A CONTRIBUTION TO THE UNDERSTANDING OF THE ETHOLOGY OF THE CICHLIDS OF SOUTHERN AFRICA

by

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FRONTISPIECE A male Pseudocrenilabrus philander from Lake Kariba.

"The Linnean categories simply do not cope
with all that living organisms have to offer."

Ethelwynn Trewavas (pers.comm.)

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2. __________ 1972 The behaviour and brain function of the cichlid fish *Hemihaplochromis philander*.
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Resumé

Allopatric populations of Pseudocrenilabrus philander were found to differ in male breeding coloration. These colours are described and attention is drawn to the possibility that male coloration might prevent population hybridisation.

Behaviour of the allopatric populations was studied in the laboratory. The execution of behaviour patterns of the various populations was found to be indistinguishable, and very similar to that of Haplochromis.

Behaviour of P. philander was recorded in three morphologically different natural water bodies. Diurnal activities were found to follow a set rhythm. Though P. philander was shown to have adapted to a variety of habitats they retained their behavioural components in an unchanged form.

Field and laboratory observations are used to propose a behavioural mechanism for the natural regulation of population density.

Although aggression between conspecific territorial Sarotherodon mossambicus habituated so that neighbours could live close to one another, it was found that P. philander are intolerant of their neighbours and are consequently forced apart.

Though the execution of behaviour patterns was apparently identical for all populations of P. philander, field observations indicated that the frequency of performance differed. An experimental procedure was established to quantitatively compare the behaviour of various populations.

As a result of comparative and choice chamber investigations, it is suggested that one of the four populations of P. philander would be unlikely to hybridise with the others if they were to become sympatric. These populations would be kept apart because of colour and behavioural differences.

Differences of egg-size, fry-size, developmental and interbrood periods were also found, providing further evidence of incipient speciation.

Evolutionary divergence of the allopatric populations of *P. philander* is discussed against a background of geological and geographical evidence. Consideration is given to the role of male coloration, ethological barriers and the importance of ethological differences to taxonomy. Behavioural evidence suggests that *P. philander* has closer affinities with the haplochromids than was initially realised. It is concluded that the clinal populations of *P. philander* should not be taxonomically separated, and it is argued that it would be premature to give the Kuruman population an elevated taxonomic status.

CHAPTER ONE INTRODUCTION

The objectives of this work

Inevitably biologists concerned with cichlid fish will at some stage become superficially or deeply entangled in the complexities of cichlid speciation. Such entanglement altered the course of the present research. Originally the behaviour of Pseudocrenilabrus philander was studied before and after brain operations with a view to determining the functions of the different parts of the fore-brain. Progress along these lines had been made (Ribbink 1971, 1972; and both papers are in the appendix). A collecting trip to Lake Sibaya, Natal, revealed that the fish of the lake were different in colour from those of Durban, on which all previous investigations had been conducted. The immediate cause for concern, at that stage, was that the Sibaya fish may have behaved differently from the Durban populations and would, therefore, be unsuitable for the continued analysis of brain function. The original specimens from Happy Valley, in the vicinity of Durban, lived and reproduced in water of less than a metre in depth, whereas in Lake Sibaya territories of this species had been found at depths greater than twenty metres which also suggested that behavioural differences must exist.

Following the discovery of phenotypic differences between two allopatric populations in Natal, further populations were obtained from other regions of the known distribution of the species to establish whether more varieties existed. All populations were found to differ from one another in colour and markings. It seemed that these allopatric populations were either in incipient stages of speciation, or, having already formed new species, were continuing on their divergent paths.

Colours and markings play an important part in cichlid communication. Excellent examples of their role as visual releasers have been given by Baerends and Baerends van Roon (1950); Wickler (1962, 1963); Eibl-Eibesfeldt (1970); (Heiligenberg, Kramer and Schulz (1972) and many others.

Of greater concern to this thesis is the fact that colour patterns probably also serve (in nature) to distinguish one species of cichlid from another. It is noteworthy that an emphasis is placed upon colour and markings during breeding when males, in particular, become brightly coloured. This intensification probably facilitates specific recognition and prevents interspecific hybridisation. Greenwood (1965, 1974) suggested that male coloration in certain cichlids may be an extremely effective barrier to hybridisation. This contention is supported by Fryer & Iles (1972) who observed that colour differences are especially well marked between species which are much alike in other respects.

The role of colour, markings and behaviour is central to the problem of cichlid speciation in the Great Lakes of Africa. The morphological similarity between the different populations of P. philander makes the species an ideal group on which to investigate the validity of the concept of ethological separation due to colour differences. Thus, against a background of suggestive, but inferential, evidence provided by Greenwood (1965, 1974) and Fryer and Iles (1972), it became pertinent to determine experimentally whether the different colour forms of P. philander would behave differently towards one another. The investigation was conducted both in the field and laboratory.

The taxonomic status of Pseudocrenilabrus philander

It is axiomatic that the problems of speciation are akin to those of taxonomy, and it is not surprising that considerable name juggling has occurred since the discovery of this widely distributed and eurytopic cichlid. The species was originally described by Weber in 1897 as Chromis philander, then in 1915 Boulenger placed the fish amongst the haplochromids. This species was widely referred to as Haplochromis philander and is still referred to as such in very recent publications (such as Axelrod 1974).

In 1963 Wickler, found that Haplochromis multicolor, the Egyptian mouthbrooder and northern counterpart of Pseudocrenilabrus philander, differed behaviourally from the other species of Haplochromis he had studied. Furthermore, H. multicolor and H. philander lacked the typical pseudo-ocelli (egg-dummies) of the Haplochromis, possessing instead an orange-red distal patch or trailing edge on the anal fin. On the basis of colour markings and behavioural differences Wickler established a new genus, *Hemihaplochromis*, for *Haplochromis multicolor*. He suggested that *philander* was also of the same genus. At that stage of our knowledge this suggestion seemed justified for even though Wickler had not worked on *philander*, the colour patterns of the two species appeared alike and especially those of the anal fin. Wickler believed that the behaviour of the two species would be similar. Consequently, *Hemihaplochromis* became the accepted generic name for both species.

Since Wickler's publication Trewavas (1973) found further evidence which seems to separate *Hemihaplochromis* from *Haplochromis*. Namely, the whole colour scheme of the two genera are in contrast, and whereas *Haplochromis* have truncate caudal fins, those of *Hemihaplochromis* are rounded. Furthermore the bases of the vertical fins of *Haplochromis* are scaled and those of *Hemihaplochromis* are unscaled.

The replacement of *Hemihaplochromis* as a generic name by *Pseudocrenilabrus*[1] resulted from the disinterment of an error on the part of the late Dr H.W. Fowler. Fowler received a consignment of fish from Durban, South Africa, which though mainly marine included a specimen of *H. philander*. Not recognising the cichlid as such (he thought it to be a member of the Labridae), he named it *Pseudocrenilabrus natalensis* (Fowler 1934). Dr J. Böhlke of Philadelphia Academy of Science showed the specimen to Dr Trewavas when she (Trewavas 1973) visited the Academy in 1963 and suggested that it might be a cichlid. Dr Trewavas recognised it as being *H. philander* (Trewavas 1973). The synonomy of the genera *Pseudocrenilabrus* Fowler 1934 and *Hemihaplochromis* Wickler 1963 had been demonstrated, and according to the Rule of Priority the older name is the correct one.

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[1] *P. philander* has also been referred to as *Haplochromis moffati* and *Tilapia ovalis*. These nomina were considered by Boulenger (1915) to be respectively senior and junior synonyms of *P. philander*. Trewavas (1936, 1973) regards both to be junior synonyms of *Tilapia sparrmanii*, the types of both nominal species being far larger than the largest recorded specimens of *P. philander*.

Jubb[1] (1971a) disliked the generic name Pseudocrenilabrus and suggested, probably in semiserious vein, that behavioural investigations might be able to distinguish multicolor from philander and thus save at least one species from the burden of the generic name. The present studies of the behaviour of P. philander have provided arguments which may justify the retention of the generic name Hemihaplochromis for multicolor (the arguments are discussed on page 190), but, of course, Fowler (1934) ensured that philander would have to remain Pseudocrenilabrus.

Though the generic status has now been established the present findings and the earlier cursory observations of Sterba (1962) indicate that the systematics of the species are a great deal more complicated than first supposed. In addition to the philander found in Natal and Zululand, Hilgendorf (1902) described a similar fish from Otavifontein (a fountain or spring) as Haplochromis luebberti. Then Trewavas (1936) studied material of P. philander from several areas of southern Africa and on the basis of her comparisons divided the species into three subspecies:

1) [2]Haplochromis philander philander (Weber 1897), native to Natal, Zululand and Mozambique;

2) Haplochromis philander dispersus (Trewavas 1936), native to westward - flowing streams from the Orange River northwards to the Congo River, thus including in its distribution South West Africa, Angola, Katanga, the Transvaal, Rhodesia, Botswana and possibly Malawi, and

3) Haplochromis philander luebberti (Hilgendorf 1902), limited in its distribution to Otavifontein.

At a later date (1967)[3] Trewavas indicated in an unpublished communication to Jubb that she was unable to distinguish H.p.dispersus from H.p.philander and suggested that H p.luebberti alone had the requirements of a subspecific category: viz, meristic and geographic identity.

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[1] Jubb (1971a) anticipated Trewavas' paper of 1973 for Trewavas in a communication to Jubb informed him of the impending name change.

[2] Trewavas (1936) used the name Haplochromis for this description, which I have followed.

[3] The generic name in 1967 was Hemihaplochromis.

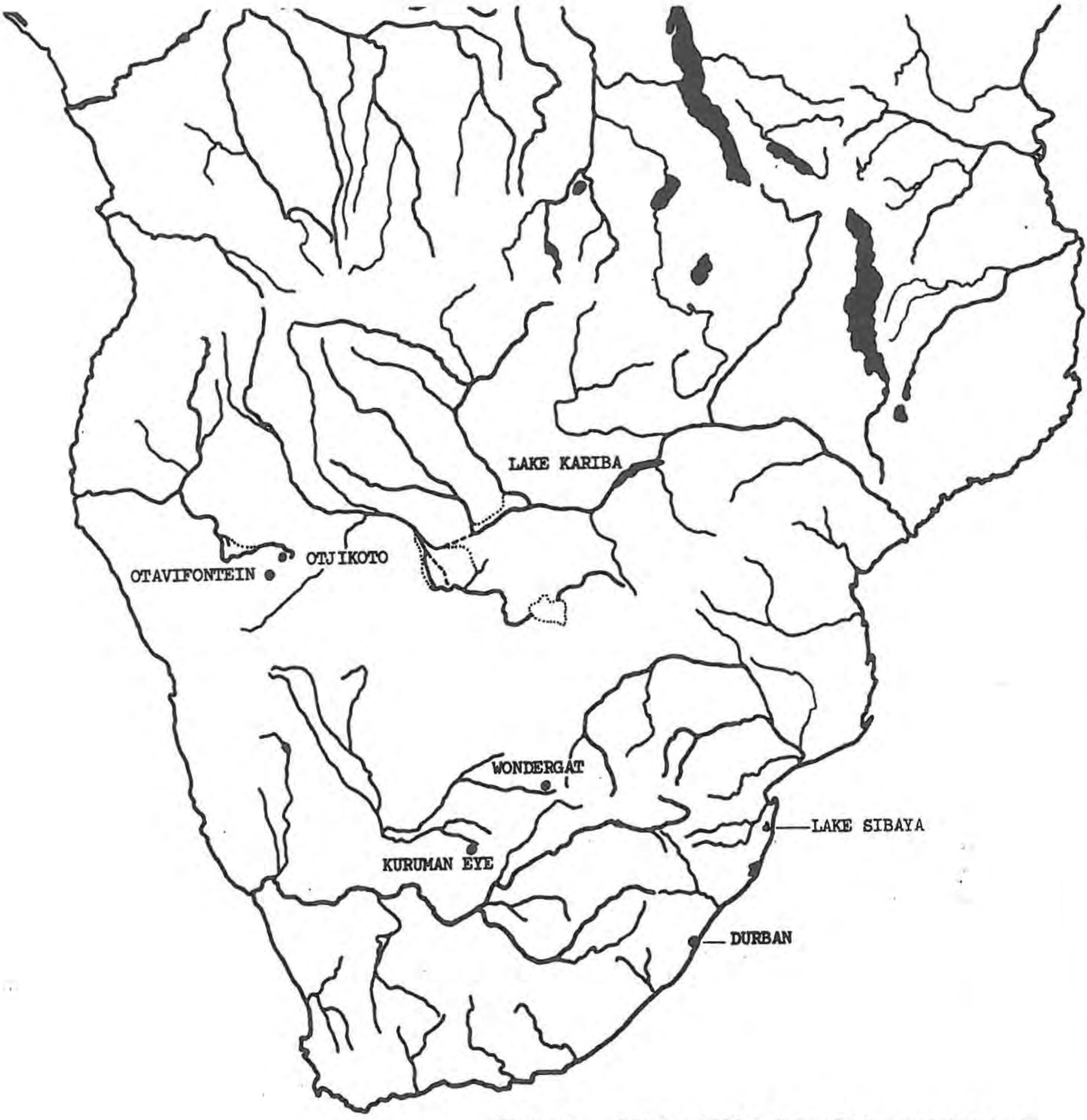

Figure 1 The localities from which populations of *P. philander* were drawn for this study.

In essence the meristic characters of Pseudocrenilabrus philander are such that conventional taxonomists have been unable to draw a clear distinction between the populations of this species.

As it was possible that behavioural studies might provide a clear distinction between the various races, the taxonomic problem was borne in mind throughout this project, and is discussed again later.

Pseudocrenilabrus, its distribution.

Members of the genus Pseudocrenilabrus are amongst the smallest of the African mouth-brooding cichlids, as the common name for philander, 'dwarf-bream', suggests. P. philander is sexually dimorphic with respect to size and colour. Males are the larger more colourful fish which usually grow to about 85mm SL, though Bruton (unpublished data) found a male of 99mm SL in Lake Sibaya and Jubb (pers.comm.) reports that 120mm SL may occur. Females caught in the field for this study were usually 40 to 50mm SL.,but can grow to 80mm SL. At present the genus appears to contain three nominal species though the position may be more involved than this; it has already been implied that P. philander is made up of a complex of distinctive allopatric populations, each of which is, to some degree geographically and reproductively isolated from the others. Furthermore, Loiselle (pers.comm.) has found that P. multicolor, the northern member of the genus, consists of two highly distinctive and possibly specifically disparate populations.

Little is known about P. ventralis, which inhabits the rivers and streams of the Congo Basin, and indeed it is not clear where the distribution of P. philander ends and that of P. ventralis begins. It is possible that P. ventralis and P. philander are the same species. Indeed, the descriptions of P. ventralis, communicated to me by Loiselle, indicate that they are identical to P. philander of Lake Sibaya.[1]

A wide distribution appears to be a feature of the genus and P. philander in particular enjoys an extensive geographical range (fig 1). This species, it seems, is especially versatile at the exploitation of a variety of habitats. It has been found in shallow pans and vleis, in streams, rivers, and in deep lakes and sinkholes. (Penrith, unpublished data, reports that P. philander is found from surface to bottom in the Otjikoto and Guinas (sinkholes), which are 36 and 90 m deep respectively).

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[1] Dr P.H. Greenwood has recently informed me that the long trailing pelvic fin, characteristic of P. ventralis, is absent from the Lake Sibaya P. philander.

It appears that *P. philander* possess a degree of tolerance to salinity. Millard and Broekhuyzen (1970) found males in breeding colours in St Lucia estuary, Natal, at a salinity of 17%.

P. philander occupies a variety of habitats and successfully colonises any water body of favourable physical conditions. Yet *P. philander* has not been found in Lake Malawi even though it enjoys a wide distribution in Malawi, including Lake Chilwa and rivers and lagoons of the Lake Malawi Basin. It lives around Lake Malawi with *Haplochromis callipterus*, but whereas *H. callipterus* enters the lake, *Pseudocrenilabrus* has not been found to do so (Jackson pers. comm., Trewavas 1973). Similarly *P. multicolor* has been found in the Nile, in streams and swamps of Uganda, round the shores of Lake Victoria, and in the shallow reed fringed channel between Lakes Edward and George (Trewavas 1973, Welcomme 1969, Loiselle pers. comm.), but does not enter the lakes. These observations gave earlier workers the impression that the genus *Pseudocrenilabrus* avoided true lacustrine habitats and was essentially riverine or to be found in swamps, backwaters and shallow-lagoons (Trewavas, 1973; Welcomme, 1969). In South Africa and Mozambique, however, *P. philander* is very successful in coastal lakes such as Sibaya and Peté, and also occupies sinkholes in the Transvaal and South West Africa which might be considered as small deep lakes. It is probable that the competition of the endemic *Haplochromis* and other cichlids of the Great Lakes of Africa excludes *Pseudocrenilabrus* from these water bodies. In the more southern parts of Africa which are inhabited by *P. philander* the genus has no close relations, and it seems that in the absence of interspecific competition *P. philander* will lead a lacustrine life.

A description of the colours of the allopatric populations of P. philander

Living specimens of P. philander were obtained from Lake Kariba (28° 30'E, 16° 20'S), Lake Sibaya (32° 42'E, 27° 21'S), Happy Valley (30° 43'E, 29° 48'S) which is a small vlei in the vicinity of Durban, Kuruman Eye (23° 20'E, 27° 12'S), Otavifontein (17° 20'E, 19° 40'S) and one male from Otjikoto (17° 25'E, 19° 15'S). Kuruman Eye and Otavifontein are shallow fountains or springs and Otjikoto is a deep sinkhole. Specimens examined at the sinkhole, Wondergat, were so heavily parasitised that they were not brought back alive to the laboratory for fear of spreading infection.

Ribbink (1971) described the ground colours of freshly caught specimens of the Natal (Durban) population as "yellowish-olive", which differs from the description which has been given below. Probably this difference is due to envrionmental conditions which do affect cichlid coloration. With the exception of the first two colour plates, descriptions have been based upon laboratory held specimens, all of which had lived under what appeared to be identical conditions for at least three months.

The principal ground or basic body colour of P. philander is yellow. The iridescence of the scales, however, has resulted in a colour trichotomy of the populations studied which are: a) the golden-yellow forms of Sibaya and Durban (plate 1); b) the blue forms from Kariba (plate 2), Otavifontein, Otjikoto and photographs of P. philander obtained from Loiselle show that P. philander of Lake Chilwa, Malawi, is also blue, and c) an intermediate coloration of the Kuruman population with pale components of both yellow and blue (plate 3). The fish of Wondergat were examined in the field and were muddy-yellow in colour (these are illustrated on a super 8 mm film submitted to Rhodes University, Zoology Department). As these fish were not maintained in the laboratory it is not known whether they would fit into any of the above groups.

The males of each population are clearly different from one another in respect of body and fin markings. These are illustrated and described by the colour plates and their legends which follow (plates 4 to 10).

Plate 1 The golden-yellow body coloration of a live Sibaya male shortly after removal from an outdoor pond in which it had lived for five months.

Plate 2 The blue coloration of a live Kariba male shortly after removal from the same outdoor pond as the Sibaya fish illustrated by plate 1. The fish had lived in the pond for five months. Note the yellow pectoral fins.

Plate 3 The relatively neutral coloration of a live Kuruman male in an aquarium, showing components of both blue and yellow. Unfortunately this population was not stored in the same outdoor pond as the fish illustrated by plates 1 and 2.

Plate 4 A territorial Sibaya male. Note its golden body coloration, black ventral surface and anal fin. The distally placed orange marking (egg-dummy) on the anal-fin may be absent or faintly visible as a beige marking. By contrast it was occasionally a conspicuous orange. The unpaired fins of the large adults are not chequered as in other populations, but in the young males a chequered pattern, resembling that of the Durban population, is present. As these males grow so the anal fin markings are masked by melanisation.

Plate 5 A Kuruman male. Note the pale, plain body coloration relative to other groups. The dorsal fin is not as vividly marked as that of any other population though the chequered pattern of coloured blocks is more distinct. The anal fin has a well defined pattern of blue and red blocks with a conspicuous yellow-orange trailing edge. A characteristic feature, not shown in this plate, nor by plate three, but which is clearly apparent in certain angles of light, is that the region immediately beneath the pectoral fins and behind the operculae is a pale, bright-blue in sexually active fish.

Plates 6 and 7 (and also the frontispiece)

The Kariba males on these plates show less blue and more yellow than is usually apparent cf. Plate 2). The antero-ventral edge of the anal fin is maroon and forms a band which passes along the ventral edge, through red to the orange colour of the egg-dummy. In sexually active males the entire ventral surface may become crimson and the orange egg-dummy becomes a bright orange-red (see plate 16).

The red and black markings of the dorsal-fin are well defined though the blocks of blue are not clear. The dorsal edge of the caudal fin may also become red in a territorial male, this is a feature which is shared by all groups, but in the Kuruman and Otjikoto males and fin edges are a rufus colour.

Plate 8 A territorial fish from Durban attacking an enflasked male intruder of the same population. The principal coloration of these fish is yellow, which is a coppery-gold dorsally, but paler ventrally and may even give way to a bluish hue (see also plate 19). The anal fin usually has a black leading edge, a chequered red and blue central region and an orange trailing edge (egg-dummy). The dark leading segment to the anal fin was frequently absent or pale, which was especially true of young males.

A distinguishing feature of male and female Durban *P. philander* is the conspicuous red eye-spot antero-dorsal to the black eye-stripe. These eye-spots are usually present, but less marked in all other populations.

Note that the enflasked male is showing an aggressive retaliation which is a behavioural aspect that receives attention later in the text.

Plate 9 An Otjikoto male in lateral display. The blue iridescence is not particularly clear in this reproduction of the colour transparency. Markings and coloration of the Otjikoto male were very similar to those of Kariba specimens: both lacked clear blocks of colour on the unpaired fins having, instead, spots of colour of which blue was the most predominant, and in both a maroon to orange band on the anal fin.

A noticeable difference between the Otjikoto and Kariba males was that the pectoral fins of the Kariba fish are yellow and those of the Otjikoto male are white to transparent. The body depth of the Kariba fish was greater than that of the Otjikoto male. The edges to the unpaired fins of the Otjikoto male were more orange than those of other populations and fringed the entire caudal fin and not just the dorsal edge.

Plate 10 An Otavifontein male. Blocks of coloration on the caudalis and analis are clear. The most distinctive feature of this population is the pale blue background against which the anal-blocks are set.

The populations of female P. philander (plates 11 to 14) are much more difficult to categorise. They are all comparatively drab and lack the numerous distinctive markings of males. All females examined had yellowish anal fins and their bodies were principally yellow. Even in the blue forms, such as those from Kariba, the blue was attenuated by yellow. Blue coloration which occurred in females was a slate blue usually associated with stressful conditions, healthy fish were light yellow to a coppery golden yellow.

Plate 11 A Sibaya female. This is the golden-yellow form. Female P. philander from Sibaya usually appear as pale yellow fish which are more numerous than the colour form presented here. Females may always be distinguished from males by their plain yellow anal fin. P. philander females lack conspicuous colours and markings, though faint red and black markings may appear on the dorsal fin during periods of aggressive and parental behaviour.

It is almost impossible to tell the difference between Sibaya and Durban females (plate 19), though as a general rule the red-eye spot of the Durban population is brightly coloured and conspicuous, whereas the Sibaya females have a less obvious rufus coloured eye spot.

Plate 12 A Kuruman female. These fish are not as deeply coloured as the other populations. They are principally yellow with a slight blue iridescence. The head anterior to the orbit appears foreshortened. The chequered pattern characteristic of the male fins appears to be represented by light, almost transparent areas on the female fins.

Plate 13 Kariba females are yellow with very little blue iridescence. The anal fin is an especially deep yellow. The feature which distinguishes Kariba females from the other populations of females are the inter-orbital bars illustrated on figure 2 below. These markings have not been found in any other population.

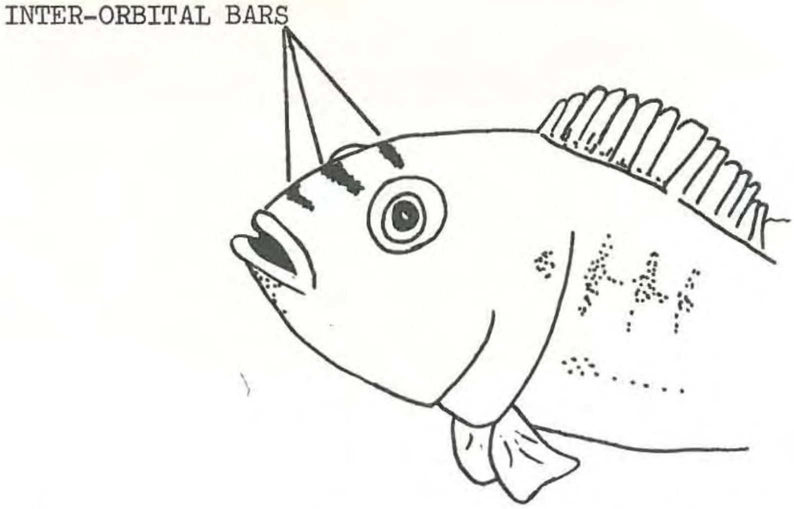


Figure 2 An illustration of a Kariba female (traced from a photograph) to illustrate the inter-orbital bars of pigmentation characteristic of this population.

Plate 14 Otavifontein females also appear as pale and dark yellow forms. The dark form is presented here. In laboratory reared broods the deeply coloured individuals occurred less frequently than the pale forms

These females could be distinguished from the other populations by the blue - white spots on the unpaired fins. The antero-dorsal part of the dorsal fin frequently had a green sheen to it which appears only faintly on this plate.

In this plate the red coloration of the dorsal fin can be seen.

CHAPTER TWO BEHAVIOURAL STUDIES

Many of P. philander's behaviour patterns have already been described (Ribbink 1971). Those behaviour patterns which were not previously described will receive attention below. Detail has also been added to the earlier work where it was found to be superficial. The behavioural terminology of Ribbink (1971) will be followed in this thesis, except that "circling, butting and biting" is replaced by the term "fins-in" (see page 21).

Most of the diagrams provided are line drawings taken from super-8mm film run at 18 frames per second. Occasional use of a zoom lens has resulted in figures of slightly different sizes.

Frequently, behavioural work of an experimental nature performed in one laboratory cannot be repeated in another. This is often because behaviour patterns measured or counted were so inadequately defined by one worker that they could not be understood by another. Therefore, where necessary and appropriate, I have explained how behaviour patterns were defined and counted.

Aggressive behaviour

Aggressive behaviour patterns need no further description, except that mouth fighting (plate 15), which Ribbink (1971) considered to be absent from P. philander's behavioural repertoire, was found to occur frequently. The manner in which jaws were locked during mouthfighting appeared very similar to that of other cichlids (Baerends and Baerends van Roon, 1950; Apfelbach and Leong 1970). While pulling and pushing with their jaws locked P. philander also attempted to chew their opponents. It appears that in addition to being a test of relative strength (Baerends and Baerends van Roon, 1950), mouthfighting may damage and discourage one of the contestants.

Several of the aggressive behaviour patterns have been illustrated (plates 16 to 18) to supplement the earlier descriptions (Ribbink 1971).

During experimental analyses it was sometimes difficult to determine whether a fish was in aggressive display or lateral display. In both forms of behaviour the fins are fully extended. The difference is that those fish which do not orientate themselves laterally to their opponents are in aggressive display. Tailbeats were counted as follows: one stroke of the tail in the direction of the adversary was a single tailbeat. In many experiments a sheet of glass, or the glass walls of a flask, separated opponents. Under these circumstances bites often fell short of their targets - the aggressor bumping its snout against the glass. Both open mouthed bites and bites interrupted by the glass before the mouth was properly opened (intention bites) were counted, each being "one bite". When a fish in lateral display swings round to bite its opponent it folds its fins in. Hence circling, butting and biting (Ribbink 1971) is more concisely described as "fins-in", in this thesis.

Plate 15 Two Rhodesian (Kariba) males with their jaws locked in a mouth-fight.

Plate 16 Two Rhodesian (Kariba) males in an intraterritorial fight. Note the crimson chin and extended fins of the fish in lateral display furthest from the camera.

Plate 17 A Sibaya male in lateral display and tail-beating. Note its conspicuous "egg-dummy".

A male in disruptive coloration is hidden behind the *Vallisinaria* in the centre of the picture.

Figure 3 Aggressive hanging

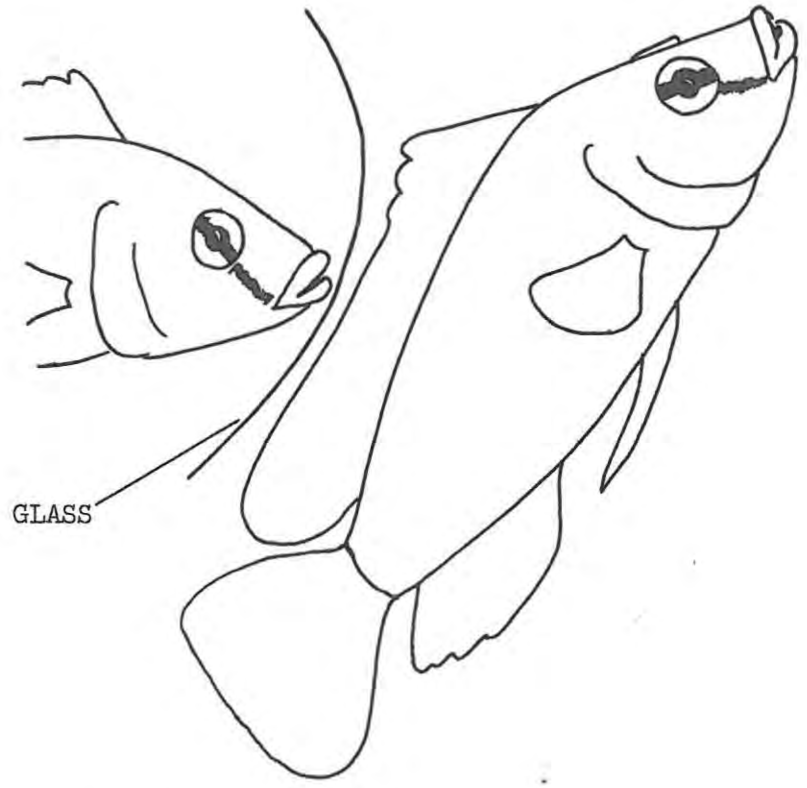


Figure 4 Hanging (submissive)

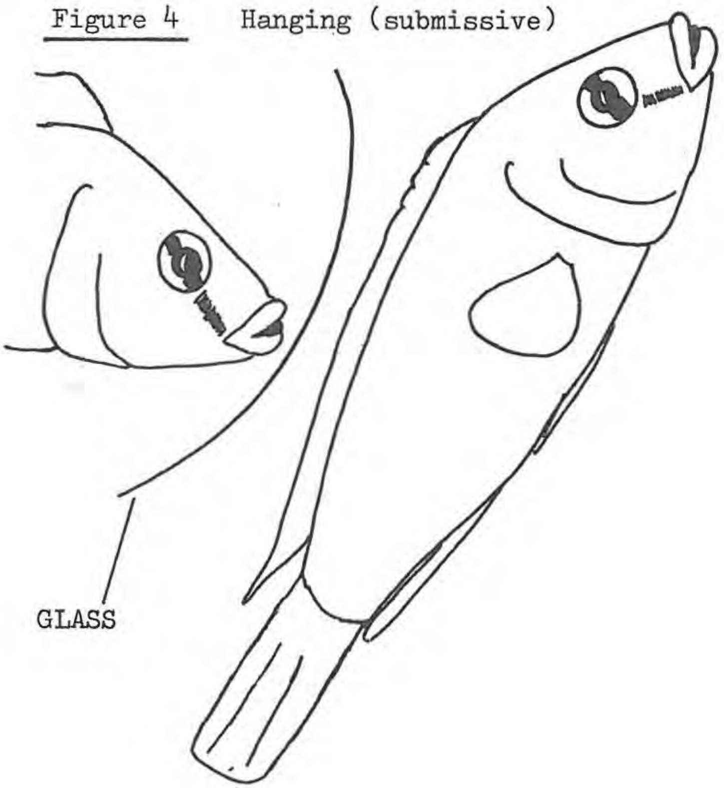


Plate 18 A Rhodesian male circling to bite its opponent.

