

AN ETHOLOGICAL STUDY OF THE HONEY GOURAMI,  
COLISA CHUNA, AND ITS CONGENERS

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AN ETHOLOGICAL STUDY OF THE HONEY GOURAMI,  
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## PREFACE

The objectives of this study on the honey gourami, Colisa chuna and its congeners were: 1) to qualitatively and quantitatively describe courtship and reproductive behavior; 2) to elucidate the biological significance of observed behaviors; 3) to describe parental behavior; and 4) to make precise comparisons of behavior among C. chuna and its congeners based on qualitative and quantitative data for possible phylogenetic relationships.

I am indebted to Dr. R. J. Miller who suggested the study, served as major advisor and furnished assistance throughout the study. Thanks are due to Drs. A. Kent Andrews, L. T. Brown, C. Beames, Jr., and J. H. Shaw who served on the advisory committee.

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## CHAPTER I

### INTRODUCTION

Anabantoidei are African and Asian perciform fishes placed by Liem (1963) into four families, largely on the basis of osteological characters. Colisa chuna (honey gourami) and its congeners C. lalia (dwarf gourami), C. labiosa (thick lip gourami) and C. fasciata (giant gourami), along with the genus Trichogaster, were placed in the subfamily Trichogasterinae, the most highly specialized group of the family Belontiidae. The genus Colisa is native to India with some degree of sympatry among the species.

In a comparative study of behavior in the Anatinae, Lorenz (1941) stated that animal groups investigated must be ones which can be maintained well in captivity and must contain a large number of comparable species and genera exhibiting the maximum possible range of degrees of relationships. In addition he said that individual species should show interspecific resemblance and yet be distinct enough to present a test case for the homology concept. Anabantoids, including Colisa, fulfill these requirements and the latter group has been selected as the subject of the present study. The suborder is characterized primarily by (1) a specialized suprapharyngeal respiratory labyrinth organ, (2) elaborate and unique behavior patterns associated with this organ, (3) the deposition of eggs into a bubble nest by most species, and (4) stereotyped courtship and reproductive behavior patterns.

Forselius (1957) deals primarily with the behavior of Colisa lalia and hybrids between C. lalia and C. labiosa. To a lesser degree the behavior of C. fasciata, C. labiosa, and other members of the family Belontiidae were also dealt with. Noteworthy is the fact that Forselius (1957) did not study C. chuna. Also included in his monograph is a review of the systematics, distribution, endocrinology, and ecology of the anabantoid fishes.

Additional studies which deal with behavioral systematics in anabantoid fishes are those by Miller (1964) on Trichogaster trichopterus; Hall (1965) on Macropodus opercularis, T. leeri, and T. trichopterus, and Robison (1971) on T. pectoralis. Miller and Robison (1974) did a comparative study on the reproductive behavior and phylogeny of the genus Trichogaster.

Forselius (1957) and Miller (1964) described the basic units of anabantoid social behavior and pointed out the significant role played by aggressive activities in courtship and in defense of the nest. Sexual and nest discrimination in several anabantoids were described by Picciolo (1964).

Liem's (1963) study, based primarily on osteological data, reviewed group systematics and briefly discussed some ecological factors believed to be involved in the group's evolution.

Miller and Hall (1968) presented the first primarily quantitative description and analysis of reproductive behavior in anabantoid fishes. Wiepkema (1961), Nelson (1964), and others have pointed out the usefulness of such quantitative studies in clarifying underlying causal factors of such overt behaviors as courtship and reproductive patterns. Other anabantoid quantitative studies are by Wimmer (1970) on the moon-

light gourami, T. microlepis, and by Robison (1971) on T. pectoralis, the snakeskin gourami.

Colisa chuna, the honey gourami, and its congeners are the subjects of this study, based primarily on courtship and reproductive behavior of breeding pairs in aquaria. There has been no published investigation on the behavior of C. chuna. Regan (1909) and Day (1958) described the species but said nothing of its behavior or ecology. The species is listed in periodicals and in general handbooks for tropical fish hobbyists (Innes, 1966; Sole, 1966) but little is cited on its behavior. Janzow (1972, unpublished master's report) conducted a qualitative ethological analysis of C. chuna.

Besides the Forselius (1957) monograph, there are few behavioral studies on members of the genus Colisa. Reser (1969) conducted an investigation primarily to provide a qualitative description of courtship and reproductive behavior of C. fasciata. Secondarily, she presented quantitative data on these behaviors which may be used in a comparative study of the genus Colisa for determining phylogenetic relationships. Miller and Miller (1970) conducted a comparative study on agonistic behaviors of the anabantoid species, Trichogaster trichopterus, Macropodus opercularis, and Colisa lalia.

The present study, designed to complement that of Miller and Robison (1974) on Trichogaster, describes both qualitatively and quantitatively the courtship and reproductive behavior of Colisa chuna and its congeners and subsequently utilizes precise comparisons to propose phylogenetic relationships among the species of the genus.

## CHAPTER II

### METHODS AND MATERIALS

This study was carried out in two phases over two years in the Animal Behavior Laboratory of Oklahoma State University Life Sciences West Building. Uniform physical conditions were maintained in the laboratory throughout the study period by installed heating and cooling systems.

During the first phase of the study essential descriptive units of courtship and reproductive behavior were determined qualitatively for each species from routine daily 10 to 15 minute observations. Observations increased in frequency and duration with increased activity of the pairs (nest building, spawning, feeding, etc.).

Quantitative data on courtship and reproductive behavior were obtained during the second phase. Frequency and duration of selected behavior patterns were recorded. Greater emphasis was placed on quantifying information from the spawning phase of each species than for pre-spawning or post-spawning phases.

Fish used in this study were purchased from local tropical fish dealers or raised in the laboratory. They were separated by species and kept in stock tanks ranging in size from 33 x 76 x 41 cm to 45 x 180 x 30 cm. For most of the study period 36-40 pairs (1 pair/aquarium) were maintained for observation in experimental aquaria as follows: C. chuna and C. lalia in 27 x 51 x 30 cm and C. labiosa and C. fasciata in

27 x 61 x 35 cm. An additional long community aquarium, 45 x 180 x 30 cm, was utilized for general observations of C. chuna in groups of four pairs. Each aquarium had a gravel bottom planted with Vallisneria sp. and/or Ceratophyllum sp. and Hygrophila sp. All had thermometers for maintaining water temperature at 72 to 85°F (22-29°C). One or two clay pots in each, as well as plants, provided shelter and some protection for females. To decrease evaporation rate aquaria were covered with glass tops but two corners diagonally opposite each other were cut to allow space for heaters and circulation of air. For separating pairs when necessary, each aquarium was sectioned into two parts by a clear glass divider.

Lighting was provided by automatically controlled ceiling fluorescent lights and individual aquarium reflectors equipped with two 15 and 25 watt incandescent bulbs to produce a light gradient. Additional incandescent bulbs in the general area of the aquaria were used to attempt to make the transition from light to dark and vice versa less abrupt. These lights also were used to facilitate continuous observations and data collection, when necessary, for those pairs which spawned when the "daylight" lights were off. The photoperiod was 15 hours (6 a.m.-9 p.m.) June through August, and 12 hours (6 a.m.-6 p.m.) September to May.

For spawning purposes, the pH was maintained between 6.7 and 8.2. Occasionally, the pH was lowered and raised in an attempt to induce spawning in Colisa fasciata during the first phase of the study.

Fish were fed commercial flake food (Tetramin) and frozen brine shrimp (Artemia) twice daily. The diets were supplemented with freshly hatched brine shrimp, Daphnia, and Chironomis larvae when available.

Data were collected by use of prepared data sheets, notebooks, stopwatches, tape recorders, and by still and motion picture photography.

## CHAPTER III

### MAINTENANCE BEHAVIOR

Activity patterns referred to as maintenance behavior in this study are those that serve to maintain vegetative functions and presumably comfort of body and body parts. These activities generally are considered to be non-agonistic and non-social and occur commonly in daily existence.

#### Feeding

All four species of Colisa eagerly accepted both prepared and non-prepared food. However, when prepared flake food is offered first and frozen brine shrimp or live food such as Daphnia and Chironomus larvae are added, the fish will change from flake food to the latter. Frozen brine shrimp seemed to be preferred. As a rule, fish hesitated with fins extended, as if inspecting all live food, before eating. This may have been due to the irregularity of feeding of such items, which were sporadically available. Snails were nipped but were never observed to be ingested. Trichogaster pectoralis readily feeds on algae (Robison, 1971), but neither this nor other vegetation was observed to be eaten by Colisa species.

Dry prepared food floats at the surface for some time before sinking slowly. Frozen Artemia sinks immediately, and live food swims. Fish feed differently on different food. At the surface they suck in

floating food, while the body usually is held stationary at a 25-45° angle with the water surface by undulations of the pectorals and caudal fin. Median fins and caudal fins are partly to fully erected, while pelvics may be slightly extended forward or held posteriorly near the ventral surface of the body. While sucking in food, C. labiosa, C. fasciata, and C. lalia sometimes expel food from the opercle openings. Though this was never observed in C. chuna, it was common to see bubbles emerge from behind their opercle flaps during feeding.

Usually fish would consume floating food, then engulf sinking food a piece at a time, and follow some to the bottom and pick it up. There was no set sequence but feeding on the bottom mostly occurred when no food was left floating or suspended through the water column.

When bottom feeding, fish maintain the head and body at an angle from 30° to 110° with the substratum while they open and close their lips and suck food into the mouth cavity and swallow it. In this position the median fins may be slightly folded to maximally extended, pectoral and caudal fins undulate, and pelvics lie near the ventral surface of the body. During the process of bottom feeding, fish may momentarily engulf a single item, and swim off, or remain stationary and feed, or move forward and backward over the bottom in a vertical head stand searching for food. The latter style of feeding is very common in C. fasciata. Often, when moving forward and backward, fish will engulf gravel and spit it out as they feed.

The angle of the body to the substratum varies according to species. C. chuna and C. lalia seldom assume an angle greater than 45° when bottom feeding, and except immediately after being fed, they are rarely seen feeding at the bottom. C. labiosa feeds in a 45° to



perpendicular angle immediately after being fed prepared food which sinks to the bottom, but hours after feeding they do not commonly search for food, as do C. fasciata. C. fasciata feed in this manner while food can be seen on the bottom and at a greater duration and frequency during early evening and late at night. Several observations made late at night and early mornings in the light of a 7½ watt bulb hanging from the ceiling revealed C. fasciata vigorously searching the substratum for food. At the same time other species were not involved in feeding activities.

Small moving organisms such as live Artemia and Daphnia usually are first approached by an individual with fins extended. The fish engulfs the organism, spits it out, and then eats it. Usually after this apparent test of the food item, the fish would then actively seek out other individuals which were eaten without being spit out. Live Chironomus larvae which hit the bottom were seized in the fashion described for bottom feeding. C. chuna preferred Daphnia to a lesser degree than did its congeners and would ignore larger individuals.

On the basis of observations made in this study, it appears that pelvic fins were not utilized in searching for Daphnia, although this is done by Trichogaster microlepis (Wimmer, 1970), and fish commonly used pelvic filaments to investigate new objects placed in their aquarium. Even though no experiment was designed to test such a conclusion, it appears that the four Colisa species depend heavily upon sight in feeding.

Perhaps the most fascinating feeding method used by Colisa spp. is a common activity referred to as jetting. Jetting, defined by Hall (1965) in a post-spawning context rather than feeding, is emission of

bursts of air and water through the nest. It is done by projecting the snout above the water surface, gulping air, moving to a spot below the surface, and forcefully squirting air and water from the mouth in the form of an arc. In a feeding context, fish observed in this study would display jetting 15-30 minutes after food was placed in the tank. The frequency and forcefulness of jetting appeared to vary with the location of the intended food object jetted at. Usually, the object was attached on the side of the aquarium. C. fasciata, in particular, often jetted among the vegetation in the corner of its tank where it routinely fed. Fish have been observed jetting while patrolling about searching for food several hours after food was last added to their tank. Jetting will be discussed further in another section dealing with post-spawning behavior in C. chuna and C. lalia.

In aquaria where social hierarchies exist, social structure tends to break down at feeding time. During lengthy feedings the fish appear to return to their previous hierarchial structure with large males dominating sub-adults and females. If surface feeding, dominant fish stay at the surface, while sub-ordinate fish hesitantly feed at lower levels. In tanks containing one male and one female, aggression toward the female by the male is very common. The intensity of aggression depends upon the motivational state of the male. Aggression directed at the female is most intense when males are in a parental stage, and the female often is not allowed to eat at all. However, in most other states the female manages to feed successfully.

#### Inspiration

Colisa spp. utilize two methods of inspiring with variations of

each depending on the ongoing behavior. The two methods will be termed stationary at surface (multiple-air snapping) and non-stationary at surface (single air snap).

Stationary-at-surface inspiration occurs when fish maintain the body at an angle (20-30°) with the water surface while breaking the water-air interface with the snout and gulping in air several times in succession for long durations. Median fins are partly to fully erect, the caudal may or may not undulate, the pelvics are slightly extended forward or depressed somewhat while the fish maintains itself in this position by undulations of the pectoral fins. This method of inspiration is used commonly by males during nest construction, by females early in the pre-spawning phase, and by both sexes when ill.

Non-stationary-at-surface inspiration is the more commonly utilized method except during male reproductive behavior. It occurs when a fish swims directly upward with dorsal fin depressed, ventral fin extended, caudal slightly moving, pectorals undulating, and pelvics held close to the body. Upon reaching the surface, the mouth is opened and air gulped (an air bubble is often released from the opercle opening). The fish then returns to ongoing activity. During periods of stress and excitement fish dash to the surface rapidly and return to original positions. Usually, when the water surface is broken a loud sound can be heard as a vertical projection of water appears.

#### Resting

Fish non-interacting and stationary for long durations were considered to be resting and sometimes sleeping. This posture was assumed at any depth, but most often within 2-4 centimeters of the surface or

on the bottom. Usually, the only moving fins are the pectorals, which undulate slightly, while others are slightly depressed. When lights are out, resting males with nests position themselves near the nest in upper water levels, while males with eggs or wrigglers (larvae) position themselves directly beneath the nest with their body appendages in much the same position they are in during stationary-at-surface inspiration. Resting was most common when lights were out, and during darkness fish did not readily move when disturbed. This state might be termed sleep. Resting was most common when lights were out, but C. fasciata was exceptional because they were less active during light and very active in the dark. When resting, C. fasciata tended to rest at the bottom. C. chuna males were active during the dark period when in the parental care phase.

#### Comfort Movements

Movement patterns which appear to alleviate discomfort for fish which are restless were first described by Baerends and Baerends-Van Roon (1950) for cichlid fishes. Miller (1963) reported that sunfishes do not usually appear restless before such movements occur or more comfortable afterwards. However, she found these movements do appear to occur with greater frequency when the animal is under stress caused by social and/or other environmental conditions. These observations apply also to Colisa spp. Movement patterns referred to here as comfort movements are those which appeared to be deliberate movements to remove irritants or stretch the body. All movements listed were not necessarily observed in all four species of Colisa and no record was made of their relative frequency.

### Yawning

Jaws appear to be opened and extended maximally while the opercles are slightly spread and median fins are partly to fully erected. The process of yawning is simultaneously carried out with median fin erection.

### Head Jerking

The head and anterior body is rapidly moved back and forth laterally. This pattern occurred in both sexes of all four species most often when fish were engaged in what has been termed erratic swimming back and forth along the side of the tank. Head jerking was reported for T. leeri (Hall and Miller, 1968); for T. microlepis (Wimmer, 1970); and for T. pectoralis (Robison, 1971).

### Mouth Snapping

This term used by Miller (1963) describes a behavior probably similar to that observed in cichlids (Baerends and Baerends-Van Roon, 1950). Fish open and shut the mouth in rapid succession, producing an audible clicking sound. At times air may be emitted from the mouth and opercle openings.

### Fin Flicking

Anal, dorsal, pectoral, or pelvic fins are individually erected and depressed with high frequency. This comfort movement, which can occur anytime, appears to be the most common one performed by all species, but especially by C. chuna. As in T. pectoralis (Robison, 1971), Colisa species tend to display dorsal fin flicking most often.

### Chafing

Chafing is accomplished by bringing some part of the body, usually the flanks or belly, into a rapid brush against some stationary object such as a plant, pot, heater, or the gravel bottom. Several of these deliberate movements are usually performed in succession, and next to fin flicking, it is the most common comfort movement recorded for Colisa spp.

Coughing, which was observed by Robison (1971), Miller (1963), and Baerends and Baerends-Van Roon (1950), was never observed during this study. C. chuna made the fewest comfort movements. Yawning, which was easily identified in C. fasciata, C. labiosa, and C. lalia, was never seen in C. chuna. Perhaps the low frequency of the other movements and absence of yawning may be due in part to the small size of C. chuna, which made some of these movements difficult to see from usual observation distances. Because of C. chuna's size and speed in performing all activities, observation and recording had to be done from less distance than with the other species, and casual observations possible on the other species were not possible for C. chuna.

## CHAPTER IV

### DESCRIPTION OF GENERAL SOCIAL MOTOR PATTERNS

Activity referred to as motor patterns in this study are patterns which are easily recognized units, occurring frequently in threat, fighting, and courtship behavior and appear as communication signals in social encounters. These patterns have been described for C. fasciata, C. lalia, and C. labiosa as well as for some species of Trichogaster by Forselius (1957), for C. lalia by Miller and Miller (1970), and for C. fasciata by Reser (1969). Forselius (1957) described them under the broad heading, "Description of Agonistic Behavior Elements," while Baerends and Baerends-Van Roon (1950) described these patterns for Cichlid fishes as "signal movements" serving as "animal language." The terminology used in this study will follow that for detailed description of motor patterns in T. trichopterus by Miller (1964) and T. trichopterus and T. leerii by Hall and Miller (1968).

#### Approach

Approach is any deliberate movement by one fish toward another without previous immediate interaction; approach varies in intensity, depending on the motivational state of the performing fish and is frequently initiated by a dominant fish. The movement may be rapid or slow with median fins maximally erected to maximally depressed. Usually, a female approaching a male under his bubble nest does so with fins

slightly to fully depressed. Aggressive approaches by male or female (less so by females) may be executed with open gape, pelvic fins extended forward, and median fins erected.

#### Lateral Display

Lateral display is accomplished when fish spread their median and caudal fins to varying degrees depending on the intensity of activity at time of display. It is most commonly observed when fish are involved in agonistic, reproductive, and group feeding activities.

#### Sigmoid Display

Sigmoid display appears to be an intense form of lateral display. Median fins are erected to a maximum degree while the lateral axis of the body curves into a S-shaped posture. It is most often observed in males during intense male-male agonistic encounters and during male-female reproductive encounters. When this posture is frequently displayed and is increasing in duration, it often develops into tail beating.

