

PROTOGYNOUS HERMAPHRODITISM AND SOCIAL SYSTEMS IN LABRID FISH

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SUMMARY

Amongst fishes of the family Labridae protogynous sex-change results in the presence of two types of males which arise by different ontogenetic processes: primary males, which are born as such, and secondary males, which are derived from females. An intriguing aspect of this pattern is the variability in the proportions of the two male identities in different species; both primary and secondary males are present in some and primaries absent in others. In this paper comparisons are made between two species of wrasses which differ markedly with respect to their compliments of primary and secondary males.

Primary males are absent in *Labroides dimidiatus*. An elaborate social system, based on permanent dominance relationships between specific individuals, is well developed. Stable social groups are formed which consist of a permanently territorial male and several females. Within the groups there is a size-based dominance hierarchy with the male at the top. This social system provides the basis for controlling sex-change. Pair spawning only occurs, between the male and each female of his group.

In *Thalassoma lunare* there are large compliments of both primary and secondary males. This species, unlike *L. dimidiatus*, exhibits a degree of sexual dichromatism; females and primary males are drab, secondary males are gaudy. This species is not permanently territorial although gaudy males set up temporary territories when spawning. A well organized social system based on individual relationships continuous in time and space does not occur. Two spawning patterns have been observed — pair spawning involving a gaudy male and a single female, and aggregate spawning in which one female and a group of drab males participate. A selection mechanism favouring the development of protogyny in this group of fishes is suggested. This mechanism accounts for the differences in male composition of the two species by considering the presence of two male types as a balanced polymorphism based on different strategies in their socio-reproductive behavior.

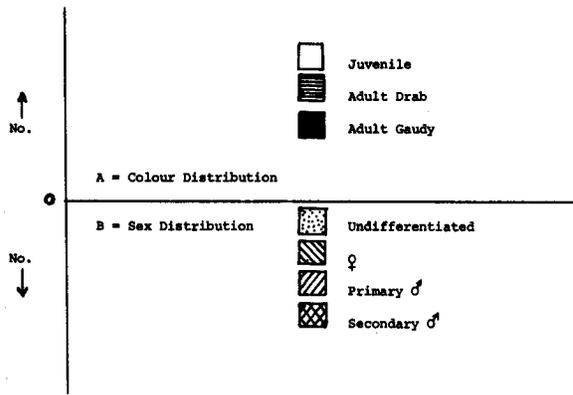
I. INTRODUCTION

Fishes, in comparison with other vertebrates, show considerable variability in their modes of sexual differentiation. This is reflected in diversity of mating systems and reproductive behaviours, a diversity which achieves its greatest expression in shallow water marine species. In the past patterns of sexuality that did not conform to an orthodox picture of separate sexes, equality of sex-ratios and life-long adherence to a single sexual identity were regarded simply as novelties. More recently an awareness has grown of the widespread nature of hermaphroditism in marine fishes, which leads to the logical proposition that the varying patterns of sexuality represent adaptations in terms of life histories.

The purpose of this paper is to consider the adaptive nature of the commonest pattern of hermaphroditism in coral reef fishes, protogynous

hermaphroditism. Such hermaphroditism is sequential, with an individual functioning first as a female and then as a male, but never having both sexes functional at the same time. In many protogynous species there are males that are born as males and show no change in sexual identity during the life cycle.

Protogyny is strongly developed in the Labridae (wrasses), Scaridae (parrot fishes) and Serranidae (groupers), all of which are abundant members of the coral reef fish fauna. Of 30 species of labrids from both tropical and temperate waters examined by various authors (including 19 Great Barrier Reef species by one of the present authors) all have exhibited protogyny (e.g. Choat, 1969; Lönnberg and Gustafson, 1937; Okada, 1962; Oliver and Massuti, 1952; Quignard, 1966; Reinboth, 1957, 1962, 1967a, 1970 and Sordi, 1962). In several others protogyny appears probable (Choat, 1965;



Key to Figures 1 and 2.

