominance establishment. An attempt will be made to determine how social, physical, temporal, or environmental parameters influence the outcome of encounters and how the outcome is related to the attendant agonistic behaviors associated with these encounters.

Studies by Collias (1943), Haldane and Spurway (1954), Wilson (1962), Nelson (1964), Altmann (1965), Hazlett and Bossert (1965),

Heiligenberg (1965), Delius (1968), and Simpson (1968) provide innovative approaches to the analysis of social behavior in animals. An attempt was made in the present study to develop experimental techniques and analytical methods which might be useful in future studies on agonistic behavior.

The concept of dominance relationships was probably introduced by Schjelderup-Ebbe in 1913 (see Schjelderup-Ebbe, 1935), who described peck order and agonistic behavior in hen flocks. Allee (1938, 1942) was a pioneer in studies on social behavior, and numerous studies on dominance and hierarchical relationships have been conducted with his influence. Bernstein (1969) pointed out that many definitions of dominance have been used and that emphasis has gradually shifted from the consequences of dominance to related responses. A review of some of the commonly used measures of dominance is presented in Chapter III. The distinction between establishing dominance and maintaining a dominance relationship, however, has not been emphasized in studies on agonistic behavior.

Since 1940 numerous studies have been conducted on hierarchical organization and agonistic behavior in fishes. Several workers have begun to analyze some of the factors which seem to play a role in dominance relationships.

Among the few who have related the outcome of a dominance encounter to the preceding and accompanying behavior patterns are Braddock and Braddock (1955), Simpson (1968), and Southwick and Ward (1968). Miller and Miller (in press) have related shifts in a prevailing social order to concomitant changes in the occurrence and frequency of certain agonistic behavior patterns.

The effect of relative size of group members in determining their hierarchical positions has been investigated in Platypoecilus maculatus (Braddock, 1945), Lepomis megalotis (Huck and Gunning, 1967), Molliniensesia latipinna (Baird, 1968), and Lepomis megalotis (Hadley, 1969). Miller (1964) noted that pairs of blue gouramis fight longer when their relative size difference is minimal. Frey and Miller (1968) suggested that in T. trichopterus and Macropodus opercularis relative size differences may be more important in dominance maintenance than in the initial outcome of a fight. Barlow (1968a) has shown that in Etroplus maculatus smaller males attack larger females more than they attack smaller females.

Prior residency as a determinant of the outcome of a dominance encounter has been investigated in Lepomis cyanellus (Greenberg, 1947) and Platypoecilus maculatus (Braddock, 1949). Baird (1968) observed in the field that smaller resident Molliensesia latipinna males successfully defended areas of residency against larger males.

The effect of social conditioning of a fish prior to subsequent dominance encounters has been studied in Platypoecilus maculatus (Braddock, 1945) and in Lepomis cyanellus (McDonald, Heimstra, and Damkot, 1968). Erickson (1967) reported that subordinate Lepomis gibbosus in social hierarchies show evidence of stress reactions such as reduced anterior interrenal weight.

The success of animals in competition for food has been used as an indicator of dominance (Carpenter, 1942; Bernstein, 1969). Magnuson (1962) in groups of medaka, Oryzia latipes, and Symons (1968) in juvenile Atlantic salmon, Salmo salar, reported increased aggressive behavior following food deprivation.

Males of many species of fish tend to dominate females, and the importance of a sex factor in dominance relationships in fish has been shown in Xiphophorus helleri (Noble and Borne, 1940), Platypoecilus maculatus (Braddock, 1945), T. trichopterus (Miller, 1964), Molliensesia latipinna (Baird, 1965), and Lepomis megalotis (Hadley, 1969).

The effect of the number of group members on agonistic behavior has been investigated in Lepomis cyanellus (Hixson, 1946 and Borkhuis, 1965), Lepomis macrochirus (Borkhuis, 1965), T. trichopterus (Miller, 1964; Miller and Miller, in press), Pelmatochromus guentheri (Myrberg, 1965), Ptychocheilus oregonense (Pfeiffer, 1965), Gasterosteus aculeatus (van den Assem, 1967), Blennius pholis (Gibson, 1968), and Macropodus opercularis and Colisa lalia (Miller and Miller, in press).

Spatial parameters and environmental complexity may influence dominance relationships and these closely relate to residency and territoriality. Agonistic behavior of several fish species has been shown to be influenced by spatial and environmental parameters. Some prominent studies in this area include Greenberg (1947), Fabricius (1951), van Iersel (1958), Morris (1958), Barlow (1962), Miller (1964), van den Assem (1967), Huck and Gunning (1967), Gibson (1968), and Hadley (1969).

The following studies have directed attention to the areas of causation and motivation of agonistic behavior: Hale (1956), Heiligenberg (1965), Baenninger (1966, 1968a, 1968b), Ward (1966), Clayton and Hinde (1968), Dunham, Kortmulder, and van Iersel (1968), Gibson (1968), Miller and Hall (1968), Southwick and Ward (1968), and McKenzie (1969).

The tendency to use quantitative tools in studies of animal behavior has received increased impetus in recent years. Collias (1943) studying chickens, seems to have made one of the initial statistical analyses of dominance relationships. Landau (1951a; 1951b) published theoretical papers on dominance relations in animal societies, and Haldane and Spurway (1954) introduced the use of cybernetics in analyzing communication between animals. Hazlett and Bossert (1965; 1966) and Dingle (1969) used information theory in an analysis of aggressive behavior. Nelson (1964) pioneered the use of the temporal patterning of behaviors in his study of courtship behavior in four species of glandulocaudine fishes. Temporal patterning has been used in studying aggressive behavior patterns in several species of fish, including Pelmatochromis subocellatus kribensis (Heiligenberg, 1965), Pelmatochromis sp. (Skaller, 1966), and Betta splendens (Simpson, 1968).

The perciform fish T. trichopterus used in this study is a member of the tropical and sub-tropical sub-order Anabantoidei found throughout southern Asia, India, and Central Africa (Forselius, 1957). Liem (1963) comprehensively reviewed the systematics of this group and constructed a proposed phylogenetic relationship. The sub-order Anabantoidei comprises about 15 genera and 53 species (Forselius, 1957; Liem, 1963). Trichogaster trichopterus belongs to the trichogasterinae, a sub-family of the Belontiidae, and a summary of some of its salient characteristics is found in Hall (1965).

The agonistic behavior patterns of several species of the Belontiidae, including T. trichopterus, have been described by Forselius (1957), Miller (1964), and Miller and Miller (in press).

CHAPTER II

MATERIALS AND METHODS

This study consisted of three phases which are referred to as the preliminary phase, pilot study, and experimental phase. They will be described in detail later.

Anabantoid Sources and Laboratory Maintenance

Fish were obtained from tropical fish dealers in Oklahoma City, Oklahoma, or directly from Florida Fish Farms, Inc., in Miami, Florida. Fifty to 75 fish were maintained in 85 liter stock tanks lighted by 15 watt fluorescent lights. Water temperatures of stock tanks and experimental tanks ranged from 21°C to 26°C, and room temperatures varied from 22°C to 26°C during the three phases. A 14-hr photoperiod was used throughout this study. Water was "aged" for several days before use in experimental and observation tanks, and periodic readings indicated a pH range of 6.8 to 7.3. Water in the stock tanks was filtered through glass wool and charcoal and partially changed every two to three weeks. Fish in stock tanks were fed a dried flake food (Tetramin) in the morning, while those in use as experimental animals were fed Daphnia sp. and Chironomus sp. larvae several hours following testing or observation. The fish used in the pilot study and experimental phase were acclimated to laboratory conditions for a minimum of three

weeks prior to testing. Identification of fish was accomplished by clipping the apex of the dorsal fin, anal fin, either point of the caudal fin, or some combination of the above.

Observation and Experimental Tanks

During the preliminary phase of this study, fish were observed in aquaria which varied in size from small tanks measuring 56x28x18 cm with a capacity of 31 liters to larger tanks measuring 60x35x28 cm with capacities of 68 liters. Eight of these smaller tanks were used in the pilot study. For the third phase, an eight-compartment experimental tank was constructed. Marine plywood was used for the bottom, back, and sides and glass for the front. The wood surfaces were painted with a white epoxy as were the seven moveable, internal, glass partitions used to divide the tank into eight adjoining compartments. Each compartment measured 21.6 cm wide and 39.4 cm long. The water level was maintained at 25.4 cm, and each compartment thus had a capacity of 21.6 liters. A pretesting isolation period was used in the pilot and experimental phases, and fish were maintained individually in opaque, white plastic buckets in 8 liters of water.

Recording Apparatus

Frequency and duration of behaviors were recorded during the pilot study; but mechanical, multichannel lab tallies were used to record frequencies rather than logging a continuous written tally. Data for each fish in a dominance encounter were then transferred to summary data sheets along with any relevant qualitative notes. The behavioral data for the third phase was recorded with a 20-pen

Esterline-Angus Event Recorder (Model A620X) wired to two 10-key keyboards. A paper (Esterline-Angus Chart #1720) speed of 7.62 cm/min was used. This apparatus made possible the preservation of records on frequency and duration as well as the temporal patterning of behaviors occurring during dominance encounters between pairs of fish. The occurrence of a discrete event, e.g., a bite, was recorded by rapidly depressing and releasing the key coded for that pattern and that fish. For behaviors in which durations were involved, e.g., fin tugging, the appropriate key was depressed for the duration of that behavior.

Preliminary Phase Procedures

Observations during this portion of the investigation were made in the Oklahoma State University Aquatic Biology Laboratory from March 1 to June 1, 1968. Approximately 100 hours were logged observing the general ethology of several anabantoid species, especially observing qualitative aspects of agonistic patterns exhibited by T. trichopterus.

Fish selected from stock tanks were established in unisexual or heterosexual groups in 20 aquaria. Aquarium size varied, and the number of fish per tank varied from two to over 20. Each tank had a sand-gravel substrate and some were planted with varying amounts of Vallisneria sp. and Ceratophyllum sp.

No definitive observation procedure was used, but groups typically were observed for periods of 10 to 30 min following their establishment and each day thereafter for 5 to 10 days. Observations were made from about 1 m directly in front of aquaria. Slight movements seemed to have minimal effects on behavior.

Pilot Study Protocol and Procedures

This research phase was carried out in the Oklahoma State University Aquatic Biology Laboratory from June 1 to October 13, 1968. The purpose of this study was to determine whether certain environmental, physical, and social factors influenced the outcome of dominance encounters and the agonistic behaviors exhibited during such fights. This phase is hereafter referred to as Experiment I.

In order to provide a variable context in which fighting could occur, a series of unisexual pairings was made according to the protocol of Table I. Eight fish from stock populations (four males and four females) were measured to the nearest millimeter (standard length) and established singly in eight, 31-liter aquaria with gravel bottoms but no plants or artificial cover. An additional four males and four females were selected from stock, measured, and isolated in white plastic containers. After 3 days, the fish in isolation containers were introduced into the tanks of residents. Standard length differences did not exceed 6 mm in this study for any pairing combination. Forty-eight hours following this initial pairing and the dominance fight, the four dominant fish of each sex were paired with each other (2 pairs) and subordinates were paired similarly. One member of each new pair remained as a resident. Fish were transferred from one aquarium to another by placing them in filter boxes and gently releasing them at the end opposite the resident fish. The third pairing followed the same design with double winners matched and their losing opponents matched; likewise, double losers were matched and their winning opponents matched. A theoretical hierarchy could be calculated

at this time from the tournament-like schedule. In the fourth pairing, higher-ranking dominant fish, based on this theoretical hierarchy, were introduced into a tank with resident, lower-ranking dominants. Lower-ranking subordinates were introduced into aquaria with resident higher-ranking subordinates. For pairing number five, dominant fish of the previous experiment were introduced into tanks of resident subordinates. The converse of this schedule was followed in the final pairing, i.e., subordinates were introduced into the aquaria of resident dominants.

TABLE I

PILOT STUDY PAIRING SCHEDULE

Pairing No.	Symbol	Combination
1	I→I	Isolated fish paired with an isolated resident
2a 2b	D→D S→S	Dominants from Pairing 1 paired and subordinates from Pairing 1 paired
3a 3b	D→D S→S	Same design as Pairing 2; theoretical hierarchy established among the eight fish
4a 4b	D→D S→S	Theoretically higher-ranking dominant paired with a lower-ranking dominant, and theoretically lower-ranking subordinate paired with a higher-ranking subordinate
5	D→S	Dominants from Pairing 4 introduced into a subordinate's tank
6	S→D	Subordinate from Pairing 5 introduced into a dominant's tank

The initial 10 min of each pairing was observed. Latencies to the first approach, lateral display, and bite were measured as were the frequencies of the behavior patterns described in Chapter III. The outcome of the ensuing encounter was noted along with qualitative aspects of each bout.

A second 10-minute observation of each pair was made 24 hr after their initial bout, and frequency measures of behaviors were recorded. This experiment was replicated three times and involved 48 fish.

Experimental Phase Procedures

The third phase of this study was conducted in the Oklahoma State University Ethology Research Laboratory at the Life Sciences West Building from December 1, 1968, to January 1, 1970. A factorial experiment and a paired experiment were conducted, hereafter referred to as Experiments II and III, respectively.

The objectives of these experiments were first, to provide a detailed, operational description of the agonistic behavior patterns of this species; second, to determine the relative importance of social, physical, environmental, and temporal factors in influencing the establishment of dominance relationships in this species; and third, to develop experimental designs, techniques, and analytical methodology which might prove useful in the study of aggressive behavior.

Only males were studied and populations of 75 to 100 fish were usually available for selection of subjects. Test fish and controls were isolated in plastic containers for 10 days prior to use. Standard lengths were measured to the nearest millimeter. All fights were conducted in the previously described experimental tank.

The factorial experimental layout followed an incomplete block design, and the following four factors selected from results of pilot experiments were tested at two levels each: residency (A_1 = resident, A_0 = non-resident); dominance (B_1 = dominant pretest experience, B_0 = subordinate pretest experience); size (C_1 = 3 to 5 mm greater in standard length than opponent, C_0 = 3 to 5 mm less in standard length than opponent); and a time function (D_1 = test immediately following pretest experience, D_0 = test 24 hours after pretest experience).

After 10 days of isolation, two fish were placed in all odd-numbered compartments of the experimental tank; and dominant-subordinate relationships developed within 45 min in each case. These pairs will be referred to as D/S pairs. A control fish which was larger or smaller than the projected opponent was then placed in each even-numbered compartment. Twenty-four hours later, one member of each D/S pair, as determined by the time factor level, was removed and returned to its isolation bucket. The control fish and the remaining members of each D/S pair were allowed to fight, with the residency factor level determining which compartment was the site of the encounter. One hour following the termination of fighting, both fish were removed, and the other member of the D/S pair was returned to its appropriate compartment. A new control fish was placed in the adjoining compartment, and 24 hr later the above procedure of testing was repeated.

Recording of an ensuing encounter was begun when a transferred fish swam from the transferring net, and recording was terminated 10 min after the end of mutual fighting. This experiment was replicated four times.

In the paired design, Experiment III, fish were taken from isolation and placed in adjoining compartments. Twenty-four hours later, a pair of fish was allowed to fight by removing the opaque partition between compartments. Forty-one pairs of dominance encounters of this type were recorded. Absolute sizes of fish in this phase ranged from 49 mm to 66 mm, and size differences varied from 0 mm to 5 mm.

Statistical and Computing Services

The data of the factorial experiment was analyzed by using the FACAOV program of the Oklahoma State University Computer Library. The linear discriminant function analyses were computed by using the Biomedical Computer Programs BMD04M program, and the entropy values of Experiments II and III were computed from a species diversity program provided by Dr. Jerry Wilhm of the Oklahoma State University Zoology Department.

CHAPTER III

BEHAVIORAL UNITS, MEASURES, AND TERMINOLOGY

Mathematical models devised by ethologists usually are unique to a particular phenomenon under study. Some behaviorists hold that such models should be translatable into a language of some related discipline, e.g., neurophysiology. While this school of thought has probably hindered the development of ethology into a sophisticated biological science, a more basic problem of animal behavior involves the lack of precise measurable units for analysis. Barlow (1968b) pointed out that instrumental responses, e.g., lever pushing, have limited usefulness since they are often indirect measures of the behavior of interest. Ethologists have traditionally used behavior patterns referred to as "fixed action patterns," but an anthropomorphic element is often injected into their usage (Hinde, 1966). The solution according to Barlow (1968b) seems to be the ability to observe and record ". . . repeatedly recognizable events."

Cybernetics have been invoked for establishing uniformity in recording behavioral events. A fight of dominance establishment between a pair of fish has been considered as a behavioral system whose intra-individual and inter-individual transitions from one state to the next correspond to those of stochastic transformations. The behavior patterns of T. trichopterus used in this study represent events which are "repeatedly recognizable" and are considered the states of this system.

Behavior Patterns

Comprehensive qualitative descriptions of some of the agonistic behavior patterns of T. trichopterus used in this study have been recorded by Forselius (1957), Miller (1964), Hall (1965), and Miller and Miller (in press). A brief operational description of the states or patterns used in the present study follows.

Approach

An approach is defined as a direct movement toward a fish when previously separated by more than two body lengths. Approach speed is variable and often includes an element of what has previously been described by Baerends and Baerends-Van Roon (1950) as "jerk-swimming." The median fins are often slightly erected, and the pelvic threads flickered forward.

Lateral Spread Display

This pattern consists of either a lateral orientation to a facing fish, a parallel head-to-head orientation, or a parallel head-to-tail position. The median fins are always strongly spread, and several body curving components are present. The head and caudal regions curve upward along with a horizontal sigmoid curving of the entire body into an S-shape. The head is always directed away from the opponent, and the pelvic threads extend ventro-posteriorly.

Opercle Spreading

The form of this behavior differs markedly from the previously described opercle spreading patterns in other anabantoids (Forselius,

1957; Hall, 1965). The opercles and branchiostegals are spread only slightly, and this behavior does not occur in a frontal approach context. The opercle spreading fish is positioned parallel and slightly behind its opponent. The head is directed toward the other fish. A sigmoid curving of the body is usually present along with a downward concave horizontal component rather than the upward concave component of lateral spread display. The head is usually higher than the tail, and both dorsal and anal fins are folded while the near-side pelvic thread may extend toward the opponent.

Tail Beating

Lateral, undulating movements of the caudal peduncle and tail of a lateral displaying fish sometimes occur and have been referred to as "tail beating" (Miller, 1964). This pattern was referred to by Forselius (1957) simply as "undulating movements."

Fin Tugging

A state of fin tugging is said to exist when a fish bites the fin of another and "hangs on" for a period of one to several seconds, or actively pulls the fin by undulating, tugging movements. Most often, it is the anal fin of a lateral displaying fish which is attacked; but the dorsal, pelvic, or pectoral fins may be seized.

Biting

Butting movements have been differentiated from biting on the basis of whether a fish actually attempts to grasp the opponent with its teeth (Miller, 1964; Hall and Miller, 1968; Miller and Hall, 1968; and Miller and Miller, in press). The rapidity of this movement and

the slight extent to which the mouth is opened in this species, however, precludes any such differentiation in recording behavior during fights. Biting during dominance formation usually follows one of two slightly different patterns. In fish oriented head-to-tail, a non-displaying fish makes contact by lateral movements of the head against the body of his opponent. When a fish faces a laterally displaying opponent, biting is accomplished by a forward thrust of the entire body against the opponent. The lower flank region and caudal peduncle are the areas most consistently bitten. After establishing dominance, the winner often bites the caudal fin of a fleeing subordinate. These former two biting patterns are considered to be equivalent, and the last biting form is not used in this study.

Bite Sessions

The temporal patterning of biting indicates a non-random distribution pattern. Bites tend to occur in clusters, and the number of bites making up any such cluster varies from one to 35. A bite session is considered terminated with the occurrence of a new behavior pattern, the occurrence of biting by the opponent or a pause of at least 4 sec between actions. This pause duration was chosen because film analysis indicates that transitions from one state to another during these encounters requires a maximum of only 1 to 2 sec.

Appeasement

The conclusion of a fight between a pair of fish comes suddenly. The loser pales, folds its median fins, and often tilts along the median axis of the body, while avoiding the other fish. This

combination of behavior patterns and coloration is termed "appeasement" here. This pattern serves only as a reference point for certain aspects of data analysis, as its function has not been experimentally verified.

Chase

Chasing is said to occur each time one fish swims vigorously after another. This term implies the fleeing of one fish from another; thus, this behavior does not enter into the patterns exhibited during the mutual fighting of a dominance encounter. As with appeasement, it serves only as a reference point following the initial period of dominance establishment.

Surfacing

Because it is a Labyrinth fish, T. trichopterus rises periodically to the surface to gulp air. During dominance fighting, sequences of agonistic behavior are interrupted approximately once a minute, during which time one or both fish rise to the surface. These pauses with concomitant inspiration are termed "surfacing."

Pausing

Pausing is defined as those periods of greater than 4 sec in duration when none of the foregoing states is occurring.

Behavior Measures

The latency of the first occurrence of each behavior pattern was recorded along with the total frequency in Phases II and III.

Durations of lateral displaying, opercle spreading, and fin tugging were totaled for each fish in the experiments of Phase III from the Esterline record charts. Corrections for varied bout lengths were made by dividing the bout length of each fight into the above-mentioned measures. The average duration of lateral displaying, opercle spreading, and fin tugging were calculated along with the average number of bites per bite session. Intra-individual entropy values and transition frequencies were calculated in the factorial experiment of Phase III, while both intra-individual and inter-individual entropy values and transition frequencies were calculated in the paired experiments of Phase III.

The value of using multiple measures in analyzing agonistic behavior apparently has been overlooked by most students of fish behavior. Tables II and III show the symbols which represent the variables used in this study, and Table III lists their coding for Appendix A.