#### Tail Beating

This usually develops during lateral display when activity is very intense. Caudal peduncles and tails are forcefully undulated laterally by two fish seemingly swimming in place side by side. In most encounters, orientation is head to tail.



### Butting and Biting

Butting is performed when one fish deliberately thrusts at or gently nudges the other with its mouth closed. When they are butting males under the nest, females usually are less intense than are males during reproductive periods or in agonistic activities. Biting is similar, except performed with extreme intensity and with the mouth open. Bites are less common than butts and may be missed by observers, especially in chuna.

### Carousel

Carousel occurs during the spawning phase, usually following incomplete clasp while male and female are engaged in intense agonistic activity well below the nest. The two fish circle each other head to tail while seemingly attempting to bite each other. This corresponds to Forselius (1957, 178) "normal swimming position [horizontal circling in a vertical position (HCIVP, Fig. 20A)]".

### Chase

This is the pursuit of one fish after another. Females are most often chased by males during courtship and reproductive periods. It is also very common during agonistic encounters when one fish tries to escape from another.

### Fleeing (Escape)

Rapid retreat by any fish from an encounter with a conspecific is termed fleeing.

### Vertical Display

There is no previous reference to vertical display in the literature on anabantoid behavior. In this study it was found to be unique to C. chuna. Males perform this behavior before females during courtship and reproductive phases and for other males at territory boundaries.

The exhibiting fish assumes a head-up vertical position with median fins maximally erected, caudal fins spread and fluttering, and pelvic fins hanging down. In most instances, this posture is assumed simultaneously with a sigmoid posture and terminates in strong lateral beats of the caudal peduncle and fin. The displaying fish is usually oriented toward and close to the conspecific, the distance varying with the situation. The display is discussed also under prespawning behavior patterns.

### Appeasement

There is considerable variation in appeasement posture within and among the four species of Colisa, depending on context and motivational state. Overall, there are two easily recognized patterns: "drooping," a common appeasement posture described throughout the literature on Trichogaster, and "breasting," a less common pattern first described by Wimmer (1970) in his study of T. microlepis.

"Drooping" is the behavior of a subordinate male or female terminating an encounter with a conspecific by folding the median fins and drooping the caudal peduncle and fin to one side. The appeasing fish in this posture immediately tilts its body laterally or vertically, downward or upward with its abdomen or flanks exposed to the attacker. The

appeasing fish may assume this posture and receive one or more butts and/or bites from the attacker or it may intermittently display this posture while fleeing from attacking fish.

"Breasting," the less common but not infrequent appeasement posture, was observed in all four species but appeared with greatest frequency in C. chuna. Wimmer (1970) introduced this term specifically to describe a female appeasement posture in T. microlepis. This posture is exhibited by male and female C. chuna, but by females only in its congeners. Generally, the posture is assumed by a subordinate fish when slowly approached by a dominant fish. The body of the appeaser is raised to an angle approximately  $60^{\circ}$ , exposing its soft parts to the attacker. Median fins are slightly erected, while pelvic fins are slightly extended forward. During approach by dominant fish, the appeasing fish may lean somewhat to the side. Breasting fish are attacked less than are fish utilizing the drooping positions.

During courtship and reproductive phases C. chuna males may perform breasting to approaching females. This posture almost appears to be a less intense stage of the vertical stand. The male moves to the edge of his nest and assumes the breasting posture for an approaching female, which begins to nudge (slight butt) his antero-ventral region as he moves slowly backwards to a position beneath the center of the nest. Functionally, this behavior pattern may decrease aggressive tendencies in both male and female as well as attracting the female to a position under the nest, thereby increasing chances of a successful spawn.

Picciolo (1964) reported that C. lalia females were significantly attracted to models which mimicked the bright blue antero-ventral

region of male conspecifics. In the breasting C. chuna male, maximum display of the dark blue-black antero-vertical region is exposed to the female, thus enhancing its signal value.

#### Opercle Spread

Opercle spread is very rare if it occurs at all in the four species of Colisa. A slight extension of the opercle flap was possibly observed in C. lalia and C. labiosa during pendulum movements which developed into mouth fighting between males and females. Opercle spread has never been observed in C. chuna and C. fasciata.

#### Mouth Fighting

In C. chuna, C. lalia, and C. labiosa mouth fighting occurs more often than in C. fasciata, where it was observed only once during this study. The pattern of performance by Colisa is basically the same as described for T. trichopterus (Miller, 1964; Robison, 1971). It was observed in male-female and male-male encounters, the latter frequently at territorial boundaries and in cornered individuals. Opponents meet each other head on in a back and forth movement (pendulum movement) with pelvic fins extended forward and dorsal and anal fins folded. Gripping of the jaws, observed by Miller (1964) in T. trichopterus, is rare or absent in Colisa, which only push with the mouth open. Opercle spreading, which occurs at this time in some species, is rare in Colisa. Mouth fighting may develop into intense butting and chasing and/or tail beating.

## Bout Terminology

Courtship and reproductive behavior patterns occur in recognizable, discrete bouts in all species of Colisa as in Trichogaster (Miller and Robison, 1974). Most of the following terms have been used by Forselius (1957), Miller (1964), Miller and Hall (1968) and Miller and Robison (1974) and are used in this study to represent various behavioral events utilized in the analysis.

### Spawning Sequence

The complete series of male-female interactions comprising pre-spawning, spawning, and postspawning activities; corresponds to "mating cycle" of Forselius (1957).

### Pre-spawning Phase

The prespawning phase is characterized by courtship and/or aggressive bouts that precede the first successful spawning bout.

### Spawning Phase

This phase includes the period from the first to the last successful spawning bout during the spawning sequence and includes all bouts and intervals within this duration.

### Post-spawning Phase

The postspawning phase is that period following the last successful spawning bout. This phase is terminated when the female remains in seclusion for long intervals and the male displays extreme aggressive behavior toward her while guarding the nest.

### Bout

This is any social interaction by two or more fish.

### Sexual Bout

Male-female interaction containing sexual responses by one or both individuals.

### Spawning Bout

Spawning bouts include sexual bouts in which clasping and oviposition occur. This definition corresponds to the "spawning cycle" of Forselius (1957).

### Swimming Inhibition

Following the release of the clasp in spawning bouts and pseudo-spawning bouts, usually both fish sink without control and orientation and for a few seconds are immobile. Swimming inhibition ends abruptly when fish regain control.

### Pseudospawning Bout

This term refers to a sexual bout which is identical to a spawning bout except that neither fish releases gametes, although swimming inhibition may be exhibited by male and/or female.

### Clasp

After preclasp as the female mounts and puts her snout above his back near his dorsal origin, the male clasps the female by bending his body around her so that his head and caudal fin nearly touch each other.

### Clasp Bout

A type of incipient spawning bout which advances only to the clasp stage. In this bout gamete emission and swimming inhibition do not occur.

### No Clasp Bout

A sexual bout that does not precede to the clasp stage.

### Interval

This term refers to the period of time between bouts when there is no visible interaction between fish.

### Pre-Clasp Time

Refers to the period of time beginning with the direct approach of the female to the male under his nest until they attempt to clasp. It does not depend on the outcome of the clasp.

### Circling

Fish orient themselves head to tail and swim in a circle.

### Circling Time

The time from the start of circling until the end.

### Multiple Clasp Bout

Bouts containing two or more clasps before the female leaves on her own or is chased away by the male.

Successful Spawn

Synonymous with a spawn or spawning bout.

Unsuccessful Spawn

Refers to any bout short of oviposition.



## CHAPTER V

### NEST BUILDING ACTIVITIES

Colisa males in the reproductive stage usually acquire a territory in which much time is spent constructing a bubble and/or bubble-vegetation nest, which becomes the center of activity throughout the spawning sequence and parental phase. The intensity of nest construction varies among species, as might be expected, as well as during the course of the spawning sequence intraspecifically. There is variation in the nest structure due to varying bubble blowing techniques and utilization of materials other than foam bubbles.

The nest serves as a repository for the deposition and development of eggs, keeping them at the air-water interface where eggs and young are exposed to atmospheric oxygen for respiration. In Colisa, as in other anabantoids, it is not an absolute prerequisite for the release of gametes. Several pairs of C. chuna, C. labiosa, and C. fasciata were observed spawning without a nest. C. lalia was the only species not seen spawning without a nest, but Forselius (1957) reports that C. lalia also will spawn without constructing a nest. Often, when there was no nest at the beginning of a spawning phase, bubble blowing was initiated during this phase and would increase in frequency and intensity through the post-spawning phase. During the parental stage, after the eggs develop into larvae, the nest appears to function as a nursery for further development of young and their protection against predation.

However, C. fasciata and C. labiosa were observed going through the entire spawning sequence without a nest, and as a result, eggs and larvae floated throughout the tank.

The presence of a ripe female is not necessary to initiate male nest building activities in Colisa. This study confirms what Forselius (1957) found in Colisa. Miller (1964) found this to be the case for T. trichogaster. Isolated males in all four species have been observed bubble blowing, which in some instances lasted several days with intervals of varying duration when no activity occurred. C. chuna, in particular, followed a pattern in which bubble blowing began shortly after lights went on and continued until approximately 10:30 a.m., resumed near 1:30 p.m., and continued until 5:00 or 6:00 p.m., and resumed again an hour or so before lights went out. This pattern of bubble blowing also occurred in the male of a pair that had previously completed a spawning sequence and the female was not ready to spawn again. In some C. chuna pairs, males would blow bubbles intensely for one to three days, then court the female and cease nest building to the point that the nest dissipated. The pair would then spawn without a nest, and during the parental stage the male would blow a raft of bubbles for the wrigglers.

Nest building activity in Colisa increased in frequency and intensity through the pre-spawning phase and reached its peak in this phase just before the onset of the spawning phase. After spawning, it increased again to its greatest intensity and duration. C. chuna males show an additional peak in nest building when the eggs develop into wrigglers.

Attempts were made initially to keep an active record of nest

size, but it was soon obvious that there was so much variation within individuals as well as among individuals that data on nest size became meaningless. Sizes ranged from a raft of bubbles the size of a quarter in C. chuna, C. fasciata, and C. labiosa to a C. chuna raft of bubbles covering one-third the surface of a 10-gallon tank. The size, depth, and shape of nests varied greatly, and no correlation between nest size and size of males was found in this study (as suggested for C. lalia by Forselius, 1957). Miller (1964) and Robison (1971) observed no correlation between male size and nest size in their studies of T. trichopterus and T. pectoralis, respectively. Wimmer (1970) found that nest size in T. microlepis is usually proportional to the amount of available vegetation suitable for nest construction.

#### Site Selection for Nest

In all four species the site selected for constructing the nest is usually in an area of the aquarium with a fair amount of protection and cover from external disturbance. However, if vegetation is too thick, males will choose an area with very little vegetation or utilize the sides of the aquarium to anchor nests. Perhaps this is done to allow space for maneuvering beneath the nest. Prior to nest site selection it is not uncommon to see males moving about the tank at the surface, stopping and engaging in rather long periods of air snapping followed by release of a few bubbles. This behavior is thought to be indicative of attempts by the male to select a nest site.

Usually C. chuna chooses areas relatively more dense than do the other species, probably because of its size and bubble blowing pattern, since a smaller body will require less space to maneuver in. Then, too,

C. chuna blows a single bubble layer nest which tends to be scattered among vegetation. Denser vegetation might be less attractive to larger fish and aquatic animals, and thereby afford more protection for C. chuna and its spawn.

Colisa fasciata and C. labiosa usually select an area of the tank with a fair amount of rooted vegetation growing upright, especially among long Vallisneria leaves with tips floating outward at the surface. Coincidentally, this area was usually in one of the back corners of the tank. Both species tended to select a corner away from the viewing side.

Colisa lalia alternated air snapping and bubble blowing activity at the surface with swimming to various areas to snip pieces of vegetation, which might then be dropped or carried to the surface where previous air snapping and bubble blowing took place. Finally, after a few hours or days the male would begin to blow bubbles in an area among vegetation with a clearing beneath. The male usually made his exit or entrance to and from this clearing. Often the chosen area would be where there was the most abundant supply of algae, which was the dominant source of plant material utilized by C. lalia males for nest construction.

#### Bubble Blowing

Colisa chuna, C. labiosa, and C. fasciata nests in aquaria are constructed entirely of air bubbles anchored to some stationary object. Forselius (1957) suggested that C. fasciata and C. labiosa actively incorporate some vegetation in their nests, but this was not seen during this study. The only species of Colisa to actively seek vegetation

and other material for construction of its nest is C. lalia (See Table 1). Vegetation makes up the major structural support portion of C. lalia nests. Bubbles are an equally important element which serve as a source of air for respiration and as a lift for elevating the vegetation portion above the water surface.

At the air-water interface anabantoid fishes inspire air that is transformed into small bubbles coated with mucus secreted from unicellular glands in the buccal cavity, and then released in several forms during bubble nest construction. Colisa species utilize two principle types of motor patterns for bubble nest construction; surface inspiration with surface release and surface inspiration with subnest release. Opercular emission of a few large bubbles was reported to be a method of bubble blowing in T. microlepis and T. pectoralis by Wimmer (1970) and Robison (1971). In this study opercular omission of a few large bubbles occurred rarely and was observed only occasionally throughout the spawning sequences among the four species. Because of this, the fact that it sometimes occurred away from the nest, and its similarity to opercle emission after air inspiration, opercle emission was not considered a source of bubble nest construction in Colisa. Jetting occurred in feeding contexts and in the parental stage.

Although Colisa females were observed blowing bubbles, none constructed or maintained a nest as reported by Forselius (1957) in C. lalia females. Bubble blowing by females seemed to appear when they were separated from their male by a clear glass partition and when there was no partition but they seemed to have a strong motivation to spawn before the male was ready. Females' bubbles are usually few and short lasting.

Table 1. Comparison of nest building among species of the genus Colisa

	<u>C. chuna</u>	<u>C. lalia</u>	<u>C. labiosa</u>	<u>C. fasciata</u>
Male nest building	present	present	present	present
Female nest building	absent	absent	absent	absent
Active incorporation of vegetation into nest	absent	present	absent	absent
Nest pushing	absent	present	absent	absent
Surface inspiration with surface release	present	present (rare)	present	present
Surface inspiration with subnest release	absent	present	present	present
Opercular air emission	present	present	present	present
Jetting	present	absent	absent	absent
Inspiration preceding expulsion of bubbles	present	present	present	present
Active formation of eggs into ball	present	absent	absent	absent
Changing egg location	present	absent	absent	absent

### Surface Inspiration with Surface Release

Surface inspiration with surface release in C. chuna, which blows a single layer raft-like nest, is the only type of bubble blowing used by that species and is performed slightly differently than in the other species. When blowing bubbles by this method, all species position themselves beneath the surface of the nest with snout up and body at about a 20-30° angle with the surface. The dorsal fin is usually slightly folded, pelvic fins are held downward, pectorals are undulated alternately, and the caudal fin moves somewhat, maintaining the fish in one location; combined action of the pectorals and caudal allow change in position. The slight difference in C. chuna and its congeners lies in the way C. chuna releases bubbles after gulping air while hovering at the surface. C. chuna males gulp in air and release a single bubble after each gulp, whereas the other males gulp in air then spew out a cluster of bubbles which form into a shallow collection. This pattern of bubble blowing by C. chuna coincides with that of Macropodus opercularis and Betta splendens (Forselius, 1957).

Colisa lalia, C. labiosa, and C. fasciata perform surface inspiration with surface release less frequently than they do sub-nest release. It occurs most commonly in the beginning stage of the prespawning phase and may appear again during the parental period. When blowing bubbles by the surface release method, the nest appears as a single raft-like structure. Forselius (1957) reported that C. lalia use only the sub-nest release method of bubble blowing. The first evidence of a C. lalia nest in this study was the presence of a small, single layer ring of bubbles blown by the surface release method. The next stage was the selection of non-bubble material which was placed beneath this raft of

bubbles.

#### Surface Inspiration with Sub-Nest Release

This is a major bubble blowing pattern for nest construction in C. fasciata, C. labiosa, and C. lalia. It was absent in C. chuna observed in this study. Functionally, sub-nest release appears to allow bubbles to pile up in the center of the nest, and eventually in C. fasciata and C. labiosa the center of the nest may extend 2 to 5 centimeters above the water surface while the diameter may extend to 20 cm. During performance the male positions himself at the surface at an angle a bit greater ( $45^{\circ}$ ) than when he uses surface inspiration with surface release. He then gulps or snaps air one to several times, swims below the nest, makes one to two turns in a circle as if searching, and releases a cloud of bubbles from the mouth. This process occurs most frequently during the pre-spawning phase and with less frequency in the spawning phase. It is repeated over and over again with occasional interruptions. The third (bottom) layer of the C. lalia nest is constructed by sub-nest release.

#### C. lalia

Colisa lalia is the only species of Colisa which actively seeks vegetation, detritus, and even gravel for nest construction. Though there was usually a population of snails in each aquarium, they were never actively incorporated in the nest, as T. microlepis males were reported to do (Wimmer, 1970). The latter also used vegetation in constructing their nests (Wimmer, 1970). To the contrary, snails near the nest were vigorously poked by C. lalia males until they descended,



usually by dropping to the bottom. During non-reproductive phases snails were ignored by C. lalia.

A detailed description of nest construction will not be presented here, since most observations agree with those of Forselius (1957), who dealt specifically with C. lalia behavior in his monograph. Only a general account will be presented and points which tend to differ from or extend the finding of Forselius (1957) will be emphasized.

C. lalia builds its nest in layers with the intensity and frequency of occurrence of the various motor patterns, varying with the phase of the spawning sequence, time of day, stage of development of the nest, and in response to other biological and physical parameters affecting the species. The nest is usually built in the following order: a single layer of bubbles, a layer of plant material and detritus, and a second lower layer of bubbles.

Most tanks contained green filamentous algae that served as the primary source of vegetation used by C. lalia in nest construction. In two C. lalia tanks which had been cleaned and contained no algae but which contained Vallisneria with leaves floating at the surface, the resident males built nests by arranging the leaves so that they crossed and were interwoven somewhat. More bubbles were used here than in nests built with algae. Also of interest was the fact that these nests were of short duration. The male had to basically rebuild them each day.

Nest building activities in C. lalia (as in its congeners) is most frequent during the pre-spawning phase. Males were never seen building their nests in the dark, as were C. fasciata males. Nest building usually began in the morning and continued all day.