Conflict behaviour

Two behaviour patterns not previously described are the conflict patterns, aggressive hanging and hanging. In aggressive hanging the male orientates itself to an intruder, usually an enflasked intruder as in fig 3, and hangs motionlessly in front of the intruder with its fins erect and head pointing upwards. Usually the sexual coloration of a male, in "aggressive hanging" fades.

Hanging is a more submissive form of behaviour. The fins are retracted and the sexual coloration is more blanched (fig 4). This behaviour pattern is similar to the symbolic inferiorism of female Hemichromis bimaculatus during the early stages of pair formation (Baerends and Baerends van Roon, 1950).

The response of a territorial individual when challenged by an intruder is the expression of the balance of two drives: to attack or to flee (Tinbergen, 1951; Thorpe, 1964). Between the two extremes, attack and flee, are a series of ambivalent patterns (an ambivalent behaviour is one in which intention movements or displays, appropriate to two tendencies, are combined into a single pattern which contains components appropriate to both, Hinde 1970).

The aggressive components of aggressive hanging are the orientation of the resident to the intruder and the extension of the fins. The intention to flee is shown by the loss of colour and upward pointing of the head, which is a submissive trait. Hanging, with the fins folded in, shows a greater tendency to submission since it has lost a further component of aggression.

Courtship and spawning behaviour

The account of courtship and spawning by Ribbink (1971) is adequate, but requires greater attention to detail and minor correction at several points. Later in this thesis (chapter seven) arguments are presented to illustrate the behavioural affinities of P. philander with the haplochromids. This is of interest because when Wickler (1963) erected the genus Hemihaplochromis, he did so as a result of observations which had shown that Haplochromis multicolor, as it was then known, behaved in a manner intermediate to the Hemichromis-type and "true" Haplochromis-type. It is my contention that P. philander has closer ties with the haplochromids than Wickler (1963) realised. Some of the evidence in support of my arguments (see chapter seven) is supplied by the behavioural descriptions below. These behavioural descriptions of P. philander are compared with those of Haplochromis burtoni, which is one of the species studied by Wickler (1962, 1963, 1968).

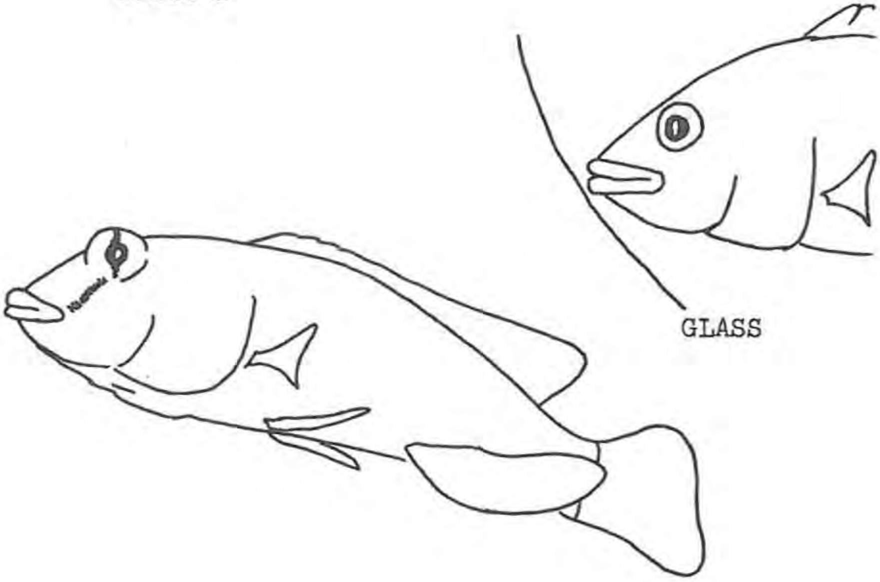
In the first set of illustrations (fig 5), the anal fin is displayed prominently as a releaser to stimulate following during the side-shake. While in this display the male orientates itself laterally towards the female. As the displaying male moves into follow-shake so it returns to a vertical position. The similarity between P. philander and H. burtoni is demonstrated by an illustration comparing the side-shake of both groups (fig 6). These initial courtship activities are in contrast with those of the early, almost aggressive, exchanges during pair formation of the Hemichromis-type (see Baerends and Baerends van Roon, 1950).

Plate 19

A Durban male in side-shake to an enflasked Durban female. By turning away from the male the female will indicate that she is not going to follow and thus terminate the side-shake. Note the female's light yellow coloration, yellow anal fin and red eye-spot. Note the male's golden-yellow coloration. The wound on the male's head was from a brain operation.

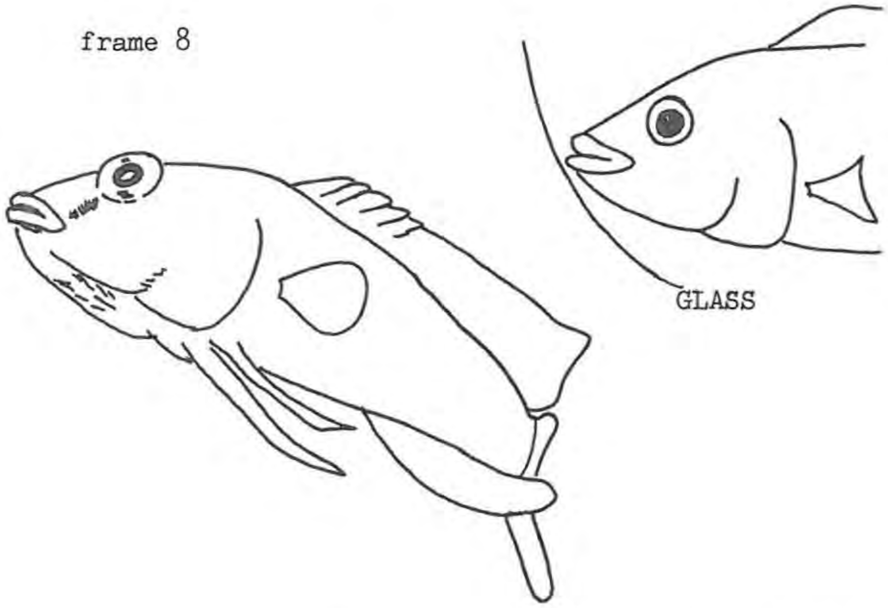
Figure 5 A sequence illustrating the side-shake and follow-shake.

frame 1



A male orientates itself in side-shake below and ahead of the female. The female is unable to follow as it is held in a glass flask.

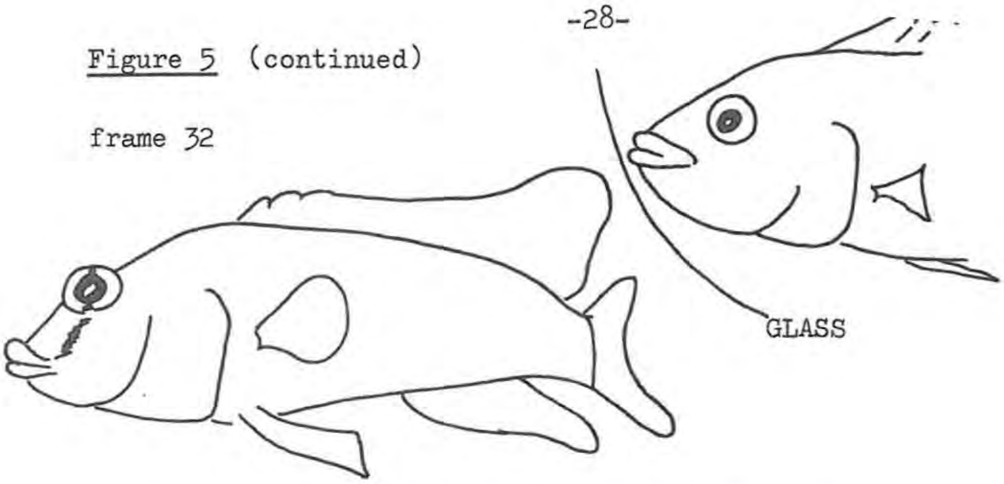
frame 8



The male in side-shake quivering. Note the extension of the anal fin.

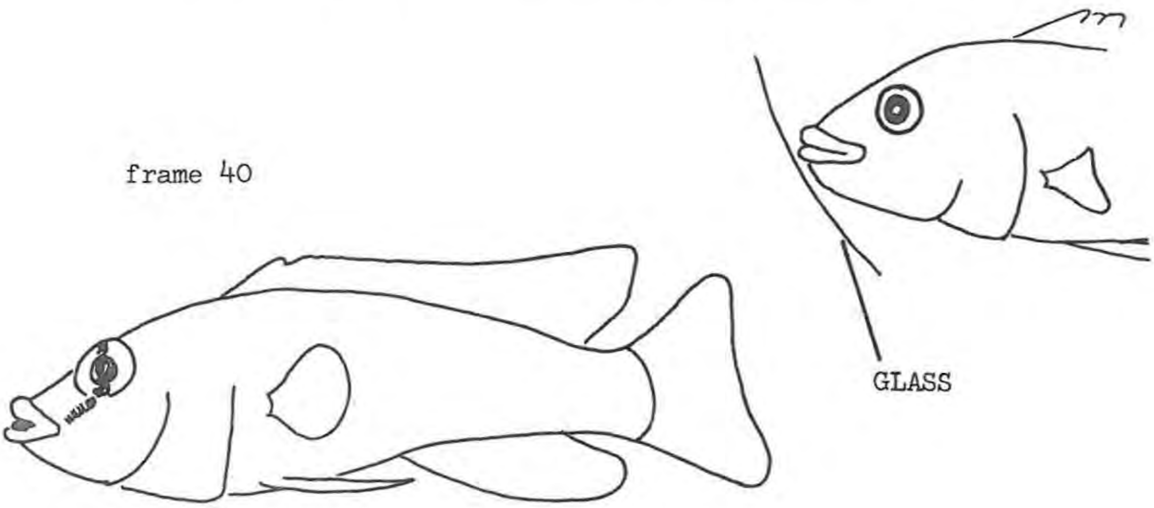
Figure 5 (continued)

frame 32



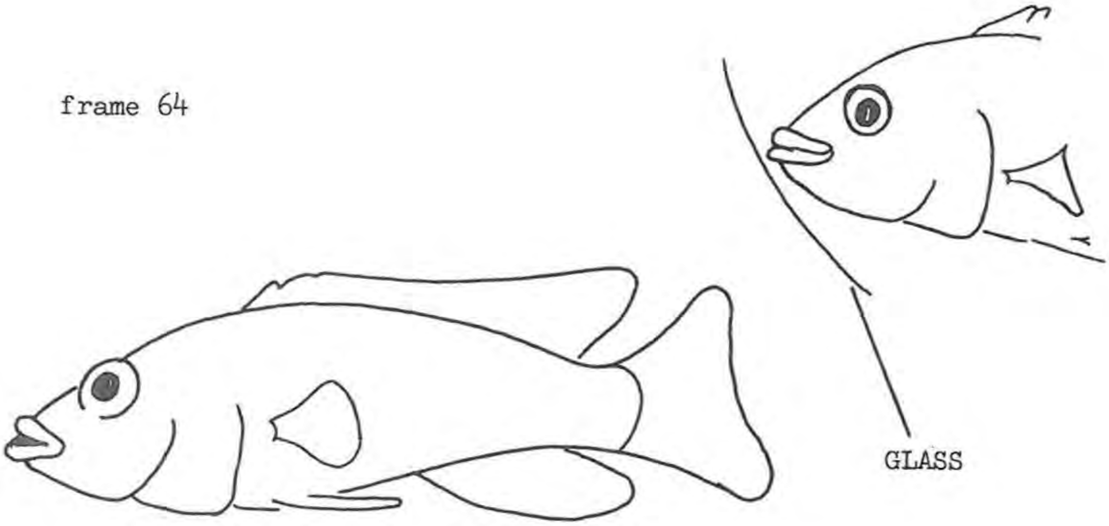
Turning from side-shake into follow-shake.

frame 40



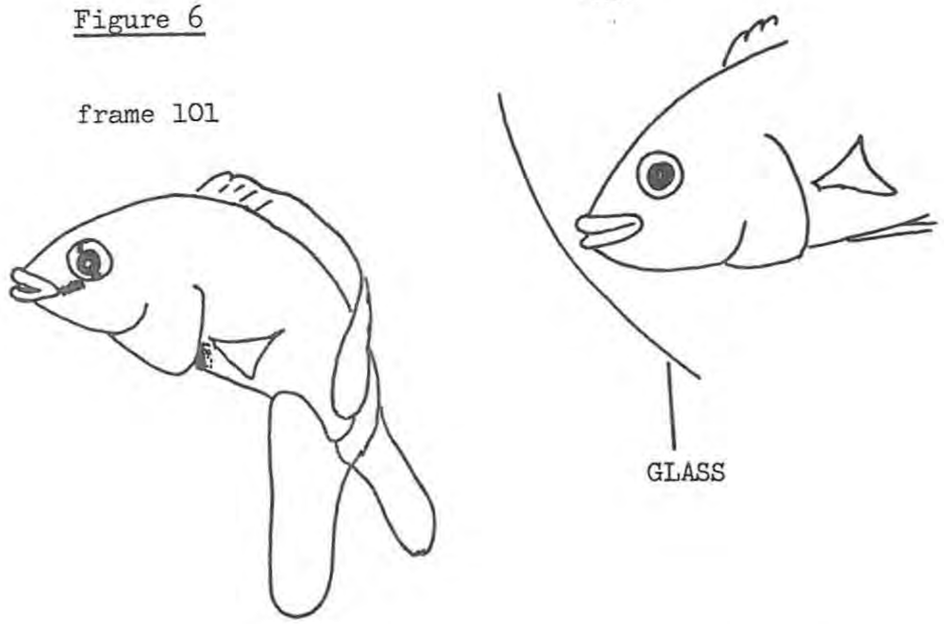
The male is facing away from the female in follow-shake.

frame 64

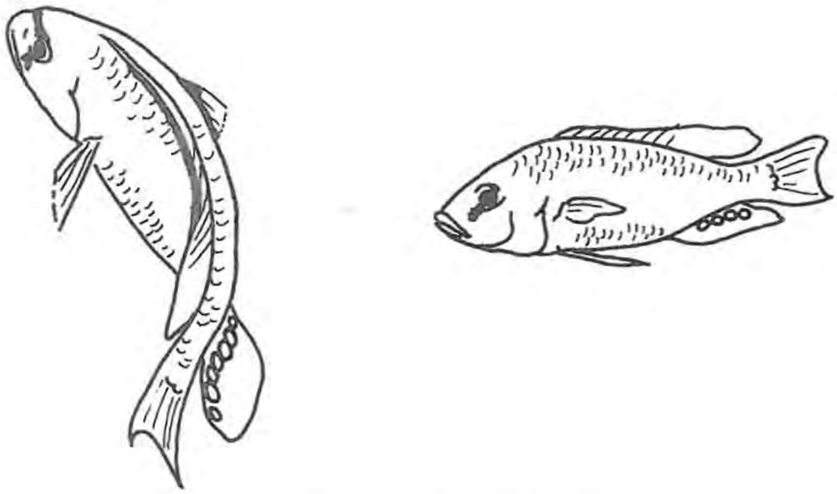


The follow-shake is lengthy because the female is unable to follow, even though she is trying to do so.

Figure 6



(a) The male returns to restimulate the following response.

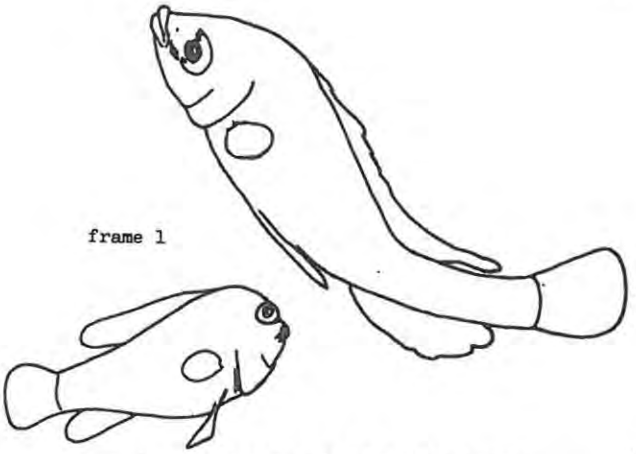


(b) A drawing, after Wickler (1968), of *Haplochromis burtoni* in side-shake. Note how both *P. philander* (fig 6a) and *H. burtoni* (fig 6b) have extended their anal fins in display.

This is an important behavioural trait which, amongst others, demonstrates the affinity of *P. philander* with the genus *Haplochromis*.

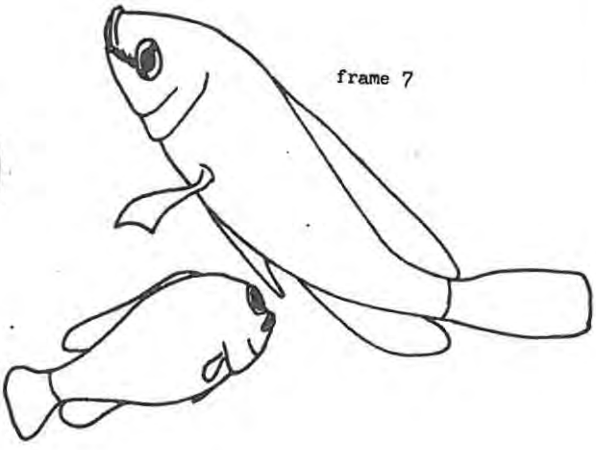
From the follow-shake _P_. _philander_ males lead the receptive females to their nests (lead swim), and stimulate them to enter the nest for courtship. The next series of figures (fig 7) illustrates the nest patterns, demonstrating the vertical nest shake and gentle butting which eventually results in oviposition.

Figure 7



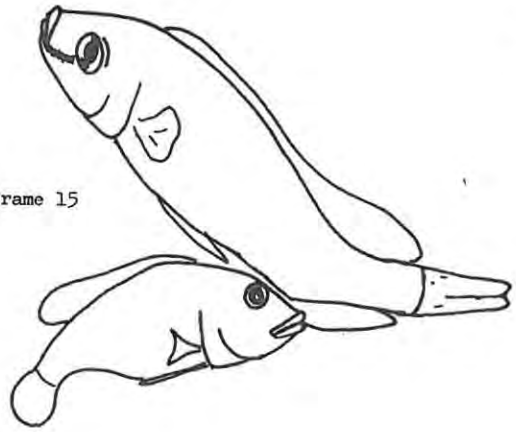
frame 1

The male lifting itself out of horizontal nest shake into vertical nest shake, initially displaying its anal fin. The female approaches in response to the courtship patterns.

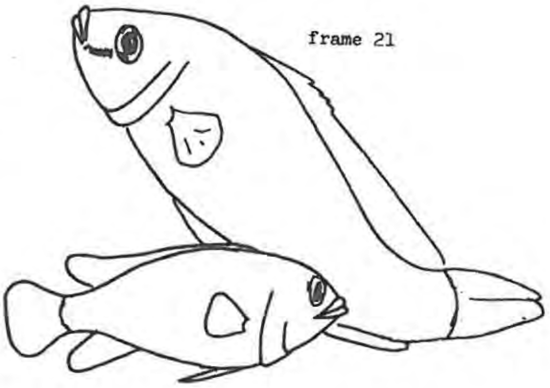


frame 7

As for frame one, but the female is closer and the caudal region of the male is more firmly planted on the substratum.



frame 15

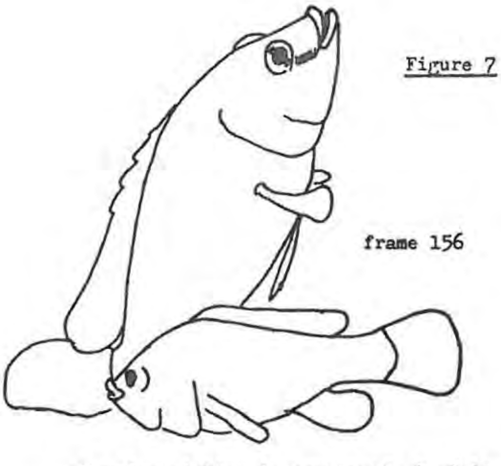


frame 21

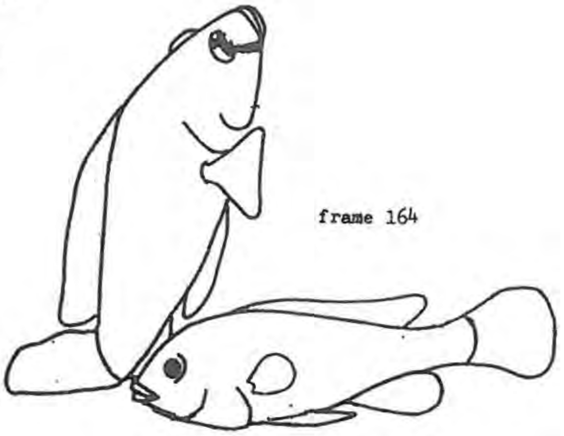
Frame 15 & 21

The female is stimulated to approach closely, and in frame 21 she begins to nudge the male: a tactile releaser.

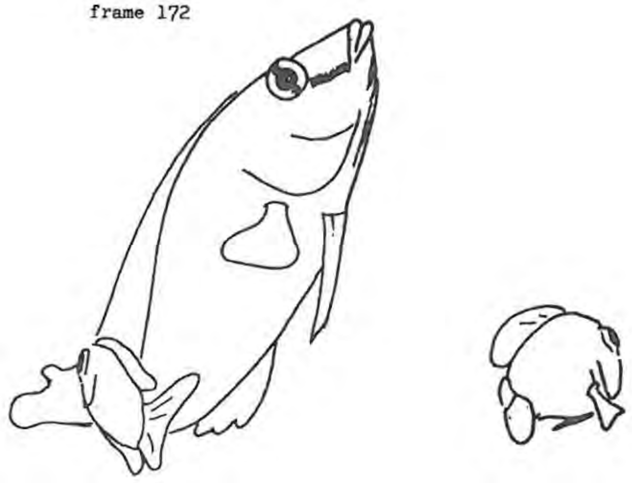
Figure 7 (continued)



The description is continued, in this new sequence the male, once stimulated by the female, becomes more erect in its vertical nest-shake.



The male, while quivering in vertical nest-shake, begins to lift itself off the substratum.

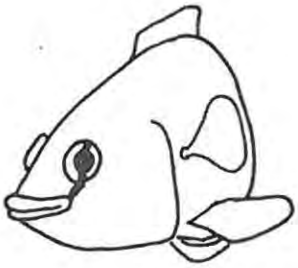


Vertical nest-shake continues as the male prepares to circle round to stimulate the female with abdominal nudges.

The male circling to nudge the female.

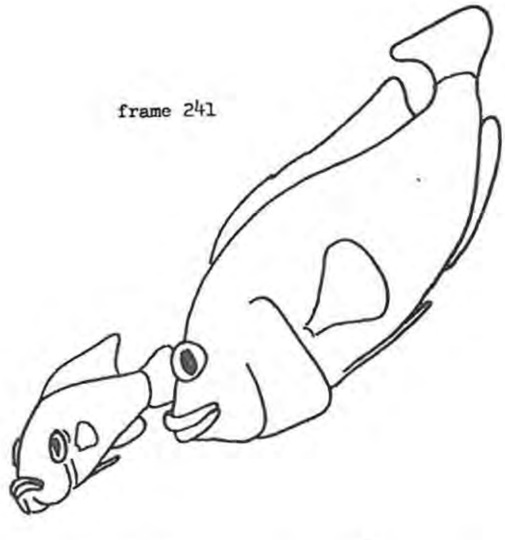
Figure 7 (continued)

frame 198



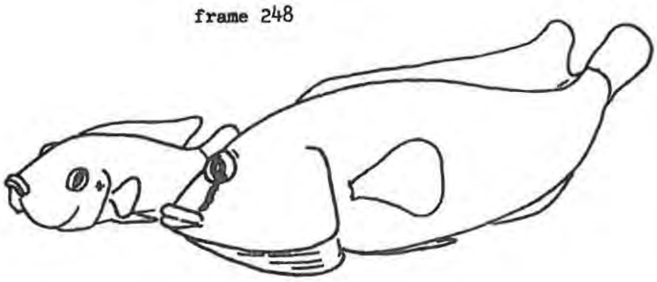
The female also circles within the nest. This mutual circling may continue for several seconds, or the female may remain still and wait for the male.

frame 241



The male about to nudge the female.

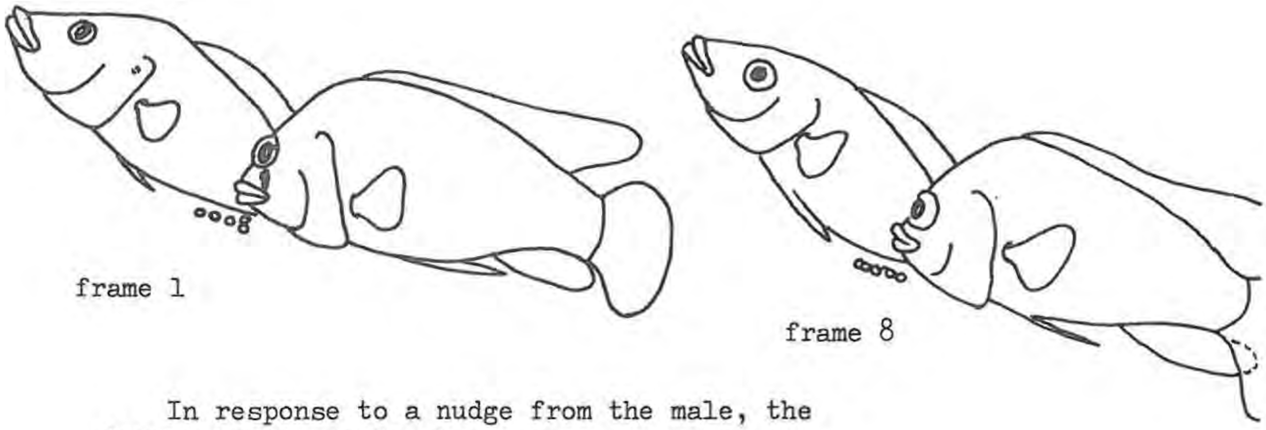
frame 248



The gentle nudging of the female eventually stimulates her to lay eggs. Egg-laying is illustrated in the next sequence of diagrams.

The sequences of *P. philander* egg-laying are illustrated (fig 8), and compared with those of *H. burtoni* (fig 9). Female *P. philander* pick up eggs immediately after laying. So rapid is the female in turning to collect the eggs (frames 64 to 74) that many eggs are picked up before the male has a chance to fertilize them. Frequently, when small batches of eggs are deposited, females may collect the entire batch before the male has had an opportunity to fertilize them. In this respect *P. philander* shows close haplochromid affinities. Females with unfertilized eggs in their mouths need to collect spermatozoa from the males. Wickler (1962, 1963, 1968) has demonstrated how this is achieved in the *Haplochromis*. In his comparison of *P. multicolor* with the haplochromids, Wickler (1963, p. 90-91) noted that the median plane of the body of *multicolor* males remained almost vertical, with the anal-fin folded, while the female collected spermatozoa. It will be noted, that during milt collection of *P. philander*, males do not remain vertical, but, in a manner reminiscent of the genus *Haplochromis*, lay their anal fin and posterior part of the body upon the substratum. (frames 670 to 730, and also 780 to 860). To do this they need to lean over laterally away from the female, so that the anal fin is extended towards the female. During this process the male glides slowly forwards while trembling in the manner described for *Haplochromis* (Wickler 1963). A comparison of the fertilization behaviour of *P. philander* with that of *H. burtoni* (fig 9) shows the similarities of these two species, both being dissimilar from *P. multicolor*.

Figure 8



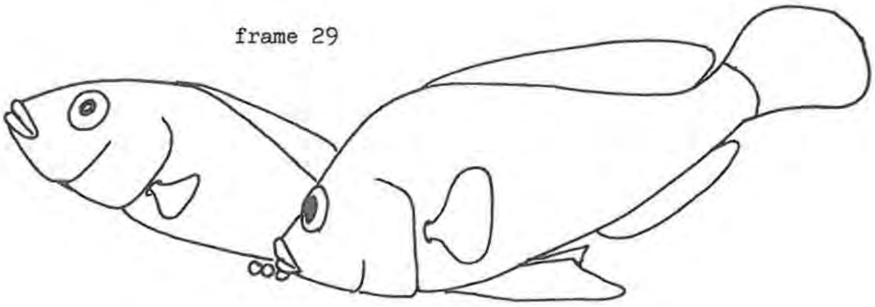
frame 1

frame 8

In response to a nudge from the male, the female begins to lay her eggs.