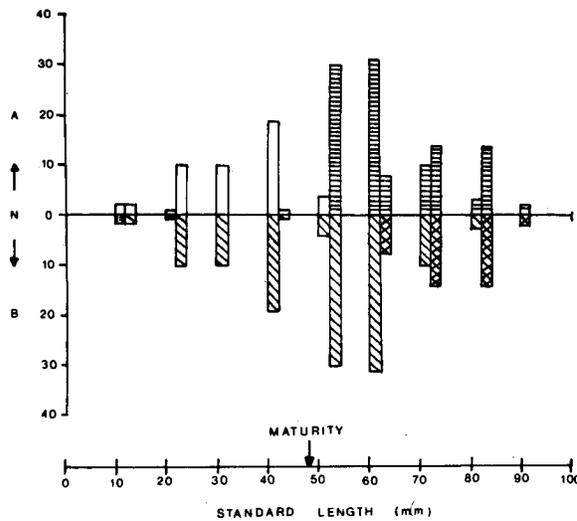


Figure 1. *L. dimidiatus* — Sex and Colour Phase Distribution, Colour Patterns (a) Juvenile — pitch black body and tail with an iridescent blue line running along the upper back and on the upper caudal peduncle and tail.
 (b) Adult — pale brown upper back; whitish belly; a black stripe running from the mouth, through the eye and along the midline, widening posteriorly to form a broad black wedge in the pale blue tail.

Reinboth 1970). The pattern of protogyny in this group conforms to the outline above.

Reinboth (1962) demonstrated the presence of two male types, which he termed primary (males born as such) and secondary (males derived from females), in the labrid *Coris julis*. Secondary males were distinguished by the remnants of ovarian structures in their testes. While in primary males the vas deferens is a large simple tube in secondary males it runs in the wall of the original ovarian lumen as a series of small ducts at the periphery of

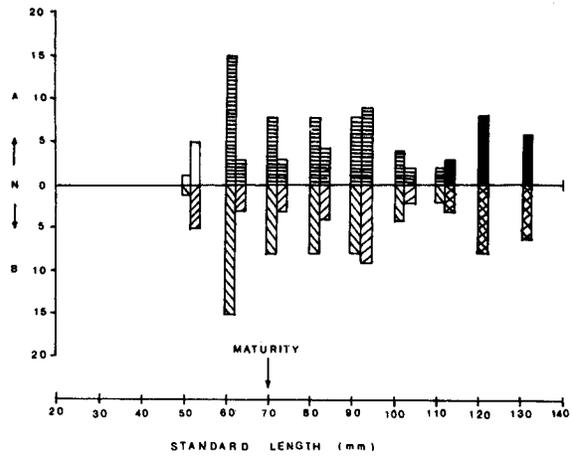


Figure 2. *T. lunare* — Sex and Colour Phase Distribution. Colour Patterns (a) Juvenile — in early juveniles upper half of body green brown, lower half blue grey; a few faint lines radiating from eye (later, body more greenish and this colour extends further ventrally); tail and pectoralis hyaline.

(b) Adult Drab — body green with blue belly; head pinkish with green lines radiating from eye; tail more lunate and is coloured; pectorals blue with pink centres; juvenile characters (e.g. body colours, one black spot on upper back and one on tail base) frequently retained till considerable size.

(c) Adult Gaudy — body and fin colours brighter; tail strongly lunate; head with distinct blue cast overall, when territorially active this blue cast intensifies considerably and spreads over most of the body.

the original oviduct. Furthermore, in secondary males the testicular tissue is often arranged in the same way as the ovarian lamellae and during the early stages of the change from female to male the remains of degenerating eggs are clearly visible in histological preparations. Later Reinboth (1967b) termed this condition of dual male identities Diandry and then divided the protogynous labrids into two main categories — diandric species, in which both primary and secondary males are present, and monandric species, in which all males are secondary (Reinboth, 1970).

In this paper two species of Great Barrier Reef labrids, one of which is monandric and the other diandric, are examined and compared and a hypothesis that accounts for the occurrence of protogyny and for the differences in male composition of these two species is presented.

II. SEX STRUCTURE

The gonads of 207 *Labroides dimidiatus* (Cuvier and Valenciennes) have been examined histologically and show this species to be monandric (Choat, 1969; Robertson, 1972; Robertson, unpub-

lished). In this species the adults of both sexes are identically coloured and a distinctively different juvenile colour pattern occurs. Figure 1 illustrates the pattern of sexual identity and colour phase distributions in 161 individuals.

