

CICHLASOMA NIGROFASCIATUM
GUNTHER (PISCES : CICHLIDAE):
A QUANTIFICATION OF FREQUENCY OF
DISPLAY AFTER PAIRS HAVE SPAWNED

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THESIS



ABSTRACT

Cichlasoma nigrofasciatum Gunther (Pisces: Cichlidae): A
Quantification of Frequency of Display After Pairs Have Spawned.

BY

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Eight mated pairs of Cichlasoma nigrofasciatum were observed under three treatment conditions (1. visually isolated, 2. visually exposed, and 3. eggs removed) during the ontological stages of their young. The data collected were the total frequency of six aggressive displays (tail beat, lateral display, nip, charge, bite at and frontal display). The data were not analyzed statistically. There was no clear indication of dominance as shown by the display frequency between males and females either in "isolated" or "exposed" treatment groups. A pattern of low displaying during the egg stage and increased displaying during wriggler and free swimming stages was consistent in both "isolated" and "exposed" treatment groups. This was thought to correlate inversely with the amount of time devoted by the parents to the young which decreased across the stages. The dead stage was an anomaly and the results of displaying during this stage were not consistent among pairs. The pairs in the "exposed" treatment group were consistent in that the majority of the "outward" displays were by the male, during the wriggler, free swimming and dead stages. In all the stages the females directed the majority of their displays "inward" toward their spouses. This agrees with the tendency of the males to protect the territory while the female stays with

the young. The male of the pair with two consecutive matings showed more displaying after the second mating and most of this was directed to the outside of the pair. . . . that experience may cause a male to increase his protectiveness of his territory and his young. The behavior of the pair that was in the "removed" treatment group suggested that removing eggs short circuits normal behavior activity. Ritualization was discussed as being the main aspect of behavior that not only holds a pair bond intact, but also prevents an individual from injuring or killing other members of the same species.

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Samoa Joane R. Wallach

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This opus minimus is dedicated to the late Sir Max Beerbohm who's satirical humor bouyed me up on the waves of this whole experience.

"Mother Earth, on whom we live, is presently in a great deal of trouble.
She is polluted by bent beer cans, coca cola containers, 'kumquats
make you horny' buttons, industrial waste, automobile exhaust,
human waste, excess humans and by an opulence of bullshit."
Dr. P.S. O'Neill

Des Esseintes Reborn

"Le génie, c'est l'enfance retrouvée." (Genius is childhood recaptured.)
Baudelaire

"Blinding paths through tables and graphs."
Joaquin

"By the sudden and unusual transition of sense at the end of the
pentameter the poet evidently suggests something or other; what we
are not sure, but the idea is none the less skillfully suggested."
Sir Max Beerbohm

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INTRODUCTION

The Family Cichlidae is distributed in tropical and semi-tropical fresh waters of the world: namely Africa, India, and the Americas as far north as Texas. This family also has diverse breeding habits in that some species are oral incubators, while others are substrate breeders. Mertz (1967) and Weber (1968) have reported the only studies to date that have quantified even a portion of the breeding behavior of Cichlasoma nigrofasciatum Günther, namely the fanning behavior during incubation of the eggs. There are, however, studies of other aspects of the breeding behavior and parental care of the young in this and related species of cichlids (Armitage, 1960; Aronson, 1945 and 1949; Aronson and Tucker, 1949; Backoff, 1969; Baerends and Baerends-van Roon, 1950; Barlow and Tate, 1962; Boulenger, 1908; Breder, 1934; Breder and Rosen, 1966; Collins, 1965; Collins and Braddock, 1962; El-Zarka, 1956; Gill, 1907; Greenberg, 1961a, 1961b 1963a and 1963b; Greenberg et. al., 1965; Innes, 1955; Liebman, 1933; Lowe, 1959; McInerny and Gerard, 1958; Myrberg, 1964, 1965b and 1966; Noble and Curtis, 1939; Oppenhiemer and Barlow, 1968; Seitz, 1942 and 1949; Shaw and Aronson, 1954; Sterba, 1962; Ward and Barlow, 1967; and Wickler, 1962 and 1965). The present study is concerned only with C. nigrofasciatum. This species is a substrate breeder from the waters of Costa Rica, Nicaragua, Guatemala, and Honduras. It is a species where both members of the mated pair participate to different degrees in caring for and protecting their young. These fish are reputed to be very pugnacious and aggressive (Innes

1955, McInerny and Gerard 1958 and Sterba 1962) whether together in heterosexual groups or separated.

Tinbergen (1968) has written that "in all animals intraspecific fighting is usually of distinctive advantage" in that it has survival value for the maintenance and continuation of the species. In C. nigrofasciatum it has been noted that the parents tend to show more and more aggressive displays towards one another as the young grow older (Armitage, 1960; and Mertz, 1967). No quantification has been made concerning this. The present investigation was designed to quantify the frequencies of aggressive displays of members of mated pairs toward one another and outsiders during the various ontological stages of their young. The pairs themselves were maintained in uniform visually isolated and non-visually isolated environments. The answers to certain questions about this so-called aggressiveness were derived from the recordings of aggressive behavioral action patterns. These questions were whether there was a difference in aggressive displaying: (1) comparing the male and female of a pair (2) during the different ontological stages of the young and (3) comparing visually isolated and non-visually isolated pairs. Also, differences were recorded between those visually isolated with eggs present and those with eggs removed.

I. Reproductive Behavior of Cichlasoma nigrofasciatum

The courtship and parental behavior of C. nigrofasciatum to be summarized here is based on my observations and those of others

such as: Breder and Rosen (1966), Innes (1955), McInerny and Gerard (1958), Mertz (1967), Sterba (1962) and Weber (1968). It resembles in general that of other substrate breeders in the family Cichlidae (Baerends and Baerends-van Roon, 1950). Courtship and parental care can be broken down into several phases: (A) Courtship, (B) Spawning, (C) Care of Eggs, (D) Care of Wrigglers, and (E) Care of Free Swimming young.

(A) Courtship

In a communal tank, as in nature, the male chooses a territory and defends it from intruders. A ripe female will attempt to enter his territory. If she successfully repels his initial aggressive attacks, she is then allowed to join the male in defending the territory. Only when a female is about to enter a male's territory is she relatively submissive to attacks by the male. Lorenz (1966 and 1969) calls this behavior the female "coyness behavior". It has been demonstrated that in fish, synchronization of mating behavior is controlled by the endocrine and central nervous systems of fish (Bastock, 1967; Baerends, 1950; Blum and Fielder, 1964 and 1965; Hoar, 1962, 1962b and 1965; Noble and Kumpf, 1936; Smith and Hoar, 1967; and Wai and Hoar, 1963).

The courtship activities prior to spawning begin with a period of mutual displaying consisting mostly of frontal and lateral displays and tail beats. Following this the male and female cooperate in cleaning off a smooth surface. This is done by nipping at the surface with their mouths. They dig one or more

pits to hold the newly hatched young using the mouth for scooping up gravel and the pectoral fins for sweeping gravel away. The female does the majority of the cleaning off of the proposed egg laying surface and the male does the chief digging of the pits. These pre-nuptial displays are said to be highly ritualized (Huxley, 1966) and follow a well-organized pattern. When these activities are completed the pair is ready to spawn. A day or so prior to spawning the genital tubes of the male and female are extended. Both male and female skim and quiver over the spawning site without contacting it in mutual indication of readiness.

During this period intensification of color occurs in this species as well as others: Kramer (1960, Mertz (1967), Neil (1964 and 1966) and Collins (1965. This is most characteristic of the female. The vertical stripes darken, heightening the contrast between these and the background color. Also, the orange color on the female's flanks increases in brightness. The iridescence of the anal and caudal fins, which signifies readiness to mate in a female, is most intense at this time. A strong pair bond based upon mutual displaying is formed between the male and female during this phase (Oehlert, 1958). It is often sufficiently strong enough to last through several spawnings in the laboratory (Weber, 1968).

(B) Spawning

The female skims along the previously cleaned surface with her ovipositor now fully extended. The ovipositor, in contact

with the substrate and seemingly guided by the pelvic fins, extrudes a row of five to twenty adhesive eggs. The male follows closely behind in the same coordinated movements and discharges milt over the eggs. Many such runs are performed for one half to two hours before spawning is complete. The time required to complete spawning is dependent upon the size of the spawn. This is usually correlated with the size of the female (Noble and Curtis, 1939; Collins, 1965; Weber, 1968; and Welcomme, 1967). In these observations spawning occurred at various times during the day. This confirmed observations of Weber (1968). The egg caring phase or incubation follows immediately after spawning.

(C) Care of Eggs

The female does most of the work during this stage, although the male alone is adequate (Armitage, 1960). She fans the eggs by rapid alternating beats of the pectoral fins. Both fins are maximally spread and the sweep of the beat is as wide as possible. Forward motion of the fish is prevented by metrical beats of the caudal, dorsal and anal fins. On occasion the male will relieve the female from her bouts of fanning. During the present study this occurred only in a few pairs and with short duration. In most pairs observed in this study, the female would not permit the male to fan the eggs. During this stage the male digs additional pits or enlarges some of those previously dug. The eggs are kept free of bacterial infection by the female who also removes infected or infertile eggs, which become opaquely

white. She does this repeatedly between fanning bouts. At 25.5° - 28.5°C the eggs hatch in three and a half to four days post-spawning. The time of hatching is temperature dependent (Greenberg, 1963a and 1963b; Peters, 1941; and Weber, 1968). All eggs in this study hatched before noon of the third or fourth day despite various spawning times. Fanning to a discrete point in space, i.e. eggs, is reported to be under hormonal control of prolactin (Blum and Fielder, 1965; and Metuzals, et. al. 1968).

(D) Care of Wrigglers

The male and female usually nip at the eggs and this assists the young in hatching. The parents then carry the young in their mouths to one of the pits dug during the courtship and incubation phases. Here the young attach to the substrate by a cephalic adhesive appendage and vigorously beat their tails. Occasionally, one or more of these wrigglers detach from the bottom and even escape from their pit. In these instances one of the parents quickly retrieves them in its mouth and returns them to the pit. While carrying the young fish a parent will move the young about apparently cleaning them. The wriggler stage lasts approximately four days, depending on the temperature. It terminates when the yolk sac is absorbed and the young become free swimming fry. During this stage neither of the parents fan the fry unlike other Cichlid species.

(E) Care of Free Swimming Young

Within a few hours after the young become free swimming,

they will swim 3-5" above the substrate. For the first few days they stay in a small, dense school and then, as time progresses, disperse farther and farther away from each other and their parents. During the night the young always school near the parents. At first stragglers from the small school are brought back in the mouth of one or the other of the parents. Later, as parental care decreases the wanderings of the young no longer evoke parental response. C. nigrofasciatum, unlike certain other species of fish (Van Iersel, 1963) do not have a tendency to eat their young after parental care ceases. The young were not observed eating mucus from their parents bodies (glancing) (Barlow and Tate, 1962; Quertermus and Ward, 1969; and Ward and Barlow; 1967).

During the Egg, Wiggler and Free Swimming stages the parents increase their displaying towards one another, but are not seen attacking, displaying or chasing their young (Mertz, 1967; Weber, 1968). These observations are concerned primarily with the aggressive displays between the parents during the various developmental stages of the young.

During the remainder of the present report the ontological stages of the young will be represented by the following abbreviations: Egg--E., Wiggler--W., Free Swimming--F.S., and Dead--D. The plan of the experiment was to terminate observations at sixteen days post-spawning. Unfortunately, the majority of the young did not live past the twelfth or thirteenth day post-spawning

and therefore did not meet this criterion of at least 16 days observation of parents with young. Hence, they were recorded as "Dead".

At first it was thought that the parents had eaten these young, but careful observation proved this to be erroneous. They had either died of a bacterial disease or starvation due to the lack of infusoria in the aquarium. The last month of the experiment, infusoria were prepared for the young and the majority of each of the broods so treated survived.

MATERIALS AND METHODS

I. Experimental Animals

Cichlasoma nigrofasciatum Günther is a substrate spawning cichlid mainly from Costa Rica, Nicaragua, Guatemala and Honduras. This species has two color varieties. The normal morph is light greyish with darker vertical stripes and is commonly known as a "zebra" or "convict" cichlid. The white morph is white or pinkish and is known as a "golden" cichlid. The individuals used in this study were sexually mature normal morphs. They were third or fourth generation descendents of specimens purchased from dealers in the Lansing and Ann Arbor areas. The history of the original specimens was not known. Due to selective breeding (for color and other characteristics) it is doubtful whether present-day domestic stocks are comparable to wild stocks of the same species.

C. nigrofasciatum is a sexually dimorphic species. It is one of the few species in which the female is more colorful than the male. A mature female has orange flanks and, when she is ready to breed, the anal and caudal fins become iridescent blue-green; otherwise they are yellowish. In some instances the opercular region also takes on this blue-green coloration. The mature male, which is much larger than the female, has dorsal and anal fins that are longer and more pointed than hers. There is also a blue-green iridescent coloration of the anal and caudal fins and of the opercular region when a male is ready to spawn. In these observations

one to ten days elapsed before a pair spawned after they were placed together.

