COURTSHIP AND REPRODUCTIVE BEHAVIOR IN THE

GIANT GOURAMI, COLISA FASCIATA

(BLOCH AND SCHNEIDER)

By

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CHAPTER I

INTRODUCTION

This investigation was conducted to describe qualitatively courtship and reproductive behavior in the anabantoid fish, Colisa fasciata (Bloch and Schneider). Several quantitative aspects of the observed behaviors have been included to facilitate and clarify the qualitative description.

Prior to this study relatively little work had been done on the courtship and reproductive behavior of C. fasciata, though several other species have been investigated. Forselius (1957) published a monograph dealing primarily with the genus Colisa, including a brief description of the courtship and reproductive behavior of C. fasciata. Special attention was paid, however, to the behavior of C. lalia and the hybrid between C. lalia and C. labiosa. Braddock and Braddock (1959) were concerned with nesting behavior in Betta splendens. Picciolo (1964) described sexual and nest discrimination by species of Colisa and Trichogaster, including C. fasciata. Miller (1964) described social behavior in Trichogaster trichopterus and included quantitative data on motor patterns, nest building, and reproductive behavior. Hall (1966a) conducted a comparative study of the ethology of three anabantoid species, and described (Hall, 1966b) the reproductive color changes in Trichogaster leeri. He also studied (Hall, 1966c) physical and physiological factors affecting spawning in two anabantoid

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species. Rainwater and Miller (1968) compared the courtship and reproductive behavior of sexually inexperienced to that of sexually experienced Betta splendens. Barlow (1962) described the reproductive color changes in Badis badis, and in a recent study (Barlow, 1968) discussed the close similarity between the spawning clasp in Badis badis and the anabantoid clasp.

The most recent investigations on anabantoids were conducted by Simpson (1968) on Betta, and by Miller and Hall (1968) and Hall and Miller (1968) on the quantitative and qualitative aspects, respectively, of courtship and reproduction in T. leeri.

All of the above studies have been useful in the preparation of this paper; those which have been especially helpful are cited throughout the manuscript.

The suborder Anabantoidei is comprised of four families: Anabantidae, Belontiidae, Helostomatidae, and Osphromemidae (Liem, 1963). C. fasciata is a member of the family Belontiidae, which includes 21-24 other species. Three general characteristics of this family, the presence of a labyrinth organ, the deposition of eggs in a bubble nest, and the employment of a nuptial clasp are found in C. fasciata. The latter two will be discussed in Chapter V. The labyrinth organ is discussed briefly by Rainwater and Miller (1968), and in greater detail by Forselius (1957).

CHAPTER II

MATERIALS AND METHODS

This study was conducted from June to October, 1967, in the
Constant Temperature Room of the Oklahoma State University Aquatic
Biology Laboratory. The room temperature was held at 24-27°C for the
duration of the investigation.

Materials

The fish were kept grouped in four 15 gallon stock tanks when not
paired. The groups varied in number of fish from 4 to 12, and fish
were not segregated according to sex. Some of the pairs were observed
in 10 gallon and some in 15 gallon aquaria. There were no apparent
differences in the behaviors shown due to different aquarium sizes.
The fish used in this investigation were obtained from pet shops.

Each breeding aquarium had a gravel bottom planted with Cerato-
phyllum and Vallisneria, and each was equipped with a thermostatically-
controlled electric aquarium heater. Pieces of clay pots were placed
on the bottom. These, along with the aquatic plants, provided some
protection for the female.

Lighting was provided by overhead fluorescent and incandescent
lamps, and by individual aquarium reflectors with incandescent bulbs.
An 11 hour photo-period was maintained by means of electric appliance
timers.

The fish were fed daily or twice-daily on prepared dried foods,
live Daphnia, and, on occasion, midge larvae (Tendipes).

Methods

Qualitative and quantitative observations were made concurrently
with the aid of notebook, wristwatch, and stopwatches.

Discrete behavior patterns, movements, and postures were defined
after several weeks of observation to facilitate quantification of the
data and description of events.

Fish were paired at least one day before spawning occurred. Pairs
were observed at least once daily to ascertain breeding condition and
presence of nests or nest-building activity. Coloration, general behav-
ior of one or both fish, territorial behavior by the male, and structure
of the nest (if present) were used as indicators of a possible spawn.

Seven spawning sequences were observed; 4 of them are believed to
have been seen in their entirety. The water temperatures in the tanks
during spawning varied from 26-27°C. Data from the 7 spawnings are
used in the qualitative descriptions of courtship and reproductive
behaviors, and data from at least 5 of the spawnings are used in the
quantitative analysis of these behaviors.

Hall (1966c) found spawning in two Anabantoid fishes to occur over
relatively wide temperature ranges, with optima approximately 29°C for
T. leeri and 27°C for Macropodus opercularis. Since spawning tempera-
tures in this study did not vary over 1°C, the range of temperatures
suitable for spawning in C. fasciata is not known. It can be said only
that this species will spawn at 26-27°C provided other conditions are
suitable.

An attempt was made to pair males and females of approximately the same size in order to reduce the danger of infection and mortality from wounds. In all observed spawning pairs, the female was slightly smaller than the male.

CHAPTER III

TERMINOLOGY AND MOTOR PATTERNS

The bouts of C. fasciata vary in duration and complexity. The
degree of completeness of a sexual bout corresponds to the level of
sexual activity attained in the bout, i.e., a complete sexual bout is
one in which gametes are released and is called a spawning bout.

Bout. Any social interaction.

Sexual Bout. This term denotes only bouts of male-female interaction
that contain sexual responses. Approach, swimming beneath the nest,
or following the male to the nest are considered to be female sexual
responses. Approach, lateral spread and sigmoid displays, curving,
clasping and attempting to lead the female to the nest are considered
sexual responses of the male.

Spawning Bout. This term refers only to those sexual bouts which
result in release of gametes by male and female and corresponds to the
"spawning cycle" of Forselius (1957). However, since it was not
possible in this species to tell whether the male had ejaculated, the
term was used whenever egg release was observed.

Pseudospawning Bout. This bout is identical to the spawning bout
except that no eggs are released.

Courtship Bout. This bout contains sexual responses by one or both sexual partners but does not reach the clasp stage.

Non-sexual Bout. This is a bout in which no sexual responses are given by either male or female.

Clasp Bout. Sexual bouts that advance only to the clasp stage are clasp bouts. Emission of gametes and swimming inhibition do not occur. The clasp bout is one type of incipient spawning bout.

