THE BEHAVIOUR OF *HEMIHAPLOCHROMIS PHILANDER*, A SOUTH AFRICAN CICHLID FISH

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INTRODUCTION

Hemihaplochromis philander is commonly found in the fresh water pans and lakes of Zululand, Natal and Rhodesia (Crass 1964, Jubb 1967). This species has also been found in saline estuaries, indicating that it is to some extent euryhaline (Millard and Broekhuysen 1970). They are relatively small, sexually dimorphic cichlids, commonly called "dwarf bream". The males may reach eleven centimetres in length, whereas the females seldom exceed eight centimetres.

A great deal of work has been done on cichlid behaviour and attention is now turning to the physiological aspects of their behaviour. This paper describes the behaviour of *H. philander*, thus providing the necessary prerequisite to the neurological studies already in progress (Ribbink 1970).

MATERIALS AND METHODS

Approximately 300 specimens of *H. philander* were obtained by netting in the fresh water lakes of Natal and Zululand. These fish were placed in aquaria which were 40 cm wide and 40 cm deep, but varied in length from 30 cm to 180 cm. The aquaria contained a sandy substrate and several aquatic plants.

The water temperatures were maintained at 25 (± 1)° C, and the aquaria were lit by overhead fluorescent tubes. Observations were made from behind a screen through a one-way mirror. Tape recordings of verbal commentaries, as well as cinematographic and still photographic records, were found to be useful aids to analysis.

The fish were fed predominantly upon commercially prepared dried food. This was supplemented by marine fish-flesh, and live *Cyclops*, *Daphnia*, and mosquito larvae.

COLORATION AND MARKINGS

In virtually all the literature concerned with cichlid fish, one finds mention of the fact that the Cichlidae are capable of a variety of both colour and pattern changes, which may either be rapid or gradual, and which are the result of their response to both endogenous and exo-

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PLATE 1
A male *H. philander* in aggressive display. The markings on the head and fins are shown clearly.

genous environmental stimuli. *H. philander*, too, have a range of patterns and colours which are described below.

(i) *The Fry and Juveniles*

The fish begin their free-swimming lives as dark fry in which a dense melanophore concentration is found; this is most marked on the dorsal surface of the head, and on either side of the dorsal fin. After seven to ten days, the melanophores become concentrated into vertical bars, and an iridescence begins to develop on the flanks and opercular regions. At the age of three to four weeks, the basic colour of the growing young is a silvery-grey. If frightened, they can rapidly develop eight to ten vertical black bars, and three longitudinal black bands. This appears to be a disruptive colour pattern.

As the young approach maturity, they develop the principal colour of the adults, in which the yellowish olive-green of the dorsal surface blends into the silvery white of the ventral surface. The females always remain paler than the males.

(ii) *The Adult Male*

At the onset of the reproductive phase, the yellowish-olive deepens to a golden-olive colour, and the fins become vividly coloured (Plate 1).

(*a*) The Fins: The dorsal fin develops a black leading edge, an orange trailing edge, and, interspersed between the trailing and leading edges is a pattern of red, blue, green and yellow checks. A black leading and orange trailing edge also appear on the anal fin, but although the checked pattern has the same colour components as the dorsal fin, the dark-coloured blocks are clearly arranged in four or five rows which converge anteriorly at the leading edge. The caudal fin, which also has a checkered pattern, lacks the orange trailing edge and is less conspicuous than either the dorsal or anal fin. The pelvic fins become black anteriorly, and a contrasting white posteriorly. The pectorals are almost colourless.

(*b*) Additional Body Colours: In addition to the fin colours, the male develops a jet black eye-band which runs from the angle of the jaw and traverses the eye across the pupil to the postero-dorsal edge of the orbit. A red eye-spot appears on the antero-dorsal edge of the eye. Dark opercular patches may emerge on the dorso-caudal region of the operculae in several, though by no means all, of the males.

In times of stress, fright, or when defeated in a fight, the nuptial male pales and assumes the disruptive colour pattern. Males which are prevented from dominating a territory are blanched in appearance, but may have faint reproductive or disruptive patterns.

(iii) *The Adult Female*

Relative to the brightly coloured males, female *H. philander* are rather drab. The basic colour lacks the golden depth of the male and tends to be a pale yellowish-white with very little olive green. The blue iridescence which is conspicuous in the young fish of both sexes is always apparent in the females.

With the exception of the yellow analis, the fins of the female lack colour, although the checkered pattern which is typical of the male is faintly discernible on the female dorsal and caudal fins.

At certain periods during courtship and maternal behaviour, the female may develop additional colours. The anal, dorsal and pelvic fins develop dark leading edges. The black eye-stripe, red eye-spot, and opercular patches also appear. These are discussed more fully in the description of courtship and parental behaviour.

(iv) *The Function of the Colour Patterns*

Since the most vividly coloured regions of the fish are also those which are associated with courtship and aggressive motor patterns, it seems likely, as was suggested by Noble and Curtis (1939), that the coloration renders the important movements of the fish more conspicuous. In addition, Baerends and Baerends-van Roon (postscript 1950) are of the opinion that the reproductive colours of cichlids act as important releasers for the prevention of cross-breeding, since similar sexual displays were found in several species of the *Tilapia* they studied.

In *H. philander* virtually all the displays and colour patterns are limited to those of the male. The female, however, does develop a facial pattern which appears to assist in the collection of her brood during maternal care.

The disruptive colour pattern breaks the outline of the fish and thus renders the animal inconspicuous. As the fry begin their lives as small black creatures, one assumes that under natural conditions they would seldom leave shaded areas.

COMFORT MOVEMENTS

The comfort movements which Baerends *et al.* (1950) found in other cichlids and described as chafing, tail-wagging, mumbling, yawning and nipping at the surface were also observed in *H. philander*. But the various forms of "fin-flicking" and "flapping and turning the pectorals" were indistinguishable, and "jumping" appears to be absent. Baerends *et al.* (1950) based their descriptive definition of comfort movements on the following statement: "before the movement is carried out the animal is restless, but after it, it looks as if it feels more comfortable." On the basis of this rather anthropomorphic statement, comfort movements in fish may be described as motor patterns which are performed by the individual without any apparent strong urges (motivation/drives) or stimuli.

FEEDING BEHAVIOUR

Stomach contents of *H. philander* caught in Zululand, and the findings of Crass (1964) reveal that these fish prefer a carnivorous diet. In aquaria they seldom eat vegetable matter.

Two methods of feeding were observed: firstly, feeding upon floating or swimming prey, and secondly, foraging on, or in, the sand substrate. They were found to be extremely aggressive, and often attacked and devoured species of fish which were larger than themselves. Small crustacea, aquatic insects and worms were swallowed whole, but larger prey and fish-flesh were held in the jaws and fragmented by the pharyngeal teeth. The fish would fight amongst themselves over large pieces of food.

To forage from the sand the fish would rise into a vertical position with their heads downward and take in food particles, other organic matter and sand. The sand particles would be shed via the gill orifices and mouth, whereas the edible portions were swallowed.

Very young fry which were just able to swim, would chase and catch moving *Artemia* nauplii. This feeding was found to be a response to visual stimuli, since the fry would attempt to catch nauplii that were enclosed in a test-tube. Adult fish also respond in a similar manner to the visual stimuli provided by food or the movement of potential prey. The early occurrence of this behaviour pattern suggests that it is either an innate response or one which matures before hatching.

After several days in an aquarium, the fish would swim to meet the experimenter in anticipation of food (appetitive behaviour). Young fry (7 to 11 days old) also learned to flock to the pipette that was used to feed them, even when it was empty. These conditioned responses disrupted ongoing behaviour, and made it necessary to use a one-way mirror and screen for behavioural observations.

SCHOOLING BEHAVIOUR

Generally, the activities of the members of a cichlid school are governed by motivations other than reproduction. Furthermore, Baerends *et al.* (1950) have shown that there is a tendency for the fish to " . . . actively seek each other's company".