A male usually began a nest by blowing a single layer of bubbles

utilizing the surface inspiration with surface release method. He then would seek out and bring clumps of algae to the surface until a very distinct mat or plate of vegetation containing bubbles released from mouth or opercle was formed. Periodically, the male would snip off frayed edges or stems of other plants and bring these to the nest. Perhaps in nature, as in aquaria, male choice of vegetation depends to some extent on the configuration of plant material available--its size, texture, abundance, and thickness. During this time nest pushing occurs frequently after each return to nest with vegetation, and appears to mend the nest and make it more compact. After an extensive period of this kind of building, the nest is often several centimeters deep and dome-shaped. Usually, after some time, the original single layer of bubbles blown at the beginning of nest construction has dissipated and the top of the nest is seen as vegetation only.

Once the vegetation layer is formed, bubble blowing by surface inspiration with sub-nest release becomes the most common pattern utilized by the male in building its nest. This pattern may be used from 1 to 5 hours, depending on the individual male and his motivational state. It is the predominant pattern during the latter portion of the pre-spawning phase, but is by no means the only method used. During this stage the male may bring additional vegetation, detritus, and even gravel to the nest.

During the spawning phase nest building activities are rare to absent. Nest building by surface inspiration with sub-nest release picks up again at the commencement of the post-spawning phase. However, in this phase it is not nearly as frequent or intense and is of short duration.

In his discussion of nest building activities, Forselius (1957) discusses glueing behavior in C. lalia. This behavior, as described by him, was not observed in this study. He also reported that C. lalia engage in fanning activities while under the nest, both during nest construction and during parental care. This behavior was not observed in this study in any species of Colisa.

Another activity which was observed and labeled by Forselius (1957) and was seen rarely during C. lalia nest building activities is opercular aeration of the nest. The male swims to the surface at the periphery of the nest, inspires, swims back to a spot below the nest, and generally, after 1 or 2 circling movements, releases a cloud of very small bubbles from the opercle opening. One or several clouds in succession may be released to rise to the nest. This activity is performed by all members of Colisa during spawning after egg release and during egg care in the post-spawning phase. The behavior has also been reported in all Trichogaster species (Miller and Robison, 1974). Forselius (1957) suggested that the function of this activity is to increase the supply of oxygen to the eggs and embryos and that when exhibited in the nest building phase it is probably a displacement activity related to the parental behavior pattern. Further study of the activity is needed in order to infer its function.

## CHAPTER VI

### QUALITATIVE DESCRIPTION OF COURTSHIP AND REPRODUCTIVE BEHAVIOR

Courtship and reproductive behavior in Colisa, as in most anabantoids, is stereotyped and occurs in discrete temporal patterns. Although it is difficult to extract any single activity from such patterns and label it "courtship behavior," there is a series of activities which can collectively be called "courtship." Miller (1964) suggested that these activities, which are usually male initiated, appear to attract and/or stimulate the female and facilitate successful spawning during the early phase of the spawning sequence.

#### Pre-Spawning and Courtship Activities

The commencement of the reproductive period in Colisa in aquaria is most striking when a ripe female with a plump belly is introduced into a tank with a mature male. However, the introduction of a ripe female is not necessary to initiate activities associated with male reproductive behavior. Male activities which become pronounced at the beginning of the reproductive period are increasing aggressiveness, acquisition of nuptial coloration, establishment of a territory, and construction of a bubble nest. All of these activities appear to depend on the motivational state of the male and female and none but the acquisition of nuptial coloration are necessary for successful

spawning. Colisa used in this study never spawned without acquiring nuptial coloration.

The duration of pre-spawning and courtship was variable among the four species as well as within the species, depending on each situation and individual differences. Pre-spawning appeared to be shortest in C. chuna and longest in C. lalia. C. labiosa appeared to be much shorter than C. fasciata. The longer duration of C. lalia was perhaps due to its utilization of vegetation in the nest.

Males spend two to six hours nest building during the early phase of pre-spawning, interrupted by periodic aggressive encounters with the female. During this time females are restricted to a specific area of the tank, where they are hidden behind a thick clump of vegetation or aquarium heater or in a clay pot. Most aggressive encounters occur when the female surfaces to inspire or to feed. Attacks by the male involve butts, bites, chases, tail beating, and sometimes pendulum movements which develop into mouth fighting. The latter movements appeared to be initiated by the female when she was in a clay pot or cornered by the male. Reproductively ready females are also attacked by males when they swim to the surface to inspire. Females would go through long periods of air snapping, as do males before selecting a nest site. As the pre-spawning phase progresses, females of all four species surface and attempt to blow bubbles in corners above their hiding places and where they previously had inspired for long durations at the surface. Gradually, females develop nuptial coloration, which becomes more evident as spawning approaches.

The advanced development of the nest created by the male, his visits and displays to the female, and the behavior of the female

appear to mark the appearance of a noticeable pattern of activities which could be labeled courtship. In C. chuna and its congeners the male approaches the female with or without fins erected and performs a display consisting of a sudden return to the nest and/or a hesitant return interrupted by several stop-lateral display, turn-lateral display, and/or swim-to-the-nest movements, termed "leading to the nest" by Forselius (1957) and Miller (1964). The latter pattern of movements appears to be species specific, and in Colisa in aquaria is more prominent in C. lalia and C. chuna. Leading is not apparent in C. labiosa and C. fasciata. In these two species the male may approach the female and give a lateral display and sometimes meets the female with a display and returns to the nest with her following him. Forselius (1957) gave a detailed description of leading to the nest for C. lalia which will not be repeated here. It should be pointed out, however, that C. lalia leading activities observed in this study would not be termed zig-zag leading, as described by Forselius.

In C. chuna leading to the nest may occur when the male approaches the female or more often when the female approaches the male near his nest. Upon her approach the male swims toward her with or without erected median fins and terminates his approach with either a lateral display or a vertical display or by passing directly in front of her as he turns toward the nest. Usually, the return to the nest is interrupted by performance of intermittent lateral and vertical displays. The female may or may not follow the male. Commonly she does not follow and is immediately attacked by the male.

As the pre-spawning phase progresses toward the spawning phase, the male becomes increasingly aggressive toward the female and the

frequency of male-female bouts increases. Most of the bouts are agonistic with some leading. Eventually, the female will fold her fins and rapidly approach the male under his nest, where the posting male commonly gives a lateral display. She may then turn and swim off rapidly, chased by the male, who butts and bites her until she appeases and even after she appeases. With an increase in frequency of female approach, the female eventually responds to the male by giving a lateral display, then one to seven butts on his side. Concomitant with such butts, the male may depress his median fins and start to fold his body into a U-shape, the initial movements of intention to clasp the female. At early stages of courtship and clasping the female often slips past the male, her snout directed toward the nest, where she pokes about as if searching for eggs or brood. The male seems incapacitated momentarily while the female is in this position, but as soon as she swims off, she is chased and attacked by him after which he usually returns to posting under his nest or resumes working on it. Gradually, this stage of pre-spawning gives way to a phase dominated by the female persistently approaching the male under his nest and the pair attempting to clasp.

In all species of Colisa sexual bouts are usually initiated by females and sometimes may contain several attempted clasps. Between these attempted clasps within a bout, the pair often circles head to tail, apparently as a result of the female changing sides to mount and adjustments made by both fish. Circling is very common in C. labiosa, less frequent in C. fasciata and C. chuna. Female C. labiosa frequently change sides. The female approaches the displaying male and butts him several times on the flank region as he begins to fold into a U-shape.

She may then drop slightly below the male at his caudal region and butt him on his side, eliciting another folding attempt. This procedure is often repeated several times in succession within a single bout and such bouts are repeated many times. If the female should change sides by passing the male's anterior end rather than his posterior, the pair may engage in violent head-on butts, with the female ultimately fleeing and being attacked by the male. Usually, after the female changes sides to mount two or three times passing by the male's caudal region and avoiding the head-on butts, the encounter develops into head to tail circling and eventual attack of the female by the male. During intervals the male usually works on his nest while the female remains hidden.

In C. chuna and C. fasciata the female often swims off after the first attempt, with a chase and attack from the male. In C. chuna, if there is a second attempt at clasping within the same bout, the male usually goes into a brief vertical display followed by the second attempted mount on the same side or the other side. These movements in C. chuna are swift.

A point that should be made here is that at this stage of the pre-spawning and courting phase as well as during spawning and post-spawning phases, the female of all four species commonly swims to the surface and inspires before she approaches the male under his nest.

One behavior which occurred during the development of the pre-spawning phase was observed only in C. lalia. It is a rather distinct behavior on the part of the C. lalia male which was not reported by Forselius (1957) in his monograph, though he describes "horizontal circling," a form of which appears to be similar to the behavior observed in this study. In this study, however, the behavior seemed to



be the rule rather than an exception when pairs first attempted to clasp during the pre-spawning phase.

Forselius (1957) described two modes of horizontal circling, one he termed (HCIVP), horizontal circling in a vertical position; and the other (HCIHP), horizontal circling in a horizontal position. The following is a quotation from Forselius (1957, p. 179) describing (HCIHP), which is most like what was observed in the present study, but occurred in different contexts than courtship.

At circling in a horizontal swimming position (Fig. 20B), the dorso-ventral body axis of the defender invariably takes a horizontal position parallel to the surface and the fins are erected. The stranger may in turn either swim in the usual swimming position up to the object of its attention, e.g., most often a nest, or assume a position with the body sides parallel to the water surface and the antagonist.

The behavior described in the latter part of this statement concerning the two fish swimming parallel to the water surface and to each other was not observed in this study. His next statement describes behavior also observed in the present study.

When only the owner performs the circling, he may thus be occupied for several minutes in succession, trying as a rule to come between the nest and the intruder, but he may also be seen circling near the bottom with the intruder nearest to the nest (p. 179).

However, the remainder of his account is not in agreement with observations in this study.

When both fishes are circling, this takes place in a horizontal track within a limited area and generally with the one close under the other. Sometimes one fish has been observed to circle clockwise, the other simultaneously counterclockwise. In the course of this process they look fixedly at each other with the facing eye, and give the impression of being bigger than they really are, owing to fin erection (p. 179).

In a footnote Forselius (1957) made the distinction between cir-

cling in connection with aggressive and threat behavior (HCIVP and HCIHP), on the one hand, and the circling movements performed by males under the nest, on the other, where the latter may be in connection with expiration, expectoration of nest material, care of eggs and fry, or just posting. Circling in connection with a nest always involves HCIVP.

In two pairs of C. lalia in this study, horizontal circling in an aggressive and threat behavioral context was recorded. Both were during the parental care stage, while males were posting under nests containing fry. Females apparently motivated to spawn approached the male under his nest with fins folded and butted him several times. This usually developed into attack with the male butting, biting, chasing, tail beating, and finally mouth fighting. The females were very persistent, so much so that each male seemed to become incapacitated, and at this point turned on his side with the female between him and the nest, which she appeared to be searching with violent thrusts for eggs or fry.

The male usually was posting under his nest, but in some cases, he would be at the periphery, either at the surface collecting air for release of bubbles under the nest, or somewhere subsurface collecting material for blowing into the nest when the female rapidly approached the nest. If she got there while he was absent, she searched the bubbles with her snout, while she alternated between fin erection and closure as if appeasing. The female in the nest invariably brought the male rapidly back, and he would give a lateral display which often evolved into a sigmoid posture, and then turn on his side into horizontal circling. In this position he swam in a circle with his lateral axis parallel to the water surface and substratum. He maintained himself in this posture with dorsal, anal, and caudal fin extended maxi-

mally, while pectoral fins beat alternately and pelvic filaments are drawn somewhat near the body (See Figure 1). The direction of swimming may be clockwise or counterclockwise. During the time that the male is in this position the female remains above him searching the nest. The male frequently made futile attempts to right himself, and attempted to butt the female, without success. There usually was 5-7 cm between the female's caudal fin (she was usually in a  $45^{\circ}$  angle with the surface) and the male. Most interesting was that the male apparently could not right himself to make contact with the female and never came out of this position until she swam off. He seemed absolutely incapacitated. Immediately after she swam away, the male instantly righted himself and chased her, inflicting several butts and bites. On several occasions, while pairs were in this position, the female defecated on the male, a most unusual action for fishes.

As pointed out, it is usual for the male C. lalia to be posting under the nest when the female approaches. He momentarily gives a lateral display, she butts him one to three times on his flank, while he folds his dorsal fins and begins to clasp her. She then slips out of the clasp toward the surface, at which time the male turns on his side as described above and swims in a circle. The frequency of this behavior ranged from three in one spawning sequence to twenty-one in another spawning sequence. The shortest duration of horizontal circling recorded was 4 seconds, while the longest was 2 minutes and 11 seconds. As this behavior increased in frequency, the pair finally would achieve longer and longer clasps until eventually the female would no longer slip out of the clasp.

Incipient bouts became increasingly frequent and longer in dura-

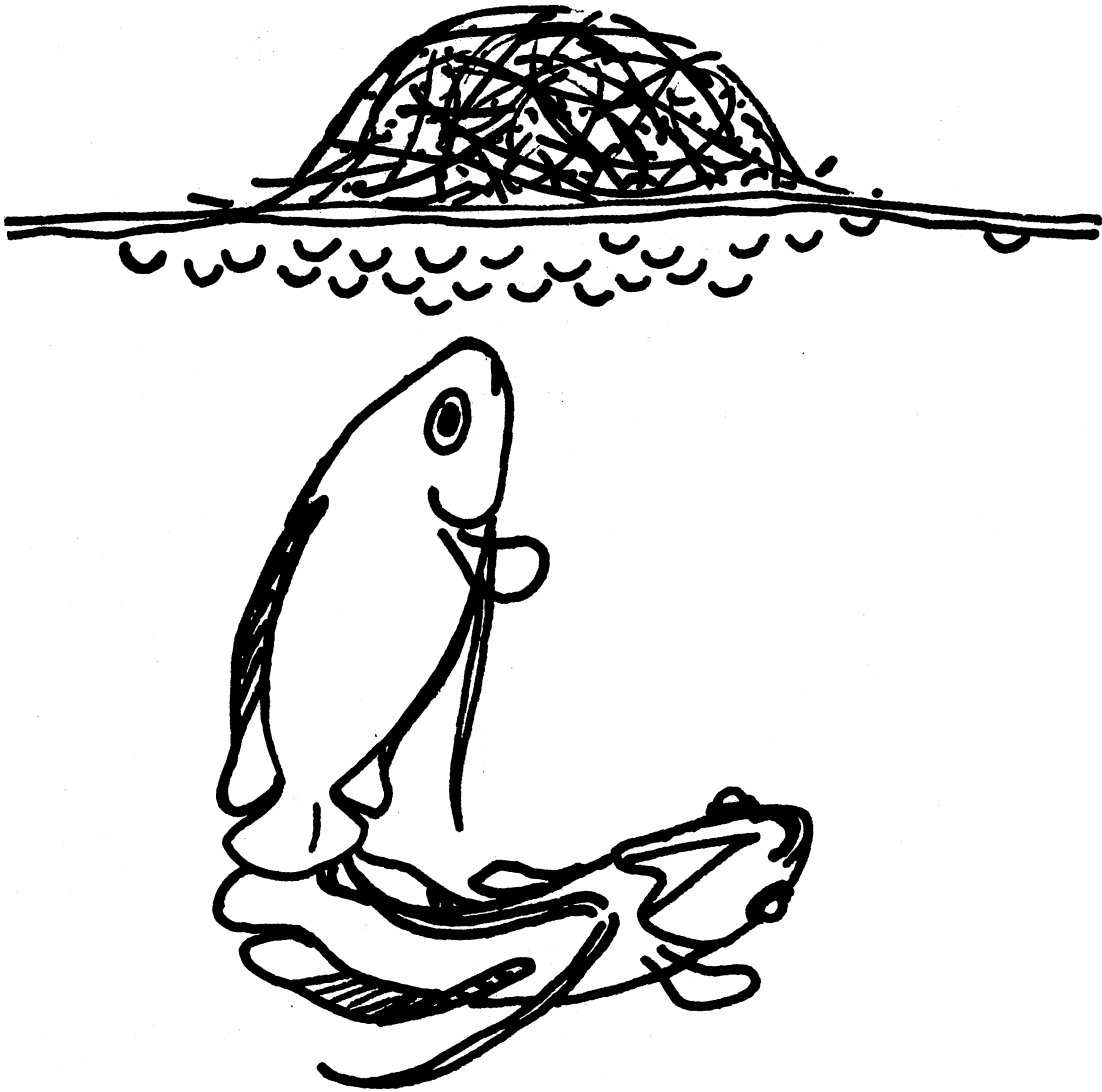


Figure 1. Horizontal circling by *C. lalia* male with female above in vertical position.

tion as the pairs in C. lalia approached the spawning phase. In general, this too was evident for its congeners. During this stage of development of the pre-spawning phase, pseudospawn bouts are common and usually precede the first spawning bout in Colisa spp.

#### Spawning

The spawning phase in Colisa spp. was considered to have begun with the first sexual bout where a pair successfully released gametes. In most spawning sequences, a successful bout followed 1 to 4 hours after the first visit by the female to the male under his nest. Most spawning bouts in all species of Colisa were initiated by the female, as they are in Trichogaster species (Miller and Robison, 1974). Male initiated bouts usually end with the female appeasing and fleeing to a hiding area.

The spawning phase is dominated by incipient bouts and some pseudospawning bouts. Bouts that do not get as far as spawning or pseudospawning include those consisting of a single approach by the female to the male with or without a butt, or those with several clasps in succession with circling in between. Successful bouts appear to depend on the female approach and once under the nest proper mounting by the female. The female approach is variable in form inter- and intra-specifically, and the response of the male to the female's approach is most important to the continuation of the bout. Forselius (1957) reported that female C. fasciata, C. labiosa, and C. lalia generally approach the male with head pointed slightly toward the bottom, and the closer one comes to the male, the more closely her head approaches the horizontal plane and sometimes higher. The findings in

this study are congruent with those of Reser (1969) on C. fasciata. The female in all species usually approached so that she appeared at the side of the displaying male rather than head on.

The position of the male under the nest during female approach differs slightly among the four species. C. chuna males are usually vertical or at a 30-45° angle 1 or 2 cm below the nest. When approached by the females, C. labiosa males often drop 8-10 centimeters below the nest and lateral display, and the female butts or nudges him 2-3 times.

Under the nest C. chuna female approach may be terminated without a butt or nudge or by one or two butts in those bouts where butting does occur. The female usually butts the male on his dorso-lateral region slightly below the dorsal fin origin. Female C. fasciata terminate their approach with one to three butts or nudges on the male lateral side slightly lower and posterior than in C. chuna. C. lalia and C. labiosa females usually butt the male closer to his posterior and caudal region. However, C. lalia females were observed to butt the male during a greater number of spawning bouts than its congeners, but with approximately one to three butts per bout, as in C. labiosa and C. fasciata where butting did occur.

A comparison of female butting during spawning bouts between Colisa species is presented in Table 3.

