

*Smithsonian Tropical Research Institute,
Balboa, Canal Zone, Panama*

The Roles of Female Mate Choice and Predation in the Mating Systems of Some Tropical Labroid Fishes

By D. ROSS ROBERTSON and STEVEN G. HOFFMAN

With 3 figures

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Abstract

The highly differentiated patterns of courtship and spawning of 3 tropical wrasses are described. We show how (a) the ability of a ♀ to freely choose her mates, and (b) risks of predation on the spawning fishes and their zygotes, affect the structure of courtship interactions and the spawning act itself. We also discuss how both these factors affect the spatial location and diurnal timing of spawning. The significance of variability in the expression of sexual dichromatism in these and other wrasses and parrotfishes is considered from the same viewpoints.

I. Introduction

Detailed accounts of courtship and pair-spawning in the labroid fishes, which include the wrasses (Labridae) and parrotfishes (Scaridae), have been presented by FIEDLER (1964), SJÖLANDER, LARSON and ENGSTROM (1972), REINBOTH (1973), POTTS (1974), NAKAZONO and TSUKAHARA (1974), and ROBERTSON and CHOAT (1974). The first two of those papers deal with temperate labrids that lay demersal eggs and exhibit male brood-care. The spawning pattern of the tropical labroids differs radically from that of the temperate species in that gametes are released free into the water and the embryos and larvae are planktonic. We have never observed any of the tropical species laying demersal eggs, on both east and west sides of the Pacific or in the Caribbean Sea and in the Indian Ocean. We have found only one sketchy and unconfirmed report in the literature of a tropical wrasse laying demersal eggs (DEBERNADO 1975).

The published accounts of labroid pair-spawnings can be summarized as follows: the ♂ approaches a ♀ and moves around and above her, while performing displays that include body-quivering and movements very like those he uses during the spawning act. The ♀ then rises to him and the two fish rush

together towards the surface, release gametes, and rush back to the substrate (see also WINN and BARDACH 1960; RANDALL and RANDALL 1963; FEDDERN 1965; BREDER and ROSEN 1966; BUCKMAN and OGDEN 1973; MOYER and SHEPARD 1975; BARLOW 1975). There have been no indications in the literature that the structure of the courtship and pair-spawning sequence can be very different in the various species of midwater-spawning labroids. Also, little attempt has been made to determine how different selective forces have shaped the construction of this sequence.

The purposes of this paper, then, are threefold:

1. We describe and compare the highly differentiated courtship and pair-spawning sequences of 3 species of tropical wrasses — *Labroides dimidiatus*, *Thalassoma bifasciatum* and *Clepticus parrae*.

2. We discuss the selection pressures that may have been involved in bringing about these differences. In doing so, we show a relationship between each species' pattern of food utilization and its social and mating system. We then demonstrate how courtship and spawning behavior has been affected by these characteristics.

3. We examine the highly variable nature of sexual dichromatism among these and other tropical labroids and discuss the significance of this variability with respect to the structure of their mating systems and the types of environments they live in.

Although the existence of 2 basic labroid spawning patterns: pair spawning and group (multimale) spawning (RANDALL and RANDALL 1963) is well known (see also ROEDE 1972; REINBOTH 1973; ROBERTSON and CHOAT 1974; WARNER, ROBERTSON and LEIGH 1975; CHOAT and ROBERTSON 1975; WARNER and ROBERTSON in press; ROBERTSON and WARNER in press), we are considering only pair-spawning patterns here.

II. Materials and Methods

A. The Species and Study Areas

Labroides dimidiatus has been studied in the field by D. R. R. at 2 widely separated locations — Heron Island, on Australia's Great Barrier Reef (23° 27' S lat., 152° 5' E long.), between 1969 and 1972; and Aldabra Island, in the western Indian Ocean (9° 25' S lat., 46° 21' E long.) from mid 1975 until early 1976.

Both of us have worked on the behavior of *T. bifasciatum* in the field, in the San Blas Islands off the Caribbean coast of Panama. Observations were made throughout much of 1974—1976 (see also WARNER et al. 1975; WARNER and ROBERTSON in press).

In the same area, D. R. ROBERTSON has made field observations on *C. parrae* over the same time period as those on *T. bifasciatum* (see also WARNER and ROBERTSON in press).

B. Types of Sexual Chromatism in the Labroid Fishes

In sexually dichromatic species, some or all mature ♂♂ are capable of developing a color pattern that mature ♀♀ cannot develop. Conversely, in a sexually monochromatic species, ♀♀ can develop all the color patterns that ♂♂ can. This definition of dichromatism derives from the fact that, in many species, large terminal phase ♂♂ have a pattern that differs greatly from the initial phase pattern shown by ♀♀ and, when they are present in the population, small ♂♂.

The dichromatic species can be categorized arbitrarily in 2 different ways, although we emphasize that this classification deals with the ends of a continuous range of states rather than perfectly divisible conditions. These conditions are (1) the degree of differentiation in the initial and terminal phase patterns and (2) the permanence of this difference. In *fully dichromatic species*, the terminal pattern contains color elements that are not present in the initial pattern. In *partially dichromatic species*, the same color elements are present in both

phases and the two are distinguished on the basis of their relative intensities. Specifically, certain elements are much more intensely developed in the terminal pattern than in the initial pattern. In *permanently dichromatic* species the terminal coloration is permanently displayed, whereas in *temporarily dichromatic* species, a ♂ can temporarily lose its terminal pattern and regain the initial pattern.

Permanently dichromatic species also fall into two classes in terms of the type of modification that the terminal pattern undergoes when its bearer is courting. During sexual activity, all or part of the terminal pattern can be considerably intensified, which we call *courtship intensification*. The terminal pattern may instead be overlaid or obscured by a different pattern, which we term *courtship alteration*.

III. Social and Mating Systems and the Structure of Courtship and Pair-Spawning

The main features of the social and mating systems, including courtship and spawning behavior of the 3 species that we will describe and discuss, are summarized in Table 1.

Table 1: Comparisons of the ecology and behavior of three labroid species

	<i>L. dimidiatus</i>	<i>T. bifasciatum</i>	<i>C. parrae</i>
1. Degree of attachment to substrate	High	High	Low
2. Feeding habits	Specialized (parasites)	Generalized (plankton, benthos)	Specialized (plankton)
3. ♂-specific color pattern	Absent	Present	Present
4. Social system	Haremic	Nonharemic, home-ranging	Nonharemic, schooling
5. Mating system	Strictly haremic	Lekking, ♂♂ territorial	Lekking, ♂♂ nonterritorial
6. Localized spawning grounds	Absent	Present	Present ?
7. Courtship:			
Active participation and displays by:	♂ and ♀	♂	♂
Color change by:	♀	♂	♂
Duration per spawning	Long	Short	Long
8. Spawning rush	Present	Present	Absent (slow rise)

A: *Labroides dimidiatus*

1. General Biology

Labroides dimidiatus is one of 5 known species within the genus (RANDALL 1958; RANDALL pers. comm. 1973). All members of the genus are cleaner-fishes, i. e., specialized feeders that remove parasites and other material from the body surfaces of various fishes.

2. Sexual Dichromatism

By definition, this species is sexually monochromatic. The normal adult color pattern consists of a black stripe running the entire length of the body that expands into a broad black wedge in the tail. Above this stripe, the body is grey or pale grey-brown and below it, white.

3. Social Organization

Labroides dimidiatus and at least one other species, *L. bicolor*, are substrate-living fishes that form social groups (harems) composed of a single ♂ and about 6 mature ♀♀ (ROBERTSON 1972; ROBERTSON, unpubl. data on *L. bi-*

color). We call this type of social system *strictly harem*. In *L. dimidiatus*, the composition of these harems is stable over long periods of time. Social relations between the members of the harem are characterized by both territoriality and the presence of a dominance hierarchy. Within a harem's area, ♀♀ are scattered about at fixed feeding areas, which they defend against equally sized or smaller ♀♀. Virtually the entire range of movements of all the mature ♀♀, and particularly those of the larger ♀♀, are contained within the territory of the harem's ♂, who is larger than and dominant over all of those ♀♀.