From the earliest stages of their lives *H. philander* form schools in which they remain until the onset of territorial behaviour. However, in aquaria which were not large enough to support several territorial males, it was found that the smaller mature males remained in the school. A school in which mature males are prevented from territorialism and are forced to practise schooling activities while exhibiting the school colours, is not considered to be a true school since the fish do not "seek each other's company", but are always ready to seize a territory should one become vacant, and continually show aggression while in the school. Under natural conditions these fish probably would not school, but would find themselves a territory.

An interesting observation of Baerends *et al.* (1950) was that adult males could be induced to form schools when conditions of temperature and dissolved oxygen became unfavourable for reproduction. Knowledge of this fact enables one to have some control of the physiological and behavioural status of the fish in the laboratory prior to experimental analyses (Ribbink, in preparation).

TERRITORIAL BEHAVIOUR

At approximately 15 to 16 weeks after hatching, the young *H. philander* males begin to show intention territorialism ("Awakening-movements", Baerends *et al.* 1950). These fish no longer tolerate the proximity of the others in the school. The intention territorial movements of the young fish gradually develop into the more complete movements, and simultaneously the reproductive coloration becomes increasingly vivid. These aspirant territorial males gain dominance, and grow more rapidly than their contemporaries because their elevated status endows them with a priority at feeding time.

Only the adult males of *H. philander* become territorial; the females and juveniles remain in schools. The initial establishment of a territory involves the chasing of all fish from a particular section of the surface waters of the aquarium. Gradually the male begins to defend a bottom area which indicates that the possession of a substrate-area on which to spawn is of greater value than the surface waters. The male now chases all trespassers and potential trespassers from his chosen site. After each chase, he returns from the surface to his bottom territory. The defence of the territory becomes more intensive, and the male's reproductive coloration more marked. The area under the male's jurisdiction is then increased until the territorial boundaries are defined (for further details see Boundary Fighting). Although these boundaries may not always be apparent to an observer or to the fish in the school, they are recognised by the territorial male and his neighbours.

As a rule, the largest and most active male in the aquarium obtains the choice of territories, the second largest male choosing his territory in the sector most remote from that of the dominant male. Several other males may adopt low intensity (pallid) reproductive colours,

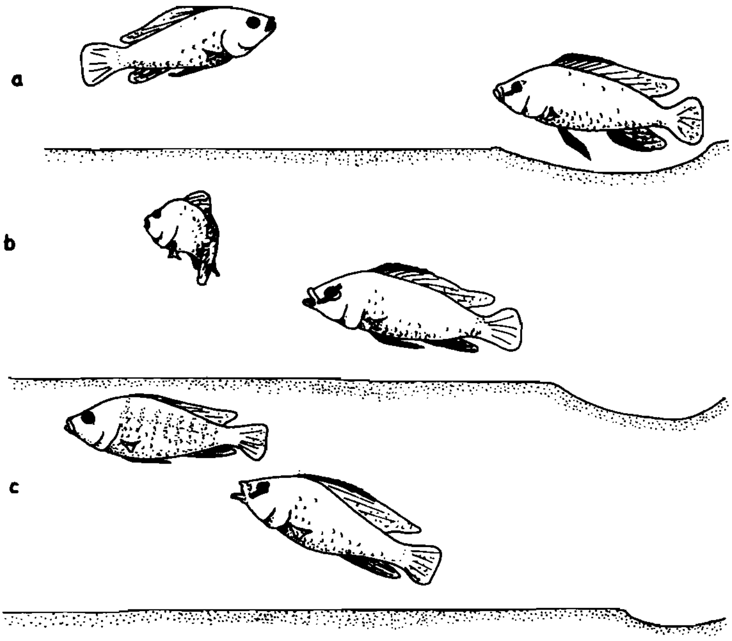


FIGURE 1
Chasing: (*a*) The resident male raises his fins in aggressive display when another fish enters his territory. (*b*) The intruder turns to flee when approached by the resident. (*c*) The resident gives chase.

but these fish are prevented from forming territories by the two largest males. Occasionally these fish may defend surface areas, but generally surface territorialism is loose, insignificant, and quickly suppressed by the dominant fish.

AGONISTIC BEHAVIOUR

The behaviour patterns involved in chasing are initiated by the approach of an intruder which is apparently unaware of the territorial boundaries. The resident male immediately extends all his median fins, depresses the pelvic fins, and remains in a motionless state of alertness termed "aggressive display" (Fig. 1; Plate 1). The duration of the aggressive display may be momentary if the intruder is relatively small and the resident is well established, or as long as six seconds if the intruder is large. A chase may develop from the aggressive display by an infolding of the unpaired fins and by the resident swimming rapidly in the direction of the intruder. Normally, when approached in this manner, the intruder will turn and flee, which in turn encourages the resident to give chase and if possible overtake and bite his fleeing adversary (Figs. 1b and 1c).

In a small aquarium (less than 40 x 40 x 30 cm), the fleeing individual may not be able to escape and may be severely or fatally bitten. If, however, there are more than eight or nine fish in the aquarium then the dominant male may be diverted by other fish, thus sparing the original offender several bites. In a larger aquarium, and presumably under natural conditions, the result of a fight is that the intruder retreats to safety across the territorial boundary, receiving at the most one or two glancing bites. After a chase, the resident returns to his nest at the bottom of the tank.

Chasing will develop only if the intruder turns to flee, but if the intruder remains in the territory, "intra-territorial fighting" will be evoked. Intraterritorial fighting begins in the same manner as chasing: the resident shows aggressive display, which is followed by a rapid approach at the intruder (Fig. 2a). The intruder's failure to turn and flee results in a marked deceleration of approach, and the resident once again raises the median fins (Fig. 2b). From a distance of five to ten centimetres from the intruder, the resident now approaches slowly and cautiously, displaying his full lateral surface with fins outstretched, seemingly to increase his apparent size. Baerends *et al.* (1950) suggest that size may be an important factor in winning a fight. If the intruder also displays laterally and adopts sexual (aggressive) coloration, then a more intensive form of lateral display, in which the branchiostegal membrane is depressed to increase further the lateral surface area, may result (Fig. 2c). The two adversaries now orientate themselves in a parallel head-to-tail position by exaggerated swimming movements. While still in lateral-display, one of the fish will powerfully beat his tail (tail-beating), and thus propel a current of water at the head of his opponent (Fig. 2d). Occasionally, the caudalis of the fish which is propelling the water will slap his adversary in the face.

After several tail-beats and a continued lateral display, one of the fish may swing round and lunge at his opponent in an attempt to bite or butt him in the abdominal region. The opponent dodges by swinging round in a circle and attempts to reciprocate the butt or bite. The result of this is that both fish circle and attempt to land their damaging blows while avoiding the other's aggression (Fig. 2e). This circling, butting and biting may become very fast, fierce and furious, but occasionally the fish pause momentarily and resume their lateral-display and tail-beating, only to plunge back once again into their circling movements, until one fish gives up and flees, adopting the "attitude of inferiority".

The attitude of inferiority in *H. philander* is manifested by the infolding of the fins accompanied by a loss of reproductive coloration (Figs. 1c and 2f). The male in flight may assume either a blanched appearance or the disruptive-pattern, both of which serve to remove the challenge advertised by the nuptial (aggressive) colours. Since the attitude of inferiority does not represent a direct challenge to a territorial male, fish in this dress (i.e. not in sexual colours) are seldom attacked, and appear to have some immunity when crossing a territory, provided they remain in the surface waters. Frequently, the defeated males hang motionless in the surface waters, with their heads pointed upwards in an attitude of inferiority. This form of inferiority is considered to be an attempt to avoid attracting the attention of the despot. This particular behaviour pattern is considered to be an aquarium artefact, since these fish would almost certainly swim away from a dominant resident under natural conditions.

A mirror placed within a territory may evoke continual attacks which last intermittently for several days because the image never turns to flee and fails to adopt the attitude of inferiority, thus constantly representing a challenge to the resident.