Terminology

Operational descriptions of certain parameters of this study that apply throughout unless otherwise qualified are the following:

Residency

The prior occupation of a given environmental space is considered to be a potential factor in determining the outcome of agonistic behavior between fish. Fish that occupied an aquarium or compartment of the experimental tank for at least 24 hr prior to the introduction of

TABLE II

BEHAVIOR STATES AND THEIR CODING

Term	Symbol	Principle Components or Posturing
Approach	A	Direct movement to within two body lengths of another fish
Lateral Spread Display	L	Erection of the median fins; sigmoid curving of the body; head directed away from opponent
Opercle Spread	O	Slight extension of the gill covers; median fins folded; head directed toward opponent
Fin Tugging	F	Biting and tugging any fin of an opponent
Biting	B	Sharp mouth contact of one fish against any region of another fish
Biting Session	BS	A cluster of bites
Surfacing	S	Pause from ongoing behavior and concomitant inspiration of air
Pausing	P	Intra-individual periods greater than 4 sec in duration during which no defined behavior occurs

TABLE III

VARIABLES MEASURED DURING DOMINANCE ENCOUNTERS

Variable (Abbreviation)	Unit	Code Number in Appendix A
Outcome	0, 1	1
Approach First	0, 1	2
Bout Length	Min	3
Surfacing/Min (S/M)	#/Min	4
Pausing/Min (P/M)	#/Min	5
Lateral Display First	0, 1	6
Lateral Display Frequency (LF)	#/Fight	7
Lateral Display Duration (LD)	Sec/Fight	8
Lateral Display Avg. Duration (L D/F)	Sec	9
Lateral Display Rate (L F/M)	Sec/Bout Min	10
Lateral Display Duration/Min (L D/M)	Sec/Bout Min	11
Lateral Display Rate by Opponent (L F/M/O)	#/Bout Min	12
Lateral Display Duration/Min by Opponent (L D/M/O)	Sec/Bout Min	13
Opercle Spread First	0, 1	14
Opercle Spread Frequency (OF)	#/Fight	15
Opercle Spread Duration (OD)	Sec/Fight	16
Opercle Spread Avg. Duration (O D/F)	Sec	17
Opercle Spread Rate (O F/M)	#/Bout Min	18

TABLE III (Continued)

Variable (Abbreviation)	Unit	Code Number in Appendix A
Opercle Spread Duration/Min (O D/M)	Sec/Bout Min	19
Opercle Spread Rate by Opponents (O F/M/O)	#/Min	20
Opercle Spread Duration/Min by Opponents (O D/M/O)	Sec/Bout Min	21
Bite First	0, 1	22
Bite Frequency (BF)	#/Fight	23
Bite Session Frequency (BS F)	#/Fight	24
Bites/Bite Session (B/BS)	#/Session	25
Bite Rate (B/M)	#/Bout Min	26
Bite Session Rate (BS/M)	#/Bout Min	27
Bites/Bite Session by Opponents (B/BS/O)	#/Session	28
Bite Rate by Opponent (B/M/O)	#/Bout Min	29
Bite Session Rate by Opponents BS/M/O	#/Bout Min	30
Fin Tug First	0, 1	31
Fin Tug Frequency (FF)	#/Fight	32
Fin Tug Duration (FD)	Sec/Fight	33
Fin Tug Avg. Duration (F D/F)	Sec	34
Fin Tug Rate (F F/M)	#/Bout Min	35
Fin Tug Duration/Min (F D/M)	Sec/Bout Min	36
Fin Tug Rate by Opponents (F F/M/O)	#/Bout Min	37

TABLE III (Continued)

Variable (Abbreviation)	Unit	Code Number in Appendix A
Fin Tug Duration/Min by Opponents (F F/M/O)	Sec/Bout Min	38
Entropy for the 6 Behaviors: {L, O, BS, F, S, P}, H(6)	Bits	39
Entropy for the 4 Behaviors: {L, O, BS, F}, H(4)	Bits	40
Number of these 6 Behaviors Shown	#	41
Total Number of these 6 Behaviors	#	42
Number of these 4 Behaviors Shown	#	43
Total Number of these 4 Behaviors	#	44

any other fish are called "residents." Conversely, a fish which has been moved into a new space or container is termed a "non-resident."

Dominance

The concept of dominance suggests a conflict or some hierarchical organization. As pointed out in Chapter I, a variety of measures of dominance have been employed. For example, primate studies often involve priority for incentives such as food as illustrated by the work of Carpenter (1942); van Lawick-Goodall (1968); and Bernstein (1969). Another measure used includes observations of relative numbers of "aggressive" responses (Marsden, 1968).

Collias (1943) used the outcome of a paired encounter as a direct measure of dominance in chickens. In most avian studies, however, dominance is often determined by observations of paired encounters usually within flocks. Peck orders are based on the relative number of peck-avoidance or threat-avoidance encounters between dyads (Craig et al., 1969). Spatial relations of "neighbors" are being used to establish factors associated with dominance (McBride et al., 1963; McBride, 1968). Landau (1951a) theoretically defined a dominance relation as ". . . a binary, asymmetric, non-transitive relation, j dominates k being written $j > k$."

No universal measure of dominance has been adopted in studies on fish behavior. Most works include some measures similar to those described for avian species or the occurrence of some subordinate posturing (Greenberg, 1947; Braddock, 1949; Barlow, 1962; Miller, 1964; Simpson, 1968; and Hadley, 1969). Baenninger (1968b) used avoidance of an opponent for 20 consecutive times as an indication of dominance.

In this study the term "dominant" refers to a fish which has previously defeated another in an encounter within the past 24 hr. A "subordinate" is one which has lost an encounter within the past 24 hr. A "dominance relationship" refers to the relative hierarchical position of a pair of fish following the initial phase of mutual fighting, i.e., a "winner" and a "loser" result. These latter two terms require no subjective interpretation since the resultant patterns of appeasement, chasing, and fleeing are self-evident of a conflict resolution.

Size

Standard length (distance between tip of snout and end of hypural plate) was used in this study. The size factor of each study concerns relative size rather than absolute size, unless otherwise indicated.

CHAPTER IV

QUALITATIVE ASPECTS OF DOMINANCE ESTABLISHMENT

The temporal patterning of the fighting behaviors shown in dominance encounters seems to be influenced by several environmental, physical, and social factors, but temporal relationships are remarkably consistent in any given context. The following description of fighting in *T. trichopterus* is intended to provide an overview of the similarities referred to above. It also provides a point of reference for the subsequent development of quantitative concepts of dominance encounters.

Protocol of a "Typical" Fight Sequence

Without considering the effect of experimental parameters on the relative occurrence of certain behaviors, a "typical" fighting sequence between two fish can be represented symbolically using the coding from Table II, as follows:

Fish No. 1:	P-A-	L-L-	O-L-S-L-B-[...]	B-L-P-F-[...]	L-APPEASE	
Fish No. 2:	P-	L- O-P-L	B-S- L-[...]	B-F-L- [...]	B-P-A-CHASE-B	
Time (Sec)	0	30	90	240	720	850

The initial reaction of most fish when given access to an unfamiliar environment is to sink to the substrate and remain motionless for a few seconds. This is represented by the pauses (P) of both fish at

time Zero; and during this time, both fish seem to explore their surroundings visually. One fish (No. 1) begins to move slowly from the bottom and orient toward the other fish (No. 2) within 30 sec. Fish No. 1 swims slowly forward (A), and Fish No. 2 may then begin to move upward and turn toward the approaching partner. When the distance between opponents is approximately 6 to 8 cm, Fish No. 2 exhibits a lateral spread display (L). Almost immediately, Fish No. 1 swims ahead of his displaying partner, orients laterally, and also displays (L). Fish No. 2, now slightly behind and lateral to Fish No. 1, exhibits an opercle spreading pattern (O). This sequence of "L-O-L" in both fish may continue for several seconds, and from a subjective point of view it seems that they "jockey" for the L position. At about 1.5 min into the encounter, Fish No. 2 turns toward his partner and bites (BS) at the lower abdomen or caudal peduncle. Mutual upward swimming follows, during which time both fish surface (S) to gulp air. The alternating sequence of "L-BS-L" follows for the next few minutes with occasional pauses to surface, opercle spread, or pause interspersed. Fin tugging becomes incorporated into the sequences of biting and displaying after about 4 min. In the terminal phases of the fight, pausing seems to occur more frequently, and Fish No. 1 suddenly exhibits the appeasement pattern (Chapter III) and moves away. A few seconds later, the winner (Fish No. 2) approaches, displays, circles, and may display again. The loser again moves away, and the dominant fish usually chases and bites the fleeing fish within a short time. This begins the second phase of a dominance relationship in these fish, i.e., a period of dominance maintenance. The intervals between approaches

and chases by the dominant fish become shorter during the next 30 min, i.e., during the first one-half hour of the second phase.

The overall picture of such initial encounters in these fish seems to be one of gradual increase in tempo and intensity of some of the agonistic behaviors. The behavior patterns, though variable in frequency and duration, are highly consistent in form, and a considerable amount of redundancy exists in their sequential arrangement.

Color Changes

Forselius (1957) has discussed the color patterns and associated chromatophore systems exhibited by several species of anabantoid fishes. The basic color patterns as well as the changes associated with courtship, reproduction, and agonistic behavior of T. trichopterus have been reviewed by Miller (1964).

The ground color of this species is a pale blue. Black ocelli occur on the abdominal region and caudal peduncle, and smaller white spots are present in the dorsal, anal, and caudal fins. Forselius (1957) has described the arrangement of melanophores ". . .that form a number of partly anastomosing vertical bands along the sides of the body. . ." The anal fin of some specimens has a light yellow tint along the ventral edge.

Fish kept in white isolation buckets or in the white experimental tank tended to be somewhat paler than fish isolated in gravel-bottomed aquaria. During the first few moments of an encounter, both fish retain this somewhat "washed out" color. The first noticeable color changes during fighting are seen in a darkening of the lateral bands. This is followed by a darkening of the iris. Following the first

several exchanges of bites, changes in the melanophores of the caudal, anal, and dorsal fins result in a darkening of these areas except for the light spots mentioned above. These spots stand out more prominently in contrast to the darker regions. In prolonged fights the lighter regions between lateral bands may begin to darken at this point and result in what Miller (1964) has described as an "inky" appearance. The black ocelli have become indistinguishable at this point.

At the conclusion of the fight, the subordinate quickly loses the above-described patterns and assumes an extremely pale color. The dominant fish also loses most of the darker colors, but more slowly than the subordinate.

CHAPTER V

PRELIMINARY OBSERVATIONS AND RESULTS OF PILOT STUDY

Blue gouramis exhibited some form of agonistic behavior and hierarchical organization under all regimes used in this study. Unisexual or heterosexual pairs or groups of fish, established for some time, often show little indication of any social conflict. Mutual fighting and displaying may be seldom observed. A dominant fish of the group may approach a subordinate, and either fish may move away without any resultant agonistic behavior. Occasionally, a dominant fish approaches and bites a subordinate, and a brief chasing-fleeing bout ensues. Miller (1964) noted that overcrowding these fish tends to suppress aggressive behavior; and tropical fish suppliers advertise this species as a "semi-peaceful" fish (Wolfsheimer, 1967). It was found during the initial stages of this study, however, that these fish fight quite vigorously during the establishment of a dominance relationship. Some factors which seem to influence a dominance relationship in this species are:

1. Familiarity with a given space, i.e., a residency factor
2. Sex
3. Absolute fish size
4. Relative size of opponents
5. Immediate prior experience relating to dominance

6. Time since this dominance-related experience

7. Duration of this dominance-related experience

The influence of several of these factors was observed during the first phase of this study, and the role they play in dominance establishment was investigated during the pilot study.

The Influence of Sex

It was consistently observed that when an encounter occurred within a group between a male and a female, the latter fled about 90% of the time. Since the males may have been larger than these females, a series of "sex tests" was conducted. Small males were introduced into aquaria with one or two larger females. The size differences were not measured but were obvious. Nine out of 10 times, the males dominated the females within several minutes of fighting. However, both sexes occasionally exhibit some form of territoriality, and the agonistic patterns of males are qualitatively quite similar to those of females with all of the patterns described in Chapter III occurring in both sexes.

The Influence of Residency

Seventy-six resident fish out of 131 pairs in Experiment I won initial encounters. The null hypothesis for testing each pairing type was that resident fish defeat non-resident partners in the same ratio that non-residents defeat residents. The number of residents winning is shown in Table IV along with the respective Chi square probability level for each. From this data the null hypothesis was not accepted during initial encounters under the following conditions:

1. When isolated fish were first introduced into resident tanks (Pairing 1)

2. When subordinates were introduced into the tanks of other subordinates (Pairing 3b)

3. When dominants were introduced into the tanks of dominants (Pairing 5)

4. When subordinates were introduced into the tanks of dominants (Pairing 6)

TABLE IV

EFFECT OF RESIDENCY ON OUTCOME OF DOMINANCE ENCOUNTERS

Pairing No.	Pairing Type	Number+ of Resident Winners or Dominants	
		Initial Encounters	24 Hr
1	I→I	17(23)*	11(24)
2a	D→D	6(10)	8(10)
2b	S→S	7(12)	6(12)
3a	D→D	6(12)	6(12)
3b	S→S	10(12)*	9(12)
4a	D→D	3(12)	1(12)**
4b	S→S	9(11)	10(12)*
5	D→S	3(24)**	3(24)**
6	S→D	15(15)**	13(15)**
Total		76(131)	67(133)

+Numbers in parentheses are the total number of cases on which Chi sq analyses were based; *.025 > p > .005; ** .005 > p.

One hundred per cent of the residents won their initial encounters in condition No. 4, while only 18% of the residents were victorious in the converse of this experiment, i.e., Pairing No. 5. Five of the 9 different pairings show decreases in the percentage of residents still dominant 24 hr later; two other pairings show equivalence; and 2 show slight increases after 24 hr.

Based on the average latencies and the first occurrence of certain behaviors, it was found that a resident approaches and bites sooner than a non-resident, while a non-resident tends to lateral display sooner than a resident.

The Influence of Relative Fish Size

The data for the influence of fish size on the outcome of encounters has been treated in much the same way as the residency data. The null hypothesis that larger fish defeat smaller fish in the same ratio that smaller fish defeat larger fish was tested. Table V shows that while as many as 80% of the winners of a particular pairing type were larger than their opponents, no pairing difference reached the .05 level (Chi sq.). A slight, but non-significant increase in the number of larger fish which were dominant over smaller opponents after 24 hr of cohabitation of a space is also seen from the totals of Table V. Four of the nine pairings show increases in the percentage of larger fish in a dominant position 24 hr after initial fights; three pairings show no change; and two show decreases after 24 hr. Though sample size is quite small, comparing these data on size with residency data seems to indicate that a residency factor probably operates independently of a size factor.

TABLE V

EFFECT OF RELATIVE SIZE ON OUTCOME OF DOMINANCE ENCOUNTERS

Pairing No.	Pairing Type	Number+ of Larger Winners or Dominants	
		Initial Encounters	24 Hr
1	I→I	12(23)*	14(24)
2a	D→D	6(8)	6(9)
2b	S→S	6(12)	5(12)
3a	D→D	8(10)	8(10)
3b	S→S	5(11)	8(11)
4a	D→D	4(9)	4(9)
4b	S→S	5(10)	5(10)
5	D→S	9(19)	10(20)
6	S→D	6(13)	7(14)
Total		61(115)	67(119)

+Numbers in parentheses are the total number of cases on which Chi sq analyses were based; *no Chi sq values are significant at .05 level.

The Influence of Prior Conditioning

The effect of immediate prior experience as a dominant or as a dominated fish on the outcome of a subsequent encounter was tested by Pairings 5 and 6 of this study. Table VI shows the number of dominants, i.e., dominant from the previous day, that won encounters with "conditioned" subordinates. From Table V it can be seen that size was not indicated as an important influencing factor in these two experiments. However, in Pairing 5 the opponent was larger in the three cases where a "conditioned" dominant did not win. Since under these

two conditions, all the dominantly conditioned fish were either the residents (Pairing 6) or the intruders (Pairing 5), the effect of residency indicated in Table IV for these two conditions seems contingent upon this fact rather than a residency factor per se.

TABLE VI

EFFECT OF PRIOR EXPERIENCE ON OUTCOME OF DOMINANCE ENCOUNTERS

Pairing No.	Pairing Type	Number of Previously Dominant Fish Winning Encounters or Dominant After 24 Hr	
		Initial Encounter	24 Hr
5	D→S	21(24)**	21(24)**
6	S→D	15(15)**	13(15)**

**.005 ≥p

Stability of Established Dominance Relationships

In contrasting the results of the outcome of initial encounters with the rank of the fish 24 hr later, some measure of dominance stability can be assessed. The number of times that the outcome of an initial encounter was reversed within 24 hr is shown in Table VII for both male pairs and female pairs. The null hypothesis that the size-related reversals are independent of fish sex was not rejected at the .05 level (Chi sq = 3.14, df = 1). Fourteen of these 22 reversals seemed to be related to a size factor, i.e., larger fish eventually became dominant. Dominance relations, once established,

thus tend to show considerable stability with only 16% of 132 fights showing reversals within 24 hr. In 41 encounters of Experiment III, only two reversals occurred within this same time period (Chapter VII).

TABLE VII

STABILITY OF DOMINANCE ENCOUNTERS OVER A 24 HOUR PERIOD

Reversal Type	Males	Females	Total	% Total
Smaller fish reversed by larger fish	8	6	14	64
Larger fish reversed by smaller fish	3	5	8	36
Total*	11	11		

*The total number of encounters in Experiment I was 136 of which only 22 had a reversal occur during the 24 hr period following dominance establishment.

Testing A Theoretical Hierarchy

By the tournament-like series of pairings in this pilot study, a theoretical hierarchy had been established as a result of Pairings 1, 2, and 3. In Pairing 4, this hierarchy was tested by subsequently fighting higher-ranking dominants with lower-ranking dominants and pairing lower-ranking subordinates with higher-ranking subordinates (see Table I). Table VIII shows the number of times this theoretical hierarchy held true, and the null hypothesis that fish which are ranked

higher theoretically win half their subsequent encounters was tested. Lower-ranking fish of this theoretical hierarchy did tend to become subordinate to higher-ranking fish ultimately.

TABLE VIII

THE VALIDITY OF THE THEORETICAL HIERARCHY ESTABLISHED BY PAIRINGS 1, 2, AND 3

Pairing Type	Number of Winners or Dominants After Initial Encounter	24 Hr
Higher-ranking dominant paired with lower-ranking dominant	9(12)*	11(12)***
Higher-ranking subordinate paired with lower-ranking subordinate	10(12)**	10(12)**

*.250 > p > .100, **.050 > p > .025, ***.005 > p

The Influence of Experimental Parameters on Agonistic Behaviors

While the outcome of an encounter may be treated as a discrete phenomenon influenced by certain physical, social, and environmental factors, the expression of agonistic behaviors during such encounters exhibits considerable variation. Such variation depends, in part, upon the context of that particular fight. For example, previously dominant fish paired with previously dominant fish (Pairings 2a, 3a, and 4a) exhibit different fighting patterns than those shown by subordinates paired with subordinates (Pairings 2b, 3b, and 4b). Fights

involving the former are characterized by significantly higher biting rates (F-test, $P > .01$); significantly higher lateral displaying rates (F-test, $P > .01$); and significantly shorter latencies to the first lateral display (t-test, $P > .025$).

It was anticipated that a winning fish would probably exhibit a higher biting rate than a losing fish. Figure 1 shows that this is not universally true since resident losers show higher rates than do their opponents, i.e., the winning non-residents. However, since the agonistic behaviors of this pilot study were recorded only for the first 10 min of fighting and fight length varies from about 2 to 30 min, this set of data does not adequately lend itself to rigorous statistical analysis concerning the dynamics of the agonistic behaviors involved in dominance establishment. Recording the temporal patterning of these behaviors was also deemed a desirable measure of agonistic patterns in the investigations described below.

From this study relative size of opponents, residency, and prior experience were indicated as contributing to either the outcome of a dominance encounter or the behaviors expressed during such an encounter. One final aspect of this pilot work concerns the reaffirmation of the existence of two phases in dominance relationships. Figure 2 illustrates the average occurrence per 10 min of several agonistic patterns during the initial encounter and during a period of dominance maintenance, i.e., 24 hr later.