4. Mating System

In *L. dimidiatus* sexual activity is essentially restricted to members of the same harem (see ROBERTSON 1972; WARNER et al. 1975), i. e., the mating system is *strictly harem*. Sexual activity occurs every day and all of the spawnings of a given group also occur within the territory of the harem's ♂ (ROBERTSON unpubl. data).

5. Breeding Seasonality

At Heron Island, *L. dimidiatus* is near the southern limit of its range, and water temperatures during the winter are probably the coldest that breeding populations of this species experience. Sea surface temperatures there are known to fall below 15 °C, and can be consistently less than 20 °C during July and August (ENDEAN et al. 1956). Aldabra is much closer to the equator, and minimum temperatures are higher. Between July and September 1975, surface temperatures in the Aldabra study area were consistently between 23 ° and 24 °C. At Heron Island, the population of *L. dimidiatus* was sexually active throughout the year, i. e., individuals went through the motions of spawning during all seasons, although egg production was restricted to the warmer months (October through May). At Aldabra, spawning was observed throughout the study period in both cold and warm months, and probably occurs throughout the year. We attribute the Heron Island spawning hiatus to the limiting physiological effects of low temperature that this species experiences at the periphery of its geographic range. We therefore consider *L. dimidiatus* to be a continuously breeding tropical species.

6. Diurnal Periodicity of Sexual Activity

At both Heron Island and Aldabra Island, the tides, which are several m in amplitude, produce distinct and predictable water movements on and off the reef. At both these islands, sexual activity in *L. dimidiatus* begins shortly after high tide, and continues for 1 or 2 h. At this time, water running off the reef would tend to carry planktonic eggs with it.

7. Courtship and Spawning Behavior

The ♂ in a *L. dimidiatus* harem visits and interacts with the adult ♀♀ of his group at regular intervals throughout the day. A day's spawning period is initiated by one of the ♀♀ approaching and displaying to her ♂ in a distinctive manner during one of his visits. Sometimes a ♀ will take a more active part by moving to the ♂'s feeding area and initiating courtship there.

Female courtship behavior is characterized by the performance of *Body-sigmoiding*, a distinctive behavior pattern that is seen only during prespawning activity. In this display (see Fig. 1) the ♀'s body is frozen in an "S" shape for a few s, with her belly bent down and curved towards the ♂. In this way her egg-distended belly and swollen cloacal region is exposed to the ♂. The ♀'s

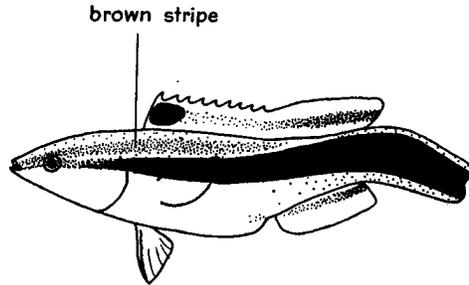


Fig. 1: *Labroides dimidiatus* ♀ (with brown-stripe coloration) body-sigmoiding

tail is also bent down and towards the ♂, with the caudal fin depressed. Her pelvic fins and anterior dorsal fin are fully extended and held stiffly, exposing a prominent black spot at the front of the dorsal fin.

While sexually active, the ♀'s color pattern also changes in a characteristic manner from the normal pattern. Her black stripe fades and often disappears in the head region. A new color element is also added which is a brick-brown stripe that runs along the front half of the body just above the level of the black stripe (see Fig. 1). This brown stripe is not shown by ♂♂ at any time. ♂♂, in fact, do not develop any special color pattern when courting.

In summary, during courtship the distinctively colored ♀ approaches the ♂, gives one or more *Body-sigmoids*, and moves slowly around him. She continues holding her anterior dorsal and pelvic fins stiffly erect, and often tilts her back towards the ♂, exposing her sexual color pattern.

The ♂ responds to the ♀'s approach by performing one or more *Flutter-run* displays. This display is also seen later when he initiates additional courtship. In one of these displays, the ♂ swims directly towards the ♀ and curves around in front of her while expanding and rapidly fluttering his tail laterally.

The performance of *Flutter-runs* is essentially restricted to ♂-♀ intra-group interactions. A ♂ *Flutter-runs* to his ♀♀ throughout the day and not just during spawning periods. In addition to courtship bouts, *Flutter-runs* are

Table 2: *Flutter running* activity by ♂♂ of *L. dimidiatus*

Type of ♂	Fish number	Day number	Number of <i>Flutter-runs</i> performed per h			
			Outside daily periods of sexual activity ^c	h of observation	During daily periods of sexual activity ^c	h of observation
Old ^a ♂♂	1	1	6.9	3.1	36.9	0.9
		2	7.6	2.5	21.3	1.6
		3	4.1	2.7	12.0	1.4
	2	1	0.4	2.8	10.0	1.0
		2	0.4	2.7	10.8	1.5
		3	2.1	1.9	8.0	1.0
	3	1	1.0	2.9	23.2	1.3
		2	4.6	2.4	21.6	1.3
		3	2.7	2.6	17.5	1.2
New ^b ♂♂	1		204	0.2	-	-
	2		124	0.5	-	-
	3		114	0.3	-	-
	4		152	0.3	-	-
	5		288	0.2	-	-

a ♂♂ at least 1 month past initiation of sex change.

b ♂♂ less than 3 h after the initiation of sex change. New ♂♂ were observed during the breeding season and old ♂♂ outside the breeding season.

c A period of sexual activity is that part of the day when ♀♀ engage in courtship and spawning behavior.

used most frequently by a new "♂" during the initial stages of its succession to the ♂ position (see Table 2), i. e., from about 1/2 h after the beginning of this process until several days later. *Labroides dimidiatus*, along with the vast majority of other wrasses and parrotfishes examined to date, is a protogynous hermaphrodite. All *L. dimidiatus* ♂♂ are derived from ♀♀. This process is socially controlled, with the dominant ♀ taking over as a ♂ upon the death of her group's ♂ (ROBERTSON 1972).

We should point out that *L. dimidiatus* has many more displays that are used in intraspecific interactions other than the two that we discuss here. Consideration of these other displays is not relevant to this discussion.

After one or more bouts of mutual displaying, including submissive displays by the ♀ and attacks and threats by the ♂, the fish move into a position where the spawning act can be initiated. The ♀ moves below the ♂ as the two perform erratic uncoordinated circling around each other, mixed with further display activity. Both fish then spiral upwards in a series of movements that become increasingly coordinated until eventually the ♂ is directly above the ♀. The pair then make physical contact, with the ♂ straddling the ♀ between his erected pelvic fins. From that position the two fish rush rapidly upwards, at an angle of about 60° above the horizontal. They remain together throughout the rush, which terminates several m above the substrate where gametes are released. Both fish then abruptly turn, and individually make rapid returns to the substrate. Because of the rapidity of this vertical looping movement, the exact positioning of the two individuals during the act of gamete release could not be determined.

In summary, courtship and spawning in *L. dimidiatus* are characterized by:

- a. The presence of both motor displays and a color pattern specific to courtship in ♀♀.
- b. The absence of both a specific male courtship color pattern and specific male courtship displays, i. e., of special behavior patterns that serve to communicate to a ♀ that the ♂ is either sexually aroused or attempting to arouse her.
- c. The active initiation and participation in courtship by both sexes.
- d. The presence of a rapid spawning rush.

B: *Thalassoma bifasciatum*

1. General Biology

Thalassoma bifasciatum is the only member of its genus in the Caribbean Sea (RANDALL 1968), although there are many more congeners throughout the Indo-Pacific region. This substrate-associated fish is usually found on coral reefs in the Caribbean, where it is one of the most abundant and characteristically present species. It is a generalized feeder taking in zooplankton, a great variety of benthic animal material, and ectoparasites from the body surface of other fish (FEDDERN 1965; RANDALL 1967).