BOUNDARY FIGHTING

It appears as though *H. philander* have large territories under natural conditions, because only occasionally was an aquarium of less than 180 cm in length divided into more than one

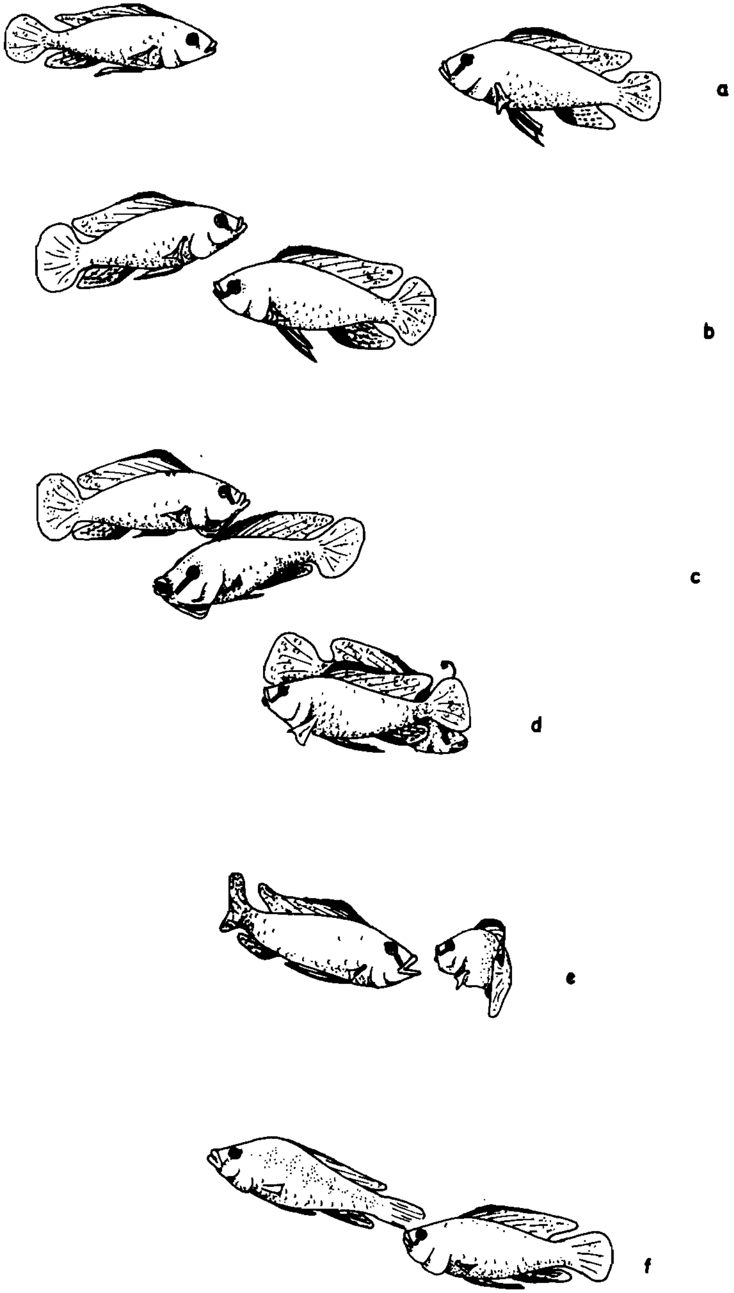


FIGURE 2
Intraterritorial fighting: (*a*) An intruding male causes the resident to raise his fins in aggressive display. (*b*) Both males in lateral display. (*c*) Both males have their branchiostegal membranes depressed in the intense form of lateral display. (*d*) Tail-beating. (*e*) Circling, butting and biting. (*f*) The loser adopts the attitude of inferiority and flees.

territory by fish of five to eight centimetres in length. Since boundary fighting can only take place over the common boundary of two adjacent territories, it was confined to fish in large aquaria.

In intraterritorial fighting the intruder approaches from the surface waters, but in boundary fighting the two adversaries approach one another along the bottom. In response to the approach of a neighbour, the resident male adopts the aggressive display and then swims to meet the encroaching fish. As the two males near one another (25 cm to 35 cm) they begin to "jerk-swim". Baerends *et al.* (1950) were of the opinion that the "jerk-swim" resulted from two conflicting drives, to flee and to attack.

At approximately eight centimetres from the boundary, both fish halt briefly in frontal display. After the brief pause and display, the males alternately charge at, and retreat from one another. The aggressor, while in frontal display, races towards the defender, who backs away for a short distance. As soon as the charge ceases, the roles are reversed; the defender now becomes the aggressor and rushes at his retreating opponent. These mock-charges always halt at a distance of three to four centimetres from the defender. This series of alternate mock-charges usually continues for approximately 40 seconds before one of the fish finds diversion elsewhere, either by displacement foraging or by chasing fish in the school. This diversion terminates the fight and the two fish return to their respective territories. The boundary fights are settled by frontal-displays and mock-charges in which some ground may be lost or gained, but more frequently they appear to serve only as a method of ascertaining and redefining the territorial boundaries.

It was noticeable that the males of six to eight centimetres in length which shared an aquarium of 180 x 40 x 40 cm built their nests as far from each other as possible. The territories of these dominant males described an arc of greatest depth over the nests to their shallowest at the boundary, thus confining the school to the interspace between the two territorial arcs (Fig. 3a). In an aquarium 180 cm long the two dominant fish shared the aquarium equally, but on the rare occasions on which a 120 x 40 x 40 cm aquarium was divided, the division was usually unequal. The larger male would claim 75 per cent of the available space, leaving the smaller territory holder with only 25 per cent of the aquarium (Fig. 3b). In aquaria smaller than 120 cm in length, a single male would dominate entirely.

DISCUSSION OF AGONISTIC AND TERRITORIAL BEHAVIOUR IN MALES

(i) *Agonistic behaviour*

A striking feature of cichlid behaviour is the similarity of the patterns that exist throughout the group. Indeed, not only are these patterns to be found in the Cichlidae, but similar patterns are also found in other groups of fish, such as the Centarchidae (Hale 1956), the Anabantidae (Lissman 1932; Braddock and Braddock 1958; Millar 1964; Clayton and Hinde 1968), the Cyprinidae (Dunham, Kortmulder and van Iersel 1968), and fish found in marine intertidal pools (*Blennius* spp., Gibson 1968). Since fish are restricted in the number of movements that they can perform, it is not surprising to find similarities of behavioural displays which traverse several groups. It is probable that these similarities arose independently in the different groups, but in the Cichlidae the agonistic behaviour patterns are so alike and well defined,

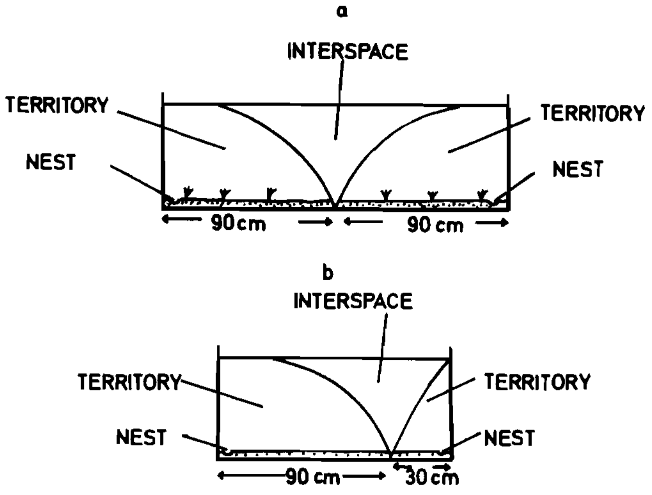


FIGURE 3

(*a*) The two dominant males have territories in which the boundaries are 90 cm from their nests. The non-territorial fish are confined to the interspace. (*b*) In aquaria which cannot accommodate two 90 cm territories, one male will have a territory with a 90 cm radius and another male may, on occasion, maintain a smaller territory.

that it is possible that these behaviour patterns arose only once, early in cichlid history.