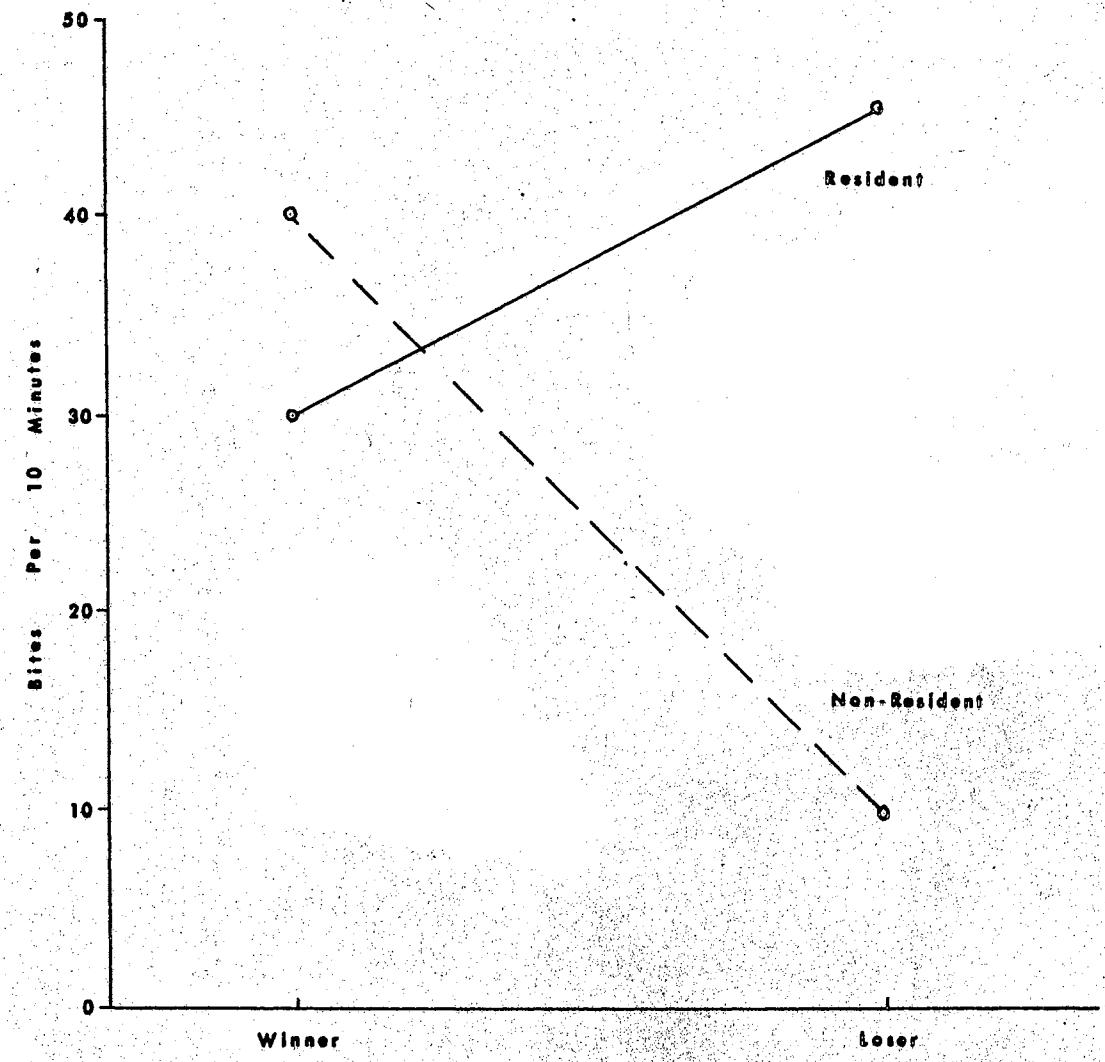


Figure 1. Residency and outcome interaction on bites given during the initial 10 min of contact between pairs of fish in Experiment I

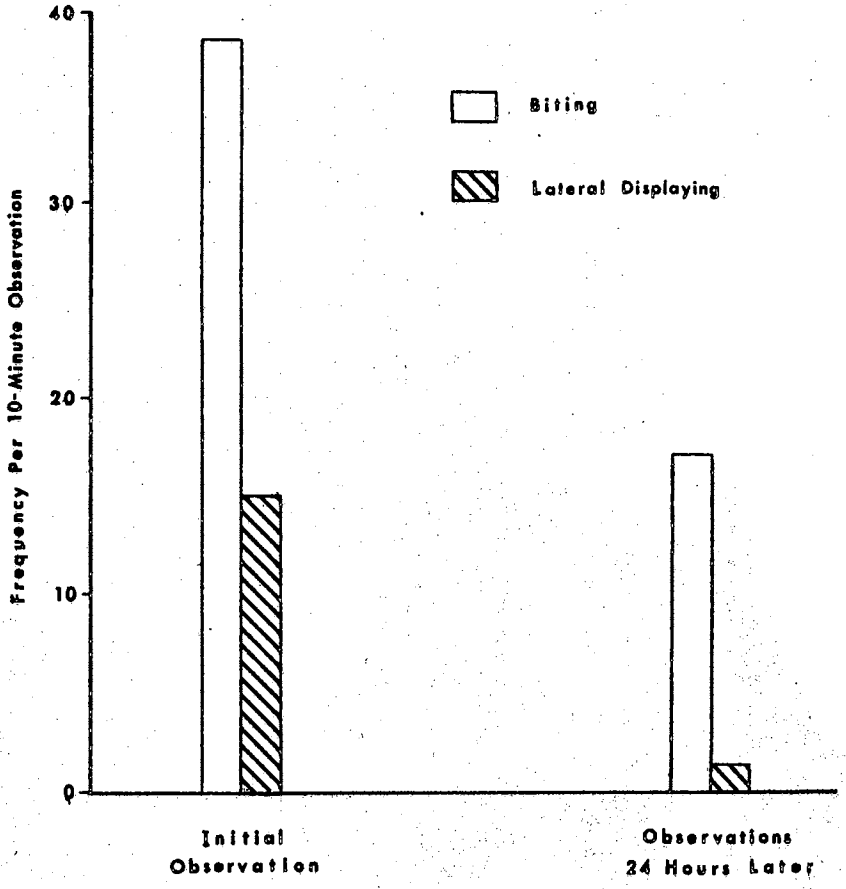


Figure 2. The frequency per 10 min observation of biting and lateral displaying by winners at time zero and 24 hr later

CHAPTER VI

THE RELATIVE INFLUENCE OF RESIDENCY, PRIOR EXPERIENCE, SIZE, AND TIME ON DOMINANCE ESTABLISHMENT

A factorial experiment, Experiment II, was conducted in order to systematically evaluate the relative influence of an environmental, a physical, a temporal, and a social factor on the outcome of dominance encounters and the behaviors associated with such encounters. These factors, defined and described in Chapter III are:

1. Residency—environmental factor (A)
2. Prior Dominance Experience—social factor (B)
3. Relative Size—physical factor (C)
4. Time Since Last Experience—temporal factor (D)

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

$$Y = R + A + B + C + D + AB + AC + AD + BC + BD + CD + ABC + ABD + ACD + BCD + ERROR$$

where the error term was a combination of the rep components and the ABCD element. The calculated F-values, error mean squares, and coefficients of variation are presented in Appendix A for the outcome of encounters as well as 43 attendant measures of dominance establishment. (Table III and Appendix A). Two- and three-way tables for interactions exceeding the .05 level of significance are presented in Appendix B.

Experimental Parameters and Outcome

Dr. Leroy Folks (personal communication) has pointed out that since the outcome of these encounters represents a discrete event, some reservations need to be employed in the interpretation of the results of this type of factorial analysis of variance. The influence of previous experience on winning subsequent fights is unequivocally significant; relative size exceeds the .005 level; and the factor time-since-experience just exceeds the .05 level (Appendix A; Variable 1 outcome; Factors B, C, and D, respectively). The number of fish which won encounters at each level of a particular factor is shown in Figure 3. When the number of fish of a particular factor winning their encounters is compared between levels of that factor by Chi sq analysis, only the prior experience parameter (Factor B) shows significance at the .05 level. A subsequent investigation confirms, however, that size plays a significant and probably differential role in dominance establishment.

The AOV of the main effects indicates that residency does not influence the outcome of an encounter. Previously dominant fish are greatly enhanced, and previously dominated fish are strongly inhibited in their ability to defeat another fish in a subsequent encounter; larger fish tend to defeat smaller opponents; and fish with immediate prior dominance-related experience are slightly less successful than fish with equivalent experience 24 hr prior to a subsequent fight.

No interactions reach significance levels, but the 3-factor interaction of dominance experience, relative size, and time-since-experience (BCD) reveals an interesting trend. No small, subordinate-

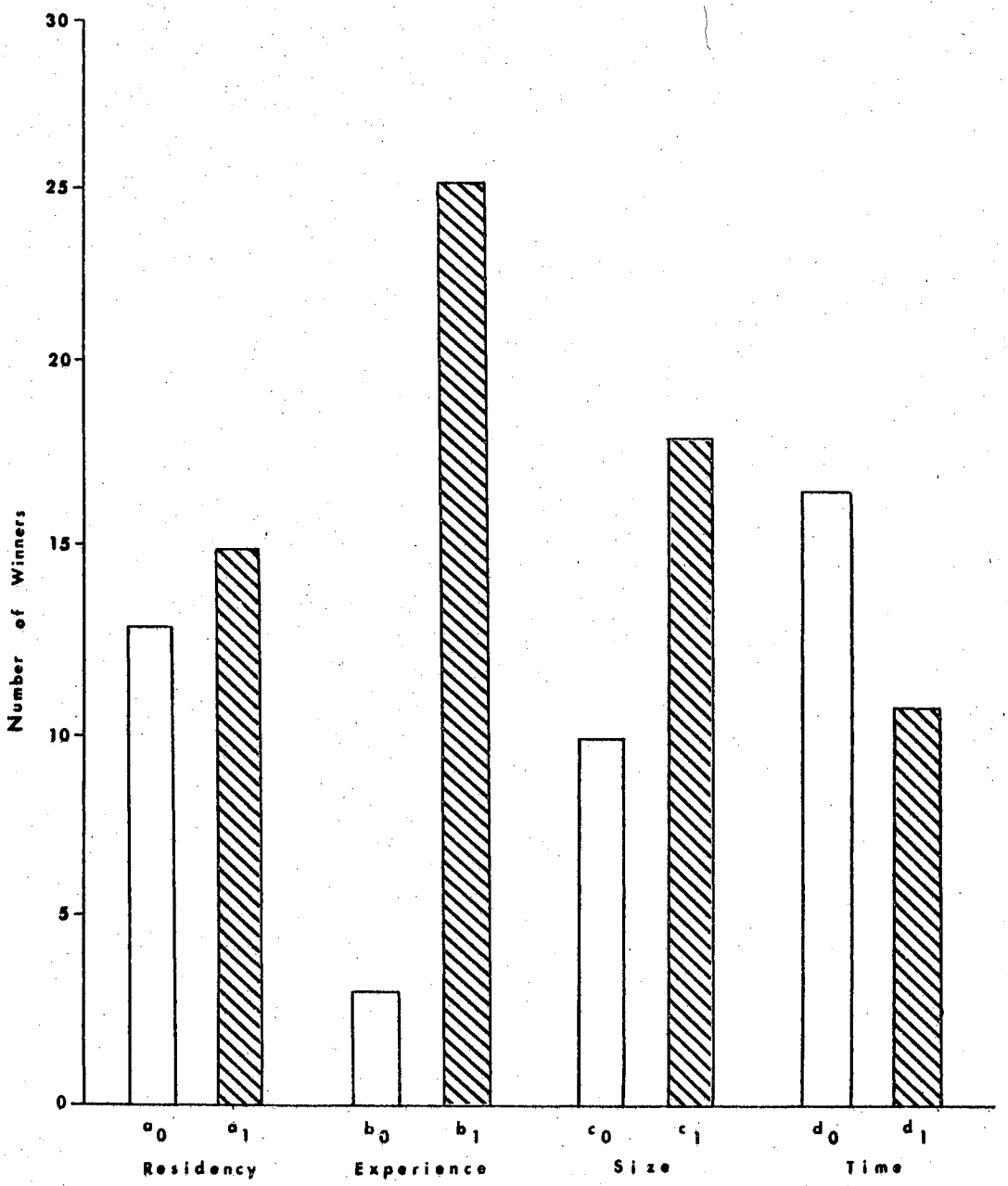


Figure 3. The number of fish winning an encounter at each factor level in Experiment II out of 32 possible cases (a_0= non-resident, a_1= resident; b_0= subordinate experienced, b_1= dominant experienced; c_0= smaller than opponent, c_1= larger than opponent; and d_0= tested 24 hr after dominance experience, d_1= tested immediately after dominance experience)

experienced fish won an encounter at either level of the time factor, i.e., fighting immediately after contact with a dominant partner (D_1) or 24 hr after that contact with a partner (D_0). No large subordinate fish won encounters immediately following the subordinating experience, but three large subordinates won encounters with smaller fish when given 24 hr of separation from their dominant partners. A waning of the effect of being dominated seems apparent.

First Occurrence of Any Behavior

The experimental parameters of this study were shown to influence the first occurrence of particular behavior patterns. Again, this represents a discrete phenomenon similar to winning or losing, i.e., fish showing a particular behavior before their partners exhibited this pattern were coded as a one (1) in the AOV, and fish not showing an initial behavior were coded as a zero (0).

One fish usually approaches another within the first 30 sec of mutual cohabitation of a space. Residency was the only factor which seemed to influence this variable (Appendix A, Approaches First, Variable 2). The residency and size (AC) interaction exceeded the .005 level, and the experience and size (BC) interaction exceeded the .01 level (Appendix B, Tables IX and X, respectively). Large, non-resident fish are inhibited from approaching first; but large, resident fish tend to initiate the first approach. The probability that a small fish approaches first is not substantially influenced by the residency factor.

As pointed out in Chapter IV, lateral displaying begins approximately 50 sec into the fight. No factors were linked with the first occurrence of lateral displaying (Appendix A, Variable 6).

The third behavior usually occurring in the repertoire of agonistic behaviors is opercle spreading. Resident fish exhibited this pattern first, regardless of prior dominance experience, relative size, or time (Appendix A Opercle Spread F-values, Variables 15 to 19, all exceed .05 for Factor A). The second factor which may promote the occurrence of this pattern is the dominance experience factor. Previously dominant fish tended to opercle spread before their partners, while previously subordinate fish "displayed" first only 25% of the time. There is some indication from examination of the non-significant experience and time (BD) interaction that subordinate fish will begin to opercle spread first about half the time, if given 24 hr of freedom from domination.

After alternating sequences of lateral displaying and opercle spreading, biting ensues. Residents and previously dominant fish bite first (Appendix A, Variable 22). The first order interaction between experience and size (BC) reaches the .05 level of significance, and Table XI suggests that a size factor might influence subordinate fish but not dominant fish in this respect, i.e., only small, subordinate fish are inhibited from biting first.

Resident fish tend to initiate fin tugging (Appendix A, Variable 31). The experience and time (BD) interaction (Appendix B, Table XII) was significant and follows the same pattern as opercle spreading, i.e., after 24 hr of freedom from domination, a subordinate is as likely to fin tug first as a dominant fish.

Behavior Rates and Durations

Multiple measures of particular behavior patterns have been recorded and analyzed in this study. This method proves useful when many tests of significance are made to evaluate which results might be due to random effects rather than real effects of some experimental parameter. As an example, consider the supposed significant first order size and time (CD) interaction for opercle spread rate by an opponent (Appendix A, CD, Variable 20). The CD interaction does not reach the .05 level for any other opercle spread variable, and it seems reasonable to assume that these results are due to random combinations rather than real effects. Similar interpretations of such random effects will be pointed out.

Lateral Displaying

The seven measures of lateral displaying described in Table III have been used in this study. The residency factor influenced only the average lateral display rate and average time spent displaying by an opponent (Appendix A, Variables 12 and 13).

The strong influence of the prior experience factor on this display can be seen by the highly significant F-values of Factor B for 5 variables (7 to 11) in Appendix A. In general, previously dominant fish display more frequently, spend more time per minute displaying, and exhibit longer duration displays than previously subordinate fish.

The main effects of relative size reached the .05 level for two (L) variables—the total time spent displaying and for the frequency of displays per minute by an opponent (Appendix A, Variables 8 and 12,

respectively). These two, somewhat isolated cases seem to indicate that the relative size factor does not influence lateral displaying to any real extent in these fish.

The main effects due to Factor D (time-since-experience) show a significant and opposite effect from the experience factor. The average duration of a display is longer, displays occur more frequently, and more time is spent displaying per minute of fighting in those fish which have their subsequent fights delayed by 24 hr, i.e., the low level of Factor D. As may be expected then a significant experience and time interaction (BD) exists. Inspection of (BD) two-way tables (Appendix B, Tables XIII to XVIII) for the six significant lateral displaying measures reveals that the parameter of "time-since-last-experience" influences subordinate-experienced fish much more pronouncedly than it does dominant-experienced fish. As previously mentioned for latency measures, and as appears to be a reoccurring phenomenon, it seems that losing a fight and being dominated by another fish has an inhibitory effect on the expression of several behavior patterns—lateral displaying included. This inhibitory effect wanes significantly within 24 hr, provided the dominating fish is removed.

The residency, experience, and time (ABD) three-way table for lateral display duration per minute by an opponent (Appendix B, Table XIX) indicates that an effect of residency may also influence these subordinates once the inhibitory effects of being dominated have waned. The non-significant ABD interaction for this variable (L D/M) in the experimental fish followed the same trend. Also, two-way tables for (AD) residency and time interaction (Appendix B, Tables XX, XXI, and XXII) provide supporting evidence for this latter point. Finally, it

is possible that fish smaller than their opponents might display differently than fish larger than their partners. The first order interactions of size and time (CD) for average length of a display and display duration per minute were found to be significant. Tables XXIII and XXIV of Appendix B indicate that when small fish fight immediately after some previous experience, their displays are shorter in duration than those of a larger fish; but the average display duration is similar to larger fish when separated from a conspecific partner for 24 hr.

Opercle Spreading

Opercle spreading, unlike the previous behavior pattern, was shown to be strongly influenced by a residency factor (Appendix A, Factor A, Variables 15 to 19). Analysis of the 2nd order resident, experience, and time (ABD) interaction of Tables XXV to XXIX illustrates that this residency factor is present only in dominant fish with immediate prior experience or in subordinate fish whose prior experience was at least 24 hr previous. Two-way experience and time (BD) interactions of Tables XXX to XXXIV confirm this point. The effect of residency then is influenced by both experience and time-since-experience. The opercle spreading rate and duration of an "untreated" opponent shows slight residency effect.

The significant main effect of prior experience on opercle spreading indicates that dominant pre-test experience increases frequency, duration per display, and total duration of this pattern. The two-way tables for BD interaction, however, show that this effect is time-dependent.

Relative size of opponents apparently does not influence opercle spreading. The significant residency and size interaction (AC) of total opercle spread duration (Appendix A, Variable 16) probably represents an artifact of random combinations of error effects.

Biting

Total number of bite sessions, bites per minute, and bite sessions per minute (Variables 24, 26, and 27, respectively, of Appendix A) showed main effects due to residency (A); but the residency and time (AD) interactions (Appendix B, Tables XXXV, XXXVI, XXXVII, and XXXVIII) indicate that this residency factor is much more pronounced in those fish whose partners have been removed for at least 24 hr. Residency also interacts with prior experience (AB) for the number of bites per biting session (Appendix B, Table XXXIX). Residency increases B/BS in subordinate fish but affects dominant fish little.

Prior experience main effects (B) were highly significant for all eight biting variables; dominant fish showed higher values than subordinate fish. The residency and experience (AB) interaction has already been pointed out, and the only other first order interaction involving experience was that of experience and time (BD). Tables XL, XLI, XLII, AND XLIII of Appendix B illustrate a similar trend. Dominant-experienced fish show no effect due to a 24 hr period of separation from a partner, but subordinate-experienced fish increase their number of bites per biting session and their BS rate by at least fourfold 24 hr after the removal of their dominant partner. Again, the inhibitory effect of subordinate experience is seen to wane with time.

Relative size (C) influenced total bites and bite sessions. This parameter interacted with residency (AC) and prior experience (BC) (Appendix B, Tables XLIV, XLV, and XLVI). Small, subordinate-experienced fish bite less per minute than large subordinate-experienced fish.

A significant effect of time-since-experience (D) was present for all biting variables except total bites and bite sessions (Appendix A, Variables 25 to 30). The magnitude of these variables increased over a 24-hr isolating period. The 2nd order interactions involving time-since-experience have been pointed out above.

Fin Tugging

The seven fin tugging measures of Table IV were recorded and analyzed. These fish were found to fin tug for about the same amount of time as they spent opercle spreading, i.e., about 2 sec/min. Slight increases in rate per minute, duration per minute, and average fin tug duration were recorded for the residency factor (A), but only Variable 32, total number, reached the .05 level for this parameter. A highly significant residency and time (AD) interaction was found for the average fin tug duration (Appendix A, Variable 34) and Table XLVII illustrates that a residency effect is probably present only if fish have been isolated from their opponents for a 24-hr period.

Prior experience as a dominant fish does not seem to increase all seven fin tugging measures, but dominated fish showed depressed rates and durations. A 1st order interaction was found between this social factor and the time factor (BD). Table XLVIII shows that dominant-experienced fish were not influenced by time-since-that-experience,

but subordinate fish showed much shorter fin tugs when fighting an immediate subsequent encounter. This inhibition wanes within 24 hr if the dominating partner is removed.

No significant trends were associated with the relative size of opponents (Factor C) and fin tugging variables.

Those fish fighting immediately after a dominance experience fin tugged less frequently and for shorter periods than fish separated from an opponent for 24 hr.

Surfacing for Air

During the fights of Experiment II, fish rose to take in air .94 $\pm$ .48 times per minute. Non-residents showed a significantly higher rate of surfacing than did resident fish (Appendix A, Variable 4). This residency factor (A) may be influenced by both the relative size (C) of the fish and "dominance state" (B). The ABC interaction (Appendix B, Table XLIX) shows that residency influences large, dominant, and subordinate fish in the same manner as described for the main effect trend; however, in small fish the residency factor does not seem to affect dominant fish but greatly influences a subordinate, non-resident to surface at a much higher rate.

The Interruption of Fighting Sequences by Pausing

None of the four experimental parameters influenced pausing (Appendix A, Variable 5). It will be pointed out in Chapter VII that this condition may be important in a contingency context rather than in the actual state of inactivity itself. Pauses of at least 4 sec occurred at about the same rate as surfacing, i.e., .94 $\pm$ .84 times/min.

Fight Duration

Fight lengths ranged from 1.03 to 36.33 min with an average of 11.96 $\pm$ 7.48 min. Three main effects were significant for bout length, i.e., residency (A), experience (B), and relative size (C) (Appendix A, Variable 3). The effects of these factors on bout duration can be summarized as follows:

1. Residents—14.22 min; non-residents—9.70 min
2. Dominant-experienced fish—16.99 min; subordinate-experienced fish—6.94 min
3. Larger fish—14.07 min; smaller fish—9.86 min

No interactions reached the .05 level for fight lengths.

The Number and Variety of Behaviors in Fighting Sequences

Fighting sequences in this study have been considered as a set of (N) elements of which (X) are distinct. For example, in the intra-sequence fighting protocol of A—L—O—L—L—BS—L—APPEASE, there are eight elements or states, but only five distinct elements, i.e., A, L, O, BS, and APPEASE. Using Ashby's (1966) definition, this sequence would have a maximum variety of 5, or more commonly ($\log_2 5$ bits). Six distinct elements of fighting sequences were recorded in this experiment as follows (see Table III for descriptions): L, O, F, BS, S, and P.

The experimental parameters of this study imposed constraint on the variety of these sequences. That is, the measure of variety used in this study was always less than the maximum which would equal $\log_2 6$ bits or $\log_2 4$ bits, depending on whether all six behaviors or only the four agonistic patterns L, O, F, and BS were considered. A measure of

variety associated with these fights has been calculated by using the following equation of Shannon and Weaver (1948):

$$H(X) = - \sum p(i) \log_2 p(i)$$

If X is a classification with categories i and associated probabilities p(i), then the information content of X is given by the above equation (Quastler, 1958). H is the entropy or uncertainty at each step of the sequence of events. As Pielou (1966) has pointed out, H is an estimate rather than an exact measure of uncertainty.