A pilot study conducted from August 7 to August 23, 1969 affirmed that the male had to be 25% larger in standard length than the female or the female 25% smaller than the male for a successful breeding to occur (Mertz, 1967; and Weber, 1968). All fish were weighed with a triple beam balance and standard length measured before pairs were assembled. The males measured from 55 mm to 73 mm standard length and weighed from 7.64 to 19.8 gm. The females measured from 44 mm to 57 mm standard length and weighed from 4.58 gm to 8.36 gm. It was uncertain whether all of the fish used had spawned prior to the study; so the sexes were isolated from each other for one month before the study began. Twenty six individuals were originally chosen for the study, of which only sixteen survived to its completion.

The food for the adult fish was derived from a mixture developed by Collins (1965). The mixture originally was ground shrimp, oatmeal, and Wardley's Supremix combined approximately 1:1:1. To this was added approximately one part Tetramin. This blend was frozen in cake form and defrosted before feeding. Supplemental foods consisted of dried preparations, e.g. Tetramin or Wardley's Supremix. Young fry were fed infusoria prepared from Beldt's Magic Infusoria Powder. As the fry aged they were fed newly hatched brine shrimp alternately with Wardley's Fryfare. The fish were fed twice daily between 9 and 11 a.m. and 3 and 5 p.m. after observation periods.

II. Experimental Aquaria

One 180 liter (121 x 56 x 34 cm) rectangular aquarium with slate ends and bottom was used as the observation tank. The front of this tank was covered with a wooden viewing port with a minimized (2") viewing aperture. This was then surrounded by a fire-proofed cloth enclosure in which the experimenter could sit (Figure 1). The back of the aquarium was covered with blue posterboard marked with dark vertical lines. This prevented the experimental animals from seeing the observer. The aquarium was transversely divided into six compartments with opaque green plexiglass partitions that were sealed along the sides and bottom with a silicone rubber sealer (silastic by Dow Corning). Each compartment held a test pair of fish. At the bottom of each partition a sliding door (10 x 10 cm) either of glass or of the previously mentioned opaque green plexiglass could be inserted. Thus visual contact could be maintained or not as desired. The aquarium was cleaned and sterilized with potassium permanganate between portions of the study to eliminate possible olfactory cues from previous occupants. In addition, two 120 litre (76 x 42 x 40 cm) aquaria with slate sides and bottoms were used as holding tanks. One contained males and the other females. Each holding aquarium was divided into two compartments by an opaque green plexiglass partition with a sliding door (10 x 10 cm) of the same opaque material. The substrate in each compartment of the experimental and holding tanks was natural colored aquarium gravel approximately 2-4 cm deep. Each aquarium was void of vegetation.

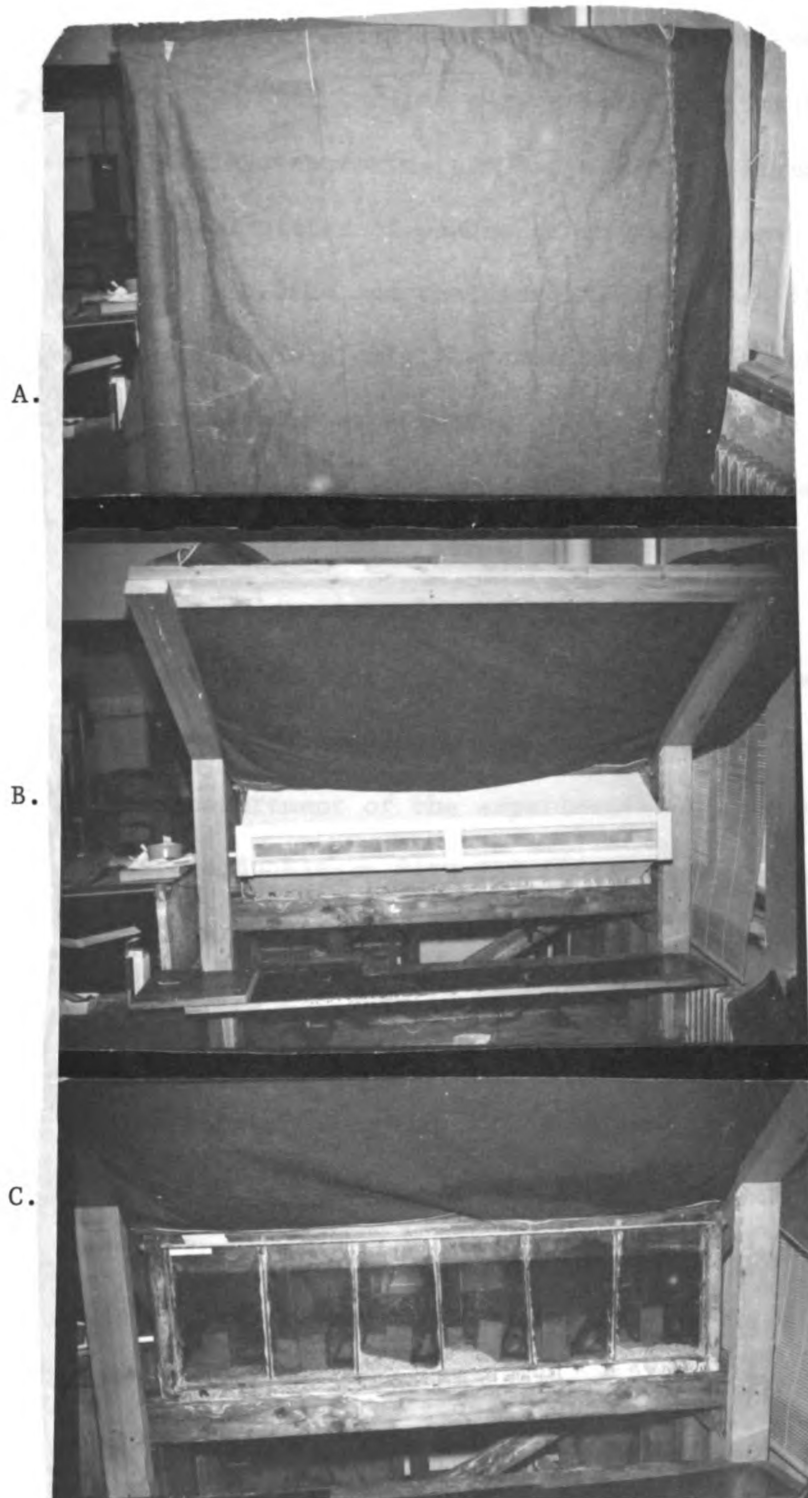


Figure 1. Experimental Aquarium. A. surrounded by fire proofed cloth, B. viewing port with two inch viewing aperature, C. six experimental compartments.

In the experimental tank each compartment contained a green plexiglass tent and one red clay brick (20 x 9 x 6 cm) with two rows of 5 holes (approximately 2.5 x 2.2 cm, Figure 2). Each tent consisted of 2 pieces of opaque green plexiglass. The horizontal piece was 8 x 6.5 cm and the diagonal piece was 15 x 8 cm. This rested against the plexiglass partition or a slate wall. The tents were used primarily as spawning places and places of shelter for the fish. The bricks were used for support of the diagonal piece of the tent and the holes served as places of refuge for females whenever the males became overly aggressive. The males were too large to enter the holes. This arrangement was patterned after a similar successful model of Weber (1968).

Each compartment of the experimental aquarium was provided with one Metaframe Bubble-up Slim Jim filter containing sterile filter floss and charcoal, which was cleaned and changed every ten days. Each compartment also contained one air stone. The air to drive the filter and air stone came from the lines that supplied the entire laboratory.

The water temperature in the experimental and holding tanks was maintained at $27^{\circ} \pm 1.5^{\circ}\text{C}$. This was done by cooling and heating units in the laboratory that were set to maintain the air temperature nearly constant. The photoperiod in the laboratory was 12 hours on and 12 hours off. This was controlled by time switches. A dawn-dusk cycle was approximated by staggering the three time switches by 15 minutes. The illumination to the aquaria was supplied by 40 W. fluorescent overhead light fixtures suspended from the ceiling.



Figure 2. One compartment in the experimental aquarium. Note: brick, plexiglass tent and fish in submissive posture.

The water in the aquaria was city water deionized by a Brune Activated Carbon Filter. Utility Seven Seas marine salt mix was added to the water, 1 gm/L as a supplement. The pH of the water ranged from 8.3 to 8.7 as measured with a Beckman Zeromatic pH meter. The pH was not artificially manipulated.

III. Quantitative Methods

The aggressive action patterns of the subjects were recorded on a ten-channel Esterline Angus multi-event recorder. The keyboard was a series of ten doorbell push buttons which were operated manually. These activated the recorder pens. The chart speed was three inches per minute.

A. Description of Aggressive Patterns.

The various aggressive displays have been described for this species, and other species, by a number of workers (Albrecht, 1966; Armitage, 1960; Baerends and Baerends-van Roon, 1950; Baerends and Blokzijl, 1963; Barlow, 1961; Dunham et. al., 1969; Gibson, 1968; Greenberg, 1947; Greenberg et. al., 1965; Miller and Hall, 1968; Mertz, 1967; Morris, 1958; Myrberg, 1965b; Neil, 1964; Riesman and Cade, 1967; Sevenster, 1961; Symons, 1966; Van Iersel, 1953; and Zumpe, 1965). The aggressive displays are expressed here as the observer saw and recorded them. In each case an abbreviated symbol is given for an aggressive pattern. These symbols will be used throughout the remainder of the paper to refer to the aggressive displays. "Pattern" and "display" are synonymous in this report.

Lateral Display (L.D.)

The aggressor spreads it's pelvic fins maximally and also

raises it's dorsal fin to various degrees depending on the individual and possibly on the intensity of the display. This is presented with the side of the displaying fish towards the adversary. This display may be held for a minute or more or for only a few seconds in duration. The purpose of this display is to make the fish look as large as possible to his or her adversary. In this species the displaying fish was not seen to circle the other fish as in other closely related species. Mertz (1967), called this display an "alert" display which is a very apt name for it. This display is mainly a threat display. Each time it was observed and the fish was in visual range of the adversary, with no obstructions between them, it was considered one lateral display (see Figure 3).

Tail Beat (T.B.)

This usually begins with a lateral display (L.D.). Next, the displaying fish, while holding the display, swims parallel to the other and beats his own tail from side to side. In most instances this contacts the other fish. The beating of the tail is said to create a current of water stimulating the lateral line of the adversary. Each full beat of the tail was considered as one tail beat.

Charge (Ch.)

The fish accelerates toward the other fish, usually pursuing it. Each time acceleration occurred and then stopped was recorded as one charge.

Frontal Display (F.D.)

The fish usually charges the other fish with opercula raised

and branchiostegal membranes extended. The charge and frontal displays were recorded as separate actions (Figure 3).

Bite At (B.A.)

This is usually a charge that ends in an effort to bite the other fish, but contact is never made. The charge and bite at were recorded as a bite at.

Nip (N)

This is usually a charge culminating in an actual biting or contact with the other fish. Nips are usually directed at the flanks of the adversary. A charge and a nip were recorded as a nip.

Lock (L)

This occurs when both fish charge each other and bite each other on the mouth simultaneously. Sometimes the mouths are closed upon one another and the fish circle. Although recorded for this species (Oehlert, 1958), this action was never observed in this study. This action however, is typical of related species.

B. Description of Submissive Actions

The submissive actions that occurred were observed but not recorded and will be described here. There were two submissive actions noted. One consists of the submissive fish's body assuming an angle of 15 degrees with the head pointed up and the pectoral fins folded against the body (Figure 2). The second submissive pattern was skimming the bottom as if laying eggs or spreading milt, but with nothing exuding from the fish. This was