Figure 8 (continued)

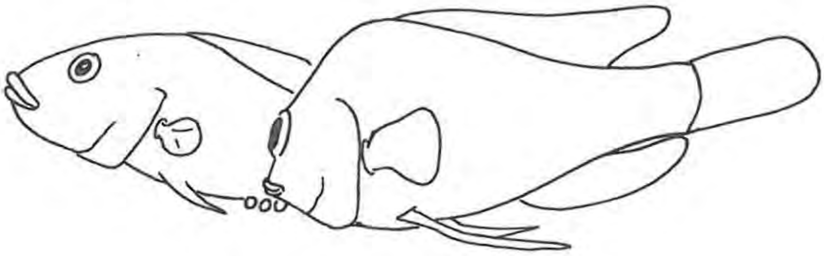
frame 29



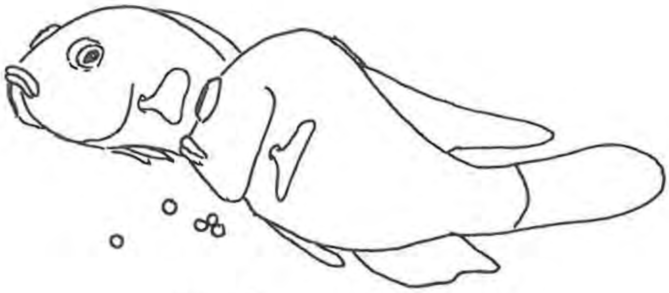
Frames 29 and 46

The female continues to lay her first batch of eggs.

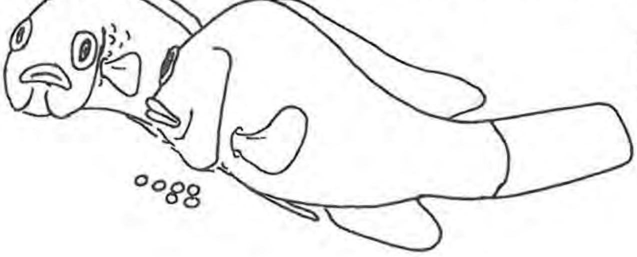
frame 46



frame 64



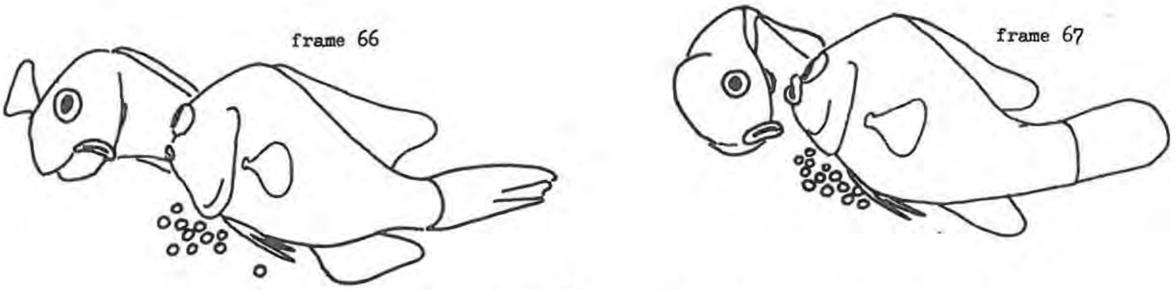
frame 65



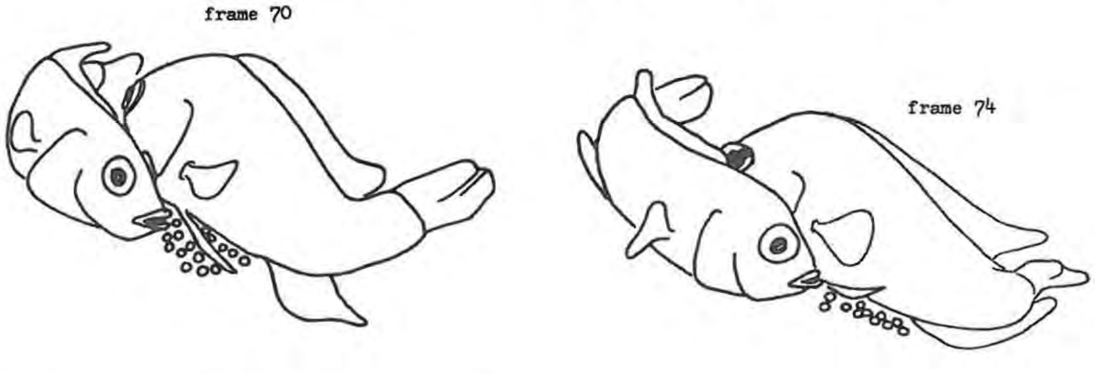
Frames 64 and 65

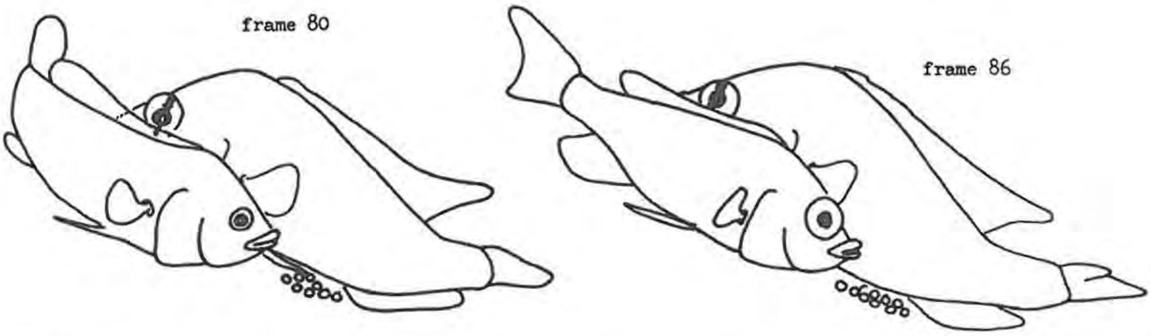
Then having laid her first batch of eggs, the female turns quickly (note consecutive frames 64-67) in order to pick them up. In turning some eggs are slightly displaced.

Figure 8 (continued)



Frame 66 and 67 The rapid turning as described above.





Frame 70 and 74

The female begins to pick up the eggs before they have been fertilized. Though the male begins to move over the eggs shortly after they are laid, females almost invariably begin to pick them up before the male arrives. This series illustrates that it takes the female approximately one second from the laying of her last egg, of a batch, to begin picking them up.

Frame 80 and 86

The female adjusts eggs in her mouth and then prepares to retrieve the remainder. The male moves into position to fertilize.

Figure 8 (continued)

Frames 92 to 121

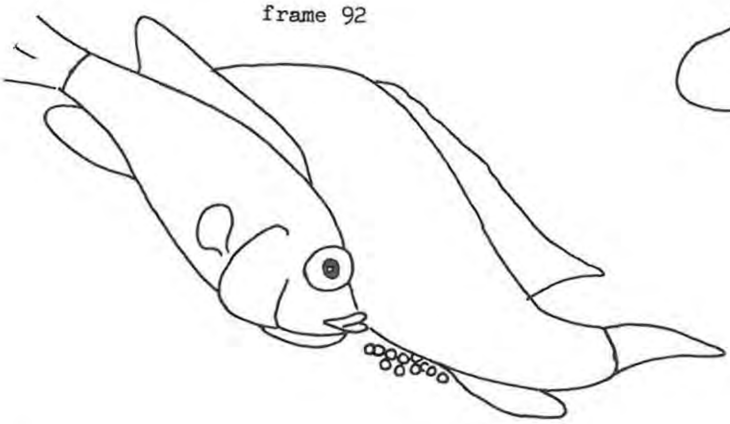
The female continues to take the newly laid eggs into her mouth at a point anterior to where the male is apparently ejecting milt.

Thus, in common with *Haplochromis* (see fig 9) *P. philander* females rapidly turn and begin to pick up their eggs before they have been fertilized. Unlike the *Haplochromis*, however, *P. philander* males may fertilize the eggs by ejecting milt when they move over them.

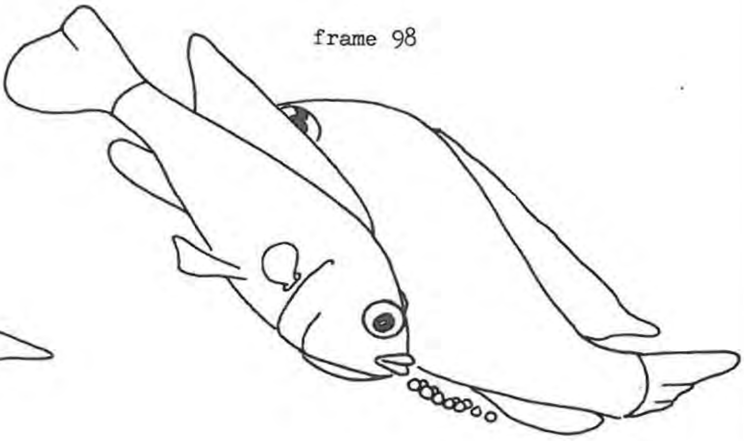
Plate 20 Eggs of an Otavifontein female. A number of sand grains, which had been accidentally picked up, were also emptied from her mouth.

Figure 8 (continued)

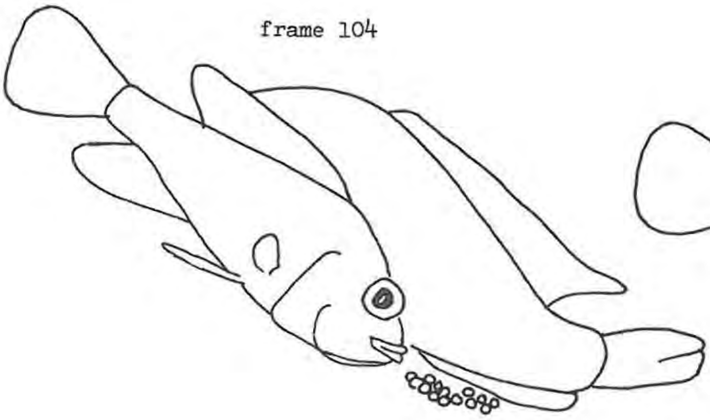
frame 92



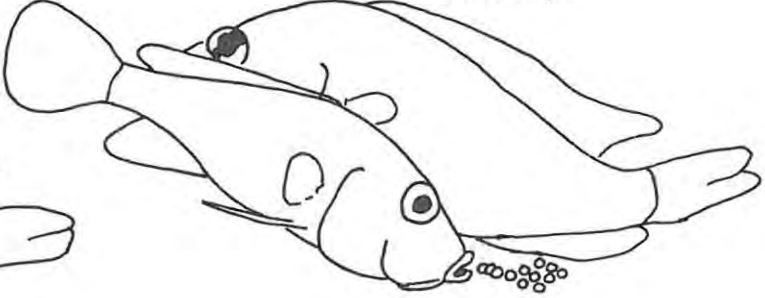
frame 98



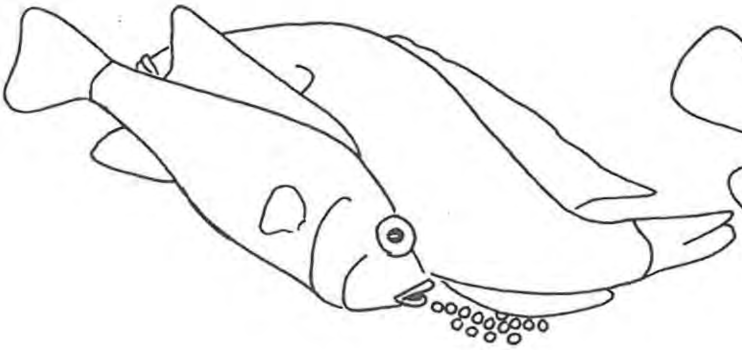
frame 104



frame 107



frame 113



frame 121

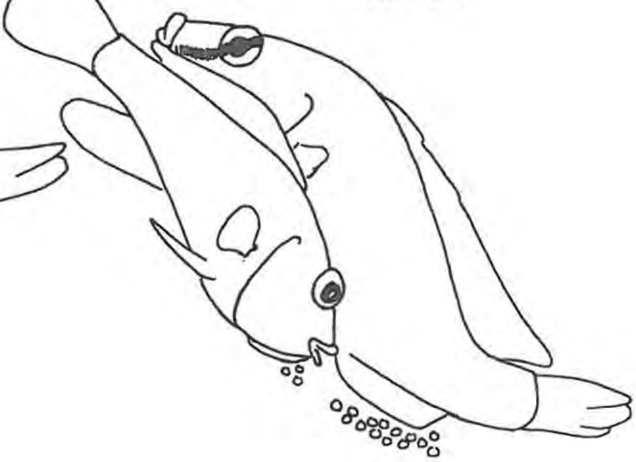
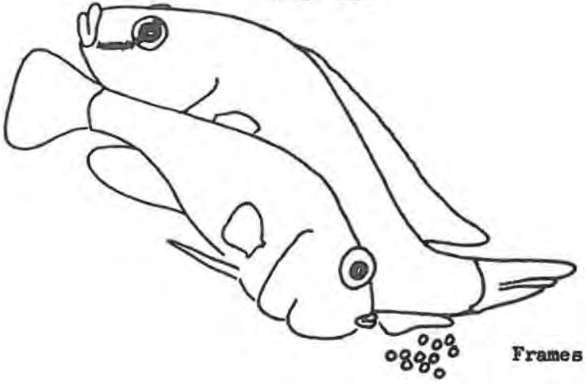
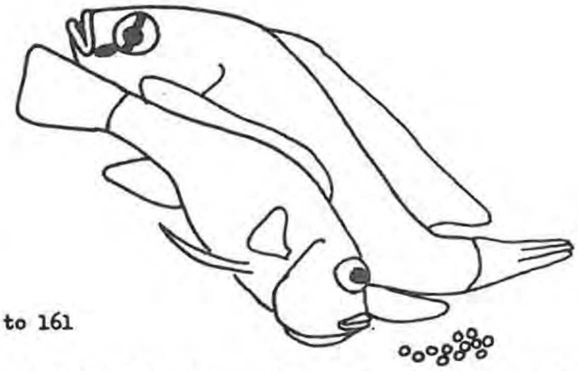


Figure 8 (continued)

frame 128



frame 142

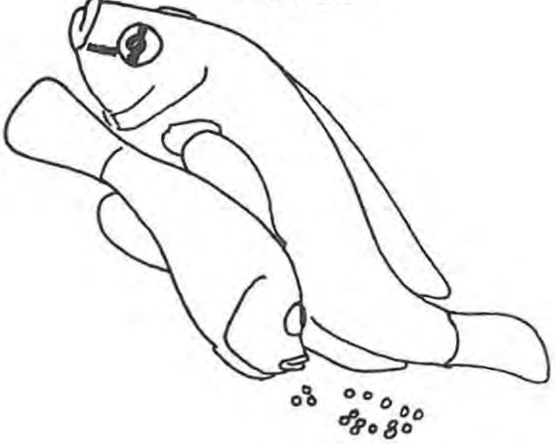


Frames 128 to 161

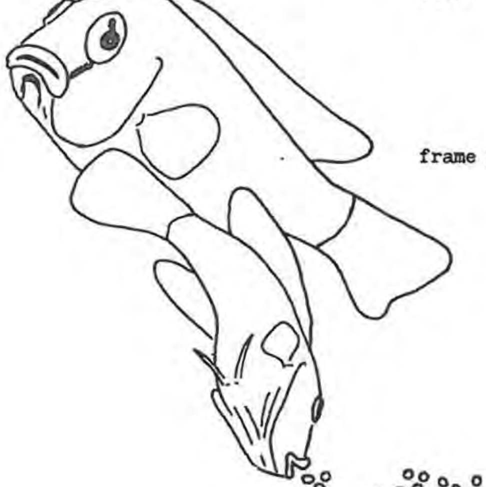
The female continues to collect the eggs. The male spreads his anal fin near to where the female is collecting eggs in a manner similar to that of the Haplochromis (see fig 9). Possibly the trailing edge of the anal fin of P. philander acts as an egg-dummy as do the pseudo-ocelli in the Haplochromis (Wickler 1962, 1963). It also appeared as though spermatozoa might be channelled over the anal fin towards the egg-dummy, propelled there by the quivering of the male.

frame 151

frame 161



frame 171

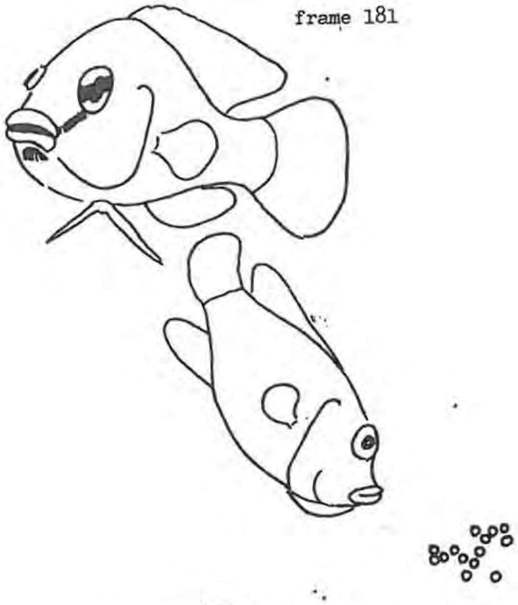


Frame 171

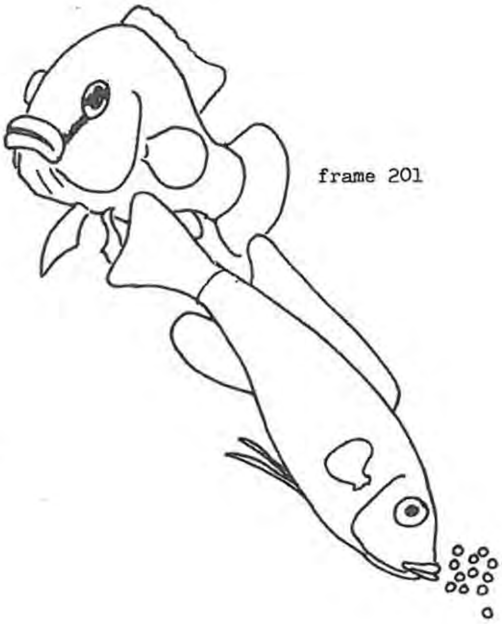
The male rises to continue spawning behaviour, while the female continues to take the newly laid eggs into her mouth.

Figure 8 (continued)

frame 181



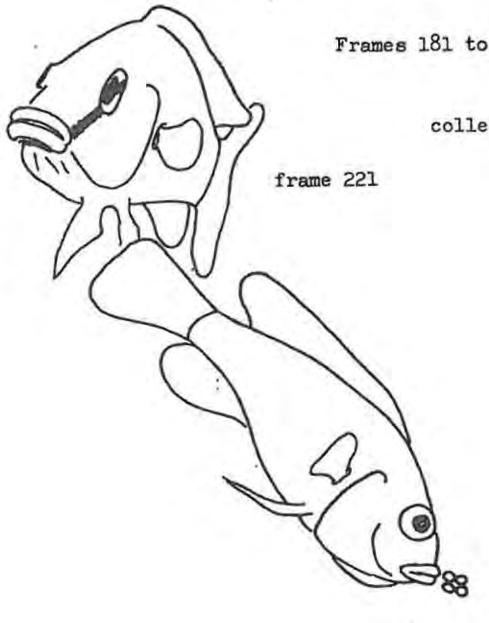
frame 201



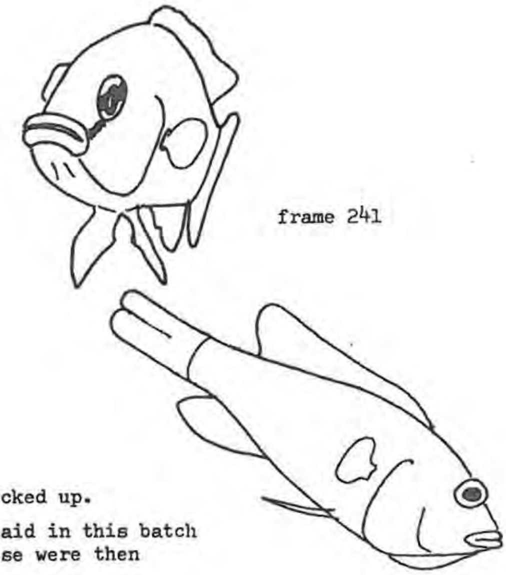
Frames 181 to 221

The male waits in close attendance while the female collects the eggs.

frame 221



frame 241

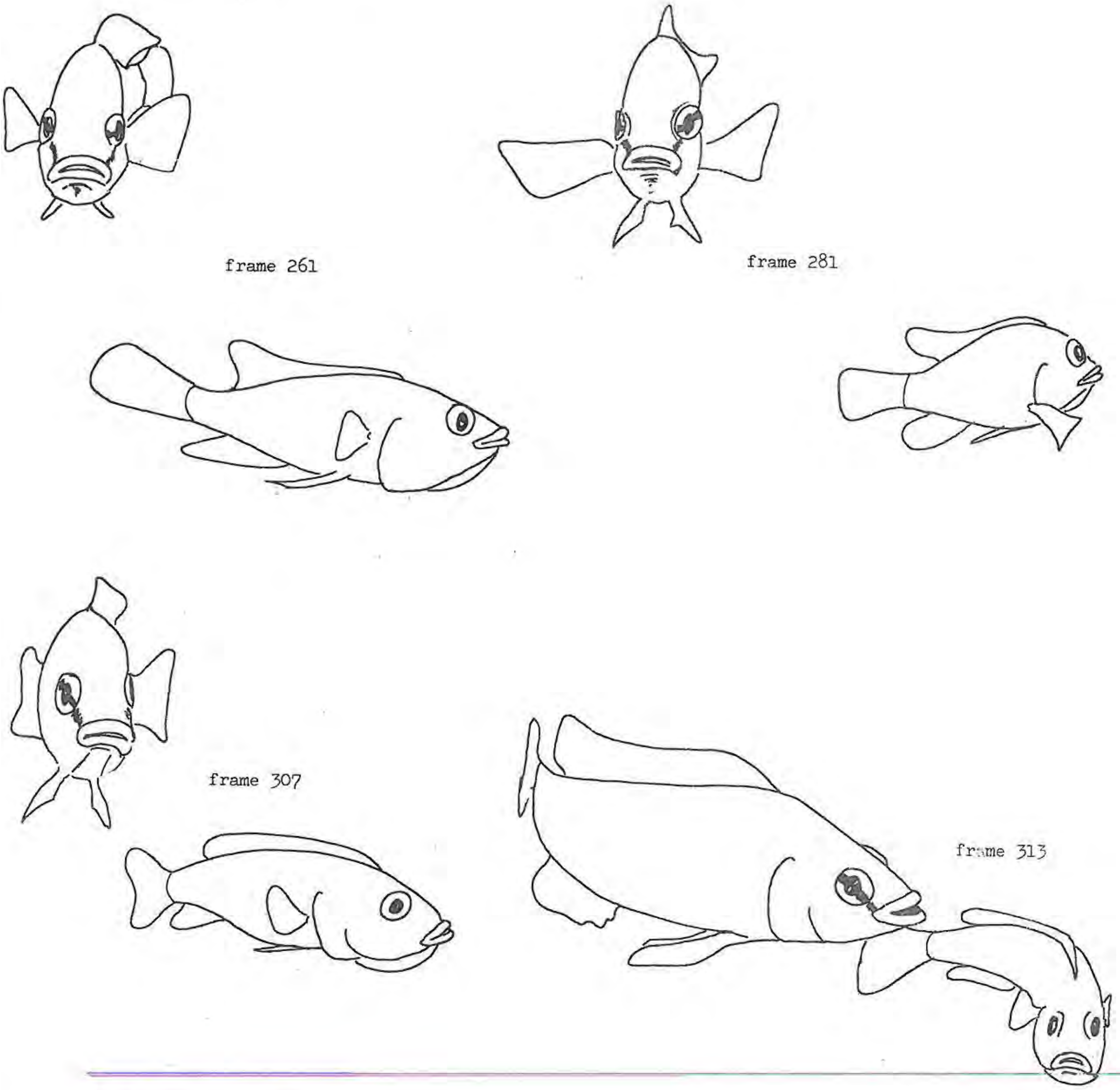


Frame 241

Finally, all the eggs have been picked up.

Approximately 20 to 30 eggs were laid in this batch in a little less than four seconds. These were then collected in the following 10 seconds.

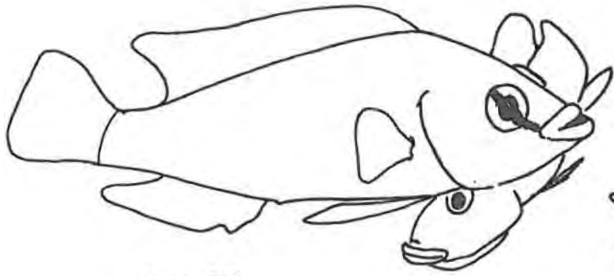
Figure 8 (continued)



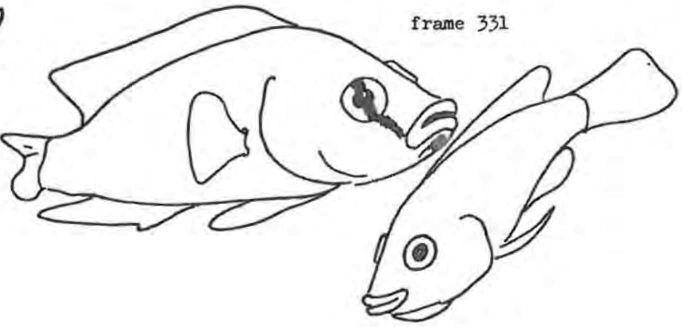
Frames 261 to 313

The female looks for any eggs which she may have missed while the male resumes sexual activities.

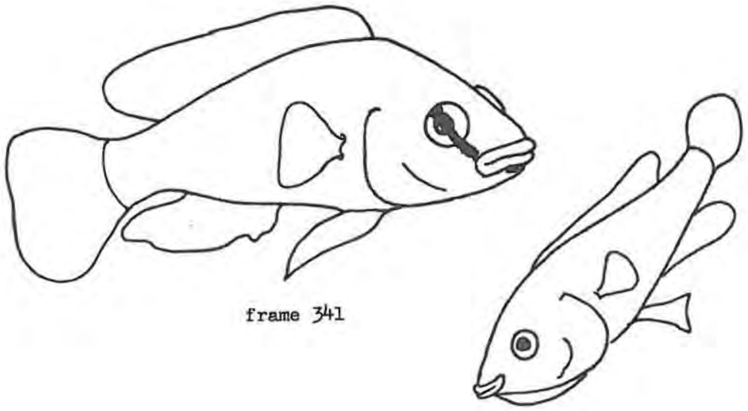
Figure 8 (continued)



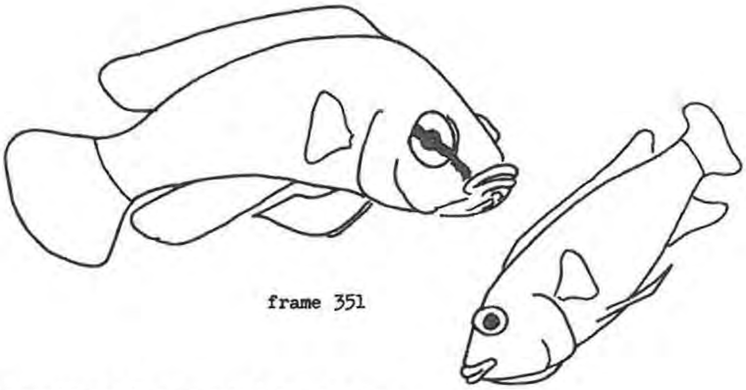
frame 323



frame 331



frame 341

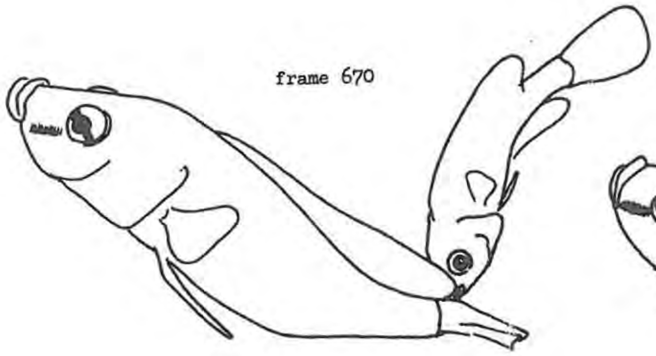


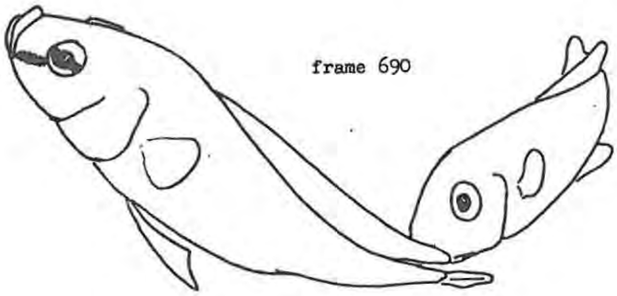
frame 351

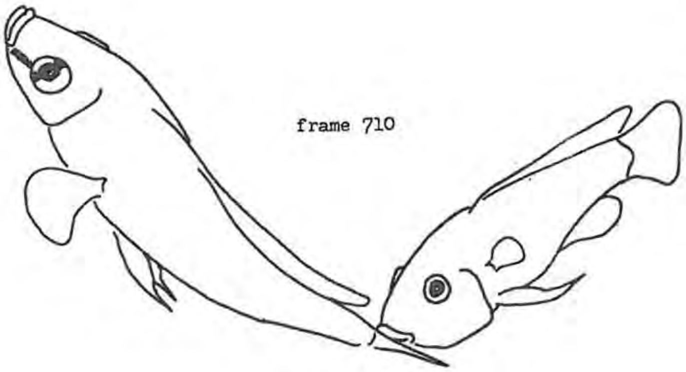
Frames 323 to 351

The female continues her search for more eggs
while the male courts her with nest-shakes (figs 331 and 351).

Figure 8 (continued)







Frames 670 to 730

After 25 seconds of searching the female responds to the male. In Haplochromis-like manner (see fig 9) male P. philander lean over to place the anal fin on the substratum. Though no clear egg-dummies are present female P. philander are nevertheless attracted to the anal fin. As the quivering of the male carries it slowly forwards, the female follows apparently sucking at the distal edge of the anal fin.