Frequency of butting or nudging in Colisa is of low intensity and short in duration, as compared to female courtship butting in T. tri- chopterus (Miller, 1964), T. leeri (Miller and Hall, 1968), and T. pectoralis (Robison, 1971). Female butting in Colisa does not precede each spawning bout as was reported by Robison (1971) for T. pectoralis and is not a prerequisite to spawning as reported by Miller (1964) for

T. trichopterus. Butting in Colisa is closer to that of T. microlepis with a frequency of approximately two to six per spawning encounter. Frequency of butts in T. leeri may exceed 40, while butting in T. trichopterus is intermediate between T. microlepis and T. leeri. Although butting does not occur in all spawning bouts in Colisa, in those bouts where butting does occur, it appears to inhibit male aggression as was suggested for Trichogaster species by Miller (1964), Miller and Hall (1968), Robison (1971) and Wimmer (1970). Morphological features, coloration, and manner of approach may also serve to identify females and concomitantly inhibit or decrease male aggression (Hall and Miller, 1968).

Usually, after delivering one to three butts to the male's side, the Colisa female commences to mount the male for clasping. Activities which occur from the point of butting until gametes are released and the pair separates or the pair pseudospawns are very stereotyped for the individual species. Mounting, which follows butting and folding of the dorsal fins by the male, is very critical to the success of spawning bouts. If the initial adjustments are not proper, the pair may alter their position in order to obtain an optimal position. The extent of such orienting movements varies considerably, ranging from slight movements to complete release and reclasp. Such adjustments appear to be critical for successful consummation of the bout.

Generally, when an incipient bout does occur, the female swims off with a chase and/or attack from the male. However, occasionally the female will slip out of a clasp, leaving the male in clasp posture which is followed by rolling over.

Immediately after or even during the single butt (often absent)

Table 2. Comparison of female butting during spawning bouts in Colisa species

	<u>C. chuna</u>	<u>C. lalia</u>	<u>C. labiosa</u>	<u>C. fasciata</u>
Total spawning bouts	141	152	167	149
Total spawn bout with butting	24	121	54	94
Total butting sessions	25	123	54	94
Total number of butts	25	247	61	116
Average number butts/ session	1.3	2.0	1.1	1.2
Average number butts/ bout	1.3	2.0	1.1	1.2
Average number sessions/ bout	1.0	1.0	1.0	1.0
Percent of spawn bouts with butting	17	80	32	63



given by the *C. chuna* female to the male, the male folds his fins and begins to curve his body around the female so that cranial and caudal regions move toward each other in a U-shape (referred to as an "invitation posture" by Rainwater and Miller (1968)). Simultaneously, the female in the curve places her snout on his dorsum in front of the anterior origin of the male dorsal fin, with her anterior-ventral region and pelvic filaments against his side. In *C. chuna*, the time between the start of the approach and the commencement of the clasp (preclasp time) is exceedingly short, with all movements of the pair very brief. If the female positions herself too far anteriorly and/or too high, the bout will likely be incomplete. In all four species the key for proceeding as far as spawning or pseudospawning is for the female to place her chin on the male's dorsum slightly anterior to the origin of the dorsal fin. Although this is the only position that females are in during successful bouts, assumption of this position does not mean that the bout always will be a complete or a pseudospawn bout.

Following curving and mounting in *C. chuna*, the male completes the clasp by wrapping himself around the female's body so that the anterior half of her body is enfolded. At this time the male's previously folded dorsal, anal, and caudal fins are extended as he tightens the clasp so that his head and caudal fin nearly touch each other. (How nearly they touch depends on size of male and female.) Simultaneously, the female's straight body is flexed into a rigid sigmoid posture with dorsal fin erect and caudal fin bent away from the male. The vents of the pair are now in close proximity and directed toward the bottom. With tightening of the clasp and flexing by the female, the

pair tilts slightly to one side with vents moving upward. Then both male and female begin to quiver. In conjunction with movements of the male's free pectoral fin and the caudal peduncles and caudal fins of both sexes, the pair rolls upward and sideways (common procedure) or all the way over until urogenital pores point toward the surface. The final position of the pair varies, ranging from positions where the male's head is pointed downward in a vertical position to positions where the head and tail are parallel to the water surface and substratum.

There are slight pair reorientations during the clasp in all species caused most noticeably by individual physical differences. Barlow (1968) noted a distinct source of variation in Badis badis male initial clasping activity which he termed "twisted-U". B. badis males apparently show the "twisted-U" before going into the "simple-U" clasp, which he found to be characteristic of elongated species (e.g., Colisa chuna Sole, 1966) based on photographs in the aquarium literature. He further states that the more disc-shaped species are regularly shown in a "simple-U" (e.g., Trichogaster leeri, Zikal, 1966; T. trichopterus, Miller, 1964). In the present study more than 40 pairs of C. chuna were observed during spawning and the "twisted-U" noted by Barlow (1968) from photographs by Sole (1966) was never observed, nor was it seen in C. fasciata, C. lalia, or C. labiosa. Barlow (1968) stated that there is no way of knowing if the elongated species always show the "twisted-U" before going into the "simple-U;" the aquarist probably waited until the enfolding was well developed before taking the picture, thereby increasing the probability of missing the "twisted-U". The "twisted-U" was not noted by Rainwater and Miller (1968) in Betta splendens, a very elongate species.

Female C. chuna quiver prior to egg release and may continue to quiver during egg release. Quivering is most pronounced before egg release. During or after quivering the female straightens her body slightly and releases eggs. Eggs, which vary in size, are few in number at the beginning of the spawning phase, increase as spawning continues, and decrease near the end of the pre-spawning phase in all species. Oviposition without previous embrace by the male, reported by Rainwater and Miller (1968) for B. splendens, was never observed in Colisa.

Male quivering ceases with a jerk of the body in all Colisa. The jerk is performed almost simultaneously with initiation of oviposition and in some instances appears momentarily before. This sudden spasm by the male may be indicative of ejaculation. There was no visible "light cloud of spermatozoa," as reported by Forselius (1957). The male body jerk in Colisa appears to be similar to the "terminal squeeze" in T. leeri (Hall and Miller, 1968).

Following the jerk and release of gametes, the male loosens the clasp and the pair slowly sinks, separately and unoriented in a state referred to as swimming inhibition (post bellum, Barlow, 1968). Swimming inhibition is also characteristic of pseudospawning bouts, with no apparent differences in duration within species. The duration of swimming inhibition varies among species as well as among individuals within species and between the sexes. Duration of swimming inhibition was greater in C. chuna by several seconds than its congeners. In C. fasciata and C. labiosa the female recovered first.

Immediately after recovery from swimming inhibition the female swims off; she may be butted and/or chased by the male, and sometimes

extremely violent attacks occur. More often, the male begins collecting eggs that have not reached the nest. He retrieves several eggs in his mouth, one at a time, before swimming to the nest, where they are released. C. chuna males search among the vegetation for eggs and rarely miss an egg.

Activities directed to the eggs in Colisa vary among species. C. chuna, the smallest member of the genus, has the smallest number of bouts per spawning sequence and releases the fewest eggs (less than 27) per spawning bout (See Table 3). It is a species that spawns just as readily with or without a nest, always handles each egg separately, and throughout the spawning phase and most of the parental period maintains its eggs in a tight rounded ball-like cluster that may extend a bit above the water level. It is a fair assumption that the eggs are coated with mucus containing anti-fungus and anti-bacterial substances. The cluster is usually attached to vegetation or the side of the aquarium. The two larger species, C. labiosa and C. fasciata, may spawn more than a thousand eggs per spawning sequence and more than 60 in a single spawning bout (See Table 2). These males do not appear to be as diligent about collecting all eggs as are C. chuna males. Eggs that are collected are blown into the center of the nest or into the center of the area used for spawning when there is no bubble nest. Some may be seen floating at the periphery of the nest or among the vegetation from which they were never collected. C. fasciata and C. labiosa do not manipulate their eggs as often as C. chuna. Generally, in the two larger species there appears to be less attention given to the eggs than in C. chuna and C. lalia.

C. lalia spent less time collecting eggs than C. chuna or the

Table 3. Number of eggs released per spawning sequence by Colisa females

	<u>C. chuna</u>	<u>C. lalia</u>	<u>C. labiosa</u>	<u>C. fasciata</u>
	271 343	322	670	1681
	220 312	679	1219	2342
	173 252	708	1527	881
	452 189	185	973	1997
	273 261	457	769	
	455		1020	
Total	3201	2351	6178	6901
Average	291	470	1030	1725
S.E.	96.29358	255.83790	477.67069	938.82509

larger members of the genus. This species was never observed to spawn without the bubble-vegetation nest present. Generally, egg release was directly under the nest and most eggs floated directly up into the nest. However, egg retrieving activities were performed and the pattern of collection and release of eggs appeared to be the same as in its congeners. Eggs were manipulated and appeared to be moved about in the nest (embedment, Forselius, 1957). Also characteristic of C. lalia and reported by Forselius (1957) was the activity pattern referred to as "nest-pushing." The male butts forcefully deep into the nest when manipulating eggs. Forselius suggested that the process renders the nest less compact and facilitates penetration of oxygen from the air to the eggs and fry at the bottom of the nest. Nest pushing in C. lalia during egg care looks much the same as when the male is constructing the nest. This activity pattern was also noted in T. microlepis by Wimmer (1970).

In Colisa during and after deposition of eggs in the nest, the male emits clouds of tiny bubbles from his opercle opening. The male often goes to the periphery of the nest and inspires after egg deposition and returns under the nest and releases streams of minute bubbles. As pointed out earlier, this activity also is observed after pseudo-spawn bouts, and during nest construction and parental care stages. The exact function is not known, but was suggested by Forselius (1957) to be a form of aeration for eggs and embryos. Although this study does not disprove his suggestion, it is hard to imagine why fish with the ability to construct oxygen-rich bubble nests at the air-water interface should need to spray the nest and eggs and embryos from below. Then, too, the fact that this behavior activity is evident during nest construction

when eggs and young are absent add reason for doubt of Forselius' suggestion. As pointed out by Miller (1964), "it seems unlikely that air from the suprabranchial organ would contain as much oxygen as air from fresh mouth bubbles, and it should be recognized that some question exists as to function of the behavior,"

During spawning bouts the pattern of activities is basically the same in all Colisa, with few noticeable species differences besides frequency and duration of bout activities. For this reason the above description of spawning in C. chuna will serve as a model for other Colisa qualitative patterns. Quantitative comparisons will be discussed in another section. Several qualitative differences do exist among the other Colisa spp. and they are discussed below.

One of the most striking differences among the species is what takes place between pairs from the time the female approaches the male until the pair engages in the clasp (pre-clasp time). As stated earlier, C. chuna has the shortest duration of pre-clasp time (9 seconds, See Table 7) with or without a single butt. At the other extreme is C. labiosa with the longest average pre-clasp time of more than 18 seconds (See Table 7).

In C. labiosa during pre-clasp when the female approaches the displaying male, he drops 8-10 cm below his nest in a lateral display. The female butts him three or more times as he curves his body into a semi-circle, and the pair ascends slowly (in a spiral) with the male slightly higher than the female. The female's fins are folded slightly and her body is also somewhat curved; her anterior region is within the folding curve of the male's body. About two centimeters below the nest, the female places her snout and anterior-ventral region on the male's

dorsum just anterior to his dorsal fin origin. The pair clasps, appearing at first as if both bodies are folded into U-shapes; then the female straightens and finally flexes her body into a sigmoid posture. The remainder of the clasp activities are much the same as in other Colisa except for differences in duration and frequency and the fact that most of the time the roll is usually all the way over, bringing the vents toward the surface.

The next greatest pre-clasp duration among Colisa was for C. fasciata. The approach of the female C. fasciata is the same rapid swim with folded fins found in other Colisa. The C. fasciata male, unlike the C. labiosa male but similar to the C. lalia male, posts a few centimeters below the nest at a 30-45° angle to the water surface in a lateral display. After 1 to 3 butts by the female the male folds his fins and assumes a horizontal position parallel with the water surface; the female remains motionless, snout touching his mid-lateral side below the dorsal fin origin. The pair remain in this position for nearly 10 seconds before the male starts to curve his body as the female moves her snout up to his dorsal origin. C. fasciata observed in this study, like those observed by Reser (1969), never assumed the "female upside-down posture" described by Forselius (1957) as occurring in C. lalia, C. labiosa, and C. fasciata, although infrequently in the latter two.

The pattern of activities for C. lalia is much the same as in its congeners; for a detailed description, see Forselius (1957). One difference that appeared unique to C. lalia occurred during the clasp adjustments of the pair. By the time the clasp behavior is completed with the roll, the pair has floated to the floor of the nest, sometimes



hitting it. This may be part of the reason the C. lalia male spends less time collecting eggs; most float directly into the nest. Another point of interest is that the eggs appear to be smaller and more closely packed when they are released from the female's vent.

Following the deposition of eggs in the nest, the Colisa male usually resumes nest care activities, deepening the nest in C. fasciata, C. labiosa, and C. lalia by expelling bubbles under it. Also, C. lalia males may collect additional detritus, especially pieces of gravel, during this time to add to the nest. The C. chuna male mostly rotates the eggs and seldom blows bubbles between spawning bouts. He may occasionally transfer the egg cluster to another spot. While the male is tending the eggs, Colisa females usually remain stationary in a far bottom corner of the aquarium or hide behind a clump of vegetation near the surface. They may utilize clay pots for protection, and some hide behind aquarium heaters. The female may surface for inspiration, and at this time she is usually approached and attacked by the male.

C. fasciata and C. labiosa females commonly ate eggs near the end of the spawning phase when eggs floated all over the surface, including over the area in which they hid. Once egg eating was initiated in these species, the activity increased and usually was followed by violent attacks by the male and the cessation of the spawning phase. Egg eating was not common in C. chuna and C. lalia, perhaps because males in these species maintained their eggs in a specific location which minimized drifting. After several observations of C. chuna spawnings, it was possible to recognize a specific body movement of the male as indicative of the end of the spawning phase. The male would approach the female (usually down in a corner), butt her, display, and tilt his

body to the side toward her and swim back to his nest directly without a vertical display, which occurred during courting and leading to the nest.

On several instances pairs, perhaps due to inexperience, attempted unsuccessfully to spawn for two and three days in succession. Other instances of frequent incipient bouts involved pairs where the female was larger than the male. In several C. chuna pairs where the female was larger the pairs tried in vain for several days to spawn. After such prolonged attempts, three females were found dead apparently from being egg bound. In another spawning sequence a large number of incipient bouts occurred as a result of improper adjustment and faulty approach and orientation by the female, which had only one eye. She often butted the male in the wrong location and tried to mount in the wrong position and usually was violently attacked by the male.

Miller (1964) pointed out that many failures (incipient bouts) doubtless are merely due to physical faults, rather than motivational inadequacy, but that the majority probably reflect the incomplete state of the motivation levels of either or both fish. This or another cause of failure noted by Miller in T. trichopterus was also seen in Colisa spp. The female in many pre-spawning proceedings would rise to the surface and feed or slowly drift away. As the spawning phase was near completion it was not uncommon to observe female C. fasciata and C. labiosa approach as if to clasp and eat eggs instead. This activity always brought on extremely violent attacks by the male.

One pattern that occurred in all four species involved a distinct conflict present in pairs which spawned with fry in the nest from a previous spawn. Often males seemed to be motivated to perform

parental care, but gave in to a persistent female highly motivated to spawn. During most such spawnings, the fry and the new spawn were eventually eaten, and the encounters appeared disrupted. Colisa chuna males, in many instances, appeared to be attempting to lead the female away from the existing nest by going through movement patterns similar to those seen in courting. Although these movements looked very much like leading-to-the-nest during courtship behavior, the context was different and the movements odd. The usual lateral and vertical displays were quicker, jerky, more frantic, and followed intense aggressive encounters. Most unusual was the increase in aggressiveness of the female. During these spawnings males in all four species bypass nest building behaviors, and in C. chuna the usual compact cluster of eggs was not evident. Males tried to hide eggs under leaves, but females ate all they could find. There was no specific spawning site as in usual spawnings.

Another phenomenon, which only occurred in C. fasciata, was a spawning sequence marked by the attainment of one to four successful spawning bouts followed by an abrupt cessation of spawning behavior when both fish separately began swimming erratically back and forth, up and down the side of the aquaria. In all these spawnings there was no bubble nest, and during this erratic swimming, the eggs floated on the surface, later to be eaten. This same type of erratic swimming occurred in a pair of C. fasciata, where the male had constructed a nest in a 7 cm wide space in a corner between a heater and the opposite wall. The female attempted several times to come between the male and the wall by approaching and swimming up under him before the male would finally clasp her. The spawning phase was short and ended

abruptly.

A point worth mentioning concerning motivation and spawning is the length of the reproductive period in the genus Colisa. C. fasciata, in most cases, resisted manipulation on the part of the researcher to get it to spawn. Fish were manipulated by addition of new water, change in temperature, change in the pH and separation of a pair by a glass divider for several days. It was characteristic for a rather quiescent C. fasciata male to begin territorial activities and spawn with several females in succession within 10 to 14 days if given the opportunity. After this the male could not be induced to spawn with the plumpest persistent female introduced into his tank. No record was maintained for periods between reproductive cycles. In general, however, it was rather extensive, lasting more than two months in some. In sharp contrast was the reproductive behavior of C. chuna, which spawn every 4-6 days if given the opportunity. C. chuna males maintain nests from May to September. C. labiosa and C. lalia appear to be similar in that they maintain nests and spawn several times within a (reproductive) period and have short non-reproductive intervals between. However, in several weeks they would resume territorial behavior, and if presented with a new ripe female, would spawn with her.

#### Post-Spawning Phase

As defined in Chapter IV, the post-spawning phase is that period beginning after the last successful spawning bout of the spawning phase and ending when the female remains in seclusion for long intervals, and the male displays extreme aggressive behavior toward her while guarding the nest. The post-spawning phase in Colisa is like the pre-spawning

and courtship phase in that there is no distinctive difference in behavior occurring in early post-spawning and late spawning phase. After a period of time it becomes obvious that spawning has ceased and that the ongoing behavior patterns have changed from those typical of the spawning phase. During many spawning sequences of Colisa spp. the post-spawning phase appears to be quite ephemeral. The time between the last successful bout and when the female remains hidden from the male is relatively brief--in some sequences lasting no more than 10 minutes. However, in a few sequences, particularly in C. lalia, the female appeared to remain motivated to spawn as indicated by the number of pseudospawnings following the last successful bout. As many as 16 pseudospawnings and many incipient bouts have been observed in C. lalia.