This quantity (H) was estimated from the intra-individual sequences of behavior for each experimental fish, and an AOV was computed on these entropy values. Since this quantity is a function of both total number of states and the variety of states, an AOV was also performed on these data (Appendix A, Variables 39, 41, and 42). A separate analysis was conducted on the variety of sequences of behavior using only the four agonistic behaviors L, O, F, and BS. The results of this data are presented in Appendix A under Variables 40, 43, and 44.

In both cases, the variety and entropy of these sequences seems to be strongly influenced by the experience factor (B) and the time-since-experience factor (D), and to a lesser extent by residency (A) and size (C). Only subordinate-experienced fish seem to be affected by a residency factor and then only 24 hr after their previous experience (Appendix B, Tables L and LI). The residency, experience, and time (ABD) interaction for H(4) clearly indicates this point (Appendix B, Table LII); and the ABD interaction of H(6), while not significant, follows this same pattern. Subordinate-experienced fish show fewer total

behaviors (Variables 42 and 44), fewer different types of behavior (Variables 41 and 43), and lower entropy values (Variables 39 and 40) than their dominant-experienced counterparts.

The possibility of a size and time interaction is seen in the significant CD interaction for H(6) and H(4) of Appendix A. Two-way Tables LIII and LIV of Appendix B indicate that the entropy of larger fish is not influenced by the length of time since their last encounter but that smaller fish show an increase in entropy with an increase in time-since-last-encounter. Chapter VII will treat this phenomenon in more detail.

Coefficients of Variation for Related Measures

As is true in most behavioral studies, considerable variation exists among experimental units. The coefficients of variation (C.V. = S/X) of the 44 variables of this experiment are presented in Appendix A. The C.V.'s ranged from 17.5% for Variable 39, H(6), to 148.0% for Variable 38, fin tugging duration/min by a fish's opponent. The C.V.'s of rate variables were slightly lower than those of duration. C.V.'s on variables for an experimental fish's opponent had the same magnitude as the C.V.'s of the test animal itself. Measures taken on the former should not be directly influenced by certain experimental parameters since none of these animals was subjected to a pretest experience factor nor any time-since-experience factor. Yet, in most cases they behaved as if they had been treated, thus some sort of "behavioral mimicry" or "action-reaction" phenomenon occurred. Finally all measures which were corrected for varied fight length showed reduced coefficients of variation.

CHAPTER VII

THE OUTCOME AND DYNAMICS OF PAIRED DOMINANCE ENCOUNTERS

The data from Experiment I suggested that relative size between fish may not be a critical factor in initial encounters of a dominance relationship, provided size differences were not extreme. The size effects in this experiment, however, were confounded with several other parameters, e.g., residency and prior experience. Experiment II clearly demonstrated that relative size does affect both the outcome and duration of dominance encounters when differences are in the range of 3 to 5 mm, but few behavior measures were influenced by size. Differences due to changes in the relative S.L. between fish could not be evaluated by this design. Furthermore, Experiments I and II provided no information regarding the role of particular behavior patterns on the outcome of encounters.

Experiment III was conducted to test the following hypotheses:

1. Bout outcome and bout duration are functions of relative size.
2. In dominance encounters, winning fish exhibit different patterns of behavior than losing fish exhibit.

Finally, the data from this experiment were used to provide information on temporal patterning and sequencing of fighting behaviors.

Effect of Size on Bout Outcome and Duration

Thirty-five of 41 bouts in Experiment III involved relative standard length differences ($1 \text{ mm} < \Delta S.L. < 5 \text{ mm}$); the remaining six pairs

of fish were the same size. Larger fish won a significantly greater number of these bouts than smaller fish (28 out of 35; Chi sq = 12.6, df = 1, "p" exceeds .005 level). It was hypothesized that winning might be a positive function of ΔS.L. Figure 4 represents the percentage of larger fish defeating smaller fish when successive classes of ΔS.L. are pooled. There is an indication that winning is a positive function of relative size difference and becomes a significant factor when a fish is 2 to 3 mm larger than his opponent. The distribution of winners which were larger or smaller than their opponents in each size category is shown in Table LV. A variance test for homogeneity of the binomial over these five classes, however, reveals no significant differences among classes (Chi sq = 4.58, df = 4, $.50 > p > .25$).

TABLE LV

THE NUMBER OF WINNERS LARGER OR SMALLER THAN THEIR OPPONENTS

	Δ S.L. in Millimeters					
	1	2	3	4	5	Total
S.L. W > L	5	7	5	4	7	28
S.L. W < L	2	3	0	2	0	7

If the absolute sizes of winners and losers are treated as random variables and the null hypothesis $\mu_D = 0$ is tested, it can be shown that winners of these 41 pairs were significantly larger than their partners (t = 4.33, df = 40, p exceeds the .001 level). The average

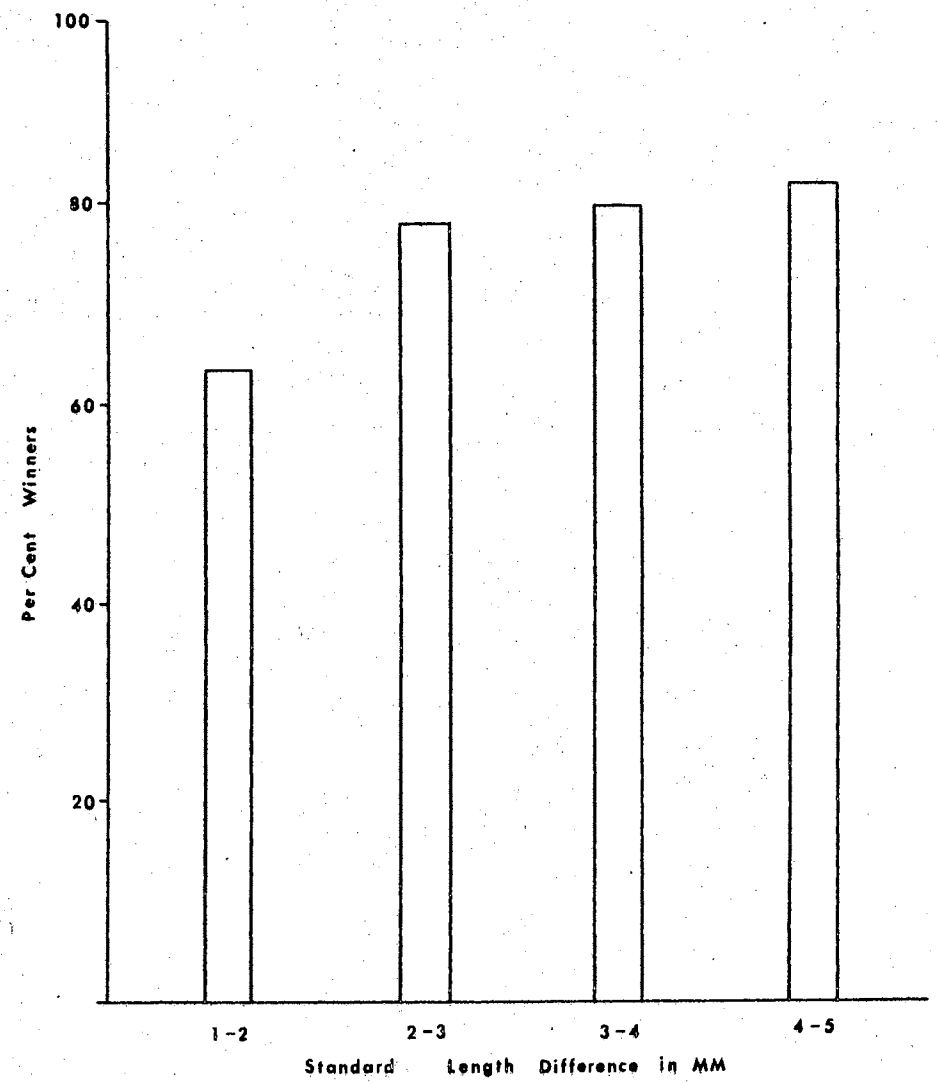


Figure 4. Percentage of larger fish defeating smaller opponents in Experiment III when classes of Table LV are successively pooled

winner was 55.4 $\pm$ .4 mm, and the average loser, 53.8 $\pm$ .4 mm in standard length. The relative size effects suggested by Experiment II are thus confirmed.

Fighting durations were fitted to the regression model

$$Y = b_0 + b_1 \Delta X,$$

where b_0 represents an overall mean duration, b_1 is the regression coefficient of the difference in standard length on bout length in minutes, ΔX is the difference between the S.L. of the winners and losers, and only $\Delta X > 0$ were considered. The model generated was

$$Y = 14.90 - .55 \Delta X,$$

and the hypothesis H_o: $b_1 = 0$, was not rejected at the .05 level. The raw data are plotted in Figure 5 and show two extremely large values for the 4 and 5 mm classes, respectively. Analysis without these two values does reject the null, indicating that relative size may indeed influence bout duration in dominance encounters. As will be shown subsequently, the absolute size of a fish did not influence bout duration.

Behavioral Differences Between Winning and Losing Fish

The behavior measures used in the factorial experiment were also recorded in these paired encounters. Differences in these measures between winning and losing fish are presented in this section along with an evaluation of their contribution to a "dominance vector."

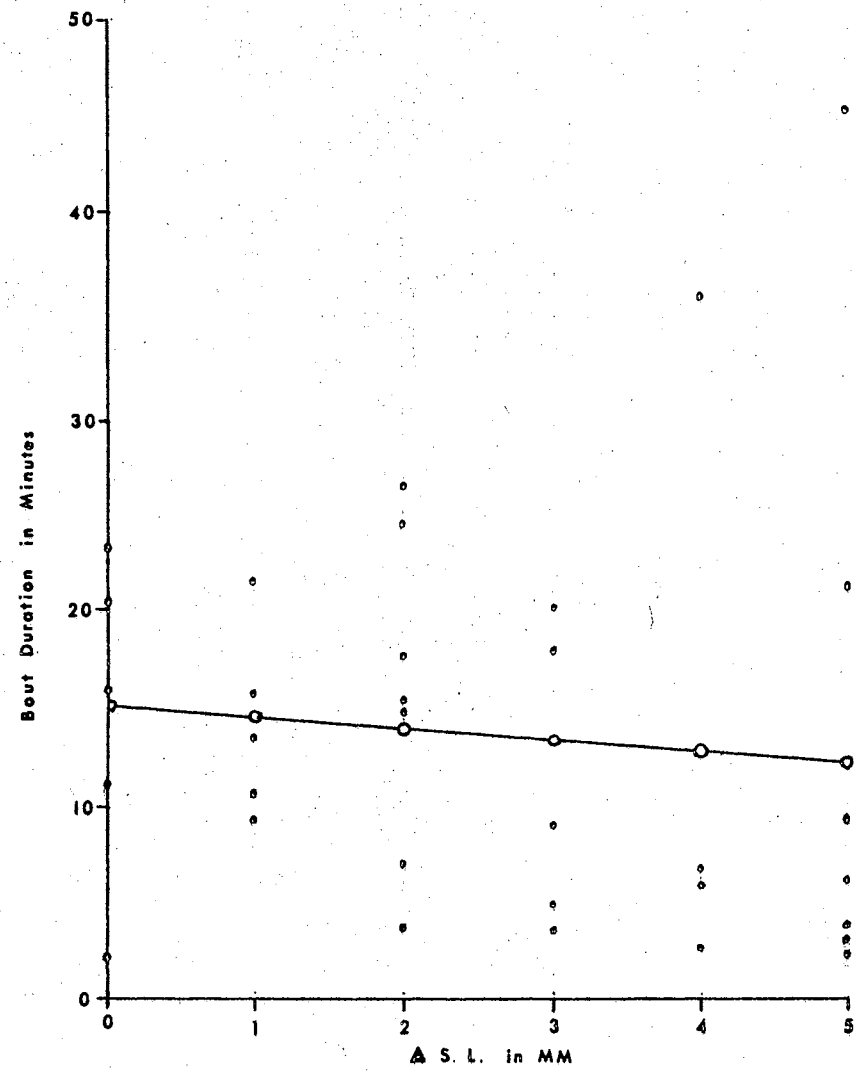


Figure 5. The linear regression of relative size on bout duration

The Linear Discriminant Function

A multivariate technique for studying the extent to which different populations overlap or diverge from one another was used initially to analyze the differences in behavior between winners and losers. The linear discriminant function is a single test of the null hypothesis that winners and losers have the same means with respect to all the measurements involved (Snedecor and Cochran, 1967). Briefly, this technique calculates a vector (Z-score) from the linear combination of a number of related measurements made on each of two groups and computed from the greatest of all squared univariate t-statistics from the linear compounds of the responses. Morrison (1967) points out that the ". . . actual linear compound with the greatest critical ratio is called the linear discriminant function, . . ." The Mahalanobis Distance Squared is a measure of the overlap between vector scores of the two groups. The greater this value becomes, the more divergent are the two groups. Figure 6 is a frequency distribution of Z-scores and illustrates the divergence of the vectors of winners and losers where the vector includes the following 11 variables previously defined in Chapter III:

$L^{F}/_{M}$, $L^{D}/_{M}$, $O^{F}/_{M}$, $O^{D}/_{M}$, $F^{F}/_{M}$, $F^{D}/_{M}$, B/BS, B/M, BS/M, S.L., and H(6).

The Mahalanobis Distance Square for this data was 1.51 and the F-value (2.46, df = 11,70) exceeded the .05 level.

The discriminant function model is represented as follows:

$$Z = L_1 X_1 + L_2 X_2 + \ldots + L_i X_i + \ldots + L_n X_n,$$

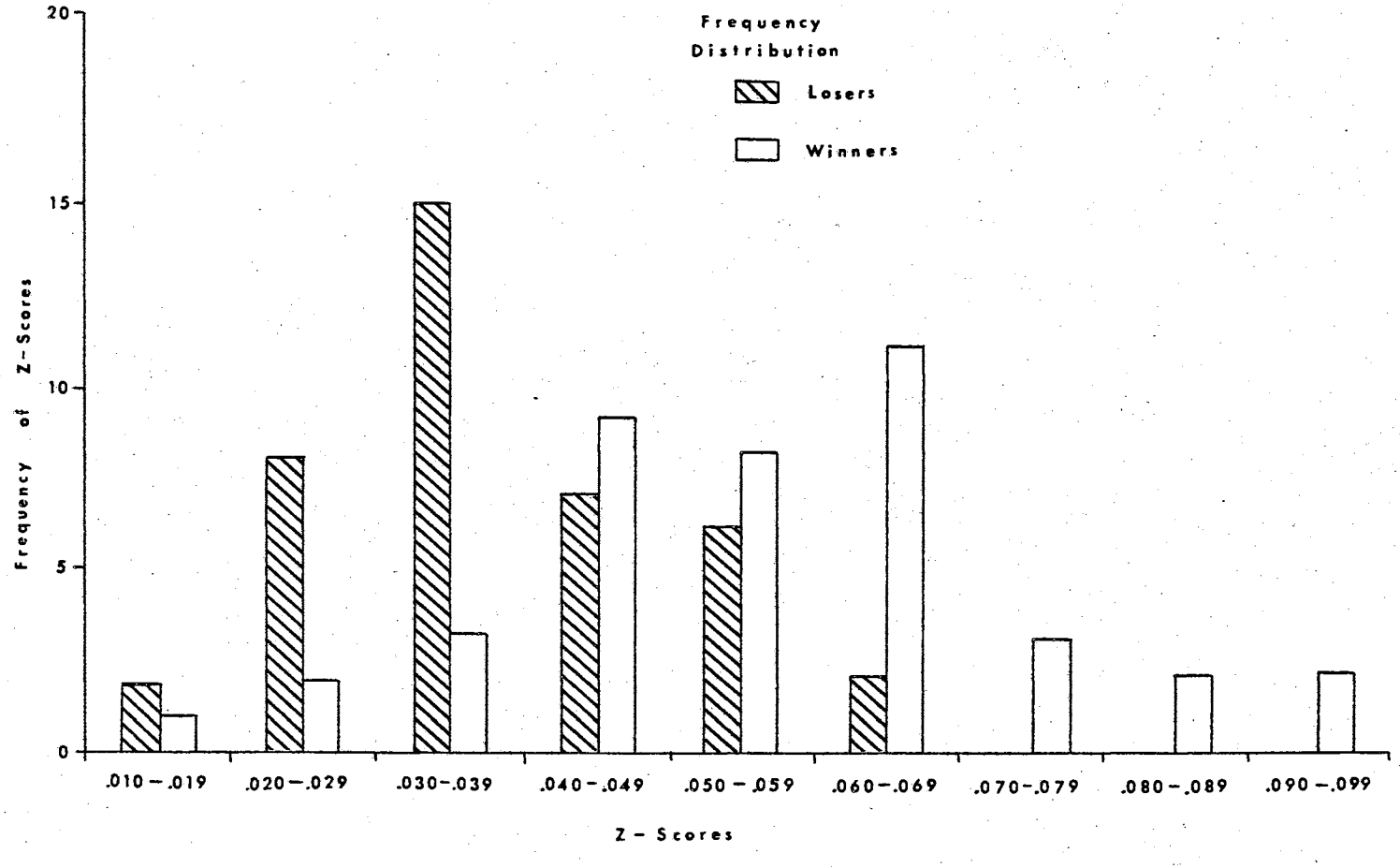


Figure 6. The divergence of vector scores (Z) between winners and losers (n = 41)

where L_i is the i-th variable coefficient and X_i is the i-th variable. Morrison (1967) points out that if the variances of the responses are nearly equal, these coefficients (L_i) in the vector give the relative importance of each variable in the F-statistic. The variance of rate measures for lateral displaying, opercle spreading, fin tugging, biting sessions, surfacing, pausing, and the entropy H(6) associated with these measures was nearly equal. The relative importance of these measures in determining the outcome of a bout was based on the absolute magnitude of their discriminant function coefficient. The linear discriminant model for this analysis was found as follows:

$$Z = -0.0066(L) + 0.0086(O) + 0.0407(F) - 0.0008(BS) + 0.0009(S) + 0.0018(P) - 0.0114(H).$$

The Mahalanobis Distance Square was .6548 and the F-value (1.77, df = 7,74) exceeds only the .25 level. The two groups are not discriminant based on this model, and the smaller value for the Mahalanobis Distance Square indicates that this model is less discriminating or overlaps more than the first model presented, i.e., the model with 11 variables. Table LVI represents a series of models which were tested using combinations of these 7 variables, and the rank of the absolute value of the variable coefficients (L_i) are indicated. From this analysis it can readily be seen that the function becomes significant in discriminating winners and losers when the two variables S/M and P/M are deleted from the model. Furthermore, the rank order of the variables (F > H > O > L > P > S > BS) in discriminating winners and losers holds in all but one case.

TABLE LVI

RANK ORDER OF SEVERAL VARIABLE COEFFICIENTS (L_i) FROM SIX LINEAR DISCRIMINANT FUNCTION MODELS

Rank of Variable Coefficients	F	Sig. Level	Mah. D. Sq.
F > H > O > L > P > S > BS*	1.773	.25	.654
F > H > O > L > S > BS	2.084	.10	.650
F > H > O > L > P > BS	2.096	.10	.654
F > O > L > P > BS > S	2.050	.10	.640
F > H > O > L > BS	2.533	.05	.650
F > O > L > BS	3.110	.025	.630

*L, O, BS, F, S, and P were defined in Chapter III. H is the entropy associated with these states. H is in bits while L, O, BS, F, S, and P are frequency per minute measures.

A second set of measures of the four agonistic behaviors (L, O, F, and BS) was calculated using L, O, and F duration per minute and the number of bites per bite session (B/BS). The discriminant coefficients (L_i) for these variables follow the rank order:

$$F^{D/}{}_{M}\ (.00349) > L^{D/}{}_{M}\ (.00046) > B/BS\ (.00031) > O^{D/}{}_{M}\ (.00021)$$

The F-value (2.78, df = 4,77) exceeds the .05 level for this analysis. The variances of these measures are approximately equal and seem to confirm the unequivocal importance of fin tugging as a determinant of bout outcome.

The overall rank ordering of all 11 measures of the initial model indicates that frequency measures ranked higher than duration measures. The original model shows greater separation of Z-scores than any other

model based on the Mahalanobis Square Distance. It should be noted, however, that the efficiency of such general comparisons is less when variables show some correlation as do some of the initial analyses (Snedecor and Cochran, 1967).

Differences Between Winners and Losers

A student's t-statistic for paired samples has been calculated for each response variable, and the null hypothesis $H_o: \mu_D = 0$ was tested. The data have been summarized in Table LVII. Mean values $\pm$ S.D. for winners and losers, the calculated t-statistic, and an indication of significance or probability level exceeded are presented. Only fin tugging rate and duration per minute are unequivocally significant. The number of bite sessions per minute approaches the 0.10 level, and the entropy associated with the frequency of L, O, F, BS, S, and P approaches the .05 level of significance. The coefficients of variation were about 1/4 to 1/3 less than those of the factorial experiment except for the three biting variables. Coefficients of variation for B/BS, B/M, and BS/M were of the same magnitude in both experiments of Phase III. The average duration per act for L, O, and F were compared between winners and losers by the Wilcoxon signed rank test; and no significant differences were indicated (Z 1.96, M = 41).