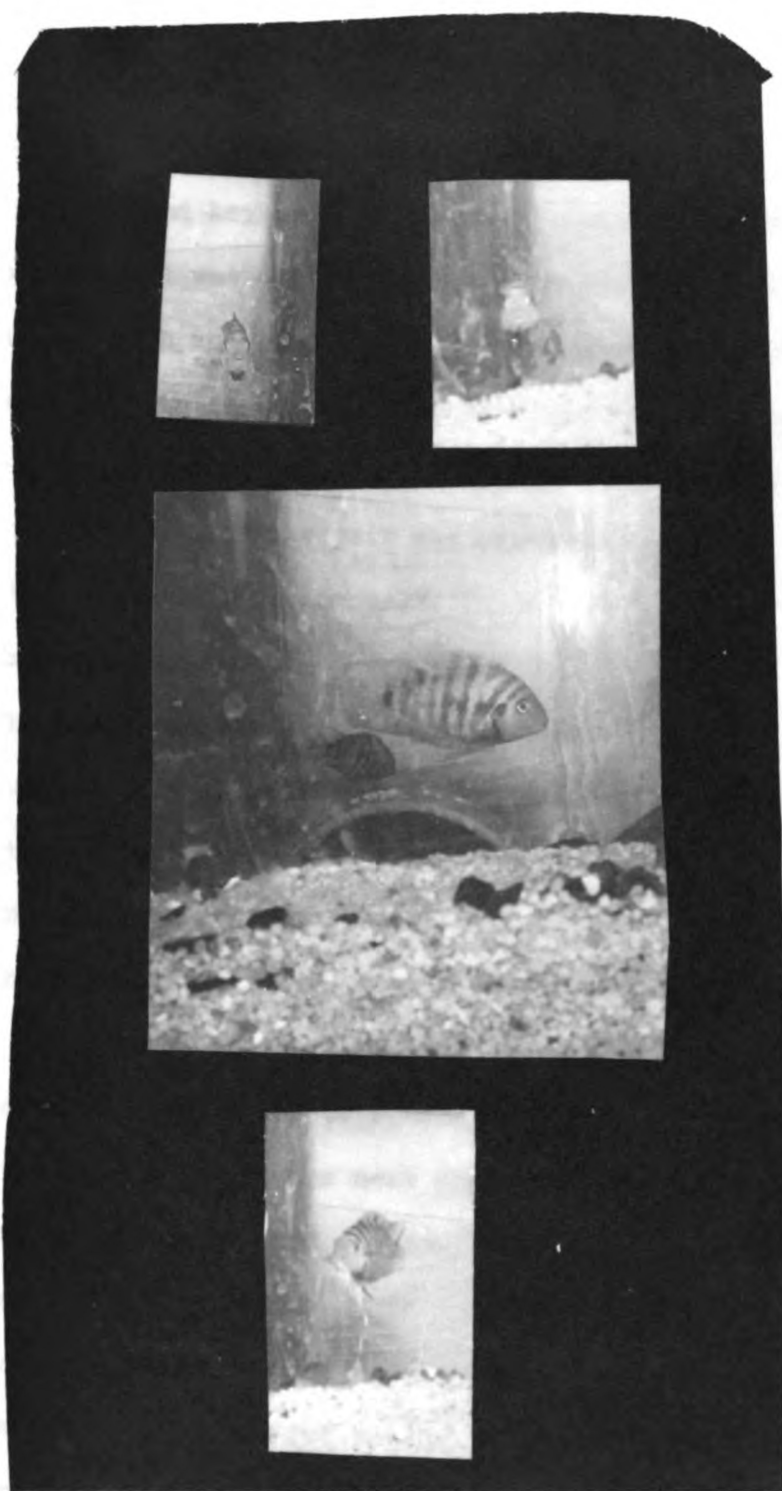


Figure 3. Fish in Displaying Postures. Top Left - branchiostegal membrane extended, beginning of frontal display. Top Right - full frontal display. Middle and Bottom - lateral display.

seen in successfully mated pairs only.

C. Recording of Display Actions

The keyboard of the multi-event recorder was so arranged that one channel was designated for each action. The male and female were each accorded a channel. There were two free channels that were used to designate which pair was being recorded and also whether the action was directed to a pair-mate or to a member of another pair to which the pair was exposed. Thus, two pairs could be recorded simultaneously.

IV. Experimental Format

The completed study utilized eight pairs of fish, each of which bred successfully at least once. Two pairs were observed one month after their first successful breeding in a second successful breeding (Pairs B and C). During that interval, males and females were in separate tanks and identified by drawing schematized diagrams of the differences in their first four vertical stripes. The fish were checked twice daily prior to spawning. After a spawning was completed the actions recorded at the next observation period were counted as observation number one and day one. There was no specified time of day when the fish spawned. This confirmed results of Weber (1968). The display interactions of male and female were recorded for fifteen minutes twice daily between 9-10:00 a.m. and between 3-4:00 p.m. for a minimum of 16 days after egg laying. This was considered to be adequate to observe their characteristic behavior.

There were three experimental groups. The first group was termed the "isolated" group. This consisted of pairs that were visually isolated from any of the other pairs after they had spawned. There were 5 successful pairs in this group. The second group was the "exposed" group. These pairs were visually exposed to one other pair after they had spawned. There were four successful pairs in this group. The third treatment group was the "removed" group. The eggs of this group were removed after the pair had spawned. There was only one successful pair in this group. There were two pairs in the study that successfully completed two treatment groups. See Table 1.

Table 1. Pairs of experimental fish and treatment groups completed.

<u>Pair</u>	<u>Isolated</u>	<u>Exposed</u>	<u>Removed</u>
A	X		
B	X	X	
C	X		X
D		X	
E		X	
F		X	
G	X		
H	X		

All three groups were treated alike so that the data could be treated statistically. All pairs were initially visually exposed to others until they spawned after which the sliding glass door in the

partition was replaced either with another sliding glass door, if the pair was to remain in visual contact or with an opaque plexiglass door if the group was to be in non-visual contact. The "removed" group was observed once with the eggs. Then the plexiglass tent piece on which the eggs were laid was removed and replaced by a blank piece of plexiglass. After this the pairs were not disturbed.

All pairs were observed for approximately sixteen days post spawning. The data used, however, varied from 14-22 days post spawn, depending on complications of second spawnings and "exposed" pairs not spawning simultaneously.

RESULTS

I. Description of the Data

Because of the low frequency of specific responses, the aggressive action response (L.D., T.B., N., Ch., B.A., and F.D.)* were pooled for each ontological stage of the young. A breakdown of the percentages of the various aggressive displays per total displaying for all pairs is graphically illustrated in Figures 4 through 14 of the appendix. The total frequency of displaying per observation period was so low in most cases that it made statistical analysis of the data impossible (except in the removed treatment group). Tables 2 through 9 show an arrangement of the data that demonstrates several trends in the display activity level of the mated pairs. These suggested trends will be mentioned in this section.

II. Male and Female Displaying

The pugnacity (aggressiveness) of Cichlasoma nigrofasciatum has been cited by numerous workers: Armitage (1960), Breder and Rosen (1966), Innes (1955), McInerny and Gerard (1958), Mertz (1967), Sterba (1962) and Weber (1968). In particular, the female of the species was cited as being extremely aggressive. There is nothing in the data that shows this. Either males or females did not dominate over the other during the entire experiment.

III. Effect of Activity of Young on Display Level

Since adults respond to the young, and the activity of the young increases through time, the effect of the developmental

* L.D. = Lateral Display, T.B. = Tail Beat, N. = Nip, Ch. = Charge,
B.A. = Bite At and F.D. = Frontal Display.

Table 2. Display Activity during the EGG Stage for Pairs in the
Isolated Treatment Group.

Pair	More Active Parent*			$\bar{X}$ - female	$\bar{X}$ - male
	Female	Male	Neither		
A	2	1	3	2.6	1.83
B	1	5	0	8.6	11.5
C	1	1	2	5.0	5.5
G	5	0	1	2.83	0.33
H	5	1	0	4.16	1.5

* = The units are "observation periods". Thus, each entry indicates the number of observation periods during which the female, the male, or neither fish showed more instances of display activity. The means are the mean number of displays per observation period.

Table 3. Display Activity during the WRIGGLER Stage for Pairs in
the Isolated Treatment Group.

Pair	More Active Parent*			$\bar{X}$ - female	$\bar{X}$ - male
	Female	Male	Neither		
A	2	3	3	3.13	2.75
B	4	4	0	12.3	13.6
C	8	0	1	29.8	15.1
G	5	1	2	1.13	0.5
H	6	2	0	7.75	4.38

* = See Table 2.

Table 4. Display Activity during the FREE SWIMMING Stage for Pairs
in the Isolated Treatment Group.

Pair	More Active Parent*			$\bar{X}$ - female	$\bar{X}$ - male
	Female	Male	Neither		
A	4	1	0	5.2	2.0
B	5	3	0	12.2	10.5
C	13	4	1	29.7	11.05
G	8	2	1	7.8	4.81
H	4	11	2	25.45	36.76

* = See Table 2.

Table 5. Display Activity during the DEAD Stage for Pairs in the
Isolated Treatment Group.

Pair	More Active Parent*			$\bar{X}$ - female	$\bar{X}$ - male
	Female	Male	Neither		
A	3	7	3	2.69	4.84
B	1	4	0	4.8	9.6
C	1	0	0	7.0	6.0
G	0	7	0	2.72	14.57
H	-	-	-	----	-----

* = See Table 2.

Table 6. Display Activity During the EGG Stage for Pairs in the Exposed Treatment Group.

Including displays directed INward and OUTward and TOTAL displaying.

		IN			OUT			TOTAL								
		More Active Parent*		$\bar{X}_f^{**}$	$\bar{X}_m^{**}$	More Active Parent*		$\bar{X}_f^{**}$	$\bar{X}_m^{**}$	More Active Parent*		$\bar{X}_f^{**}$	$\bar{X}_m^{**}$			
Pair		Female	Male	Neither	$\bar{X}_f^{**}$	$\bar{X}_m^{**}$	Female	Male	Neither	$\bar{X}_f^{**}$	$\bar{X}_m^{**}$	Female	Male	Neither	$\bar{X}_f^{**}$	$\bar{X}_m^{**}$
B	4	1	0	5.4	1.8	3	0	2	0.6	0	5	0	0	6.2	1.8	
D	3	2	1	2.0	1.4	0	0	5	0	0	3	2	1	2.0	1.4	
E	4	2	1	1.57	0.43	0	0	7	0	0	4	2	1	1.57	0.43	
1st mating																
E	0	5	2	2.29	4.43	0	6	1	0.29	16.14	0	7	0	2.57	20.57	
2nd mating																
F	2	1	1	5.75	3.0	0	1	3	0	0.5	2	2	0	5.75	3.5	

* = See Table 2. ** = $\bar{X}$ - female and $\bar{X}$ - male.

Table 7. Display Activity During the WRIGGLER Stage for Pairs in the Exposed Treatment Group.

Including displays directed INward and OUTward and TOTAL displaying.

		IN			OUT			TOTAL								
		More Active Parent*		$\bar{X}_f^{**}$	$\bar{X}_m^{**}$	More Active Parent*		$\bar{X}_f^{**}$	$\bar{X}_m^{**}$	More Active Parent*		$\bar{X}_f^{**}$	$\bar{X}_m^{**}$			
Pair		Female	Male	Neither	$\bar{X}_f^{**}$	$\bar{X}_m^{**}$	Female	Male	Neither	$\bar{X}_f^{**}$	$\bar{X}_m^{**}$	Female	Male	Neither	$\bar{X}_f^{**}$	$\bar{X}_m^{**}$
B	6	2	0	0	9.0	4.0	3	0	5	0.88	0.13	7	1	0	9.88	4.13
D	4	4	0	0	3.9	2.1	0	5	3	0.25	14.12	3	5	0	3.9	2.1
E	3	5	0	0	5.13	5.25	2	3	3	0.75	1.38	3	4	1	5.22	5.88
1st mating																
E	0	6	0	0	0.5	3.83	0	6	0	0.43	41.66	0	6	0	0.5	3.83
2nd mating																
F	8	1	1	1	9.1	4.2	0	9	1	1.7	8.4	4	6	0	10.8	12.6

* = See Table 2 ** = $\bar{X}$ - female and $\bar{X}$ - male

Table 8. Display Activity During the FREE SWIMMING Stage for Pairs in the Exposed Treatment

Group. Including displays directed INward and OUTward and TOTAL displaying.

Pair	IN			OUT			TOTAL		
	More Active Parent*	More Female Parent*	Neither $\bar{X}_f^{**}$ $\bar{X}_m^{**}$	More Active Parent*	More Female Parent*	Neither $\bar{X}_f^{**}$ $\bar{X}_m^{**}$	More Active Parent*	More Female Parent*	Neither $\bar{X}_f^{**}$ $\bar{X}_m^{**}$
B	3	11	0	12.56	11.2	4	21	0	6.28 19.8 9 15 1 18.84 30.88
D	10	8	1	8.68	7.05	6	11	2	2.84 6.57 6 9 4 11.79 13.6
E	8	4	0	10.58	6.75	0	5	7	0.5 2.58 8 4 0 11.08 9.33
1st mating									
E	1	4	0	8.2	14.2	0	5	0	0 49.8 0 5 0 8.2 64.0
2nd mating									
F	7	2	0	13.88	8.44	3	5	1	1.77 2.77 6 2 1 13.88 8.44

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* = See Table 2. ** = $\bar{X}$ - female and $\bar{X}$ - male.

Table 9. Display Activity During the DEAD Stage for Pairs in the Exposed Treatment Group.

Including dis

Including displays directed INward and OUTward and TOTAL displaying.

Pair	IN			OUT			TOTAL		
	More Active Parent*	More Female Parent*	Neither $\bar{X}_f^{**}$ $\bar{X}_m^{**}$	More Active Parent*	More Female Parent*	Neither $\bar{X}_f^{**}$ $\bar{X}_m^{**}$	More Active Parent*	More Female Parent*	Neither $\bar{X}_f^{**}$ $\bar{X}_m^{**}$
B	-	-	-	-	-	-	-	-	-
D	-	-	-	-	-	-	-	-	-
E	3	11	1	3.86	7.64	0	6	8	0.14 1.5 2 10 2 4.0 9.14
1st mating									
E	0	2	1	8.66	11.66	0	3	0	2.0 8.33 0 3 0 8.25 20.0
2nd mating									
F	4	5	1	6.9	10.1	0	9	1	2.5 19.8 1 9 0 9.4 29.9

* = See Table 2. ** = $\bar{X}$ - female and $\bar{X}$ - male.

stages on adult display level was looked for. A pattern of low frequency of displaying during the Egg stage with increasing frequency of displaying during the Wiggler and Free Swimming stages is evident in both the "isolated" and "exposed" treatment groups. See Tables 2 through 9. The females show a decrease in the frequency of displaying during the Dead stage. This or any other trend was not suggested for the males during the Dead stage. In terms of the evolutionary development of the parental behavior, the Dead stage is an anomaly. Therefore, one should expect inconsistency in behavior of the parents when the young die.