H. philander shows all the intra-territorial patterns of other cichlids (Baerends *et al.* 1950; Apfelbach and Leong 1970) except mouth-fighting. Although on two occasions males involved in circling and biting momentarily interlocked their jaws, mouth-fighting is not considered part of *H. philander's* repertoire of aggressive activities because these occasions appeared to be the result of accidents which arose from both fish simultaneously swinging round to bite each other.

In a comparative study of cichlid agonistic and territorial behaviour, Apfelbach and Leong (1970) found that all substrate-spawners of the genus *Tilapia* were specialised in mouth-fighting, whereas mouthbrooders tend to rely more heavily on displaying behaviour whilst fighting. It appears as though these findings may be extended to other cichlid genera since Myrberg (1965) found that mouth-fighting in the oral-brooder, *Pelmatochromis guentheri*, occurred less frequently than in other cichlids, and in the present work *H. philander* was not observed in "mouth-fighting".

The aim of territorial encounters is to obtain, or defend, a territory by means of a series of formalised signals (display patterns or aggressive activities) which are directed at establishing superiority and not necessarily at damaging the adversary. The ritualised patterns appear to provide a series of cues which enable the fish to assess their relative sizes and strengths, and this in turn prompts the weaker or smaller fish to terminate the fight when expedient, thereby avoiding unnecessary damage to itself. For example, mouth-fighting and the subsequent backward and forward pushing are considered to be a means whereby fish may assess their relative strengths and thus determine the winner of a contest (Baerends *et al.* 1950; Apfelbach *et al* 1970).

Although the outcome of encounters between *H. philander* individuals were not determined by mouth-fights, there appeared to be a behavioural scale (Fig. 4) in which size, displays and aggressive activities decided the result of a fight. An aggressive display followed by a rapid approach is sufficient for a relatively small male to become aware of his inferiority and flee, whereas in a better matched pair, the fight may reach the stage of lateral-display before the smaller one flees. Tail-beating, probably a test of relative strengths, will be reached in a fairly evenly matched pair, while for a well-matched pair, the final test will be one of stamina in maintaining the circling, butting, and biting movements. In all cases, the loser adopts the attitude of inferiority and flees. Although Sietz (1940) found that size had no influence on the display of an opponent in *Astatotilapia* males, it is generally agreed that both the size and strength of fish are important factors in winning a fight. Certainly this appears to hold true for *H. philander*. Baerends *et al.* (1950) suggested that fish have a knowledge of their own size. However, it is more likely that fish do not have a knowledge of their own size, but rather that experience has provided them with a knowledge of the sizes of the fish which they would defeat, and which would defeat them in an encounter. This knowledge would influence the course of a fight, and is presumably what prompted Baerends and Baerends-van Roon to make the above suggestion.

Motivation also affects the result of a fight. For example, a male on his home territory will fight with more determination and often defeat a larger fish, while a fish which is outside his territory will behave with less resolution and therefore further increase the advantage of the resident. Hinde (1966) observed that certain territorial animals do not merely respond to the stimuli presented by the appearance of an intruder or trespasser, but that they also have "fighting moods", and when they are in a fighting mood they will show appetitive behaviour for fighting. They also respond to sub-maximal stimuli (domestic cocks and *Betta splendens*), indicating that the threshold of aggression has been lowered. Similarly, *H. philander* males in a fighting mood are more likely to win a fight than a fish which is merely responding to stimuli. Fighting moods and the tendency to flee may wax and wane within the individual, and consequently produce inconsistent results, even in closely controlled experiments. Therefore the ethological scale (Fig. 4) based on responses to the size and strength of an opponent must be viewed as a working model, which does not take into consideration the full effects of motivation.

(ii) *Territorial behaviour*

According to Baerends *et al.* (1950) *Tilapia mossambica* of seven to ten centimetres in length divide an area of 100 x 50 x 50 cm into three of four territories, but one male will dominate an aquarium of 60 x 35 x 35 cm. These authors also found that *Hemichromis bimaculatus* of four to five centimetres in length divide a 60 x 30 x 30 cm aquarium into two or three substrate territories and considerably more mid-water territories. Since *H. philander* of comparable size will not share aquaria of 120 x 40 x 40 cm it appears as though these fish have larger territories for their size than other species. It is possible that under natural conditions individuals of these three species have territories which are commensurate with their

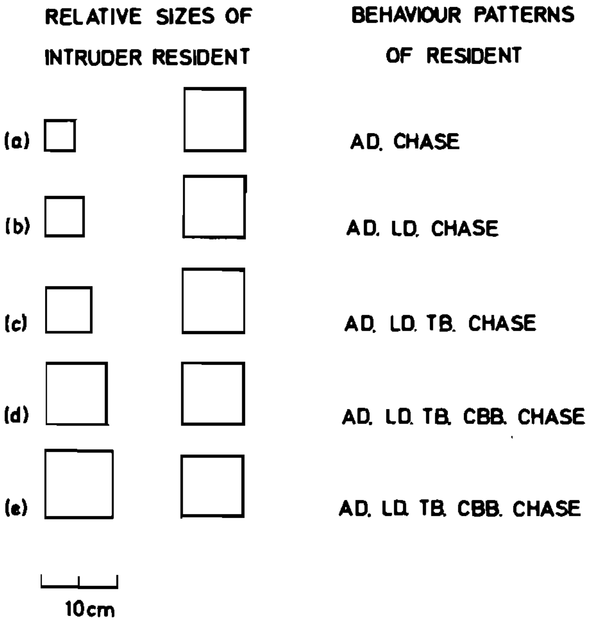


FIGURE 4

A diagrammatic representation of the effect of the relative sizes of the intruder and resident on the extent of an intraterritorial fight. The number of behaviour patterns were found to increase as the size discrepancy of the two fish decreased. Abbreviations: AD – aggressive display; LD – lateral display; TB – tail beating; CBB – circling, butting and biting. The scale refers to the relative lengths of the fish.

size, but that in aquaria *H. philander* will not tolerate a reduction in the size of its territory as readily as the other species.

It is apparent that a certain minimum area must belong to a territorial male before it will tolerate a neighbour. One of the factors which determines the size of a territory might be the maximum distance from the nest that a fish is prepared to chase an intruder. In aquaria *H. philander* (of six to eight centimetres in length) have a maximum chasing distance of 90 cm from their nests. Preliminary observations of *H. philander*, by the use of SCUBA diving techniques, have shown that the distance from the nest to the boundary is also about 90 cm under natural conditions (Ribbink in preparation).

Three patterns found in boundary fights in other cichlids (Baerends *et al.* 1950) are omitted from the boundary disputes of *H. philander*. Firstly, mouth fighting, which does not appear in *H. philander's* intra-territorial fighting, is also absent from its boundary activities. Secondly, the pattern in which other Cichlidae "oscillate" in order to mark their boundaries is absent. Finally, the pattern in which the caudal region is placed against the nest for a "last-ditch" fight, subsequent to the loss of several boundary disputes, is also missing from *H. philander's* complement of boundary patterns.

Hinde (1966) observed that territorial male chaffinches will feed in close proximity to other males, which they tolerate at distances of a few feet or even inches. In *H. philander* as well, the territorial male permits other fish to feed and forage in his territory at feeding time. One presumes that while the fish are feeding, the territorial drive is less powerful than the drive to feed. Once, however, the dominant male approaches satiety, he expels all intruders.

AGGRESSION IN FEMALES

Female *H. philander* do not dominate when in the presence of a male. Females which are isolated from males form straight-line hierarchies (peck orders), in which the largest or most highly motivated female will dominate. The behavioural components employed by females in establishing and maintaining their peck orders are essentially the same as those utilised by males in intra-territorial fighting – lateral display, tail-beating, circling, butting, biting and chasing. Normally, these feminine fights are of shorter duration than the masculine encounters. The fights are terminated by the loser swimming away and being pursued, but the attitude of inferiority is never shown by females.