Correlation Among Behaviors in Dominance Encounters

Several correlations exist among the measures employed in this study. The intra-individual correlation coefficients among 13 variables are shown in Tables LVIII and LIX for winners and losers,

TABLE LVII

DIFFERENCES BETWEEN WINNERS AND LOSERS FOR 13 VARIABLES ASSOCIATED WITH THE BEHAVIOR OF DOMINANCE ENCOUNTERS

Variable*	Mean + S.D.		t-Cal	Probability Exceeded
	Winner	Loser		
L Rate	2.15 ± .68	2.26 ± .63	1.300	N.S.**
L D/M	23.64 ± 8.42	25.55 ± 6.56	1.255	N.S.
O Rate	.68 ± .50	.68 ± .48	.019	N.S.
O D/M	2.53 ± 2.44	2.90 ± 2.76	.626	N.S.
F Rate	.42 ± .33	.22 ± .22	4.050	.001
F D/M	3.33 ± 3.02	1.59 ± 1.79	4.486	.001
B/BS	3.98 ± 2.48	4.02 ± 2.04	.088	N.S.
B Rate	7.16 ± 4.22	7.35 ± 4.84	.268	N.S.
BS Rate	1.94 ± .85	1.72 ± .75	1.507	.2
S Rate	.62 ± .35	.63 ± .36	.335	N.S.
P Rate	.86 ± .56	.86 ± .48	.110	N.S.
Entropy, H(6)	2.17 ± .16	2.10 ± .22	1.774	.1

*L, O, F, BS, S, and P rates are frequencies per minute, while H(6) is in bits.
**N.S. = Not Significant

TABLE LVIII

INTRA-INDIVIDUAL CORRELATION COEFFICIENTS FOR
WINNERS OF DOMINANCE ENCOUNTERS

L-Rate	L Dur/M	O-Rate	O Dur/M	F-Rate	F Dur/M	B/BS	B-Rate	BS-Rate	S.L.	S-Rate	P-Rate	H(6)
L-Rate	.576*	.311	.014	.163	.045	.064	.122	.210	-.278	.300	-.224	.070
	L $\frac{Dur}{Min}$	.032	-.164	.140	.094	.332	.214	.170	-.216	.288	-.472	.096
		O-Rate	.554	-.170	-.196	-.288	-.196	.100	-.209	.002	.056	.235
			O $\frac{Dur}{Min}$	-.112	-.150	-.223	-.256	-.088	.060	-.253	.150	.198
				F-Rate	.838	-.029	.372	.416	.081	.082	-.166	.532
					F $\frac{Dur}{Min}$	-.015	.338	.400	.025	.104	-.288	.542
						B/BS	.640	-.190	-.157	-.007	-.247	-.215
							B-Rate	.389	-.078	.302	-.437	.234
								BS-Rate	-.007	.388	-.260	.523
									S.L.	-.020	-.222	-.063
										S-Rate	-.554	.370
											P-Rate	-.284

*The .05 and .01 levels for r-tabulated (df = 39) are .308 and .398, respectively.

TABLE LIX

INTRA-INDIVIDUAL CORRELATION COEFFICIENTS FOR
LOSERS OF DOMINANCE ENCOUNTERS

L-Rate	L Dur/M	O-Rate	O Dur/M	F-Rate	F Dur/M	B/BS	B-Rate	BS-Rate	S.L.	S-Rate	P-Rate	H(6)
L-Rate	.334*	.284	.062	-.003	.101	-.024	-.008	.090	-.262	.067	.103	-.053
	L $\frac{Dur}{Min}$	.140	-.016	-.264	-.168	.162	-.052	-.144	-.150	-.164	-.194	.047
		O-Rate	.813	-.214	-.264	.108	.094	.150	-.244	-.068	.032	.392
			O $\frac{Dur}{Min}$	-.142	-.204	-.079	-.075	.016	-.196	-.132	.232	-.334
				F-Rate	.896	.102	.382	.600	.182	.232	-.187	.440
					F $\frac{Dur}{Min}$	.016	.256	.528	.126	.250	-.166	.362
						B/BS	.798	.288	.142	.268	-.574	.372
							B-Rate	.718	.284	.342	-.588	.376
								BS-Rate	.270	.320	-.368	.527
									S.L.	.146	-.240	.146
										S-Rate	-.478	.316
											P-Rate	-.339

*The .05 and .01 levels for r-tabulated (df = 39) are .308 and .398, respectively.

respectively. Measures of rate and duration per minute for both winners and losers are positively correlated for L, O, and F; B/BS is positively correlated with B/M but not with BS/M; and B/M is positively correlated with BS/M. This was expected since the factorial experiment showed that a particular factor influenced rate and duration measures in the same way. The correlation matrices for winners and losers show several other similarities. Fin tugging rate and duration is correlated with bites per minute and bite sessions per minute ("r" for $F^{D}/_{M}$ and B/M of losers just fails to reach the .05 level). Bites per session is highly correlated with bites per minute in both groups. Since B/BS was not correlated with BS/M, it is suggested that the number of bites a fish shows is dependent upon both the frequency of biting sessions and also the number of bites in a session, but that the two variables may be influenced by different mechanisms. Thus, while B/M and BS/M are correlated, they are not equivalent measures.

Pauses greater than 4 sec duration (P/M) were negatively correlated with bite rate and surfacing rate. Surfacing rate is probably positively correlated with biting rate and bite session rate.

Some apparent differences in the two matrices are present. Opercle spreading rate was not correlated with the entropy H(6) values for winners but positively correlated for losers. Bites per session (B/BS) were negatively correlated with H(6) in winners but positively correlated in losers.

In order to determine whether agonistic behavior rates were temporally organized, their correlations with bout length were determined for winning fish. Only B/M and BS/M were significantly correlated with fighting duration ($n = .458$ and $r = .630$, $df = 39$).

While no measures were correlated significantly with fish size (S.L.), BS/M and S/M of winners were slightly negatively correlated with S.L.; however, these two measures were positively correlated in losers.

Behavior Sequences

Intra-individual and inter-individual sequences of behavior in dominance encounters are considered in this section. A contingency analysis on two-act sequences of behavior is presented. The method used to obtain two-act sequences follows that of Nelson (1964), Hazlett and Bossert (1965), Miller and Hall (1968), and Dingle (1969). As an example, the intra- individual sequence of ...L–O–B–S–L–... was broken down into the four 2-act sequences L–O, O–B, B–S, and S–L. Two matrices, one for each fish, were thus produced from each fight. The inter-individual sequences,

Fish No. 1: ...L———O–L———B...
Fish No. 2: ....O–L————B——...

also produces two matrices, where one first considers the initial acts of Fish No. 1 and the following acts of Fish No. 2 (...L–O, L–L, O-No Change, L–B...). The second matrix results from the initial acts of Fish No. 2 and following acts of Fish No. 1 (...O–NC, L–O, L–L, B–B...).

Only states or acts which are mutually exclusive are incorporated into this analysis. For example, tail beating occasionally occurs simultaneously with lateral displaying and therefore is not considered in this data processing. Six behaviors or states (L, O, F, BS, S,

and P) were a part of the intra-individual analysis, while an additional category of "no change" (NC) is added in the inter-individual sequences. If a particular behavior by one fish occurred with no visible change in the ongoing behavior of the other fish, a condition of NC was recorded.

Intra-Individual Sequences

The frequency distribution of 3816 intra-individual, two-act sequences pooled from the 41 winning fish of Experiment III is shown in Table LX. The equivalent data from 3596 two-act sequences for their partners is present in Table LXI. The distribution of following acts (row totals) was used to calculate the expected values enclosed in brackets.

Column totals, i.e., the distribution of all initial acts regardless of the following behavior, were compared between winners and losers by Chi sq. The same test was applied to the following behavior totals. Significant differences were found in both cases. Opercle spreading was found to be both a preceding and following behavior more often in losers than in winners. Fin tugging showed the opposite trend. Lateral displaying was an initial behavior of two-act sequences more often in losers than in winners. Results from such analysis are probably due to a greater or lesser absolute frequency of occurrence for fin tugging and reveals no new information, but the above relationships for L and O seem to merit further investigation.

By comparing the observed and expected values of Tables LX and LXI, the deviation from randomness or a measure of independence can be estimated for any two-act sequence. Hazlett and Bossert (1965)

TABLE LX

OBSERVED AND EXPECTED FREQUENCY DISTRIBUTION OF 3816 INTRA-INDIVIDUAL TWO-ACT SEQUENCES FOR 41 WINNING FISH

Following Act	Initial Act						
	L	O	F	BS	S	P	Total
Lateral Display (L)	107 (370)*	136 (99)	84 (90)	459 (388)	235 (130)	173 (120)	1194
Opercle Spread (O)	105 (96)	7 (26)	14 (23)	145 (99)	16 (33)	29 (30)	316
Fin Tug (F)	18 (90)	4 (24)	6 (22)	238 (193)	11 (32)	14 (29)	291
Bite Sessions (BS)	641 (380)	122 (101)	124 (92)	63 (394)	148 (133)	150 (122)	1248
Surface (S)	239 (122)	32 (32)	27 (30)	83 (126)	2 (42)	10 (39)	393
Pause (P)	75 (116)	16 (31)	32 (28)	242 (120)	3 (40)	6 (37)	374
Total	1185	317	287	1230	415	382	3816

*In this and succeeding tables, numbers in parentheses are expected values.

TABLE LXI

OBSERVED AND EXPECTED FREQUENCY DISTRIBUTION OF 3596 INTRA-INDIVIDUAL TWO-ACT SEQUENCES FOR 41 LOSING FISH

Following Act	Initial Act						
	L	O	F	BS	S	P	Total
Lateral Display (L)	137 (408)	156 (125)	43 (49)	469 (370)	211 (129)	184 (118)	1200
Opercle Spread (O)	134 (128)	7 (40)	6 (16)	191 (116)	16 (40)	25 (37)	379
Fin Tug (F)	24 (50)	1 (15)	3 (6)	112 (44)	3 (16)	3 (14)	146
Bite Sessions (BS)	576 (385)	159 (118)	63 (46)	47 (349)	154 (118)	135 (112)	1134
Surface (S)	258 (130)	36 (40)	14 (16)	66 (118)	3 (41)	5 (37)	382
Pause (P)	93 (120)	17 (37)	19 (14)	223 (109)	1 (38)	2 (34)	355
Total	1222	376	148	1108	388	354	3596

described sequences which occurred more frequently than expected as "directive" and those occurring less often than expected as "inhibitive," i.e., a preceding behavior may be directive or inhibitive on a following behavior in a statistical sense. As an example, compare the observed and expected values for the sequence L—L in Table LX (107 vs. 370). Lateral displaying clearly follows lateral displaying less often than expected, based on the overall distribution of L as a following act. In this respect, intra-individual sequences differ little between winners and losers. However, a salient feature of both matrices is that a particular behavior follows itself less often than expected in each case (see the diagonal terms in the matrices). The degree to which a behavior is directive or inhibitive on a following behavior can be estimated by the Chi sq value associated with that sequence.

Finally, the conditional probabilities for the occurrence of lateral displaying and biting following particular behaviors differs between winners and losers. The probability, $P(E_1|E_2)$ is greater in losers than in winners when E_2 is a lateral display or pause and when E_1 is a lateral display, i.e., given that a fish has just displayed or paused, losers are more likely to L than are winners. These values were as follows:

$$p(L_{loser}|L_{loser}) = .112,\ p(L_{winner}|L_{winner}) = .090;$$
$$p(L_{loser}|P_{loser}) = .520,\ p(L_{winner}|P_{winner}) = .453.$$

The opposite trend is shown for sequences where E_1 = BS. Winners tend to bite following an L or P more often than do losers. The $p(E_1|E_2)$ for these sequences were as follows:

$$p(B_{loser}|L_{loser}) = .471,\ p(B_{winner}|L_{winner}) = .540;$$
$$p(B_{loser}|P_{loser}) = .381,\ p(B_{winner}|P_{winner}) = .393.$$

Certain directive and inhibitive relationships of these matrices will be discussed in the following chapter.

Inter-Individual Sequences

In the preceding section, behaviors were treated independently of the role that an opponent's behavior might have on their occurrence. Inter-individual relationships were analyzed to evaluate the influence of a conspecifics behavior on the partner. The two-act, inter-individual sequences from the 41 dominance encounters of Experiment III are shown in the matrices of Table LXII for initial acts of winners and in Table LXIII for initial acts of losers. As in the previous section, the distribution of following acts was used to calculate expected values.

Initial-act distributions differed significantly between winners and losers (Chi sq = 58.52, df = 5). Lateral displays and opercle spreads were more often initial behaviors in losers than in winners, while fin tugging was a preceding behavior more common to winners. Biting, surfacing, and pausing were apparently not different. When following-act totals were compared by the same method, winners showed significantly less O and P states but a greater-than-expected number of F, BS, and NC states.

A lack of independence obviously exists between certain behavior sequences in Tables LXII and LXIII (compare the observed and expected values). Again, certain behaviors can be described as inhibitive or

TABLE LXII

OBSERVED AND EXPECTED FREQUENCY DISTRIBUTION OF 4574 INTER-INDIVIDUAL TWO-ACT SEQUENCES FOR WINNERS AND LOSERS

Following Act by Loser	Initial Act by Winner						
	L	O	F	BS	S	P	Total
Lateral Display (L)	419 (436)	33 (78)	36 (74)	407 (303)	100 (83)	76 (96)	1071
Opercle Spread (O)	279 (132)	12 (24)	1 (22)	13 (92)	12 (25)	8 (29)	325
Fin Tug (F)	72 (50)	0 (8)	11 (8)	18 (35)	7 (9)	14 (10)	122
Bite Sessions (BS)	549 (353)	14 (61)	57 (60)	129 (245)	67 (67)	51 (78)	867
Surface (S)	138 (132)	32 (23)	31 (22)	56 (91)	52 (25)	14 (28)	323
Pause (P)	159 (103)	0 (18)	34 (18)	28 (72)	7 (20)	26 (22)	254
No Change	248 (656)	241 (117)	148 (112)	644 (456)	110 (125)	221 (144)	1621
Total	1864	332	318	1295	355	410	4574

TABLE LXIII

OBSERVED AND EXPECTED FREQUENCY DISTRIBUTION OF 4307 INTER-INDIVIDUAL TWO-ACT SEQUENCES FOR LOSERS AND WINNERS

Following Act by Winners	Initial Act by Losers						
	L	O	F	BS	S	P	Total
Lateral Display (L)	428 (422)	29 (86)	20 (36)	298 (252)	113 (78)	72 (85)	960
Opercle Spread (O)	199 (100)	15 (20)	1 (8)	5 (60)	5 (18)	2 (20)	227
Fin Tug (F)	172 (86)	0 (18)	6 (7)	5 (52)	6 (16)	8 (17)	197
Bite Sessions (BS)	565 (412)	22 (84)	27 (36)	181 (246)	74 (77)	70 (83)	939
Surface (S)	129 (128)	33 (26)	19 (11)	50 (76)	44 (23)	16 (26)	291
Pause (P)	185 (125)	14 (26)	14 (10)	32 (74)	15 (23)	25 (25)	285
No Change	212 (618)	274 (126)	76 (53)	560 (370)	97 (116)	189 (124)	1408
Total	1890	387	163	1131	354	382	4307

directive upon the subsequent behavior of opponents. To illustrate this point, observe that the L_{winner}——BS_{loser} sequence occurs much more often than expected (Table LXII); and L would be considered directive on BS. Winners and losers follow similar patterns. As a rule then, particular two-act sequences are either directive or inhibitive in both winners and losers in the same magnitude and direction. Variations from this pattern are reflected in the conditional probabilities associated with the occurrence of certain events.

Three conditional probabilities seem to merit inspection. Ultimate winners are more likely to fin tug a lateral displaying partner than vice versa, i.e., $p(F_{winner} | L_{loser}) = .091$ and $p(F_{loser} | L_{winner}) = .038$. A somewhat similar relationship exists in BS–BS two-act sequences. Winners are more likely to bite upon being bitten than are losers, $p(BS_{winner}\ BS_{loser}) = .160$; $p(BS_{loser}\ BS_{winner}) = .100$. Lateral displaying following BS sequences show a relationship opposite to the above, i.e., $p(L_{winner} | BS_{loser}) = .263$; $p(L_{loser} | BS_{winner}) = .314$. Since fin tugging rate was shown to differ significantly between winners and losers, the expected and observed values were compared for all acts following fin tugs. It was found that fin tugging by winners is directive on pausing by losers but the converse relationship showed independence.

The Uncertainty Associated with Fighting Sequences

In Chapter VI it was shown that prior dominance-related experience strongly influenced the number of different types of behavior that a fish exhibited during subsequent fighting. A measure of uncertainty associated with each step in a fighting sequence was also responsive to

this experience factor. This "uncertainty factor" or entropy has further been shown to be greater among winning fish than losers.

The relationship between entropy of dominance encounters and relative size has been investigated in this study. The absolute size of fish in this study was not correlated with fighting entropy (Table LVIII and LIX). It seemed reasonable, however, to suspect that uncertainty at each step might be a function of relative size. The average entropy H(6) for 11 winners and 11 losers in each of two different relative size ranges was compared. Figure 7 shows that winners exhibit greater uncertainty as stated previously. It also shows that this entropy seems to be a negative function of standard length difference, i.e., the greater the difference in size between opponents the less uncertainty will be shown by both winners and losers.

The simple linear regression model of relative size effect on entropy H(6) of 28 winners was

$$Y = 2.3062 - .0440\Delta X,$$

where a 1 mm $< \Delta X <$ 5mm range of winners larger than losers was considered. The null hypothesis $b_1 = 0$ was not quite rejected at the .05 level.

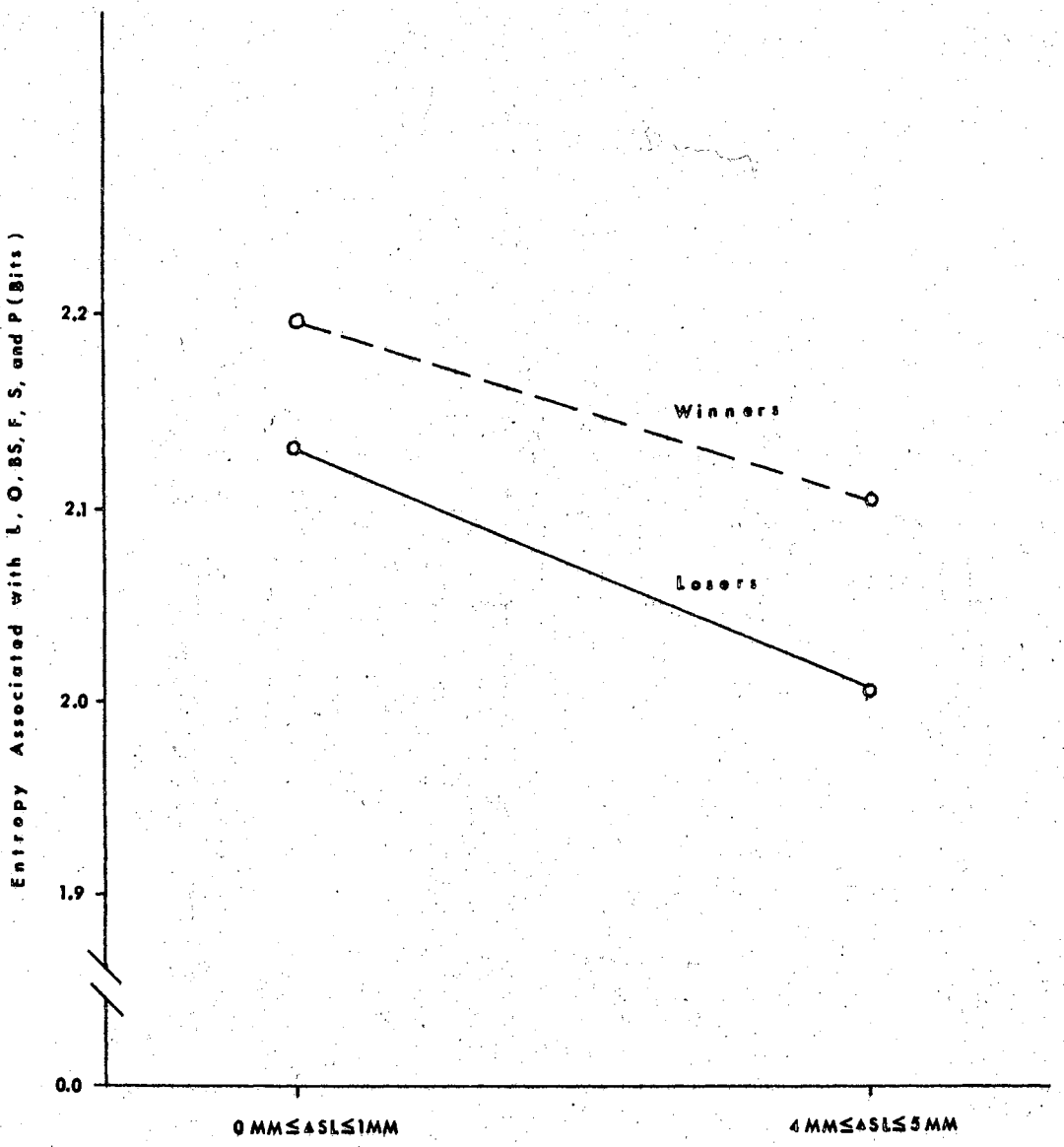


Figure 7. The influence of relative size of opponents on the entropy of fighting sequences (n = 11 pairs in each Δ S.L. class)

CHAPTER VIII

DOMINANCE ESTABLISHMENT—A SYNTHESIS OF THREE APPROACHES

Pairs of male blue gouramis usually establish a hierarchical relationship within the first 45 min of their association, generally as a result of mutual fighting. Occasionally, the fights are brief and one-sided, but some sort of mutual agonistic behavior always occurs. The discussion below will attempt to evaluate the relative significance of several factors previously shown to influence dominance and attendant activity, and will seek to develop a series of models which may clarify some of the relationships among them.

Three rather different types of studies have generally been conducted by students of social order in lower vertebrates. The first type investigates the relationships among parameters such as size, sex, and previous experience and the outcome of agonistic encounters. Many of the works cited in Chapter I fit this model. A second type considers the same parameters but determines their effects on the agonistic behaviors occurring in hierarchy fights rather than on outcome per se (see Dennis, 1970). Finally, a few studies (i.e., Braddock, 1955; Simpson, 1968; Miller and Miller, in press) consider the influence of particular behavior patterns on outcome or social structure. None of these works has attempted to combine the three approaches in synthesizing a general theory of dominance-determination; therefore, the

discussion below will seek to develop simple descriptive models based on each of the three types, then combine them to produce an overall model for dominance encounters.

Model I. Experimental Parameters Determining A Dominance Relationship

The effects of prior residency, relative size of opponents, previous dominance experience, time since last contact with a dominant or subordinate partner, and their first or second order interactions on the outcome of fights between pairs of blue gouramis have been evaluated previously (see Chapters V, VI, and VII).