During the post-spawning phase the male may show activities characteristic of the two previous phases of the spawning sequence, i. e., aggressive behavior, nestbuilding behavior, parental behavior, and courtship behavior. Commonly, there are one or more pseudospawning bouts, with many incipient bouts in between, following the last successful spawning bout. Perhaps the most striking activity, other than frequent and violent attacks by the male on the female, is the intensity of nest building activities. Miller (1964) found that in T. trichopterus nesting activity per se was greatest immediately before and after spawning, but greater in duration after spawning when eggs and young were in the nest. Although no quantitative measurement of this activity was made, this also seems to be characteristic of the genus Colisa. Male C. chuna, especially, spent most of their time manipulating eggs, releasing streams of fine bubbles from opercle openings, and blowing bubbles at the surface. C. fasciata, C. labiosa,

and C. lalia spent much time deepening nests by sub-surface release of bubbles made previously while they collected air at the surface near the nest periphery. They, too, continue to release many fine bubbles from their opercles.

Some females will attempt to feed at the bottom, but the usual female behavior pattern is to remain motionless near the bottom behind some object, emerging for quick and infrequent rushes to the surface for air. When the female surfaces, she is immediately attacked by the male. Aggressive encounters in C. chuna often develop into lengthy tail beating sessions. Generally, the frequency of female surfacing for inspiration seems to be affected by the level of aggressiveness towards her by the male as well as by her actual physiological needs. Occasionally, a very aggressive female will remain at the surface, approach the male under his nest, and in some encounters even eat eggs. Females which persist very long at this are equal to or larger than the male and may eventually consume all the eggs which may be abandoned by the male. On occasion, C. labiosa and C. lalia females were killed by males following spawning. After several spawnings it was necessary to remove the female or separate her from the male by a glass divider in order to keep her from being killed.

## CHAPTER VII

### PARENTAL BEHAVIOR AND DEVELOPMENT OF THE YOUNG

Parental behavior includes those activities carried out by the male in the process of maintaining and protecting eggs, embryos, larvae (wrigglers), and fry in a viable environment. In a strict sense, parental care activities begin immediately following the first spawning bout and continue until the male ceases to maintain its progeny. Therefore, commencement of parental behavior occurs when the pair appears to be dominated by sexual or spawning motivations. As the spawning sequence proceeds, parental activities by the male become increasingly dominant. From the end of the spawning phase and the onset of the post-spawning phase until the male deserts his fry and nest, he spends an increasing amount of time in purely parental activities. Of these, maintaining the young in a central location is the most important activity for all four species of Colisa. In C. chuna, C. labiosa, and C. fasciata this is accomplished by maintaining a raft of bubbles, which appears to function as a nursery in which young develop. However, a bubble nest is not necessary for successful development of the young. Several spawnings occurred without a nest. As the parental period proceeds in C. lalia, the eggs are first maintained in a nest containing bubbles and vegetation but after the bubbles dissipate development occurs in the vegetation. The length of the parental care

stage varies from 3-4 days in C. chuna to 5-7 days in C. fasciata. Colisa females take no part in parental activities. Instead, they remain as far from the nest as possible.

#### Early Parental Activities

In bouts where gametes are released, the pair usually ends the encounter with swimming inhibition. During swimming inhibition, as the pair sinks slowly, separately, and without control to the bottom, some eggs ascend slowly to the nest, while others either adhere to the incapacitated pair or are dispersed somewhat horizontally by a current created by the sinking pair. Although the pair usually sinks to the bottom, in some pairs, especially in C. chuna, one or both fish may float near the surface while in swimming inhibition. The male commonly is in a head up position with median fins partially to fully erected. Both often appear to be in a posture similar to the sigmoid posture.

Recovery time varies between sexes as well as among species. There are also individual recovery time differences within a species. It is not uncommon to see the male actively try to recover and to commence to collect eggs before complete recovery. In some instances, the male recovers before the female and may begin to retrieve eggs without attacking her. However, he may attack first and then return to retrieve eggs. Usually, in C. fasciata, C. labiosa, and C. chuna, the female recovers first and swims off without an aggressive encounter with the male.

The male collects eggs one at a time by sucking them into the mouth where they are coated with mucus. Several are retrieved before the male swims beneath the nest and releases them. Release of eggs



varies slightly among the four species. In C. fasciata and C. labiosa the male appears to spit eggs into the thick center of the nest or into a central location when a nest is absent. As Forselius (1957) noted, it is not uncommon to see C. lalia males thrust the mouth into the nest when releasing eggs. In C. chuna the male releases the eggs into the nest, where they scatter slightly. He then collects them individually, and after his manipulation they adhere in a ball-like cluster. In all four species several retrieval trips are made after eggs are released, and the frequency of these trips depends on the number of eggs released and the number collected per trip. Often C. fasciata and C. labiosa fail to collect all eggs, but C. chuna usually collects them all. C. lalia's eggs float directly into the nest.

In most cases after a deposit of eggs into the nest, many tiny bubbles are released from the male opercle opening. Sometimes he swims to the periphery of the nest, gulps air, returns beneath the nest, and releases a stream of these tiny bubbles before manipulating the eggs.

Males spend some time during the spawning phase between bouts rotating eggs and blowing bubbles. However, bubble blowing then is not as frequent as before and after spawning. As the spawning phase proceeds to completion, nest care increases as does male aggressiveness toward the female.

Near the end of the spawning phase and continuing through post-spawning and early parental care period air snapping and subsurface bubble release beneath the nest is very frequent in C. lalia, C. labiosa, and C. fasciata. This process appears to enclose the eggs in foam bubbles above the water surface for a few hours after spawning. It may also aid in separating the eggs so that gas exchange is facili-

tated. Perhaps because C. chuna eggs are clumped, males during this same period spend most of their time rotating the ball shaped egg cluster so that proper gas exchange occurs. It is at this time, shortly after oviposition, that cleavage is most rapid and developing embryos require the most oxygen. C. chuna's maximum peak of bubble blowing usually occurs much later in the parental stage, around the time of hatching and later.

Rotation and changing location of the ball shaped egg cluster by C. chuna is the most striking and frequent activity during the post-spawning phase and lasts until the wriggler stage of development. None of C. chuna's congeners spend as much time manipulating their developing embryos. However, just before embryos hatch, nest building activities become the dominant behavior of the male, accompanied by extreme aggressiveness towards anything that moves near the nest. At this time the male appears to include the entire tank as his territory.

Jetting by C. chuna males commonly occurs after he changes the location of the egg cluster; however, it also may occur at other times. In the first situation, the male transfers the spawn either by pushing the entire mass to a new location or by collecting several eggs individually into his mouth and transferring them to a new location. In the latter method several trips are necessary to move the entire cluster. Upon completion of the transfer to a new location, the male returns to the old location repeatedly and jets an arch of water, as if to make sure no eggs were left behind.

One particular case illustrated this behavior: a pair spawned without a nest and then the male attached the egg cluster to the near side of the aquarium. The male appeared to become disturbed by the

observer's presence. Approximately twelve minutes after spawning was over and the female had retreated to a corner where she remained, the male commenced to transfer the spawn to a new location under a clump of emergent leaves near the back side of the tank away from the observer's view. The male jetted an arch of water against the aquarium wall, collected eggs, transferred them to the new location, returned and jetted again, collected eggs, and transferred repeatedly. After all the eggs had been transferred, a period of six minutes lapsed and the male was observed jetting onto the glass wall at the original spot. Again, approximately twenty-five minutes later, the male returned to the original egg location and jetted four separate powerful jets against the aquarium wall, more than 4 cm above the surface. Functionally, this activity appeared to insure maximum collection of eggs.

Other jetting during the post-spawning phase appeared to occur randomly. Usually, when the male was posting under the nest or involved in nesting (egg rotations) activities, he would suddenly jet an arch of water onto the cluster.

Male C. chuna and C. lalia have been observed on occasion to jet water upon the side of the aquarium wall to dislodge wrigglers and fry. Wrigglers and fry often become trapped against the side of the tank at the water surface where the water meets the tank wall. From this area males have difficulty sucking young into their mouths. Wimmer (1970) noted that male T. microlepis jetted as far as 4 cm beyond the upper surface of the nest while nest pushing after collection of eggs. He also stated that it is impossible to establish the frequency with which such jetting occurs, since the thick vegetation nest often prevents the spurting water from penetrating it. Only when executed beneath a thin

portion of the nest may a jet be observed. In the present study C. lalia performed nest pushing movements when placing eggs in the thick nest constructed in part of vegetation. Males may very well jet water when nest pushing, only the jets would not penetrate for the reasons noted by Wimmer (1970). Robison (1971) reported jetting as a rare activity in a post-spawning context in T. pectoralis. Jetting probably helps to keep the eggs moist.

#### Late Parental Care Activities

Beginning about an hour after the last spawning bout all male behaviors are associated strictly with parental care. By this time the female is hiding and the male is posted under his nest manipulating the eggs, blowing bubbles at the surface in C. chuna, or releasing them subsurface beneath the nest in the other species. Males continue to release streams of tiny bubbles from their opercle openings while tending the young and nest for as long as four hours after spawning. Males will eat anytime after spawning until shortly before the young hatch; thereafter, they will not readily accept food until several hours after the young are in the wriggler stage of development.

Unfortunately, complete records were not kept for comparative purposes on the frequency and duration of nest building activities for the spawning sequence and parental period in the four Colisa species. More attention was given to C. chuna than the others during the parental period. From descriptive notes it is evident that C. chuna spends much more time tending the young and nest during the 3-4 days of development of young than do the other species. After the first 6-8 hours following the cessation of the spawning phase, parental activities in

the other species appear to decline in frequency. When the eggs hatch, C. fasciata and C. labiosa males build bubble rafts which serve as a nursery for the young, but they give it less time and attention than C. chuna. When the wrigglers drop below the surface or fry swim away from the nest, males of all species will retrieve them. However, after the first day of hatchings, C. fasciata in particular may spend a good amount of time well below the nest, even on the bottom. Time spent away from the nest is also greater in C. lalia and C. labiosa than in C. chuna. C. lalia males spend a considerable amount of time posted 2-3 cm under the nest. C. chuna males are more aggressive and restrictive towards female movements than males of the other species during the latter half of the parental period. If there is space between an aquarium heater and the corner walls of the aquarium, the C. chuna female in most instances remains there, near the surface in appeasement posture, following hatching of the eggs until the end of parental care.

Parental behavior activities appear to be influenced by the presence or absence of light. Even the most active male decreases his activities when lights are out. Immediately following spawning most males remained extremely active until dark. In the dark with embryos in the nest, C. chuna males remained 1-2 cm below the nest, posting at a 30-45° angle with median fins partially to fully erected. The male nudges the egg mass occasionally and perhaps rotates them as he does in the light. C. chuna eggs at 27-28°C hatch in 18-20 hours, and somewhere between 14-17 hours after spawning, males usually break egg clusters up and the eggs spread out among the bubbles. During the dark C. lalia males with or without fins erected post at the periphery of the nest a few centimeters below the surface, but not directly beneath the nest, as

in C. chuna. Females remain hidden in a corner. C. fasciata males usually posted at the substratum near the nest.

The parental behavior patterns of C. chuna appear to be adaptive for a fish its size. The smallest member of the genus, individuals used in this study ranged from 25 mm to 31 mm standard length. Among C. fasciata, the largest member of the genus, standard lengths ranged from 45 mm to 60 mm. The number of eggs released per spawning sequence by C. chuna females ranged from 189 to 455, whereas the range in C. fasciata was from 881 to 1997 (See Table III). It seems reasonable that C. chuna males spend more time guarding eggs and progeny to compensate for the smaller number of eggs produced.

With water temperature at  $27.7 \pm 1^{\circ}\text{C}$ , hatching of C. chuna took 18-20 hours. At  $27.7 \pm 1^{\circ}\text{C}$  eggs of C. lalia hatched between 22 and 24 hours, C. labiosa hatched in 24-25 hours, and C. fasciata 28-32 hours. C. chuna eggs left in a petri dish at room temperature approximately  $23^{\circ}\text{C}$  hatched somewhere between 38 and 44 hours. Of interest was the fact that these eggs received no care from the males. To emphasize the durability of the eggs, a pair of C. fasciata spawned and the eggs were removed for counting. Because the counting could not be done immediately, they were left in water in a jar in the refrigerator for more than three hours. After they were removed, counted, and placed in aquarium without fish a few hatched.

Eggs at first appear as yellowish spheres, but shortly after hatching become increasingly darker until just before hatching, when they look black. If observed closely or under a dissecting microscope they can be seen to move slightly. After hatching the larvae (wrigglers) are in an upside-down position in the nest. Movement during this

stage is very limited due to lack of differentiated fins and presence of the heavy yolk sac. Larvae in this stage mostly adhere to the foam bubbles (or bubbles and plants in C. lalia) but occasionally slowly sink from the nest and then spurt upward towards the nest or surface. The male often retrieves them in his mouth and spits them back into the nest. His movement patterns are much the same as when retrieving eggs. At this stage the extremely territorial C. chuna males spend most of their time blowing bubble rafts which surround the wrigglers.

Wrigglers of C. chuna become progressively more active as they get older and by the time they are 12 hours post-hatching (30 hours since spawned), they will stray a considerable distance horizontally and vertically from the nest, only to be retrieved by the attentive male.

C. chuna wrigglers remain upside-down until about 48 hours after spawning or 30 hours after hatching. Anytime after 30 hours post hatching some begin to turn right side up and become more active swimmers. The male at this time is still protective and actively blowing bubbles. The young, now referred to as fry, become active swimmers and move further from the nest.

By the time they are 72 hours old, fry are moving all over the tank. At this time the male is noticeably less busy blowing bubbles and retrieving young. Up to about 96 hours post-hatch the male guards the fry, which are extremely active throughout the tank. Bubble blowing activity is infrequent. At 108 hours post-hatch he no longer retrieves fry; he may blow bubbles and appears to tolerate movement by the female, which until this time has rarely moved from her hiding place. Usually at about 120 hours post-spawning the parental care

period is over. From this time progeny fend for themselves and may even be eaten by the male.

Although several fry could be seen in one area of a tank in some form of aggregation, it is questionable that these groups should be called "schools." Forselius (1957) suggested that Colisa with which he worked may have schooled.

#### Colisa chuna Exchange Experiments

Qualitative observations suggested that a measure of regulation of parental activity could be obtained by experiments involving the exchange of eggs and young at various stages of the parental period. Because of time limitations, only preliminary experiments were carried out. This included the following simple exchange experiments designed to see if C. chuna males would accept (adopt) and take care of the eggs and young of its conspecifics. No attempt was made to measure the intensity of parental activities directed towards such foster offspring in those males which accepted spawn from other pairs.

The experiments were carried out as follows:

Exp. #1 TK #25 contains pair that completed spawning 10 minutes earlier; male tending eggs, female in corner.

Step 1. Eggs were removed for counting.

Step 2. Eggs were replaced 36 minutes later. Male retrieved eggs and placed them in cluster in original spot.

Exp. #2 TK #25 contains pair that completed spawning 25 minutes earlier; male tending eggs, female hiding behind clay pot.

TK #28 contains a pair, plus wrigglers (<8 hrs old); male tending wrigglers, female off to side.



Step 1. Removed eggs from TK #25 to count, portion was placed into TK #28. Male collected eggs and placed them among wrigglers and guarded them. He then changed color by losing his black beard.

Step 2. Removed wrigglers from TK #28, placed them in TK #25 with male whose eggs were removed. He immediately ate the introduced wrigglers.

Step 3. A portion of eggs removed from TK #25 were replaced, male immediately collected them and placed them into a cluster and guarded them.

Step 4. Another batch of wrigglers from TK #28 were then placed into TK #25 with male guarding reintroduced eggs. He collected them and placed them among reintroduced eggs and guarded them.

Exp. #3 TK #26 contained a pair; male tending eggs, female hiding.

TK #27 contained male tending fry and female hiding.

TK #25 and #29 contained pairs that appeared to be courting.

Step 1. Fry were removed from TK #27 and placed in TK #25 and 29. They were immediately eaten.

Step 2. Eggs were removed from TK #26 and placed in TK #25 and 29. Males collected them and placed them into clusters and guarded them.

Exp. #4 TK #26 contained pair in the process of spawning (had not completed).

TK #27 contained pair and fry (approximately 24 hours old, spawned 48 hours earlier). Male tending nest. Female hiding.

- Step 1. Eggs and female removed from TK #26. Male appeared to be searching for eggs.
- Step 2. Fry were removed from TK #27 and placed into TK #26. Male immediately ate fry that did not get away. Some fry escaped.
- Step 3. Eggs from TK #26 placed into TK #27 with male guarding fry. At first he continued to collect fry; hesitated and then commenced to collect eggs and placed them into a cluster among fry. He guarded eggs and fry.
- Step 4. A portion of eggs were returned to TK #26. Male gathered them, placed them into a cluster, and later, while taking care of eggs, he gathered fry which had been placed in his tank (step #2) and attempted to keep them among the eggs. Observation next day.—Eggs (step #3) placed in TK #27 from #26 had hatched and male was guarding them. An obvious difference in size of wrigglers and fry existed as well as in swimming ability. Some swimming upright (original fry) and others upside down (foster fry).

Exp. #5 TK #29 contained single male with no nest.

TK #26 contained a pair without much interaction and without eggs, fry, or nest.

TK #25 contained a pair in process of spawning.

TK #27 contained a pair plus fry (72 hours old); male guarding, female off in corner.

- Step 1. Some fry removed from TK #27 were placed into TK #25 while the pair was in swimming inhibition. Male, col-

lected eggs and fry, and spat them among the cluster as soon as he became active. Fry swam away, but he retrieved them with eggs and put them into the cluster repeatedly. Male continued to take care of both eggs and foster fry during post-spawning phase.

Step 2. A cluster of eggs from TK #25 was removed during post-spawning phase. Twenty were replaced; male collected them and placed them back into the cluster in exact location from which they were removed. Male continued to retrieve introduced fry and attack female.

Step 3. Eighty-three eggs removed from TK #25 were placed in TK #27 among free swimming fry with male guarding them. This male was not intensely active because fry were three days old and no bubbles were present. He retrieved the eggs and placed them in a cluster. He did not release fine bubbles from opercle openings, as did the male in TK #25, which was still in post-spawning phase. (Perhaps release of bubbles is associated with early development of nesting behavior, spawning, and the early stage of parental care and is a function of physical activity.)

Step 4. Eighty-five eggs removed from TK #25 were placed in TK #26 among inactive pair. Male hesitated, collected some eggs, swam around in jerky pattern as if searching for a place to put the eggs and finally spat them out next to a leaf. He collected more and formed a cluster. Occasionally, between collecting eggs he would display at the

female.

Step 5. Seventy-five eggs removed from TK #25 were placed in TK #29 with a single male without a nest. He hesitated at first and then commenced to collect eggs and form them into a cluster under a leaf. After collecting all the introduced eggs he guarded them and rotated them.