During courtship the female may assist in the defence of the male's territory, the nest site in particular. Later, during the period of incubation, she may again aggressively defend a small area against intruders of both sexes (see maternal behaviour), but generally the females of this species are not at all territorial.

NEST CONSTRUCTION

The ability of the cichlids to construct saucer-shaped depressions (nests or pits) on the substrate is well known, and in several African lakes, *Tilapia mossambica* nests of more than a metre in diameter are commonly found (Jubb 1967). Nests of *H. philander* may be as large as 12,5 cm in diameter and six centimetres in depth, but they are usually smaller than this.

In aquaria in which two males have territories, the nests are constructed in the regions most remote from those of their neighbour. In aquaria in which one male dominates, the choice of the nest-site appears unimportant, although a preference is shown for sites near plants and corners.

Once the nest site is chosen the male circles over the site, then digs his mouth into the sand. The mouthful of sand is deposited at the edge of the site, and then further mouthfuls are collected and deposited until a hollow is formed which is encircled by a sandy ridge. Roots, plant stems and small stones are forcefully jerked, pushed or pulled out of the way.

The construction of more than one nest by *Cichlosoma meeki*, *Haplochromis multicolor* (Baerends *et al.* 1950), and *Astatotilapia* (Sietz 1940), and the excessive enlargement of nests by other species of cichlids, prompted Baerends *et al.* (1950) to suggest that this was done as an outlet for accumulated energy associated with mating. It was found that the number of nests constructed by *H. philander* males varied according to the circumstances. For example, in a small aquarium (40 x 30 x 40 cm), which was inhabited by one large male and only about five other fish, the entire substrate would be covered by six to nine nests, each of four to six centimetres deep. In large aquaria (180 x 40 x 40 cm), in which there were two territorial males and approximately twenty fish in the inter-territorial space, there were seldom more than two nests of two to three centimetres deep to be found in each territory. It appears therefore, that in large, well populated aquaria the males have adequate opportunity in which to dissipate their reproductive energies through guarding their boundaries, asserting their dominance and frequent attempts at courtship and hence they have little opportunity to dig pits. In small sparsely populated aquaria, the males have little else to do but turn their reproductive energies to nest construction. Although males may construct more than one nest, only one of these is chosen for courtship. Nests are not an essential prerequisite for courtship and spawning, because these fish frequently spawn without a nest.

COURTSHIP

During the initial stages of the formation of a territory, the aspirant territorial males will aggressively chase away intruders of both sexes. However, once the territory is established, the males will readily court.

The courtship patterns may conveniently be divided into two categories: the "inviting-motor-paterns", which are performed outside of the nest area, and which serve to entice the female to follow to the nest; and the "nest-patterns" which apparently play an important role in the synchronisation of the pair.

The Inviting Patterns

Stage I

Females enter a territory from the surface school, and thus elicit the same response as any intruder, i.e. aggressive display followed by the rapid approach of the resident towards the female (Fig. 5a). A gravid female will hold her ground, whereas a casual intruder will flee and be chased. Since a gravid female does not flee, and does not brandish the male breeding dress, the resident male will slow down as if he were going into lateral-display, but instead he raises his fins in a brief aggressive display, followed by a side-shake. The "side-shake" which develops instead of lateral display (the pattern shown to an intruding male), consists of the male swinging into an arched position antero-ventral to the female in such a manner as to expose his flank and colourful fins to her. In this curved position (three to five centimetres away from the female), and facing slightly away from her, he partially retracts his fins and sends a rapid series of undulating quivers through them all, particularly his dorsal (Fig. 5b).

The actions of the female on entry into the territory dictate the course to be followed by the male; for example, should she turn and flee she will be chased; but, if she shows willingness to court, either by remaining stationary and watching the male, or slowly swimming further into the territory while watching the male, then the side-shake is elicited. Should the female turn and move away from the male during his side-shake, then the display ceases immediately, and the male may either attempt to intercept her with another side-shake, or chase her out of his territory. Occasionally a female, while still watching the male, backs away during the display, while the male, in an effort to maintain his position relative to her and to continue his invitation, swims backwards, using his pectorals. Signs of willingness in a female encourage the male to continue to Stage II.

Stage II

The male moves out of the side-shake into a position in front of the female in which he faces away from her, with his head pointing downwards in the general direction of the nest. While in this position, he wags his caudal fin from side to side and quivers his dorsal fin (Fig. 5c). This is the "follow-shake" which is a pattern of short duration (2,5 seconds maximum), and which is considered to be an invitation to follow.

An unreceptive female turns away and releases chasing, or she may be intercepted again by a side-shake. A receptive female will remain watching the male, and may begin to move forwards. This encourages the male to proceed to Stage III.

Stage III

The male now swims with exaggerated caudal movements in the direction of his nest (Fig. 5d). During this pattern (the lead-swim), he may pause to check on the female's progress, but usually he will reach the nest without a pause. A willing female will follow to the vicinity of the nest, and there she will wait, watch, and show displacement foraging. The male, encouraged by the female's presence, enters the nest and proceeds to Stage IV.

Stage IV

This is the last of the invitation patterns. The male enters the nest and, while remaining just above the substrate so that his pelvic, anal and caudal fins just touch the nest, he will quiver all his unpaired fins (horizontal nest-shake; Fig. 5e). As a rule, the female is a little hesitant at this stage and may require frequent invitations. Occasionally the female swims into the nest immediately and thus releases Stage V.

The Nest Patterns

Stage V

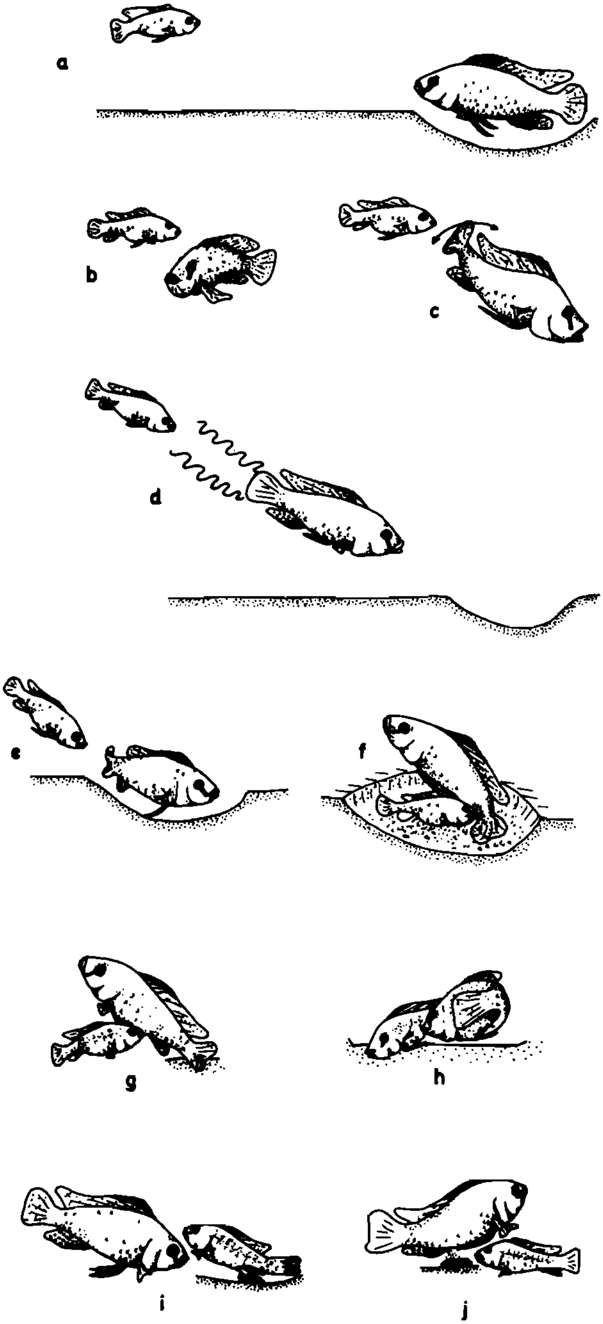
The female's entry into the nest releases the "vertical nest-shake" in which the male raises his head into an almost vertical position, while the caudal region of the body is kept on the substrate by means of a body-flexure in the region of the anal fin (Fig. 5f). As the male rises up from the horizontal nest-shake, the fin-quivering and body vibrations become more marked, which suggests that the vertical nest-shake is an intense form of the horizontal nest-shake. While the male is in the vertical nest-shake, the gravid female may gently butt or prod the male in his abdomen (Fig. 5g).