IV. Sexual Differences in Externalizing or Internalizing Display Within a Pair.

Lorenz (1969) reported that males direct displays toward "hostile neighbors". This suggested that possible differences in the direction of display by males and females was present. The data can be seen in Tables 6 through 9. The data show that males did most of the aggressive displays OUT (to the outside of the pair) during the Wiggler, Free Swimming and Dead stages and IN (within the pair during the Egg stage. The females directed most of the displays IN (within the pair) during all of the stages.

V. Effect of Consecutive Mating on Displaying

Pair E of the "exposed" treatment group had two consecutive matings while under observation. After the second mating the mean number of displays, per observation period per stage, increased considerably over those after the first mating (see Tables 9 through 9).

VI. Eggs Removed

Pair C was the only pair in the "removed" treatment group. A Chi-square test (Rohlf and Sokal, 1969; and Sokal and Rohlf, 1969) using the total frequency of displaying after the eggs were removed was performed to determine whether the male and female showed an difference in displaying. The male showed significantly more displaying than the female (Table 10).

Table 10. Chi-Square Table and Results for Pair C of the Removed Treatment Group.

=====			
Male	Female		
392.0	157.0	P	.005*
	<u>549.0</u>		

* = Statistically Significant

DISCUSSION

Very little research has been done on the quantification of display patterns of a pair of fish after they have mated, since in most families only one of the parents cares for the young or the young are left to fend for themselves. In part, this section will discuss the data and literature when pertinent and will propose hypotheses and suggestions for further research.

I. Male and Female Displaying

The data on both "isolated" and "exposed" treatment groups demonstrated that there was no clear indication that females display more than their mates or vice versa. Several aquarists such as Innes (1955), McInerny and Gerard (1958) and Sterba (1962) noted the pugnacity of the female, probably because this is an occurrence. In general, females of most popular tropical fish tend to be very submissive. (The submissiveness of the female Homo sapiens was an expected role for many centuries and now this too is changing.) Perhaps in Cichlids this is an evolutionary adaption. Lorenz (1966 and 1969) observed that the only time a female cichlid is submissive is prior to mating, since if she returns the male's displaying she will abort the pre-nuptial sequence and consequently mating. Since the data of this experiment showed that neither males nor females were dominant all the time, it may be that balance is reached that helps to maintain the pair bond after spawning.

II. Effect of Activity of Young on Display Level

Mertz (1967) and Weber (1968), although only observing incubation behavior, noted that the female increases her frequency of displaying (aggressiveness) toward the male as the egg stage progresses. The data of this experiment showed that the trends in activity level of the parents suggest a consistent pattern during three of the stages (E., W., and F.S.). The pattern involves a low level of activity during the E. stage and an increased level of activity during the W. and F.S. stages. The results suggest that the adult display level increases within active stages as from the W. stage to the F.S. stage. The D. stage, however, is not in the normal sequence, and behavior during this stage is not consistent among pairs.

Although the fanning behavior and reduced aggressiveness during the E. stage is reputedly under the control of prolactin (Bern, 1967; Blum, 1968a and 1968b; Blum and Fielder, 1964 and 1965; and Metzals et. al., 1968), only the display behavior per se was measured here. Thus, this study was not directly involved with the endocrinological control of behavior. It would be interesting to learn if in a dominance situation injecting prolactin could mitigate the aggressiveness of the alpha animal enough to change his/her position in the hierarchy. Another possibility might involve changing the activity levels of a parent fish by injection throughout the post-spawning cycle of stages.

Perhaps the increase of activity of the parent fish during the various stages concerns the amount of time a fish spends caring for the young. During the E. stage the female is almost constantly fanning or cleaning the eggs and the male, usually hovering near, is ready to relieve her when she takes a break from these duties. Therefore, during this stage there is little time for displaying activity. During the W. stage the young occupy a small area and receive care only when one of them comes detached from the bottom, or the parent wants to move or clean them. The F.S. stage, however, poses a more complex problem. It is during this stage that the young are moving about and must be protected from possible predators. During the W. stage and especially the F.S. stage displaying is not only exclusively mutual between the parents. Males protect their territories containing young if the pair is not isolated. Thus possible predators are excluded. As the stages progress both parents spend less and less time actually caring for the young and therefore have more time for displaying. This is only an hypothesis and it should be tested.

III. Sexual Differences in Externalizing or Internalizing Display Within a Pair

Lorenz (1969) in On Aggression stated that it is a common behavior in cichlids for the male to "vent" his "aggression" on a "hostile territorial neighbor". The data of the "exposed group" confirmed that the males of all pairs did most of the displaying

to the OUTside of the pair in the direction of a member of the pair to which they were exposed during the W., F.S. and D. stages. The females all directed most of their displays withIN the pair towards their mates. These results agree with the trends associated with the activity level per se in that this occurred at higher display levels, during the W. and F.S. stages. The direction of the display also correlated with the major duties performed by the male and female in relation to their young. The female is always with the young while the male makes constant forays to check and defend the periphery of the territory.

Lorenz (1969) also states that in cichlids if a neighbor is not present, all of the male's hostility is vented on the female and more often than not she is killed. Armitage (1960), in observing C. nigrofasciatum noted that unless an object (e.g. another fish of the same species) toward which the male can direct his aggressiveness was present, the pair bond broke. This is similar to Lorenz's observation, because once the pair bond is broken injury to the female is sure to follow unless she can escape. Fortunately in this experiment, five pairs in visual isolation of their neighbors successfully cared for young. There were no observations of killing or severely injuring of the female or male. There may have been olfactory cues or sound cues from the neighbor. Myrberg (1965a) notes that females of C. nigrofasciatum produce sound. These were not studied during

the present observations. Visual contact prior to spawning may have conditioned individuals to the presence of a neighbor but this is only a possibility. Experimentation concerning the role of cues given by an unseen neighbor or the necessity of the presence of a neighbor at all, to maintain a pair-bond is necessary to clear up these conflicting observations.

IV. Effect of Consecutive Mating on Displaying

Pair E mated twice while it was under observation. It was shown in the data that the male showed far more displaying after the second mating and the majority was directed to the outside of the pair. The male appeared to be protecting his territory more intensely and was thus taking better care of the young. Lehrman (1961), after adorning his ideas with many references, proposes that the care of young is enhanced and more efficient after the birth of a second brood. This suggests that the first brood serves as a learning experience. Although Lehrman was referring to birds and lower mammals there is no reason why this may not be assumed for those fish which also care for their young. Weber (1968) observed that it is not unusual for a pair of this species to remain together for several spawnings in the laboratory. Thus they could be increasing their coordination and care of the young following the first breeding. Work to confirm this hypothesis in fish is greatly needed.

V. Eggs Removed

Pair C was the only pair that was in the "removed" treatment group. The eggs and young are objects to care for and a normal occurrence after mating. If the eggs are removed this constitutes a short circuiting of behavioral events usually performed by the parents. In this case the female had no eggs to care for or defend and this may explain her reactions. The male also acted unusually since he displayed much more than in a previously completed brood care cycle and much more than the female. Many reasons for this behavior of the pair could be postulated and could also be termed "anthropomorphic presumptions". One pair, however, is an insufficient basis for generalization concerning the behavior of an entire population. Obviously more experimentation is necessary.

VI. Ritualization of Behavior

This discussion would not be complete without mentioning ritualization of behavior as one of the main components of this experiment. Ritualization, as defined by Baerends (1957) is "the process through which a behavior has acquired in the course of evolution a new function as a social releaser and has changed in relation to this new task". The behavioral action pattern does not change but the communicative meaning changes. Oehlert (1958) did quite a comprehensive nonquantitative study on mating and other behaviors in sixteen or more species of Cichlidae.

C. nigrofasciatum was one of the species studied. She concluded

that intraterritorial fighting was entirely ritualized in this species. She also mentioned that she had never seen a male pursue a female for purposes of injury. Probably a majority of the displays observed in this project were ritualized. The communicative nature was not aggression, but rather had other communicative functions, such as recognition of the mate in greeting ceremonies. Lorenz (1969) asserts that greeting ceremonies tend to renew and strengthen the pair bond.

In discussing retualization in cichlids Lorenz (1969) suggests that retualization and redirection of attack help to act as forms of a braking mechanism, with the result that members of the same species do not injure one another. This is probably why in this project none of the fish were injured or killed. Displaying towards a neighbor which looks more aggressively intense still contains a great deal of ritualization.

SUMMARY

Eight mated pairs of Cichlasoma nigrofasciatum were observed under three conditions: 1. visually isolated, 2. visually exposed, and 3. eggs removed during the ontological stages of their young. The data consisted of the total frequency of six aggressive displays (tail beat, lateral display, nip, charge, bite at and frontal display). The conclusions were:

1. There is no clear indication that females display more than their mates or vice versa. This applied both to "isolated" and "exposed" treatment groups.
2. There was a consistent pattern in frequency of display of males and females of "isolated" and "exposed" treatment groups. This traversed three of the ontological stages of the young. This pattern involved little display during the egg stage and increasing displaying during the wriggler and free swimming stages. The dead stage was inconsistent across pairs because this stage does not normally occur.
3. In the "exposed" group the males did most of the displaying to the outside of the pair during the wriggler, free swimming and dead stages, while the females directed most of their displays toward their mates during all stages. This is consistent with the tendency of the male to guard the territory while the

female stays with the young.

4. The male of Pair E, which had two consecutive matings showed an increase in displaying after the second mating. The majority of these displays were to the outside of the pair. This suggests that experience may cause a male to increase his protectiveness of his young and his territory.
5. The male of Pair C when in the "removed" group displayed more frequently than the female. This suggests that removing eggs may short circuit behavior.
6. There was no pair bond breakage, severe injury or killing of a mate in the "isolated" pairs as reported by other researchers.
7. Ritualization is the main aspect of behavior that holds a pair bond intact and prevents injury or death to members of the same species.

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APPENDIX

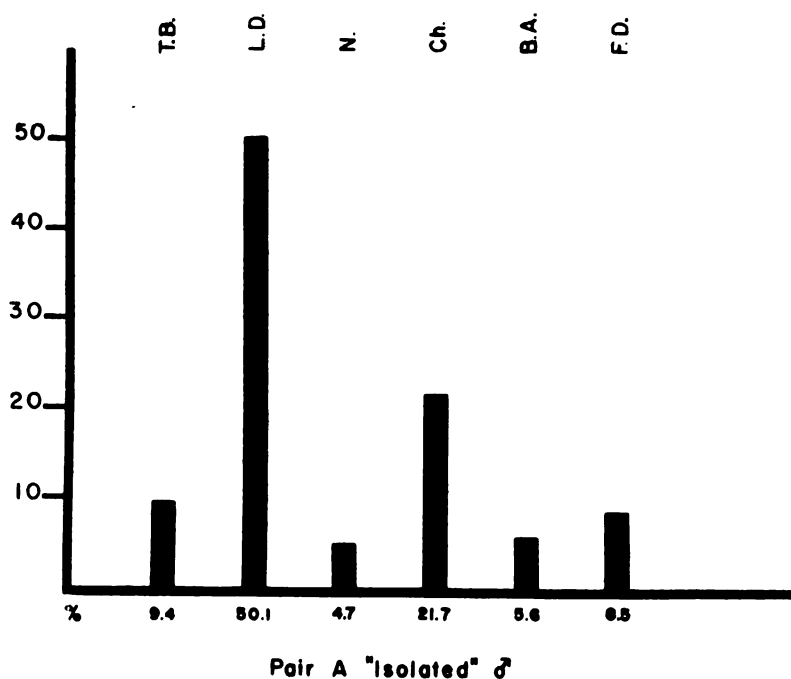
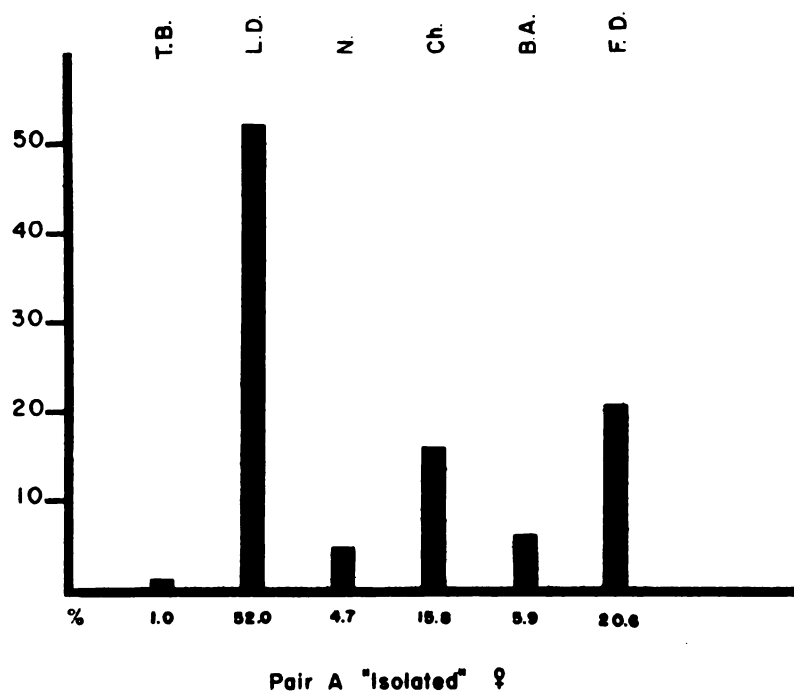


Figure 4. Pair A "Isolated". Percentages of the various displays per total displaying during all observation periods (T.B. = tail beat, L.D. = lateral display, N. = nip, Ch. = charge, B.A. = bite at, and F.D. = frontal display).