Spawning Sequence. The complete series of sexual bouts and non-sexual periods making up the prespawning, spawning, and postspawning periods is called the spawning sequence and corresponds to the "mating cycle" of Forselius (1957). The spawning sequence of C. fasciata may last from 2 to 6 hours.

Nest-posting. Any time during a spawning sequence the male is positioned beneath the nest but is not actively engaged in caring for nest or eggs, he is referred to as nest-posting.

The nest is the focus of the male's territory. A nesting male is more aggressive than at any other time, thus better able to defend his territory (Forselius, 1957). This has adaptive significance for the matings that follow. Braddock and Braddock (1959) found that Betta splendens males would not mate with a female anywhere but under the nest. This is also true of C. fasciata males.

Forselius (1957) observed that most anabantoid males direct their heads strongly upward to the water surface when nest-posting, but in C. lalia and C. fasciata the angle is much larger, often up to 45°. C. fasciata males in the present study were usually observed

nest-posting with their bodies and heads parallel to the water surface.

Prespawning Period. All of the sexual bouts and non-sexual periods
(bout intervals) up to, but not including, the first spawning bout
comprise the prespawning period. It is characterized by male approach,
lateral spread and sigmoid display, butting, biting, chasing, and nest-
building, and by female appeasement and approach. Male and female
approach will be described in the discussion of the C. fasciata
ethogram (Chapter V). Lateral spread and sigmoid displays, butting,
biting, chasing, nest-building, and appeasement have been described
for T. leeri by Hall and Miller (1968), and their descriptions will
apply to the same motor patterns in C. fasciata, with the following
exceptions: "jetting" is not a bubble-blowing pattern observed in this
species, and vegetation is not incorporated in the nest; however, the
males show a marked tendency to construct their nests on the underside
of overhanging Vallisneria leaves, and in the absence of nests males
have been observed to deposit eggs directly against the undersides of
these leaves. There is apparently no critical nest size for this
species since males will spawn in the total absence of a nest; and
there seems to be no correlation between size of the male and size of
the nest, although it would not be surprising to find that the quality
(form, depth, durability, etc.) of the nest tends to increase in direct
proportion to experience of the male.

Hall and Miller (1968) noted for Anabantoid fishes that the size,
form, and materials used in construction of the nest may vary greatly,
even at the species level.

Spawning Period. The period from the first to the last spawning bout is the spawning period and includes all bouts and bout intervals occurring during this period. Behavior patterns typical of this period include: male curve and clasp; female nudging or butting, mounting, sigmoid posture and quivering; male quivering and ejaculation; egg release; swimming inhibition; male egg retrieval and some nest care. The above behaviors are described in Chapter V.

Postspawning Period. This denotes the period following the final spawning bout and is characterized by female retreat and male aggressiveness and nest care. The nebulous end of this period is marked by the female remaining in hiding for long periods at a time. She may feed occasionally but she rarely surfaces. The male is aggressive toward the female and spends most of his time nest-posting or caring for nest and eggs.

One or two pseudospawning bouts are characteristic of the prespawning period and may also occur infrequently in the spawning period and rarely in the postspawning period.

All of the motor patterns listed in prespawning and spawning periods, with the exception of ejaculation and egg release which, by definition, are characteristic only of the spawning period, may occur during either period but occur more commonly in the period under which they are listed.

CHAPTER IV

REPRODUCTIVE COLOR CHANGES IN C. FASCIATA

Color changes, especially in the male, during the reproductive cycle are startling and serve as indicators of the motivational states of the sexual partners. As Hall (1966b) stated, "The functional implications of many of these changes are unknown."

Picciolo (1964) showed that visual cues are important factors in intraspecific sex discrimination in the genus Colisa. Among the important visual cues is color of dorsal and anal fins. He also notes that the black horizontal chin bars, which are strongly accentuated in the nuptial male, serve as a strong hostile stimulus to males of the species. It is interesting to note that both male and female possess these chin bars. The red vertical striations on the lateral surface of C. lalia function as a visual stimulus for sex discrimination, but the longitudinal bars on the lateral surface of C. fasciata do not.

Reproductive color changes have been described for Badis badis (Barlow, 1962), T. trichopterus (Miller, 1964), T. leeri (Hall, 1966b) and for B. splendens, C. lalia, C. labiosa, C. fasciata, and several other anabantoid species (Forselius, 1957). The above authors note that reproductive color changes closely resemble agonistic color changes in these species, except that the former are more striking, the colors being more intense than in the latter. Miller (1964) and Forselius (1957) point out the significant role played by male

aggressive behaviors in nest area defense and courtship of the female.
It should also be remembered that even during the spawning period, when
the male is assumed to be at the height of his sexual motivation for
the spawning sequence, he continues to defend his territory against
other males and may show aggressive activity toward the female. This
suggests that the expression of agonistic and reproductive color
changes may be mediated by the same central neural mechanisms.

In a study on chemical communication in C. lalia, Mainardi and
Rossi (1968) found that of 13 heterosexual pairs in which the male and
female of each pair were in chemical communication with each other, all
13 males assumed typical courtship coloration and built bubble nests;
while of 13 like pairs in which the partners had only visual communi-
cation with each other, the males neither assumed reproductive colora-
tion nor built nests. These findings seem to leave the impression that
chemical stimulation from the female is necessary for the development
of reproductive coloration in the male; yet many people have observed
the acquisition of reproductive coloration and the initiation of nest-
building in males lacking any kind of contact with females, as well as
in males with only visual communication with conspecific females, in
C. lalia, C. fasciata, C. labiosa, T. trichopterus, and several other
anabantoid species. Visual and chemical stimulation from conspecific
females undoubtedly plays an important role in acquisition of repro-
ductive coloration and initiation of nest building in the male, but
these phenomena may also occur in the absence of any female stimulation.

Female colors in the genus Colisa show greater interspecific
similarity than do those of the males, the male of each species having
a characteristic nuptial coloration. This might indicate that species

discrimination is based on female recognition of conspecific male
coloration (Forselius, 1957). The male of C. fasciata shows a far
greater variety of colors in his nuptial coloration than any other
Colisa species.

Females removed from the aquarium with a net and those stimulated
to flee by an intruding hand or a tap on the side of the aquarium show
color changes remarkably similar to those in breeding females, which
fact suggests the possibility that the expression of the color patterns
for fear and for breeding may be mediated by the same neural mechanism.