Stage VI

In response to the "abdominal butt" the male swings round and reciprocates by gently prodding the female's abdomen (Fig. 5h). The female remains in a horizontal position and may occasionally produce horizontal nest-shakes, but never the vertical nest-shake. The pair will now "circle and butt" alternately.

Stage VII

An abdominal prod will eventually induce oviposition. While quivering slightly and moving slowly forwards, the female lays a batch of oval yellow eggs upon the substrate, while the male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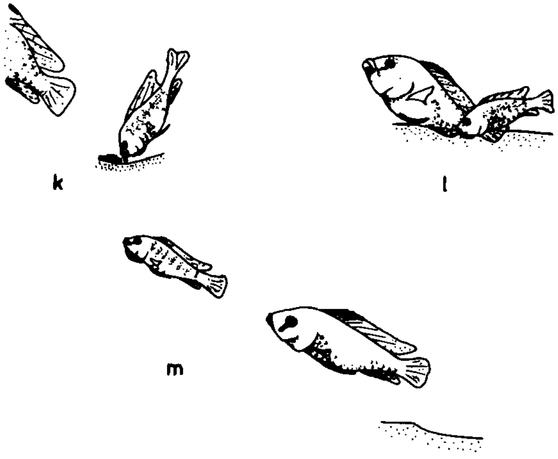

FIGURE 5

Courtship: (*a*) A female enters a male's territory and evokes aggressive display; (*b*) side-shake; (*c*) follow shake; (*d*) lead swim; (*e*) nest shake; (*f*) vertical nest shake; (*g*) the female prods the male; (*h*) the male prods the female; (*i*) the male observing oviposition; (*j*) the female observing fertilisation; (*k*) the female gathers the eggs while the male chases potential intruders; (*l*) the female collects milt from the male; (*m*) the female carrying her eggs is chased off by the male.

looks on (Fig. 5i). As soon as the female stops laying, the male moves over the batch of eggs and ejects a fine shower of milt upon them, quivering gently and holding his caudal region slightly to one side as he fertilises (Fig. 5j). Immediately the male stops fertilising, and often before he has ceased, the female begins to pick up the gametes, and appears to mix and/or manipulate them in her mouth. While the female picks up the gametes, the male reasserts his authority and reiterates his boundaries by chasing all the fish that have encroached on his territory during the period spent in spawning (Fig. 5k).

Once all the eggs are in the female's mouth, the pair begin their butting and circling afresh until all the batches of eggs have been laid. In *H. philander*, two large batches of eggs are laid (15–40 eggs, depending on the size of the female), followed by several smaller batches of usually less than 10 eggs.

Stage VIII

After the female has collected each batch of eggs, and especially after she has collected the last batch, she then appears to collect sperm from the male genital opening. The male rises into the vertical nest-shake, and lays his anal fin upon the substrate so that it is slightly concave. The red and black markings on the anal fin appear to act as "guide-lines" which converge towards the male's genital opening. The sharply contrasted black and white of the pelvic fin also appear to act as a guide. The female follows these guides and when she is over the concavity of the anal fin and near the male's genital opening she performs biting-sucking movements, which are considered to be for the collection of additional spermatozoa. The milt collected in this manner is then mixed with the eggs (Fig. 5l).

Occasionally during this period, the male circles round and begins to give the female abdominal butts. However, if the last batch of eggs has been laid, these attempted abdominal-butts may be met by tail-beats from the female.

Eventually, after approximately 48 minutes (average of 36 observations) from the female's entry into the nest, the female fails to respond to the male's vertical nest-shake, and, having produced frequent tail-beats at his attempted abdominal butts, she is expelled from the territory (Fig. 5m). The male now turns his attention to other females, leaving his last mate to cope with all the parental duties.

DISCUSSION OF COURTSHIP BEHAVIOUR OF *H. philander*

(i) *The Behaviour Patterns*

As a rule, the courtship sequence does not follow smoothly through the eight stages described above. Normally, the male has to repeat his invitations on numerous occasions before the female will follow him. The earlier inviting patterns need to be repeated more frequently than the latter patterns, probably because the gravid female is not quite ready to respond fully.

The most frequently performed invitation is that of the side-shake, which indicates that, at this stage, the female offers most resistance to courtship. The initial invitations of *H. philander* appear to be similar to those of *Haplochromis multicolor*, since both these species remain in a horizontal position while they perform their initial "side-shake" or "quiver", whereas in *Tilapia mossambica* (=*natalensis*) the initial invitation is performed in a vertical position with the head downwards (see Baerends *et al* 1950).

Only during the early courtship, while the female is rather hesitant, is the follow-shake used as a form of encouragement. However, once a sexual momentum is gained, this pattern may be omitted. It is suggested that the tail-wags characteristic of the follow-shake are a manifestation of an intention lead-swim. This contention is supported by the observation that a male in lead-swim may occasionally pause to ascertain the position and response of the female, and, during these pauses, the follow-shake appears again. Although the follow-shake may be an intention lead-swim, it is nonetheless an important inviting pattern which encourages a hesitant female to follow, and only once the female is responding in a positive manner can the male afford to omit this additional encouragement.

Sometimes both the side-shake and follow-shake are omitted, but again these omissions may be made only if the female is willing to co-operate.

The lead-swim is not often omitted from the sequence, but, on occasions when the female is close to the nest, the male may drop down into the nest while performing a side-shake.

Often a female which has followed to the nest is reluctant to enter, and displaces (foraging) in the vicinity of the nest. In response to the female's failure to respond to his nest-shake, the male becomes aggressive, and may dissipate his aggression on potential intruders, but seldom, at this stage, will a male chase away the female he is courting. Normally, but not invariably, the yellow colour of the anal fin of the waiting female may deepen and a dark leading edge may appear. In addition faint vertical bars and longitudinal bands, the diagonal eye-stripe, opercular patches, and a red eye-spot may develop; occasionally, the pelvic fin darkens on the leading edge, whilst the dorsal fin becomes faintly red. These colours deepen as courtship proceeds, and are at their most vivid during spawning.

After a period of 3 to 7 minutes, the hesitancy of the female comes to an end, and she enters the nest, where she begins to respond to the male's nest activities. The male may now have occasion to leave the nest to chase intruders, during which time the female will remain passively in the nest, waiting for his return; however, should an intruder of either sex slip past the male unnoticed, the female will demonstrate her acceptance of the male and his territory by chasing the trespasser. This is one of the few periods of territorialism shown by female *H. philander*. The female's period of waiting in the nest and its environment may be of benefit to the sexual synchronisation of the pair, in that the nest-environment may provide additional sexual stimulation. A further advantage of this period of courtship and intermittent waiting, is that the male reiterates his dominance and boundaries by chasing other fish, thereby decreasing the chances of interruption during spawning.

The ultimate synchronisation of the pair appears to be more dependent on the nest patterns than on the inviting patterns, since the nest activities are not omitted from the sequence, and each nest pattern appears to carry more stimulating weight involving both visual and tactile cues. Seitz (1940) is of the opinion that the butting also provides chemical stimuli. In the nest, the courting individuals watch each other carefully, and maintain a harmony by responding to visual sign-releasers, and possibly pheromones.

In the oral-brooder *Pelmatochromis guentheri*, the females assume relatively bright colours and play an active role in both the inviting and nest patterns (Myrberg 1965), and in substrate spawners, the females again play an active part throughout courtship (Baerends *et al.* 1950). However, in *H. philander*, the female remains passive throughout the invitations, but once in the nest she assumes an active role and, in some instances, wrests the initiative from the male.