2. Sexual Dichromatism

The strong sexual dichromatism of this species is well documented (see LONGLEY and HILDEBRAND 1941; RANDALL and RANDALL 1963; FEDDERN 1965; ROEDE 1972; WARNER et al. 1975). ♀♀ and small ♂♂, which are in the *initial color phase*, can be striped in yellow and black or can have a series of grey-green bars on a pale brown background. Large ♂♂ in the *terminal color phase* have blue-grey heads separated from green bodies by a sandwich of 3 bars, black-white-black. The tails of fishes in the terminal phase have much longer filaments than those of initial phase fishes. The tails of terminal phase ♂♂ are dark blue along the filaments with a hyaline center. Anteriorly, the dorsal fin is black and posteriorly, green. The anal and pelvic fins are blue-green and the pectoral is hyaline, except for a dusky tip. Terminal phase ♂♂ that are sexually active and inactive differ slightly in the intensity of their color patterns. In sexually active fish the body is blue-green rather than green, the

head has a greenish rather than bluish cast, and the pectoral tips carry a large prominent black spot rather than being sooty or hyaline.

3. Social Organization

In this species no permanent social groups similar to those of *L. dimidiatus* have been found, on either large reefs (our own observations) or small reefs (WARNER and HOFFMAN unpubl. data). Sexually inactive fishes maintain home ranges, which they may use continuously for months at a time (ROBERTSON unpubl. data). In addition, during the nonbreeding portion of the day there are extensive overlaps in the ranges of individuals of both sexes. However, terminal phase ♂♂ are not distributed at random with respect to size along a reef. One tends to find the largest of those ♂♂ spaced apart, with each having several smaller terminal phase ♂♂ living in the same area. There is no tendency for this species to form feeding territories, although during substrate feeding larger fishes will displace smaller ones from specific food items. In addition, large aggregations often form during plankton feeding or when the fishes find a concentration of food on the substrate.

4. Seasonality and Diurnal Periodicity of Sexual Activity

Sexual activity occurs daily throughout the year, and within each day is restricted to several hours around midday (WARNER et al. 1975; WARNER and ROBERTSON in press).

5. Mating System

The species shows lek-forming tendencies. On large reefs, fishes of both color phases commonly migrate up to $1/2$ km to areas where spawning activity is concentrated. These migrations sometimes follow well-defined trails. At such spawning grounds, terminal-phase ♂♂ set up temporary spawning territories, with individual ♂♂ returning repeatedly to the same territories (WARNER et al. 1975; ROBERTSON unpubl. obs.).

6. Courtship and Pair Spawning

We can construct an idealized courtship and spawning sequence of *T. bifasciatum*, i. e., one involving the full range of component interactions, from a combination of REINBOTH's (1973) descriptions and our observations. A territorial ♂ moves actively about his territory and will perform one or more *Loopings* upon, or before, sighting an initial phase fish moving in or near his territory. These are rapid rushes up and down in the water column, describing a loop or inverted "U" in a single smooth movement.

When a ♀ approaches, the ♂ responds by approaching her and circling slowly overhead, while giving bursts of rapid lateral quivering of the expanded tail and posterior trunk (*Quivering*). Anterior-posterior flutterings of his horizontally extended pectoral fins (*Pectoral-fluttering*) are also performed, which expose the black coloration of those fins. This displaying may be mixed with *Loopings*.

Unlike the situation in *L. dimidiatus*, there is no evidence that the characteristic displays that *T. bifasciatum* ♂♂ perform during courtship (*Looping*, *Quivering* and *Pectoral-fluttering*) are used by them in any context other than courtship, or are ever used by ♀♀.

If the courting pair are located at a suitable spawning site, and the ♀ is receptive, she will rise slowly off the bottom in a head-up position, with her unpaired fins expanded. The ♂ responds by circling upwards in a slow spiral while continuing *Quivering* and *Pectoral-fluttering*. He then moves to the ♀,

sits on her back, and wriggles his body from side to side against her, with further *Quivering* and *Fluttering*. This leads to a pair-spawning rush, which the ♀ initiates by moving off upwards. She takes off at an angle of 30–45° above the horizontal, but changes more towards the vertical as she accelerates and ascends. The ♂ remains with, or slightly behind the ♀ during this spawning rush. At its terminus, 0.5 to 1 m from the start, the ♀ momentarily stops, releases eggs, and returns rapidly to the substrate. The return is often to the approximate take-off point of the rush. The ♂ also pauses a moment at the egg-release point, releases sperm, and then returns to the substrate. REINBOTH'S (1973) film analysis of pair spawnings shows that at the top of the rush, the ♀ turns more or less upside down and that the ♂ flexes his body, bringing his genital opening close to hers.

In practice, elements of this idealized sequence are often omitted. The number of *Loopings* a territorial ♂ performs during a daily spawning period varies considerably. Although the frequencies of spawnings per spawning period and *Loopings* per spawning period are positively correlated (Spearman Rank Correlation Coefficient $r_s = 0.33$, $p < 0.01$, $n = 66$ spawning periods), the relationship is a very loose one. Many spawnings are not preceded by the ♂ *Pectoral-fluttering* or *Quivering* (only 56% of 1968 spawnings by 15 ♂♂ were), and the ♂ usually does not sit on the ♀'s back prior to the spawning rush (contact was made in only 28% of 177 spawnings by 16 ♂♂). In fact, the ♀ often takes off in a spawning rush before the ♂ is in position above her, so that the two meet halfway up the rush. The ♂ can also arrive at her egg-release point after a ♀ has left it and is returning to the substrate. A group of ♀♀ will often form at a spawning site and rise together to the one ♂. A series of pair spawnings can then occur in rapid succession, with no display activity between each. We have seen as many as 18 pair spawnings in 1 min by a single ♂.

Male courtship is easily triggered in this species. An initial phase fish merely entering a ♂'s territory can elicit his courtship and ♂♂ will often *Quiver* and *Pectoral-flutter* over a sexually unresponsive fish that has moved up in the water column while feeding on plankton. Little beyond the ♀'s rising seems necessary to stimulate the ♂ to move to her and ready himself for the spawning rush. ♀♀ do not usually spread their fins while rising (only 37 of 75 ♀♀ we observed did so). ♀♀ also do not adopt a specific courtship color pattern, and may show any of 4 patterns immediately prior to spawning (see Table 3).

In "Barred" fishes the body has a series of pronounced grey-green bars. In fishes with the "Entire Stripe" pattern the body is yellowish to whitish with an unbroken black stripe running its length on each side. The "Interrupted Stripe" pattern is intermediate between "Barred" and "Entire Striped". In an "All Yellow" fish, all of the body is yellow and white.

Although in both *L. dimidiatus* and *T. bifasciatum* the ♀ rises to the ♂, in the former species she precedes that rise with a specific set of displays and activities that the ♀ of the latter lacks. Thus the ♀ plays a much more quiescent part in courtship than does the female *L. dimidiatus*.

Tab. 3: Color patterns of female *T. bifasciatum* approaching a courting ♂ prior to spawning

Color pattern of fish	Proportion of ♀♀ with that pattern (n = 73)
Barred	0.37
Interrupted Stripe	0.39
Entire Stripe	0.14
All Yellow	0.10

- Courtship and pair spawning in *T. bifasciatum* are thus characterized by:
- The absence of a specific female sexual color pattern, the near-absence of specific female sexual displays, and the quiescent role of the ♀ in courtship.
 - The presence of special male sexual displays and of a specific male sexual color pattern.
 - The ♂ being very active in courtship.
 - The presence of a rapid spawning rush.

C. *Clepticus parrae*

1. General Biology

Clepticus parrae, the only known member of its genus and subfamily (JORDAN and EVERMANN 1896), is restricted to the tropical western Atlantic region (RANDALL 1968). It is unique among the labrids of that area in that it feeds and spends most of its time in mid-water, next to reefs. It is, however, ultimately reliant on adjacent reefs for shelter. This species has undergone considerable morphological modification from the typical labroid type as an adaptation to its planktivorous, semipelagic mode of life (DAVIS and BIRDSONG 1973; RANDALL 1967).

2. Sexual Dichromatism

Clepticus parrae is sexually dimorphic, with the dorsal and anal fins of ♂♂ having filamentous extensions that those of the ♀ lack. It is also sexually dichromatic (see Fig. 2). Sexually inactive and active ♂♂ have the same color pattern, although that of courting ♂♂ is much more intensely developed.