Besides aiding in sexual discrimination and emphasizing gestures
important in attracting the female, nuptial coloration may serve to
repel rivals. As Noble (1938) stated, in fishes as in birds, "the
greater the display, the less the fight."

Reproductive changes in coloration of male and female are shown
in Figure 1. The following text numbers correspond to the diagram
numbers in Figure 1.

Male

1. **Opercular Ocellus.** A blue opercular ocellus is characteristic of
both breeding and non-breeding males, but in territorial and breeding
males its color is highly intensified.

2. **Horizontal Chin Bars.** These are brown in the non-breeding male,
but their color is darkened to nearly black in the breeding male, and
they appear to be continuous with the jugular darkening.

3. **Jugular Darkening.** Hadley (1967) coined this term for a color
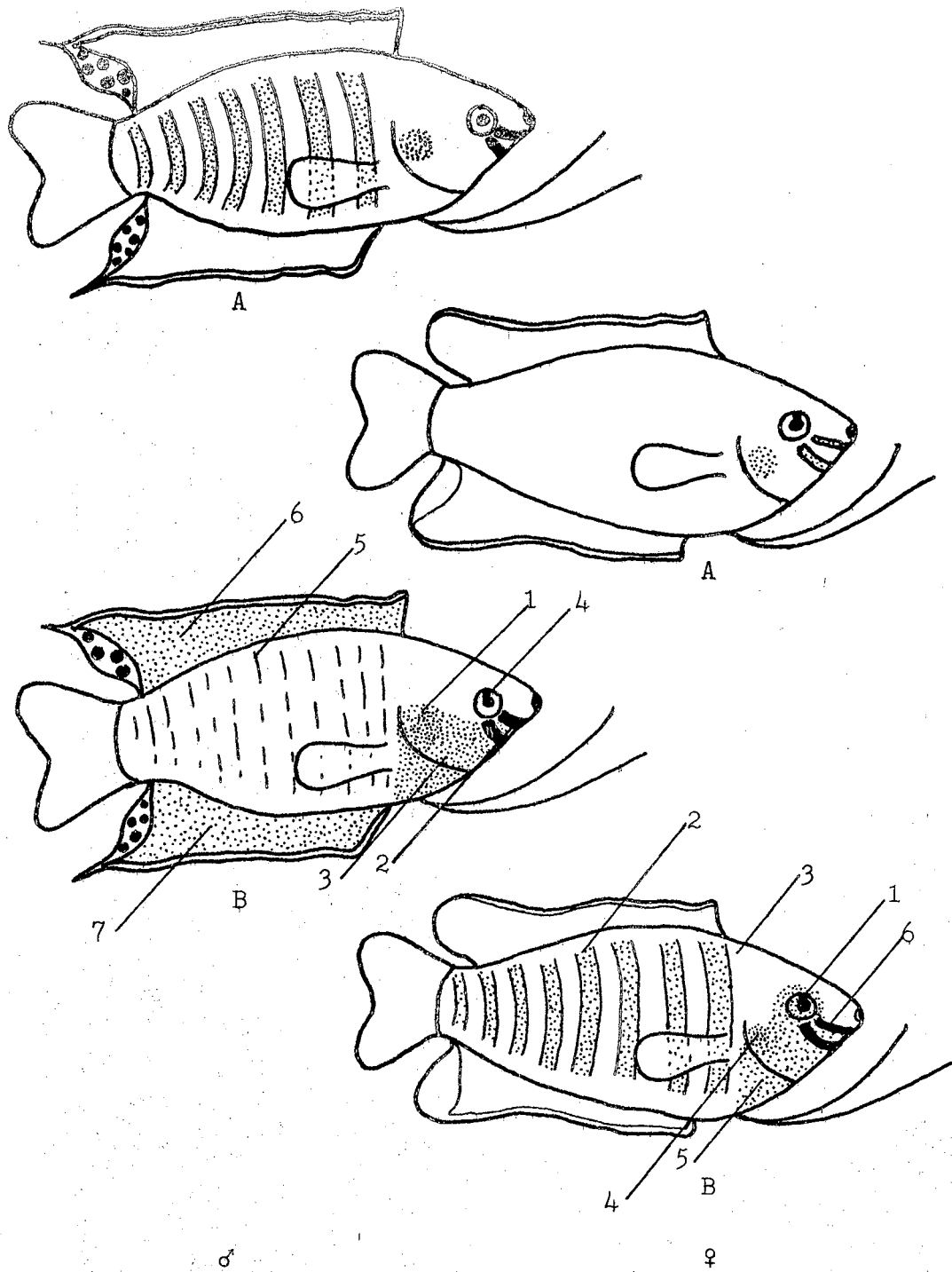pattern shown in Lagodon rhomboides and it seems appropriate here. The

Figure 1.   Reproductive Color Changes in C. fasciata Male and Female.
A. Non-breeding.   B. Breeding.

area on the venter of the breeding or territorial male from the chin bars across the breast to the level of the pectoral fins becomes a very dark blue, often approaching black. In the non-breeding male this area is usually silvery.

4. Eye Color. The area around the eye of the breeding male becomes uniformly dark, contrasting with the deep orange of the iris, which is interrupted by a short supraorbital vertical bar. The bar is very dark, nearly black, as is the pupil. The area around the eye of the non-breeding male is light bronze. The iris is light orange, the pupil is dark, and the dark bar is present, though not as conspicuous as in the breeding male.

5. Longitudinal Bars. These bars are present in breeding and non-breeding males, but in the former they are extremely dark brown and nearly blend in with the darkened body and fins, while in the latter they are light blue against a light, almost silvery, background.

6. Dorsal Fin Color. The dorsal fin is normally light turquoise blue, the distal edge of the fin tipped in white. Contrast is increased in the breeding male when the blue turns to deep, iridescent blue-black in color and the distal edge of the fin remains white. The soft dorsal has black spots on an orange background in breeding and non-breeding conditions, but here again contrast is greater in breeding males.

7. Ventral Fin Color. In breeding and non-breeding males the ventral fin is blue with orange along its exterior margin. There are very diffuse black spots in the orange area along the posterior margin of

the fin. In the breeding male the blue area turns from turquoise blue
to a deep, iridescent blue-black, and the orange color is greatly
intensified.

Female

1. **Eye Color.** Usually the area around the eye is light and silvery,
the pupil is dark and the iris a pale orange. In the breeding female
the whole eye appears uniformly dark.

2. **Longitudinal Bars.** Varying from nearly transparent to a light
frosted turquoise blue in color in the non-breeding female, these bars
turn dark gray in the sexually responsive female. During actual
spawning they take on a tone of color that is more dark bronze than
gray.