Residency

Noble and Curtis (1939), Greenberg (1947), Braddock (1949), Baird (1968), and others have implied that familiarity with a given area gives a resident an advantage in dominance encounters in several teleost species. The accuracy of such a generalization for blue gouramis is questionable, since residents (occupants of a space for at least 24 hr) did not defeat non-residents significantly more often than non-residents defeated residents in Experiment I, nor was there a significant residency main effect in Experiment II for bout outcome. It should be mentioned, however, that size was a confounding variable in Experiment I. Two points support the postulation of a residency factor as a bout outcome determinant in this species. First, in the initial bouts of Experiment I, residency was a significant factor in one pairing type, i.e., where isolated fish were placed in aquaria with isolated residents. Second, inspection of the non-significant, 3-way

interaction between residency, experience, and time (ABD of Experiment II for bout outcome) suggests a tendency for residents to win more often than non-residents where these fish have had 24 hr to occupy that habitat without a dominant or subordinate partner. Since the prior experience factor was found to be unequivocally significant in regulating bout outcome, its potential role in masking the possible subtle influence of factors like residency must be considered. As time elapses after a previous dominance experience, the effect of the experience factor lessens and the modest advantage of being a resident may become measureable.

An alternate hypothesis might follow the idea that fish which occupy their environs in the absence of conspecifics either "build up" some tendency to dominate another fish or perhaps the "defeat" thesh-old for these fish is raised. However, it seems simpler to assume that these fish, in the absence of a partner to dominate or upon being free from domination, have more opportunity to become "familiar" with their environment. The behavioral effect may be due to a decrease in fearfulness produced by the initially strange environment. If a residency factor exists relative to bout outcome, it is subtle and clearly is influenced by a time function and can be readily masked by other factors like prior experience.

Size

While an earlier work (Frey and Miller, 1968) indicated that relative size was not an important determinant of fighting outcome, the present study shows that the relative size of opponents significantly influences dominance relationships. Larger fish tend to defeat smaller

opponents, as is true for several other teleosts (Braddock, 1945; Huck and Gunning, 1967; Baird, 1968; and Hadley, 1969). Other factors being equal, the probability of winning a fight seems to be a positive function of relative size. Data from Experiment II (p. 42-44) suggested that, like the residency factor, the influence of relative size becomes more prominent as the powerful inhibitory effect of being dominated wanes.

Prior Experience

The masking effects of the experience factor were mentioned above. In Experiment II, 78% of the dominant-experienced fish won encounters, while only 9% of the subordinate-experienced fish defeated controls. The F-statistic for this factor was highly significant and exceeded the next greatest factor sevenfold. Considering the magnitude of the influence of this factor, it is interesting to note that few people have studied previous experience as a determinant of hierarchical order or fighting outcome.

The data clearly show that while dominating another fish for 24 hr produces a slightly higher probability of winning a subsequent encounter, being dominated for 24 hr virtually eliminates the possibility of winning a subsequent encounter (p. 42-44). The inhibitory effects of being beaten thus seem most striking. Within 24 hr, however, even this factor wanes (if the dominant is removed); and other factors such as size begin to exert more influence.

Thus, ranking the importance of the residency (A), prior experience (B), and relative size (C) factors would produce the order:

B $\gg$ C $>$ A, initially, in determining the winner of a fight. Changes in relative importance of the factors may occur over a period of time, however, subsequent to the last encounter or experience.

Model II. Experimental Parameters Influencing Measures Associated with Dominance Establishment

Many of the behaviors occurring in these fights were shown to be affected by residency, size, experience, time since that experience, and interactions among these parameters (see Chapters V, VI, and VII).

Residency

While residency was shown to have a limited effect on the outcome of a bout, it significantly influenced the performance of the fish (Experiment II, p. 44-53). Residents tend to approach first, but this tendency is complicated by the effects of size. Fish larger than their opponents approach more readily when in a familiar environment and much less when they are non-residents (Experiment II, p. 44). Fish smaller than their opponents approach first about 50% of the time, regardless of residency.

Resident fish also opercle spread first slightly more often than their partners (controls), but non-residents show a greatly reduced probability of first occurrence for this pattern (16%; p. 45). Frequency and duration measures of opercle spreading were slightly greater in residents (p. 48). The residency, experience, and time (ABD) interactions suggest that depressed values for subordinate-experienced fish are due to a "fright component" associated with being dominated, which wanes significantly within 24 hr. Such fright-induced inhibition

can be re-established by the frightening effects of transfer to a strange environment (see Chapter VI and Appendix B, Table XXVIII). This idea is supported by the fact that ABD interactions were not significant in the opponents of these fish where no experience factor was involved. Thus, dominance state may influence the effect residency has on opercle spreading and other activities discussed below.

Resident fish usually bite first and fin tug first; but among the several quantitative measures associated with these two expressions of overt aggressiveness, only the number of bite sessions per minute were highly influenced by residency. The ABD interaction of this variable indicates that the residency effect is also liable to the influence of the dominance state (p. 49). Apparently, a fish must be free of domination in a home space for about 24 hr before the residency effect appreciably influences these activities.

Under such circumstances, residency influences not only the frequency and latency of the behaviors shown in these encounters, but also the measure of sequence uncertainty, or entropy (p. 53).

A "fright-residency" hypothesis may then be stated as follows: When the inhibitory effect due to prior experience of being dominated wanes sufficiently, a subordinate fish may respond to a conspecific in the same manner as would a dominant, resident fish at that time; but any additional fright input such as that due to an unfamiliar environment may inhibit normal fighting behaviors. Perhaps the residency factor may not be a positive effect due to environmental familiarity but rather a negative factor associated with unfamiliarity. Barlow (1961) implied that "new surroundings" produce a lowering of a "fright threshold" in Badis badis. There is no way to presently determine

whether "fright inhibition" is a unitary process or a more complex system. Clearly, both non-residency and subordination affect it, but the temporal pattern of their effects clouds the issue.

Prior Experience

The factor of paramount importance in the responses of these fish was the prior dominance experience factor. From Appendix A (of the 43 measures tested in Experiment II), it can be seen that the only variables not significantly affected by this parameter were first approach, first lateral display, first fin tug, surfacing rate, and pausing rate. Dominant fish or partners of these fish showed the highest values in all other cases.

Nearly all agonistic variables and the two entropy measures for the dominant-experienced fish were of the same magnitude whether this experience was 0 hr or 24 hr prior to an encounter. Values for dominated fish approached those of dominant fish after 24 hr of waning of inhibitory effects. Thus, based on responses, there is no evidence in support of an arousal phenomenon due to previous winning. An argument congruent with the foregoing "fright-residency" hypothesis seems more reasonable: The effect of dominating a fish does not result in a positive input for subsequent aggressiveness. Rather, the predominant factor which is relevant to this parameter and which is important in influencing subsequent behavior is the degree of inhibition of the dominated fish. The experience factor may, of course, result from defeating or being defeated, plus the maintenance of that relationship for 24 hr, rather than from the experience of winning or losing per se.

Short-term arousal processes due to the latter seem probable but cannot be evaluated by this data. It should also be remembered that the dominant-experienced fish won 78% of their subsequent encounters with non-experienced partners.

Although it seems impossible to obtain any direct measure of the effect referred to as fright, the relative influence of an unfamiliar environment (Factor A) or being dominated (Factor B) can be assessed for those fish fighting immediately after their previous dominance experience. Consider any variable from Appendix A for which a significant residency, experience, and time (ABD) interaction exists, e.g., the entropy associated with L, O, F, and BS (Appendix A, Variable 40 and also see Table LI) or the average O duration per display (Variable 17, and Table XXVII). The inhibitory influence of being dominated can be measured by

$$\Delta f[B_i] = A_1B_1D_1 - A_1B_0D_1,$$

and the inhibitory effect of an unfamiliar environment would equal

$$\Delta f[A_i] = A_1B_0D_1 - A_0B_0D_1,$$

where $\Delta f[B_i]$ and $\Delta f[A_i]$ are the decrements of variable i due to factors B and A; and $A_1B_1D_1$, $A_1B_0D_1$ and $A_0B_0D_1$ are the values found for those treatment combinations from the 3-way table of that variable. The relative inhibition due to being dominated can be calculated as:

$$\text{Per cent Inhibition} = \Delta f[B_i] \times (\Delta f[B_i] + \Delta f[A_i])^{-1} \times 100$$

while the relative inhibition due to an unfamiliar environment can be calculated as:

$$\text{Per cent Inhibition} = \Delta f[A_i] \times (\Delta f[B_i] + \Delta f[A_i])^{-1} \times 100.$$

Using the dimensionless variable entropy H(4), these indices of relative inhibition are 88.5% and 11.5%, respectively, for domination and residency. Using a variable with a considerably higher Coefficient of Variation such as O D/F, the indices are 87.4% and 12.6%, demonstrating unequivocally the greater effect of domination.

The influence of time-since-last-experience was shown in Chapter VI and also mentioned above. The effect of domination wanes significantly within 24 hr. While the nature of this waning process has not been investigated here in any detail, it is probably not completed by 24 hr because response values are not yet up to normal levels at that time. Although Barlow (1962) implied that the "background" of the fish involved in any encounter may influence the course of that encounter, few studies indicate the pre-test conditions of the fish involved; and only the work of McDonald, et al. (1968) on Lepomis cyanellus seems to have tested for the role of this variable. Confounding existed in their study, however, because their "pre-conditioning" measures were taken 6 hr after establishing a pair, while "post-conditioning" observations were recorded immediately after establishment. Their data clearly illustrates that in the former case a period of dominance maintenance was being evaluated while in the latter, the period of dominance establishment was in progress. A somewhat analogous confounding seems to exist in studies which ascribe changes in "aggression" to some duration of pre-testing isolation per se. Southwick and Ward (1968) concluded for Macropodus opercularis that an intermediate isolation period resulted in maximum aggressiveness.

Pal (1968) reported that longer periods of isolation from conspecific Macropodus cupanus resulted in increased aggressiveness. Such "isolation" effects may well be partly due to changes in the effects of "dominance factors" determined prior to isolation.

Size

Relatively few variables of this study were influenced by a size factor. As pointed out in Chapter VII, the absolute size of participants was not correlated with any of the measures associated with dominance encounters. Hadley (1969) found an absolute size factor to influence established groups of Lepomis megalotis, but Dennis (1970) found no such factor for Lepomis humilis.

Relative size is a more significant variable than absolute size. Barlow (1968) noted that in Etroplus maculatus, ". . . males attacked more when interacting with larger females, . . ." Most other references to relative size effects in the literature seem to concern only established groups, observed during a dominance maintenance phase. In the present study, male blue gouramis tended to bite more often when fighting a slightly larger male opponent than a slightly smaller partner (see Appendix A, Variable 9), though this trend may be masked by more powerful factors.

No other direct effect of relative size on behavior rates or durations was found in the data, i.e., no variable was significantly correlated with Δ S.L. The number of bite sessions per minute tends to decrease as the relative size differences between opponents becomes larger, but this trend may be due to a time dependent factor. Fights tend to be shorter as Δ S.L. increases (Figure 5), and it was pointed

out in Chapter VII that shorter fights have lower bite session rates. Thus, BS rate may be indirectly related to relative size. An increase in BS/M which occurs in longer fights may provide some evidence of a short-term arousal process occurring during fighting.

While relative size was not directly linked to behavior differences between opponents in fighting sequences, the uncertainty associated with these events (entropy) was shown to decrease for winners as they become progressively larger than their partners (Chapter VII). The winners in Experiment III (Figure 7) exhibited a greater amount of behavioral uncertainty than the losers, yet the AOV for the effect of size on entropy (Experiment II, Appendix A, Variables 39 and 40) was not significant. This seems to indicate that being larger or smaller in itself does not influence fighting entropy directly but that the uncertainty of sequences is related to the interplay between a relative size factor and the overall "dominance" state of a fish. As size differences increase, so does the advantage conferred to an individual in obtaining dominance.

Finally, it should be noted that the four factors tested here or other untested parameters may strongly influence agonistic behaviors in some unmeasured fashion. For example, it seems reasonable to suggest that a larger fish is more capable of inflicting physical damage to an opponent than could a smaller fish, yet no means of quantifying bite or fin tug intensity was possible.

Model III. Behavioral Variables Regulating Bout Outcome

During dominance encounters, it is usually quite difficult in this species to detect obvious behavioral differences between the ultimate

winner and loser. Simpson (1968) and Braddock (1955) found that both members of a pair of Siamese fighting fish tend to "keep in step" for most of the fight and only toward the end does the winner outstrip the loser in some display pattern. The only behavior in which the winner outstrips the loser in T. trichopterus seems to be fin tugging. During the course of a fight, fin tugging rate usually increases slightly in the ultimate loser but markedly in the winner.

There are several ways in which behavioral events might prove directive on bout outcome. Simpson (1968) stated that he did not feel that widely separate events influence the outcome of an encounter. His concept of bout determination implies that a bout would be terminated when a critical difference in some display rate was reached. The cumulative effects of intervening behaviors are not considered to be of direct significance. A second hypothesis might consider the cumulative noxious physical effects of the fight. Finally, the possibility that the outcome of a bout may actually be determined before the fighting nears a terminal stage should also be considered. In this case, the participants only continue to "act out" some pre-established stereotyped pattern.

The first hypothesis seems questionable in this species since some fights fail to include appreciable fin tugging (the only overt response which could qualify as an evaluator) by either fish. If physical damage is the criterion for cumulative deleterious effects, then the second hypothesis cannot account for bouts which are determined without body contact, i.e., bouts in which only displaying occurs. The third paradigm will be dealt with below.

In his formulation of a mathematical construct for hierarchical organization of animal societies, Landau (1951a) assumed that ". . . each member is characterized by an 'ability vector,' $X_j = (X_{j1}, X_{j2}, \ldots, X_{jn})$. The X_{ja} measures the individual characteristics which make for dominance such as size, . . . etc." He also noted that if dominance probability is the weighted sum of several independent components, as the number of components increased, the probability of establishing a dominance outcome would decrease. Z-scores of the linear discriminant model of Chapter VII of this study do not represent ability vectors; but it was found that Z-scores were influenced principally by two variables, fin tugging and behavioral uncertainty.

The analysis of behavior measures influencing fighting outcome is considered here in terms of a dominance vector. This vector is not comparable to Landau's "ability vector," which is a function of experimental parameters such as size. The dominance vector is a function of behavior-related variables such as biting rate, F-rate, or entropy. All of its components cannot possibly be determined from these data, but many of its probable components can be postulated. Thus, the dominance vector, $F(X)$, is quite likely a complex function of several components, $X_1, X_2, \ldots X_i \ldots X_n$. These components are in turn functions of certain parameters such as size, experience, etc., whose interrelationships will be the subject of the next section. For the model under consideration, however, we will concern ourselves with the X_i-components of the vector.

In a recent paper, Kalmus (1969) has reviewed some of the principles of game theory as they apply to social behavior. He noted that many ". . . kinds of animal interactions are analogous to a zero sum

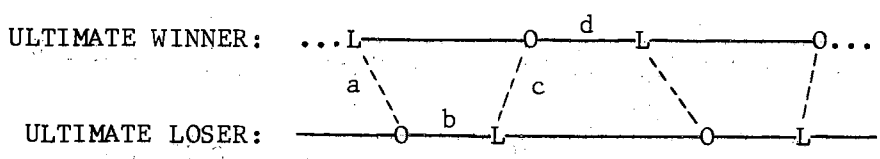
game." In other words, one or the other member of the pair must lose. Fighting in T. trichopterus seems to fit this definition. A principle of such theory involves the degree of determinateness involved in the "moves of the game." One extreme of this phenomenon is pointed out by Kalmus (1969) when he notes that in certain games, given two competent players, ". . . there always exists one particular winning move, even if the actual players do not realize this." Such a game might be comparable to a completely ritualized fight. Eibl-Eibesfeldt (1961) concluded that fighting in vertebrates includes a high degree of innate determinateness. Heiligenberg (1965) and Skaller (1966), in their analyses of attacking behavior by cichlid fish, concluded that the bouting of behaviors was primarily endogenously determined. Studies proposing endogenous control seem to imply a high degree of determinateness associated with behavior sequences.

Some of the data in Experiment III indicate a level of determinateness suggesting a degree of endogenous control. For example, the occurrence of a particular behavior seems to inhibit the reoccurrence of that behavior by the same fish at least for the next four seconds (note that the diagonal terms of Tables LX and LXI are always less than their expected values). It also seems as if the repeating intra-individual sequences of (L—B—L—B . . .) and (L—S—L . . .) are "self-generating" sequences. That is, lateral displaying is strongly directive in a statistical sense on both biting and surfacing, while biting and surfacing are directive on lateral displaying, i.e., their observed occurrences greatly exceed their expected values. The "links" between (L—B) and (B—L) are probably greater for winners than losers since the directive Chi sq values associated with this dyad are more for winners

than losers (179.2 vs. 104.0 and 128.0 vs. 26.6, respectively). This suggests that by having a greater control of the sequencing of their own behavior, winners essentially control the course of the fight. Losers are more responsive to the actions of the winner and thus appear to be less able to influence the trajectory of a fight. This situation might be compared to one of making more of the right moves in a somewhat determinant game. In addition to the conditional probabilities associated with the above dyads, several other conditional probabilities pointed out in Chapter VII are probably important vector components.

Collias (1943) studying fighting in hens, concluded that a large number of unknown or as yet undetermined factors influence the outcome of encounters. Among these factors he postulated the roles of the behavior of the opponent and "chance blows." The former can be considered as an exogenous influence on an animal's behavior.

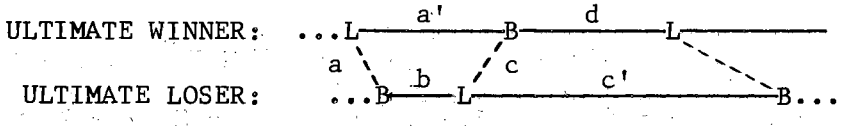
The behavior of one fish does influence that of another fish as indicated by the lack of independence in Tables LXII and LXIII. As with intra-individual sequences, certain inter-individual sequences seem to be "self-generating." The relationship between endogenous and exogenous influences in these cases, however, can readily be seen by an analysis of two commonly-occurring sequences. The first of these involves L and O, as follows:



From Tables LXII and LXIII it can be shown that lateral displaying by one fish tends to be followed by an opponent's opercle spread (dashed

segments "a" and "c" represent these tendencies). The intra-individual two-act sequence O-L can likewise be shown from Tables LX and LXI to occur much more frequently than expected by mere chance ("b" and "d" represent these tendencies).

Upon observing the Esterline records for one fish only, intra-individual sequence (L-O-L-O-) appears at first to be a "self-generating" and perhaps endogenously controlled sequence. However, Tables LX and LXI show that the L-O sequences occur no more often than expected. As pointed out in Chapter IV, there seems to be a "jockeying" for the L position; that is, the anterior position of a lateral spreading fish seems to influence the opercle spreading opponent to rapidly swim forward and display. Contrary to the O-L sequence, therefore, the L-O sequence is mediated more by exogenous factors than endogenous factors. Biting tends to replace opercle spreading in these inter-individual sequences after a few minutes into the encounter. The protocol for these sequences tends to follow the pattern:



where the same relationships exist as in the protocol for lateral displaying and opercle spreading. The principal difference seems to be a tendency for intrasequence lateral displaying to be followed by biting by the opponent ("a" and "c" represent these tendencies). This sequence seems to be less determinant than that for L and O sequences perhaps because of the two competing tendencies "a" vs. "a'" and "c" vs. "c'." The above sequence would occur only as long as the following tendencies existed: "a" > "a'" and "c" > "c'." As found for intra-

individual, two-act sequence analysis, the pooled data of the 41 fights in Experiment III suggest that the directive influence (based on Chi sq magnitude) of a winner's behavior in these sequences is considerably greater than that of their partners. Winners thus seem to control the "direction" of a fight, and the degree of directive control might be considered a dominance vector component.

It seems highly probable that more successful fish would also be quicker to react to an opportunity to attack. It would be highly instructive to investigate time associated with segments "a" and "c." Such a reaction-time hypothesis would predict that time associated with "c" was less than that associated with "a."

Finally, concerning inter-individual sequence constraints, it can be shown from Tables LXII and LXIII that biting by an ultimate winner seems to be followed less frequently by an opponent's attack than vice versa. The Chi sq values associated with these inhibitory relationships were 55.2 and 17.4, respectively.

The second undetermined factor mentioned by Collias (1943) was "chance blows." Kalmus (1969) pointed out that chance moves exist in many games as well as being ". . . fairly characteristic of much animal behavior, which as a consequence is notoriously unpredictable." Miller (1965) equates the entropy of a system with unpredictability, and that definition has been followed in this study. This uncertainty measure has been used by Hazlett and Bossert (1965) and Dingle (1968) in analyzing aggressive communication systems of crustaceans and has been described previously in Chapter VI. This measure is the equivalent of species diversity indices used by some ecologists. Wilhm (1969) has cautioned that such a measure must be independent of sample

size in order to be of value in comparative work. In brief encounters between a dominant-experienced fish and a subordinate fish, the entropy is considerably less than that exhibited during a longer fight which involves much mutual interaction. In plotting the H(6) values of Experiment II for all 64 bouts against time, it was found that when a fight exceeded about 2 min an asymptotic level seemed to be reached. The 41 bouts of Experiment III all exceeded 2 min in duration.

Barlow (1968b) discussed behavioral uncertainty in terms of variability vs. stereotypy. He noted two reasons stereotypy seems to have evolved. The first reason concerns the efficiency of a response. He pointed out that ". . . conditioned responses tend to become parsimonious" and found no reason to assume that natural selection should operate otherwise. Second, he suggested that stereotypy is probably adaptive in a signal function context by reducing chances for communication errors. However, he did note that a certain amount of unpredictability may be favored in certain reproductive contexts.

The data of Experiment III (Figure 7) clearly indicated that winning patterns of behavior show greater uncertainty than losing patterns. This function, i.e., overall sequence uncertainty, may be as important a factor in a dominance vector as the redundancy of particular two-act sequences discussed on p. 70-77.

Altman (1965) noted that stereotypy is a measure of the degree of determinateness of behavior sequences. His index of stereotypy S(X) has been applied to the data of this study. The index,

$$S(X) = 1 - \frac{H(X)}{MAX\ H(X)},$$

ranges from 0 to 1, where a value of 0 represents events that are

completely independent of preceding events and 1 represents completely stereotyped sequences. Only first order S(X) approximations were determined, i.e., the stereotypy associated with a preceding event. The data was not analyzed for evidence of "memory" beyond a preceding event.