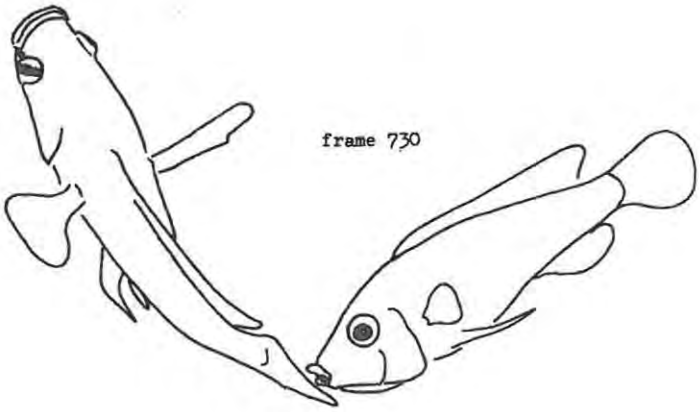
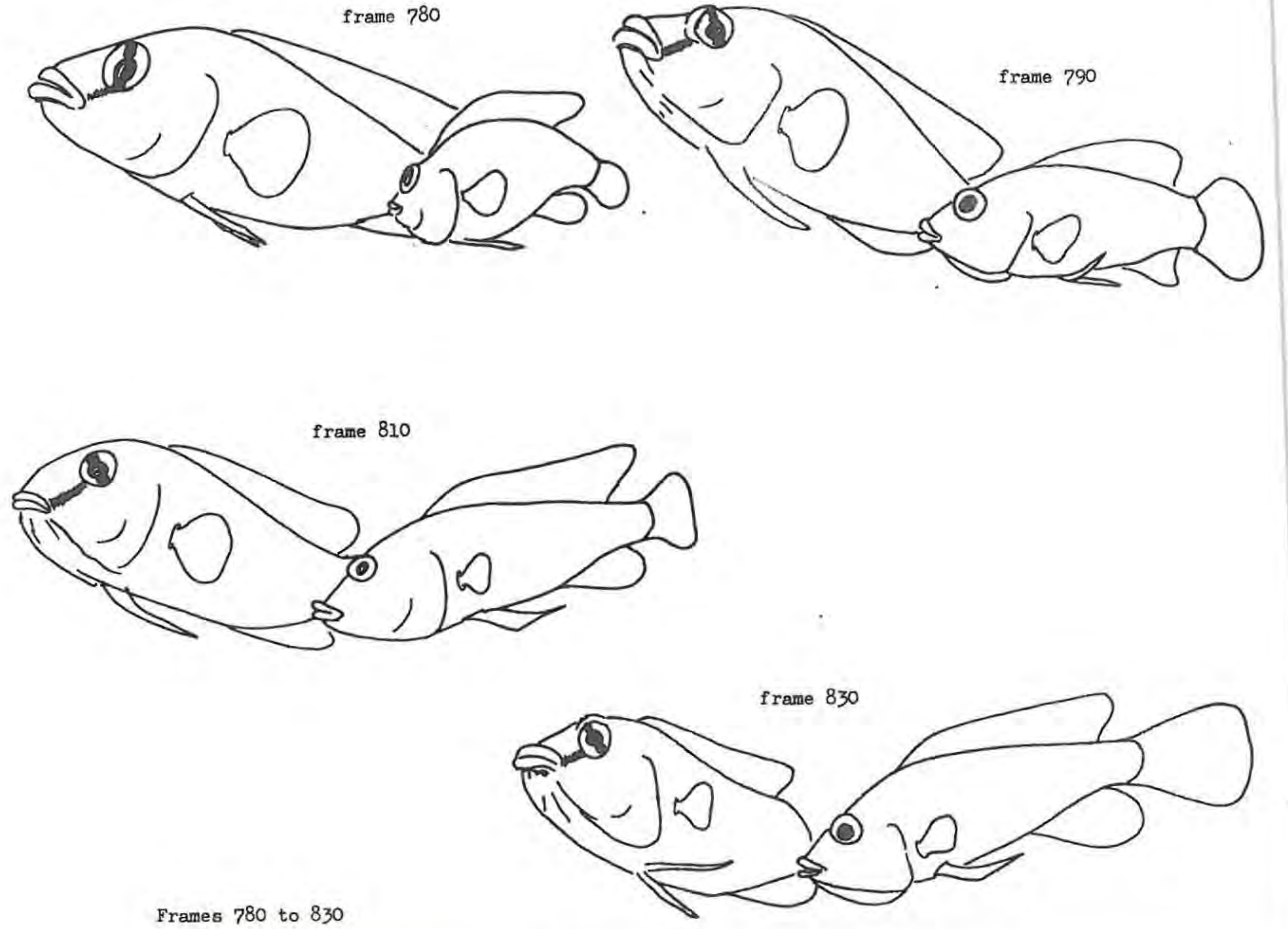


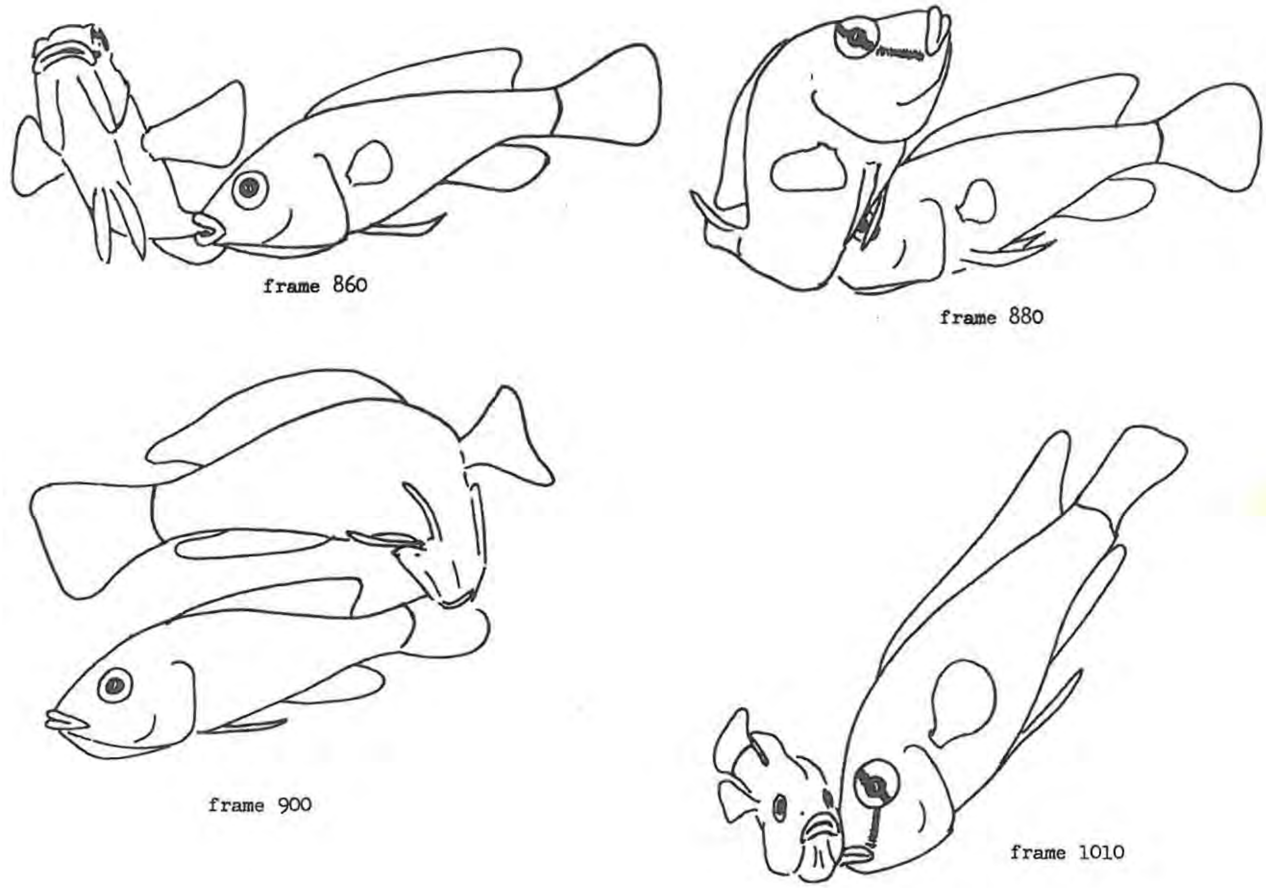
Figure 8 (continued)



Frames 780 to 830

The female following the male sucking at the anal fin. I believe that a combination of visual releasers (anal fin markings) and chemical releasers, from the male's genital aperture (perhaps spermatozoa itself), stimulate the following anal sucking movements of the female. As the male moves forwards, quivering, so spermatozoa are released and pass onto the anal fin instead of into the substratum. The female, drawn to the anal fin, collects the spermatozoa and mixes them with the eggs. This aspect of P. philander behaviour is very similar to Haplochromis fertilization behaviour described by Wickler (1962, 1963), except the overt egg-dummies are absent from P. philander. Wickler (1963), and Ribbink (1971), suggested that the brightly coloured trailing edge of the Pseudocrenilabrus anal fin may act as an egg-dummy. The egg-dummy is not always necessary, however, for many large Sibaya males have completely black anal fins. Probably chemical releasers play a more important role in the fertilization of Pseudocrenilabrus eggs than initially realised.

Figure 8 (continued)



frame 860

frame 880

frame 900

frame 1010

Frames 860 to 1010

The collection of spermatozoa continues (frame 860) until the male swims around (frames 880 and 900) to nudge the female into laying her next batch of eggs (frame 1010).

Many spawning and fertilization sequences were filmed and in all cases the behaviour was very similar. The time from the cessation of laying to collecting the eggs was usually of the order of 1 second (11 frames to 18 frames, N = 12).

These sequences outlined above are typical of P. philander spawning. The egg-laying and fertilization behaviour of Haplochromis burtoni, a typical Haplochromis, is shown in figure 9 to illustrate the behavioural similarities of H. burtoni and P. philander. Unfortunately, the frame counts were not given by Wickler and so it is not possible to make a direct comparison of the time-course of the patterns of the two species.

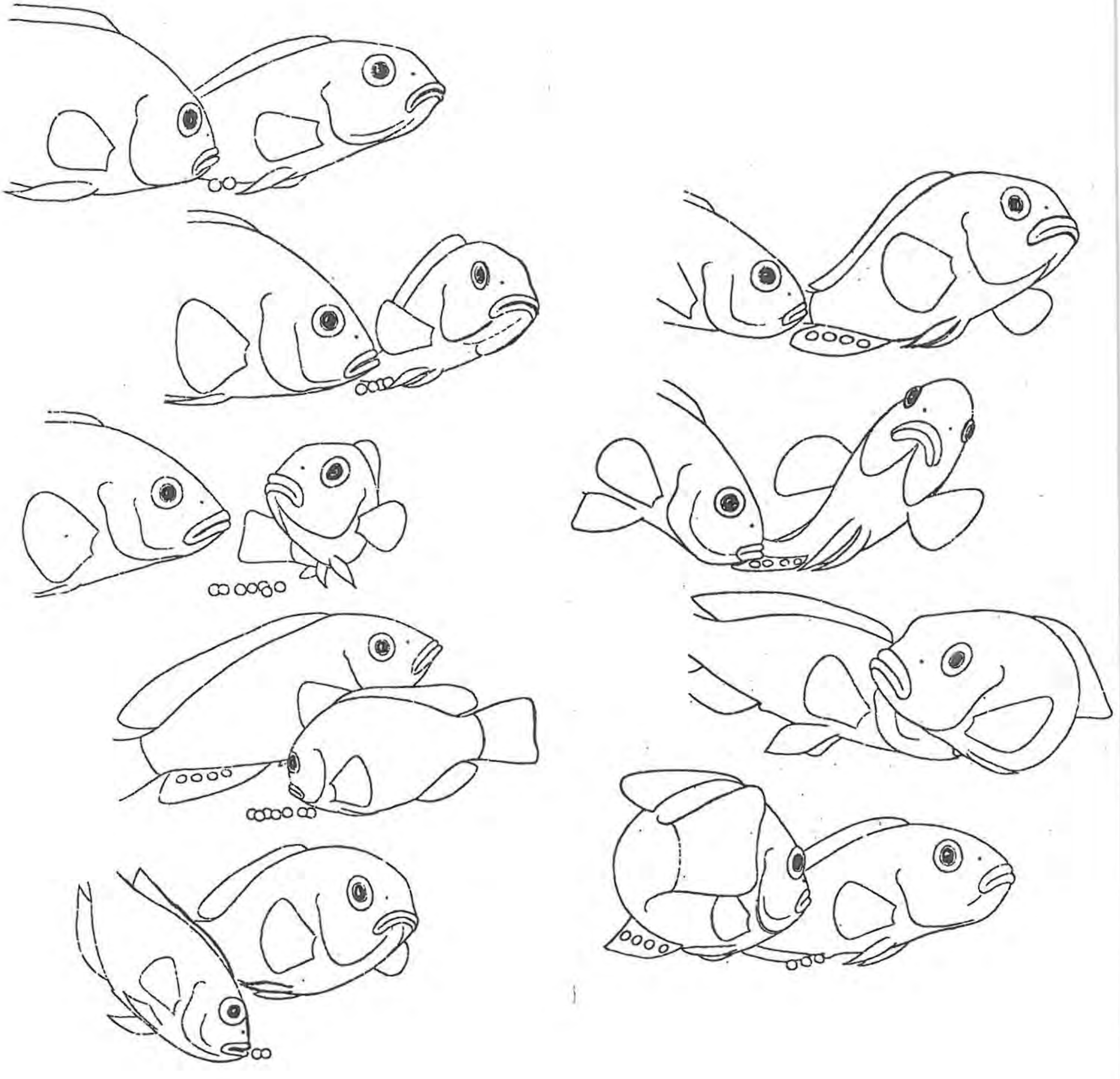
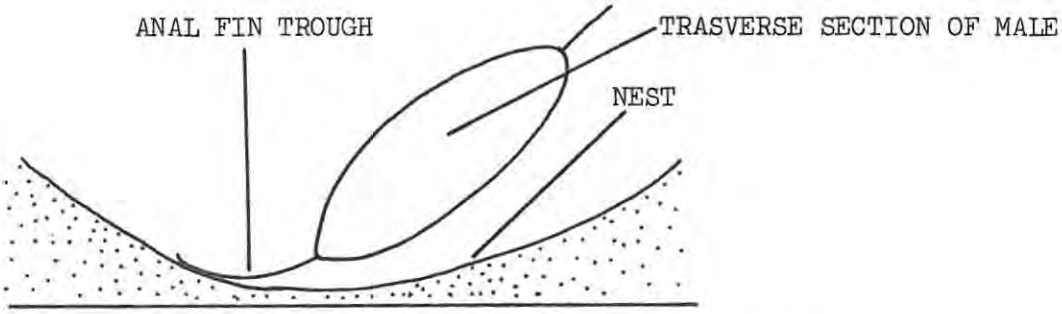


Figure 9

Egg-laying and fertilization of Haplochromis burtoni is similar to that described for P. philander (fig 8), as this illustration demonstrates. The sequence is after Wickler (1968) and taken from Fryer & Iles (1972).

While the female collects spermatozoa, the anal fin of P. philander is slightly folded to form what appears to be a concave receptacle to catch, hold and concentrate the spermatozoa.

Figure 10



A transverse section of the posterior regions of a male haplochromid-like fish in its nest. The anal fin is formed into a trough to facilitate milt collection, and prevent loss of spermatozoa.

Spermatozoa might otherwise be lost in the substratum. In all cases, it seems as though the female is drawn to the anal fin, and as the male glides slowly forwards around the nest, the female follows collecting spermatozoa funnelled along the anal fin (fig 11). This might explain why in the Haplochromis[*], and in Pseudocrenilabrus, the egg-dummies are placed posteriorly on the anal fin, and not close to the genital opening. My observations indicate that it is only the section of the anal fin posterior to the spines that is placed on the substratum to form an anal fin trough. The spiny, inflexible anterior region is usually held off the substrate. Goldstein (1970) and Axelrod (1974) do not accept fully Wickler's interpretation of the function of egg-dummies. An objection they levelled was that, if the egg-dummies served the purpose proposed by Wickler then they should be nearer to the genital opening. My interpretation may answer these objections, and also explain why the Pseudocrenilabrus egg-dummy is placed on the trailing edge of the anal fin. An examination of frames 670 to 730, and also 780 to 830 (fig 8), shows the female collecting milt from the trailing edge.

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[*] A look at the illustrations of various Haplochromis in Greenwood's excellent papers will show that in all species the egg-dummies are posteriorly placed (Greenwood 1956, 1957, 1959, 1962, 1965, 1967, 1973, 1974).

Figure 11

By pressing the anal fin and caudal region of the body onto the substratum, flexing the body to lift it anteriorly off the substratum, and moving slowly forwards around the nest, males ensure that spermatozoa pass into a trough formed by the anal fin trough to facilitate milt collection. Arrows indicate the proposed route for spermatozoa. Females may follow sucking at the distal edge of the anal fin, or move up and down the fin, collecting spermatozoa from within the trough.

Figure 12

Three different forms of Haplochromis anal fin with the proposed route for spermatozoa indicated by the arrows. In (a) egg-dummies are smaller than the eggs, in (b) they are super-releasers and in (c) the dummies are true mimics of the eggs. Note: egg-dummies do not occur anteriorly, on the spiny inflexible region of the fin.

Figure 11

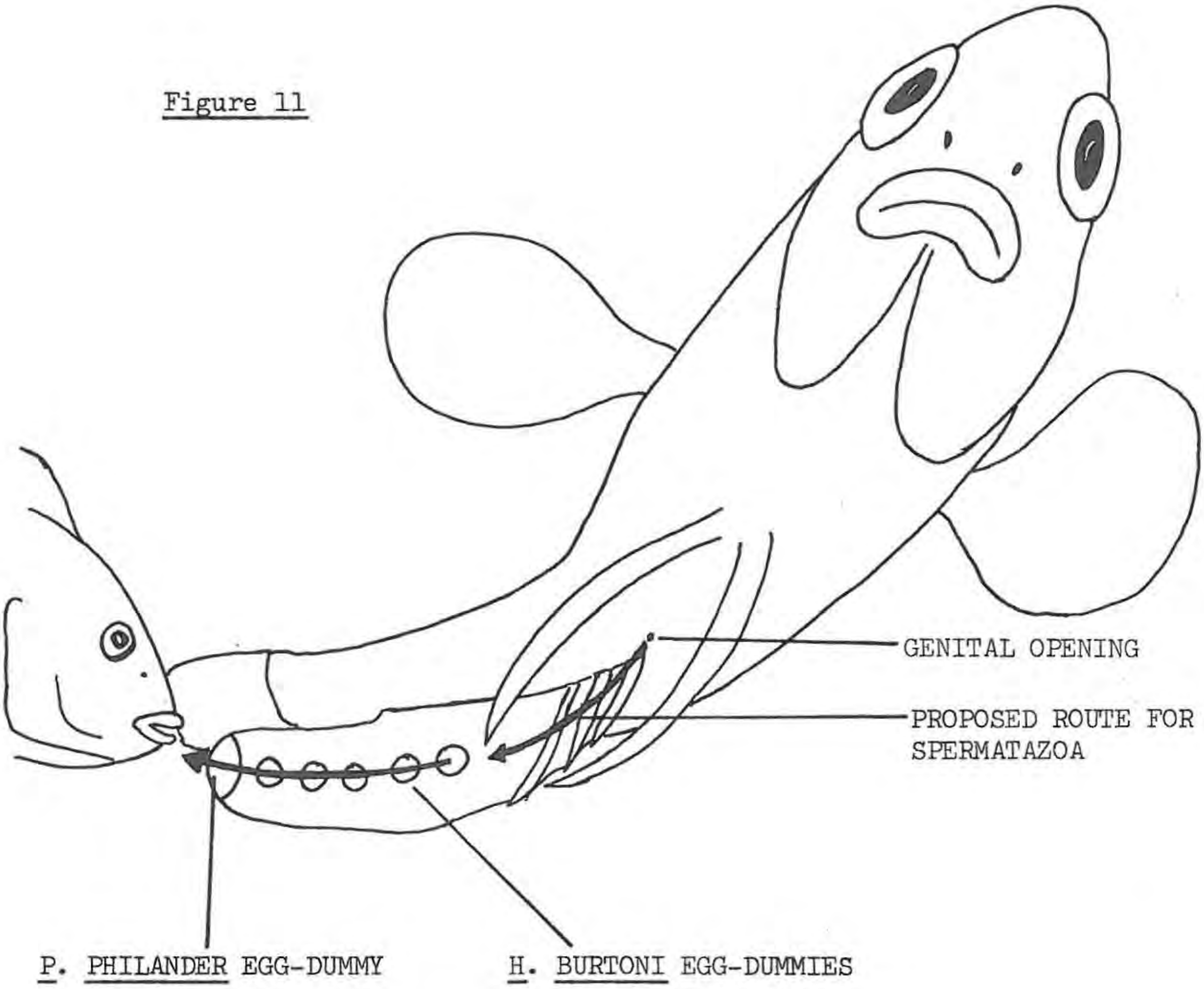
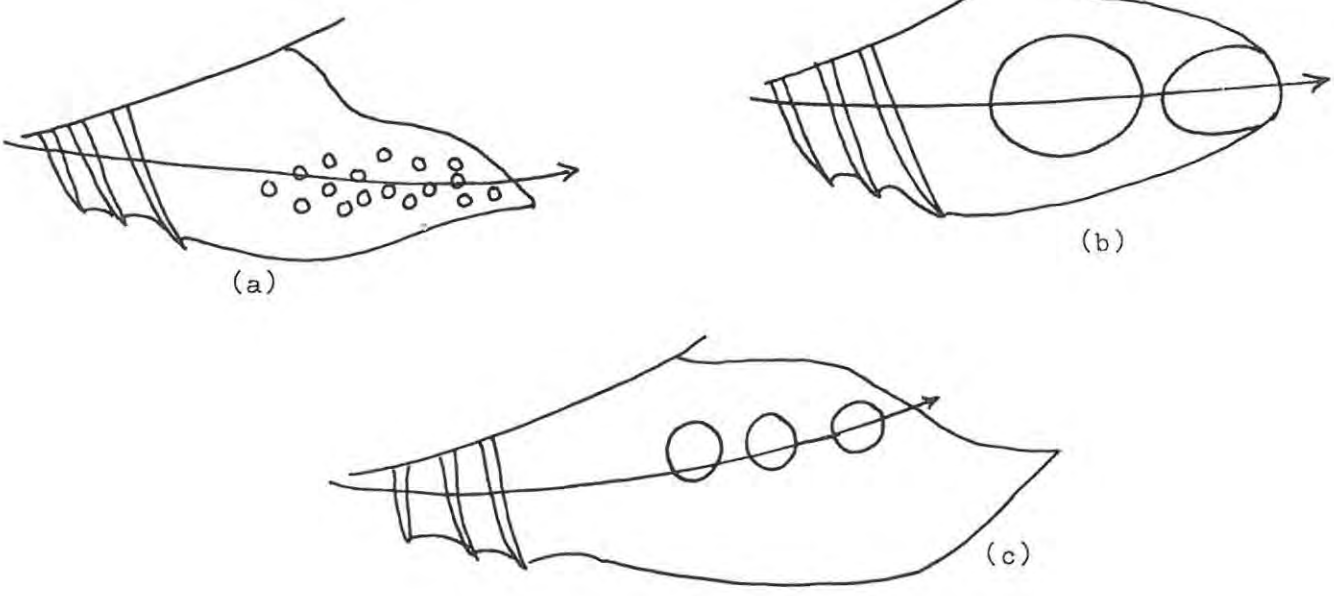


Figure 12


(a)
(b)
(c)

Egg-dummies are not always the same size and colour as the eggs of the species which possess them, as Wickler (1962, 1968) would have us believe. Goldstein (1970) and Axelrod (1974) used this observation as a further criticism of Wickler's proposal. The criticism, however, is of little behavioural consequence. What is important is that egg-dummies are releasers: those egg-dummies larger or more vividly coloured than the eggs of the species may be super-releasers, in those species with egg-dummies smaller or less vivid than the eggs, it is probable that they have their behavioural stimulus-response systems adjusted accordingly, and finally the role of those egg-dummies which are perfect mimics of the eggs has been beautifully described by Wickler (1962, 1965).

Though I have never seen the spermatozoa when released by the males, and assume that Wickler has also not seen the milt, the behavioural evidence strongly suggests that the proposed role of the anal fin in fertilization is correct. Nevertheless, absolute confirmation is required for one to be certain that the anal fin of the _Haplochromis_ and _P. philander_ is used to perform the functions described.

Feeding behaviour

In aquaria, P. philander caught and fed on floating or swimming food. Food which lay on the surface of the substratum was picked-off and swallowed. If food had not been recently supplied then the fish foraged, as is illustrated by fig 13. Foraging from the substratum was the principal manner of feeding in the natural environment.

A swimming fish about to dig into the substratum would slow down and stop (fig 13a) then lower its head and apparently examine the site (fig 13b), move downwards to dig its mouth into the sand (fig 13c). A mouthful of sand would be withdrawn, "mumbled" or "chewed", and finally passed out via the gill rakers (fig 13d).

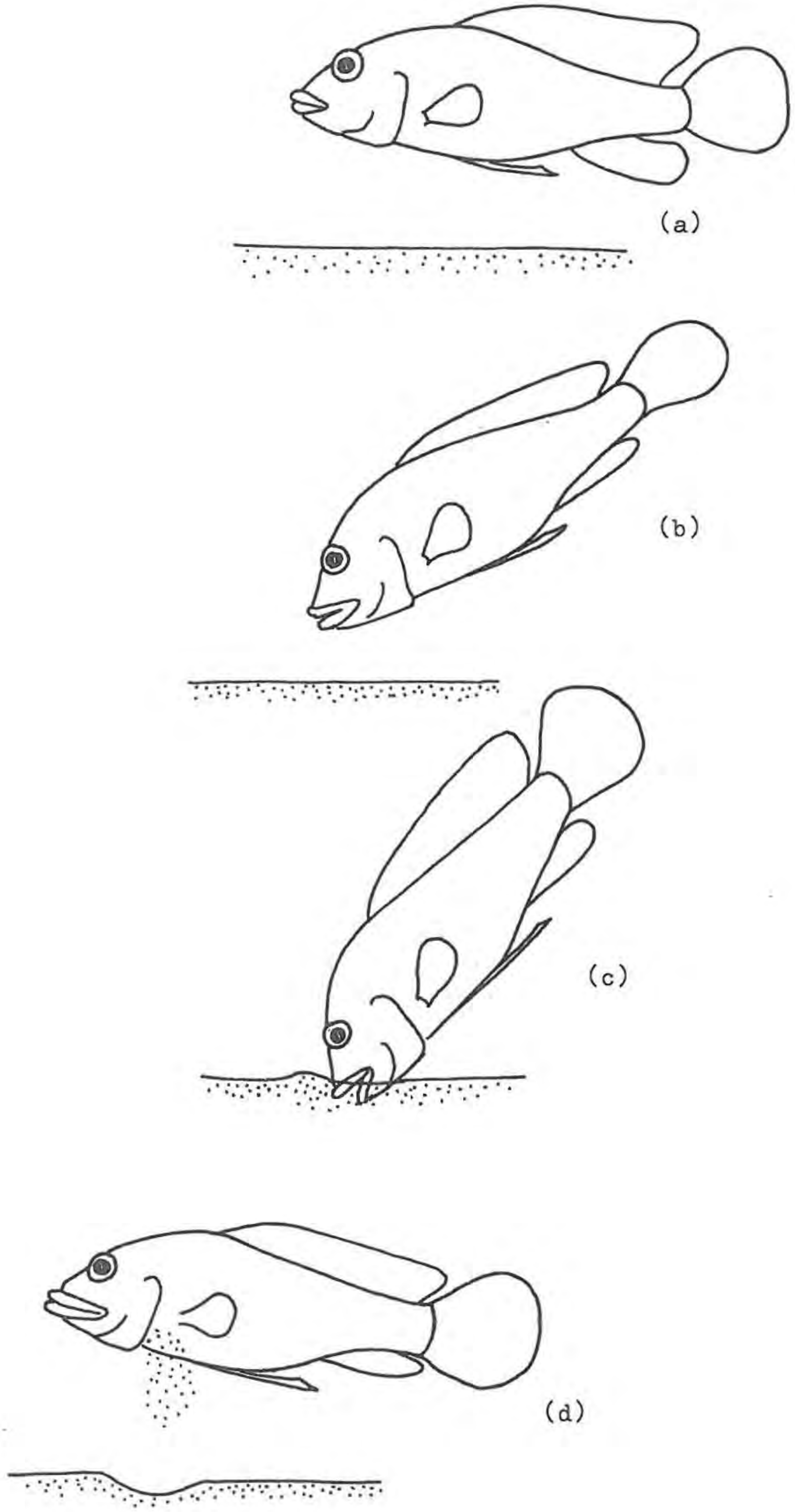
For experimental analyses, a single foraging activity was recorded each time a fish took a mouthful of sand. The duration of the activity was recorded from the moment the fish angled itself, as in fig 13b, until the entire mouthful of sand had passed through the gill orifices. If, however, a fish suddenly performed some other activity while its mouth was still full, such as chasing, then it was recorded that foraging had ceased the moment the new activity was initiated.

Nest-building

P. philander nests are constructed by mouth. Sand is either carried or shovelled to the perimeter of the nest and deposited there. Nest-building activities were recorded each time a fish dug its jaws into the substratum to excavate. The activity was recorded to have ceased once the mouthful of sand had been spat or shovelled onto the rim of the nest. Particles which came to rest in the nests were removed. Though these are strictly cleansing and maintenance activities they were nevertheless recorded as nest-building behaviour.

Figure 13 Foraging behaviour

The successive positions of *P. philander* as it forages in the substrate.



CHAPTER THREE : FIELD OBSERVATIONS

With the background information provided by the behavioural descriptions in the previous section, I was able to examine and compare the behaviour of three allopatric populations of P. philander in their natural enfironment. Other species in the habitat are mentioned only when their behaviour affects that of P. philander. Several laboratory investigations were also carried out to confirm and add to field observations.

The behaviour of P. philander in natural habitats

Observations of aquatic animals in their natural environment have been limited by the fact that the observer has been physically unable to venture under water for more than a brief time. Consequently the main deductions concerning the behaviour of aquatic animals has resulted from surface sightings, and the information gained by examination of the specimens caught by netting, poison or hook which was then correlated with measurements of the environmental parameters. Over the past 15 to 20 years, however, marine biologists have literally moved into the sea as the refinements of Self-Contained Underwater Breathing Apparatus (SCUBA) have extended the time and versatility of underwater observation. In addition, improvements in manned submersibles (Nakamura 1972; Emery 1973), underwater television (Myberg 1972; Nakamura 1972), underwater telescopes (Emery 1968) and an array of underwater sensing devices have all contributed to the opportunities and output of in situ studies. Most impressive of all is the extremely well equipped and massive underwater station at 15 m depth in Lameshur Bay, St John Island (Virgin Islands), where aquanauts have lived and worked for up to 60 days as part of the 'Tektite Program' (Collette and Earle, 1972). As a result of technical advances the information and literature concerning marine life, its behaviour and ecology, have exploded and are already in need of review.

Despite the progress made by submarine ecologists, those interested in the interactions of freshwater animals are still, by and large, standing on the shore or in a boat making surface observations and examining caught specimens. The need for underwater studies of cichlid fish behaviour and ecology has been pointed out by Fryer and Iles (1972) who have also shown that the Great Lakes of Africa provide environs which are biologically as exciting as the sea. Undoubtedly, in response to their publications, underwater research in the Great Lakes will blossom, and already SCUBA divers are exploring the fauna (e.g. Axelrod 1974).