3. Social Organization

Sexually inactive ♂♂ and ♀♀ mingle freely in midwater schools composed of hundreds or thousands of fishes. This species does not form permanent social groups like those of *L. dimidiatus* or have small home ranges like those of *T. bifasciatum*.

4. Seasonality and Diurnal Periodicity of Spawning

In the study area, breeding occurred throughout the year, and spawning was observed in mid to late afternoons (WARNER and ROBERTSON in press).

5. Mating System

We have observed over 100 pair spawnings by this species. All occurred in the same shallow (< 10 m depth), 0.1 ha area, situated at one end of a single reef. The ♂♂ that courted ♀♀ in this area were not territorial. However, there were frequent ♂-♂ fights, as a courting ♂ with a ♀ would attempt to chase away approaching ♂♂. We have seen a large ♂ displace a smaller one

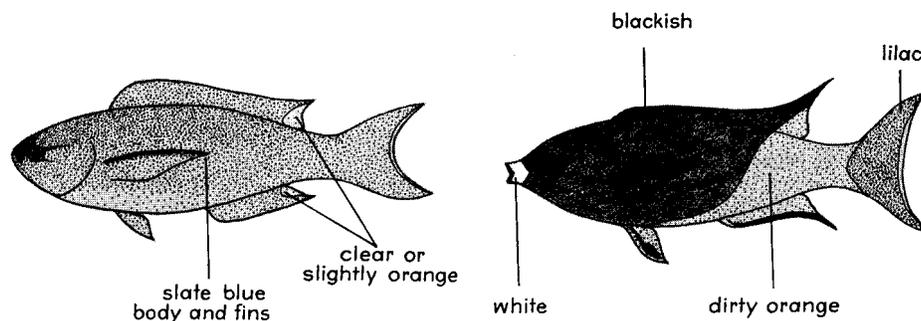


Fig. 2: *Clepticus parrae* ♀ (left) and Pouting ♂ (right)

from a ♀ and spawn with her on two occasions. Thus dominance ability, as determined by size, appears to play a part in determining spawning success of ♂♂ of this species. Spawnings were not associated with particular sites or specific substrate features within this spawning area. Pairs of ♂♂ and ♀♀ criss-crossed freely throughout the spawning area, with spawnings often occurring just below the water's surface. Thus, sexually active ♂♂ do not hold spawning territories.

Although all the spawnings seen occurred in a definable area, we often noted that a sexually active ♂ would leave this area after spawning. The ♂ apparently would return later with another ♀ that he had found outside the spawning ground. During a spawning period there were also cycles in the amount of spawning activity at this spawning ground. Groups of 5 or 6 mating pairs would often arrive simultaneously, court and spawn more or less synchronously and leave, with little or no activity before the next group arrived.

6. Courtship and Pair Spawning

Courtship in this species is initiated by ♂♂. A ♀ swimming along in the water column at a normal pace will be approached by a ♂, who attempts to take up a position immediately above her, with his belly against one side of her back. While doing so, the ♂ *Pouts*, i. e., his mouth is extended forward, which exposes its conspicuous white membranes. Additionally, his tail and his posterior dorsal and anal fins are spread (see Fig. 2). This posture can be held for minutes at a time as the two fish swim along together by pectoral sculling. *Pouting* is only performed by ♂♂ and only in the context of courtship.

The ♂'s threshold for the release of courtship behavior is evidently quite low. We have seen ♂♂ approaching, *Pouting* to, and attempting to initiate spawning with juvenile conspecifics, adults of the damselfish *Chromis multilineata*, and individuals of both initial and terminal phases of the scarids, *Scarus croicensis* and *Sparisoma rubripinne*. While adult *C. multilineata* superficially resemble *C. parrae* juveniles, neither of the scarids resembles *C. parrae*, in either shape or color. In addition, while *S. croicensis* is about the same size as *C. parrae* adults, *S. rubripinne* ♂♂ can weigh about six times as much as the largest *C. parrae*.

A nonreceptive ♀ responds to the ♂'s approach by speeding up and trying to avoid him, although he may follow her closely for up to at least 10 min. If a ♀ is receptive, she will eventually slow down, usually quite near the substrate, and allow the ♂ to move to a position immediately beneath her. The ♂ then begins *Pushing* the ♀ upwards with the back of his forehead. During this courtship sequence, receptive ♀♀ do not change their color pattern or behave in any special manner other than slowing down and ceasing avoidance of the ♂ as the two fish swim near the substrate. Subsequently, ♀♀ usually show some resistance to the *Pushing* ♂ and attempt to move away. This leads to the ♂ swimming after the ♀, while attempting to maintain his courtship position. The two fish circle rapidly and erratically during this activity.

Male *Pushing* can eventually lead into the spawning act as the pair moves further off the bottom. The ♂ places his snout against or under the ♀'s slightly flared operculum just above the pectoral fin. With his mouth and fins in the *Pouting* position, he then pushes the immobile ♀ up through the water, while vibrating his tail with rapid, low-amplitude, lateral beats. One or 2 m above the starting point of this spawning rise, and 5—7 m above the substrate, the ♂ stops pushing as the ♀ releases a cloud of eggs. The ♂ briefly moves into the cloud, presumably to release sperm, and then swims off. The ♀ hangs motionless for 1—2 s at the apex of the rise, and then also swims off. During the

spawning rise the pair move in a curved path that begins with the ♂ nearly vertical and the ♀ leaning to one side with her head up. The rise ends with the ♂ more or less horizontal and the ♀ leaning on the opposite side, and often head down. It is not clear whether the ♂ is merely pushing against or actually gripping the ♀ with his mouth during the spawning rise.

Courtship and spawning in this species are thus characterized by:

- The absence of specific female sexual displays and of a specific female sexual color pattern.
- The presence of a specific male sexual display and of a specific male sexual color pattern.
- Active initiation and participation in courtship by the ♂ alone.
- The absence of a rapid spawning rush and the presence of a slow spawning rise.

IV. Sexual Dichromatism in the Labroid Fishes

Sexual dichromatism occurs very commonly among the wrasses and parrotfishes. The differences between the color phases of the same species are also often radical enough to have created confusion as to their taxonomic status (see SCHULTZ 1958, and ROSENBLATT and HOBSON 1969, for example). A careful examination of the literature and observations in the field show that there is a considerable range of variation in the degree and form in which species are sexually dichromatic. WARNER and ROBERTSON (in press), and ROBERTSON and WARNER (in press), have partly discussed this variation in the Caribbean labroids. We expand on that work here.

CHOAT and ROBERTSON (1975) indicated that the presence or absence of sexual dichromatism in labroid fishes is related to the type of mating system

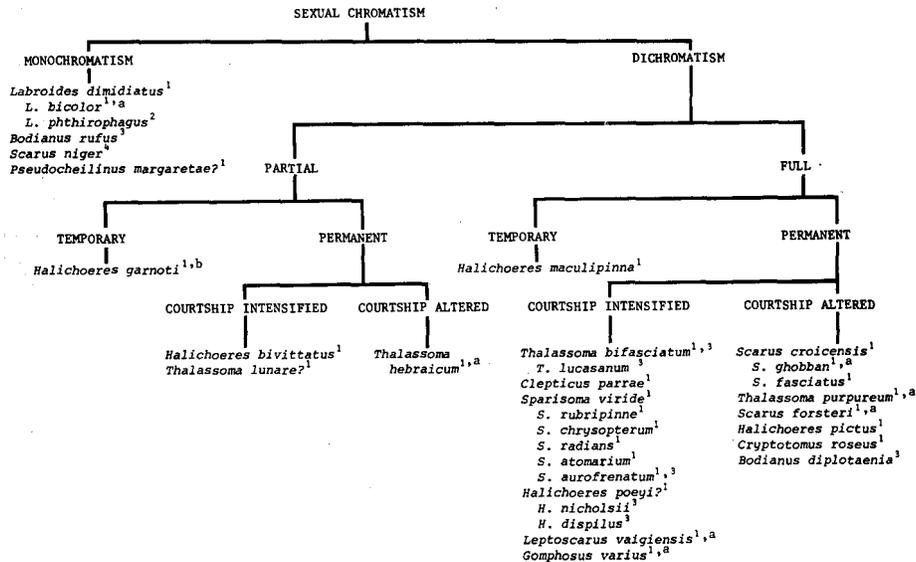


Fig. 3: Patterns of sexual chromatism in some tropical labroid fishes. 1) ROBERTSON, observations. 2) YOUNGBLUTH 1968. 3) HOFFMAN, observations. 4) CHOAT and ROBERTSON 1975. a) Indian Ocean form. b) There is some doubt that this species is truly dichromatic (see WARNER and ROBERTSON, in press)