Thalassoma lunare (Linnaeus) is diandric (Choat, 1969). In this species the juveniles differ in colour from the adults, but not as markedly as in *L. dimidiatus*. Adult *T. lunare* also retain more elements of the juvenile colour pattern and lose them more gradually with age. Amongst the adults there are two colour phases — a duller "Drab" pattern and a more brightly coloured "Gaudy" pattern. Figure 2 illustrates the pattern of sexual identity and colour phase distribution in 89 *T. lunare* of various sizes. Drab adults may be either females or primary males. In the sample obtained all gaudy individuals were secondary males. Underwater censuses indicate that gaudy individuals constitute about 20 per cent of the adult ($\sigma^7 + \text{♀}$) population. Gaudies are restricted to the upper end of the size range.

Several other species of the genus *Thalassoma* examined are also diandric — *T. bifasciatum* (Bloch), *T. hardwicki* (Bennett), and *T. janseni* (Bleeker) (Choat, 1969; Reinboth, 1970). In *T. bifasciatum* the sex-change process is completed while the individual is in the drab phase (Reinboth, 1972) and it is probable, therefore, that some drab male *T. lunare* are secondary males in the process of changing sex and colour phase. The details of the processes of sex-change and colour change of this species in the field have yet to be worked out.

In a number of Great Barrier Reef species of labrid examined by Choat (1969) a strong correlation between male sexual identity and gonad size also exists — the testes of primary males are markedly heavier than those of secondary males. Figures 3 and 4 show the relationship between gonad weight, size of the individual (standard length) and sexual identity in *L. dimidiatus* and *T. lunare* respectively. In the latter the differences between testes weights of primary and secondary males are clearly evident. Both Feddern (1965) and Roede (1972) noted differences in testes size in a variety of males of *T. bifasciatum*. Drab males nearly all had large testes while in gaudy males although both large and small testes were present very few were large — 7 per cent according to Roede. Neither author made determinations of sexual identity of these males but Reinboth (1972) reported that the gaudy phase of this species contains both primary and secondary males. Gaudy males of a variety of Great Barrier Reef labrids and scarids are basically secondary but with a small proportion of primaries (Choat, 1969). In view of the small size of

the sample of gaudy *T. lunare* (17 individuals) primary gaudies may occur but would be very much in the minority.

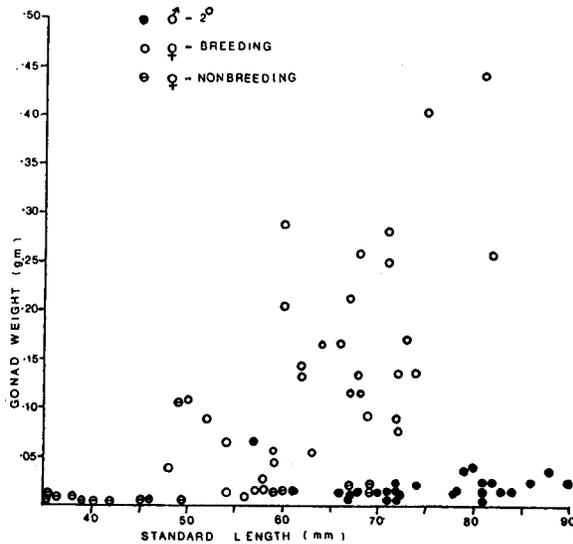


Figure 3. *L. dimidiatus* — Gonad weights.

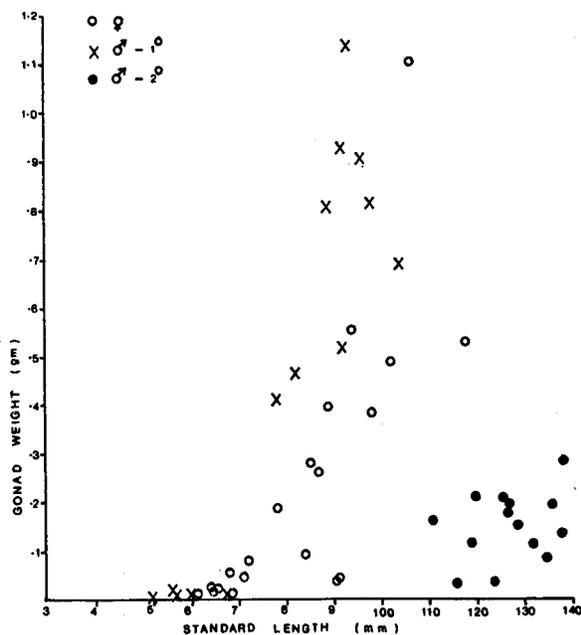


Figure 4. *T. lunare* — Gonad weights.