Detailed descriptions of cichlid ethology in the natural environment are scarce. Lowe (1956), Ruwet (1962, 1963) and Coe (1966) have produced surprisingly comprehensive reports of cichlid interactions, considering the difficulty of making observations from without the water. In addition,Fryer and Iles (1972) have commendably synthesized the fragmentary information from a variety of sources and included their own observations to form an excellent general picture. However, in the presentation of the behavioural aspects Fryer and Iles relied heavily upon aquarium studies. Cichlid behaviour in aquaria is well documented (a) because these fish are excellent laboratory animals and (b) as a result of the enthusiasm of aquarists. The study of cichlid fish in aquaria prior to field work produces a familiarity with behavioural displays, activities and sequences and consequently provides a powerful field tool. Indeed for efficient field-studies aquarium observations are an essential prerequisite. Then, as a feedback, observations and experimental work on fish in their natural habitat serve to confirm or disprove hypotheses which originated in the laboratory.

Behavioural investigations of P. philander in their natural environment were carried out with the aid of SCUBA and by means of free diving techniques.

On each dive a watch, compass and depth gauge were worn. Distance measurements were made with a 30m underwater plastic tape. All observations, and distance, time and depth measurements were recorded upon plastic writing slates attached to the diver's forearm. Observations were made whilst swimming on compass transects, by following individuals and groups of fish, and by lying quietly on the substrate watching and recording behaviour. Provided divers did not move rapidly or approach too closely disturbance caused by their presence and expiratory bubbles interfered very little with the behaviour of the fish.

Observations at night and in poor visibility were made with the aid of underwater torches.

P. philander breeding stations were marked by small coloured floats (fig 14 plate 21) placed at the nests of territorial individuals.

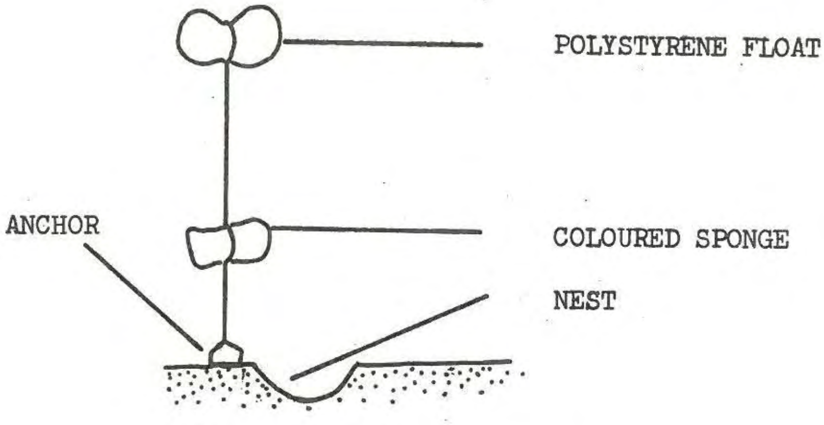


Figure 14 An illustration of a marker placed at the nest of a tagged-territorial male.

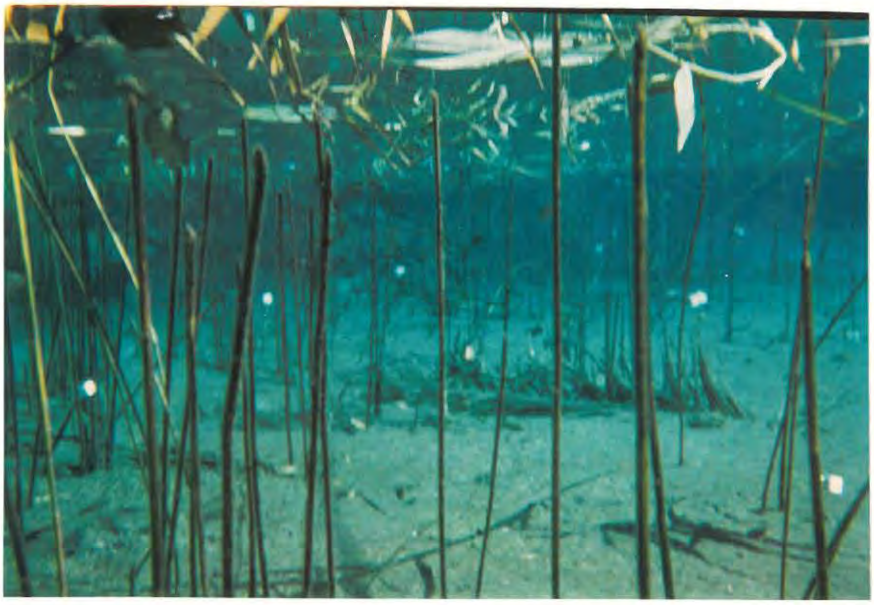


Plate 21 The distribution of marker floats in an arena at Kuruman Eye.

To identify the territorial males they were tagged with FLOY FTF 69 fingerling tags which had been painted various colours. The tag colour corresponded with that of the float placed at the nest. Tags were sewn into the musculature anterior to the dorsal fin.

Plate 22 A tagged male at its nest. The line to the float is visible. Another nest is indicated by the arrow.

Care was taken to avoid damage to the muscles associated with the dorsal fin since this would have affected the ability of the fish to raise or lower its fin for behavioural displays. Under natural conditions tags did not alter the ability of fish to maintain their territories or to court successfully. In aquaria, however, resident tagged males were usually defeated in fights with rival conspecific males.

The behavioural observations described below are the result of a total underwater observation period of 56 hours in Kuruman Eye, 21 hours in Lake Sibaya and 9 hours in Wondergat.

The habitats

Three different habitats were chosen for this investigation: Kuruman Eye, a spring or fountain which flows into what Jubb (1971b) calls a miniature lake; Sibaya is a freshwater lake and Wondergat a deep sinkhole with sheer rocky walls. The location of these water bodies is given by fig 1.

Plate 23 A photograph of Kuruman Eye taken from the northwestern corner. The grassy embankment provided a rhizome cover for fry. The water flow is towards the camera.

Brief descriptions of these water bodies will be given here as Ribbink (1975) has provided greater detail of the habitats and associated cichlid fauna.

Kuruman Eye (plate 23)

Kuruman Eye is a shallow, small clear water body in which P. philander territories were grouped together to form an arena running along the fringe of the reeds and lilies of the south basin (figs 15 and 16). Pairs of Tilapia sparrmanii occupied regions in which cover offered by the embankment, reeds and lilies was more dense (plate 24; fig 15 and 16).

Probably because the water entering the "Eye" from below the ground is always warm (21.9^{o}C), P. philander were found to breed in summer and winter. Only male P. philander were territorial and the centre of each territory is invariably marked by a nest. P. philander nests are saucer shaped depressions excavated in the sand substrate by mouth.

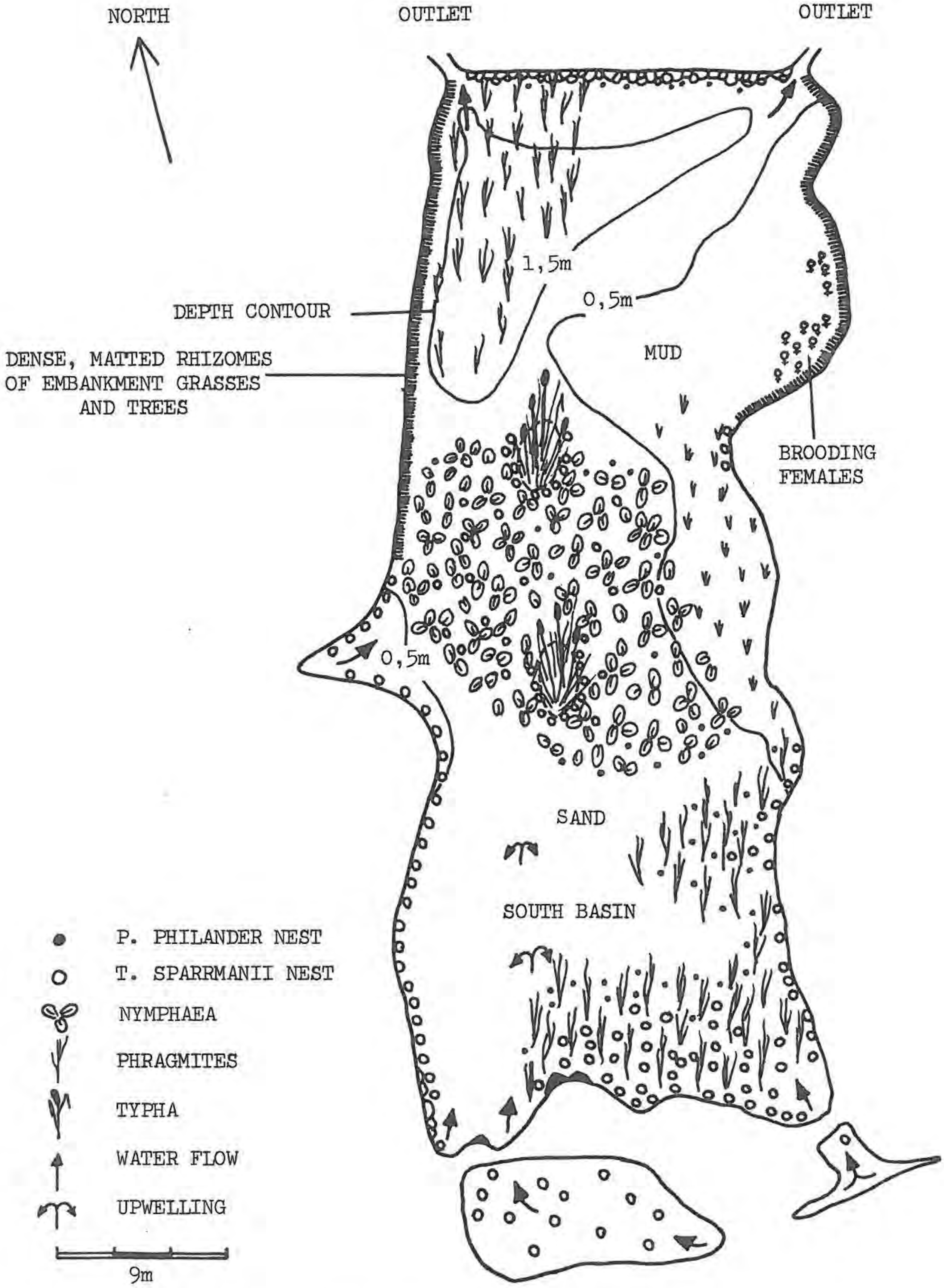


Figure 15 Plan view of Kuruman Eye showing distribution of P. philander nests, T. sparrmanii territories and macrophytes. Direction of water flow and depth contours are also given.

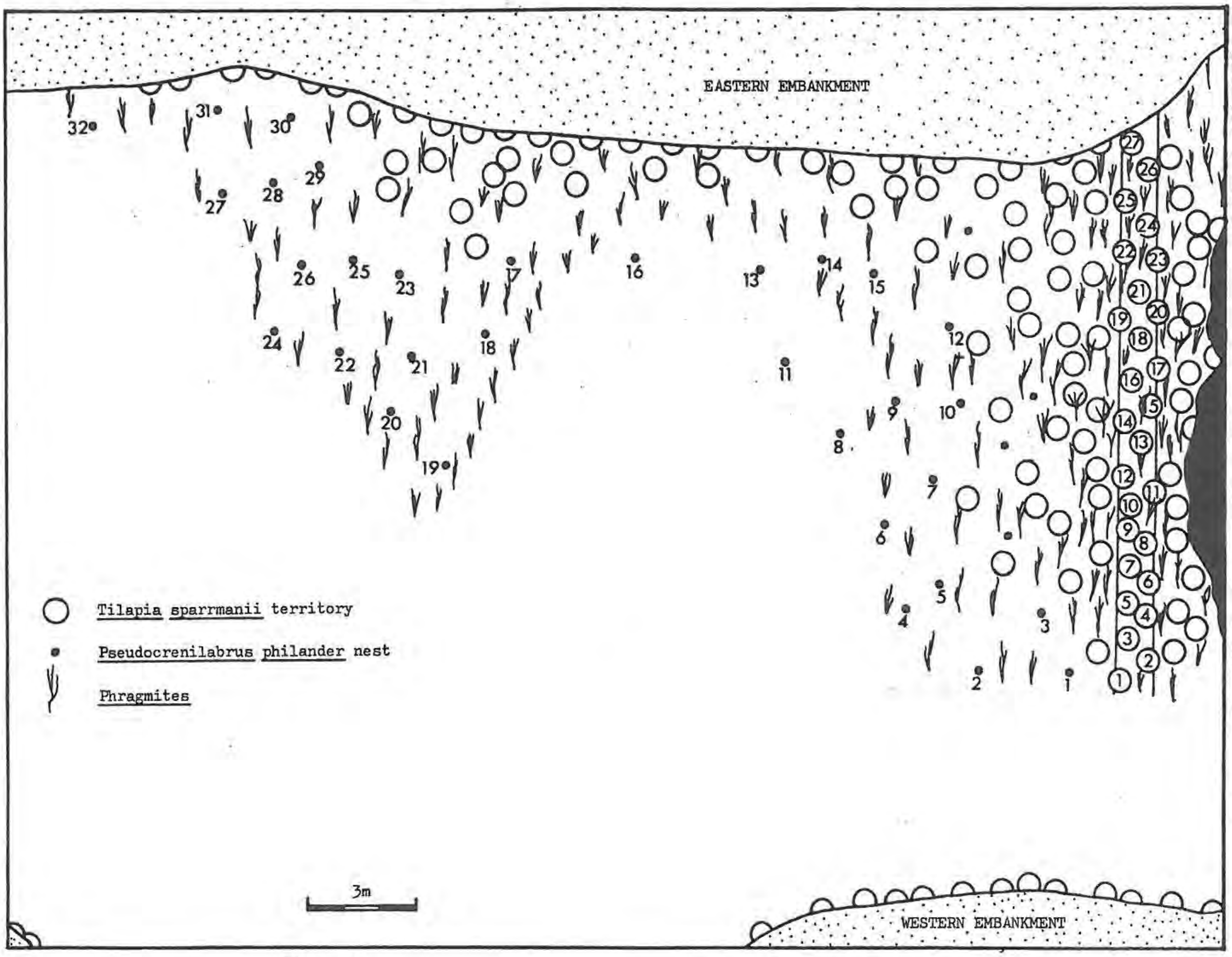


Figure 16

Horizontal distribution of P. philander and T. sparrmanii territories in reed beds of the south basin in Kuruman Eye.

Numbered P. philander territories were marked by floats, and the distances between them measured. Their distribution is drawn to scale. Unnumbered nests of P. philander are in a bispecific arena. Distances between these nests were estimated. Parallel lines through the T. sparrmanii arena represent a transect, 1 x 16 metres in which the nests were counted and measured.

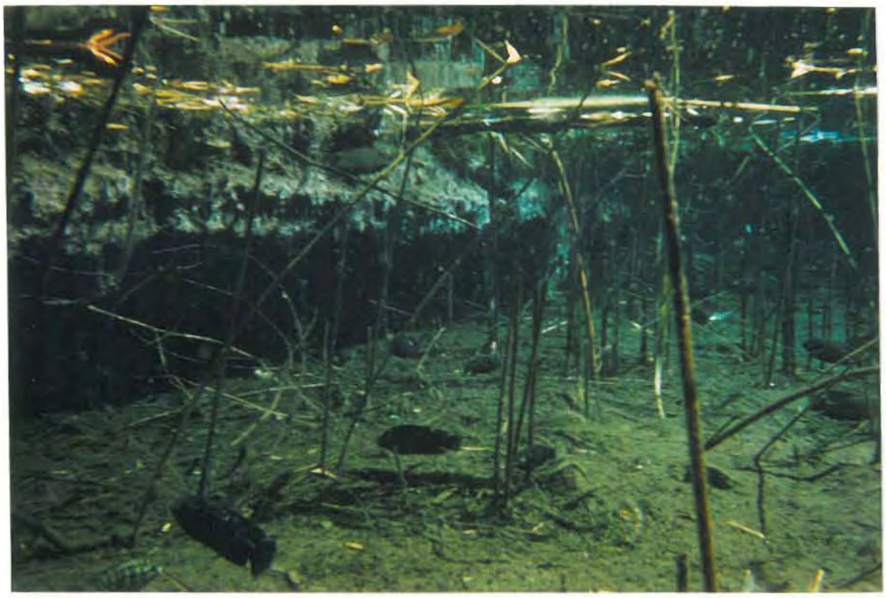


Plate 24 Pairs of *Tilapia sparrmanii* in Kuruman Eye.

Plate 25 SCUBA divers in Lake Sibaya.

Lake Sibaya (plate 25)

Lake Sibaya of Northern Zululand is a land locked fresh-water lake 65 sq. km in area, and has a mean depth of 13m with a maximum depth of 40m (Hill 1969). P. philander were found from the shallowest fringes to the deepest waters of the lake, and territorial arenas were found on the gently sloping sand substrate from depths of 3.5 to 24.0m in summer. This species was not territorial in winter in Sibaya.

Wondergat (plate 26)

Wondergat is a 65m deep sinkhole in the watershed of south-western Transvaal. It was of interest to find out how P. philander, which normally spawns and holds territories on a relatively level sand-substrate, had adapted to the sheer, vertical rock walls in the absence of both macrophytes and sand in the sinkhole.

Though the walls were steep they sometimes formed massive overhangs and also had regions which jutted from the vertical face to form platforms or ledges. These platforms, and rocky outcrops were used to support the nests of territorial male P. philander. Males ranged out from these ledges to chase intruders and court females.

Plate 26 Wondergat.

Pseudocrenilabrus philander: population structure in natural habitats

P. philander formed several distinct natural groups:

1. Territorial males These were large sexually mature fish which were conspicuously coloured and which actively defended and maintained territories.
2. Supernumerary males Sexually mature males of which many were in breeding dress while the remainder were neutrally coloured— although the male sexual colours were distinguishable. None of these fish was territorial.
3. Gravid females Adult females which had swollen abdomens due to the presence of mature eggs. It was this sector of the female population which were responsive to the males' courtship.
4. Brooding females Once females had spawned they held eggs in their mouths until the fry developed. Thereafter the fry were cared for by their parent. Maternal fish in all stages of parental care have been referred to as brooding females.
5. Spent females Adult females which had recently ceased their parental activities. These fish were relatively hollow bellied and were unresponsive to male courtship displays.
6. Fry Fish estimated to be less than a month old and shorter than 15mm SL.
7. Juveniles Subadult fish which were old enough to be sexed by visual means, but were sexually immature.

The behaviour of these groups will be described below.

The behaviour of the territorial males

Territories and nests

Territorial males were recognised by their vivid coloration and aggressive way in which they dominated their territories. After each brief excursion to chase, court or forage, they returned to their nests and thus identified themselves with their nests. It was therefore relatively simple to locate and tag a territorial male, and to mark its nest. P. philander were found to defend actively territories of approximately a meter radius in which one or more nests were centrally placed. Territories were usually established in groups to form arenas. The term 'arena' is used here in the sense followed by Fryer and Iles (1972); that is, a group of territories constitute an arena. Arenas are monospecific if occupied by one species only, but bi-, tri- or multispecific if shared by two, three or more species. Usually P. philander arenas were monospecific, though overlap regions between Sarotherodon mossambicus and more frequently T. sparrmanii were found. Occasionally territories of P. philander which were isolated from the arenas were formed, usually these were unstable and shortlived. Stable arenas were established in regions which were considered to be the most suitable, if not always optimal.

The establishment of a territory was not observed in Lake Sibaya or Wondergat, but in Kuruman Eye, nests were constructed within the first two to three hours of occupation of a territory. Throughout this period nest construction was punctuated by frequent attempts at courtship and bouts of aggressive behaviour. Work on the spawning-depressions never ceased because even established nests were cleansed and reconstructed frequently each day.

In Lake Sibaya nests were little more than a circular disk of cleansed sand, and were usually less than 100mm in diameter with a depth of 5mm or less. By contrast, the Kuruman Eye population constructed large, deep nests; the largest of those measured was 127mm in diameter and 56mm deep. At Wondergat, cleansed patches on the rock sometimes marked the nest-site and occasionally, where a little sand had collected on the ledges, nests were surrounded by a rim of sand. Frequently, however, the spawning sites were recognised only because the males' behaviour indicated their function.

Lake Sibaya a single nest marked the centre of a P. philander territory, but at Kuruman Eye two to four nests were not uncommon (table 1).

TABLE 1

The number of nests found in ten marked territories of male P. philander in summer and in winter at Kuruman Eye

	SUMMER		WINTER	
Territory number	Float and tag colour	Number of nests per territory	Float and tag colour	Number of nests per territory
1	WHITE	4	GREEN	2
2	YELLOW	1	RED	2
3	BLUE	1	WHITE	2
4	YELLOW	1	BLUE	1
5	GREEN	2	YELLOW	4
6	RED	2	RED	2
7	WHITE	3	GREEN	1
8	GREEN	2	WHITE	2
9	BLUE	4	YELLOW	3
10	YELLOW	2	RED	1

Fish with more than one nest usually favour a particular nest, the principal nest, to which they preferentially lead a female and in which they rest. Generally, secondary nests were within a radius of 40cm of the principal nest. In one exceptional case, however, a male with a territory remote from the arena, had three secondary nests which were 112cm, 135cm and 120cm from the central nest. It is possible that in the absence of neighbours this fish occupied several territories.

Any one of the secondary nests could become the favoured spawning site, or an entirely new principal nest could be constructed some distance away from the original nest which was then abandoned or treated as a secondary pit. The relocation of a territorial hub probably resulted from a change in the relationship of a territorial male with one or more of its neighbours, however, no evidence has been found to confirm this suggestion. At Sibaya, males

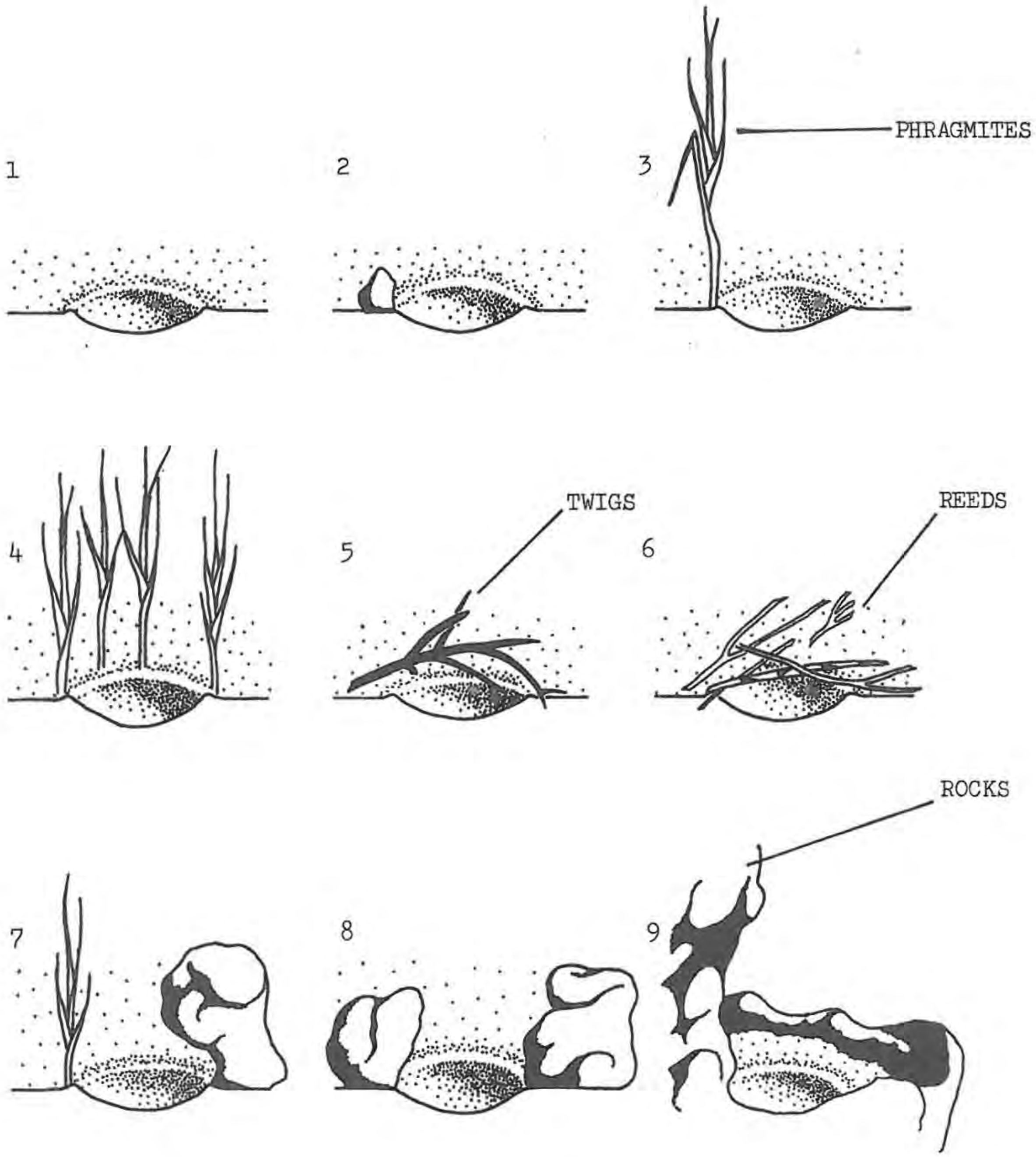


Figure 17 *P. philander* preferred some cover for their nests, but were frequently forced to construct their nests in exposed regions.

Nest types 1 to 8 were found in Kuruman Eye.
Nest types 1 to 6 were found in Sibaya except that *Myriophyllum* replaced *Phragmites*.
Nest type 9 was unique to Wondergat.

in the roped-off transect (see Ribbink 1975) retained a single nest which was not moved, the territories appeared to be stable and static (observations at Kuruman Eye and Sibaya were over seven and six day periods respectively). Stability of territories at Wondergat was not determined.

Where possible nests were constructed alongside or beneath a shelter in which the male could rest or spawn. Optimal nest conditions were not always available and many territorial males were fully exposed when in their spawning stations (fig 17).

As far as it was possible to discern, the execution and sequences of behaviour patterns in natural waters appeared inditinguishable from those performed in the laboratory. The greater space available in natural systems, however, meant that males chased and ranged further than in aquaria.

Diurnal behavioural rhythm

In Kuruman Eye, where P. philander bred in summer and winter, the behavioural activities of nine tagged territorial males were recorded for two minute periods at different times throughout the day.

Figures 18 and 19 illustrate that during the morning, irrespective of season, the number of territorial activities (courtship, nest-building and aggressive activities such as chasing and fighting) is greater, with a peak at about midday. In the afternoons the males were not as active in their territories.

The increase in behavioural activity is due largely to aggression and courtship (fig 20 and 21). Activities associated with nest-building remained fairly constant.

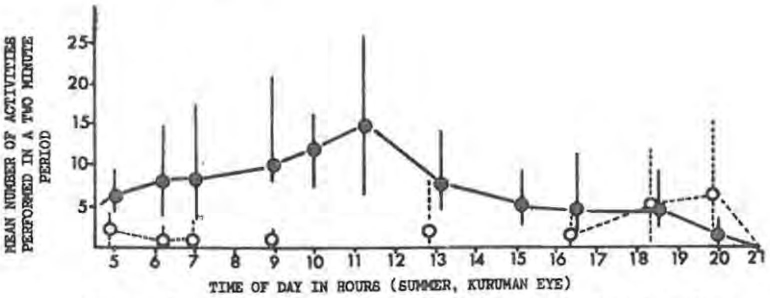


Figure 18 Summer diurnal rhythm of territorial *P. philander* males in Kuruman Eye. The closed circles show the mean number of territorial activities performed by the nine fish. The open circles represent the mean number of foraging activities performed. The vertical lines through the points give the total variation shown by the nine fish.

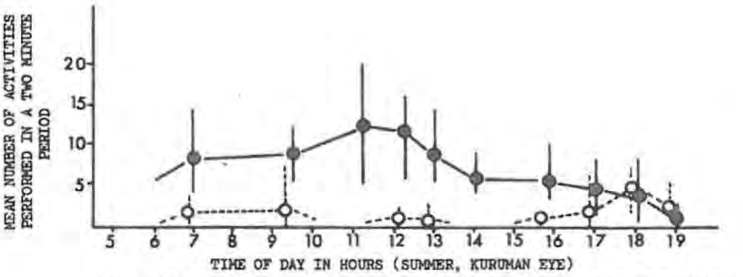


Figure 19 Winter diurnal rhythm of territorial *P. philander* males in Kuruman Eye. The closed circles show the mean number of territorial activities performed by the nine fish. The open circles represent the mean number of foraging activities performed. The vertical lines through the points give the total variation shown by the nine fish.

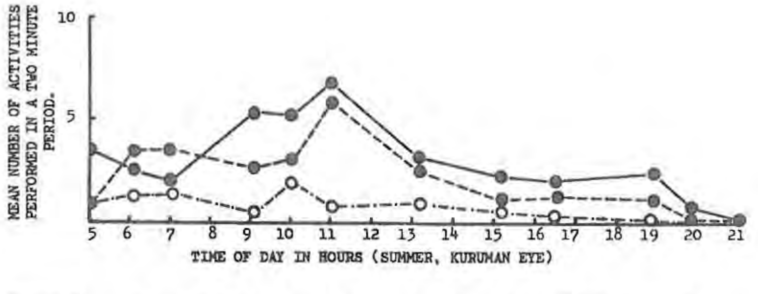


Figure 20 Territorial behaviour is composed of three forms of behaviour. The component behaviour patterns have been separately illustrated to determine their respective contributions to the diurnal rhythm. Aggressive behaviour ●——● , courtship behaviour ●-----● , and nest-building behaviour ○-·-○.