The final releaser for oviposition is an abdominal butt from the male, which then watches closely as the eggs are being laid. It is apparent that the appearance of a batch of eggs and/or the shudder given by the female as she lays the eggs acts as a visual releaser to the male (see also, spawning intrusions), which moves over the eggs and fertilises them. Whether an additional chemical releaser is also produced is not known. The female may begin to pick up the eggs before the male has completed his fertilisation, but she usually does not show any signs of haste. Wickler (1962) found that in *Haplochromis wingatii*, the females snap up the eggs before the male has fertilised them. In this species, fertilisation takes place once the eggs are in the mouth of the female when she attempts to take up "egg-dummies" from the male's anal fin, but instead merely collects the male's ejected milt. In *Tilapia mossambica*, the female lays her eggs upon the substrate; the male then moves over the eggs and ejects his milt. The female gathers up both sets of gametes and mixes them in her mouth (Baerends *et al* 1950). *H. philander* follows the same procedure as *T. mossambica*, but also collects milt from the male's anal fin. However, instead of attempting to grasp "egg-dummies" as in *H. wingatii*, the female follows the guide lines to the male's genital opening to gather sperm. It is possible, however, that the orange trailing edge of the male's anal fin may also act as an egg-dummy. This collection of sperm from the anal fin of the male as a supplement to the previous fertilisation in *H. philander*, is a safety factor which, one presumes, was introduced because the female may begin to gather her eggs before the male has completed the fertilisation. In *H. wingatii* the process of fertilisation in the mouth is developed to perfection; the first fertilisation is omitted, and egg dummies have evolved.

(ii) *Sex recognition*

Occasionally, a neutrally coloured male will behave as a female and follow the resident male to the nest, where he will be exposed as an impostor and evicted. This occurs in other cichlids, and Baerends *et al.* (1950) suggested that the exposure of the impostor resulted from his failure to produce the appropriate female pheromones when receiving the abdominal butts. Whether a chemical or behavioural failure causes the sequence to misfire is unknown. However, the willingness of the resident to continue through the early stages of courtship, shows that the role of the behavioural motor patterns is more important than the external appearance of the partner in the early stages of courtship. This was also shown by presenting either a gravid female, a spent female or a non-nuptial male in turn to eight different territorial males in the following manner: each fish was placed in turn into a 500 ml round bottomed flask which was suspended five centimetres above the substrate, and 25 to 30 cm from the nests. In all cases these fish were orientated so as to face the nest and anaesthetised with Sandoz MS 222 so that they would not turn away when the territorial male approached. Without fail the territorial males invited the anaesthetised fish to follow.

When males in nuptial dress were presented to the territorial males they evinced aggression. The anaesthetised male in the flask would retain his nuptial colours, provided that he had not been too severely frightened while the anaesthetic was administered.

From these observations, it is postulated that a resident divides all the fish entering his territory into two categories, those which represent a challenge, and those which do not. All those which might challenge him are treated aggressively, while those which do not threaten to usurp him are courted. The coloration of the trespasser appears to be an important releaser at this stage. The identification of the non-challenging intruders now depends upon their responses to the invitations of the male. The correct responses encourage further courtship, the incorrect responses evoke aggression, illustrating that movement is an important factor in sexual discrimination.

Since the males cannot vacate their territories to find a female, it is likely that, under natural conditions, the gravid females would visit the males in their territories. The males, which are brightly coloured and highly active, would attempt to attract the females, since colour and activity have been shown to play an important role in the selection of a mate (Noble and Curtis 1939).

(iii) *Courtship Abnormalities*

(*a*) *Accelerated Spawning*

Gravid females which have been isolated from males appeared to develop a high specific action potential, so that when reintroduced to a heterosexual community they would immediately follow the nuptial male to his nest, and lay eggs within a minute or two of their meeting. The sudden appearance of the eggs would prompt the male to fertilise them. The female's drive to spawn is so great that if the experimenter pushed the female from the nest with his hand, she would repeatedly swim between his fingers and back to the nest.

These observations indicate that the process of synchronisation is for the benefit of the female only, since the male was quite capable of fertilising the eggs at short notice, and that the displacement behaviour and hesitancy of the female during conventional spawning is an integral part of the process of synchronisation, which is not required if the threshold is already lowered.

(*b*) *Courtship Intrusions*

Shortly after a large male and an oestrous female had been placed in an unfamiliar aquarium, they would begin courtship. Although the male had not had time to establish a territory, or dig a nest in that aquarium, the other males in the tank remained within the school by recognition of their inferior size. When the eggs appeared, however, the smaller males, unafraid of the large male, descended to push between the spawning pair, eject milt, and in some instances devour the gametes. The original spawning couple would unsuccessfully attempt to drive the intruders away and would salvage as many eggs as possible.

Several points emerged from these observations. Firstly, the formation of a territory and dominance in an aquarium are necessary for privacy during courtship. Secondly, the eggs, or the movement of the female during spawning, appear to act as a visual releaser which summons the males in the school. Chemical stimuli would have taken too long to reach these males at a distance of 25 to 40 cm away, and to produce the immediate response shown. Finally, the confinement of the males to a school is artificial, for they have a spawning potential awaiting release.

(*c*) *In-vacuum Activities*

It was observed that isolated gravid females may lay eggs, pick them up, and after several days swallow the eggs. Kühme (1964) found that the young of substrate spawners produced a chemical releaser (pheromone) which encouraged the adult fish to maintain parental behaviour. It is possible that a similar chemical is required to prevent oral-brooders from swallowing their progeny, and that since unfertilised eggs would not promote parental care, they would be swallowed.

MATERNAL BEHAVIOUR

In several oral-brooders the males do incubate the eggs (Liebman 1933; Myrberg 1965; Iles and Holden 1969), but in *H. philander* the male does not participate in any parental duties. Once spawning is over, he expels the female with her eggs from his territory and turns his attention to other females. The female leaves the territory to become a passive member of the school, or to choose a quiet area in which to remain.

A female which is carrying eggs or young is easily distinguished from the others in a school by her lack of participation in certain facets of the behaviour of the school, such as her refusal to take food and also by the expanded branchiostegal membrane, through which the eggs, or young, are visible.

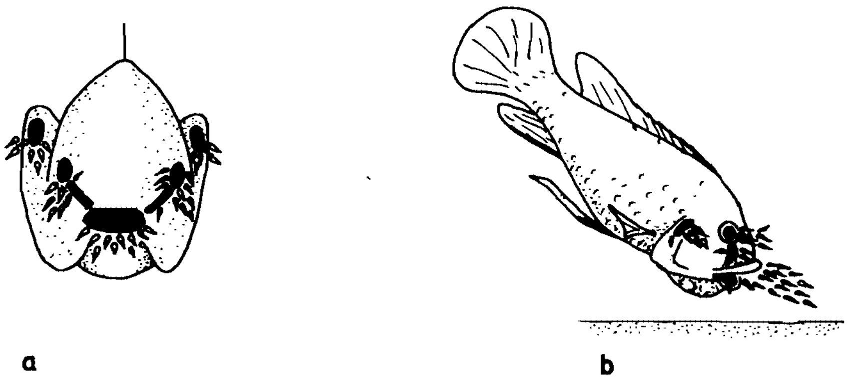

FIGURE 6
(*a*) The facial pattern of the maternal fish showing the markings which attract the fry. (*b*) A female gathering her brood.

Incubation

The number of eggs laid is dependent upon the size of the female; a small fish carries fewer eggs in her mouth than a large female. The incubation at 25 (± 1)°C takes 11–14 days, during which time the female does not feed, and respires in an exaggerated manner which ventilates the fry. Eggs and young may be seen to be moved about during ventilation.