3. **General Body Color.** In the non-breeding female the body is rather
uniformly silvery-white. In the breeding female the venter is
silvery-gray, while the dorsum appears somewhat darker gray, though
not as dark as the longitudinal bars.

4. **Opercular Ocellus.** A very faint blue opercular ocellus is present
in the non-breeding female. It becomes very dark blue in breeding
females.

5. **Jugular Darkening.** This is not present in the non-breeding female.
In the breeding female it is very similar to that in the breeding male,
but the color in the female is not as intense and the darkening appears
more diffuse.

6. <u>Horizontal Chin Bars.</u> These change little from non-breeding to breeding female. In the former they are light brown; in the latter, darker brown.

These colors and patterns are subject to a great deal of variation in intensity and appearance among and within individuals.

CHAPTER V

THE C. FASCIATA ETHOGRAM

The ethogram for C. fasciata (Table I) provides a means for
qualitative description, in stylized terms, of a highly variable
sequence of behaviors. It is an attempt to show the main units of
courtship and reproductive behavior in their regular occurrence without
the variation that can result from interruption at any one of these
stages.

Stages 1a and 1b. Both male and female acquire nuptial coloration,
which is described in Chapter IV. No spawnings occur in the absence
of this presumably necessary preliminary phase; however, its duration
may vary greatly among spawning sequences of the same and different
males. The male establishes a territory, initiates nest building,
and approaches the female, showing some courtship and aggressive
activity. The female stays in the opposite end of the tank, away from
the male. She does not defend a territory or aid the male in nest
building or the defense of his territory.

In his approach the male swims directly toward the female, often
touching her with his pelvic filaments, which are extended forward
except during very rapid approaches. His approach is accompanied by
partial to full median fin erection and usually terminates in a
lateral spread display or an attack. At high intensity the lateral
spread display may be accompanied by a sigmoid display. Attack may

TABLE I

COLISA FASCIATA ETHOGRAM

Male	Female
1a. acquires nuptial coloration; establishes territory; initiates nest building; approaches female; some courtship & aggressive activity	1b. acquires nuptial coloration; stays away from male in opposite end of tank
2. male lateral spread	2. female approach – variable in form and duration
3. male curve	3. female may nudge or butt male on dorsum
4. male clasp	4. female mounting & caudal fin vibration
5. male quivering	5. female sigmoid posture; begins quivering
6. male stops quivering with a jerk of his body (ejaculation?)	6. female partially straightens; stops quivering; egg release
7. loosening of clasp; swimming inhibition	7. swimming inhibition
8. male egg retrieval	8. swims slowly away from nest
9. egg and nest care	9. remains stationary on bottom at opposite end of tank; surfaces rarely; occasionally feeds OR
	10. swimming inhibition may be followed by male chase with butting and/or biting

consist of butting and/or biting and may result in chasing with
subsequent butting and/or biting on the part of the male. The female
often responds to attack with behaviors of apparent appeasement
function.

The bubble nest usually built by the male during this stage seems
to have definite survival value for eggs and fry. It keeps them at the
air-water interface where atmospheric oxygen is available for respira-
tion. It keeps them together, thus facilitating nurture, and it
attracts microorganisms required as food by fry (Forselius, 1957).

2. Male Lateral Spread Display and Female Approach. Typically, the
male approaches the female, performs a lateral spread display and
returns to the nest. The female then approaches the male in a variety
of manners as described by Hall and Miller (1968). Before her actual
approach, however, the female of C. fasciata usually swims to a
position from which the nest-posting or nest-tending male is visible,
and her caudal and pectoral fins beat rapidly in opposition for
several seconds, often up to a minute, before she begins her approach.
This movement may be interpreted as showing an intention to approach
the male. Manner of approach, coloration, and general body shape may
serve to identify the female and thus inhibit male aggression. Plump-
ness of the abdomen seems to be an important factor in sexual recogni-
tion in the genus Colisa (Picciolo, 1964).

The female of C. fasciata, C. labiosa, and C. lalia generally
approaches the male with her head pointed slightly toward the bottom,
but the closer she comes to the male, the more closely her head
approaches the horizontal plane (Forselius, 1957). In the present

study, the C. fasciata female usually held her head in the horizontal plane, sometimes slightly higher, during her approach to the male.

Male response to female approach appears to be extremely important to the continuation of the bout. Male lateral spread display releases female nudging or butting, but the male's facing the female or moving toward her results in female flight, which is often followed by male chasing and butting. Approach of the T. leeri female appears to be facilitated if the male turns so the female does not approach head-on (Hall and Miller, 1968).

3. Female Nudging or Butting and Male Curve. Once under the nest, the female often nudges or butts the male lightly on his dorsum. This nudging or butting is of low intensity and very brief duration and does not compare to female courtship butting in T, trichopterus. Miller (1964) states that in T. trichopterus the first prerequisite for a successful spawning is the butt or bite of the female. Butts are usually sharp, and butting is of fairly long duration. Under the nest, butting is usually followed by male rubbing, a behavior unique in this species, which in turn is followed by male circling. He further states that the more the male circles, the greater the chance that the female will lose her orientation to him and, likewise, that he will cease behaving sexually and chase her. Circling in T. leeri is followed almost 5 times as often by aggressive behavior as by clasping, which suggests a strong underlying aggressive component of circling (Miller and Hall, 1968).

Circling is also present in Betta (Forselius, 1957; and Rainwater and Miller, 1968), but it is not found in the genus Colisa (Forselius, 1957). In C. fasciata clasping never occurs without prior curving,

but curving and subsequent clasping were occasionally observed to
occur without proper mounting by the female who usually swam out of
the male curve and away from the nest area. The behavior of the
C. fasciata male while the female is next to him under the nest does
not suggest the presence of a strong aggressive component as does the
circling of T. leeri males.

Male curving is elicited more quickly if the female places her
snout on the dorsum of the male just anterior to his dorsal fin, her
pelvic filaments against his side. The male was, on occasion, seen to
curve without any previous tactile stimulation from the female. Male
curving is referred to as an "invitation posture" by Rainwater and
Miller (1968). As the female touches the male with her snout and
pelvic filaments, her caudal fin begins to quiver. This generally
results in immediate curving by the male (if he is not already curved),
mounting by the female, and the clasp. Increased activity of the
female at this time decreases the probability that the pair will
become properly oriented, thus decreasing the likelihood of a complete
spawning bout, and often terminates in the male chasing the female
away from the nest area.