that each species has. Species such as *L. dimidiatus* that have *strictly harem* mating systems are monochromatic, and those with mating systems similar to that of *T. bifasciatum* are dichromatic. Fig. 3 shows the degree of sexual dichromatism exhibited by various species. Information available on many of the species referred to in that figure supports this observation (WARNER and ROBERTSON in press; ROBERTSON and WARNER in press; ROBERTSON and CHOAT 1974; ROBERTSON and HOFFMAN, unpubl. data). Species with intermediate mating systems are also dichromatic. For example, we have observed that permanently territorial, terminal phase ♂♂ of the scarid, *Scarus croicensis*, mate with both the ♀♀ of their harem and passing ♀♀. BARLOW (1975) reports that terminal phase ♂♂ of that species can also set up temporary spawning territories that they defend for only the duration of the daily spawning period.

V. Discussion

A. Social and Mating Systems

1. Effects of Patterns of Resource Utilization on Social and Mating Systems

We suggest that the specialized feeding habits of *L. dimidiatus* are responsible for the development of its social system. The predictable availability of a limiting resource in space and time enables that resource to be defended (BROWN 1964; BROWN and ORIANI 1970). We hypothesize that the continuing attachment of a ♀ to a fixed and limiting resource, such as a foraging site, enables a larger ♂ to exert behavioral control over her by aggressively dominating her. He can penalize the ♀ if she is sexually uncooperative by reducing her access to that resource. A ♂ can set up a harem by controlling a number of such ♀♀.

Several sets of observations on *L. dimidiatus* indicate that food is predictably available at a restricted number of sites, and that food availability is limiting to the individual. Firstly, adult ♀♀ defend fixed feeding sites against smaller adults belonging to their own or other social groups. Secondly, when an adult ♀ dies, a smaller, more subordinate individual takes over the vacated feeding site. This leads to continuity of occupancy of the same feeding sites over successive generations (ROBERTSON 1972).

♂♂ of this species do seem to impose restrictions on the movements of the adult ♀♀ of their groups. If a ♂ finds a ♀ at the edge or outside the border of his territory, he will attack her strongly and drive her back inside (see Table 4). A ♂ could quite conceivably expel a ♀ from his group if she was frequently absent from his territory and did not spawn with him. If food is limiting, such expulsion would place the ♀ at a distinct disadvantage in her attempts to obtain food and ultimately to change sex, as she would have to try and force her way into another social group against the opposition of the resident territorial ♀♀. The successful repulsion by one group of ♀♀ against the repeated attempts of a large ♀ to enter their group has been observed at Heron Island. The ability of a ♂ to dominate a known group of ♀♀ thus enables him to ensure that they mate with him and him alone.

The existence of a nonharem social system in *T. bifasciatum* probably relates to differences in the pattern of availability of its food resources in comparison to that of *L. dimidiatus*. *T. bifasciatum* is a generalized feeder that feeds on plankton as a main food item. As such, its potential food resources are probably not predictably available in time and space, and may not even be limiting. ♀♀ would have to move about freely to obtain their food require-

Table 4: Intensity of *L. dimidiatus* ♂♂' aggression to their own adult ♀♀ relative to the location of the ♀♀ in the ♂♂' territory

Intensity ^a of male aggression	Proportion of aggressive acts of each intensity level	
	Near territory border ^b n = 140	Away from territory border ^b n = 1017
n ♂♂ = 24		
Low	0.17	0.73
Medium	0.44	0.21
High	0.39	0.06

There is a significant difference between the intensity of male aggression near to and away from the territory border:

Chi Square (using raw data) = 324, $p \gg 0.01$

^a With increasing intensity the ♂ switches from threats and intention-to-attack movements to attacks of increasing vigor and persistence.

^b Near border = less than 2.5m from sites on the border where neighboring ♂♂ normally interact; away from border = greater than 2.5 m from such sites.

ments. Thus, a ♂ could not exert permanent control over one or more ♀♀ because he would be unable to penalize a mobile ♀ by reducing her access to food. We suggest that the planktonic feeding habits of *C. parrae* are similarly responsible for its nonharemic social system.

Thus, the type of food resource utilized by a species can have marked effects on its social and mating system. In both *T. bifasciatum* and *C. parrae*, planktivory results in an inability of ♂♂ to permanently control groups of ♀♀, as well as enabling ♀♀ to freely choose their mates. This has promoted continuing competition among the ♂♂ for access to ♀♀ during the temporally restricted spawning periods. Conversely, in *L. dimidiatus*, economic defendability of food has led to female territoriality, dominance by ♂♂ over ♀♀, and a relative lack of both female mate choice and ♂-♂ competition during spawning periods.

2. Localization of Spawning Activity

RANDALL and RANDALL (1963) suggested that the areas where labroids concentrate their spawning activity are those that provide the best chance of eggs being carried off a reef and away from reef-based egg predators. *Thalassoma bifasciatum*, and possibly *C. parrae*, concentrate their spawning activity at specific areas, the location of which may be independent of where the fishes feed. In *L. dimidiatus*, ♂♂ invariably spawn within their permanent feeding territories. *Thalassoma bifasciatum*'s and *C. parrae*'s spawning grounds are located at the type of sites described by the RANDALLS, i. e., the downcurrent edges of reefs (WARNER et al. 1975). Why then should *L. dimidiatus* spawn in permanent territories rather than move to areas that are perhaps more favorable for egg dispersal? We hypothesize that the ♂ gains more by staying in his area where he is guaranteed spawnings rather than moving elsewhere. A large reproductive cost would result from such a move, by the ♂ trying to insert himself into an area already occupied by the permanent territories of other ♂♂. This would be difficult, as groups seem to be scattered throughout the available substrate. ♀♀ are unable to leave the group to spawn for reasons that we had discussed above.

Terminal phase ♂♂ of *T. bifasciatum* spawn at specific sites within their spawning territories, which are concentrated in certain parts of reefs. *C. parrae* also restricts its spawning to only part of a reef, although it spawns in mid-water rather than at specific sites or circumscribed territories. This difference

is related to the degree to which each species relies on the substrate for shelter. The territoriality of *T. bifasciatum* ♂♂ is related to the existence and defensibility of specific substrate features that are preferred spawning sites because they reduce the risk of predation to a shelter-reliant species. *T. parrae*, lacking such strong reliance on the substrate for shelter, would not be expected to spawn near specific substrate features. The basis for the development of male territoriality — the existence of preferred spawning sites that are fixed in space — is thus lacking in *C. parrae*.

3. Diurnal Periodicity of Spawning Activity

The timing of daily spawning can vary and depends on local conditions. In some areas a large tidal range produces strong, predictably timed water movements. In such areas, which include those where we have studied *L. dimidiatus*, the production of zygotes occurs at that part of the tidal cycle when they are most likely to be moved off a reef. This evidently overrides the effects of other factors. However, where the tidal range is small, as it is in the San Blas Islands, strong predictably timed tidal currents are lacking and the time of day at which spawning occurs is more dependent upon other factors.

At the beginning and end of each day light intensities are low, and piscivorous fishes have an advantage over their prey in visual capabilities (MUNZ and MACFARLAND 1973). These predators are evidently most successful by feeding at such times (HOBSON 1968, 1972, 1975). During periods of reduced light availability, the feeding ability of planktivorous fishes is probably reduced, and their activity curtailed by the predation risk they face. This would result in both higher egg-predation risks and lower risks to the spawning fishes at midday in comparison to mid to late afternoon. We have observed well over 100 attacks by a variety of predatory fishes on spawning *T. bifasciatum*, and often see planktivorous fishes feeding on newly spawned eggs of that species. We suggest that the timing of *T. bifasciatum* and *C. parrae*'s spawning periods is determined by differences in the strength of the predation risk to the spawning individuals of each species.