For the first ten or eleven days of incubation, the female adopts the school colours and remains a passive member of the school, or if in isolation, she adopts the disruptive pattern. After the tenth or eleventh day, the female becomes increasingly aggressive and develops new markings: a black eye-stripe, a red eye-spot, a black leading edge to the anal and dorsal fins, the bars and bands characteristic of the disruptive pattern, and the two opercular patches. All fish which approach the female are chased away, and those which are reluctant to leave are encouraged to move away by tail-beats and "push-butts". Proper bites and butts are not possible since the young are in her mouth. Instead, the premaxillae, maxillae, and dentary are held rigidly and pushed into the intruder's flank.

Two females placed together during their last few days of incubation will fight for lengthy periods, pause and fight again continuously through the day. Neither female will show inferiority, and since they are kept together by the confines of the aquarium, this constant urge to drive the potential danger away is never satisfied. In general it was found that maternal fish with fry would attempt to drive away fish which were approximately their own size, but avoided fish that were substantially larger than themselves. It is assumed that under natural conditions, a female which is in the last stages of incubation will seek a quiet area in which to liberate her brood. She may defend this area against intruders of comparable size, but would probably avoid intruders that were larger than she.

The female ejects the brood while swimming backwards, and some of the young turn and attempt to re-enter the mouth immediately. Once all the young are liberated, the female assumes a horizontal position near the young, and, after a brief period of gaping to adjust the branchiostegal membrane, she swims slowly away from the young in an attempt to lead them. Initially the young lie on the bottom, and they can only follow their mother by means of short bursts of swimming. However, after approximately half an hour the fry are more capable of swimming, following, and feeding, which they do as a school. A disturbance which startles the female will cause her to move suddenly, and the young will scatter and hide on the bottom in response to the disturbance, their mother's reaction, or both stimuli. After approximately 10–20 seconds, the school re-forms and approaches the parent who collects her brood. To gather the brood, the female slowly approaches the school (it was observed that a frightened female may approach her brood too rapidly, with the result that the brood scattered and fled to the bottom, thus thwarting her efforts to retrieve them), and then, displaying frontally, the female bobs backwards and upwards at an angle of 25–35 deg. to the horizontal. Baerends *et al.* (1950) found a similar movement in other cichlids which they termed the "calling-movement", because it induces the fry to return to their mother. In *H. philander* the fry swarm to the mouth and other dark areas of the female's anterior region, and are either taken in by their mother or push their way into her mouth of their own accord (Fig. 6).

Experiments with models

In frontal display a maternal fish shows a facial pattern consisting of a black mouth (open), eyes, eyestripe, opercular patches and red eyespot (Fig. 6a). The presentation of this facial pattern to the fry causes them to swarm to the female, and especially to the dark spots. These facial patterns were painted on to models and discs, but dark spots or patches had been omitted from or added to several of these models. In all cases the fry were attracted to the models, and it was found that those models which had the largest number of dark patches subdivided the main swarm into the largest number of minor swarms. The facial pattern on the maternal fish probably serves to subdivide her school of fry.

It was also found that the fry were attracted to objects such as pencils, rubber tubing, painted light bulbs of 5,5 cm diameter, and fibre glass models of fish of various colours and shapes, provided these objects were bobbed up and down at an angle of 25–35 degrees to the horizontal. This slow bobbing movement appeared to be an essential prerequisite to swarming. The fry would then be attracted to the dark spots or patches, against which they would press, presumably in an attempt to enter. If any of the objects, models, or discs were moved too rapidly the fry would scatter and dive to the bottom.

Mutual recognition

The experiments with models, discs and other objects have shown that the fry do not readily recognise their parent by her morphology, and that recognition of movement is of great importance. Apparently imprinting of the mother on the fry does not occur. It was also found that foster parents adopt foreign young of the same species, and that the young readily accept their foster parent.

The reactions of *H. philander* maternal fish to disturbances were basically the same as in other Cichlidae: anticipated danger (something which is not an immediate threat such as the appearance of the experimenter) will result in the recall of the young, whereas an unanticipated danger (sudden, unexpected appearance of another fish in the incubation aquarium) evoked immediate ferocious attack. In response to the maternal fish's sudden movement the fry would scatter and then re-form as a school. The female would return, gather a few of her fry and attack the intruder again. This would be repeated until all the young had been collected, while the intruder was kept at bay. The sudden appearance of a large intruder (12 cm *Tilapia mossambica*) resulted in a rapid gathering of her young and a retreat to a safe distance.

Decrease of maternal care and increased independence of the fry

Initially, a relatively minor disturbance will induce the female to gather her young, but after three to six days, the tendency of the young to respond to the female's "calling movements" will have decreased, and the willingness of the female to summon the young will have virtually disappeared. Normally five to seven days after "hatching", the young could be induced to respond to calling movements made by a model. This indicates that the willingness of the fry to respond lasts longer than the female's willingness to summon them.

DISCUSSION OF MATERNAL BEHAVIOUR

The parental behaviour of *H. philander* is very similar to that of the oral-brooders described by Baerends *et al.* (1950) The eggs are incubated until the fry are ready to be released, and once the fry have been liberated, they may be recalled by the maternal fish, which also protects them against predators.

The calling movement of *H. philander* was shown to be a releaser which prompted swarm ing. Experiments by Baerends *et al* (1950), and Peters (1937) have shown that the young of oral-brooding cichlids respond to models which are moved in the correct manner, and that these young attempt to enter the dark patches or hollows on the models. If a dark patch or hollow was not to be found on the model, then the fry would wander over the surface in search of an "entrance". The young of *H. philander* responded in a similar manner. It is therefore suggested that the facial pattern (Fig. 6a), found on the maternal *H. philander*, facilitates the incorporation of the fry as follows: the young swarm towards the female in response to her "calling-movements", and then congregate in small groups at the dark patches (eyes, mouth, opercular patches) against which they push in an attempt to enter. Those young which have swarmed to the mouth are gathered in, and the female then moves upwards and backwards, leaving the little swarms behind. The swarms follow the dark spots which originally attracted them, but the female will intercept one of these groups by a quick sideways manoeuvre in which she substitutes her mouth for one of the dark spots; at the same time she will move slightly forwards to facilitate the entry of the fry. She will then repeat the performance, and take in another group. This backwards and upwards movement, followed by a sideways and slight forward movement to take in the young, produces the bobbing "calling-movement". The calling-movement is thus probably an intention collecting-movement.

Since the minor swarms which require collection are always above her mouth, the female must move upwards and backwards to substitute her mouth for the dark spots which attract the fry. Thus the facial pattern apparently facilitates the gathering of the young by dividing the main swarm into several groups which may then be conveniently and efficiently taken into the mouth by the collecting movements.

Baerends *et al* (1950) found that vibrational stimuli of an agitated parent (rapid movements) were a prerequisite for the collection of young *T. mossambica=natalensis*. The fry of *Haplochromis multicolor* and *H. philander* can be summoned from behind glass, which eliminates vibrational stimuli as an operative cue. In *H. philander* the rapid movement of the female, or the vibrations caused by this movement, induced the young to scatter and dive. This reaction of the fry appears to prime them for collection, because shortly after scattering they swarm and search for the female (appetitive behaviour prior to entry into the mouth).

Although Noble and Curtis (1939) thought that imprinting occurred in young *Hemichromis bimaculatus*, subsequent work on *H. bimaculatus* and other cichlids (Baerends *et al.* 1950; Greenberg 1963) and the present work on *H. philander*, indicate that imprinting does not take place in the Cichlidae.

SUMMARY

Hemihaplochromis philander is a sexually dimorphic oral-brooding cichlid fish which has agonistic behavioural elements similar to those of other cichlids, except that mouth fighting and boundary "oscillation" are absent. It is suggested that the males have relatively large territories for their size.

The courtship behaviour patterns may be divided into eight stages: the first four entice the females to the nest, and the subsequent behaviour patterns are performed in the nest. The eggs appear to be fertilised while on the substrate and when the female gathers milt from the male.

Imprinting does not occur and the parents are unable to distinguish between their own fry and those of another female.

It is suggested that the facial pattern of the maternal fish facilitates the collection of the fry by dividing the brood into smaller groups.

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