III. SOCIAL AND REPRODUCTIVE BEHAVIOUR

A detailed field study of the social organization of *L. dimidiatus* at Heron Island, Great Barrier Reef has demonstrated the intimate relationship between the pattern of social organization and the control of sex-change in this species (Robertson, 1972). All individuals of this species, juveniles and adults of both sexes, exhibit territoriality. The elements of this territoriality — attachment to a particular site and hostility towards conspecifics — form the basis of a stable social system in this species. Protogyny and the absence of primary males results in a sex-ratio heavily biased in favour of females, and social groups are formed which consist of a male, usually 5-6 mature females and several juveniles. A juvenile upon settling out of the plankton remains where it is for some time, then becomes more mobile as it approaches and passes the onset of maturity when it may leave the group it originally settled in. Older adults normally remain in the one group permanently. The male's territory forms the spatial basis of the group and all older individuals normally confine their activities to within it. The male is the oldest, largest individual and dominates the females of his group by his active aggressive activities, regularly moving about his territory and visiting and interacting with his females and visiting sites on his territory's border where he is likely to meet neighbouring males. Each individual has a feeding area that forms the focus of its territory; the male's feeding area is situated roughly centrally in his territory. Amongst the females there is a simple dominance hierarchy based on size. The largest female dominates and her feeding area coincides with that of the male. She excludes other females from that area and her territory as a whole is roughly superimposed on that of the male. The feeding areas of the other large females are well separated from each other and are scattered about away from the male/dominant female's area. The smaller females have their areas in between those of larger ones and wherever they are tolerated. Female territoriality is frequently obscured by the dominance hierarchy imposed on it. Females are also more sedentary and aggressively and territorially less active than males and the borders of their territories are not as clearly defined. The spatial distributions and dominance relationships of the older members of the group are stable over long periods of time and the same areas are frequently occupied for a year or more until death. Death produces an instability and results in a reorganization of the group if the dead individual occupied a high position in the hierarchy. In such cases an individual lower in the hierarchy moves into and takes over

the vacant territory and position. This pattern of reorganization is carried through to the highest level — if the male dies the dominant female takes over his territory and group, rapidly changing sex at the same time. This change in turn creates a vacancy and lower level females move up in position. The whole pattern of social organization in this species is thus based on stable relationships between specific individuals with these relationships defined in terms of dominance and spatial distribution. Within the group there is a continual testing and reaffirmation of these relationships by the movement of individuals within the group's area and a high level of social interactions. This can perhaps best be seen in the rapidity with which the behavioral changes associated with sex-change and the reorganization of the group, following the death of its male, occur. Within one hour of the male's death the dominant female is behaving as a male to the other females of the group and is capable of performing the correct behaviour patterns of male reproductive behaviour within a further one hour. In this species reproductive activities are confined to a fairly discrete period shortly after high tide when the current of the ebb tide is at its peak. Spawning occurs within the group's area and the females of a group normally spawn with their male only. All of the many hundreds of spawnings and pseudospawnings (no release of eggs) observed have been pair spawnings, involving a male and a single female, although partial interference between females may occur when several females courting with the same male simultaneously.

The literature provides sketchy information on general behaviour patterns relating to social organization in members of the genus *Thalassoma*. Juveniles of *T. bifasciatum* are usually found in schools while feeding on the bottom (Feddern, 1965) while the adults form loose aggregations. Feeding aggregation of large numbers of adults can be induced by crushing sea-urchins. This species is also sexually dichromatic and gaudy individuals are more solitary and roam more widely than drabs. Aggregations of drab phase adults are maintained during periods of sexual activity. Reinboth (1972) noted that gaudy males of this species hold temporary reproductive territories.