One behavior observed on several occasions in several different
females, but in striking contrast to that usually observed, is performed
by the female once she is next to the male under the nest. Rather than
interacting with the male, she swims slowly to the surface and gulps a
mouthful of bubbles. It is possible that the motivational level in the
female is in an incomplete state, which is reflected by her loss of
interest in prespawning proceedings and subsequent rise to the surface
to eat (Miller, 1964). An alternative explanation of the behavior

might be profferred in terms of a displacement activity arising from
a conflict between an urge to mate and an urge to flee. This activity
also often resulted in the female being driven away from the nest area
by the male.

4. Female Mounting and Male Clasp. Mounting consists of the female
swimming into the male curve, placing her snout against his dorsum
just anterior to the dorsal fin origin, and placing her pelvic filaments
against his side. The median fins of both fish are partially folded.
As the female mounts, the male tilts his venter slightly toward her,
and she presses her venter vertically against his side. Forselius
(1957) noted that C. fasciata females seem to orient themselves toward
the head region of the male. The female mounts with her snout at the
anterior base of the male's dorsal fin, which appears to be farther
forward on the male than in C. lalia as described by Forselius (1957).

Male clasping usually occurs simultaneously with or immediately
following mounting by the female, and consists of the male bending his
body around the female so that his head and caudal fin nearly touch
each other. The pair is now oriented with male and female vents in
close proximity and directed toward the bottom, and the caudal half of
the female pointing toward the surface. The pair is usually a few
centimeters below the nest, and the orientation is apparently main-
tained by movements of the caudal fins. Miller (1964) stated that
maintenance of the T. trichopterus clasped pair near the surface
appeared to be effected through movements of the caudal fin and pos-
terior anal rays of the female.

Proper mounting and orientation of male and female to each other
are important for the continuation of the bout. The female is

apparently responsible for this orientation, and excessive adjustments in body position by the female or her failure to mount properly may terminate the bout.

5. Female Sigmoid and Quivering. Following mounting and the clasp, the female bends her body in a sigmoid posture and the male flexes his body, thus tightening the clasp. The median fins of the male and the dorsal fin of the female are now fully erected. The pair may tilt slightly to one side, the venter of the female pointing laterally in relation to the water surface, before egg release. A C. fasciata female was never observed, however, to assume the "female upside-down posture" described by Forselius (1957) as occurring in C. lalia, C. labiosa, and C. fasciata, though infrequently in the latter two. This posture corresponds to "rolling over" in T. trichopterus (Miller, 1964), B. splendens (Rainwater and Miller, 1968), and T. leeri (Hall and Miller, 1968).

Although the exact function of clasp tightening is not known, the pressure of the male's body around the female may facilitate egg release. The caudal fin of the female is bent away from the male, and the median fins of both male and female are partially to fully, usually fully, erected. Both male and female begin quivering their bodies and fins, but quivering in the female becomes most pronounced just prior to egg release.

On several occasions the female was observed to drop vertically out of the male's clasp and swim away. That the male continued clasp posture and quivering for several seconds, apparently unable to terminate it sooner, is evidence of a possible critical period in clasping

after which this activity must be continued to its end. Miller (1964) found evidence for a critical duration of the T. trichopterus clasp, which, once surpassed, almost invariably led to spawning. The persuasive evidence for this critical duration (30-35 sec) derives from the fact that only 4 records of clasps exceeded it, and all of these clasps resulted in pseudospawnings, in which all activities of the spawning bout occur except for egg release.

Barlow (1968) suggests the existence of a close relationship between Badis badis and the anabantoid fishes due to the remarkable similarity of the spawning clasp. He found that the female Badis badis, once she has approached, butts the male's side; this leads to circling about one another, male hooking (similar to curving), female mounting and male clasp by his closing of the hook. Barlow stated that an important feature of clasping, for comparative purposes, is that the male first clasps the female in a posture called "twisted U," which is converted to a "simple U" as the clasp progresses toward oviposition. He states that, although there are photographs showing the twisted U only in elongate species such as C. chuna, and showing only the simple U in the more disc-shaped species (e.g., T. leeri and T. trichopterus), there is no way of knowing whether the elongate species always show the twisted U before going into the simple U, or if the deep bodied species ever show the twisted U, since the photographer probably waits until the clasp is well developed before taking the picture, thereby increasing the probability of missing the twisted U. The twisted U was never observed in C. fasciata in the present study, nor was it noted in B. splendens, a very elongate species, by Rainwater and Miller (1968).

6. <u>Egg Release</u>. The female partially straightens her body and stops quivering. Male quivering ceases with a jerk of his body, which may indicate the moment of ejaculation, although no cloud of milt was ever observed. A movement similar to the male body jerk in C. fasciata is the "terminal squeeze" in T. leeri (Hall and Miller, 1968). Terminal quivering is reported for Badis badis by Barlow (1968). Egg release usually occurs just before or as the female relaxes her sigmoid posture; however, eggs have often been seen emerging from her genital pore during swimming inhibition.

7. <u>Loosening of the Clasp and Swimming Inhibition</u>. Following the body jerk the male loosens the clasp and the pair sinks slowly through the water in a state referred to as swimming inhibition. Male and female are otherwise motionless and tend to lose their orientation to each other. Swimming inhibition may last from 2.5 to 17 seconds in the male and usually terminates 1 or 2 seconds earlier in the female of the pair. It occurs in both spawning and pseudospawning.

8. <u>Male Egg Retrieval</u>. As the female swims away from the nest area following swimming inhibition, the male may give chase to the female and then return to the nest area to gather eggs. More often, however, he does not give chase but begins collecting eggs that have not reached the nest and spews them out through his mouth into the nest. The eggs of C. fasciata are buoyant and rise to the surface, most of them accumulating in the nest since all spawnings take place directly under the nest when a nest is present.

9. <u>Egg and Nest Care</u>. After the male collects the eggs and deposits

them in the nest, he resumes nest care, deepening the nest by expelling bubbles beneath it. Through his opercula he expels fine streams of tiny bubbles underneath the nest. This opercular aeration is described in more detail by Forselius (1957), who also noted that C. fasciata, C. lalia, and C. labiosa males generally show the same patterns of egg retrieval. These bubbles are short-lived but may serve to aerate the eggs in the nest. During this time the female usually remains stationary in a far bottom corner of the aquarium. She feeds occasionally on the bottom but rarely surfaces. Surfacing rate may be determined by the level of male aggressiveness as well as actual physiological need (Hall, 1966a).