Step 6. Removed fry from TK #27 and placed them into TK #29, where a lone male was guarding eggs from TK #25. Male collected fry and guarded them along with adopted eggs. On second day after adoption of eggs and fry by this male in TK #29, there were no eggs or fry.

The above exchange experiments indicate that C. chuna males will accept and take care of conspecific's eggs throughout the parental period and even when not in the parental period. On the other hand, the experiments suggest that there might be a critical period during the spawning period when males will not accept wrigglers or fry. These experiments also suggest that chemical or visual cues are not used to identify an individual's own spawn, or that the need to care for eggs and young overrides the tendency to eat foreign eggs.

The outcome of these preliminary exchange experiments suggest that more detailed exchange experiments could be designed to measure the intensity of parental activities at various developmental stages. Critical periods of acceptance and cues used to differentiate among eggs and wrigglers of different age and origin may come out in more detailed and carefully designed experiments.

## CHAPTER VIII

### COLOR CHANGES IN COLISA

Color changes in Colisa are most evident by changes in color intensity, colors present, and color patterns. The changes appear to be situation dependent, suggesting that color variations are associated with motivational factors present during certain social interactions. The most obvious differences in colors and markings associated with their changes are observed when individuals change from a non-reproductive pattern to a reproductive (nuptial) pattern. During these two phases the differences appear to be greater and more striking in males than in females. Individuals involved in agonistic encounters undergo similar changes as those involved in reproductive encounters, but with less change in color intensity. Picciolo (1964), in a study of sexual and nest discrimination in Anabantid fishes of the genera Colisa and Trichogaster, reported that the species used in his study were able to discriminate visually between fishes of their own and alien species. He further stated that because test males could distinguish their own species visually from closely related species which possess similar behavior (movements) they reacted to specific color and morphological characteristics which are independent of movements. He did, however, caution that it is possible that fishes are able to perceive extremely slight differential movements.

In the present study discussion will be limited to the more

obvious differences in coloration between males and females during non-breeding and breeding periods. For a more detailed presentation, see Forselius (1957) and Picciolo (1964).

#### Non-Breeding Colorations

All Colisa are rather pale during non-breeding periods and in non-agonistic situations. Dark anterior-ventral markings (beards) which are characteristic of breeding males are usually absent. C. lalia, C. fasciata, and C. labiosa males and females all have ocelli present on the opercle flap. During the spawning phase the ocelli in males become indistinguishable from the darkening of the beard and in females the ocelli become more prominent. When present, the ocelli appear rounded in males and irregularly shaped in females. Females during non-breeding periods appear to have a silver sheen to their bodies and their fins are almost transparent. Of the four species, C. fasciata females appear to be the most colorful at non-breeding and breeding times, particularly due to median and caudal fin coloration and markings.

C. chuna exhibits fewer body stripes, bars, and number of different colors than other Colisa. C. chuna males and females are also less distinct from each other in body shape. The pointedness of the posterior portion of the dorsal and anal fins and the caudal fin in males is not as striking in C. chuna as in its congeners. Neither is the tail as deeply lobed in C. chuna as are the tails of C. labiosa and C. fasciata. C. lalia has a fan shaped tail without any lobes. The color and shape of the median fins and caudal fin of C. lalia, C. labiosa, and C. fasciata accentuate the body, and intricate markings

appear in the posterior pointed regions of the fins of C. labiosa and C. fasciata. A point of interest is that non-breeding C. chuna males look very much like breeding females. Non-breeding males are characterized by an overall beige color darker on the dorsum, fading to a silver beige on the ventral region. Between these two regions is a dark brown lateral band extending from the caudal peduncle to the opercle. The band appears to wax and wane in intensity, depending on motivation of the male. A lateral band of the same color is characteristic of the breeding female but absent in the non-breeding female except in agonistic encounters. However, there are slight differences in the male and female. The band in the breeding female extends through the eye, but it stops at the opercle opening of the male. In the female the band also appears to be outlined above by a silvery white border.

During the non-breeding period C. labiosa males and females appear to exhibit a lateral band as a result of concentration of color in the center of their vertical stripes. This band is also characteristic of the spawning C. labiosa female, but it is not evident in the dark spawning male. The distinctiveness of the band is not as evident as in C. chuna. Forselius (1957) stated that the lateral band in C. labiosa appears from the base of the caudal fin to the eye. Individuals observed in this study showed a lateral band extending from the base of the caudal fin to the opercle opening. When non-breeding C. lalia females in this study were observed at certain angles, they appeared to have a faint lateral band, a phenomenon also noted by Forselius (1957).

Horizontal chin bars characteristic of non-breeding and breeding

males and females of C. labiosa and C. fasciata are absent in C. chuna and C. lalia. In both species in non-breeding coloration the chin bars appear to be dark brown, separated by silvery white areas between the once distinct brown bars.

Color changes evident during agonistic encounters are similar to changes seen in breeding fish and will not be discussed in detail. Changes from one phase to the other and vice versa are very rapid. Although the colors are much the same as those in spawning individuals, the detail and intensity are not as pronounced. This suggests that agonistic and reproductive color changes may be mediated by the same physiological mechanisms. Dominant individuals tend to be more intensely colored than do subordinate individuals during aggressive encounters.

#### Reproductive Color Changes

Reproductive color changes have been described for cichlid fishes (Baerends and Baerends-van Roon, 1950), B. splendens, C. lalia, C. labiosa, C. fasciata, and several other anabantoid species (Forselius, 1957), T. trichopterus (Miller, 1964), T. leeri (Hall, 1966), C. fasciata (Reser, 1969), and T. pectoralis (Robison, 1971). However, in these studies and many others on color changes in fish, the functional significance of many of the changes are not well understood.

During the spawning sequence there are slight to extreme variations in colors. No spawning occurred during the course of this study without individuals acquiring nuptial coloration. Although nuptial colorations appear to be inevitable, their intensity may vary among individuals and throughout the sequence.



Generally, body markings such as stripes and bars become darker as nest building and courtship proceeds during the pre-spawning phase. Individuals develop colors in regions of the body previously void of markings such as the very prominent anterior-ventral bearded regions in all Colisa males. Accompanying the changes in body markings is an overall darkening of the ground color of the body and fins, especially in the males. In C. lalia the markings remain basically the same as in non-breeding males but the intensity is more striking and the blue beard and blue markings in the median fins stand out. Darkening of the ground color is of such intensity in C. labiosa and C. fasciata males that in the former the appearance is a dark chocolate brown to black with iridescent markings. In the latter, the body becomes a deep brown-red to maroon with blue iridescent stripes and splotches and orange-red fin margins. The C. chuna male changes from a silvery beige with a dark brown lateral band to a gold-orange with a blue-black anterior-ventral region and yellow median fin markings. The females undergo changes in coloration not nearly as striking as those of males. Female C. chuna during pre-spawning vary in intensity. The female in C. chuna's congeners may wax and wane in coloration during this phase.

Nuptial colors are most striking, intense, and permanent during the spawning phase of the spawning sequence. However, between spawning bouts, particularly during the early stage of the spawning phase, females may suddenly darken prior to approaching the male under his nest and maintain or increase in color intensity during the clasp, only to lose it following the clasp. C. chuna females often acquired a dark brown lateral band just before approaching the male and lost it once they returned to the hiding area. Usually, females maintain their dark

coloration throughout the middle and latter portion of the spawning phase.

Whereas acquisition of nuptial coloration seems to be a gradual process in males as well as females, the loss of nuptial coloration following the spawning phase appears sudden in females. Post-spawning color change in males are not so abrupt, but a noticeable change in intensity and markings does occur. As males enter the parental period color may vary with the presence of the female or interference by the observer, other fish, other conspecific males, or snails. Basically, anything that moves near its nest causes an intensification of coloration. When the male approaches the female, he becomes very dark, but once she is in a corner hiding and he is back under his nest he may become less brilliant. C. chuna males during parental care usually lose their blue-black beard but maintain a rather intense gold-orange color as opposed to the silvery beige color of the non-reproductive phase. In some C. chuna males throughout the spawning sequence and during the parental care period, depending on the angle of observation, a remnant of the lateral band may be seen.

Forselius (1957) indicated in his studies on members of the genus Colisa that species discrimination might be based on female recognition of conspecific male coloration. Females are not characterized by the brilliant colors that are possessed by the males. Picciolo (1964) found that neither non-silvery nor the more natural silvery colored aluminum models attracted males. However, the silvery model could be brought up to nest-posting males without eliciting escape behavior. This finding was in agreement with Forselius' (1957) conclusions based on model presentation.

The following are descriptions of color changes which occur at the onset of the reproductive period and remain throughout. Numbers correspond to numbers in Figures 2, 3, 4, and 5.

#### Male Nuptial Coloration

##### 1. Eye Color

C. chuna--During the spawning sequence the eye appears to be solid black.

C. lalia--The eye is traversed by a black vertical bar above and below the black pupil, while the remaining portion is orange-red.

C. labiosa--The eye above the black pupil is traversed by a black bar. The rest of the upper half is orange-red, while the lower half is silvery.

C. fasciata--Eye coloration is same as in C. labiosa.

##### 2. Opercular Ocellus

C. lalia, C. labiosa, and C. fasciata--In breeding males the ocelli are indistinguishable from the gular coloration.

C. chuna--The ocellus is absent.

##### 3. Anterior-Ventral Region

C. chuna--A blue-black coloration appears on the cheeks below the lower lip and eye and extends along the gular region and breast onto the anal fin.

C. lalia--An iridescent blue extends from under the eye and lip, along the cheek, and onto the gular and breast regions with a white patch on the breast where the pelvic fins attach.

C. labiosa--A blue tract extends from along the lower cheek past

the point of attachment of the pelvic fins to the origin of the anterior part of the anal fin. The more ventral gular region is a deep chocolate brown.

C. fasciata--The entire anterior-ventral region is blue except for chin markings.

#### 4. Horizontal Chin Bars

C. labiosa--The chin bar effect appears to be a result of prominent white markings separated by continuations of the blue anterior-ventral tract.

C. fasciata--Basically the same as in C. labiosa.

#### 5. Pelvic Fins

C. chuna--Coloration is light yellow, as in non-breeding individuals.

C. lalia--The proximal portion appears white, while the remainder is orange-red.

C. labiosa and C. fasciata--The entire filament is orange-red.

#### 6. Vertical Stripes

C. lalia--The alternating blue and red vertical stripes extend from behind the opercular cover into the caudal fin. Also, the red stripes appear to extend into the anal fin.

C. labiosa--The vertical blue stripes on a chocolate background extend from behind the opercular into the caudal fin and into the soft ray portion of the anal fin.

C. fasciata--The posterior part of the soft ray shows orange-red and blue diagonal stripes. Blue is characteristic of the remainder of the fin except for a narrow white margin.

#### 7. Dorsal Fin

C. chuna--The gold-orange fin is bordered by a rather wide yellow margin.

C. lalia--The margin of the fin is orange-red, while the spiny ray portion is blue with orange-red splotches and the soft ray portion exhibits orange-red and blue diagonal stripes.

C. labiosa--Orange-red splotches appear on a chocolate background on the proximal portion of the soft ray and the remainder of the fin is blue with a narrow orange-red margin.

C. fasciata--The posterior part of the soft ray shows orange-red and blue diagonal stripes. Blue is characteristic of the remainder of the fin except for a thin white margin.

#### 8. Anal Fin

C. chuna--Most of the spiny rays are black, as are the ends of the soft rays with a narrow yellow margin on the anterior half of the spiny ray portion. A slightly posterior proximal area of the spiny rays and most of the soft rays are gold-orange, as is most of the lateral surface of the body.

C. lalia--Blue which extends from the anterior-ventral region dominates the spiny ray portion, with a white border between the blue and orange-red margin. The soft ray is dominated by orange-red in the form of vertical or horizontal stripes with a faint blue background.

C. labiosa--The orange-red margin of the spiny ray portion is bordered by a broad blue band extending to the margin of the soft ray. The remaining area of the fin is chocolate brown with blue vertical stripes extending from the body into the fin.

C. fasciata--Most of the fin is blue with a prominent orange-red margin, and the posterior portion of the soft ray appears deep red.

#### 9. Caudal Fin

C. chuna--Solid orange-gold as most of the body.

C. lalia--Alternating orange-red and blue vertical stripes cover the tail.

C. labiosa--Chocolate-brown with a few vertical blue stripes.

C. fasciata--A wide red band borders the deeply lobed fin. Red splotches on a blue background cover the rest of the fin.

#### Female Nuptial Coloration

#### 1. Eye Color

C. chuna--The eye is silver with a black pupil and a dark horizontal band appearing as an extension of the dark brown lateral band.

C. lalia--A dark vertical band extends through the eye. The pupil is black and the remaining portion outside the band is red-orange.

C. labiosa and C. fasciata--Same as in the male.

#### 2. Opercular Ocellus

C. lalia, C. labiosa, and C. fasciata--All exhibit a small irregular blue ocellus.

#### 3. Lateral Band

C. chuna--Broad dark brown band extends horizontally from the caudal peduncle through the eye. This band also appears to be bordered above by a light silver band. The overall body

color appears beige, as opposed to the silvery color during non-breeding periods.

C. labiosa--The vertical blue stripes are much darker on the midline, giving the appearance of a broken horizontal band. Forselius (1957) states that this band extends from the root of the caudal fin to the mouth. However, individuals used in this study only exhibited it to the opercular opening.

#### 4. Horizontal Chin Bars

C. labiosa and C. fasciata--Same as in the males, but less pronounced.

#### 5. Pelvic Fins

Not nearly as brilliant as in the males.

#### 6. Vertical Stripes

C. lalia--Stripes appear the same as in the male except they are less intense and blue is much more dominant.

C. labiosa--Color appears to be concentrated in the center of the blue stripes, giving the appearance of a horizontal band.

C. fasciata--The colors are the same as in the male except the intensity is not as great.

#### 7. Dorsal Fin

C. chuna--Silver with a narrow yellow margin.

C. lalia--Silver with blue markings and a gray-black margin on the spiny portion.

C. labiosa--Silver with an orange-red margin.

C. fasciata--Silver with a blue tinge, a white border, and red spots on the posterior part of the soft ray.

#### 8. Anal Fin

C. chuna--Mostly silver with a slight black area on the spiny ray portion and a yellow margin.

C. lalia--Mostly silver with blue markings and a rather dark margin.

C. labiosa--Silver with blue markings and an orange-red margin.

C. fasciata--Blue with an orange-red margin and a light red area on the posterior portion of the soft ray.

9. Caudal Fin

C. lalia--Smoky gray with a few light blue stripes.

C. labiosa--About the same color as in C. lalia except there are no stripes or other markings.

C. fasciata--The deep lobed tail has a broad red margin and the rest is characterized by red and blue markings.



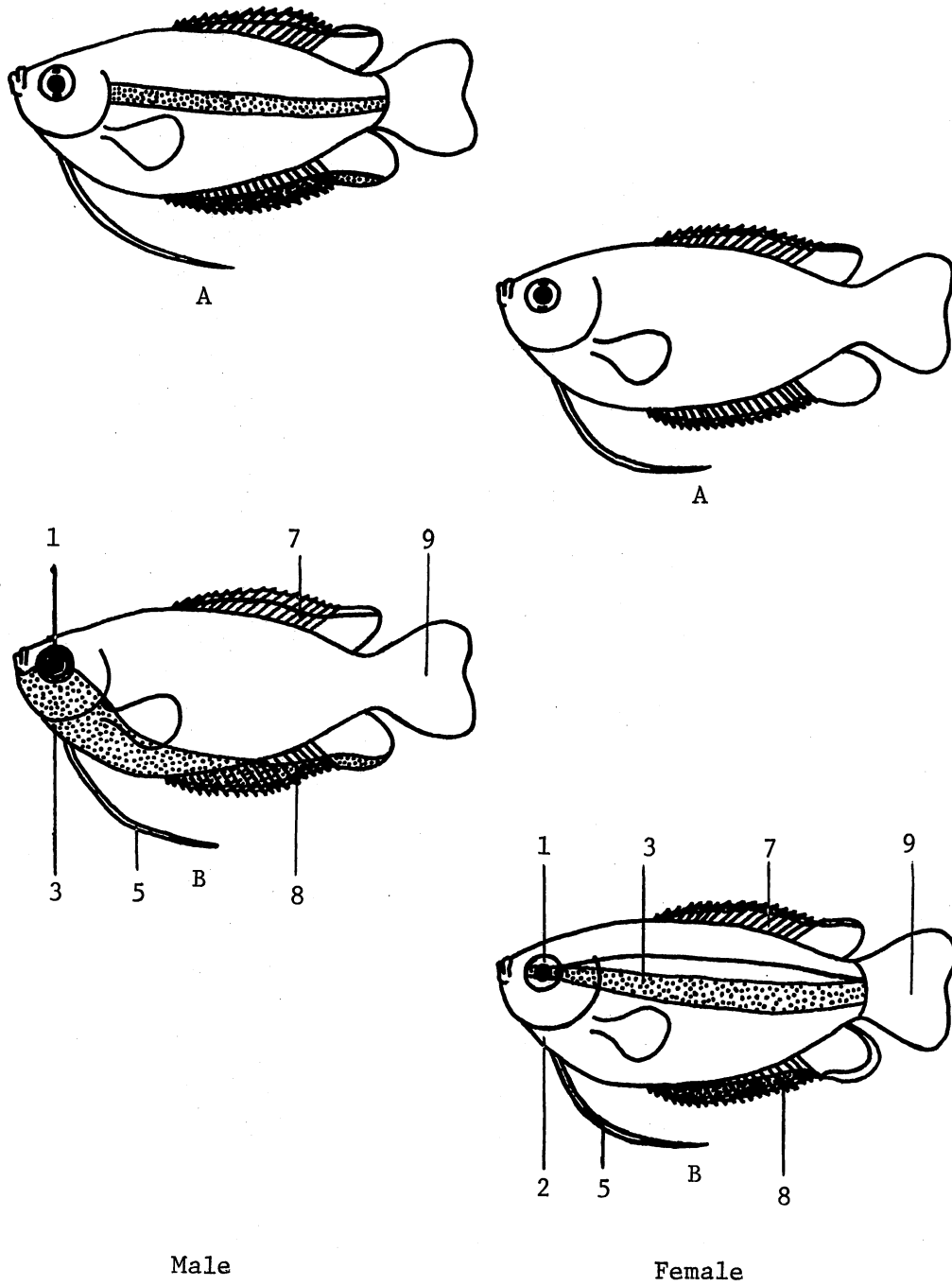


Figure 2. Reproductive color changes in *C. chuna* male and female. A. Non-breeding. B. Breeding.