Thalassoma lunare is abundant and widely distributed over Heron reef where it is found in all habitats with a good shelter component. There is some degree of habitat segregation between juveniles and adults in both *T. lunare* and *L. dimidiatus* and although small juveniles are strongly bonded to the substrate the adults move about freely both on and off the bottom. Adults of *T. lunare* often feed in mid-water.

Although no observations have been made on individually marked *T. lunare* over long periods of

time an outline of the pertinent features of the pattern of social organization of this species has been gained. No well defined, permanently defended territories are established, although gaudies hold temporary territories when reproductively active. Short term observations show that individuals have home ranges and that there is a very high degree of overlap in the areas occupied by different individuals of all ages. This overlap appears to be largely independent of social factors and individuals do not attempt to exclude others from their home areas. When not sexually active, adults, both drab and gaudy, move about singly or in loose aggregations with individuals in close proximity to one another. There are few social interactions and the main dominance type interactions that occur, apart from now level sexual-aggressive activity by gaudy males, are low intensity disputes over food. Feeding aggregations as described by Feddern in *T. bifasciatum* occur at natural and artificial food sources. Juveniles behave similarly although the aggregations they form are not as large as those of adults.

A large part of the population of this species at Heron Island occurs on the outer parts of the shallow reef flat (which is exposed at low tide) and the reef slope which shelves off from the reef flat to a depth of 10-15 metres over a distance of about 30-60 metres. Most of the observations on *T. lunare* were made in this area and during periods of sexual activity gaudy males occupy territories on the reef slope, usually on the higher points at the middle level of the slope. Sexual activity is restricted to the same period after high tide as in *L. dimidiatus*. During this period the basic colour of gaudy males is considerably intensified (see Fig. 2). In *T. bifasciatum* the reproductive territories of gaudy males are also temporary and are occupied for short periods each day (Reinboth, 1972). Territories of *T. lunare* are not as strongly associated with the substrate as are those of *L. dimidiatus* and each territorial male swims about very actively off the substrate about 1-2 metres up in the water column, ranging over an area roughly 10-15 metres across. Neighbouring territory holders are frequently engaged in aggressive interactions with vigorous chasings and displaying with erected unpaired fins. Territory borders are ill defined and alternate chasings carry the males well into each others territories. Serious fights between males have not been observed.

During the reproductive period drab adults, as in *T. bifasciatum* (Feddern, 1965), are commonly seen moving about in small schools, as well as singly or in loose aggregations, often near gaudy males' territories. Drabs remain close to the substratum and gaudies react to their presence near their territories, by approaching and swimming ra-

pidly about and above them and giving aggressive and sexual displays. These sexual displays consist of short bouts of rapid fluttering of the brightly coloured pectoral fins, brief bursts of body vibrating and incipient and complete spawning rushes. The drab schools consist of up to several dozen individuals moving in the same direction. They are compact, with the individuals usually less than a body length apart, and the fish at the front of the school are closely bunched up and frequently touching each other. When drab schools approach a gaudy male's territory he responds by approaching and displaying aggressively and sexually and chasing individuals for short distances. If one of the school members flees at his approach or shows marked avoidance it is often vigorously and persistently attacked and chased.

Pair spawning occurs when a gravid female approaches a territorial male and responds positively to his displays and chasings by moving up off the bottom. The male's actions intensify with increased emphasis on sexual displays and he moves to a position immediately above the female as they move up further in the water column together. After a brief pause and a burst of male body vibrating the two fish rush very rapidly upwards at an angle of about 60 deg. for several meters then turn abruptly and swim back down less rapidly, separating as they descend. At the point of the turn milt is released and can be seen as a small pale cloud which fades in a second or two. A similar spawning rush occurs in *L. dimidiatus* although the events and displays preceding spawning are different in this species. Randall and Randall (1963) gave a brief description of pair spawning in *T. bifasciatum* — gaudy males chase drab individuals with fin raising displays and a very short chase of the female is followed by an upward spawning rush.