Innes (1966) reports that males of this species take mouthfuls of sand and blow it among the eggs in the nest. The bottoms of the aquaria used in the present study were covered with gravel rather than sand, which may explain whey this behavior was not observed by this author; however, the behavior itself seems to have no apparent function.

10. This phase was discussed under Male Egg Retrieval.

Discussion

Although the behaviors from Female Approach to Egg and Nest Care appear to be somewhat more stereotyped than the rest, each of these phases varies in duration and form of its composite elements and may be interrupted at any time by inappropriate responses from the male or female, lack of synchronization of the pair, or sudden environmental change. However, Female Approach and Male Curve seem to be the most critical stages in this respect.

In contrast to the findings of Hall (1966a) for _T. leeri_, it is the female of _C. fasciata_ who seems to be responsible for most of the interrupted bouts. Interruptions of various types, as from a third fish or an increase in brightness of light, do not cause immediate termination of swimming inhibition. In fact, it appears that once the pair is engaged in this behavior there is little that will interrupt them.

Within the genus _Colisa_ the courtship and reproductive activity has heretofore been described in detail only for _C. lalia_ (Forselius, 1957); therefore, the scope of any comparative discussion of species within the genus is necessarily limited. Forselius also made some general comments concerning courtship and reproduction in _C. labiosa_ and _C. fasciata_ which will be useful in the following discussion.

During the prespawning and spawning periods the male of _C. lalia_ and _C. labiosa_ may approach the female and perform a display posture which corresponds to the lateral spread display, after which he either moves slowly toward the nest in a manner termed "leading-to-the-nest" or moves rapidly and directly to the nest (Forselius, 1957). Leading-to-the-nest was also observed in _T. trichopterus_ (Miller, 1964), _B. splendens_ (Rainwater and Miller, 1968), and _T. leeri_ (Hall and Miller, 1968). This behavior pattern, or its equivalent, was performed several times during one spawning sequence by only one male _C. fasciata_ observed during this entire study. It is possible that this performance was indicative of a high sexual motivation in the male and a relatively low sexual motivation in his partner. A great majority of the female approaches to this male occurred during or immediately following leading. After the first spawning bout, leading-to-the-est

was not again observed until the postspawning period. The same male spawned the following day with a different female, and leading-to-the-nest was not observed.

It is possible that leading-to-the-nest was once a behavior pattern typical of this species, and that it served to stimulate the female to approach the male at the nest. Perhaps with the evolution of the now brilliant coloration of the nuptial male, leading-to-the-nest was performed less and less often as a behavior to stimulate the female to approach the male under the nest. The male usually approaches the female, shows a lateral spread display and returns to the nest. This pattern was carried out 2 or 3 times in the one C. fasciata who showed leading-to-the-nest before he began actual leading. In other spawnings the female usually approached the male after the first 1-3 approaches followed by lateral displays. It may be that leading-to-the-nest as a behavior pattern is still in the repertoire of C. fasciata males, but that it is seldom initiated due to the early success of lateral spread display and male nuptial coloration in stimulating the female to approach.

The nest of C. labiosa males is typically composed of one or a few bubble layers and contains little vegetation; whereas, a C. lalia nest is frequently composed of 3 layers, an upper thick one of foam bubbles, a middle layer with dense mats of vegetation, and a thinner bottom layer of bubbles and some plant parts (Forselius, 1957). Although algae, as well as Ceratophyllum and Vallisneria, were present in all breeding tanks, none of the C. fasciata males in this study was ever observed to incorporate vegetation into his nest. Nests varied from several small aggregations of bubbles to several-layered bubble

nests of large diameter (up to 10 cm), although spawning was observed
to occur in the absence of a nest.

Forselius (1957) noted that female upside-down posture (rolling
over) occurs typically in C. lalia, and frequently in C. labiosa and
C. fasciata. Barlow (1968) stated that in species that leave their
eggs in a bubble nest, release of the eggs tends to occur when the vent
of the female is directed laterally or straight up toward the water
surface. Since spawning in Colisa, and most other anabantoids, usually
occurs directly beneath the nest, rolling over so that the female vent
is directed upward during oviposition would be an added assurance that
a large number of eggs would reach the nest in species with buoyant
eggs; and in species with non-buoyant eggs, directing the eggs upward
at oviposition would give the male more time to collect them before
they fall to the bottom, thus becoming extremely hard to find.

C. fasciata presents a striking contrast to the general pattern
of spawning followed in the suborder Anabantoidei and in Badis badis.
Female upside-down posture or rolling over seems to be present in
nearly every other anabantoid species, even in other members of the
genus Colisa. The slight tilt of the C. fasciata spawning pair, as
previously described, may be an indication of rolling over that is
never carried through to its completion. If rolling over was at one
time a behavior pattern commonly occurring in C. fasciata spawning
bouts, it is not at this time apparent why it was never observed in
the present study, unless it occurs only at extremely high levels of
sexual motivation which were never attained by the individual fish in
this study. This, however, seems unlikely since this pattern occurs
so commonly in other anabantoids, and since many spawnings observed in

this study were thought to indicate a relatively high level of sexual
motivation due to the high degree of synchronization of the pair,
increased amount of quivering in male and female, and the relatively
large number of eggs released.

The male of C. lalia usually recovers from swimming inhibition
before the female and rouses her by thrusting with his snout at her
sides; male chase usually ensues (Forselius, 1957). The C. fasciata
female usually recovers from swimming inhibition shortly before the
male and swims away from the nest area; seldom does the male give
chase.

One very apparent difference between C. lalia and C. fasciata and
labiosa is the relative speed of the movements performed. C. fasciata
and C. labiosa are similar in general body shape and proportions, both
are longer and shallower-bodied than C. lalia and have longer, more
flowing dorsal and ventral fin extensions. C. lalia is a short, deep-
bodied fish, almost disc-shaped when its median fins are erected. The
movements of C. lalia have a fluttery or jerky coordination and the
fish go forward or backward in swift, darting movements (Miller and
Miller, in press). The movements of C. fasciata and C. labiosa are
much less rapid and more fluid, and they do not dash and dart about as
C. lalia. Miller and Miller (in press) propose the hypothesis that
qualitative differences in behavioral traits among the three anabantoid
species observed in their study may be "closely associated with certain
morphological specializations which impose a form or rhythm to movement,
producing a recognizably unique pattern." This may help to explain
the pronounced zig zag leading of C. lalia (Forselius, 1957), which
involves quick, interrupted movements, as compared to the more gliding

movements of C. fasciata during leading.