4. The Structure of Courtship Interactions

Courtship interactions serve various functions that ensure successful mating (MORRIS 1956). They enable an individual to find a conspecific mate of the appropriate sex, to sexually arouse that mate, and to synchronize the activities of the two individuals.

a. The *L. dimidiatus* Pattern

The *Flutter-run* of male *L. dimidiatus* serves several social functions. EIBL-EIBESFELDT (1970) has pointed out that among group-living animals, greeting displays that serve a group integration function are common. *Flutter-running* serves such a function in *L. dimidiatus*. ♂♂ of this species have a very specific social role in the group. The *Flutter-run* is the only means by which the ♂ can be rapidly and positively identified by his ♀♀. As part of serving as a general male display, it also acts as a courtship display.

There are several reasons why male courtship activity in *L. dimidiatus* is not developed beyond increasing the frequency of performance of a display that is used in other social contexts. This species lives in permanent social groups in which there is constant ♂-♀ interaction. Thus a ♀ can easily locate and identify a conspecific ♂. All ♂♂ in the population maintain harems and are sexually active. Thus harem ♂♂ do not have to differentiate themselves from any class of inactive or nonterritorial ♂♂ and indicate their sexual

capability. There are no strong selection pressures for $\delta\delta$ to adopt special activities that would serve to attract and arouse those or other ♀♀ , because a δ is assured of reproductive access to the ♀♀ of his group and to only those ♀♀ .

Why then should we find the development of a special female display and emphasis on female activity during the initial stages of courtship in this species? δ - ♀ intragroup interactions occur frequently throughout the day and usually involve the δ being aggressive to the ♀ . This expression of male dominance is important to each δ 's sexual success, as it enables him to control numerous ♀♀ and prevent any member of his harem from changing sex and reducing the size of his harem (ROBERTSON 1972). A ♀ mates only with her harem's δ . She therefore must identify her sex and differentiate her sexual state from the normal. A ♀ must also act specifically to reduce the δ 's normal social aggressive tendency and stimulate him to respond sexually (TINBERGEN 1954). Sexual monomorphism also presents a δ with the problem of ensuring that his spawning success is not reduced by the activities of other $\delta\delta$.

b. The *T. bifasciatum* Pattern

Breeding $\delta\delta$ of *T. bifasciatum* are competing continuously to attract and induce spawning in ♀♀ that pass by their territories. In promiscuous species, a premium is placed on increased development of sexual signals in $\delta\delta$ and low threshold of male responsiveness to ♀♀ . By such behavior, a δ can maximize the number of ♀♀ he attracts, encounters, and attempts to spawn with (SELANDER 1972). There are a number of types of attraction displays that *T. bifasciatum* $\delta\delta$ use. *Looping* functions in long-distance communication, and indicates the presence and location of the territorial δ . *Quivering* and *Pectoral-fluttering* are better designed for short-distance communication and actual spawning induction. The change in pectoral coloration presumably enhances the visual effect of pectoral movements of the δ when he is moving above the ♀ .

Low thresholds of responsiveness in promiscuous species often result in $\delta\delta$ attempting to mate with ♀♀ , independent of the ♀ 's behavior (e. g., TRIVERS 1972). This may explain the lack of development of a specific sexual color pattern and a complex set of display and activity by female *T. bifasciatum*. Here, ♀♀ need only to move to a δ to obtain a spawning. There is no tendency for $\delta\delta$ of *T. bifasciatum* to be strongly and continuously aggressive to specific ♀♀ , as is normally found in the harem *L. dimidiatus* $\delta\delta$. Aggression by terminal phase $\delta\delta$ of *T. bifasciatum* can in fact be detrimental to their spawning success. We have seen gravid ♀♀ of that species leave such a δ 's territory when attacked by him and spawn elsewhere. Thus, ♀♀ do not have to actively reduce male aggressiveness by any special activity.

c. The *C. parrae* Pattern

As in *T. bifasciatum*, the mating system of *C. parrae* can be characterized by a combination of promiscuity, free female mate choice and continuing male competition for spawnings. In *C. parrae* this has similarly led to the development of specific male sexual displays, persistent male courtship activity, a reduced threshold of male responsiveness to ♀♀ , and the absence of specific courtship displays and coloration in the ♀ .

5. The Duration of Courtship Interactions

While *C. parrae* $\delta\delta$ have to invest much time and persistent effort to induce a ♀ to spawn, spawning can be much more easily triggered in *T. bi-*

fasciatum ♀♀. This difference can be related to differences in both the mechanisms of female mate choice, and the potential risk of predation to sexually active individuals of each of these species.

For a small species such as *T. bifasciatum* that relies strongly on the substrate for shelter, minimizing the time spent in courtship, especially above the bottom, should reduce the risk of predation for a ♀. A lower risk in *C. parrae*, resulting from reduced reliance on the substrate for shelter, could allow the development of more lengthy courtships. Also, in *T. bifasciatum* fairly rapid choice of a mate by a ♀ may be facilitated by the interactions that have occurred between ♂♂ prior to the ♀'s arrival at the spawning ground. That is, larger ♂♂ are predictably fixed in space and defend sites that are probably the best spawning sites, from the ♀'s point of view. In *C. parrae*, if a ♀ is to choose between ♂♂ she must allow sufficient time for a number of ♂♂ to find and compete for her, because ♂♂ are only found in general spawning areas and are not fixed at specific spawning sites in any predictable pattern.

6. The Structure of the Spawning Act

RANDALL (1961) made the suggestion that the rapid up and down spawning rush of labroids and other fishes such as surgeonfishes, "served the purpose of confusing predators", which JONES (1968) interpreted as referring to egg predators. When spawning, all three species that we are considering here need to be sufficiently above the substrate to minimize reef-based predation on their eggs, and to ensure that the eggs are carried off the reef by the currents.

Spawning fishes are exposed to both predators on their zygotes and themselves since the conspicuous nature of sexual displays and activity inevitably attracts predators (MORRIS 1956). The spawning rushes of *L. dimidiatus* and *T. bifasciatum* represent an attempt to reach the most favorable gamete release site and return to the shelter of the substrate as soon as possible. This type of behavior should reduce both types of predation risk in fishes reliant on the substrate for shelter from predators. A rapid spawning rush increases the difficulty with which egg predators locate freshly spawned zygotes.

Fish that clean piscivores might be expected to be immune to those predators' attacks. Thus, one might not expect cleaners to have a spawning rush to avoid being eaten. However, many piscivorous predators attack from below (HOBSON 1968), and would be less able to recognize the specific identity of a small fish such as *L. dimidiatus* that was silhouetted high in the water column. Thus, spawning *L. dimidiatus* do face a risk of being eaten.

We would expect that a substrate-associated species would be more prone to predation when spawning in midwater than those fishes that normally live up in the water column. *C. parrae* normally moves in mid-water and thus has no need to move rapidly up and down to reduce the risk of predation on the pair. This species is not as strongly reliant on the substrate for shelter as *T. bifasciatum* and *L. dimidiatus*.

Egg predation can be reduced by means other than rapid spawning rushes. We have observed terminal phase ♂♂ of some labroids (e. g., *Scarus sordidus*, *Labrichthys unilineatus*, *Bodianus rufus*, *B. diplotaenia*, and, rarely, *T. bifasciatum*) attacking egg predators. A spawning rush would not be expected to develop unless egg predation was important and rushing was the optimal method available to the fish to reduce the likelihood of this risk.

Why should we see the development of a "♂ pushing ♀ up" spawning rise in *C. parrae*, with the ♀ playing such an inactive part in both courtship and spawning? We have discussed the reasons for the development of persistence and lowered thresholds of responsiveness in male courtship in species with a

promiscuous type of mating system, as is found in *C. parrae*. *C. parrae*'s spawning rise probably developed as a result of persistent male courtship leading to the ♂ physically attempting to manoeuvre the ♀ to the best place to release her eggs, i. e., high up in the water column.