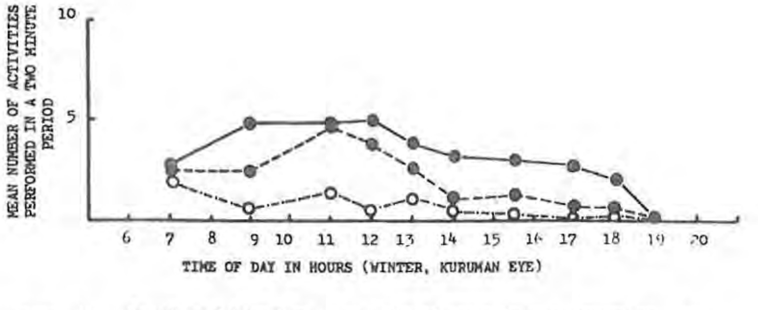


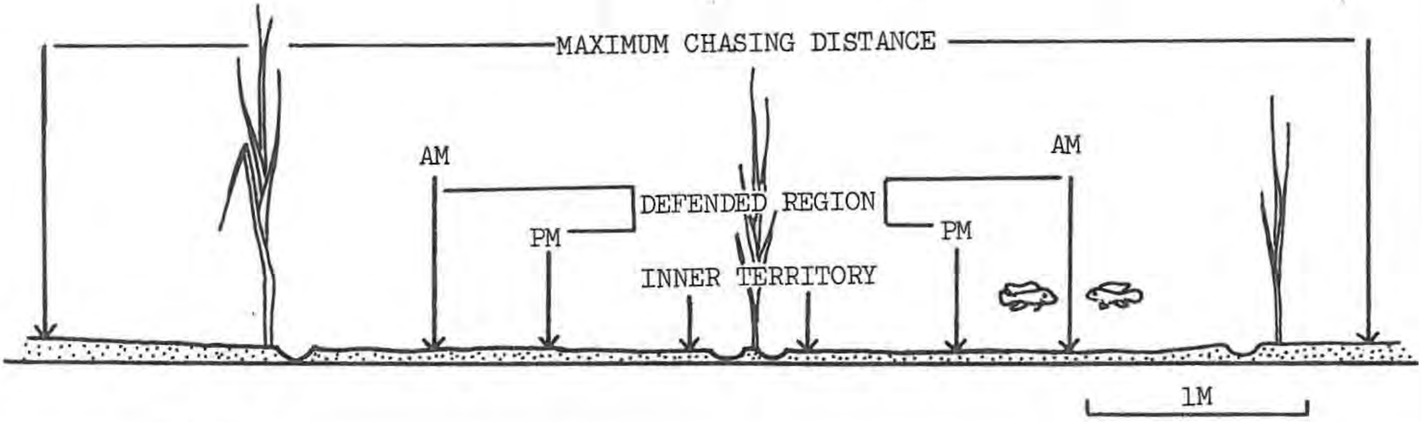
Figure 21 Territorial behaviour is composed of three forms of behaviour. The component behaviour patterns have been separately illustrated to determine their respective contributions to the diurnal rhythm. Aggressive behaviour ●——● , courtship behaviour ●-----● , and nest-building behaviour ○-·-○.

At dawn, and particularly in the evenings, territorial fish foraged extensively (figs 18 and 19) and also permitted non-territorial fish to enter and feed in the arenas. Throughout the afternoon tolerance to trespassers increased, so that the defended territory became effectively smaller (fig 22). At no stage, however, were conspecific intruders allowed to remain in the inner regions of the territories. In Kuruman Eye a responsive, gravid female which arrived at the arena in the afternoon would usually stimulate a male so that it increased its territory, clearing it of trespassers to enable courtship to proceed undisturbed.

In Lake Sibaya territories of P. philander within the roped off transect (Station two, Ribbink 1975) were marked. As a result of five morning and six afternoon dives it was established that, like territorial fish of Kuruman Eye, the males remained in their territories throughout the day and that they were very active and dominant in the mornings.

The diurnal rhythm at Sibaya was similar to that of Kuruman fish, but whereas Kuruman males appeared to become more tolerant of intruders in the afternoons, it seemed that at Sibaya the arenas were so inundated by intruders that territorial males had no option but to accept them. Indeed, territorial males were often seen in desperate defence of their nest-sites. In contrast to Kuruman Eye, the overwhelming number of afternoon intruders into the Lake Sibaya arenas prevented territorial males from paying much attention to females. So marked and so sudden was the change in Lake Sibaya that initially it was thought that territorialism occurred only in the mornings and that all but a few of the males formed foraging schools in the afternoons. Only once the territories had been marked and the males identified with their nest-sites it was established that the territorial males remained on site throughout the day.

At night P. philander rested on the substrate or against macrophytes. Thirteen of the fifteen tagged males in Kuruman Eye were found in their principal nests, which suggests that the nests are the preferred resting places. The other two males were not seen at night.



<u>Figure 22</u>

The boundaries of <u>P</u>. <u>philander</u> territories were not fixed. In the mornings aggression of the males increased territory size. In the afternoons, however, intruders were allowed to approach the inner territory more closely. This illustration is based on observations in Kuruman Eye.

Dirunal rhythm was not investigated at Wondergat. It was observed, however, that males vacated their nest-sites in the late afternoon and it has been assumed that this was done to enable them to feed elsewhere, because in Wondergat it was not possible to depend upon the territory for food.

A discussion of the dirunal rhythm

Behavioural rhythm have been known for centuries: especially prominent was the awareness of seasonal reproductive and migratory cycles and, of course, the menstrual cycles. Diurnal or circadian rhythms have been investigated since 1900, and rhythms appear to exist for almost every animal or function in which they have been sought (Klopfer and Hailman, 1967). A profusion of reports is to be found in the literature concerning the seasonal changes of behaviour in fish. On the other hand, with the exception of the work on the coral reef fish (Collette and Talbot 1972), the daily rhythms of fish behaviour appear to have been largely overlooked, or just tacitly accepted. This observation is surprising since marine and freshwater anglers have an awareness of the circadian and tidal periodicity of fish behaviour, and organise their efforts accordingly.

Attention to circadian rhythms is important in the standardization of experimental procedure. For example, as a result of the information obtained in the field it became apparent that all investigations designed to evaluate the behaviour subservient to the territorial drive should be conducted between 09.00h and 14.00h. Similarly those experiments concerned with a quantification of feeding behaviour should be confined to the late afternoon and evening. Furthermore, it appeared important, in the absence of evidence to the contrary, that P. philander in aquaria should be fed at a time which corresponds to the daily feeding period in the natural environment. It is possible that one of the factors which regulate the rhythm is the daily filling and emptying of the gut, and therefore irregular feeding times would conceivably disrupt the normal rhythm, and upset what would otherwise have been a standard procedure.

The findings of this subsection illustrate the importance of field observations in the development of an awareness of behavioural traits which had previously been unnoticed in the laboratory. It is likely that without the knowledge gained from Lake Sibaya and Kuruman Eye the circadian rhythm might have evaded discovery. It is often argued that animals in captivity behave abnormally. To a limited extent this is true. However, an enormous amount of invaluable information comes from the study of laboratory held animals. This information has even greater value when field observations can be used to strip the behavoural artefacts from the genuine behaviour patterns or trends.

Finally, Lowe (1956) in her study of territorial male Tilapia karomo found an increased activity from midday towards evening. This is exactly the opposite of what was found for P. philander which were more active in the mornings increasing their activity to a peak at midday. The importance of the asynchronization of circadian rhythms as a behavioural isolating mechanism amongst cichlids is an untapped field of investigation which is filled with potential. The potential is especially great when viewed against a background of the cichlid complexities of the Great Lakes of Africa. Not only would an asynchronization of behavioural rhythms act as an isolating mechanism, but it could also reduce competition between species and explain how two or more species could occupy the same niche and feed from the same food source in an equitable manner. The necessity to harness the potential and power of ethological tools and apply these to the complexities of cichlid ecology and speciation in the African Great Lakes is becoming apparent.

The effect of other fish on territorial male behaviour

Returning to observations of territorial *P. philander* in natural waters, it was apparent that in addition to the influence of the inherent rhythm on behaviour, their behaviour was also affected by other fish. In the field, visits by the non-territorial fish and the activities of their neighbours affected the behaviour of the territorial individuals.

Casual cichlid intruders were approached by a territorial male swimming rapidly in a threatening manner. Usually intruders fled upwards and out of the territory without offering any resistance and were always chased. Because casual intruders were the most frequent visitors, chasing was the most commonly performed intraterritorial behaviour (figs 20 and 21). It was usual for an intruder to be chased for approximately one metre, however several chases of three to five metres were recorded and two of over five metres were measured. To chase such great distances the pursuer would have to traverse several territories. Usually they evoked little aggression from their neighbours on the outward or return journeys, provided they remained a metre or more above the lake bottom. On the other hand, should a sexually coloured male attempt to cross its neighbours' territory near the substrate, it would be chased. The chase usually ceased once the fleeing male reached its own territory and turned to face its pursuer, which would then retreat.

Boundary fights between neighbours could develop in the manner described above, but most frequently resulted from what appeared to be accidental meetings between neighbours. In the mildest form of boundary encounter the neighbours would display frontally for a moment then turn away and move apart. More overt encounters involved the sudden approach of one of the fish in frontal display towards its neighbour, which would back away. The retreating fish might swim away, or, by suddenly advancing in frontal display cause the initial aggressor to retreat. After a series of alternate backward and forward movements of this nature, the two fish might find diversion in their respective territories. Alternatively the contest could develop into a series of mouthfights with tail-beats and body bites. Such fights were terminated when one of the individuals swam off to redirect its aggression elsewhere. Though brief displays were common between neighbours, fierce boundary fights were witnessed only four times in Kuruman Eye, once in Lake Sibaya and not at all in Wondergat. Animals at the edge of their territories are usually considerably less aggressive than at the centre (Tinbergen 1951; Manning 1967; Hinde 1970), and therefore displays at mutual boundaries would probably be more frequent than fierce fighting.

Though territorial fish may gain or lose ground as a result of boundary fights in aquaria (Baerends and Baerends van Roon 1950; Fryer and Iles 1972; Ribbink 1971), I did not discover whether territories changed size as a consequence of naturally occurring boundary encounters.

Usually, neighbouring males of an arena were of much the same size and status with little evidence of a hierarchy amongst the territorial individuals. In Kuruman Eye, however, a particularly large male completely dominated a sector of the winter arena. Its territory was almost twice the size of that of its neighbours in addition to which it was not challenged when it trespassed, unless the nest site of a neighbouring fish was approached too closely. To find an exceptinnally large male was very unusual.

Challenges from supernumerary males were rare. Only six full-scale fights between a challenger and territorial male were observed at Kuruman Eye, and only one intraterritorial encounter was observed in Lake Sibaya. All seven encounters occurred in the late afternoon. Of the seven fights, five were in progress when first discovered and the other two were observed from start to finish. The one lasted 2 minutes 14 seconds and the other 3 minutes and 4 seconds. Both fights were initiated when a supernumerary sexually dressed male refused to flee when chased, but challenged the resident. The conflicts followed the ritualized sequence of lateral display, tail-beating, frontal display with mouth fighting and circling to butt and bite. Two of the seven encounters were with tagged males and in both cases the resident tagged fish retained its station. It was not possible to be certain whether the untagged residents had won the other fights, but the immediacy and direct manner in which the fish returned to the territorial nests after chasing away the defeated fish suggested that this was the case.

An unusual encounter was witnessed in Kuruman Eye in July 1973. A newly formed pair of T. sparrmanii took up residence under a rocky overhang which was already occupied by a tagged P. philander male which had built its nest there. Though the relationship appeared awkward the two species shared the nest-site for approximately 36 hours with few aggressive exchanges. Eventually the P. philander male, which was too small to contest the right of the new owners, left and immediately challenged his untagged neighbour. The fight lasted 28 minutes and was won by the tagged male. It is unusual for a challenger to defeat a resident territorial fish in an intraterritorial fight. Presumably in this instance as the intruding male was not a casual supernumerary but a territorial male in search of better site, its motivation was such that it managed to reverse the normal trend. The severity of the fight was illustrated by its duration - nine times longer than the previous longest recorded intraterritorial fight. It is assumed that the defeated male joined the supernumerary schools.

The new owner, that is the tagged P. philander male, took over the nest of the previous occupant and was eventually seen to spawn in that nest.

Interspecific reactions of P. philander and T. sparrmanii

The manner in which the pair of T. sparrmanii forced a male P. philander to vacate its territory (described in the previous subsection) demonstrates how interspecific competition for space could increase intraspecific competition, and tighten intraspecific selection of territorial males.

Where the two species occurred together, T. sparrmanii nests were often overlapped by P. philander territories, though the principal nest-site of *P. philander* was never within 40cm of the edges of *Tilapia* nests.

Territorial *P. philander* tolerated *T. sparrmanii* which shared their territories, and treated them aggressively only when they (*T. sparrmanii*) approached their nests too closely. *P. philander* were especially aggressive towards their *Tilapia* and conspecific neighbours and other intruders when spawning. Under these circumstances their increased ferocity usually kept the *Tilapia* at bay and could even force them to take avoiding action. Frequently, however, *T. sparrmanii* pairs paid scant attention to aggressive threats from the smaller species and on occasion inhibited further attacks with a brief threatening display.

Those individuals of *P. philander* which trespassed into *T. sparrmanii* territories were usually chased, though non-breeding pairs occasionally permitted *P. philander* to forage in their nests. In dense *T. sparrmanii* arenas *P. philander* were actively excluded.

From the observation and behavioural analyses of territorial males a number of general principles emerged. Most intruders into a territory were not motivated by the drive to possess a territory and therefore the threatening approach of the resident was sufficient to cause them to flee. The few intraterritorial fights observed were all in the late afternoon and early evening. Studies of the circadian rhythm of *P. philander* have shown that at these times the territorial males were less zealous in the defence of their territories and that territories were effectively reduced in size with only the central area being well defended. It would be opportune for a supernumerary male to attempt to drive a wedge between territories at this time of day. Such an attempt would result in a fight with the resident male. The outcome of the fight would depend upon the concentration of territories within an arena; a poorly inhabited arena with a few well spaced territories would be more susceptible to the claims of supernumeraries than well populated arenas which could not absorb further territories.

Laboratory reared *P. philander* were found to be capable of breeding from 12 to 15 weeks of age. The males at that stage were as small as 25mm SL. It took a further two years for the fish to reach a standard length of 75mm which appeared to be the average size of territorial males in the field. Acknowledging that the fish might not grow at the same rate under laboratory conditions as they would in natural waters, these data nevertheless indicate that males would have a relatively long wait from the time they became sexually mature to the time when they could occupy a territory and breed. Implicit in this observation is the fact that the three water bodies studied had a large reserve of males capable of breeding, but prevented from doing so by the larger occupants of the arenas.

Many cichlids have fixed, recognisable physical boundaries to their territories (Baerends and Baerends van Roon 1950, Fryer and Iles 1972) and observations of territories of *S. mossambicus* and *T. sparrmanii* confirm these findings. However, *P. philander* do not. Firstly, the boundary positions are believed to alter during the course of the day. Secondly, neighbouring territories have no "invisible barrier" between them. Neighbours will trespass when chasing and occasionally when foraging, which implies that neighbouring territories overlap and no boundary is recognisable to the males. The degree of trespassing will depend upon the respective ranks of the neighbours and also on whether the resident is close to or far from the site at which its neighbour enters the territory. Thus in *P. philander* the boundary is not fixed, indeed there is probably no boundary at all: the size of the defended area fluctuates as the territorial drive waxes and wanes with altering circumstances.

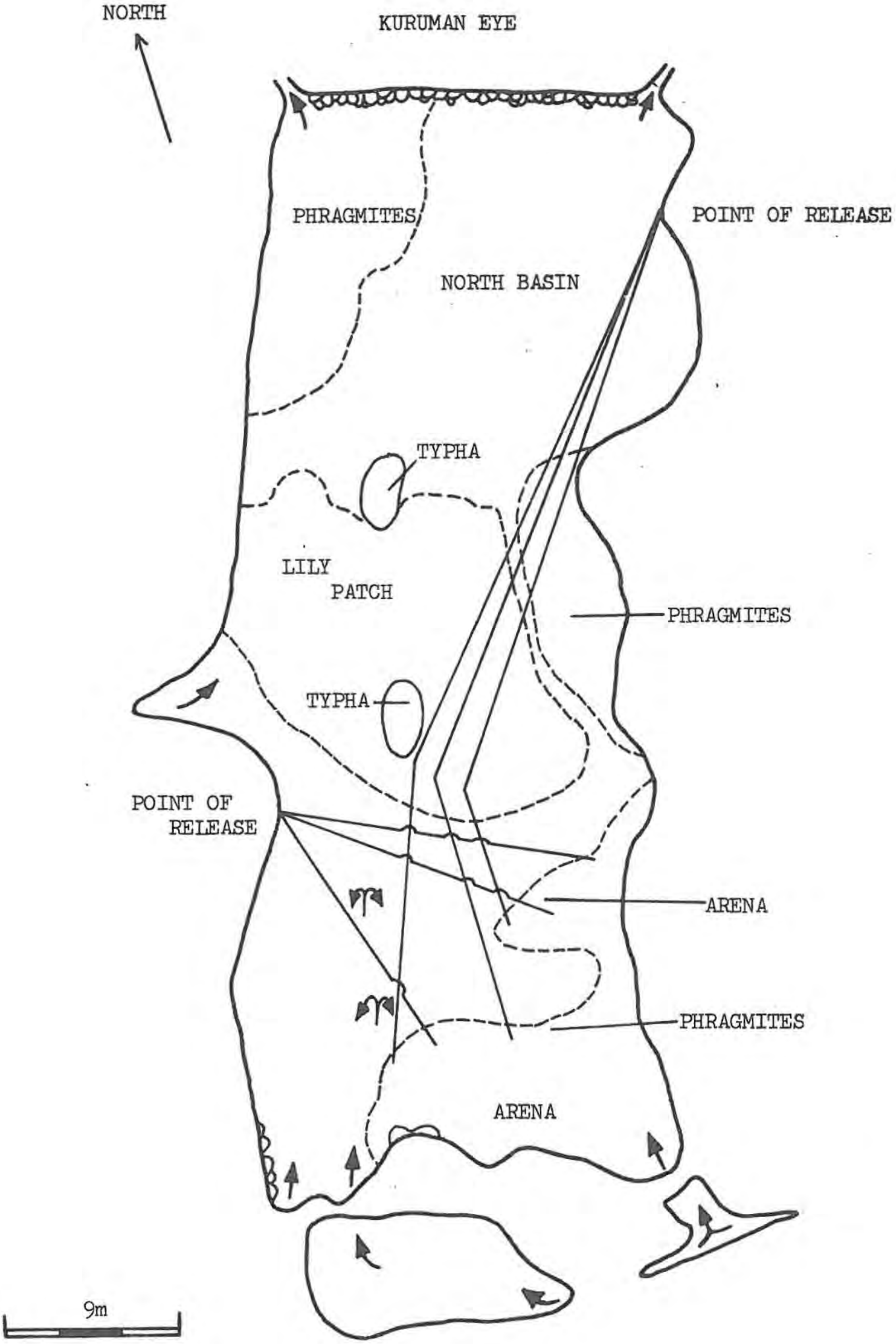


Figure 23

Approximate routes and distances covered by territorial males returning to the territories from which they had been removed in Kuruman Eye.

Territorial males displaced from their territories

To determine whether a territorial male would give up territorialism and join the supernumerary schools or find its way back to its territory after being removed from it, six tagged males at Kuruman Eye were removed from the arena and placed with the non-territorial fish at some distance from their territories (fig 23). All six fish reclaimed their territories within 49 minutes of their release. Those fish which I followed swam directly towards their territories though they occasionally stopped to forage and even to court.

Five other tagged territorial males were caught and held overnight. On returning these fish to the arena the next morning it was found that all five territories had new owners. Only two of the five previous owners made an attempt to regain their original holdings and these were quickly defeated. Because these fish made no attempt to regain their territories and two made half-hearted attempts,it was assumed that the territorial drive of the fish had dissipated while they were held in captivity. All five tagged males joined the supernumerary schools and were seen periodically thereafter.

These findings show that P. philander can navigate over short-distances and do recognise the location of their territories. Whether P. philander males could find their way over the greater distances possible in Sibaya is not known.

This experiment also demonstrated that amongst the supernumerary males are individuals which will sieze an opportunity to occupy a territory. Territorial fish defeated in a fight were found to join the supernumerary shoals.

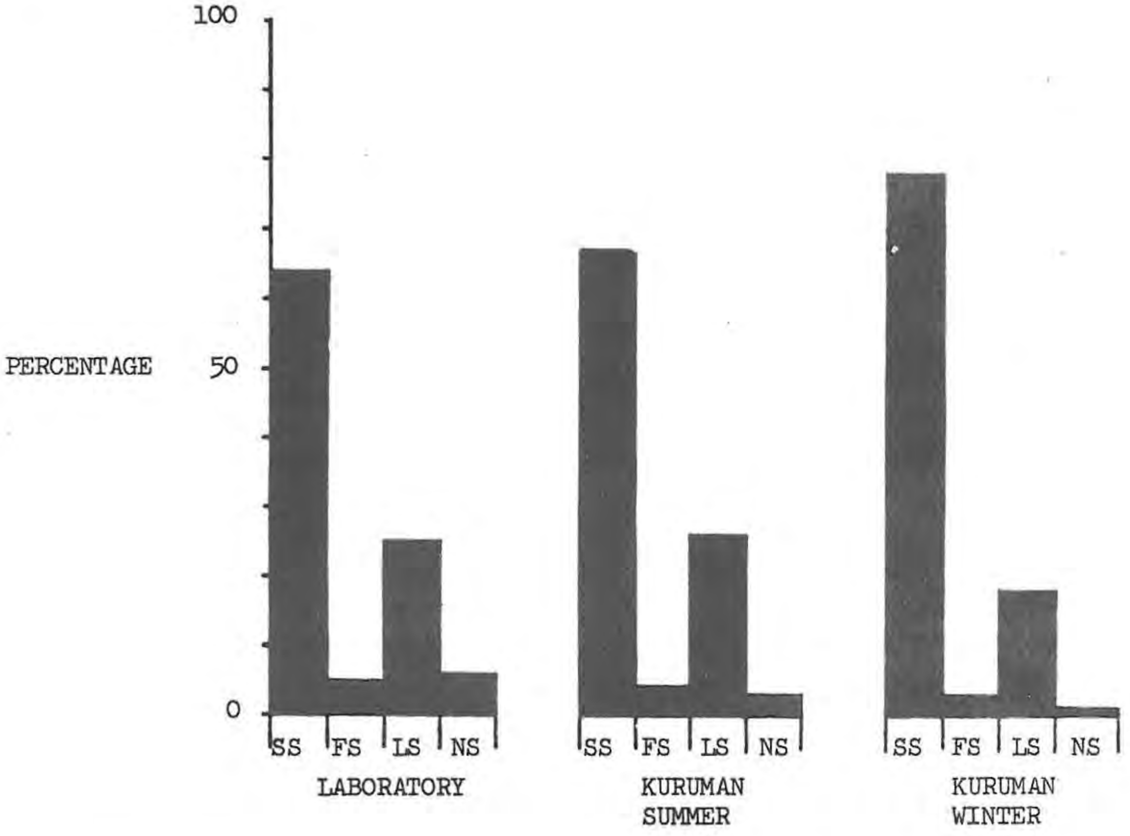


Figure 24 A comparison of the percentage of each of the invitation courtship patterns of territorial, Kuruman male, *P. philander*. Note the similarity of the laboratory and field frequency patterns.

SS = side shake
LS = lead swim

FS = follow shake
NS = nest shake

Courtship and spawning in natural waters

As far as I could judge, courtship displays and sequences in the field were identical to those performed in the laboratory. In the natural environment groups of non-territorial fish were continually passing over the arenas approximately 0.6m above the substrate. Usually these groups were small containing only a few members, but in Lake Sibaya large shoals estimated at several hundred individuals also visited territories. Territorial males swam to meet groups of visiting fish to initiate courtship and stimulate the following response in gravid females. Often females followed to the nest then left almost immediately to rejoin the school. A little further on they might respond to the courtship of another male, enter its nest for a brief period, then hurry after the school. Every now and again a female would remain to spawn.

Four entire spawning sequences were observed in Kuruman Eye, in which the time taken from the laying of the first batch of eggs to the stage at which the female left the territory with the fertilized eggs in her mouth was 34, 42, 46 and 51 minutes. These times were found to be comparable with the duration of spawning sequences recorded in the laboratory (Ribbink 1971, reported that the average duration was 48 minutes).

Though entire courtship and spawning sequences were not observed in Sibaya and Wondergat, many fish in courtship and often involved in spawning were seen. So similar was the execution of these behaviour patterns by each allopatric population that I was unable to distinguish between them.

The most commonly performed courtship pattern was the side-shake. The mere appearance of a female in the territory frequently elicited this initial invitation pattern, whereas the subsequent patterns were dependant upon a positive response from the female for their initiation. Usually the merest indication of a response from the females was sufficient to elicite the follow-shake and/or lead swim (Ribbink 1971; fig 5 of the present work).

A comparison of the frequency of occurrence of the invitation courtship patterns performed in the laboratory, and in Kuruman Eye in summer and in winter is given in fig 24 . All three histograms show the same trends, but in the winter it became apparent that the percentage of side-shakes appeared to have increased at the expense of the follow-shakes, lead swim and nest shake. This observation may be tentatively attributed to the decreased number of receptive females which were available in winter, relative to summer. As a result a large number of side-shakes were performed, but the unresponsiveness of the females meant that the subsequent patterns were not frequently released.

P. philander exhibit both polygyny and polyandry, and the specific name, philander, is descriptive of both sexes since each consorts with many of the other sex.

A female will spawn only once she is fully stimulated to do so. By following receptive females through the arenas it became apparent that they visit a number of males before they eventually spawn. The sojourn at the nests may be very brief or last as long as twelve minutes. While the female remained in the nest the pair would go through the motions of the sexual activities, but eggs were not laid and presumably little or no milt was ejected. After these periods of sexual exchange the female would suddenly leave the nest and respond to another male further along in the arena. It seemed likely that as they visited one male and then another, the female P. philander became increasingly sexually motivated. Furthermore by wandering through the arenas in this manner the females were placed in a better position to select a spawning partner and its nest. As yet it is not known how important the nest is in influencing a females' choice of a mate.

In aquaria where only one male dominates, the female would be restricted to one nest and one male. Female P. philander in aquaria may begin to visit the nest three to four days before they spawn. This is a behavioural trait analagous to the visitations to many males in the lakes. Initial visits and bouts of courtship in an aquarium nest-site were brief. Later sojourns in the nest became longer. When eventually a female accepted a male and its nest she would remain there until spawning was completed, and during this time would participate in the defence of the nest-site if required to do so. By contrast, the females of many of the Haplochromis have such tenuous relationships with their mates and their territories that they never assist in the defence of the spawning-site, and as often as not they wander promiscuously from male to male laying small batches of eggs to be fertilized by each of their different partners (Wickler 1963, Fryer & Iles 1972).

One cannot be certain that female *P. philander* visit numerous males as a behavioural ploy to increase sexual motivation, though the evidence suggests that this is the case. Furthermore, Aronson (1949) found that the ovaries of *Tilapia macrocephala* would develop only if the fish received stimulation from their male conspecifics. Possibly, development of the reproductive system of *P. philander* females is hastened by visual, tactile and olfactory stimuli provided by a succession of visits to various territorial males.

Protracted periods of prespawning activity necessary to produce the correct physiological and behavioural receptivity does not appear to be a prerequisite of all female cichlids. Lowe (1956) observed a female *Tilapia karoma* which swam over several territories in an arena to a particular nest where it spawned immediately, with almost no preliminary display. The entire spawning sequence, from arrival to departure, lasted only two minutes. The directness and rapidity with which this mating took place implies that the female had some previous association with that male; either immediately before the observation took place, or, it is possible that they had spawned together on a previous occasion. This rapid spawning without preliminary courtship appears to have been exceptional, because Lowe (1956) also reports that *T. karoma* males may lead into the nest a female which is not ready to spawn. Then, in a manner similar to that of *P. philander*, the pair would go through many of the motions of courtship and spawning after which the female would leave without laying eggs.

It is unlikely that male *P. philander* select their mates. They attempt to court all females which enter the territory and responsive females select themselves for spawning. On the other hand, it has been tacitly assumed that female mouthbrooders select their mates from those which display from the arenas. The males which occupy an arena, however, represent a small uniform sector of the population. For example, the space suitable for an arena at Kuruman Eye was limited, but the population of males which might fill this space was large. Those males which occupied optimal sites in an arena appeared uniform in size and coloration, and showed little variation in rank and behavioural vigour (an exception was the single extraordinarily large male which occupied the winter arena). Therefore as females courted from nest to nest they would encounter males which were all very similar. Furthermore, as it is likely that as females move from one male to the next they become increasingly sexually stimulated, it seems that at the time of spawning the females would be least selective about their mates - the threshold to spawn having been lowered. Thus, if selection occurs it probably does so where a female is first induced to respond to the males of the arenas. And, as Fryer & Iles (1972) pointed out, that before the females even appear on the scene, these males have already undergone a good deal of selection as they competed for holding sites in the choice sector of the arena. It seems that a female would probably select the group of males occupying the optimal regions of the arena. The individual male is thus probably not selected by the females.

Finally, the field observations demonstrate that laboratory studies of courtship and spawning reflect very accurately the true nature of events the only real exception being that the aggression of the males was such that in an aquarium only one male could dominate a territory with the result that only one male was visited, and the relationship between the pair was abnormally lengthy.

The Supernumerary Males

Approximately half of the large non-territorial males in Kuruman Eye were sexually coloured (in breeding dress), and at Sibaya and Wondergat the percentage of these fish appeared greater. Were it not for the behavioural evidence to the contrary, these fish would have been taken for breeding males as they looked identical. A field biologist without recourse to behavioural observation would be inaccurate if he assumed that the males he caught in breeding-dress were in fact breeding males. Furthermore, he might also erroneously assume that the fish had been caught over breeding grounds. Supernumerary males do not frequent the arenas, indeed in the mornings they were largely excluded from these regions. Fryer (1961) caught male T. variabilis in breeding dress with females over brooding grounds. He assumed therefore that the brooding ground was near the breeding ground. This may have been incorrect if the males caught were supernumeraries in breeding colours.

Those supernumerary males not in breeding dress were neutrally coloured but nevertheless retained many of their sexual markings and were easily identified.

Though supernumeraries were barred from territorialism they frequently practised intention territorialism and attempted to establish territories in sub-optimal regions. To investigate their behaviour a square of $9m^2$ area was roped off over a mud substrate. Table 3 shows that the territories formed were ephemeral. Within these transient territories nests were dug and passing females were invited to court.

TABLE 3

Table 3 illustrates that the number of "territorial" males which occupied the $9m^2$ area, fluctuated. These are transient territories. This contrasts with the permancy of the reed-bed territories in Kuruman Eye in which the males remained on station throughout each day.

DATE	TIME OF OBSERVATION	NUMBER OF MALES
7.12.72	0730	6
7.12.72	1143	8
7.12.72	1700	3
8.12.72	1630	9
9.12.72	0755	4
9.12.72	1430	5

Supernumerary males within the schools showed intention courtship and made unsuccessful attempts to stimulate females to follow to imaginary nests. This behaviour implies that possession of a territory and construction of nests are not prerequisites to courtship, which in turn suggests a rather flexible hierarchical sequence of behaviour patterns.

It appeared that in many supernumerary males the territorial drive had been thwarted and that the intention behaviour provided a partial expression of these drives.

It has already been mentioned that supernumerary males would become territorial if an opportunity presented itself. In aquaria, adult cichlids form straight line hierarchies. Removal of the α- fish results in increased status and coloration of the β - fish, which assumes the α- position; removal of this fish results in the ascendancy of the next in line. In this respect a well populated water body was not greatly different from an aquarium, except that it has a greater number of fish at each level of the hierarchy.