The second pattern of spawning observed in *T. lunare*, aggregate spawning, has also been observed in *T. hardwicki*. In *T. lunare* aggregate spawning occurs in the same general area as pair spawning, near, but not usually in, gaudies' territories. Conglomerates of the small roaming drab schools form close to the bottom and may enlarge to contain up to several hundred individuals milling around in a small area. Most of the aggregate spawnings observed have been in those large groups and consequently this spawning pattern is more localized than pair spawning. Drabs of all sizes, from maturity on, participate and there appears to be a heavy preponderance of males. Although no large collections were made from these aggregations gravid females can be distinguished on close inspection and were far in the minority. In a gravid female the belly, which is visibly distended with eggs, is green and blends in with the general body

colour. Drab males' bellies are blue grey. In *T. hardwicki* the numerical superiority of males amongst drabs during spawning certainly holds — of 15 drabs collected from a spawning aggregation, 13 were males and only 2 females. The true ratio of drab males to drab females is the reverse of this situation — of 55 drab *T. lunare* collected from a variety of sites outside the spawning period 38.1 per cent were males and 3 of 32 drab *T. hardwicki* were males. Feddern (1965) and Randall and Randall (1963) made pertinent observations on aggregate spawning in *T. bifasciatum* and the latter authors also on the scarid *Sparisoma rubripinne*; a species which exhibits a similar dichromatism to that in *Thalassoma*. In both these species aggregate spawning occurs when large milling aggregations of drabs form. Collections of ripe drab *S. rubripinne* from these aggregation showed a heavy preponderance of males (77 per cent) which contrasted with a ratio of about 1:1 amongst non-spawning drabs. Roede (1972) found a similar situation in *T. bifasciatum* — 86.6 per cent of 127 drabs collected from spawning aggregations were males as opposed to 21.8 per cent males in a sample of 1528 drabs which she considered representative of the population.

In *T. lunare* the schools which form both in and out of the large spawning aggregations are composed either of a single female with an attendant group of up to several dozen males, or a group of males alone. In the former situation the school is much more compact with the gravid female being very closely followed and partly surrounded by males, who are often in body contact with her. Schools composed entirely of males are much more transient than bisexual schools and are much less compact. Apparently the female is acting as a focal point for the formation and maintenance of the school. In bisexual schools the female does not appear to be responding positively to the attendant males and often attempts to avoid them by moving into cover and hiding.

Aggregate spawning is performed by the bisexual schools. As the school moves up off the bottom the males cluster more tightly about the female often jostling her and each other. The female still remains roughly at the head of the school. The school then moves up at a steep angle in a series of hesitating movements followed by a very rapid spawning rush. At the peak of the rush a large cloud of milt is released and the school plunges more slowly back towards the substrate, breaking up as it does so.

Randall and Randall (1963) made careful observations and analysis of motion pictures of aggregate spawning of *S. rubripinne* and showed that the small spawning groups consisted of a single lead female being followed by 3-12 males. The actual

position of female *T. lunare* during the spawning rush could not be determined. Immediately after spawning the female has a noticeably collapsed belly. During the tightening up of the school prior to the spawning rush the only sexual displays made by attendant males are the occasional short bouts of body quivering. No aggressive interactions, fin raising displays or pectoral fluttering displays were observed.

After a spawning rush, whether consummated or not, other drab individuals often converge rapidly on the spawning school and single individuals will make spawning rushes to the immediate area of just released milt and release their own. All male schools frequently perform unconsummated spawning rushes. In large milling aggregations the performance of one aggregate spawning is frequently followed by a number of further rushes in quick succession. Randall and Randall (1963) noted a similar situation in *S. rubripinne*. The performance of aggregate spawning rushes acts as a general stimulus to other individuals in the area.

As noted earlier, gaudy *T. lunare* males often chase individuals from drab schools which approach their territories, individuals which are apparently males. When large spawning aggregations occur near gaudies' territories the territory holders react aggressively to them, more strongly when actual spawning occurs. Randall and Randall (1963) noticed similar aggressive responses of gaudy *T. bifasciatum* and *S. rubripinne*. No participation of gaudies in aggregate spawning was observed by those authors and none has been seen in *T. lunare* and *T. hardwicki*. Drab male *T. lunare* do sometimes participate in pair spawning. Immediately following pair spawning single drabs moving nearby occasionally make incipient and consummated spawning rushes to the site of the pair's milt release. Thus, although pair and aggregate spawning are usually spatially separated, a degree of mutual interference does occur.