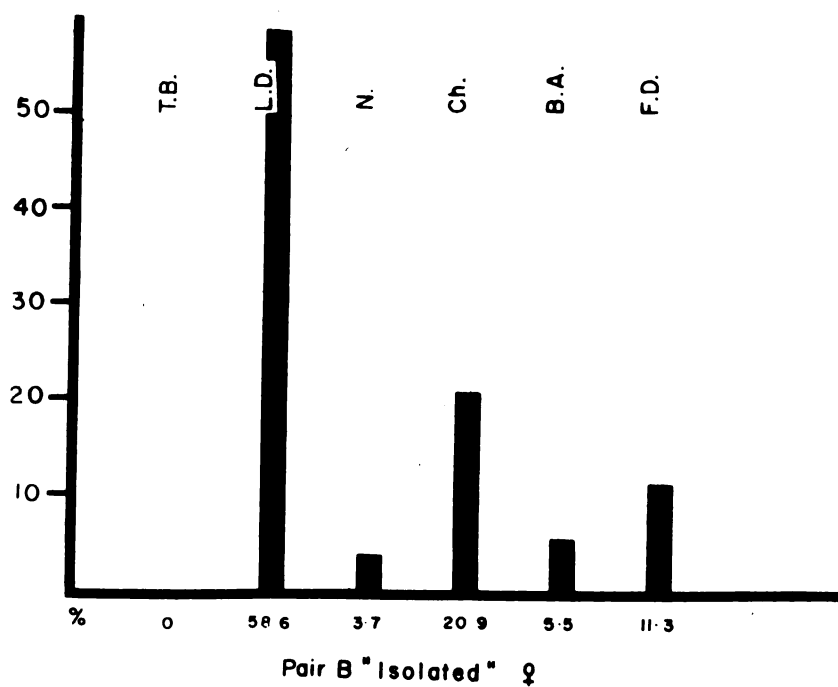
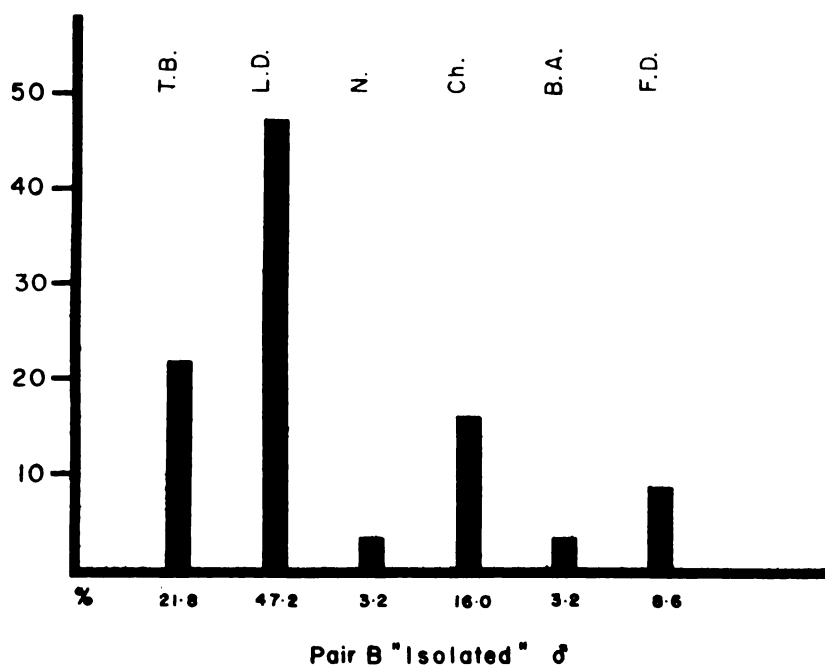


Figure 5. Pair B "Isolated". Percentages of the various displays per total displaying during all observation periods (T.B. = tail beat, L.D. = lateral display, N. = nip, Ch. = charge, B.A. = bite at, and F.D. = frontal display).

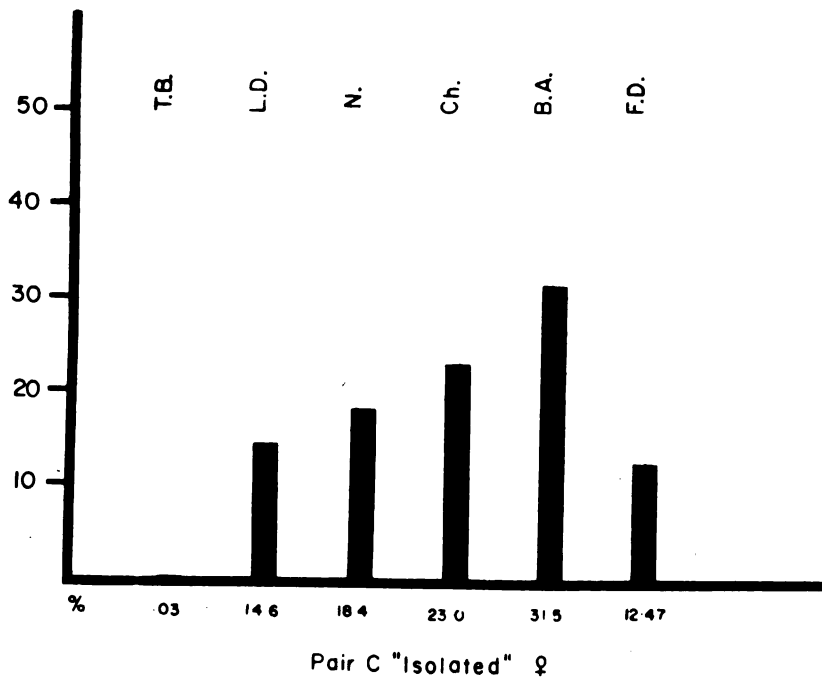
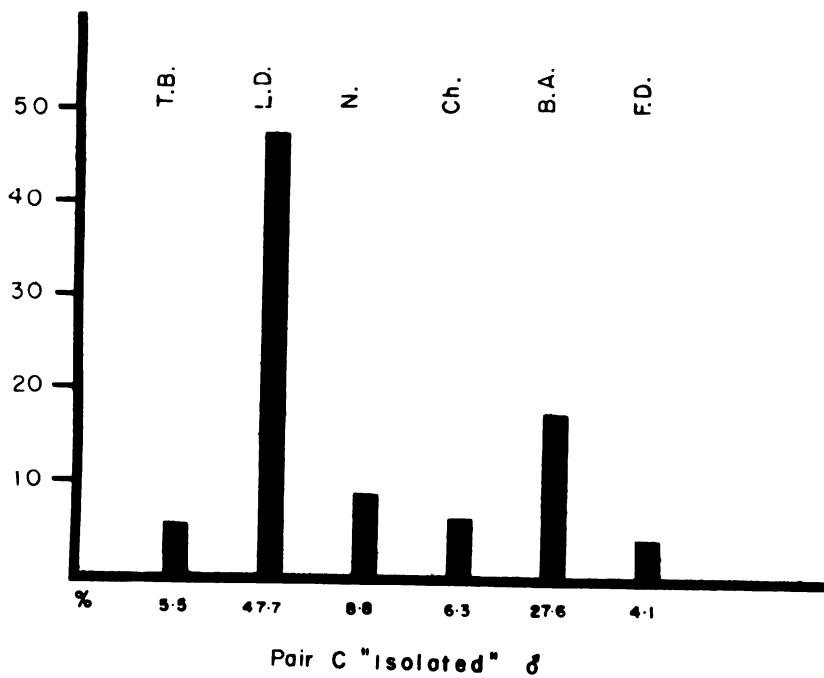


Figure 6. Pair C "Isolated". Percentages of the various displays per total displaying during all observation periods (T.B. = tail beat, L.D. = lateral display, N. = nip, Ch. = charge, B.A. = bite at, and F.D. = frontal display).

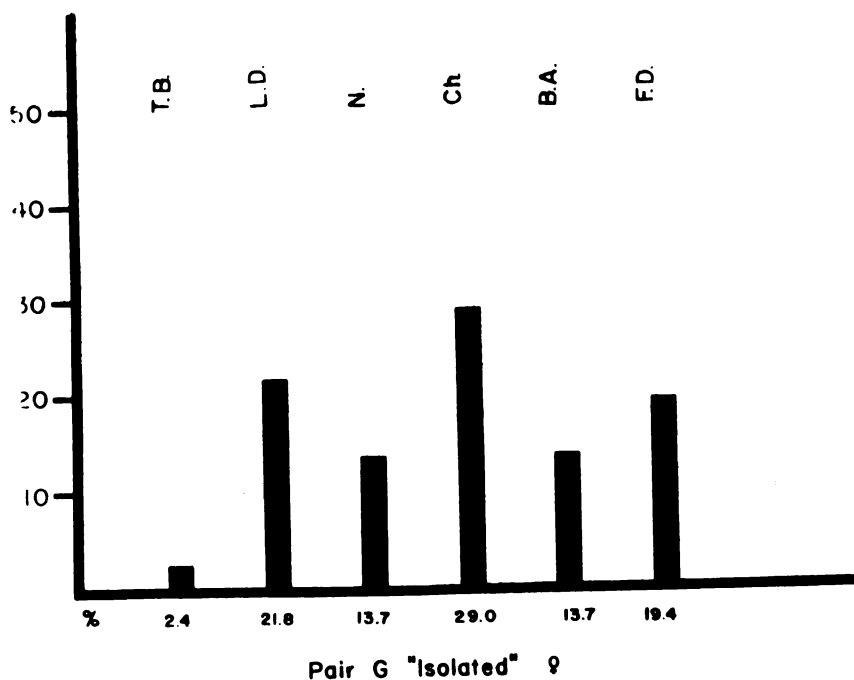
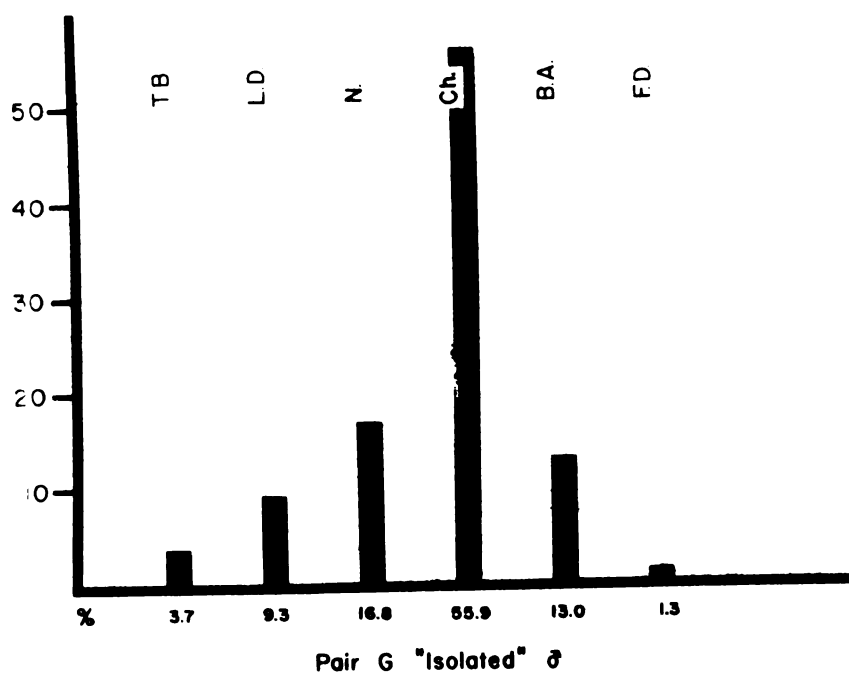


Figure 7. Pair G "Isolated". Percentages of the various displays per total displaying during all observation periods (T.B. = tail beat, L.D. = lateral display, N. = nip, Ch. = charge, B.A. = bite at, and F.D. = frontal display).