Another conspicuous divergence between the behaviors of C. lalia
and C. fasciata occurs following swimming inhibition. In C. lalia
the male first recovers from swimming inhibition then rouses the female
by butting her and usually chases her away. In C. fasciata the female
recovers 1-2 seconds before the male and swims away from the nest
area; the male rarely chases her. It would appear that the male of
C. lalia is highly aggressive toward the female, but Miller and Miller
(in press) suggest that, although overt aggressive movements, such as
chasing and butting, play a more prominent role in male C. lalia
interaction in terms of frequency, they appear to be less violent and
possess more signal value than equivalent actions of contra-specifics.
This may apply also to C. lalia male-female interactions since the
female of a spawning pair rarely shows mutilated fins or missing
scales. Females of C. fasciata spawning pairs likewise rarely show
wounds or mutilated fins due to male aggressive activity since the
males display little overt aggressive activity toward the female
during courtship and spawning.

CHAPTER VI

A DISCUSSION OF THE QUANTITATIVE ASPECTS OF

REPRODUCTIVE BEHAVIOR IN C. FASCIATA

Since this study was conducted primarily to provide a qualitative
description of the courtship and reproductive behavior of C. fasciata,
the quantitative data collected are not extensive, but they provide a
basis for further quantitative study on the reproduction of this
species and, in this respect, it should prove valuable to briefly
consider them. Tables II and III will serve as bases for the following
discussion.

A total of seven spawning sequences was observed, but one of them
has been eliminated from quantitative analysis due to the lack of
sufficient timing devices for recording bout durations.

Spawning sequences lasted an average of 3.3 hours, and all
occurred between 11:00 am and 7:00 pm. One spawning sequence that was
neither observed nor recorded occurred sometime between 7:00 pm one
evening and 8:00 am the following morning, as eggs were then found to
be in the nest. This is the only time such a situation was noted.

Table II shows the bout category analysis. Bout types are defined
in Chapter III.

Average number of bouts per spawning period is 53.8; and the
average number of spawning bouts per spawning period is 18, spawning
bouts on the average comprising 33.5% of the total.

TABLE II

BOUT CATEGORY ANALYSIS OF SEXUAL BOUTS OCCURRING
DURING THE SPAWNING PERIOD IN C. FASCIATA*

1. Total number of bouts   323
   a. Male initiated   112
   b. Female initiated   211
   c. Average number bouts   53.8

2. Total number spawning bouts   108
   a. Male initiated   2
   b. Female initiated   106
   c. (male and female) % of total bouts   33.5
   d. Average number spawning bouts   18

3. Total number of pseudospawning bouts   5
   a. Male initiated   2
   b. Female initiated   3
   c. (male and female) % of total bouts   1.5
   d. Average number pseudospawning bouts   0.8

4. Total number clasp only bouts   11
   a. Male initiated   3
   b. Female initiated   8
   c. (male and female) % of total bouts   3.4

5. Total number of courtship bouts   116
   a. Male initiated   24
   b. Female initiated   92
   c. (male and female) % of total bouts   35.9

6. Total number of non-sexual bouts   83
   a. Male initiated   81
   b. Female initiated   2
   c. (male and female) % of total bouts   25.7

7. Average duration of spawning bouts (sec)   56.8

8. Average duration of pseudospawning bouts (sec)   65.5

9. Average duration of clasp only bouts (sec)   19.7

*1-6 based on 6 spawning sequences; 7-9 based on 5 spawning sequences

Sexually inexperienced pairs of B. splendens successfully spawned in 28.3% of the bouts performed during the spawning period; sexually experienced pairs in 45.6% (Rainwater and Miller, 1968). The spawning efficiency of C. fasciata lies between these two figures and would seem to be rather high, slightly over one third of all bouts in the spawning period culminating in actual spawning.

TABLE III

AVERAGE CLASP DURATION IN SPAWNING, PSEUDO-
SPAWNING, AND CLASP ONLY BOUTS*

	Avg. Dur. Clasp (sec)
Spawning Bouts	20.6
Pseudospawning Bouts	18.5
Clasp Only Bouts	5.7

*Averages based on data from 4 spawning
  sequences

It is assumed that the sexual receptivity and readiness of the female to spawn is of extreme importance since 98.2% of all spawning bouts were female initiated. The female was also found to initiate the great majority of spawning bouts in T. trichopterus (Miller, 1964), B. splendens (Rainwater and Miller, 1968), and T. leeri (Miller and Hall, 1968). The average duration of spawning bouts is 56.8 seconds, which closely resembles the average spawning bout duration of 55.23 seconds in T. leeri (Hall, 1966a) and 52.9 seconds in sexually experienced B. splendens (Ranwater and Miller, 1968).

Pseudospawning bouts rarely occur during the spawning period, as evidenced by the 0.8% average per spawning period. One to four

pseudospawning bouts commonly occur prior to the spawning period, but
they rarely follow it. The percent of pseudospawning bouts per total
bouts in the spawning period in sexually experienced and sexually
inexperienced B. splendens was 14.8 and 13.4, respectively, much higher
than in C. fasciata; while the average respective duration of the
pseudospawning bouts was 40.4 and 32.2 seconds (Rainwater and Miller,
1968), somewhat lower than the average duration of 65.5 seconds in
C. fasciata.

Clasp only bouts comprise only 3.4% of the total and occur on the
average of 1.8 per spawning period in C. fasciata. Clasp only bouts in
sexually experienced B. splendens comprised 3.5% of the total bouts in
the spawning period (Rainwater and Miller, 1968), a figure almost
identical to that for C. fasciata. The female of C. fasciata initiates
72.7% of the clasp only bouts, and the termination of bouts prior to
attainment of the spawning or pseudospawning stage seems to be due
most often to inappropriate responses by the female. The duration of
clasp only bouts is 19.7 seconds and falls between 17.9 and 29.9
seconds, respectively, for sexually inexperienced and sexually
experienced B. splendens (Rainwater and Miller, 1968).

Courtship bouts comprise 35.9% of the total number of bouts during
the spawning period, compared to 31.2 and 51.8%, respectively, in
sexually inexperienced and sexually experienced B. splendens (Rainwater
and Miller, 1968). In both species the female initiated the majority
of these bouts.

Non-sexual bouts make up 25.7% of the total spawning period bouts
and are almost exclusively male initiated. This is in sharp contrast
to all other bout types occurring during the spawning period, each of

which is female initiated over 50% of the time.