At Kuruman Eye, five supernumerary males were tagged and thereafter whenever one of these fish was found, its location and behaviour was recorded. Tagged supernumerary males were observed at many different sites of Kuruman Eye, usually they were foraging with other non-territorial fish. These observations indicated that supernumeraries did not confine themselves to a particular locus and that their principal activity was foraging which they did in the company of female and juvenile P. philander.

In Kuruman Eye the supernumerary males seldom entered the arenas. By contrast, the supernumeraries at Sibaya were common over the arenas, however, the greater depth of Sibaya allowed these fish to remain a metre or more above the substrate which was just out of range of the territorial males which would otherwise chase them.

In all three water bodies supernumeraries were found to accompany schools of mouthbrooding females. Whether these fish learned to follow the maternal fish to prey on their fry or whether they form some other, perhaps protective function, is unknown.

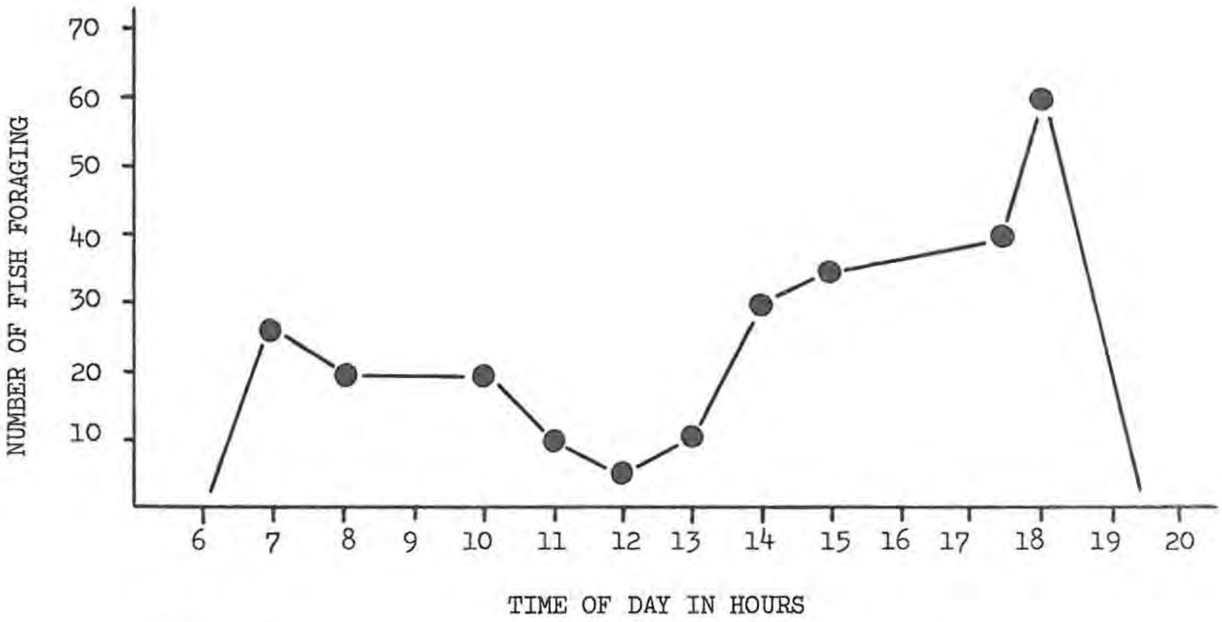


Figure 25

The number of non-territorial fish foraging in a one square metre patch at different times of the day. Observations were made in Kuruman Eye, in winter, in what appeared to be an optimal feeding site.

Non-gravid (spent) females and juveniles

Spent females and juveniles foraged in slow moving, diffuse shoals throughout the day. These shoals were usually accompanied by a number of supernumerary male and gravid females which differed from the others of the shoal by showing appetitive sexual behaviour in addition to foraging. Over the *Myriophyllum* beds of Lake Sibaya several shoals of faster moving, more densely packed fish, numbering two hundred or more, were also observed. The difference in behaviour was not understood, but it is possible that in late January when the observations were made, *P. philander* breeding season was drawing to a close and the shoals heralded the formation of winter schools. Bruton (1973) reported that the breeding population of *S. mossambicus*, in Lake Sibaya, showed a marked numerical decline in January followed by school formation. It is possible that *P. philander* follow the same trend.

Foraging of non-territorial fish was most marked in the late afternoons and evenings. This was quantitatively determined by counting the number of fish which foraged in a roped-off square metre adjacent to the arenas in Kuruman Eye (fig 25) at different times of the day. Foraging fish were to be found throughout Kuruman Eye, though the juveniles showed a preference for the warmer regions.

In summer, these fish were to be found from the shallowest to deepest parts of Lake Sibaya. The juveniles, however, were slightly more common on the terrace than at the bottom of the slope, and both spent females and juveniles were found most densely in the weedbeds of the slope and the *Myriophyllum* areas. In winter all the *P. philander* moved into deeper water.

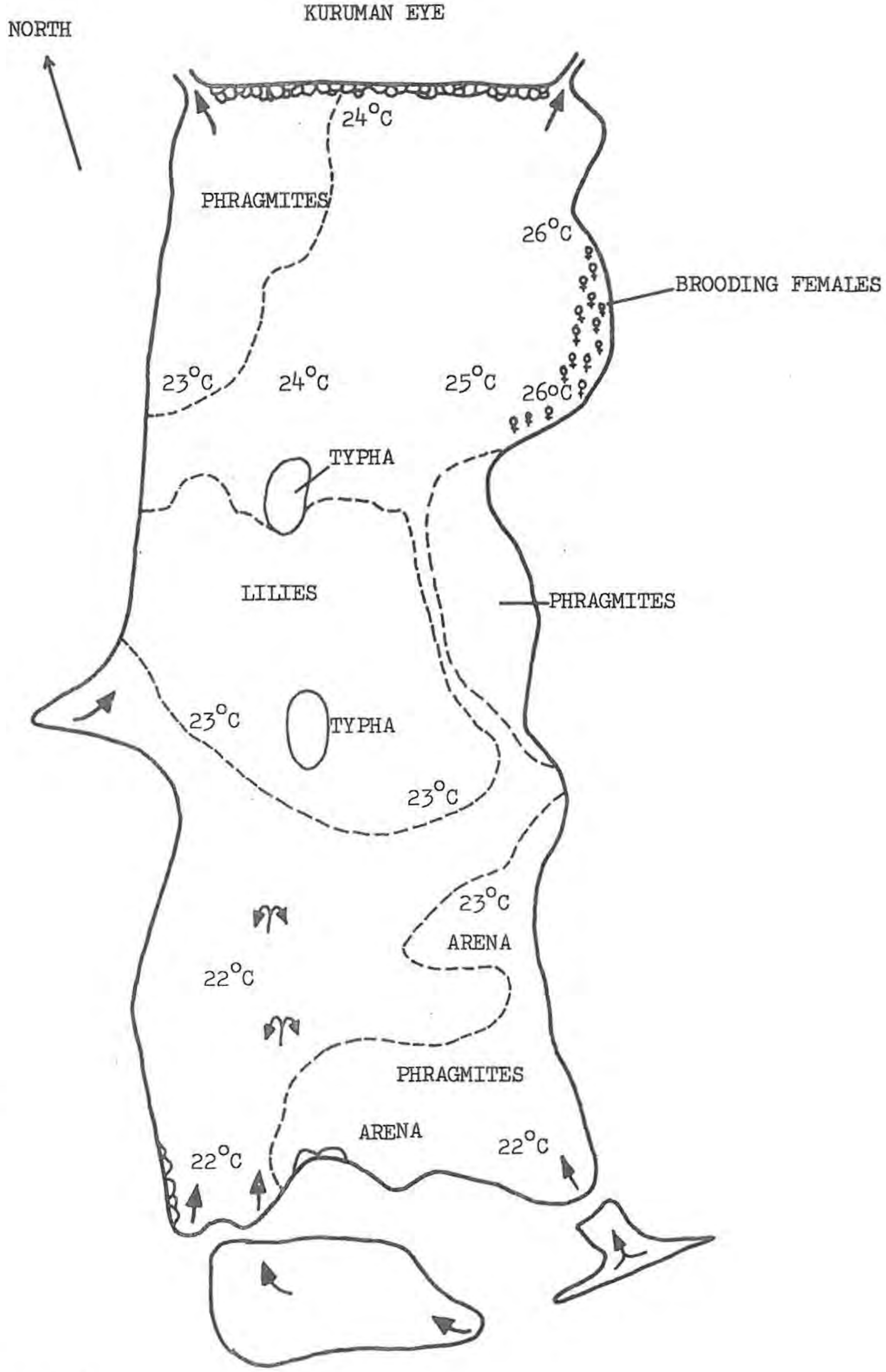


Figure 26

Brooding females were found in the warmest water of Kuruman Eye. Temperature data taken in December (summer) 1972.

Brooding females and fry

At completion of spawning females would voluntarily leave, or were chased from the territories once their responses to the males' courtship displays ceased. The fertilized eggs were carried away from the arenas to regions where maternal mouth-brooders congregated to incubate their eggs. Schools of fish carrying eggs, or fry, varied numerically from as few as five, in winter at Kuruman, to an estimated several hundred in Sibaya during summer.

In December at Kuruman Eye the brooding females were found just below the surface along the embankment of the eastern shore of the north basin. Water temperature in this region was higher than elsewhere in the Eye at that time (fig 26). The brooding females remained quietly hidden in the densely matted roots of the grass and shrubs which lined the embankment. When disturbed they fled rapidly as a school and then returned to the warmer region immediately after the danger had passed.

Towards the end of the incubation period individual females carried their fry away from the shoals of brooders to seek, what appeared to be, relatively isolated areas in slightly deeper waters. At these sites they released their fry onto the substrate where the fry and parent would feed. Maternal fish guarding clouds of fry were found at several sites in the Eye: among the lilies and reed beds especially and also over the ooze of the north basin. These sites were not as heavily populated by potentially cannibalistic predators, as the south basin and arena regions, and were warm though not as warm as the surface waters in which incubation had taken place.

A large number of young fry were found singly or in small groups in the densely matted roots just beneath the surface of the water of the eastern and especially the western embankment. Whereas fry were never found unguarded in the deeper water, the fry of the embankment were never seen with their parents. Two suggestions might provide an explanation for these observations. Firstly, in deeper more exposed regions communication between parent and fry, and the shepherding of the shoal of fry over the substrate would be relatively easy. In regions of dense cover, such as those found on the vertical embankments, however, communication and shepherding would be extremely difficult. The adult and fry would rapidly lose contact with one another and the relationship would therefore be terminated in a quick but passive manner. This explanation does not account for the observation that unguarded fry were not found in the deeper water, but only along the surface waters of the embankment. At some stage it would be necessary for the fry to be carried to the fringe waters for they would be unlikely to survive the journey unaided through predatory schools of P. philander. A second, more likely, suggestion is that in Kuruman Eye parental care is a three stage phenomenon, consecutively:

(a) the period of incubation which takes place in warm surface waters;

(b) a period when the parent avoids other fish and guards its fry while they feed from the substrate, and finally,

(c) a stage when the fry are carried to the extreme shallows and released into the warm protected waters, after which the spent female would rejoin the foraging benthic shoals.

The sudden cessation of parental duties would not have been anticipated from aquarium studies in which the ties between a parent and its progeny were gradually broken. As one might reasonably expect, maternal fish in an aquarium would be unable to carry its fry elsewhere, and might eventually eat them.

Bruton (1973) observed that under certain circumstances in Lake Sibaya, usually after heavy rain, the association between maternal S. mossambicus and their fry would terminate suddenly. Brooding shoals of S. mossambicus were observed to carry their fry over sand bars which were so shallow that the adults had to flap on their sides to get across to reach "nursery ponds" at the edge of the lake. Once in the "nursery-ponds" the fry were released and the association between the parent and fry broken by the adult fish returning to deeper water. Bruton observed that not all of the brooding shoal entered the extreme shallows and he assumed that only those fish with fry old enough to be released entered nursery ponds.

P. philander fry fed upon epiphytic growths on the rhizomes of the embankment of Kuruman Eye. They spent the entire day nipping at the surfaces of these plants. Those fry at the surface were very small and young, but those near the base of the embankment were approximately two centimetres in length. It seemed that as fry grew older they moved down the bank into deeper water and eventually left the protection of the banks to join the benthic shoals as juveniles. Whereas the southern basin of Kuruman Eye harboured all the arenas and most of the adults, the warmer north basin contained all the fry and most of the juveniles.

In winter, there were very few females carrying eggs or fry in Kuruman Eye, and the small groups that were found were always in the warmest water. During the course of each day these females tended to follow the sun-warmed water even if it meant that they were completely exposed in the bare patches between weeds. On these occasions it appeared that they had foregone their cryptic tendencies in order to fulfil their thermophilic requirements.

Only two shoals of fry were found with their parents in winter. These fry were released in relatively exposed regions between the lilies and close to the schools of oral-brooding females. Both groups of fry were spewed out onto the substrate and not into the surface waters: one group into a small hole in the sand where they nipped at the detritus and the other into the root system of a lily. The parental females recalled their fry at the appearance of the diver. The only other fry found in winter were in the rhizomes of the embankment.

At Wondergat shoals of 30 to 80 brooding females were found in the warm surface waters. Schools of brooders moved around the sinkhole during the course of the day. In the absence of macrophytes parental fish hid in cracks and crevices which had been formed in the limestone walls.

Females with shoals of fry were found as isolated individuals on shelves or slopes usually within a few centimeters of the surface, though one group was found at approximately 60cm and another at almost 90cm depth. As a general rule, the fry were in holes or crevices guarded by the parental fish, but some broods were found on exposed surfaces. In all instances the shoals of fry remained as a discrete group and responded quickly to the females' recall. There appeared to be a closer communication between parent and fry in Wondergat than that found at Kuruman. Possibly in the barrenness of Wondergat the relationship between parent and progeny is closer and longer lasting than that in densely vegetated conditions where contact might easily be lost.

Fry spent their time feeding upon epilithic growths (aufwuchs). When no longer protected by the parental fish, fry remained in deep narrow cracks in the rock face where they fed. Cracks and holes in the rocks were used in lieu of the cover which would be afforded by macrophytes elsewhere.

In Lake Sibaya individual females carrying eggs were frequently seen swimming over the arenas. These fish were probably en route to the brooding grounds where large schools, of several hundred females congregated. Shoals of brooding females remained quietly in the macrophytes at four to five metres depth. A female guarding its brood was found only once, and this was in the weedbeds of the south basin (Station 3, Ribbink 1975).

Despite searching for them, using fine nylon gauze nets, P. philander fry were not found along the shallow fringes of the lake, in January 1972 nor January 1973, though many S. mossambicus fry were caught in these nurseries. Bruton (pers.comm.), however reports catches of P. philander of 15 to 20mm SL in the eulittoral pools. Probably these fry were carried to the fringe regions by their parents. Hart (1973), however, caught P. philander fry in his substrate bins at 38m depth. It is possible that P. philander females carry their fry into the deepwaters of Sibaya when the deep water is warm in January and February. At these depths the fry would be beyond the reach of the adult cichlids of the Lake which cannot compensate to the pressures at those depths (Caulton 1973).

To confirm that fry are actively taken to deepwater nurseries, as well as into the shallows, would demonstrate a remarkable dichotomy of behaviour within the species, and an unusual behaviour for mouthbrooding cichlids which usually bring their fry to the fringe regions (Fryer 1961; Bruton 1973) or rear them, as do the 'mbuna', same habitat as that in which they mate and habitually live (Fryer & Iles, 1972).

Discussion of parental behaviour

Aquarium parallels

In the natural environment and in aquaria females with eggs and fry in their mouths were easily recognised by the distension of their branchiostegal membranes and their more pronounced ventilatory movements. In aquaria, brooding females became dissociated from other fish because they appeared more quiescent and did not participate in the day to day activities of other fish. Furthermore they tended to form inactive groups in a neutral part of an aquarium where they avoided behavioural interaction with other occupants. These groups would be analogous to the shoals of brooders found in the brooding grounds of natural waters.

In an aquarium the females with broods adopted a disruptive colour pattern and showed cryptic and thermophilic tendencies when given a choice. This also parallels the behavioural traits of these fish under natural conditions.

Finally, the release, collecting, shepherding and defence of the fry in natural waters appeared indistinguishable from that described by Ribbink (1971) who studied the fish in tanks. Further parallels and dissimilarities will be discussed under the appropriate sub-headings below.

Temperature effects

In Kuruman Eye and Wondergat brooding shoals were always found in the warmest water, within a few centimetres of the surface. To remain exposed in the surface waters would make the brooders unnecessarily easy targets for avian predators, such as kingfishers, and therefore the thermophilic behaviour was found to be coupled with cryptic tendencies where possible. At Kuruman the grassy root verges and in Wondergat the rock cracks and crevices hid the maternal fish. In winter, at Kuruman Eye, it appeared more important to the fish to remain in the warm waters than to hide away, for they were occasionally found in exposed sunny regions which were slightly warmer ($23^{\circ}C$ instead of 22.5 and $22.0^{\circ}C$) than areas with cover close to where they had congregated, seemingly to bask.

In Lake Sibaya individual fish with eggs were observed swimming over arenas and were assumed to be en route to the brooding grounds. As the arenas at 20m depth were usually at the same temperature as the brooding grounds in three to six metres water in January (temperature data from Allanson & van Wyk, 1969), temperature differences per se and thermophilic behaviour would not adequately account for the migration to the brooding grounds. At present it is not known what it is that makes the females congregate in the macrophytes of the relatively shallow waters of Sibaya. Though one might guess that once chased from the arenas the parent fish swims towards the shallows in response to an inherent drive and remains in the macrophytes gaining protection afforded by both the plant cover and schooling behaviour.

In laboratory experiments, Donnelly (1968) found that young P. philander had a preferred temperature which was higher than that chosen by the adults. It is possible therefore that one of the many physiological changes which occurs at the time of spawning is that the female's temperature preference changes from that of the adult to one better suited to the fry.

The incubation period is shorter at higher temperatures, for example, Evans (1974) found that P. philander from Kuruman took 20 days to absorb the yolksac at 22°C, and only 13 days at 29°C. An important advantage of shortening the incubation period is that it would allow the production of more broods within a given time interval. This would effectively increase the fecundity of the population.

Nutrition

P. philander, in common with most[1] mouth-brooders, does not actively feed during the incubation of their young.

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[1] Apparently some species of mouthbrooder do feed during the periods of incubation (see Coe 1966, and also Chlupoty, cited by Fryer & Iles 1972).

The observations presented on page 168 show that the number of eggs laid by P. philander do, as a rule, exceed the number of fry released. It has been suggested that a proportion of the eggs and young of mouthbrooders are swallowed to sustain the parent during the period of incubation (Liebman 1933, Welcomme 1973). It is more appropriate to discuss this interesting aspect of their biology later (page 169).

In aquaria, females with mature fry become aggressive and may vigorously attempt to increase their individual distance. In crowded tanks the release of fry may be delayed by several days. Under natural conditions females leave the brooding grounds to release their fry in quiet protected areas.

Under laboratory conditions, parental care appears to have two distinct stages: the period of incubation and the period of parent-fry behavioural interactions. Thereafter there is usually a passive and gradual termination of the parent-fry relationship. In the field three distinct stages appear likely because the period of parental care is actively terminated when the parent finally releases her brood in the fringe regions.

Fryer (1961) clearly described the advantages of conferred upon fry living in the shallow nurseries. Principally, larger fish would have difficulty in entering these regions to prey upon fry, and that avian predators which dived for their food would find a few centimetres of water inadequate for fishing. One can add to this that a further deterrant to adult fish would be the higher temperatures of the nursery regions.

At Kuruman and Wondergat, the respective embankments and rock walls were found to be vertical, therefore the advantages of the extreme shallows of other nursery regions were not available. Whereas fry in Lake Sibaya could safely remain exposed in their nurseries, in Kuruman and Wondergat, they would have to remain hidden in order to survive. Probably in both these small water bodies mortality of fry, as a result of cannibalism by adults, would be high.

Fry behaviour in feeding and growth

Initially when released the fry remained in discrete groups and were responsive to the movements of their parent and siblings. By the time they were observed in the nurseries, approximately four days after their initial release, most of the groups had dispersed, though some remained together. One group, in Kuruman Eye, was induced to respond to calling movements (described by Ribbink, 1971) simulated using the pencil attached to the under water slate.

As the fry grew so they moved from the nurseries into deeper and deeper water, by the time they had grown to juveniles they were foraging in the substrate in an adult manner for benthic fauna. This movement from the nurseries into deeper water parallels that of the *Sarotherodon* species described by Fryer (1961), Coe (1966), Fryer & Iles (1972) and Bruton (1973).

Further field observations

Spawning intrusions and nest robbing

A behaviour observed in the laboratory and referred to as courtship intrusions (Ribbink 1971) was considered to be an aquarium induced artefact which resulted from crowded conditions of fish in aquaria. These intrusions were especially common in aquaria in which the largest male was not fully dominant. When this behaviour was observed on several occasions, in both Sibaya and Kuruman Eye, greater consideration was given to its biological value. Consequently spawning intrusions of *P. philander* and *S. mossambicus* were cinematographically recorded on Super-8mm film, in the laboratory, for closer study under different conditions of population densities.

Spawning intrusions occur when a spawning pair is interrupted by groups of non-territorial fish, of both sexes, descend to the nest and force their way between the courting pair. Frequently intruders perform many of the spawning motions themselves either in isolation in the nest or with other intruders, and even with one or other of the original spawning pair. The original occupants of the nest treat intruders aggressively and usually drive them away within a few minutes. Most intruders seem reluctant to leave and frequently dodge back into the nest. Once clear of intruders courtship continues. The resumption of courtship usually stimulates an immediate reinvasion.

Nest-robbing occurs when eggs are laid. Either the appearance of eggs or possibly egg-laying behaviour, acts as a releaser to the non-territorial fish which immediately descend and force their way between the spawning pair. Intruders of both sexes then rob the nest of its eggs. In addition, male intruders may eject milt and fertilize eggs. Stolen eggs are usually held within the mouths of the robber fish for several days before being swallowed, though they may be swallowed immediately. Occasionally females would rear the stolen brood and correctly perform all the appropriate maternal behaviour.

An important laboratory observation was that a dominant male with few attendant fish in the aquarium would be undisturbed by intruders during courtship. Whereas a dominant male in crowded aquaria would be plagued by interruptions and thieving during courtship and spawning.

The biological function of spawning intrusions and nest-robbing appears to be one which provides a mechanism for the regulation of population size. This will be discussed below.

Natural regulation of P. philander population density

> "In looking at Nature it is most necessary never to forget that every single organic being may be said to be striving to the utmost to increase in numbers."
>
> Darwin (1859)

According to Wynne-Edwards (1965) those views of Darwin, given above, have dominated the thinking of biologists, who, like Darwin, believed that the only "checks to increase" of population density were of four extrinsic kinds, namely: the effects of food availability which provides the extreme limit to the increase of any population; the effects of predation; effects of physical factors such as climate, and the effects of disease. Only relatively recently have intrinsic factors (physiological and behavioural) assumed importance, in the eyes of biologists, as means for natural regulation of animal numbers, with Wynne-Edwards (1962) stimulating much of the thinking.

Almost all the work on self-regulation of population density has been done on the small arctic mammals (Krebs 1964, Chitty 1967 and others), on birds (Lack 1966, Wynne-Edwards 1962) and insects (Dempster 1968, Klomp 1964) with little work being done on fish. In his review Le Cren (1965) alluded to the possible regulatory role of territorialism in fish density regulation but concentrated principally upon the extrinsic factors. Yet the work of Silliman and Gutsell (1958) suggests that fish might be extremely useful animals with which to study population homeostasis. In their experiment, which lasted over three years, they showed that when stable aquarium held populations of Lebistes, the guppy, were cropped by removal of a proportion of the fish, the remainder responded by producing more young which survived. Thus, in the absence of extrinsic regulators the population density remained constant by the matching of recruitment and loss.

In control tanks the stocks were left untouched and though the guppies went on breeding, cannibalism consistently removed all the surplus young produced. In other animals the surplus is not cropped but reproductive output is lowered by behavioural and physiological means (Chitty 1967).

There are two largely distinct behavioural methods of regulating reproductive output, one is to limit the number of adults that are permitted to breed, which may result from the adoption of a territorial system, or any other system in which the number of permissible breeding sites is limited. The other is to influence the number of young that each breeding pair is permitted to produce. The two methods can easily be combined (Wynne-Edwards 1965), and they appear to be combined in the regulation of the population density of P. philander.

Fryer and Iles (1972) believe that cichlids have a means which enables them to regulate the size of their own populations. Following the thesis of Wynne-Edwards (1962), they suggested that arenas might serve to control population density (a) because an arena would be unable to support more than a fixed number of territories, thus placing a ceiling on population numbers, and (b), by implication, they proposed that epideictic displays (as defined by Wynne-Edwards 1962, 1965) may provide indications of population density and pressure, which, acting as releasers, might stimulate or inhibit reproductive behaviour. Applying their hypothesis to P. philander it was found that space in arenas was restricted which also limited the number of males permitted to breed. Only boundary fights appeared to serve as overt epideictic releasers which might influence the number of young produced. In addition to these facets, observations strongly suggested that the presence or absence of particular behavioural activities provides P. philander with a mechanism for population homeostasis.

As a population grows the arena fills up and also the number of non-territorial fish increases. Surplus males, females and juveniles would provide a negative feedback to population growth, firstly, they would make intrusions into the territories and need to be chased out. The number of intrusions would increase with an increase in population density and less time, and possibly energy, would be available to territorial males for courtship and spawning. By way of example, a comparison between Kuruman Eye and Sibaya populations may be made. In Kuruman Eye the territorial males may court and spawn at any time of the day. Though sexual activity usually takes place in the mornings, the arrival of a receptive female in the late afternoon will so increase a male's sexual and aggressive drives that it then, as a general rule, keeps all other fish at bay and spawns. In Lake Sibaya the arenas were so inundated by supernumeraries and other intruders in the afternoons that territorial individuals were too occupied in the defence of their inner territories to take advantage of an opportunity for courtship. Thus, an increase in the population beyond a certain level appears to decrease the productivity of an arena. Secondly, and in similar vein, an increase in competition for space on an arena probably results in a greater number of territories being squeezed into the arena. Neighbours would therefore be involved more frequently in boundary encounters and have less opportunity for sexual activity. It appeared that Lake Sibaya might be more densely populated than Kuruman Eye because, in addition to the other indications mentioned above, territories of P. philander were smaller in the lake.

A third and powerful means of population regulation is provided by spawning intrustions and nestrobbing behaviour. These behavioural activities, which may have evolved specifically as a mechanism for population regulation, provide a direct and effective means of reducing the number of young produced by a population. Spawning intrusions would interfere with courtship and inhibit spawning. More effective still is nest-robbing as eggs would be lost, because stolen broods are usually swallowed. During the interruption the original spawning female attempts to frantically rescue its eggs taking many of them into its mouth before fertilization. Then, assuming the intruders permitted the pair to continue their spawning undisturbed, which they seldom did, the delay whilst attempting to drive-off persistent intruders might be so long that by the time milt was collected the eggs would have become water hardened and never fertilized.

A further device which would tend to reduce a population is that supernumerary fish are cannibalistic and prey upon fry. Therefore a large supernumerary population could drastically increase the incidence of fry mortality. Small waterbodies such as Kuruman Eye and Wondergat, where fry were not well protected, would be particularly sensitive to such regulatory mechanisms.

If a population were drastically reduced by a natural disaster then the behavioural restrictions on population growth would be removed. All males would have territories and become involved in courtship and spawning. In the absence of non-territorial fish sexual activity would proceed undisturbed, furthermore a great deal more time would be available to forage and build up energy reserves between bouts of sexual activity. Predation on broods of fry and intraspecific competition for space and food would be minimal. All factors point to a rapid population regrowth to a stage where the non-territorial fish would slow and possibly even stop the numerical growth rate of the species.

The self-regulating feedback mechanism proposed for P. philander, (fig 27) and S. mossambicus in which spawning intrusions and nest-robbing was also observed, is based upon specific behaviour which increases mutual interference to reduce population density, or reduces interference to stimulate numerical growth, rather like the somewhat more complicated feedback postulated by Krebs (1964), as a result of his studies of mammals.

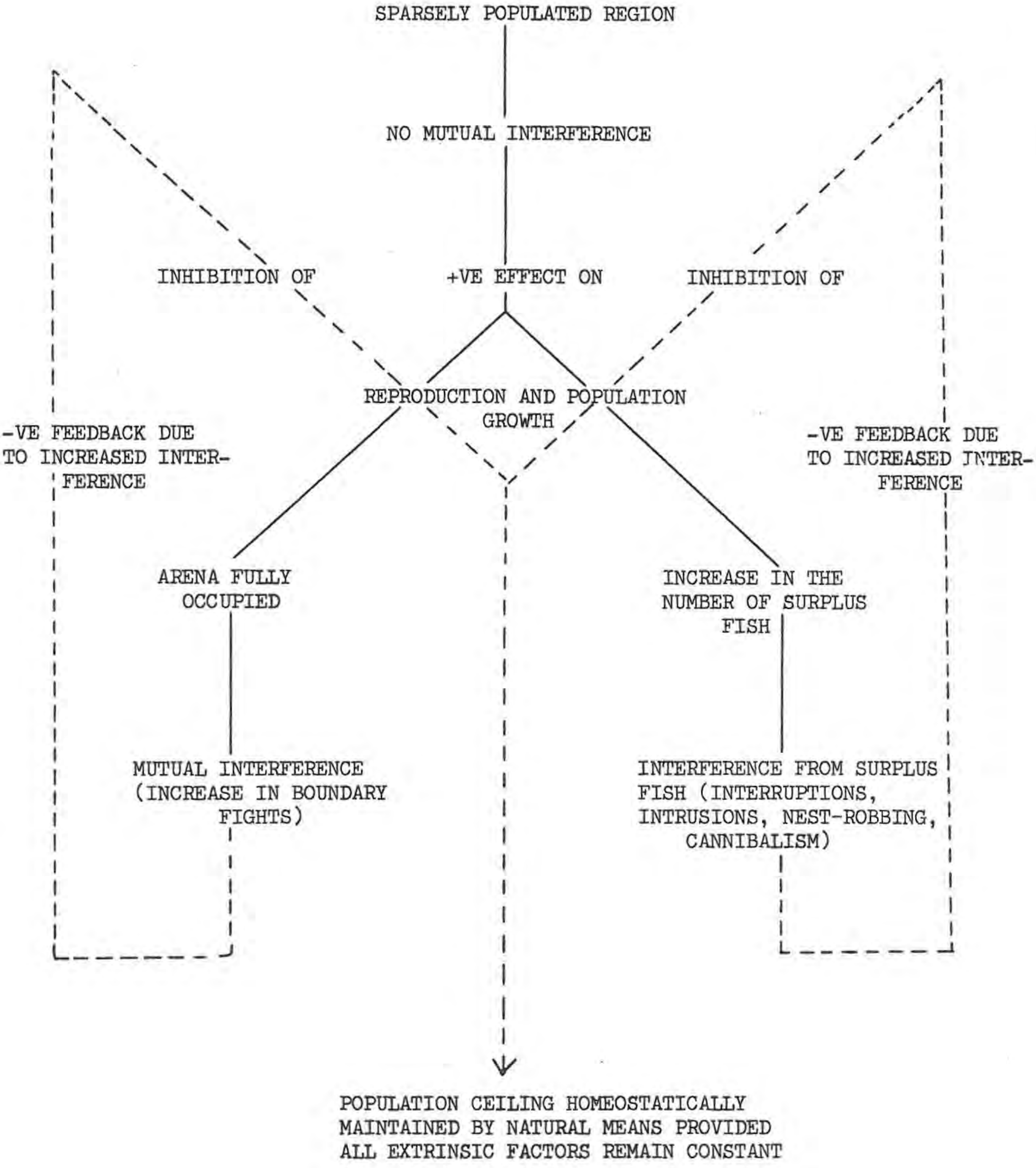


Figure 27 The postulated self-regulatory feedback system for population homeostasis of the cichlid fish, P. philander and S. mossambicus.