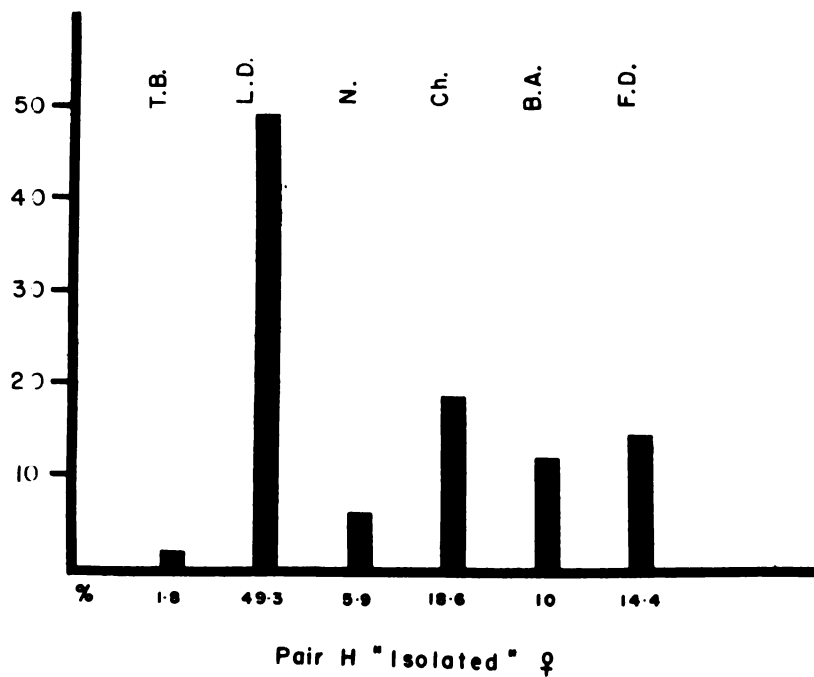
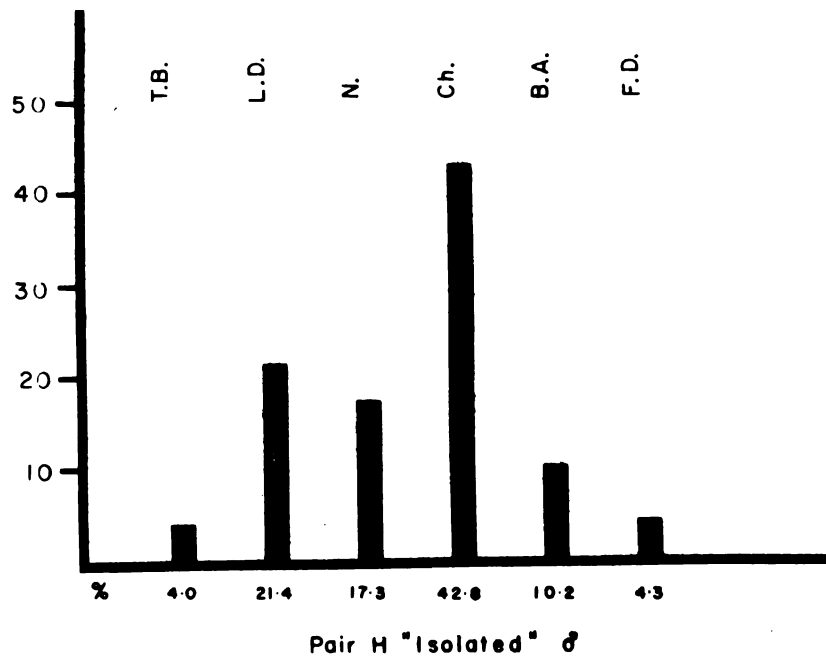


Figure 8. Pair H "Isolated". Percentages of the various displays per total displaying during all observation periods (T.B. = tail beat, L.D. = lateral display, N. = nip, Ch. = charge, B.A. = bite at and F.D. = frontal display).

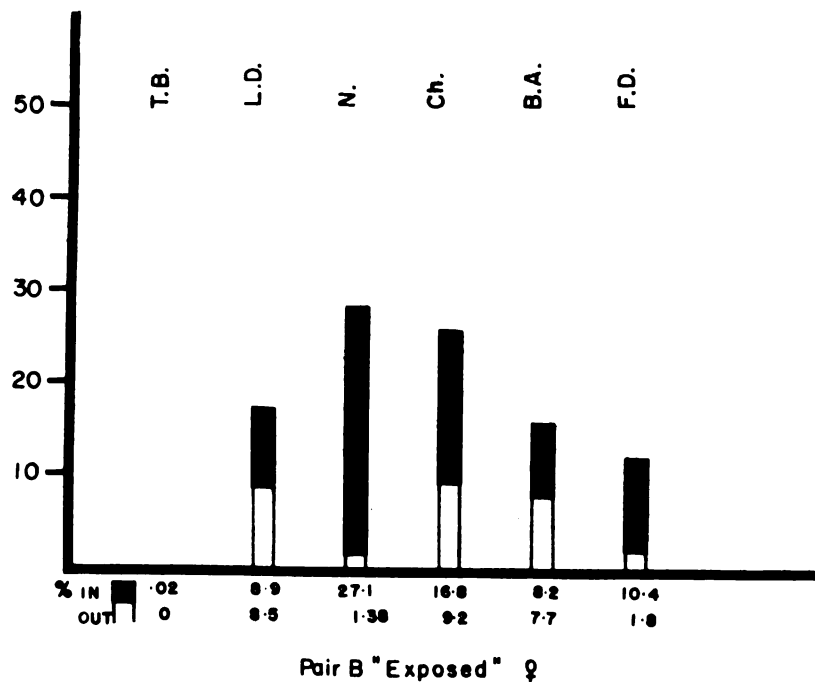
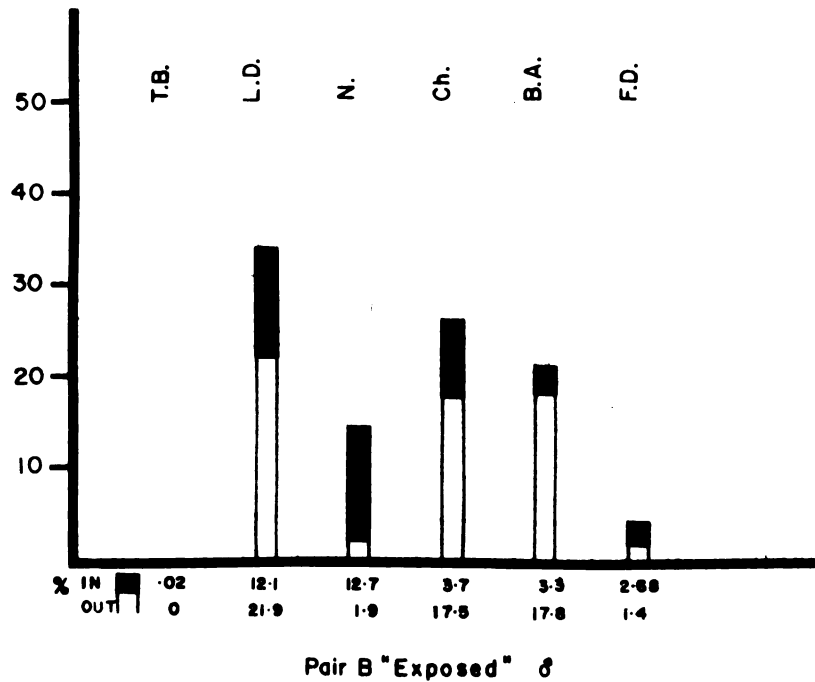


Figure 9. Pair B "Exposed". Percentages of the various displays (directed IN and OUT) per total displaying during all observation periods (T.B. = tail beat, L.D. = lateral display, N. = nip, Ch. = charge, B.A. = bite at, and F.D. = frontal display).

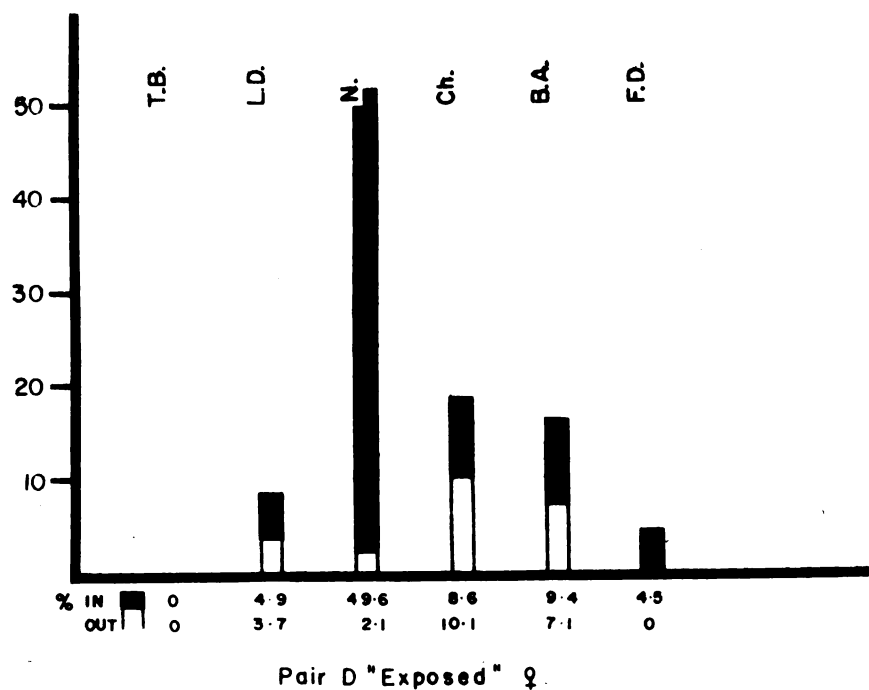
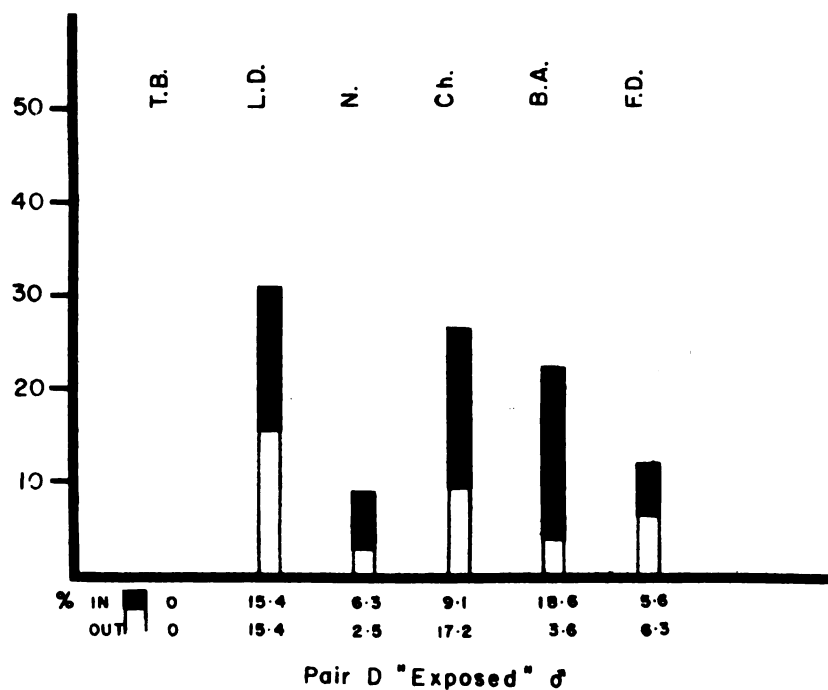
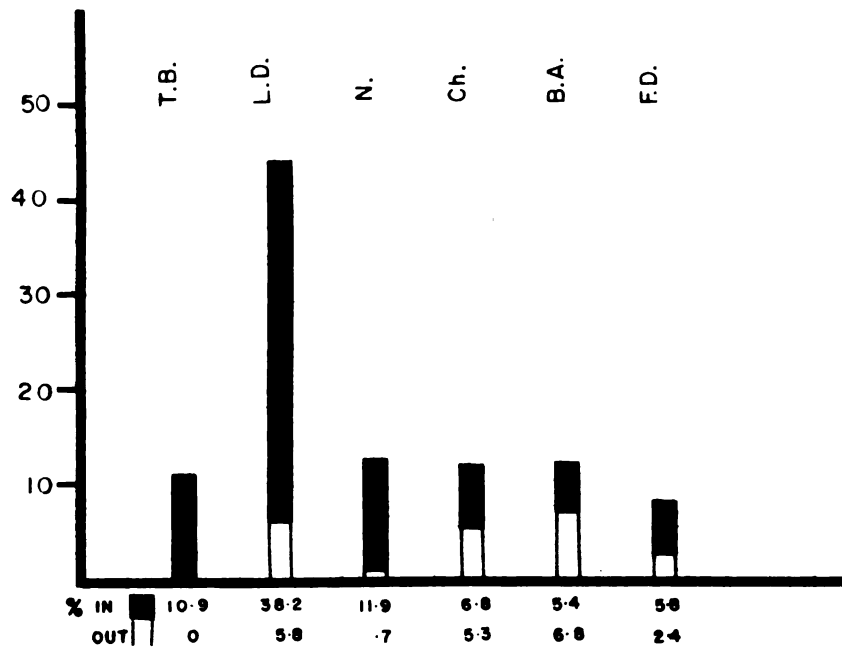
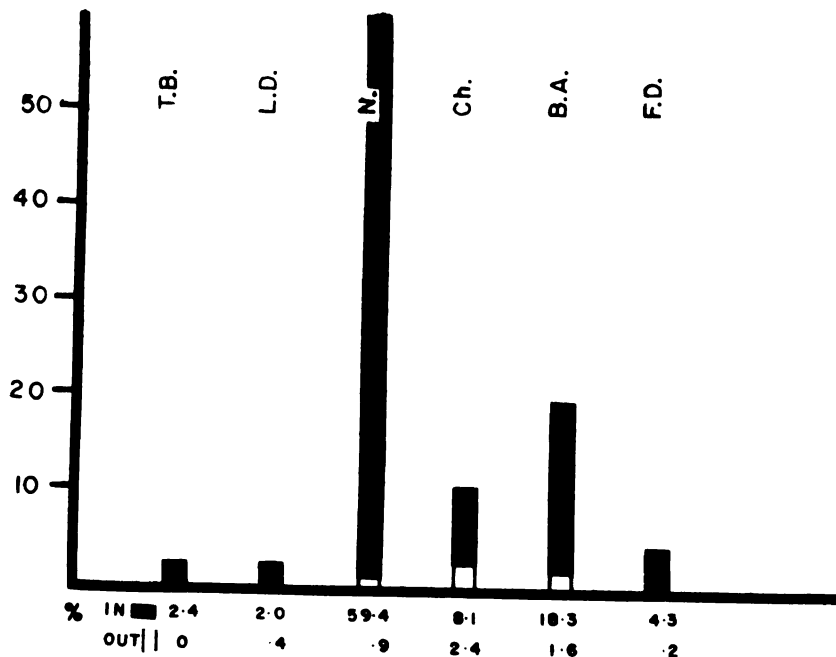


Figure 10. Pair D "Exposed". Percentages of the various displays (directed IN and OUT) per total displaying during all observation periods (T.B. = tail beat, L.D. = lateral display, N. = nip, Ch. = charge, B.A. = bite at, and F.D. = frontal display).