The S(X) values for the winners and losers of Experiment III were .1216 and .1508 when the four agonistic patterns (L, O, F, and BS) were considered, while equivalent measures for all six states (L, O, F, BS, S, and P) were .1064 and .1263, respectively. As expected, higher stereotypy is associated with the behavior of an ultimate loser. It also seems that surfacing and pausing are more random in their occurrence and thus may function in increasing uncertainty in an animal's fighting pattern. The average stereotypy shown in Experiment II was greater than that in Experiment III. Apparently, manipulating parameters such as prior experience, residency, etc., produces greater stereotypy than the size parameter alone.

Finally, the behavior sequences tend to become more stereotyped as a fight progresses. The pooled S(X) values from the first third of the bouts in Experiment III were compared to the S(X) values for the last third of the bouts. The following S(X) estimates were determined:

LOSERS: 1st third = .1347, last third = .1549

WINNERS: 1st third = .1187, last third = .1347

The foregoing discussion suggests that two tendencies toward stereotypy may be operating in opposition to one another. An endogenous stimulus would thus tend to compete with the signal coming from an opponent. Depending on the states of the animals (size, sex,

experience, etc.) and feedback from the actions occurring in the fight, one of them might begin to develop a behavioral sequence more dependent on endogenous stimuli, which would permit him to gain control of the fight. Any deviation from expected responses to signals emitted by the ultimate loser would probably contribute to confusing and upsetting him, thereby increasing the winner's control of the fight. Thus, greater unpredictability could be seen as a major factor in attaining ascendency in a fight. It is interesting to note that even in the first third of a bout, a difference between S(X) values exists between ultimate winners and losers.

The Establishment of Dominance Relationships

Intra-specific fighting occurs in every major vertebrate group, and several authors have speculated on its adaptive significance (among others, see Eibl-Eibesfeldt, 1961; Wynne-Edwards, 1962; Lorenz, 1966; Ardrey, 1966; and Etkin, 1967). Collias (1943) has noted that the initial encounters between pairs of animals, ". . . lie at the basis of the social order in flocks of chickens, as is known to be the case with a number of vertebrates." For this reason, it seems important to determine which factors influence this phenomenon and how they seem to work.

Three models related to the establishment of dominance have been discussed in this chapter. Model I described the effect of several experimental parameters on the outcome of these encounters. Model II showed that certain experimental parameters influence the agonistic behaviors of these fights. In Model III agonistic behaviors were shown to influence outcome and a dominance vector was hypothesized.

A synthesis of the three models suggests an overall framework in which two levels of integration may exist. The experimental parameters of the first model influence agonistic behaviors, resulting in a new integrated variable, the dominance vector (D-vector). This vector functions during a hierarchy fight in determining which fish will become dominant.

To facilitate understanding of this concept, Figure 8 diagrams some of the suggested relationships. Some of these vector components, such as fin tugging rate, unpredictability, redundancy of more successful inter-individual dyads, and biting intensity have been postulated above. Such components (X_i's of Figure 8) are influenced by a set of environmental, physical, temporal, social, and other parameters (P_i's of Figure 8). In other words, the D-vector components (X_i's) are functions of n-parameters where the number and set of P_i's influencing any X_i probably varies at any given time. In Figure 8 for example, the parameter P_4 is not influencing any vector component at the time while P_1 is operating to enhance two vector components and inhibit a third. These parameters may be main effects or interaction effects of factors such as those tested in Experiment II, e.g., residency, relative size, etc. The importance of any P_i would vary for different D-vector components. The time factor of Experiment II, for example, was relatively more influential on fin tugging rate than on behavioral entropy, though both are quite likely vector components. Similarly, the relative size factor did not affect behavior rates but undoubtedly affects certain behavior intensities, such as biting.

The X_i's may likewise vary in importance as vector components, depending on the particular set of parameters or the level of any one

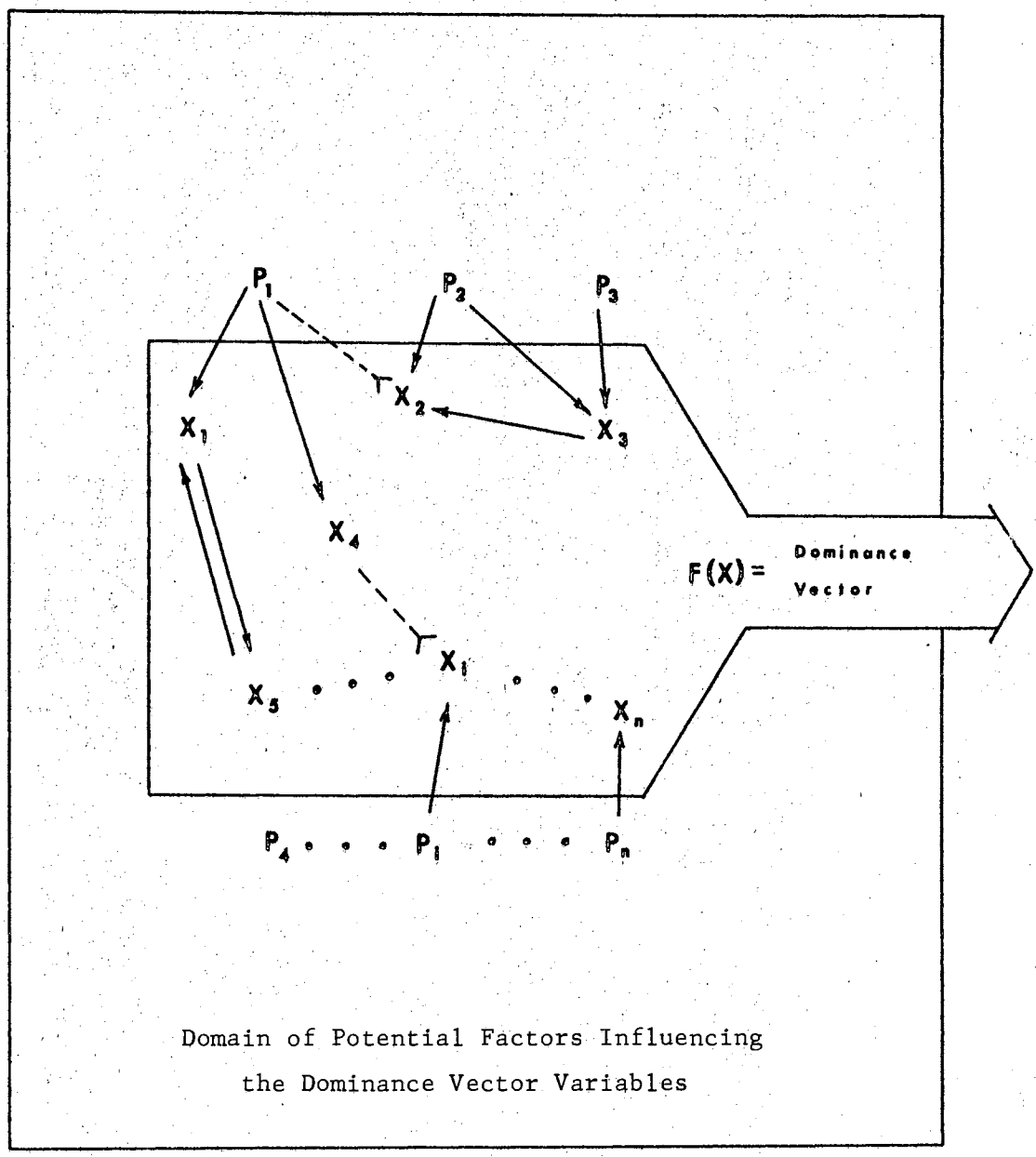


Figure 8. A hypothetical model for the formation of a dominance vector (Solid arrows represent either positive effects due to any P_i or a directive effect by any X_i. Broken lines represent either negative effects due to a P_i or an inhibitive relation for any X_i.)

parameter. Behavior entropy is considerably lower when more parameters are influencing the system than when only a few are present. Another example is associated with relative size and behavior entropy. As Δ S.L. approaches zero, H(6) increases in importance as a dominance vector component. This suggests that entropy reflects a more significant behavioral control system operating when fighting is needed to determine relative sizes and strengths. Directive and inhibitive relationships probably exist among some of the components; a few are shown in Figure 8.

The outcome of a dominance encounter might be viewed as the result of a "test" between two D-vectors. Figure 9 represents one way of describing such a test within the framework of a threshold model. The D-vector levels (D_j and D_i in Figure 9) for fish j and i, respectively, are shown to diverge steadily as the fight progresses, while in reality considerable fluctuation would probably occur. The difference between D_j and D_i is shown as Δ D. Between time (t) and (t + 1) this difference exceeds a critical level (submission threshold) and fish i ceases to exhibit aggressive behavior. This threshold can perhaps best be considered as a theoretically static level of difference between the two highly variable D-vectors. The D-vector curves might be higher and much closer together, initially, where two well-matched fish who had recently won fights were matched in territory familiar to both. Nonetheless, as the fight proceeded, the Δ D would eventually increase until it reached the critical level.

Based on the data presented in this paper and abundant supportive observations, the following scheme summarizes a proposed model for dominance determination under the conditions of this study. The winner

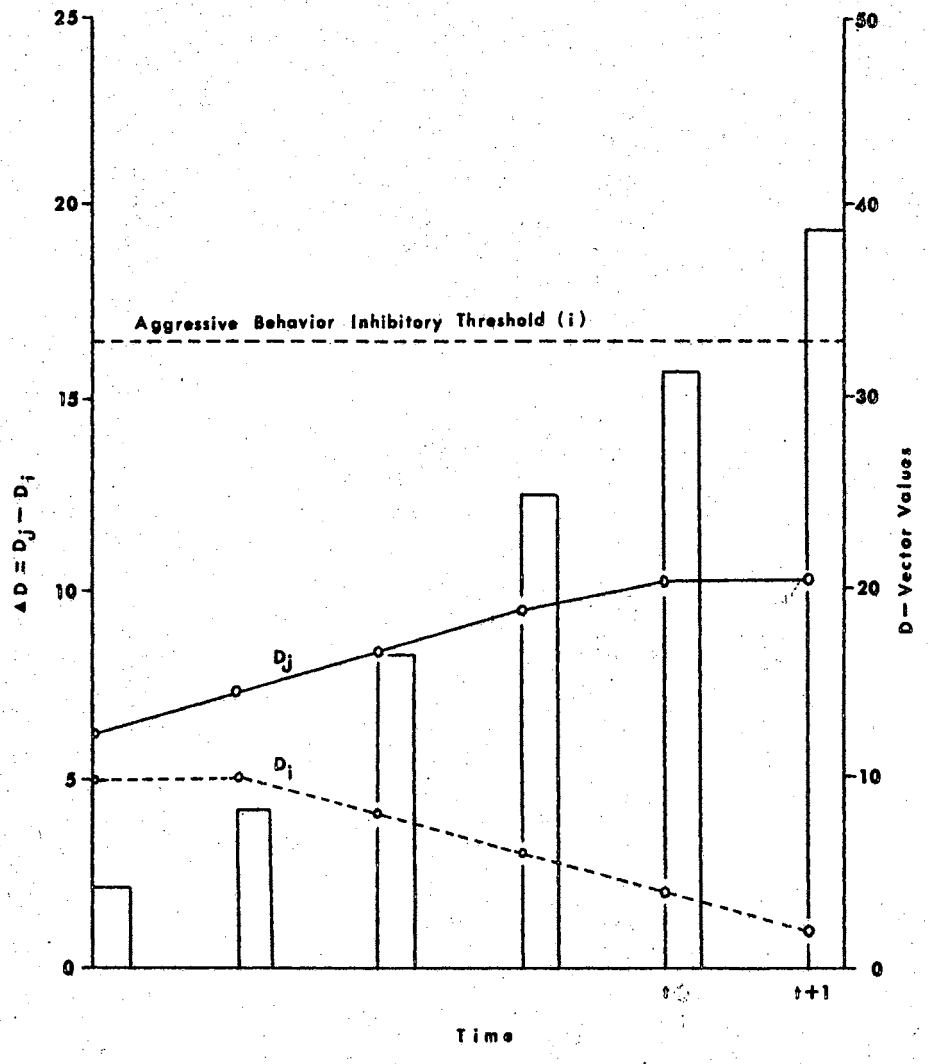


Figure 9. A hypothetical model for the outcome of a dominance encounter (The solid line, D_j, represents the D-vector of the winner; the broken line, D_i, represents the D-vector of the loser; and the bar graph, ΔD, represents the difference between D_j and D_i.)

and loser in a two-fish interaction are determined through a complex evaluative process which is not directly accessible to study by the present techniques. The overt manifestations of this process, however, are changes in the frequency and patterning of behavior, and occasionally, subtle qualitative differences in motor patterns. The present study suggests that these changes are not only indicative of changes in psychological "dominance sets," but also contribute to inter-individual communication about the state of such sets or moods. It further seems likely that some of these changing patterns contribute to speeding the evaluative process, and must be thought of as truly directive. The concept of a dominance vector is proposed to provide a probabalistic construct (greater or lesser likelihood of winning) as an alternate to the mentalistic concepts of "set" or "mood."

The present study confirms the importance of several parameters (P_i's of Figure 8) such as relative size, previous experience, and residency in influencing the outcome of dominance encounters, and suggests that they exert these influences via directive variables (X_i's of Figure 8). The net activity of these behavioral variables communicates the level of the dominance vector to the opponent, and contributes to enhancing the trajectory (towards winning or losing) of the dominance vectors.

In this type of system, one can conceive of a match between a much larger, positively experienced resident fish and a smaller, previously intimidated intruder. Most of these factors could be identified very soon after initial contact, and the difference in D-vectors would be large almost instantaneously, requiring only a short fight to confirm and reinforce D-vector trajectories. In this case,

differences in behavior patterns (X_i's) would be largely communicative, rather than directive. In cases where the fish were well matched, D-vectors would be very similar initially, and the pattern of development of the fight would be very important in influencing the outcome. The fish that gains control of the fight (see p. 93-99 for discussion of entropy and determinateness) ultimately becomes the winner, but the point at which such control occurs is difficult to determine. It seems therefore that there is a significant interplay between complex cognitive evaluations and feedback derived from behavioral interactions more accessible to study. With the present data, it seems prudent simply to demonstrate the associations among experimental parameters, behavioral variables and outcome, and present simple descriptive models (Figures 8 and 9) for overall operation of the system. Future studies will test some of the hypotheses rendered above.

CHAPTER IX

SUMMARY

1. Hierarchical relationships in the blue gourami, T. trichopterus are characterized by two distinct temporal phases—an ephemeral period of dominance establishment and a period of hierarchical maintenance. Variable behavior patterns are shown in the mutual fighting during dominance establishment between pairs of fish, but the initial outcome is always a discrete event, i.e., one fish dominates the other. The influence of several parameters on this period of dominance establishment has been investigated in this study, and the probable relationships between these parameters and patterns of behavior characteristic of ultimate winners and losers has been discussed.

2. Prior residency per se does not increase the "dominance potential" of this species. Residency was not found to act as a positive input for increased aggressiveness, rather it was concluded that the "fright" component due to moving a fish into unfamiliar surroundings acts to inhibit the "normal" expression of aggressive behavior. The residency factor interacts both with prior dominance experience and with time since that experience.

3. Prior experience as a dominant increases the probability that a fish will win a subsequent encounter, while fish previously dominated within the last 24 hr seldom win subsequent encounters. Forty-three behavior measures recorded during these subsequent encounters did

not indicate an arousal phenomenon due to dominating a partner for 24 hr, but a highly significant inhibitory effect on all agonistic behaviors was observed for those fish which had been dominated for 24 hr. These inhibitory effects wane during the next 24 hr, provided the dominating partner is removed. It is conceivable that short-term arousal input due to winning per se may temporarily lower aggressive thresholds, but whether these lowered levels would be "transferred" into a new fighting context is questionable. The phenomenon of dominance-related inhibition has been considered as a parameter which influences the "dominance vector" of each fish.

4. The inhibitory effects of "non-residency" are in part dependent upon the "dominance state" of a fish. Dominant-experienced fish are only slightly inhibited by non-residency, while subordinate-experienced fish are strongly inhibited by this factor. As the prior experience effect wanes, the fright due to environ unfamiliarity is less inhibiting.

5. Initially, the decrement in responses due to prior experience is much greater than the decrement due to non-residency.

6. Prior experience did not influence surfacing or pausing. This seems to indicate that these patterns are not a part of the agonistic repertoire in this species. For this reason, two measures of behavior uncertainty (entropy) were calculated. The first included the uncertainty associated with all the elements defined for the system, i.e., [L, O, BS, F, S, and P], while the second entropy values were based on only the agonistic set [L, O, BS, and F]. The prior experience factor influenced both entropy values more strongly than it did any single variable.

7. The relative size of opponents is probably paramount in deciding bout outcome when Δ S.L. is beyond the range tested here, i.e., where Δ S.L. $>$ 5 mm. As the time since the last dominance experience increases, the influence of Δ S.L. also increases. The length of time that two fish fight was shown to depend upon Δ S.L., while the only behavior correlated with relative size was BS rate. Smaller fish bite more frequently than did their counterparts. Finally, entropy measures were found to be functions of Δ S.L. As Δ S.L. approaches zero, entropy values increase, indicating that other variables, such as biting intensity, may become more important as a "dominance vector" component when one fish is considerably larger than his partner.

8. The absolute size of fish did not seem to be correlated with any measures associated with dominance establishment.

9. A "dominance vector" was defined in this study as that complex of variables which contribute to the defeat of one fish by another. Such a complex, highly integrated variable must remain hypothetical. Some possible components of this vector indicated by this study include: variables associated with fin tugging rate or duration, biting intensity, unpredictability, and redundancy of certain inter-individual or intra-individual dyads such as $[B_1\text{-}B_w]$ or $[L_1\text{-}B_w]$ where their conditional probabilities may be important.

10. A simple descriptive model relating environmental, experiential, size, temporal or other parameters to the dominance vector was presented. A mechanism describing how such a vector might operate in determining bout outcome was also postulated.

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APPENDIXES

APPENDIX A

CALCULATED F-STATISTICS FOR EXPERIMENT II

The same variable coding is used in Appendix A as is employed in Table III and the text. Appendix A includes the following variables:

1. Outcome
2. Approach first
3. Bout length
4. S rate
5. P rate
6. L first
7. L frequency
8. L duration
9. Duration/L
10. L rate
11. L duration/min
12. L rate by opponent
13. L duration/min by opponent
14. O first
15. O frequency
16. O duration
17. Duration/O
18. O rate
19. O duration/min
20. O rate by opponent
21. O duration/min by opponent
22. B first
23. B frequency
24. BS frequency
25. B/BS
26. B rate
27. BS rate
28. B/BS by opponent
29. B rate by opponent
30. BS rate by opponent
31. F first
32. F frequency
33. F duration
34. Duration/F
35. F rate
36. F duration/min
37. F rate by opponent
38. F duration/min by opponent
39. Entropy associated with [L, O, BS, F, S, P]
40. Entropy associated with [L, O, BS, F]
41. Number of elements of [L, O, BS, F, S, P]
42. Total (L+D+BS+F+S+P)
43. Number of elements of [L, O, BS, F]
44. Total (L+O+BS+F)

Factor or Interaction	F-Statistic for Variable: 1	2	3	4	5
Replications	0.00*	0.56	0.99	0.76	0.48
Residency (A)	0.52	15.00	5.82	5.35	3.72
Experience (B)	62.53	2.21	28.85	0.07	0.15
Size (C)	8.26	0.08	5.07	1.75	0.00
Time (D)	4.65	0.79	1.04	1.65	0.17
AB	0.00	2.21	0.58	3.08	0.70
AC	0.51	10.74	2.32	0.02	0.00
AD	2.06	0.08	1.26	0.98	0.86
BC	0.51	7.36	0.57	3.85	3.96
BD	0.00	0.79	3.37	0.56	0.23
CD	0.51	0.08	0.27	5.80	2.08
ABC	2.06	0.08	0.32	6.01	0.69
ABD	0.51	2.21	1.26	1.08	0.09
ACD	0.00	0.79	0.58	0.33	0.04
BCD	2.06	0.79	3.50	1.59	1.48
Error	0.12	0.17	56.03	0.22	1.48
C.V.	74.47	86.59	62.55	50.91	89.67

*Tabulated F-values for (d.f. = 46,1) are 4.05, 7.21, and 8.80 for $\alpha = .05$, $\alpha = .01$, and $\alpha = .005$, respectively.