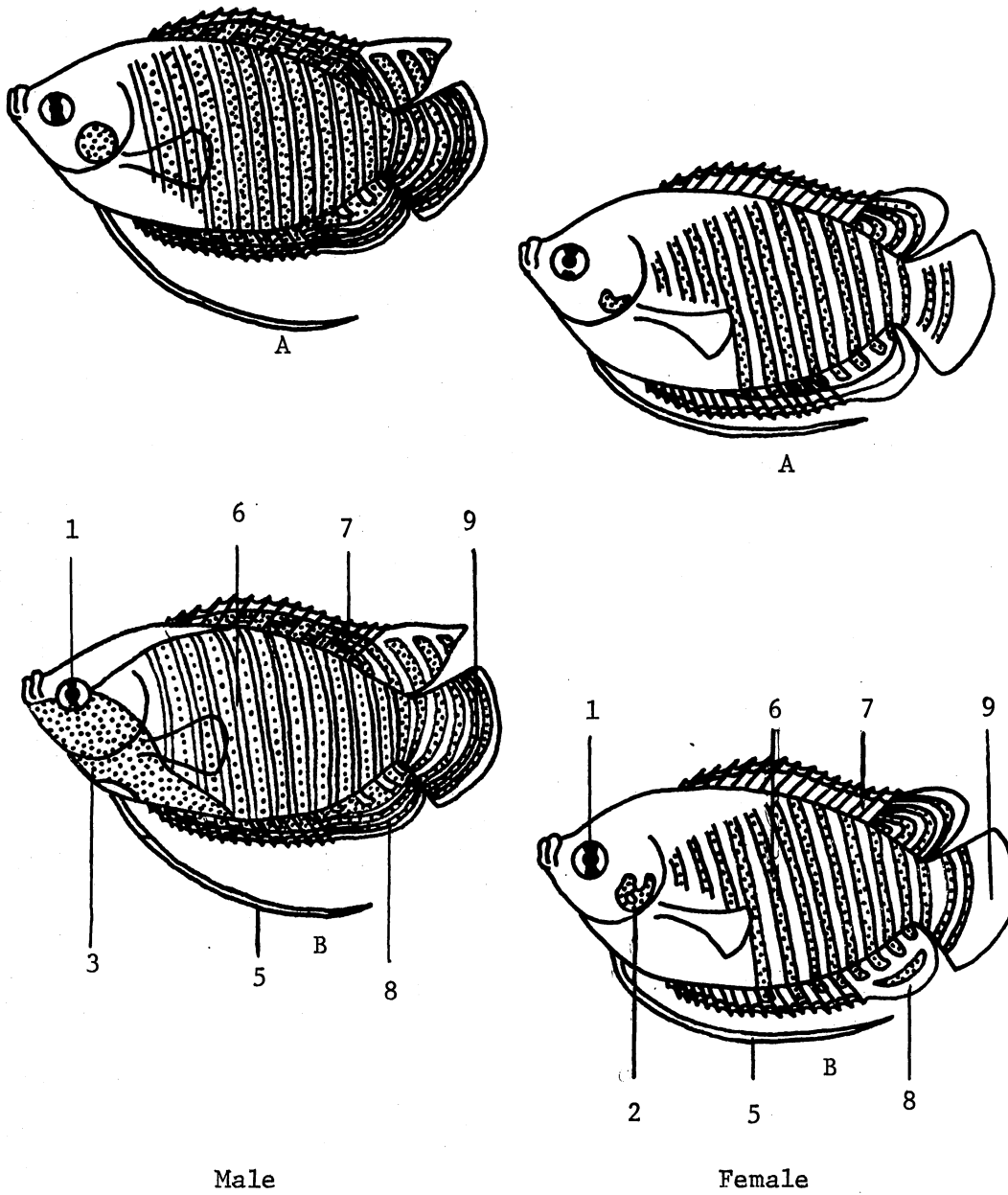


Figure 3. Reproductive color changes in *C. lalia* male and female.  
 A. Non-breeding. B. Breeding.

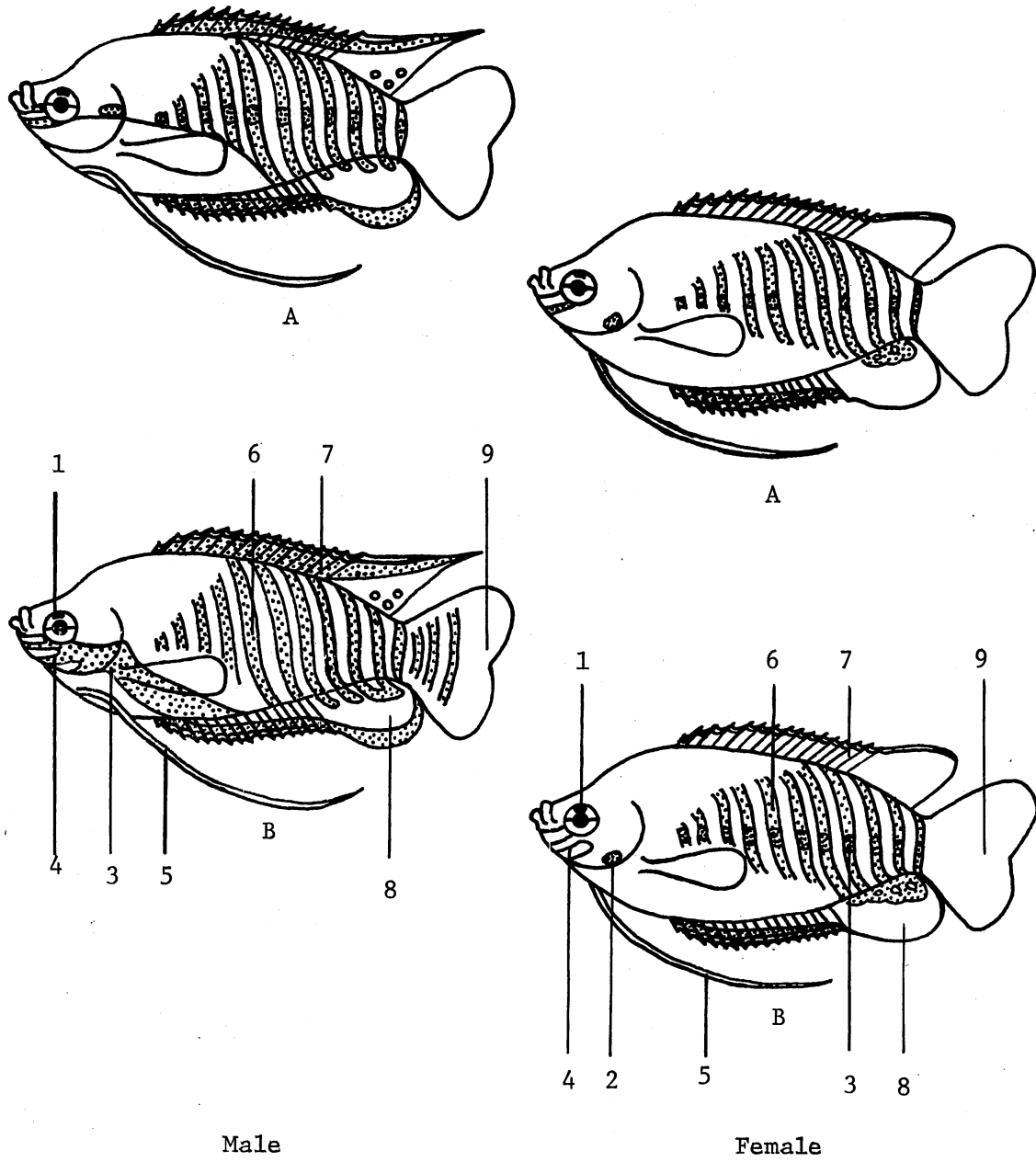


Figure 4. Reproductive color changes in *C. labiosa* male and female.  
 A. Non-breeding. B. Breeding.

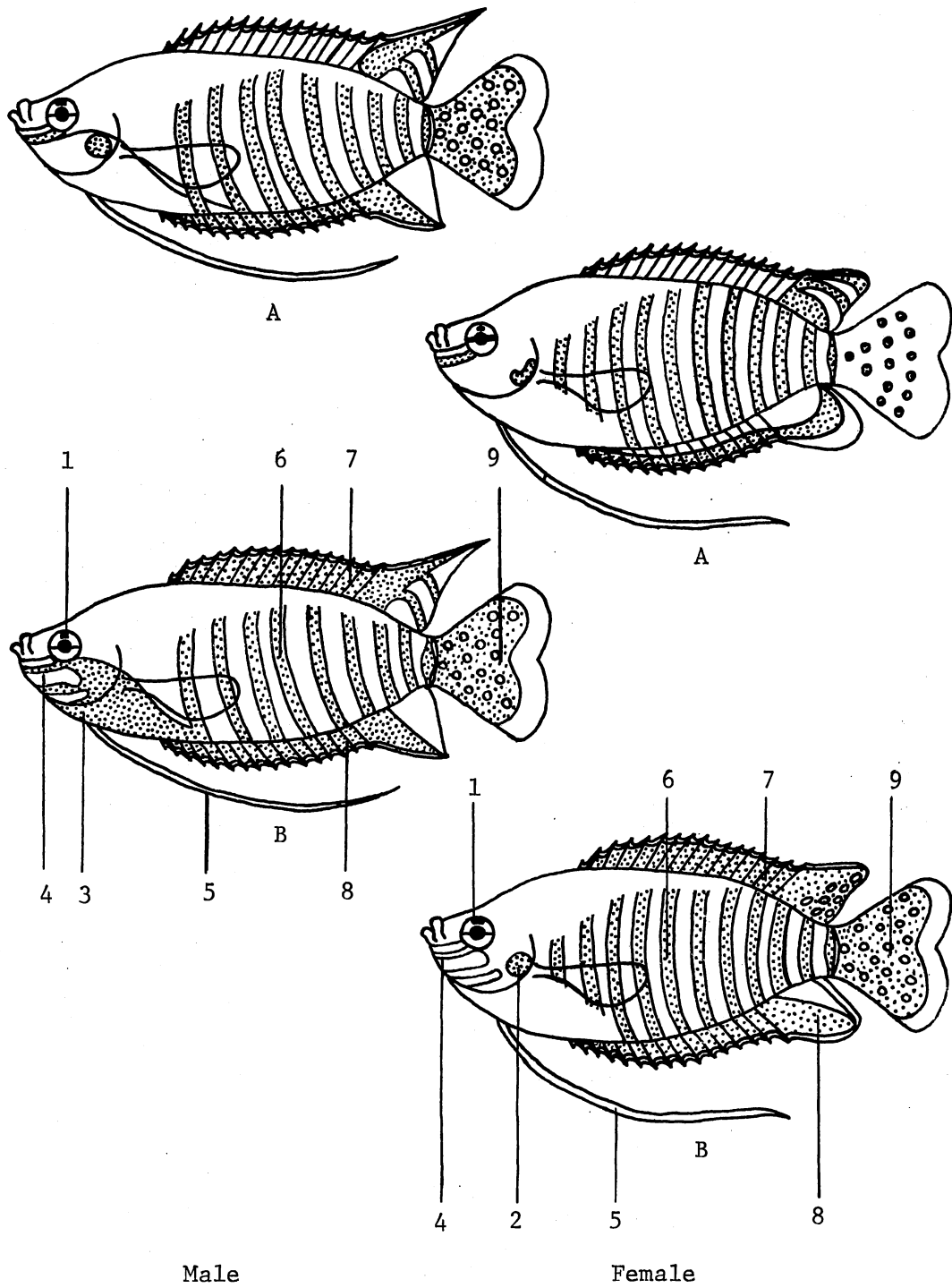


Figure 5. Reproductive color changes in *C. fasciata* male and female. A. Non-breeding. B. Breeding.

## CHAPTER IX

### QUANTITATIVE ASPECTS OF SPAWNING IN

#### THE GENUS COLISA

In addition to describing the qualitative differences in behavior among the species of Colisa as discussed above, several features useful in providing comparative information on the genus were studied in a more detailed, quantitative manner. All of the latter pertain to behaviors occurring in the spawning phase.

General discussion of quantitative aspects of the four species will be based on data found in Tables 4 and 5. C. chuna data were obtained from 12 complete recorded spawning phases which had a total of 586 bouts. Data were obtained on complete spawning phases of 6 pairs of C. lalia, 5 pairs of C. labiosa, and 6 pairs of C. fasciata. The total number of bouts for the three species were 568, 358, and 720, respectively.

The average number of bouts per spawning phase was greatest in C. fasciata with 120.00, while the lowest was C. chuna with 48.83. C. lalia had an average of 94.67, the second greatest, and C. labiosa, ranking third, had an average of 71.60. Females initiated most of the bouts in all Colisa spp. C. chuna females initiated 52.21 per cent of all bouts, while C. lalia females initiated 70.77 per cent. C. labiosa females initiated 73.74 per cent, and C. fasciata females initiated 57.00 per cent. This contrasts with data for Trichogaster leerii (Miller

Table 4. General quantitative data on spawning activities in Colisa<sup>1</sup>

	<u>C. chuna</u>	<u>C. lalia</u>	<u>C. labiosa</u>	<u>C. fasciata</u>
Total number of bouts	586	568	358	720
a. male initiated	280	166	94	310
b. percent of total				
initiated by male	47.78	29.23	26.26	43.00
c. female initiated	306	402	264	410
d. percent of total				
initiated by female	52.21	70.77	73.74	57.00
Total duration of all bouts (sec.)	9210.00	7617.50	9852.50	13020.00
Average bout duration (sec.)	14.01	13.41	27.52	18.10
Total duration of spawning phase				
a. minutes	743	626	553	975
b. seconds	44556	37586	33150	58475
c. average duration per complete spawning phase (minutes)	61.92	104.33	110.60	162.50
Average number of spawning bouts/spawning sequence	11.75	25.33	32.80	22.67
Average number of pseudospawning bouts/spawning phase	1.08	8.16	4.00	2.66
Average number of clasp bouts/spawning phase	17.33	39.83	50.81	34.83
Average number of non-clasp bouts/spawning phase	31.50	54.83	20.80	84.66
Average duration of swimming inhibition in spawning bouts (male)	11.87	3.52	6.48	5.70
Average duration of swimming inhibition in spawning bouts (female)	11.80	4.05	5.74	3.55

<sup>1</sup>Based on 12, 6, 5 and 6 complete spawning phases in C. chuna, C. lalia, C. labiosa and C. fasciata.

Table 5. Bout category analysis of sexual bouts in C. chuna, C. lalia, C. labiosa, and C. fasciata<sup>1</sup>

	<u>C. chuna</u>	<u>C. lalia</u>	<u>C. labiosa</u>	<u>C. fasciata</u>
Total number of bouts	586	568	358	720
a. male initiated	280	166	94	310
b. female initiated	306	264	264	410
c. average number of bouts per spawning sequence	48.83	94.67	71.60	120.00
Total number of spawning bouts	141	152	164	136
a. male initiated	3	4	12	3
b. female initiated	138	148	152	133
c. (male and female) percent of total bouts	24.06	26.76	45.81	18.80
d. average number per spawning sequence	11.75	25.33	32.80	22.67
Total number pseudo-spawning bouts	13	49	20	16
a. male initiated	1	4	2	0
b. female initiated	12	45	18	16
c. (male and female) percent of total bouts	2.21	8.63	5.59	2.22
Average duration of pseudo-spawning bouts (seconds)	26.00	24.53	37.45	48.63
a. male initiated	17.00	25.75	64.50	0.00
b. female initiated	26.00	24.42	34.44	48.63
Total number of clasp only bouts	51	38	70	56
a. male initiated	3	4	2	5
b. female initiated	48	34	68	51
c. (male and female) percent of total bouts	8.70	6.69	19.55	7.08
Average duration of clasp only bouts (seconds)	19.47	17.51	30.14	33.16
a. male initiated	22.00	17.25	55.00	35.80
b. female initiated	19.31	17.54	32.90	32.90
Total number of clasp bouts	205	239	254	208
a. male initiated	7	12	14	8
b. female initiated	201	227	240	201

Table 5. (Continued)

	<u>C. chuna</u>	<u>C. lalia</u>	<u>C. labiosa</u>	<u>C. fasciata</u>
c. (male and female) percent of total bouts	35.59	42.08	70.95	28.88
Average duration of clasp bouts (seconds)	27.36	23.72	35.53	43.64
a. male initiated	28.85	22.92	49.14	42.13
b. female initiated	26.85	23.03	34.48	43.88
Total number of non-clasp bouts (aggression only bouts)	378	329	104	508
a. male initiated	273	156	80	301
b. female initiated	105	173	24	207
c. (male and female) percent of total bouts	64.50	57.92	29.05	70.56
d. average number per spawning sequence	31.50	54.83	20.80	84.67
Average duration of non- clasp bouts (aggression only and courtship only bouts)	9.52	6.42	6.78	7.76
a. male initiated	8.93	6.10	5.15	4.31
b. female initiated	11.00	6.72	12.21	12.56

<sup>1</sup>Based on 12, 6, 5 and 6 spawning sequences, respectively.



and Hall, 1968:128), where males initiated slightly more bouts than females during the spawning phase.

The average duration of the spawning phase in minutes was 61.92 for C. chuna, 104.33 for C. lalia, 110.60 for C. labiosa, and 162.50 for C. fasciata.

Spawning bouts in C. chuna, C. lalia, C. labiosa, and C. fasciata, respectively, comprised 24.06, 26.76, 45.81, and 18.80 percents of all bouts during the spawning phase. The average number of spawning bouts per spawning phase were 11.75 for C. chuna, 25.33 for C. lalia, 32.80 for C. labiosa, and 22.67 for C. fasciata. Most spawning bouts in all species were initiated by females, which may be indicative of the receptivity and physiological readiness of the females to spawn. Female C. chuna, C. lalia, and C. fasciata initiated 97 percent of all spawning bouts, while C. labiosa females initiated 92.68 percent of the spawning bouts. As pointed out by Miller and Hall (1968), female initiated bouts tend to contain more of the activities associated with the terminal act of spawning and, therefore, are considered more successful.

The average duration of spawning bouts in seconds was 30.00 in C. chuna, 23.91 in C. lalia, 38.13 in C. labiosa, and 47.50 in C. fasciata.

Pseudospawn bouts were few in number and were similar in average duration to spawning bouts. Most pseudospawns were initiated by females and comprised fewer than 2.5 percent of the total bouts in C. chuna and C. fasciata. C. lalia had the greatest relative number of pseudospawn bouts, 8.63 percent of the total number of bouts, while 5.59 percent of the C. labiosa bouts were pseudospawnings.