Pair E "Exposed" (1st mating) ♂



Pair E "Exposed" (1st mating) ♀

Figure 11. Pair E "Exposed". (1st mating). Percentages of the various displays (directed IN and OUT) per total displaying during all observation periods (T.B. = tail beat, L.D. = lateral display, N. = nip, Ch. = charge, B.A. = bite at, and F.D. = frontal display).

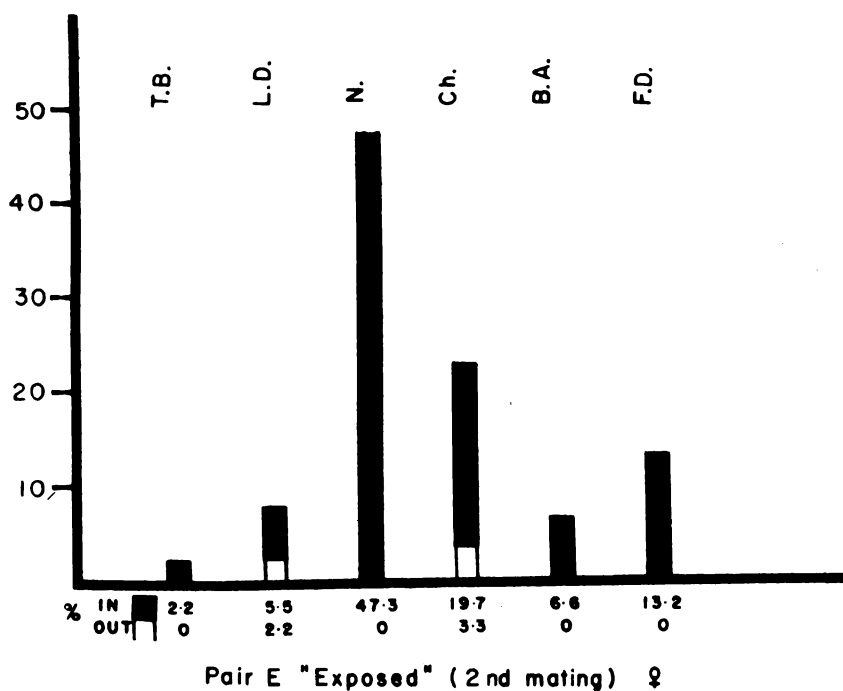
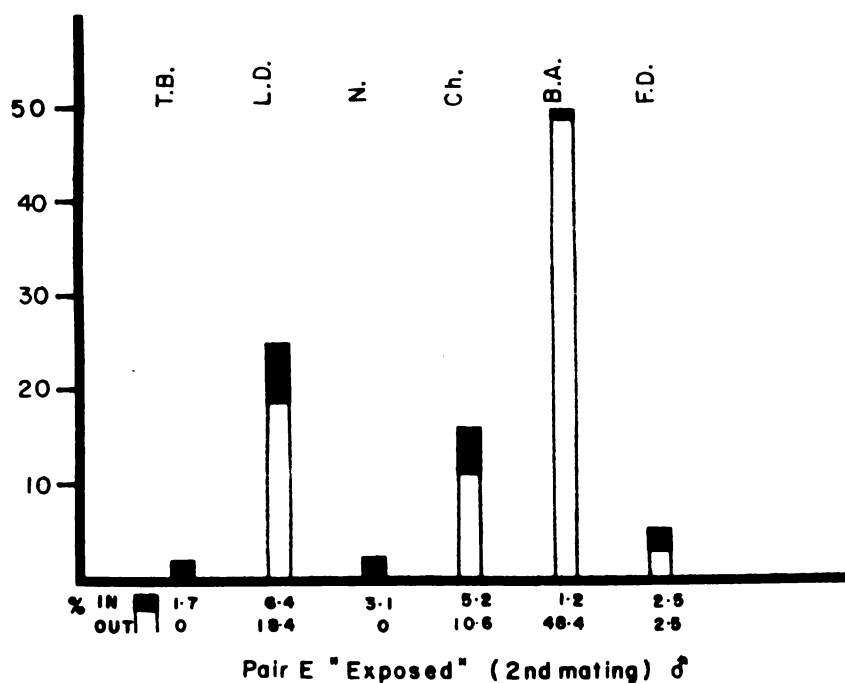


Figure 12. Pair E "Exposed" (2nd mating). Percentages of the various displays (directed IN and OUT) per total displaying during all observation periods (T.B. = tail beat, L.D. = lateral display, N. = nip, Ch. = charge, B.A. = bite at, and F.D. = frontal display).

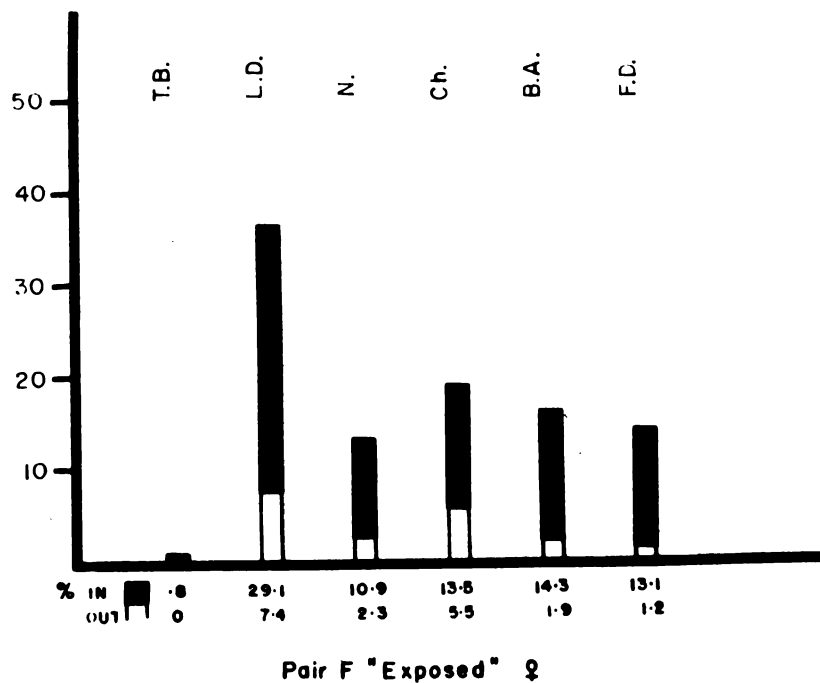
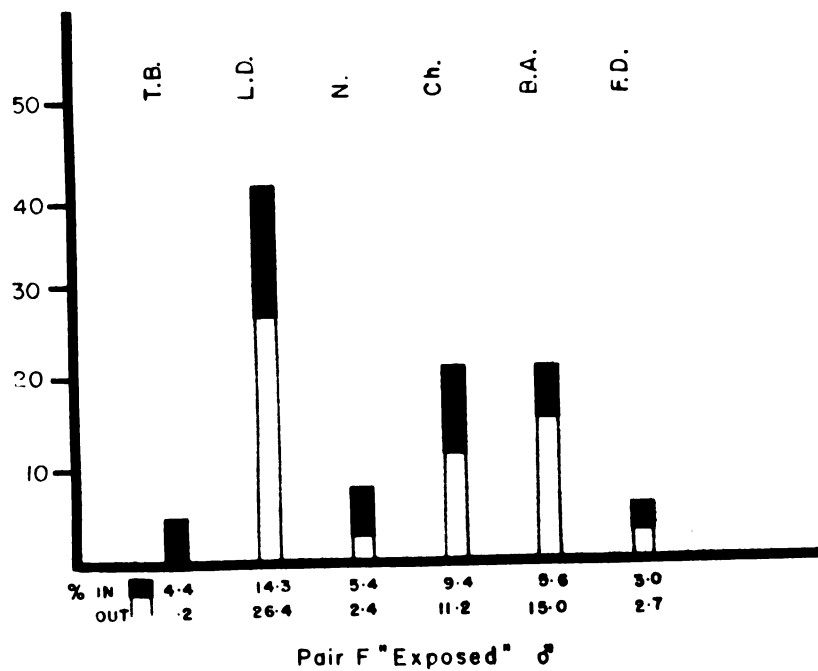


Figure 13. Pair F "Exposed". Percentages of the various displays (directed IN and OUT) per total displaying during all observation periods (T.B. = tail beat, L.D. = lateral display, N. = nip, Ch. = charge, B.A. = bite at, and F.D. = frontal display).

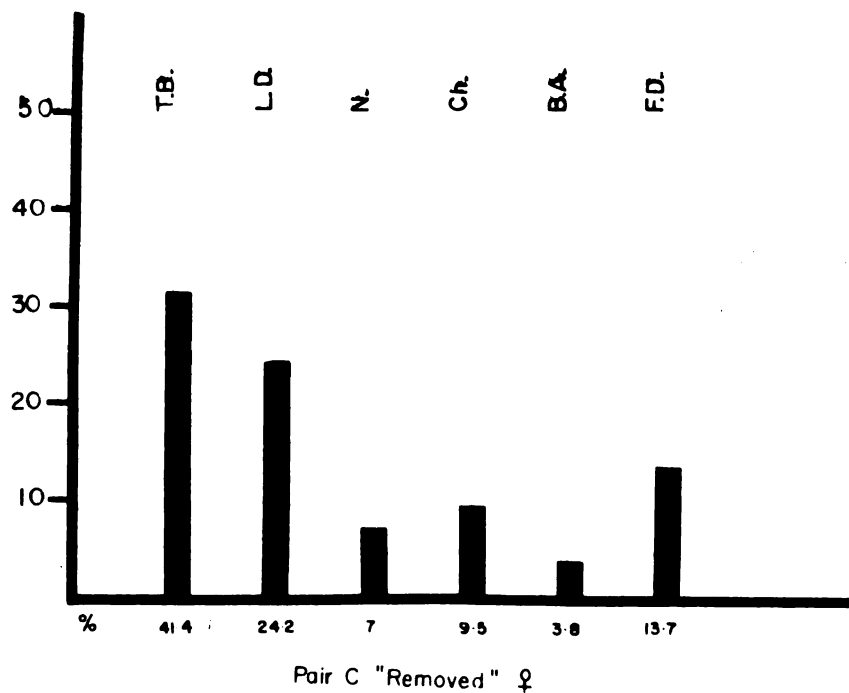
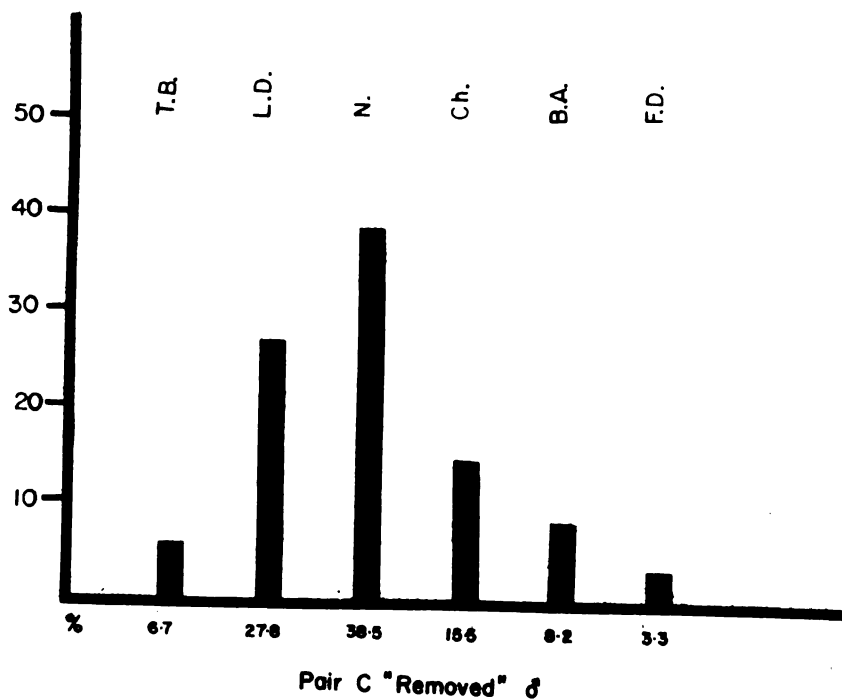


Figure 14. Pair C "Removed". Percentages of the various displays per total displaying during all observation periods (T.B. = tail beat, L.D. = lateral display, N. = nip, Ch. = charge, B.A. = bite at, and F.D. = frontal display).