Factor or Interaction	F-Statistic for Variable: 6	7	8	9	10
Replications	0.97	0.24	0.66	3.46	0.74
Residency (A)	0.00	3.66	1.80	1.90	0.87
Experience (B)	2.19	31.40	36.54	12.58	23.38
Size (C)	0.00	3.52	5.38	3.16	0.56
Time (D)	0.00	1.67	1.39	6.54	11.04
AB	0.24	0.52	1.22	1.12	4.12
AC	0.00	1.95	2.78	0.02	0.21
AD	3.89	3.05	0.95	0.09	6.41
BC	2.19	0.47	2.09	0.00	0.02
BD	2.19	3.76	5.75	10.13	8.04
CD	0.97	0.60	2.48	6.67	3.31
ABC	0.24	0.11	0.32	0.25	0.00
ABD	0.24	1.09	3.23	1.94	1.64
ACD	0.97	2.06	3.00	0.02	2.85
BCD	0.24	1.41	2.97	0.19	0.41
Error	0.25	373.10	41368.20	23.81	0.55
C.V.	101.34	81.88	77.09	57.11	49.14

Factor or Interaction	F-Statistic for Variable:				
	11	12	13	14	15
Replications	1.96	2.85	0.76	0.95	0.49
Residency (A)	0.35	6.17	13.16	17.47	4.69
Experience (B)	29.18	35.17	55.21	5.70	19.83
Size (C)	1.80	5.27	2.67	0.35	0.06
Time (D)	12.99	4.29	16.59	0.35	0.15
AB	6.85	1.87	6.43	0.35	0.69
AC	0.01	0.21	0.07	0.00	2.97
AD	2.35	5.37	14.20	0.00	0.27
BC	1.07	0.28	0.01	3.20	0.04
BD	11.22	5.06	13.87	3.20	12.47
CD	8.73	1.31	2.55	0.00	2.51
ABC	0.00	0.75	1.77	0.00	1.08
ABD	2.59	1.67	6.87	1.42	5.15
ACD	1.14	0.54	0.22	3.20	1.15
BCD	0.02	2.85	0.04	1.42	3.50
Error	68.33	0.53	50.33	0.17	53.65
C.V.	50.61	45.77	43.23	111.64	102.58

Factor or Interaction	F-Statistic for Variable: 16	17	18	19	20
Replications	1.00	0.94	1.79	1.54	0.65
Residency (A)	5.47	7.58	4.16	5.14	0.16
Experience (B)	15.74	30.64	13.54	11.41	20.13
Size (C)	0.03	0.00	1.51	1.05	0.00
Time (D)	0.35	6.57	0.58	0.08	3.08
AB	0.40	5.31	2.71	1.81	1.66
AC	4.11	1.48	0.00	0.14	0.09
AD	0.09	2.12	0.83	0.43	0.00
BC	0.76	0.19	0.02	0.91	0.00
BD	13.73	14.66	11.91	14.20	1.78
CD	0.53	0.02	2.49	0.26	5.29
ABC	0.64	0.35	0.60	0.02	0.34
ABD	6.60	5.15	4.13	6.75	2.28
ACD	0.49	0.00	0.00	0.25	2.38
BCD	2.86	0.46	0.05	0.00	1.82
Error	933.19	2.24	0.19	3.32	0.14
C.V.	111.44	60.26	92.53	102.71	92.50

Factor or Interaction	F-Statistic for Variable: 21	22	23	24	25
Replications	0.02	0.13	0.43	0.44	2.89
Residency (A)	0.12	49.71	3.73	8.40	1.01
Experience (B)	17.79	16.66	18.12	29.15	39.07
Size (C)	0.30	1.23	5.57	6.37	1.07
Time (D)	2.52	1.23	2.39	2.36	8.61
AB	1.30	3.44	0.23	0.17	7.45
AC	0.91	3.44	1.39	5.11	0.21
AD	0.01	3.44	6.53	5.11	9.91
BC	0.09	6.74	0.56	0.00	0.12
BD	2.99	1.23	0.77	2.75	4.40
CD	1.90	1.23	0.44	0.61	1.04
ABC	0.14	0.13	0.10	0.00	1.51
ABD	0.51	3.44	0.00	0.92	0.18
ACD	1.81	1.23	0.47	0.19	0.11
BCD	2.46	0.13	0.35	0.85	0.26
Error	2.29	0.11	11211.65	432.12	2.12
C.V.	97.42	74.34	113.74	87.95	59.25

Factor or Interaction	F-Statistic for Variable: 26	27	28	29	30
Replications	1.50	0.27	2.97	3.87	2.35
Residency (A)	5.06	17.31	1.46	1.28	1.42
Experience (B)	32.79	62.16	9.84	18.61	15.94
Size (C)	3.16	2.55	0.07	3.31	4.35
Time (D)	5.74	5.08	5.20	7.98	4.12
AB	1.21	0.81	15.27	9.52	0.32
AC	0.01	0.38	0.00	0.01	0.62
AD	11.09	5.43	5.79	5.93	5.72
BC	0.05	5.51	1.32	4.89	0.96
BD	1.01	6.02	4.69	5.05	2.35
CD	0.72	1.97	2.99	2.02	0.00
ABC	1.46	1.87	0.08	0.07	0.05
ABD	0.09	3.09	1.10	1.30	0.23
ACD	1.68	5.38	0.07	0.08	2.45
BCD	0.43	3.76	0.26	0.09	0.24
Error	15.30	0.53	2.49	9.95	0.68
C. V.	73.10	46.79	56.10	64.41	58.33

Factor or Interaction	F-Statistic for Variable: 31	32	33	34	35
Replications	0.28	3.61	4.68	2.75	2.97
Residency (A)	6.31	4.16	1.88	1.53	3.00
Experience (B)	1.94	16.44	11.45	7.88	8.98
Size (C)	0.07	0.37	0.09	0.08	0.28
Time (D)	3.82	4.38	5.22	8.49	8.83
AB	1.94	0.08	0.05	3.07	0.00
AC	0.07	1.97	0.76	0.50	0.11
AD	0.70	1.68	1.08	8.07	2.74
BC	0.07	0.25	0.31	3.61	0.03
BD	6.31	0.03	0.01	8.20	0.14
CD	1.94	0.30	0.89	3.85	0.92
ABC	0.07	0.00	0.19	1.71	0.04
ABD	1.94	0.43	0.45	0.54	0.65
ACD	3.82	0.00	0.15	0.12	0.24
BCD	0.07	2.12	2.92	0.05	0.00
Error	0.20	22.23	2113.63	14.89	0.06
C. V.	114.61	122.16	141.80	87.24	113.63

Factor or Interaction	F-Statistic for Variable: 36	37	38	39	40
Replications	3.72	1.46	2.87	0.15	0.12
Residency (A)	1.17	1.54	0.71	2.85	5.29
Experience (B)	5.20	16.36	11.28	58.18	65.83
Size (C)	0.43	0.82	0.46	0.28	0.11
Time (D)	8.46	0.00	0.17	17.53	16.25
AB	0.47	4.25	1.56	4.50	8.06
AC	0.00	0.01	0.07	0.01	0.50
AD	2.29	0.87	1.09	0.45	2.54
BC	0.14	0.20	0.00	3.05	1.13
BD	0.21	0.73	0.67	24.37	20.45
CD	2.82	0.68	0.57	4.45	6.48
ABC	0.11	0.42	1.42	0.04	0.10
ABD	0.33	0.73	0.99	2.33	4.20
ACD	0.23	4.15	3.07	0.38	0.67
BCD	0.10	1.81	2.83	0.27	0.35
Error	6.66	0.03	2.42	0.10	0.17
C. V.	133.88	136.94	148.02	17.53	37.72

Factor or Interaction	F-Statistic for Variable: 41	42	43	44
Replications	0.45	0.32	1.88	0.26
Residency (A)	4.84	6.39	22.58	6.96
Experience (B)	68.19	33.98	217.02	34.58
Size (C)	0.30	3.93	2.03	4.02
Time (D)	21.59	1.63	65.26	1.86
AB	2.72	0.44	14.45	0.39
AC	0.30	3.49	0.00	3.95
AD	1.89	3.10	8.12	3.74
BC	0.30	0.00	2.03	0.02
BD	27.35	5.02	81.52	4.72
CD	3.71	0.02	11.06	0.09
ABC	1.21	0.90	0.06	1.89
ABD	1.89	1.83	8.12	1.74
ACD	0.07	0.34	0.90	0.36
BCD	1.89	1.82	5.64	1.91
Error	0.82	3401.53	0.27	2127.52
C. V.	18.86	73.85	18.91	78.33

APPENDIX B

TWO- AND THREE-WAY TABLES FOR INTERACTIONS OF EXPERIMENT II EXCEEDING THE .05 LEVEL

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

A_0 = Non-resident
A_1 = Resident

B_0 = Subordinate pre-test experience
B_1 = Dominant pre-test experience

C_0 = Smaller than opponent
C_1 = Larger than opponent

D_0 = 24 hr since pre-test experience
D_1 = 0 hr since pre-test experience

TABLE IX

RESIDENCY AND SIZE INTERACTION FOR PER CENT OF FISH APPROACHING FIRST

	C_0	C_1	$\bar{X}$
A_0	43.75	12.50	28.12
A_1	50.00	87.50	68.75
$\bar{X}$	46.88	50.00	-

TABLE X

EXPERIENCE AND SIZE INTERACTION FOR PER CENT OF FISH APPROACHING FIRST

	C_0	C_1	$\bar{X}$
B_0	25.00	56.25	40.62
B_1	68.75	43.75	56.25
$\bar{X}$	46.88	50.00	-

TABLE XI

EXPERIENCE AND SIZE INTERACTION FOR PER CENT OF FISH BITING FIRST

	C_0	C_1	$\bar{X}$
B_0	12.50	43.75	28.12
B_1	68.75	56.25	62.50
$\bar{X}$	40.62	50.00	-

TABLE XII

EXPERIENCE AND TIME INTERACTION FOR PER CENT OF FISH FIN TUGGING FIRST

	D_0	D_1	$\bar{X}$
B_0	56.25	6.25	31.25
B_1	43.75	50.00	46.87
$\bar{X}$	50.00	28.12	-

TABLE XIII

EXPERIENCE AND TIME INTERACTION FOR LATERAL DISPLAY DURATION/FIGHT*

	D_0	D_1	$\bar{X}$
B_0	201.1	19.1	110.1
B_1	386.5	448.6	417.5
$\bar{X}$	293.8	233.8	-

*All duration variables in Appendix B are reported in seconds.

TABLE XIV

EXPERIENCE AND TIME INTERACTION FOR AVERAGE DURATION/LATERAL DISPLAY

	D_0	D_1	$\bar{X}$
B_0	9.88	2.88	6.38
B_1	10.32	11.09	10.70
$\bar{X}$	10.10	6.98	-

TABLE XV

EXPERIENCE AND TIME INTERACTION FOR LATERAL DISPLAYS/MINUTE

	D_0	D_1	$\bar{X}$
B_0	1.632	0.490	1.061
B_1	2.004	1.913	1.958
$\bar{X}$	1.818	1.202	-

TABLE XVI

EXPERIENCE AND TIME INTERACTION FOR LATERAL DISPLAY DURATION/MINUTE

	D_0	D_1	$\bar{X}$
B_0	17.94	3.56	10.75
B_1	22.18	21.65	21.96
$\bar{X}$	20.06	12.60	-

TABLE XVII

EXPERIENCE AND TIME INTERACTION FOR LATERAL DISPLAYS/MINUTE BY OPPONENTS

	D_0	D_1	$\bar{X}$
B_0	1.446	0.658	1.052
B_1	2.118	2.150	2.134
$\bar{X}$	1.782	1.404	-

TABLE XVIII

EXPERIENCE AND TIME INTERACTION FOR LATERAL DISPLAY DURATION/MINUTE BY OPPONENTS

	D_0	D_1	$\bar{X}$
B_0	16.74	2.90	9.82
B_1	23.30	22.69	23.00
$\bar{X}$	20.02	12.80	-

TABLE XIX

RESIDENCY, EXPERIENCE, AND TIME INTERACTION FOR LATERAL DISPLAY DURATION/MINUTE BY OPPONENTS

	A_0			A_1		
	D_0	D_1	$\bar{X}$	D_0	D_1	$\bar{X}$
B_0	5.60	3.10	4.35	27.87	2.70	15.28
B_1	21.32	22.74	22.03	25.29	22.64	23.96
$\bar{X}$	13.46	12.92	-	26.58	12.67	-

TABLE XX

RESIDENCY AND TIME INTERACTION FOR LATERAL DISPLAYS/MINUTE

	D_0	D_1	$\bar{X}$
A_0	1.496	1.350	1.423
A_1	2.140	1.054	1.597
$\bar{X}$	1.818	1.202	-

TABLE XXI

RESIDENCY AND TIME INTERACTION FOR LATERAL DISPLAYS/MINUTE BY OPPONENTS

	D_0	D_1	$\bar{X}$
A_0	1.344	1.389	1.366
A_1	2.220	1.419	1.820
$\bar{X}$	1.782	1.404	-

TABLE XXII

RESIDENCY AND TIME INTERACTION FOR LATERAL DISPLAY DURATION/MINUTE BY OPPONENTS

	D_0	D_1	$\bar{X}$
A_0	13.46	12.92	13.19
A_1	26.58	12.67	19.62
$\bar{X}$	20.02	12.80	-

TABLE XXIII

SIZE AND TIME INTERACTION FOR AVERAGE DURATION/LATERAL DISPLAY

	D_0	D_1	$\bar{X}$
C_0	10.59	4.32	7.46
C_1	9.61	9.64	9.62
$\bar{X}$	10.10	6.98	-

TABLE XXIV

SIZE AND TIME INTERACTION FOR LATERAL DISPLAY DURATION/MINUTE

	D_0	D_1	$\bar{X}$
C_0	21.72	8.16	14.94
C_1	18.38	17.05	17.72
$\bar{X}$	20.06	12.60	-

TABLE XXV

RESIDENCY, EXPERIENCE, AND TIME INTERACTION FOR OPERCLE SPREADS/FIGHT

	A_0			A_1		
	D_0	D_1	$\bar{X}$	D_0	D_1	$\bar{X}$
B_0	0.62	0.00	.31	11.25	0.38	5.81
B_1	8.00	12.00	10.00	7.25	17.62	12.44
$\bar{X}$	4.31	6.00	-	9.25	9.00	-

TABLE XXVI

RESIDENCY, EXPERIENCE, AND TIME INTERACTION FOR OPERCLE SPREAD DURATION/FIGHT

	A_0			A_1		
	D_0	D_1	$\bar{X}$	D_0	D_1	$\bar{X}$
B_0	1.75	0.00	.87	46.50	0.75	23.62
B_1	28.25	43.87	36.06	24.00	74.12	49.06
$\bar{X}$	15.00	21.94	-	35.25	37.44	-

TABLE XXVII

RESIDENCY, EXPERIENCE, AND TIME INTERACTION FOR AVERAGE DURATION/OPERCLE SPREAD

	A_0			A_1		
	D_0	D_1	$\bar{X}$	D_0	D_1	$\bar{X}$
B_0	1.000	0.000	0.500	4.294	0.500	2.396
B_1	3.354	3.524	3.440	3.218	3.996	3.607
$\bar{X}$	2.177	1.762	-	3.756	2.248	-

TABLE XXVIII

RESIDENCY, EXPERIENCE, AND TIME INTERACTION FOR OPERCLE SPREADS/MINUTE

	A_0			A_1		
	D_0	D_1	$\bar{X}$	D_0	D_1	$\bar{X}$
B_0	.1394	.0000	.0697	.8661	.0814	.4738
B_1	.5678	.7389	.6534	.4878	.9048	.6963
$\bar{X}$	.3536	.3694	-	.6770	.4931	-

TABLE XXIX

RESIDENCY, EXPERIENCE, AND TIME INTERACTION FOR OPERCLE SPREAD DURATION/MINUTE

	A_0			A_1		
	D_0	D_1	$\bar{X}$	D_0	D_1	$\bar{X}$
B_0	0.361	0.000	0.180	3.494	0.162	1.828
B_1	1.982	2.686	2.334	1.518	3.990	2.754
$\bar{X}$	1.172	1.343	-	2.506	2.076	-

TABLE XXX

EXPERIENCE AND TIME INTERACTION FOR
OPERCLE SPREADS/FIGHT

	D_0	D_1	$\bar{X}$
B_0	24.12	0.38	12.25
B_1	26.12	59.00	42.56
$\bar{X}$	25.12	29.68	-

TABLE XXXI

EXPERIENCE AND TIME INTERACTION FOR
OPERCLE SPREAD DURATION/FIGHT

	D_0	D_1	$\bar{X}$
B_0	5.94	0.18	3.06
B_1	7.62	14.81	11.22
$\bar{X}$	6.78	7.50	-

TABLE XXXII

EXPERIENCE AND TIME INTERACTION FOR
AVERAGE DURATION/OPERCLE SPREAD

	D_0	D_1	$\bar{X}$
B_0	2.646	0.250	1.448
B_1	3.286	3.760	3.523
$\bar{X}$	2.966	2.005	-

TABLE XXXIII

EXPERIENCE AND TIME INTERACTION FOR OPERCLE SPREADS/MINUTE

	D_0	D_1	$\bar{X}$
B_0	.5028	.0407	.2718
B_1	.5278	.8218	.6748
$\bar{X}$	.5153	.4312	-

TABLE XXXIV

EXPERIENCE AND TIME INTERACTION FOR OPERCLE SPREAD DURATION/MINUTE

	D_0	D_1	$\bar{X}$
B_0	1.928	0.081	1.004
B_1	1.750	3.338	2.544
$\bar{X}$	1.839	1.709	-

TABLE XXXV

RESIDENCY AND TIME INTERACTION FOR BITES/FIGHT

	D_0	D_1	$\bar{X}$
A_0	54.1	80.88	67.5
A_1	173.0	64.3	118.6
$\bar{X}$	113.6	72.6	-

TABLE XXXVI

RESIDENCY AND TIME INTERACTION
FOR BITES/MINUTE

	D_0	D_1	$\overline{X}$
A_0	3.793	4.708	4.250
A_1	9.251	3.650	6.450
$\overline{X}$	6.522	4.178	-

TABLE XXXVII

RESIDENCY AND TIME INTERACTION
FOR BITE SESSIONS/MINUTE

	D_0	D_1	$\overline{X}$
A_0	1.178	1.192	1.184
A_1	2.366	1.526	1.946
$\overline{X}$	1.772	1.359	-

TABLE XXXVIII

RESIDENCY AND TIME INTERACTION
FOR BITES/BITE SESSION

	D_0	D_1	$\overline{X}$
A_0	2.240	2.318	2.278
A_1	3.756	1.537	2.646
$\overline{X}$	2.998	1.927	-

TABLE XXXIX

RESIDENCY AND EXPERIENCE INTERACTION
FOR BITES/BITE SESSION

	B_0	B_1	$\bar{X}$
A_0	0.640	3.917	2.278
A_1	2.004	3.289	2.646
$\bar{X}$	1.322	3.603	-

TABLE XL

EXPERIENCE AND TIME INTERACTION
FOR BITES/BITE SESSION

	D_0	D_1	$\bar{X}$
B_0	2.240	0.404	1.322
B_1	3.756	3.450	3.603
$\bar{X}$	2.998	1.927	-

TABLE XLI

EXPERIENCE AND TIME INTERACTION
FOR BITE SESSIONS/MINUTE

	D_0	D_1	$\bar{X}$
B_0	1.275	0.412	0.844
B_1	2.270	2.306	2.288
$\bar{X}$	1.772	1.359	-

TABLE XLII

EXPERIENCE AND TIME INTERACTION FOR BITES/ BITE SESSION BY OPPONENTS

	D_0	D_1	$\bar{X}$
B_0	3.072	1.316	2.194
B_1	3.455	3.410	3.432
$\bar{X}$	3.263	2.363	-

TABLE XLIII

EXPERIENCE AND TIME INTERACTION FOR BITES/MINUTE BY OPPONENTS

	D_0	D_1	$\bar{X}$
B_0	5.049	1.046	3.047
B_1	6.978	6.523	6.751
$\bar{X}$	6.014	3.784	-

TABLE XLIV

RESIDENCY AND SIZE INTERACTION FOR BITES/FIGHT

	C_0	C_1	$\bar{X}$
A_0	16.25	17.62	16.94
A_1	19.56	44.44	32.00
$\bar{X}$	17.90	31.03	-

TABLE XLV

EXPERIENCE AND SIZE INTERACTION
FOR BITE SESSIONS/MINUTE

	C_0	C_1	$\overline{X}$
B_0	0.482	1.205	0.844
B_1	2.356	2.219	2.288
$\overline{X}$	1.419	1.712	-

TABLE XLVI

EXPERIENCE AND SIZE INTERACTION FOR
BITES/MINUTE BY OPPONENTS

	C_0	C_1	$\overline{X}$
B_0	3.202	2.892	3.047
B_1	5.160	8.342	6.751
$\overline{X}$	4.181	5.616	-

TABLE XLVII

RESIDENCY AND TIME INTERACTION FOR
AVERAGE DURATION/FIN TUG

	D_0	D_1	$\overline{X}$
A_0	3.860	3.790	3.825
A_1	7.798	2.245	5.022
$\overline{X}$	5.830	3.017	-

TABLE XLVIII

EXPERIENCE AND TIME INTERACTION FOR
AVERAGE DURATION/FIN TUG

	D_0	D_1	$\bar{X}$
B_0	5.857	0.281	3.069
B_1	5.802	5.753	5.778
$\bar{X}$	5.830	3.017	-

TABLE XLIX

RESIDENCY, EXPERIENCE, AND SIZE INTERACTION
FOR SURFACING/MINUTE

	A_0			A_1		
	C_0	C_1	$\bar{X}$	C_0	C_1	$\bar{X}$
B_0	1.521	0.815	1.168	0.722	0.640	0.680
B_1	0.814	1.167	0.990	1.024	0.824	0.924
$\bar{X}$	1.168	0.991	-	0.872	0.732	-

TABLE L

EXPERIENCE AND TIME INTERACTION FOR
ENTROPY OF 6 BEHAVIORS, H(6)

	D_0	D_1	$\bar{X}$
B_0	1.931	1.183	1.557
B_1	2.152	2.213	2.182
$\bar{X}$	2.042	1.698	-

TABLE LI

EXPERIENCE AND TIME INTERACTION FOR ENTROPY OF 4 BEHAVIORS, H(4)

	D_0	D_1	$\bar{X}$
B_0	1.137	0.238	0.688
B_1	1.514	1.566	1.540
$\bar{X}$	1.326	0.902	-

TABLE LII

RESIDENCY, EXPERIENCE, AND TIME INTERACTION FOR ENTROPY OF 4 BEHAVIORS, H(4)

	A_0			A_1		
	D_0	D_1	$\bar{X}$	D_0	D_1	$\bar{X}$
B_0	0.676	0.160	0.418	1.598	0.316	0.958
B_1	1.566	1.570	1.568	1.462	1.562	1.512
$\bar{X}$	1.121	0.865	-	1.530	0.939	-

TABLE LIII

SIZE AND TIME INTERACTION FOR ENTROPY OF 6 BEHAVIORS, H(6)

	D_0	D_1	$\bar{X}$
C_0	2.106	1.590	1.848
C_1	1.976	1.806	1.892
$\bar{X}$	2.042	1.698	-

TABLE LIV

SIZE AND TIME INTERACTION FOR ENTROPY OF 4 BEHAVIORS, H(4)

	D_0	D_1	$\bar{X}$
C_0	1.442	0.750	1.096
C_1	1.210	1.054	1.132
$\bar{X}$	1.326	0.902	-

VITA

3

Dennis Frederick Frey

Candidate for the Degree of

Doctor of Philosophy

Thesis: THE ESTABLISHMENT OF DOMINANCE RELATIONSHIPS IN THE BLUE GOURAMI TRICHOGASTER TRICHOPTERUS (PALLAS)

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