IV. DISCUSSION

In a review of the evolution of animal hermaphroditism Ghiselin (1969) proposed that one of the situations in which sex-change should evolve is when one sex benefits from being larger or smaller than the other. A sequential hermaphroditism with a female to male change could be expected if it were more advantageous for males to be larger or older than females. It has been further suggested that protogyny would be favoured in a polygynous species in which breeding amongst males is restricted to the older segments of the male population (Robertson, 1973). Polygyny is used here in its widest sense and refers to any species in which there are fewer males than females in the breeding

population. The male-female relationship or bond may be either very transient or more permanent. Transient bonds are restricted to the brief period of courtship and mating and a male mates promiscuously with a number of different females. Longer term bonds occur when, for instance, a male and a number of females form a stable group with mating being restricted to within the group. The aggressive dominance of older (often larger) males over young males in species which form stable social groups and a combination of male dominance and female choice of mates in species in which males set up temporary breeding territory systems is the basis of polygyny with older males doing most of the mating in many species of animals. The necessary ingredients are clearly present in the social and mating systems described here.

In such a polygynous species early in their reproductive life males would be breeding at a low level and young females, which would be breeding at their potential rate, would thus be reproductively more successful than young males. Later in life the situation would be reversed and older males, by breeding with a number of females, would have greater reproductive success than old females. A protogynist would then, by functioning first as a female and then as a male, produce over its lifetime proportionately more offspring than either normal males or normal females. Through their greater reproductive success protogynists would contribute proportionately more to the next generation than normal females or males and, if this fitness advantage were maintained, would eventually replace them in the population.

The evolutionary development of a social system such as that occurring in *L. dimidiatus* provides the basis for the elimination of primary males through the maintenance and enhancement of the protogynists' fitness advantage. Stable social groups are formed and within each group there are, at the level of the individual, stable dominance-subordination and spatial relationships. The structure of this system enables polygyny to be rigidly enforced by the dominant male of a group. Selection would favour those dominant males that reduced the participation in breeding of subordinate males. The chances of a young male existing undetected in a group and competing effectively with the dominant male would be very reduced. Subordinate males (i.e. young primary males) would have little or no chance of increasing their reproductive success at the expense of dominant males (either secondary or primary). In such a case primary males would be unable to offset the fitness advantage protogynists had and would eventually have been eliminated from the population, as they have been in *L. dimidiatus*.

The life history pattern of species such as *T. lunare* and *L. dimidiatus* can be envisaged in terms

of subordination and dominance phases. In females which did not change sex the subordination phase would occupy the entire life history. In both primary males and protogynists there would be a chance from a subordination phase to a dominance phase, with the subordination phase being male and female respectively. Protogynists achieve their reproductive success by breeding during both phases. If primary males were also able to breed during both phases the evolutionary stage would be set for their continued existence. By subordinate males competing effectively with dominants and lowering their reproductive output the relative reproductive success of protogynists would be reduced and that of primary males increased and a balanced polymorphism (of primary males and protogynists) could result.

In *T. lunare* a highly organized social system based on precise spatial and dominance relationships between individuals does not occur. In the non-breeding phase numerous individuals move about in a unorganized, completely overlapping manner, and aggregations are often formed. Aggressive interactions are minimal and are unrelated to spatial relationships. Subordinate primary males can exist largely undetected and undiscriminated against at this time. This looseness of organization carries over to the reproductive periods when gaudy males set up territories to which females come to spawn. These territories are not well defined in terms of a strong association with substrate features and the territory owners don't have complete control of the substrate area. At this time subordinate primary males can move about in the same general area again with a low probability of detection by gaudy males. The results of apparent detection are vigorous attacks by gaudy males.