Females initiated most of the clasp only bouts as well as the

total number of all bouts containing clasp (spawning and pseudospawning included). In C. chuna clasp bouts constituted 8.7 percent of the total, while in C. lalia, C. labiosa, and C. fasciata they represented 6.69, 19.55, and 7.08 percents, respectively. Female C. labiosa initiated 70.95 percent of all bouts containing clasps, about 30 percent more than any of the other Colisa species.

Non-clasp bouts contain only courtship and aggressive activities and made up a major portion of the spawning phase. In C. chuna, C. labiosa, and C. fasciata the males initiated most of the non-clasp bouts with percentages running 72.22, 76.92, and 59.25, respectively. In C. lalia the males initiated 47.56 percent. Average duration of non-clasp bouts was brief compared to clasp bouts, 9.52 in C. chuna, 6.42 in C. lalia, 6.78 in C. labiosa, and 7.67 in C. fasciata. Female initiated non-clasp bouts in all four species were longer than male initiated non-clasp bouts, suggesting that male initiated bouts are more likely to be incomplete, perhaps due to reproductive unreadiness on the female's part. The male initiated bouts undoubtedly also contain a fairly high percentage of bouts in which the male was primarily aggressively motivated, a situation which generally results in a short attack or chase.

Table 6 presents data on intervals which follow all bouts and intervals which come before and after spawning bouts. The average interval duration following bouts was 61.60 in C. chuna, 53.42 in C. lalia, 65.77 in C. labiosa and 73.36 in C. fasciata. When comparing average intervals before and after spawning, those before were shorter than those after in all species. However, looking at interval durations after spawning bouts among the species, C. chuna had a markedly

Table 6. Analysis of sexual bout intervals in Colisa<sup>1</sup>

	<u>C. chuna</u>	<u>C. lalia</u>	<u>C. labiosa</u>	<u>C. fasciata</u>
Total interval duration following bouts	35356.00	30022.50	23297.50	45455.00
Total interval duration before spawning bouts	11887.00	9245.00	10720.50	9715.00
Total interval duration after spawning bouts	14657.00	10381.50	11970.00	13333.00
Average interval duration following bouts	61.60	53.42	66.00	64.20
Average interval duration before spawning bouts	84.91	60.82	65.77	73.36
Average interval duration after spawning bouts	105.45	68.30	72.99	98.25

<sup>1</sup>Time in seconds, based on 12, 6, 5 and 6 spawning sequences, respectively.

greater average duration than its congeners. Average interval duration in seconds after spawning bouts for C. chuna was 105.45, C. lalia 68.30, C. labiosa 72.99 and C. fasciata 98.25, while the average interval duration before spawning bouts was 84.91, 60.82, 65.77, and 73.36, respectively. Longer average intervals after spawning bouts, particularly in C. chuna, may be indicative of time spent by males taking care of eggs just spawned. As discussed in the qualitative section, C. chuna males spend a greater amount of time tending the eggs than do other Colisa males. Post-spawning interval duration of C. lalia (68.30) males reinforce the conclusion that females of this species spend less time tending the eggs than do other Colisa males.

Table 7 shows the average pre-clasp duration in spawning, pseudospawning, and clasp only bouts. Pre-clasp duration is the time from the beginning of the female approach to the male under his nest until the clasp is initiated. Pre-clasp only bouts (4.21) is shortest in C. chuna. C. lalia, with a pre-clasp duration in spawning bouts of 5.12, in pseudospawning bouts of 6.11, and clasp only bouts of 6.14, has the next shortest time. The average pre-clasp duration is 18.40 in spawning bouts, 18.20 in pseudospawning bouts, and 18.28 in clasp only bouts for C. labiosa. C. fasciata average pre-clasp duration is 17.05 in spawning bouts, 19.01 in pseudospawning bouts, and 15.30 in clasp only bouts. Perhaps average pre-clasp duration is shortest in C. chuna because female C. chuna usually do not butt the male before clasping. Also, there is no pause or long orientation and adjustment period by C. chuna as there is in C. labiosa and C. fasciata, species with longer average pre-clasp periods. The average pre-clasp duration in C. lalia was only slightly greater than that in C. chuna. In Chapter IV it was stated

Table 7. Average duration (sec.) of pre-clasp in spawning, pseudo-spawning and clasp only bouts in Colisa<sup>1</sup>

	<u>C. chuna</u>	<u>C. lalia</u>	<u>C. labiosa</u>	<u>C. fasciata</u>
Average pre-clasp duration in spawning bouts	3.86	5.12	18.40	17.50
Average pre-clasp duration in pseudospawning bouts	3.84	6.11	18.20	19.01
Average pre-clasp duration in clasp only bouts	4.21	6.14	18.28	15.30

<sup>1</sup>Averages based on data from 12, 6, 5 and 6 spawning phases in C. chuna, C. lalia, C. labiosa and C. fasciata.

that upon approach by female C. lalia to the lateral displaying male under his nest during spawning bouts, the female averages two butts per bout and that C. lalia females butt more frequently than do other Colisa females. Since they butt more and have relatively brief pre-clasp times, it may be concluded that pre-clasp butts of C. lalia females are delivered rather quickly. Pre-clasp butting in female C. lalia appears to function to inhibit male aggression by serving as a signal releasing lateral display which leads to clasp and spawning.

A comparison of average clasp duration in spawning, pseudospawning and clasp only bouts in seconds is shown in Table 8. The average clasp duration in clasp only bouts is much shorter than in spawning bouts, with pseudospawning bout clasps intermediate. The short duration of clasp in clasp only bouts may indicate lack of pair synchronization, failure of the female to mount properly, and failure of the female and male to continue responding sexually to each other.

Average clasp duration in all bout types was greatest in C. fasciata (Table 8). In all four species average duration of pseudospawning bout clasps were a bit lower than the durations of spawning bouts.

Average duration of swimming inhibition in seconds (see Table 4) varied slightly between male and female in Colisa species. However, there was considerable variation among C. chuna (11.87, males and 11.80, females) and its congeners. C. lalia had the shortest average swimming inhibition duration, with 3.52 in males and 4.05 in females. If swimming inhibition were shorter in C. chuna, its average bout time would perhaps be shorter.

Table 8. Average clasp duration<sup>1</sup> (sec.) in spawning, pseudospawning and clasp only bouts in Colisa

	<u>C. chuna</u>	<u>C. lalia</u>	<u>C. labiosa</u>	<u>C. fasciata</u>
Average clasp duration in spawning bouts	12.86	10.74	13.75	23.63
Average clasp duration in pseudospawning bouts	9.39	9.84	13.42	20.30
Average clasp duration in clasp only bouts	4.69	4.57	6.50	7.89

<sup>1</sup>Averages based on data from 12, 6, 5 and 6 spawning phases in C. chuna, C. lalia, C. labiosa and C. fasciata.

## CHAPTER X

### SUMMARY AND DISCUSSION

Several non-social activities occur commonly in all species of Colisa and are referred to as maintenance behaviors in this study. Feeding, perhaps the main vegetative activity, is quite similar in the four species and may take place at the surface, between surface and bottom and at the substratum, depending mostly on the nature of the food. C. fasciata tends to spend more time bottom feeding than other Colisa, and it was the only species observed bottom feeding in a vertical head down position (occasionally tipping farther over than 90°), engulfing gravel, and spitting it out. It was not uncommon to see C. fasciata, the species most active at night, feeding vigorously during the night. Perhaps this finding, coupled with the fact that C. fasciata is darker in coloration than its congeners, points to its possible adaptation for a bottom existence or living in dense vegetation in its natural habitat.

Jetting, a method of feeding unique to Colisa, was reported for Trichogaster by Hall (1965), Wimmer (1970) and Robison (1971) in post-spawning contexts or as a method of bubble blowing.

Maintenance activities such as inspiration, chafing, fin flicking and yawning are very similar in all species of Colisa and are of no use in comparative study.

Summarizing the existing data on the distribution of the four



Colisa species, Forselius (1957) found that sympatry occurs among C. chuna, C. lalia and C. fasciata. He also stated that "whether any ecologic and/or ethologic barriers preventing hybridization exist in nature between the species remains to be investigated." Subsequently he was able to produce a Colisa hybrid, C. labiosa x lalia, which was subjected to detailed observation. It should be pointed out that this cross was between two species that apparently are allopatric in nature.

The three species of Colisa existing sympatrically may largely depend on courtship and reproductive behavior as an isolating mechanism; assuming geographic separation at some time in the past, sympatry may have occurred subsequent to the development of behavioral isolating mechanisms. Spieth (1958) suggested that behavioral differences may be the most effective isolating mechanism. He also reported that in many species exhibiting territorial behavior, specific and unique recognition ornamentation and movements have evolved. That such is the case in Colisa, as it is in Trichogaster (Miller and Robison, 1974), has been demonstrated above in the section on color patterns (Chapter VIII).

Most anabantoid genera utilize a bubble nest for spawning, but the form and composition of the nest and nest building behavior vary even at the species level (Miller, 1964). From Table 1 it can be seen that species specific variation in nest building behavior exists among the species of Colisa. The most striking difference in nest building behavior is in the use of vegetation in nest construction. C. chuna, C. labiosa, and C. fasciata utilize plants or other objects in the area selected for nesting to anchor the nest, but do not actively seek vegetation for construction. C. lalia actively seeks vegetation for con-

structing an elaborate dome shaped nest, an indication of specialization probably related to an as yet unknown ecological adaptation.

Wimmer (1970) reported that T. microlepis not only always uses plant material in its nest construction, but actively seeks out vegetation and either uproots such vegetation or snips off leaves of plants and transports them back to the nest for incorporation. C. lalia showed a preference for filamentous algae and chose other plant material and detritus secondarily.

Another unique pattern shared by C. lalia and T. microlepis is nest pushing. Nest pushing is accomplished by thrusting the snout into the nest. Miller (1964) suggested that the absence of nest pushing in other Trichogaster may be due to less extensive use of vegetation. It is reasonable to reach a similar conclusion for Colisa species which do not actively seek out vegetation for incorporation in the nest.

C. chuna, the smallest member of the genus, is unique in its method of nest construction in that it blows a single layered bubble nest. Differences in bubble blowing patterns used in nest construction are found among the species of Colisa paralleling those found in Trichogaster species (Miller and Robison, 1974). C. chuna was unique in that it only utilized surface inspiration with surface release as a method of bubble blowing. C. lalia, C. labiosa, and C. fasciata utilize this method as well as surface inspiration with subnest release, the most commonly used. Although C. lalia does exhibit surface inspiration with surface release, it was rather rare. T. microlepis, the only Trichogaster which actively seeks vegetation for nest construction shares with C. lalia the predominant use of subnest release. This striking convergence indicates the strong influence of ecological fac-

tors on behaviors subserving such adaptations.

Stereotyped threat and courtship movements have provided a rich source of material for studying the evolution of behavior (Hinde, 1970). Because of the sterotypy of social behavior in anabantoid fishes such behaviors are perhaps the most useful for comparison in Colisa species. However, Hinde and Tinbergen (1958) have pointed out that all characters of the living animal, including behavioral and morphological features are products of environmental factors as well as inherent potentialities and care must be taken to ensure that behavioral differences are in fact indicative of genetic diversity and not merely of dissimilar environments. C. chuna and its congeners were spawned in the same laboratory, during the same period under the same conditions and therefore it is assumed that behavior differences in courtship and reproductive behavior are largely indicative of genetic diversity.

The four species of Colisa are characterized by distinctive courtship and reproductive patterns. These patterns vary in temporal relationship of behaviors, inclusion and deletion of behavioral elements, and frequency and intensity of certain behaviors.

The initial development of the nest created by the male, his visits and displays to the female, and the responsive behavior of the female mark the appearance of a noticeable pattern of activities which could be labeled courtship.

Leading, an activity pattern described by Forselius (1957) for Colisa and by Miller (1964) for T. trichopterus appears to be species-typical among the species of Colisa. In aquaria, leading is more prominent in C. chuna and C. lalia and less so in C. labiosa and C. fasciata. Leading appears to be most unique in C. chuna due to its

display of a complete vertical stand and median fin spread. Upon the approach of the female to the male, the male swims toward her with or without erected median fins and terminates his approach with either a lateral display or a "vertical display" or by passing directly in front of her as he turns towards the nest. Usually, the return to the nest is interrupted by performance of intermittent lateral and vertical display. Interestingly, this same motor pattern is observable when it appears that the male is attempting to divert attention away from his nest following spawning. Such behavior activity may have the same neural basis and is adaptive in that it appears in response to specific situational needs.

Another behavior, horizontal circling, which occurred during the courtship period was unique to C. lalia and at this point there are no clues as to its adaptive significance (see Chapter VI).

Behaviors exhibited during the reproductive period are distinctive, but not as outstanding as pigmentary and morphological differences. As noted above, these activities occur in discrete units (bouts), random in sequence, separated by intervals of varying duration. The bouts vary in duration, complexity, and success (completeness).

Each species of Colisa has unique pre-clasp behaviors in spawning bouts which may serve, along with differences in coloration and morphological differences based on size, to enhance isolating mechanisms. In C. chuna, the smallest, pre-clasp time was shortest, female pre-clasp butting was rare, and few position adjustments were made before the fish almost "jumped" into a clasp. In C. lalia, the next smallest, pre-clasp time was slightly greater than in C. chuna, female pre-clasp butting was quite common, averaging 3 per spawning bout when they occurred, and

butts were delivered on the flank near the caudal peduncle. C. labiosa, almost equal in size to C. fasciata (the largest species), had the longest pre-clasp time. The male usually met the female several cm below the nest in a lateral display and circled with his body in a semi-circle, positioned slightly above the female, who was almost perpendicular, with her snout against his side during the ascent. Subsequent to the ascent, the pair commonly went through adjustments before the clasp. C. fasciata pre-clasp time was almost equal to that of C. labiosa. Upon approach the female butted the posting male who folded his fins and remained almost motionless in a position perpendicular to her for approximately ten to fourteen seconds before clasping. If the male attempted to move, the female often butted him. Careful scrutiny may show that success of the bout may be correlated with a minimum time spent in this stationary position because there was little body adjustment following this period. Any adjustment usually occurred before the pause. This also may be the closest parallel to a "rubbing position" found in T. trichopterus and T. microlepis (Miller and Robison, 1974).

Activities occurring during the clasp are basically the same among Colisa species, most noticeably differing in duration and in the position of the pair following the turn, which will be to the side or all the way over (roll). The three sympatric species, C. chuna, C. lalia, and C. fasciata commonly rolled only to the side. However, C. lalia appeared to roll all the way over more often than did the other two. C. labiosa, the allopatric species, commonly rolled all the way over with vents pointed upward. It should be pointed out that this is the species which Forselius (1957) crossed with C. lalia. C. lalia and C. labiosa females are more similar in coloration than the other species

and C. lalia and C. labiosa, in addition to rolling over during the clasp, have similar clasp durations, a point worth mentioning in considering phylogenetic relationships.

Following release of the clasp, Colisa pairs sink without control in a state of swimming inhibition. C. chuna is unique in that it remains in this state an average of 11.83 seconds, close to five seconds longer than C. labiosa, the species with the next highest average.

Intervals following successful bouts are characterized by males tending nests while females are hiding. C. chuna, which produces the fewest eggs per bout and per spawning phase has the longest average bout interval following spawning bouts. C. chuna males, perhaps in correlation with low egg number, are unique in the methods used in egg care. The male collects individual eggs and forms them into a ball-like cluster which he usually attaches to emergent vegetation or some stationary object emerging from the water. C. lalia, which utilizes a nest made of vegetation, has the shortest average interval following spawning bouts and spends less time collecting and manipulating its eggs. C. lalia also appear to release their eggs closer to the nest than do the other species and when released, the eggs appear to be more clustered. Both C. labiosa and C. fasciata fall between C. chuna and C. lalia in time spent manipulating their spawn following bouts. Both average several hundred more eggs than the two smaller species and this may be related to their decreased attentiveness to the spawn.

Specialization is most obvious in C. lalia and C. chuna. The former spends less time manipulating its eggs, perhaps because of the nest made of vegetation which may allow for protection from predators above and below. The latter spends more time with its eggs, placing

them into a compact form which can be easily hidden among vegetation and moved about by pushing with the snout. Jetting, in the post-spawning context, was only observed in C. chuna and C. lalia. When changing the cluster location, C. chuna males would return to the original location and jet several times as if to make sure no eggs were left behind. Males of both species utilized jetting to collect fry lodged against the aquarium wall at the water-air interface.

Quite clearly, C. chuna and C. lalia are the most specialized forms with respect to over-all parental activities. C. chuna males spent far more time guarding and rotating eggs and fry than did the other species. Prior to hatching, rotation of eggs is perhaps advantageous for proper gas exchange since they are in a compact form. C. lalia can afford to spend less time tending its eggs since they are probably reasonably safe in the dense, plant-filled nest. C. lalia males did spend less time posted near the nest when eggs or young were present. C. labiosa and C. fasciata also showed less nest-care than C. chuna. However, in the case of the latter two species, C. fasciata in particular posts on the bottom, oriented towards the nest. Both species may show less of a tendency to post close to the nest because of the larger number of eggs spawned and consequently greater chance for survival based on numbers alone.

C. chuna, C. labiosa, and C. fasciata construct a single layered raft of bubbles prior to hatching of the young and may maintain it for 1 or 2 days. However, the frequency and duration of such activities are greater in C. chuna than in the others. As the young develop, become free swimming, and move further from the center of the nest, C. chuna males extend their bubble blowing range over the surface, some-

times covering large portions of the tank.

Forselius (1957) pointed out that related species are generally characterized by more or less pronounced differences in reproductive behavior, frequently accentuated by the evolution of distinctive markings and color patterns in different species. Colisa species illustrate this principle in that each species has its own characteristic markings and color patterns, particularly prominent during the reproductive cycle.

C. chuna, C. lalia, and C. fasciata, the three sympatric species, are markedly different in color intensity, color patterns, and size. C. labiosa, the species with a disjunct distribution, is closest in size to C. fasciata. Among the sympatric species these striking differences in coloration and size may function to prevent hybridization.

Color pattern differences give few clues to phylogenetic relationships, however (see Chapter VIII). C. chuna is the only species that lacks red and blue stripes, but C. labiosa and C. fasciata share prominent chin bars in both nuptial and non-reproductive dress.

Based on the totality of behavioral (qualitative and quantitative) and morphological (color patterns) evidence examined in this study, it appears that the three sympatric species, C. chuna, C. lalia, and C. fasciata have diverged most markedly in color patterns, nestbuilding, courtship and reproductive activities, care of eggs and young, and cycling of general maintenance activities. Most overlap exists between the disjunct species, C. labiosa, and either C. lalia, or C. fasciata, depending on the characteristic being considered. C. chuna, the smallest Colisa, appears to be the most highly specialized form, overall.



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