Table III shows average clasp duration in spawning, pseudospawning, and clasp only bouts.

Miller (1964) noted that average duration of a clasp in T. trichopterus spawning bouts is 44.7 seconds, while that of T. leeri is 25.3 seconds. Very similar to the average clasp duration in spawning bouts of T. leeri is the average clasp duration in spawning and pseudospawning bouts of C. fasciata, 20.6 and 18.5 seconds, respectively. This contrasts sharply to clasp only bouts, in which the average clasp duration is 5.7 seconds. The possible explanations for this short duration are obvious: lack of pair synchronization; failure of the female to mount properly; failure of the female to continue responding sexually to the male (several times the female swam out of the male clasp); failure of the male to continue responding sexually to the female.

Swimming inhibition in the male has an average duration of 8.4 seconds. The female of C. fasciata usually recovers from swimming inhibition approximately 1-2 seconds before the male and begins to swim away from the nest. The male seldom chases the female after swimming inhibition, possibly due, in part, to the long latency of his recovery (the female has time to move out of the nest area), which could function in reducing male aggression toward the female at this time as well as in allowing his attention to be directed toward eggs and nest.

Forselius (1957) noted that generally in the anabantoids the male is first to recover from swimming inhibition after which he gathers eggs, deposits them in the nest, then thrusts at the female before she has recovered and/or attacks her afterwards. In T. trichopterus

(Miller, 1964), T. leeri (Hall and Miller, 1968), C. lalia and

C. labiosa (Forselius, 1957), both male and female of the species

terminate swimming inhibition at approximately the same time, and the

male often chases the female as she begins to swim away. The chase

may terminate in male aggressive activity directed at the female.

During swimming inhibition in B. splendens (Rainwater and Miller,

1968), the clasp is maintained temporarily, then the female rises to

the surface where she lies resembling a dead fish, while the male

remains in his U-position under the nest or sinks slowly. Upon

recovering, the male catches most of the eggs in his mouth and deposits

them in the nest. The female recovers, swims to the bottom where she

picks up bottom material or eggs, then moves under the nest beside the

male where she deposits any eggs she has retrieved. Apparently there

is seldom, if ever, any male aggression directed at the female during

this time. It is possible that the long latency of swimming inhibition

in the female of this species, rather than attracting the attention,

and possibly aggression, of the male, as movement of the female might,

serves to allow the attention of the male to become focused on the

falling eggs, thereby assuring that a large percentage of them will be

retrieved and deposited in the nest. The focusing of the male's

attention on the eggs would not seem to be as crucial in Colisa and

Trichogaster species since the eggs float to the surface.

The average number of eggs per spawning bout is estimated at 23.5.

This is a very rough estimate since the eggs were counted visually as

they were exuded from the female; yet it corresponds well with the

10-50 eggs per spawning bout in C. fasciata noted by Forselius (1957).

He further mentions that at times a C. fasciata female may release

75-100 eggs at one time, or more. The distribution of eggs per bout for each spawning period is few eggs (often only 1-2) at the very beginning, a fairly consistent higher number of eggs per bout over most of the spawning period, and few eggs (again 1-2, sometimes up to 10) per bout at the end of the spawning period).

CHAPTER VII

SUMMARY

The onset of the reproductive cycle in C. fasciata is characterized
by marked color changes in both sexes, initiation of territorial
defense and nest-building by the male, enlarged abdomen in the female,
and a general increase in activity. Although most males build nests
before they spawn, the presence of a nest is not a prerequisite for
spawning. However, in the absence of a nest, the male will spawn only
in a particular area of the aquarium.

C. fasciata males usually choose nest sites around or underneath
floating or overhanging aquatic vegetation.

The spawning period begins with the first spawning bout and
terminates with the last. After the first or second spawning bout,
the interval between spawning bouts becomes relatively short. This
continues until the last 2-3 spawning bouts when the bout interval
again increases. Female approach to the nest becomes less frequent,
and male aggressive activity usually increases. Pseudospawning bouts
are rarely performed during this period, but often occur during the
prespawning period shortly before the first spawning bout.

The early part of the postspawning period is characterized by
increasing male aggressive activity toward the female. Pseudospawning
bouts seldom occur. The female exhibits an increasing tendency to
remain on the bottom, hidden from male view. She feeds frequently and

gulps air at the surface, often over extended periods. As this period is terminated, the male shows an increasing tendency to care for nest and eggs.

The courtship and spawning of C. fasciata is distinct from closely related Anabantoid species in that the male rarely leads the female to the nest, the female does not assume an "upside-down posture" or "roll over" during spawning, and the female recovers first from swimming inhibition and is seldom chased by the male afterwards.

Females never show aggressive behavior toward the males during the spawning or postspawning periods. Appeasement postures are often displayed during these periods, but they apparently do little to ward off male aggression. The females seldom show signs of fin or body mutilation, however, and female appeasement may serve to decrease the frequency and intensity of aggression.

The pelvic fin filaments of C. fasciata females are often placed against the lateral surface of the male during mounting and may aid in orientation of the female with respect to the male or serve as a tactile stimulus to the male. Picciolo (1964) stated that the function of the pelvic fin rays was unknown, but he found that amputated or cauterized fin rays resulted in markedly fewer successful spawnings than in controls.

The role of the female in determining the success of the spawning sequence seems to be one of singular importance since 98.2% of the spawning bouts observed were female initiated. The female also initiates the majority of spawning bouts in several other anabantoid species.

Pseudospawning bouts rarely occur during the spawning period in C. fasciata but were found by Rainwater and Miller (1968) to occur frequently during the spawning period in B. splendens.

The termination of bouts prior to spawning or pseudospawning seems to be due most often to inappropriate responses by the female.

The distribution of eggs per spawning bout for each spawning period was few eggs per bout at the beginning, a fairly consistent higher number per bout over most of the period, and few eggs per bout at the end of the spawning period.

Interruptions of spawning bouts occurred at any time during several stages due to inappropriate responses on the part of one or both members of the spawning pair, though usually the female, or to lack of pair synchronization. Interruptions also were caused by environmental changes.

Speculations were made as to the possible explanations for the infrequent leading-to-the-nest and the absence of rolling over in the C. fasciata spawning pair.

A brief comparative discussion of the differences in behaviors between the species of the genus Colisa (primarily fasciata and lalia) was facilitated by the application of an hypothesis about a "morphologically-influenced locomotory pattern" (Miller and Miller, in press).

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