Subordinate primary males are thus capable of competing with gaudy males in terms of physical access to females. However, a major problem that drab males have, and which must be overcome if they are to compete successfully, is mate choice by females and the characteristics by which females recognize potential mates. As Selander (1965), in discussing the relationships between the strength of sexual selection and the type of mating system, pointed out (p. 130), in promiscuous mating systems "there is an increased selective premium on morphological, behavioural and physiological characters which function in epigamic and intrasexual interactions directly related to mating". The mate recognition patterns of females of promiscuously mating species, such as *T. lunare*, are involved in these processes and would operate on the broad classification of gaudy = mate, with finer discrimination as a secondary process. In addition Selander (p. 139) observed that in promiscuous (bird) breeders "male competition for territory selects for unusually strong aggressive tenden-

cies and it is not unreasonable to expect that the heightened aggressiveness of males in turn places a strong selective premium on those female morphological and behavioural characters which minimize the probability that the female will elicit aggressive responses on the part of the male". The differences between gaudy males and drab females/males would then tend to be strongly marked and drab males, by (i) not being gaudy and (ii) closely resembling females would, in visual terms, be largely unrecognizable as potential mates to females. The display of gaudy male visual signals (colours, general level of excitement, aggressiveness, body vibrating and pectoral fluttering) by drab males would tend to increase the degree of responsiveness of females to them but would also tend to increase the probability of their recognition and attack by gaudies. Drab males may also be largely incapable of sending all or some of these signals if the ability to do so is an integral part of being in the dominance phase.

This recognition problem is overcome by drab males through their activities which lead to aggregate spawning. Aggregate spawning principally occurs when drabs form large concentrations in which males heavily outnumber females. Because these large concentrations tend to be away from gaudies' territories the probability of a direct choice situation arising is reduced. When a choice does arise it is of many drabs against perhaps a single gaudy, which would help to reduce the relative stimulus value of the gaudy. The stimulation a gravid female receives from the attendant males clustering tightly about her, together with that received from numerous other individuals spawning in close proximity in the large drab concentrations, presumably overrides the effects of the female's mate recognition system by raising her level of excitement to a sufficient point at which she spawns with the male cluster.

As well drab male participation in pair spawnings several other aspects of the drab male — gaudy male competitive interaction would also tend to work in favour of drabs. Aggressive interference by only 1 or 2 gaudies could be rendered largely ineffective by the sheer numbers of drabs in large spawning concentrations. Gaudy males are frequently interacting with one another, sometimes to the exclusion of responses by them to drabs, including soliciting females. On one such occasion an attendant drab male group induced aggregate spawning with the responding female.

Aggregate spawning enables drab males as a whole to compete with gaudy males but places a greater burden in terms of gamete production on drab males than gaudies. In an aggregate spawning

each drab male is competing with up to several dozen others. To reduce the number of drab males participating would reduce the effectiveness of the manner in which drab males overcome female recognition patterns and raise her level of excitement sufficiently. Consequently, for a drab male to compete effectively with gaudy males each drab male must participate in a far greater number of spawnings. Increased sperm production by a drab male would also tend to increase the proportion of the eggs in each aggregate spawning that it fertilized. The results of selection for the capacity of drab males to produce these quantities of gametes are the much heavier testis weights of drab (primary) males as compared to gaudy (secondary) males (see Figure 4).

We suggest, therefore, that a balanced polymorphism, in which the two morphs in balance are primary males and protogynists, has arisen in *T. lunare* and that its primary basis is a loosely organized social system. Such a system allows subordinate males (i.e. drab primaries) to exist indiscriminated against in the population when not breeding and also allows them to compete successfully with dominant males (gaudies, mainly secondaries) during breeding periods. Primary males have thus been able to strike a balance with protogynists by maintaining their relative reproductive success at the protogynists' expense.

Discussion in this paper has been limited to the two species of wrasses on which the most comprehensive information is available. The sex structure of populations of a number of other species of labroid fishes (labrids and scarids) from within the same study area have been examined in some detail and preliminary observations have been made on social and mating systems. The literature also contains a few sketchy outlines of social systems and references to spawning patterns as well as more detailed information on the sex structure of labroid species from other areas, including the Caribbean and Mediterranean. There are strong indications that the two species dealt with here lie near opposite ends of a spectrum. There is a considerable range in the degree of sexual dichromatism, from monochromatic species to species in which the gaudy and drab phases are much more strongly differentiated than in *T. lunare*, for example many parrotfishes. Monandry grades into diandry with varying proportions of primary and secondary males in different species. Correlated with this gradation there appears to be a gradation of social and mating systems with a series extending from the *Labroides* type to the *Thalassoma* type, which includes species, such as many parrotfishes, that form schools during the non-breeding phase.

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