B. Sexual Dichromatism

Two major questions can be asked about sexual dichromatism in these fishes: (1) what is the function of a ♂-specific color pattern, and (2) what is the adaptive significance of the variation in the strength of dichromatism among the dichromatic species.

1. The Function of ♂-specific Color Patterns

DARWIN (1871), in developing his theory of sexual selection observed that two separate processes were involved — selection concerned with ♂-♂ interactions and that concerned with ♂-♀ interactions. This distinction has been repeatedly emphasized since then (e. g., FISHER 1930; HUXLEY 1938; MAYR 1972; SELANDER 1972; TRIVERS 1972).

CHOAT and ROBERTSON (1975) reasoned that dichromatism developed when there was free and continuing competition among ♂♂ for access to ♀♀, because the possession of a distinctive ♂-specific color pattern enhanced the ability of a ♂ to attract the attention of conspecific ♀♀. They also pointed out that rapid, accurate identification of conspecific ♂♂ by ♀♀ was an important factor in influencing selection for a conspicuous and distinctive color pattern in the ♂♂ of such species. In those areas of a coral reef in which a number of similar species with similar mating systems are simultaneously sexually active, each ♂ competes with ♂♂ of both his own and other species to attract the attention of conspecific ♀♀. Coral reef fish communities characteristically have a high species diversity (see, for example, GOLDMAN and TALBOT 1976), and contain groups of many closely related species, as well as those with similar sizes and morphologies. This has undoubtedly promoted the development of distinctive ♂-specific color patterns and displays that do more than merely insure the reproductive isolation of species (MAYR 1963). Both natural and sexual selection are important in the development of sexual dichromatism for animals living in an environment well suited to the use of visual communication.

In species with a mating system similar to that of *L. dimidiatus*, there is little selection pressure for the ♂ to develop a distinctive color pattern to attract roving conspecific ♀♀. Other strictly harem labroids that have been investigated, including *L. bicolor* (ROBERTSON unpubl. data), and *Bodianus rufus* (HOFFMAN unpubl. data) are also sexually monochromatic.

Thus far we have dealt with the influence of ♂-♀ interactions on the development of labroid sexual dichromatism, in terms of species and sexual recognition as well as female mate choice. Several sets of observations strongly suggest that in the labroids, ♂-♀ interactions are of far greater importance than ♂-♂ interactions to the development of sexual dichromatism. First, in both monochromatic and dichromatic labroids, ♂♂ can successfully defend territories. Thus a male labroid does not need to be distinctively colored to be territorially competent and compete successfully with other ♂♂. Second, in dichromatic species it appears that the display of the ♂-specific color pattern has little to do with ♂-♂ interactions, including success in territorial disputes. In the temporarily dichromatic wrasse, *Halichoeres maculipinna*, we have observed the loss of distinctive coloration in sexually active terminal phase

♂♂ during their territory border fights. When fighting, sexually active *T. bifasciatum* terminal phase ♂♂ also tend to lose the color elements that they develop most intensely when courting. We have also seen large initial phase ♂♂ of the latter species engage and defeat smaller terminal phase ♂♂ in aggressive interactions during periods of sexual activity. While ♂-♂ aggressive interactions do influence spawning success in the labroid fishes, color plays no significant part in determining the outcome of these interactions.

In *L. dimidiatus*, as well as other strictly harem species, all ♂♂ are derived from ♀♀ by sex change (ROBERTSON 1972; ROBERTSON unpubl. data for *L. bicolor*; HOFFMAN unpubl. data for *B. rufus*). The succession process from ♀ to ♂ is very orderly and is accomplished with a minimum of competitive interactions and disruption within and between social groups. This and year-round breeding results in long-term group stability. In such species there are no periods during the year when ♂♂ are competing to set up breeding territories and attract ♀♀ to a harem, such as one finds in some cyclically breeding birds and mammals. These factors have all contributed to a minimization of female mate choice and thus conditions favoring the development of sexual dichromatism.

2. The Expression of Sexual Dichromatism

a. Effects of Habitat Type

The conflicting necessity of concealment from predators and for species and sexual recognition should influence the type of dichromatism a species exhibits. Consider the costs involved in developing and maintaining the different types of dichromatism. We think that it is reasonable to assume that the cost of developing a pattern that can selectively be turned on and off is greater than developing one that is permanent. Thus, one would predict that temporary dichromatism should be found in species living in environments where the continuous display of a conspicuous signal would significantly increase the risk of predation. Any selective compromise that determined the degree of expression and form of dichromatism must be affected by whether or not the result can be alternatively achieved by the increased use of motor displays.

Let us now consider aspects of the biology of some of the dichromatic Caribbean wrasses and parrotfish, including *T. bifasciatum* and *C. parrae*, to see if variation in the expression of sexual dichromatism in these fishes can be related to potential risks of predation. In Table 5, information on 17 species is summarized. Note that the species that are associated with coral habitats are those with the strongest and most permanently developed dichromatism. Conversely, those that live among benthic plant communities, in midwater, or in sandy environments are less strongly or permanently dichromatic. The differentiation between the color patterns of sexually active ♂♂ and ♀♀ is also less in the plant community species than in reef-living species.

The pattern seen in Table 5 results from the risk of predation to fishes that permanently bear a conspicuous color pattern, being higher if they live away from the refuge of coral. The solid, but extremely cavernous construction of coral allows an individual to rapidly enter a refuge and thus put a physical barrier between itself and a predator. In benthic plant communities, such physical barriers are particularly absent and cryptic coloration becomes more important for prey fishes than in coralline environments. The initial phase color pattern of those species living in plant beds are indeed cryptic, as are the terminal phase patterns. A similar situation prevails in *H. garnoti*, which lives where coral shelter is relatively sparse.

Table 5: Comparisons of the size, habitat types and strength of sexual dichromatism of some Caribbean labroid fishes*

Species	Approximate maximum standard length (mm) ^a	Main habitat ^a (from coral-rich to coral-poor)	Degree of difference ^b between initial- and terminal-phase fish when terminal-phase fish is:	
			Sexually inactive	Sexually active
<i>Thalassoma bifasciatum</i>	120	coral areas	5	5
<i>Sparisoma viride</i>	340	coral areas	4	4
<i>Sp. aurofrenatum</i>	250	coral areas	2	3
<i>Scarus vetula</i>	330	coral areas	4	no data
<i>Sc. croicensis</i>	180	coral areas	3	4
<i>Sc. taeniopterus</i>	270	coral areas	4	no data
<i>Halichoeres pictus</i>	100	coral areas above bottom	1	4
<i>Clepticus parrae</i>	190	mid water	1	3
<i>H. garnoti</i>	170	sand with scattered coral	0	5
<i>H. maculippina</i>	120	coral areas and benthic plant beds	0	3
<i>Sp. rubripinne</i>	320	benthic plant beds near coral areas	1	2
<i>Sp. chrysopterus</i>	280	benthic plant beds near coral areas	2	3
<i>H. bivittatus</i>	150	benthic plant beds near coral areas	1	1
<i>Sp. atomarium</i>	100	benthic plant beds	1	2
<i>Sp. radians</i>	190 (120 ^c)	benthic plant beds	1	2
<i>H. poeyi</i>	150	benthic plant beds	1	1
<i>Cryptotomus roseus</i>	90	benthic plant beds	1	2

^a Data from WARNER and ROBERTSON (in press) and ROBERTSON and WARNER (in press).

^b In considering the degree of difference between the patterns of the two color phases of each species, we have taken into account (a) the relative general conspicuousness of each pattern, (b) differences in the types of color elements each pattern is composed of (bars, stripes, spots, etc.); and (c) differences in the main color(s) each pattern is composed of (red, green, blue, etc.). We have estimated the degree of difference subjectively, by comparing a fish of each phase 3 m distant from the observer. This procedure tends to emphasize the differences between the color phases of large species as compared to those of small species. A scale of 0 to 5 is used for the degree of difference, 0 indicating no difference and 5 the greatest difference observed.