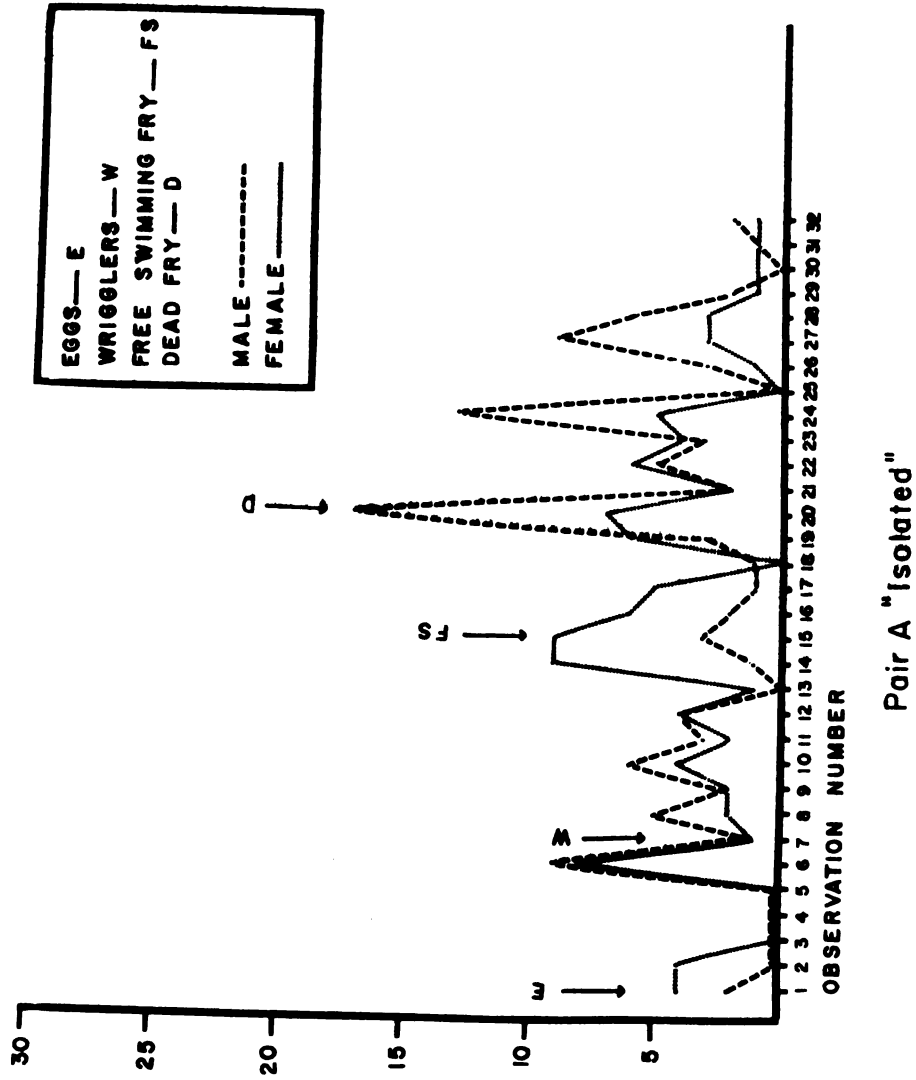


Figure 15. Pair A "Isolated". Number of total displays per observation period (number) during all ontological and viable stages of the young.

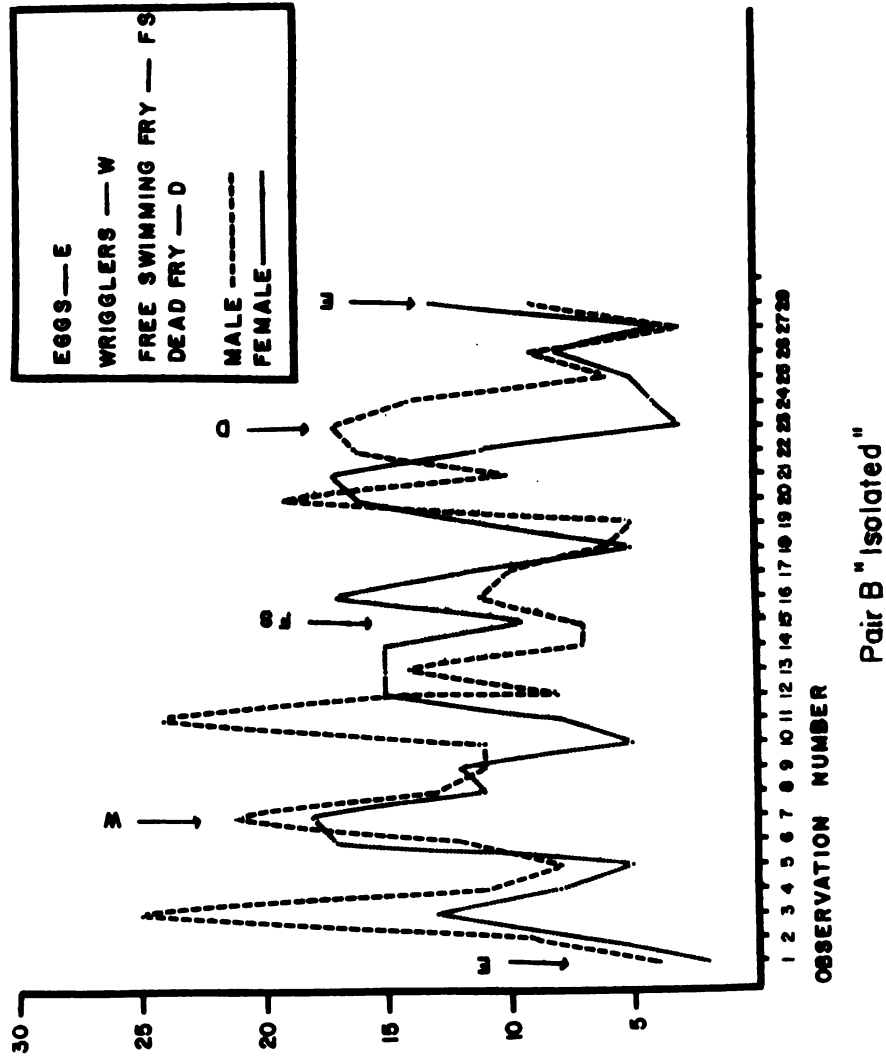


Figure 16. Pair B "Isolated". Number of total displays per observation period (number) during all ontological and viable stages of the young.

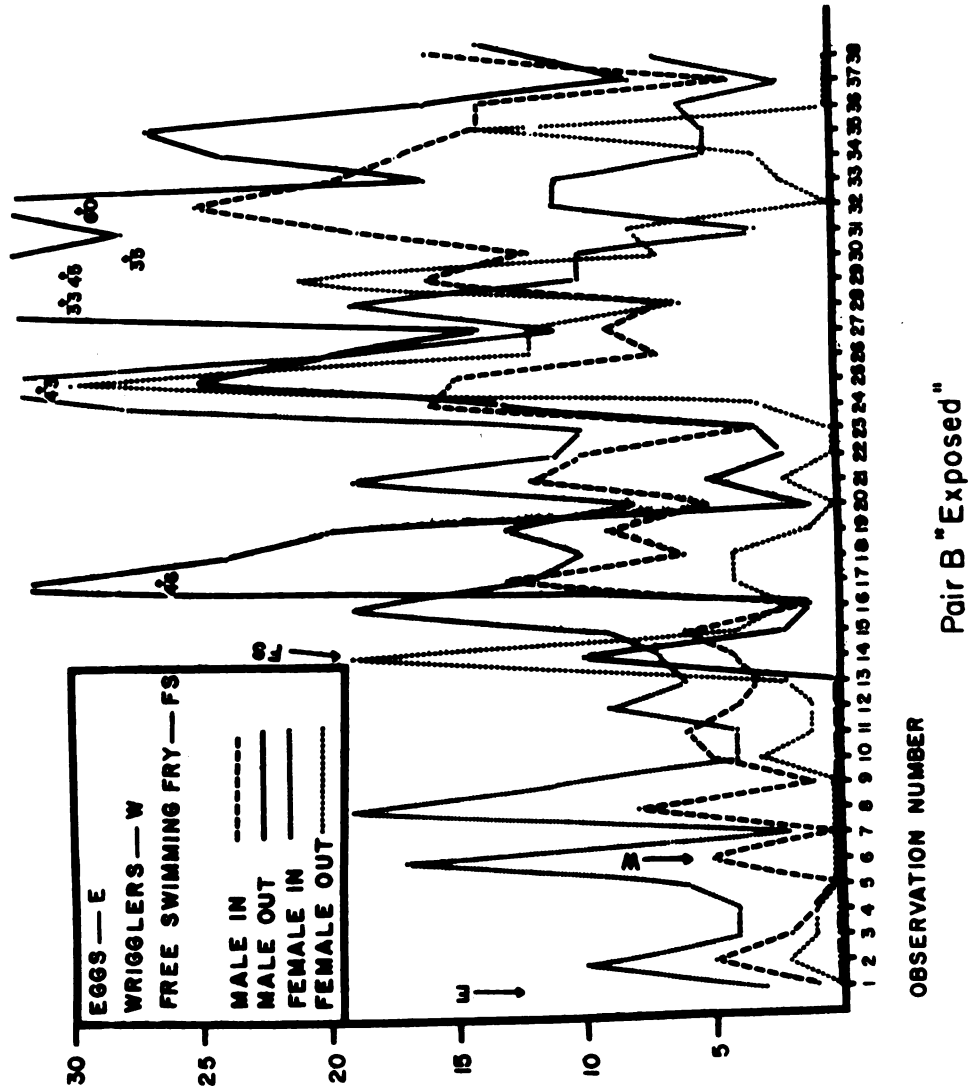


Figure 17. Pair B "Exposed". Number of total displays directed IN and total displays directed OUT per observation period (number) during all ontological and viable stages of the young.

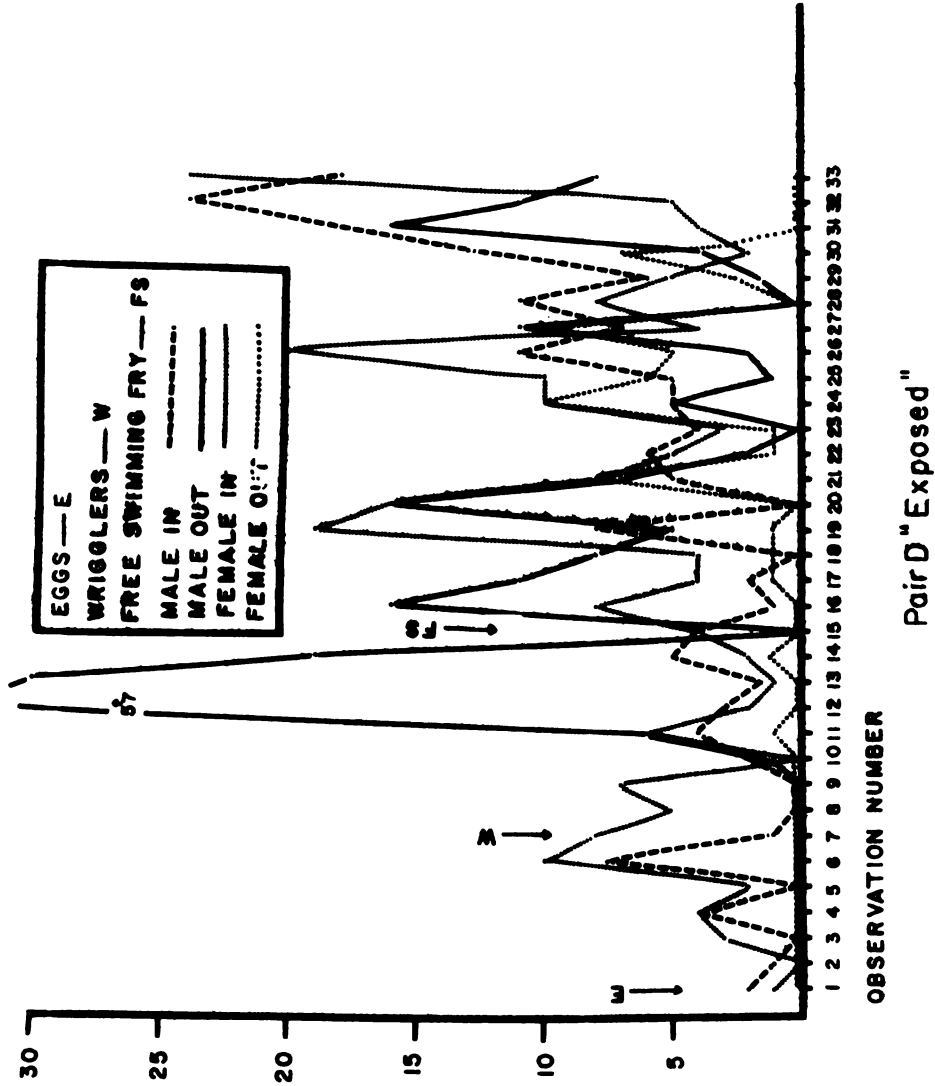


Figure 18. Pair D "Exposed". Number of total displays directed IN and total displays directed OUT per observation period (number) during all ontological and viable stages of the young.

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