^c Very few individuals actually grow above 120 mm SL.

* See RANDALL 1968, BOEHLKE and CHAPLIN 1968, and CHAPLIN and SCOTT 1972, for descriptions and figures of the color patterns of all these species.

MORRIS (1956) pointed out that many species of animals are unable to offset the increased risk of predation that arises from displaying conspicuous morphological features by being able to conceal permanent structures (see also SELANDER 1972) or, as in the case of fishes, to change color. Of the species that we are considering here, the ability of terminal phase ♂♂ to change color is best developed in those species that live in coral-poor environments (see Table 5).

Size can also have marked effects on the cryptic appearance and distribution patterns of fishes. Only small species are capable of rapidly immersing themselves in the comparatively dense benthic plant stands. Thus, most of the

species that tend to remain continuously in plant-bed environments are small (these include the last five listed in Table 5).

DAVIS and BIRDSONG (1973) reviewed aspects of the behavioral ecology of fishes that live in the water column over reefs. They discussed a number of morphological convergences present in such fishes, including color, which often tends to be violet blue. In *C. parrae*, the ♀♀ are plain blue, and selection for reduced conspicuousness in the midwater environment might explain the lack of strong permanent dichromatism in ♂♂ of that species. *H. pictus* tends to remain removed from coral shelter and the need to reduce conspicuousness could explain the ability of ♂♂ of that species to greatly alter their color from the striped pattern of inactive ♂♂ to one consisting of a lot of iridescent blue in sexually active ♂♂.

Predators sometimes tend to select odd prey (SALT 1967; MUELLER 1971). Since fishes in the terminal color phase of labroids are characteristically in the minority in a population (see WARNER and ROBERTSON in press, and ROBERTSON and WARNER in press, for data on the Caribbean species), it may be especially important for a sexually inactive ♂ to resemble the predominant initial phase morph in a schooling species that relies on schools for protection from predators.

b. Effects of a ♂'s Ability to Alter its Color on Social Interactions

The ability of a ♂ to alter his color pattern may have other advantages beyond reducing predation risks in high-risk environments. We can suggest several advantages:

1. In many species, the terminal color pattern is not particularly conspicuous from a distance, and alteration or intensification during sexual activity may enhance its long-distance communicative qualities (e. g., in *Thalassoma hebraicum* and the Indian Ocean form of *Scarus ghobban*).

2. ♂♂ probably change their patterns to advertize that they are members of a special class of ♂♂, i. e., sexually active as opposed to inactive ♂♂. Such a specific color pattern could also indicate that the bearer was the holder of a spawning territory as opposed to a fish that was unable to obtain one. For example, the scarid, *Scarus croicensis*, has two distinct social classes of initial phase fish. Members of the territorial class have some elements in their color pattern that nonterritorial fishes lack (BUCKMAN and OGDEN 1973).

3. The ability of a ♂ to control the expression of a ♂-specific pattern would enable him to immediately assume the sexual role implied by the exhibition of that pattern at the most appropriate time. Thus, a sexually inactive ♂ in a system similar to that of *T. bifasciatum* could enjoy the protection of the more cryptic female pattern until an opportunity arose to fill a vacant reproductive territory. A permanently dichromatic, sexually inactive ♂, having adopted the conspicuous terminal phase coloration, would suffer the penalties but gain none of the rewards associated with its color until such a vacancy arose. Also, a ♂ of a permanently dichromatic species that took over a newly vacated territory while still displaying the female pattern could suffer in competing with fully colored terminal phase ♂♂ for the ♀♀, who would be less attracted to him during the time it took him to develop the ♂-specific pattern.

4. In some dichromatic species, the external similarity of ♀♀ and initial phase ♂♂ allows those ♂♂ to enter the territories of terminal phase ♂♂ and interfere with the latter's spawning activity (ROBERTSON and CHOAT 1974; CHOAT and ROBERTSON 1975). ♂♂ of dichromatic species that are able to switch off the ♂-specific pattern can similarly gain protection by displaying

the female pattern at appropriate times. For example, we have observed small ♂♂ of *Halichoeres maculipinna* and *Bodianus diplotaenia* enter the territory of a large terminal phase ♂ while displaying the initial phase color pattern, and then rapidly assume the terminal pattern when an opportunity arose to pair-spawn with a ♀ there. *T. bifasciatum* ♂♂ in the process of changing to the terminal phase coloration tend to develop that pattern most strongly when courting ♀♀ and tend to lose it when being attacked by larger, territorial terminal phase ♂♂.

Summary

1. The feeding ecology of a labroid species limits the options available in the evolution of its social system. It determines whether a ♂ can exert continuing control over a set of ♀♀. If a ♂ can, he can maintain a permanent harem.

2. The structure of a species' social system affects the nature of its mating system by determining whether or not a ♀ is able to freely choose which ♂ she mates with. When ♀♀ are able to freely choose, leks develop.

3. The structure of courtship interactions and the spawning act is strongly influenced by:

- a. The degree to which a ♀ can freely choose her mate. Free choice is positively correlated with the presence of greater and more specific male courtship activity and with reduced and less specific activity by the ♀. Conversely, with minimal female choice, reduced male courtship activity and greater female activity is found.
- b. Variation in the probability of predation on the mating pair and its zygotes. A rapid up-down spawning rush minimizes the time that spawning fishes are away from shelter and exposed to piscivores. A spawning rush also increases the difficulty in locating a planktonic zygote concentration by egg predators.

4. The spatial location and timing of spawning is determined by whether a ♀ can freely choose her mate as well as the risk of predation on the mating pair and its zygotes. With free female mate choice, localized spawning grounds develop at sites most favorable to egg dispersal. In areas with strong tidal currents, spawning occurs at that stage of the tidal cycle most favorable to movement of the eggs off the reef.

- a. The development of sexual dichromatism has been promoted by free choice of mates among ♀♀. In dichromatic species, ♂-♀ interactions during sexual activity are of prime importance in the development of the dichromatism and ♂-♂ interactions are of little or no importance.
- b. The degree to which sexual dichromatism is expressed in a dichromatic species can be highly modified and is dependent upon the options available for minimizing predation risks in different environments. Solid shelter is more readily available in coral areas than in seagrass beds, therefore cryptic coloration is more important as an antipredator mechanism to grass-bed labroids. Sexual dichromatism is more strongly and more permanently developed in species that live in coral areas than it is in those species that live in grass beds.

Zusammenfassung

Die Nahrungs-Ökologie begrenzt die Möglichkeiten zur Entwicklung des Sozialsystems bei Lippfischen. Sie entscheidet, ob das ♂ mehrere ♀♀ überwachen kann und dann einen Dauer-Harem aufbaut.

Das Sozialsystem einer Art bestimmt, ob das ♀ sich seinen Geschlechtspartner frei wählen kann. Wenn ja, entstehen Arena-Ordnungen („Leks“).

Balz und Laichakt werden stark beeinflusst von der Männchenwahl durch das ♀. Wählt das ♀, zeigt sie selbst weniger spezielle Aktivitäten, während das ♂ stark und auffällig balzt. Entscheidend ist ferner die Gefahr für das Paar und die Eier, Feinden zum Opfer zu fallen. Ein schnelles Auf-Ab-Schwimmen verkürzt die Gefahrenzeit und verstreut die Eier. Wenn die ♀♀ wählen, entwickeln sich feste Laichgründe und Laichzeiten, die mit starker, seewärts gerichteter Gezeitenströmung zusammenfallen.

Sexualdimorphe Arten sind solche mit Partnerwahl durch die ♀♀. Interaktionen zwischen ♂♂ spielen dafür fast keine Rolle. Auffällige Färbungen kommen eher bei Riffbewohnern, die Verstecke haben, als bei Seegrassbewohnern vor.

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Authors' addresses: D. ROSS ROBERTSON, Smithsonian Tropical Research Institute, P. O. Box 2072, Balboa, Canal Zone, Panama; STEVEN G. HOFFMAN, Department of Biological Sciences, University of California, Santa Barbara, California, U.S.A., 93106.