The negative feedback provided by interference behaviour appears to be a prerequisite to population homeostasis of mouth-brooding cichlids which, as a rule practice polygyny. Assuming that extrinsic factors controlling population density remained optimal, it should be clear that in an arena crowded to capacity and in the absence of interference behaviour, the number of receptive females being served by the arena would continue to increase. These females would add their progeny to an ever bulging population from which additional females requiring fertilization would arise. The ceiling to a population under such conditions would be very high and would ultimately depend upon how many spawnings each male in an arena could manage per day. An exhausted male could be passively replaced by a supernumerary thus keeping the production line operative. It seems that restrictions imposed by limited territorial space alone would set a high relatively uncontrolled ceiling to population density, but when combined with the regulatory effects of interference-feedback-behaviour a lower ceiling with a finer homeostasis is achieved.

P. philander provide an excellent illustration of how the two behavioural methods described by Wynne-Edwards (1965) may be combined to regulate population density: they limit the number of adults permitted to breed and they reduce the number of young produced.

Nest-robbing does not appear to have been reported elsewhere amongst the cichlids, though evidence which suggests it may occur comes from Lowe-McConnell (1955) who reports finding small numbers of fry in the mouths of juvenile fish. Possibly these were stolen and held. And Welcomme (1967) suggests that fish may be interrupted in the spawning act by other fish, due to crowded conditions.

A similar form of nest-robbing behaviour has been observed in sticklebacks (Morris 1952; Van den Assem 1967 and Wootton 1971). Morris and Van den Assem recorded this behaviour during aquarium studies, and Wootton witnessed the behaviour in natural habitats. Notwithstanding the inherent behavioural differences which exist between the sticklebacks and P. philander, the nest-raiding behaviour of the two groups is strickingly similar. Morris (1952), who noted that the behaviour may serve to regulate population density, emphasized that the behaviour was probably a behavioural outlet for sexually frustrated fish. Such a conclusion might be equally applicable to

P. philander and S. mossambicus raiders. Van den Assem (1967) argued that egg-stealing and fertilization of neighbours' eggs increases the number of eggs fathered by each male and synchronises breeding, because the intrusions and egg-robbing he observed were usually between neighbours.

Nest-raiding, according to Wootton (1971), is normally a response to a shortage of food or material for building nests. Though Wootton (1971) apparently did not recognise it as such, it seems clear that this stickle-back behaviour is geared to regulate population density. For as he (Wootton) puts it, "... if prevalent it will prevent any males from successfully rearing young, because of the frequent destruction of nests." Further on he accounts for nest-robbing as a "... a response to a shortage of some resource", which appears to indicate a population density in excess of its resources and therefore in need of a reduction of growth rate.

It seems that in the cichlids, P. philander and S. mossambicus, and in the sticklebacks population numbers may be regulated by the density dependent fluctuations of interference behaviour.

Population stability

These behavioural studies suggest a means which might enable one to immediately evaluate the stability of a breeding population of P. philander. For example, an arena occupied by the largest males in a population would be stable as these would be selected by intraspecific competition. Such an arena would have a large number of supernumeraries in attendance representing the breeding reserve. On the other hand, an arena tenanted by territorial males which vary in size from small sexually mature fish to the largest size group would be less stable and probably growing rapidly. Such a population might already be utilizing its breeding reserve and few, if any, supernumeraries would be attendant on the arena.

An extrapolation of this theory to many of the maternal-brooding cichlids of some of the Great Lakes of Africa could provide a basis for the recommendation that fishing is stopped, if a population is utilizing its reserve, or continued if a large reserve population is present. Stock assessments made in this way would be much more rapid than currently employed techniques. In such an assessment one should also consider the effects of recent environmental changes.

If the environment changes so that more space for arenas becomes available then the reserve population would be able to utilize this additional area and spawn. An example of this has recently been communicated to me by M.N. Bruton from Lake Sibaya. The level of the lake has recently increased by more than 1.5m with the result that the available space for S. mossambicus arenas has increased dramatically. At the previous lake level only the largest male specimens held territories, but in February and March 1975, small and large males were territorial and reproductively active. Thus, if one were to assess the stability of a population by the behavioural criteria outlined above, a prerequisite would be an accurate knowledge of the constancy of that environment.

Bruton's observation indicates a mechanism which enables S. mossambicus to promptly take advantage of increased opportunity. Should the lake level drop then the number permitted to breed would decrease. That the small males representing the reserve population should immediately form territories when space became available, confirms the opinion that supernumeraries would breed if given the chance. That they do not breed when space on the arena is unavailable is because they are prevented from doing so by the larger males.

Aggression in P. philander: its affect on territory size.

While territories of P. philander were found to comprise one or more centrally placed nests surrounded by a large defended area, it was observed that T. sparrmanii and S. mossambicus constructed large nests which also served as entire territories. In densely packed arenas, nests of P. philander remained far apart, by contrast, those of the other two species were frequently found to be rim to rim within their respective arenas. Though P. philander is the smallest of the three species, their territories were considerably larger than those of the other two species. Behaviourally, P. philander were the least tolerant of their conspecific neighbours and they apparently maintained a level of aggression higher than that of the other species. Though many fish have been shown to habituate to their conspecific territorial neighbours (Clayton and Hinde 1968; Peeke, Wyers &

Herz 1969; Peeke, Herz & Gallagher 1971), yet P. philander appeared not to do so. I decided, therefore, to investigate this behaviour.

To determine whether neighbouring territorial P. philander maintain a high level of aggression, or show a waning of aggression (habituation), males of equal size were placed on either side of an opaque partition (partition 'A' in fig 28) which divided an 88 x 38 x 30 cm aquarium.

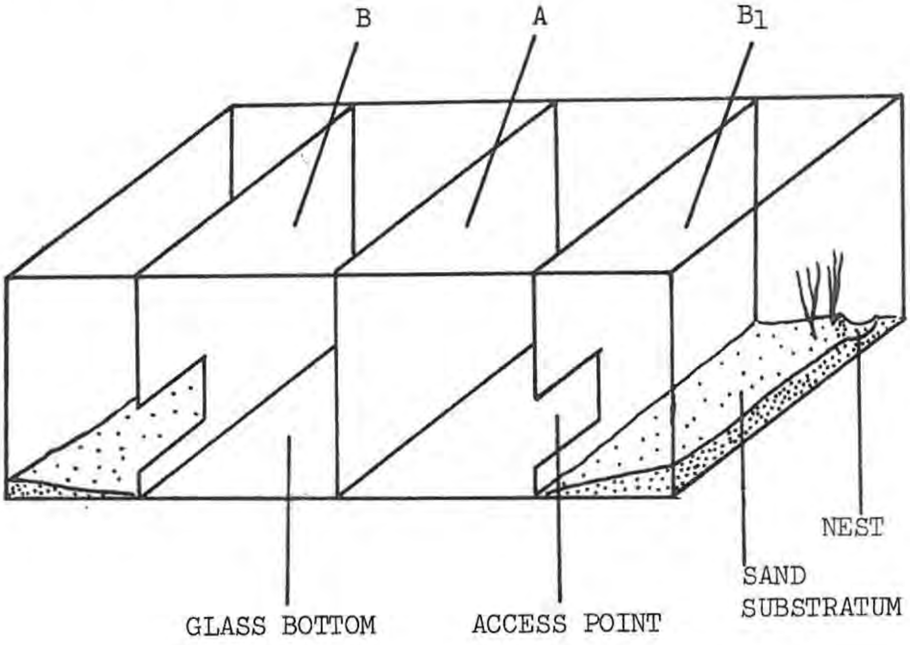


Figure 28 An aquarium partitioned to simulate boundary conditions between two territories.

The region between partition A and the nest-screens B and B^1 had a plain glass substrate, however, behind the nest-screens a layer of sand covered the subgravel filters, and plants were arranged in a ring around the screened off corners in a manner which would ensure that the nests were constructed in these corners. This meant that the centres of each territory would be equidistant from the boundary screen "A". In each compartment seven or eight attendant fish were present at all times.

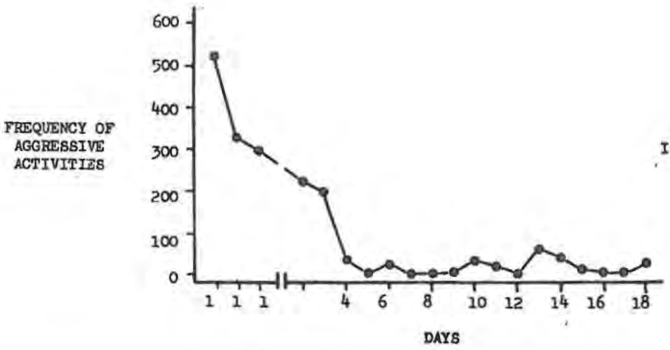


Figure 29 The waning of aggression between two conspecific neighbours. Bites and tail-beats of both fish were counted and are presented as a single curve. Behavioural activities were recorded for three consecutive 10 minute periods on the first day, thereafter for only one 10 minute period each day.

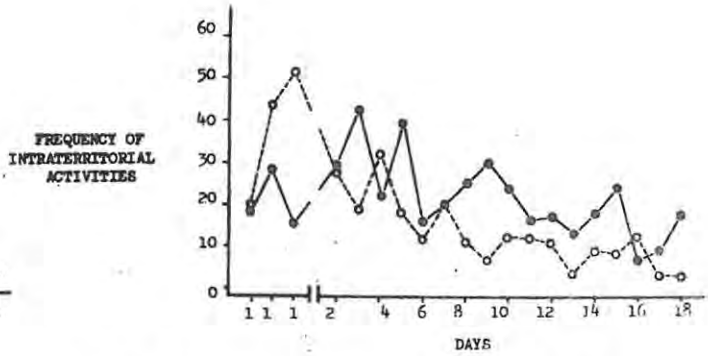
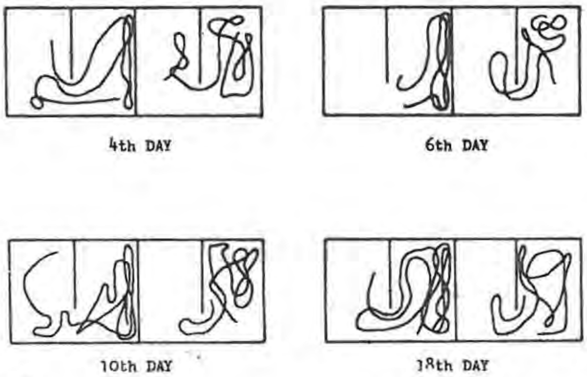


Figure 30 Intraterritorial activities recorded daily, and presented separately for each neighbour (closed circles for the dominant fish; open circles for the submissive fish). Behavioural activities were recorded for three consecutive 10 minute periods on the first day, thereafter for only one 10 minute period each day.


4th DAY

6th DAY

10th DAY

18th DAY

Figure 31 Traces of the positions of the left and right hand fish in their respective territories. The subordinate fish (right hand) avoided its neighbour. Each trace was plotted for 60 seconds.

Once the males had become fully dominant within their territories (usually five or six days were required), the opaque partition "A" was replaced by a clear glass partition. The ensuing behavioural activities were recorded for three 10 minute periods (the first 30 minutes) on the initial day, and thereafter for a 10 minute period from 10h00 on each following day. Records were made at midmorning because the diurnal rhythm had indicated that the fish were territorially active in the morning. The number of aggressive activities performed by each of the neighbours was recorded.

To show that habituation had occurred it can be argued that, not only should the waning of the particular response to a specific stimulus be demonstrated, but also that the animal having learned to ignore the stimulus resumes its normal daily activities. Therefore a better index of habituation might be an increase of intraterritorial activities such as nest-building, courting and chasing of attendant fish. Consequently aggression and all other behaviour was recorded.

In the first experiment aggressive exchanges were numerous initially, but declined in time (fig 29). Intraterritorial activities remained at a relatively high constant level (fig 30). Contrary to expectation the results given above indicate that a dominance heirarchy had been set up between the two fish. This would have outwardly an effect similar to that expected if habituation had occurred - e.g. a decline of aggressive and an increase in intraterritorial activities. That an hierarchy had been established is illustrated (fig 31) in which it is shown that the one fish avoided the other. Both practiced intraterritorial activities, but the subordinate fish did so in a more confined space.

On the 19th day of the experiment the glass partition was removed and the dominant fish took over the entire aquarium after a brief fight. Had habituation occurred the neighbours would have remained in their respective territories.

The experiment was repeated on two further occasions with fish that had not been used before, and the initial result was confirmed (figs 32-35).

As the hierarchies may have been established because neighbours were placed too close to one another, the experiment was repeated using larger aquaria in which the distance from the central partition to the nest screens was 71cm instead of 27cm. A waning of aggression similar to that in smaller aquaria was recorded (fig 36-41) which suggests that

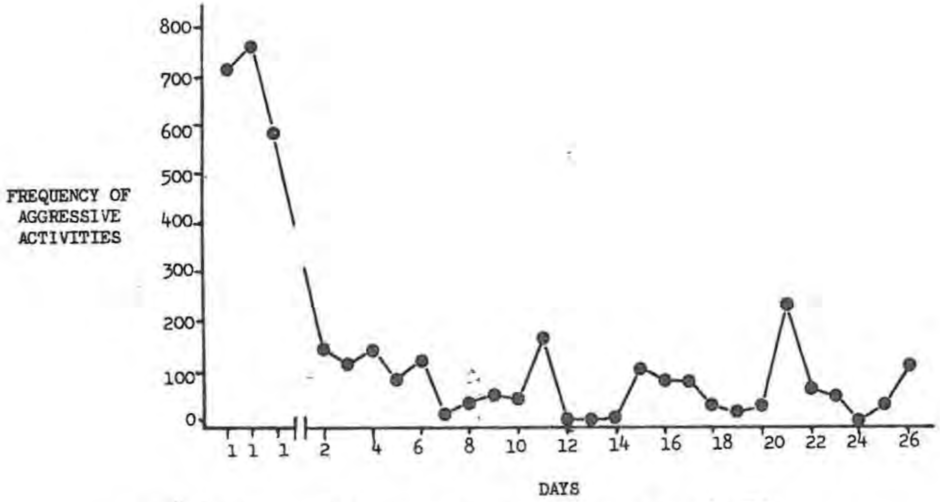


Figure 32 The waning of aggression between two conspecific neighbours. Bites and tail-beats of both fish were counted and are presented as a single curve. Behavioural activities were recorded for three consecutive 10 minute periods on the first day, thereafter for only one 10 minute period each day.

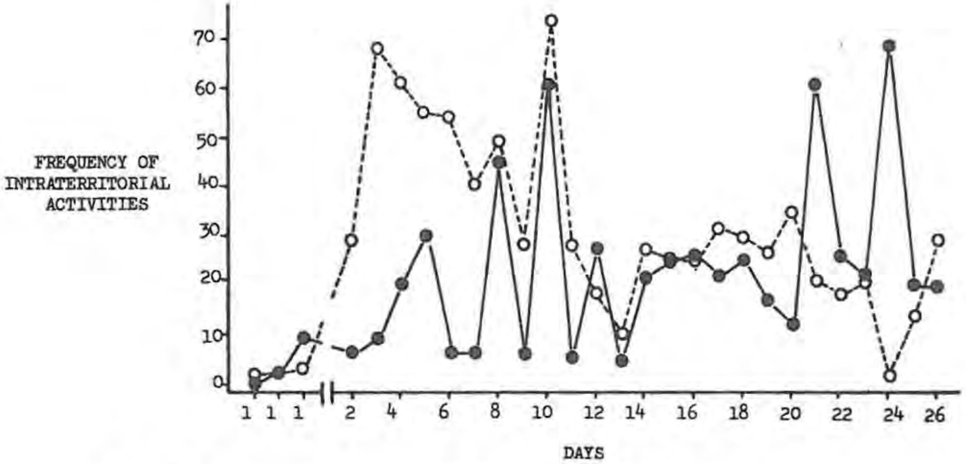


Figure 33 Intraterritorial activities recorded daily, and presented separately for each neighbour (closed circles represent activities of subordinate fish; open circles the activities of the dominant fish. Behavioural activities were recorded for three consecutive 10 minute periods on the first day, thereafter for only one 10 minute period each day.

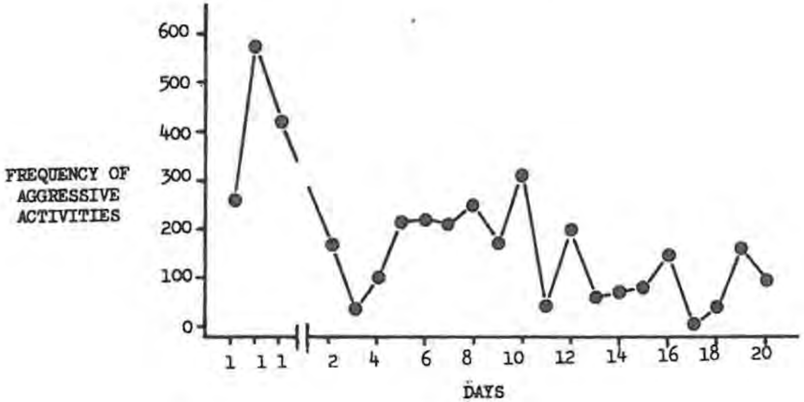


Figure 34 The waning of aggression between two conspecific neighbours. Bites and tail-beats of both fish were counted and are presented as a single curve. Behavioural activities were recorded for three consecutive 10 minute periods on the first day, thereafter for only one 10 minute period each day.

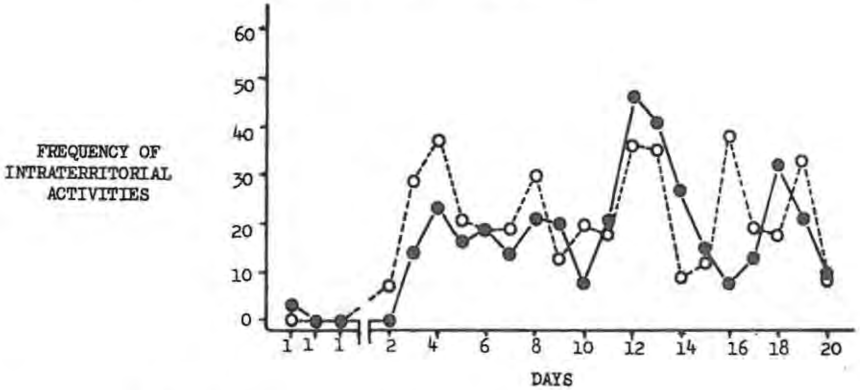


Figure 35 Intraterritorial activities recorded daily, and presented separately for each neighbour (closed circles represent activities of subordinate fish; open circles the activities of the dominant fish. Behavioural activities were recorded for three consecutive 10 minute periods on the first day, thereafter for only one 10 minute period each day.

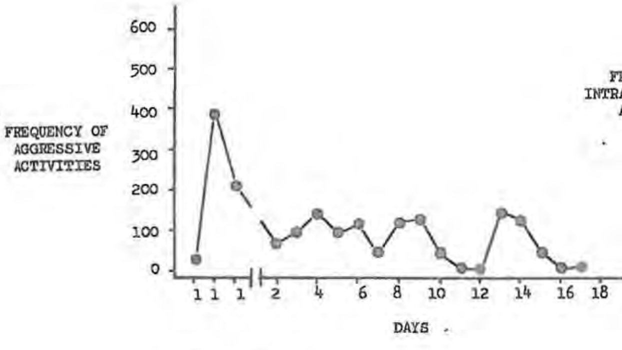


Figure 36

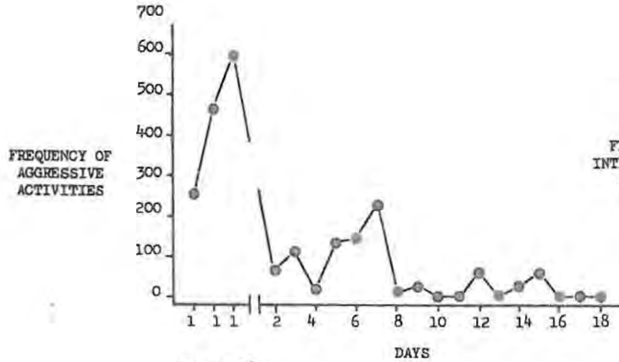


Figure 38

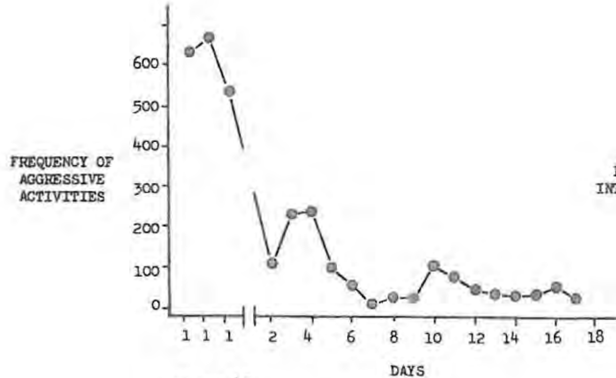


Figure 40

Figures 36, 38 and 40

The waning of aggression between two conspecific neighbours. Bites and tail-beats of both fish were counted and are presented as a single curve. Behavioural activities were recorded for three consecutive 10 minute periods on the first day, thereafter for only one 10 minute period each day.

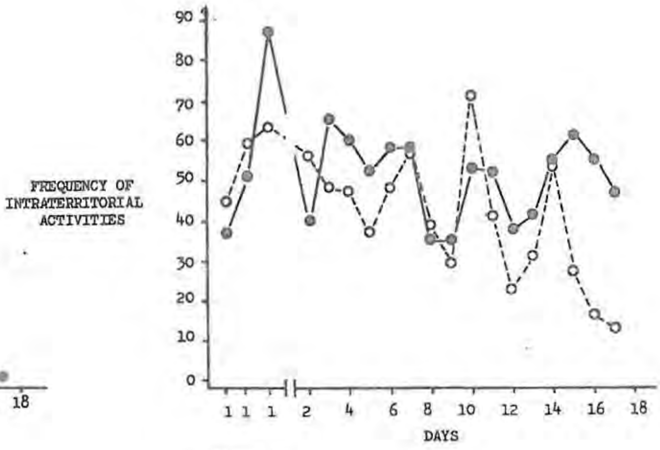


Figure 37

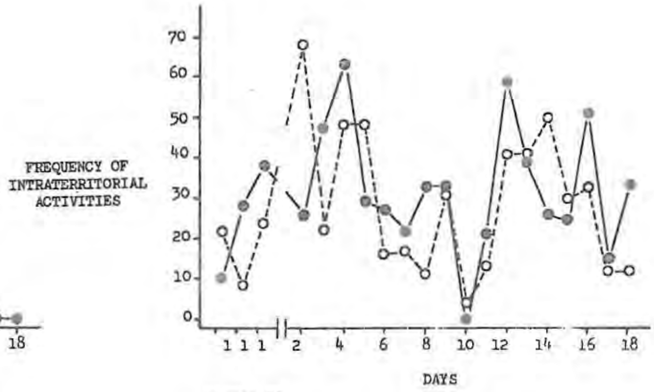


Figure 39

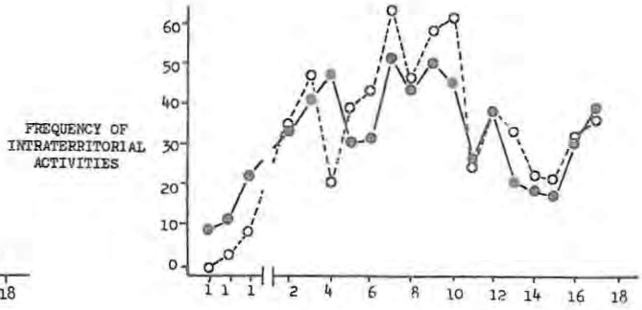


Figure 41

Figures 37, 39 and 41

Intraterritorial activities recorded daily, and presented separately for each neighbour (closed circles for the dominant fish; open circles for the submissive fish). Behavioural activities were recorded for three consecutive 10 minute periods on the first day, thereafter for only one 10 minute period each day.

the distance between the neighbours was still not great enough. An analysis of the number of aggressive encounters of fish in large and small aquaria showed that from the second day (after the initial period of intense aggression of the first day) the average number of daily aggressive activities was 79 and 74 respectively. The similarity of these results may seem surprising since it can be argued that males in large aquaria would meet infrequently and should therefore have had fewer encounters. It was found that in the larger aquaria neighbouring males actively sought conflict, but in the smaller aquaria the submissive fish avoided encounters.

Though appetence[1] for aggression was evident in larger aquaria it was also apparent that a peck-order had been established. Dominant fish were usually the aggressors and did not show displacement, redirected or avoidance behaviour, whereas the other fish often exhibited these submissive traits in addition to subordinately seeking confrontation. Furthermore, the removal of the partition always

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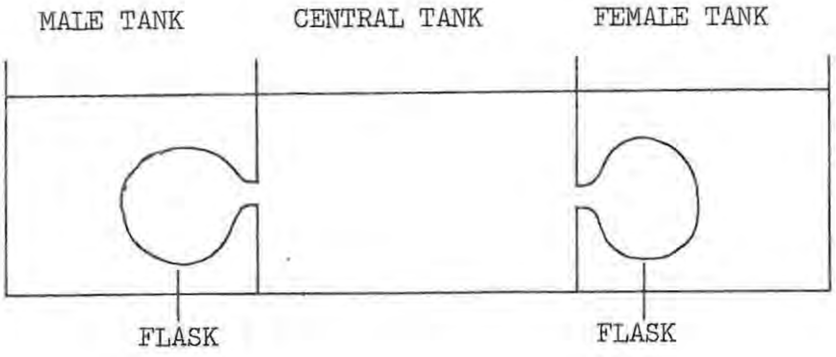
[1] Appetence for aggression was demonstrated in P. philander in an experiment in which a male placed in a central compartment could visit a sexually coloured conspecific male on the one hand, or gravid females on the other merely by swimming through a hole into a flask suspended in the lateral compartment (fig in footnote).



It was found that the subject male spent significantly more time fighting and seeking his adversary than in the female compartment. Since this work is not directly relevant to the theses it will be reported more fully elsewhere, however, as a result of these experiments the appetetence for aggression could be recognised with some confidence.

resulted in the domination of one fish over the whole aquarium.

In large aquaria, males could get further from one another, consequently the subordinate fish were less inhibited and never as submissive as those in small tanks.

A further observation was that in the small tanks the dominant males forced the attendant fish to hang submissively in surface waters. These motionless attendant fish provided an environment poor in stimuli which resulted in the performance of relatively few intraterritorial activities by the males (a daily average of 26 activities per fish per 10 minute observation period taken from the second day of observation). On the other hand, in the larger aquaria the greater freedom of movement of attendant fish enriched the stimulus environment resulting in a greater number of intraterritorial activities performed (a daily average of 42 activities per fish).

It appears that aggression and the need for confrontation are inherent in territorial P. philander. Probably interaction between neighbours only ceases when their nest-sites are so far apart (estimated to be about three metres) that communication between the territorial individuals is reduced to a minimum. Within these limits P. philander would be intolerant of their neighbours.
By contrast, my field observations indicated that S. mossambicus were tolerant of their neighbours. To establish the validity of these observations I placed two male S. mossambicus, of similar length (92mm SL and 93mm SL), one on each side of a partitioned 88 x 38 x 30cm aquarium.

Once they had become dominant over the attendant fish, acquired full sexual coloration and begun nest-construction the opaque partition was replaced by one of transparent glass. Aggressive and all other activities were recorded for both males for three consecutive 10 minute periods on the first day, and thereafter for ten minutes in the morning of each of the following days.

Removal of the opaque partition resulted in an initial exchange of aggressive activities, but by the second day a third smaller male had formed a territory between the two subject fish and

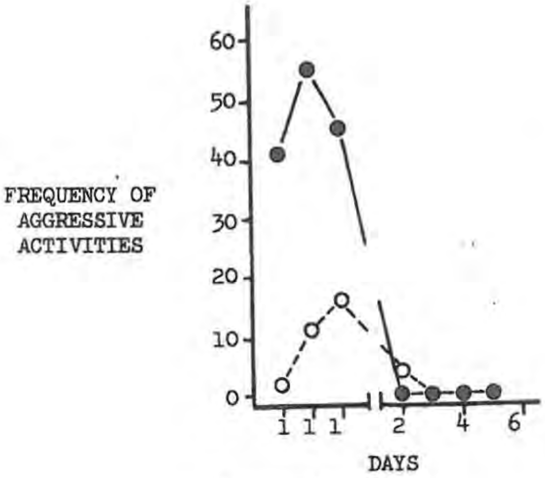


Figure 42

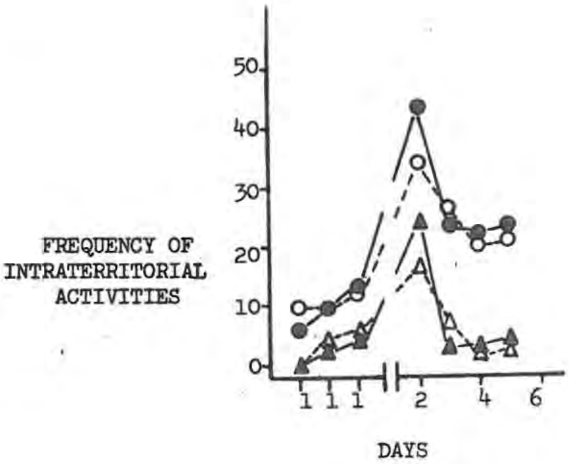


Figure 43

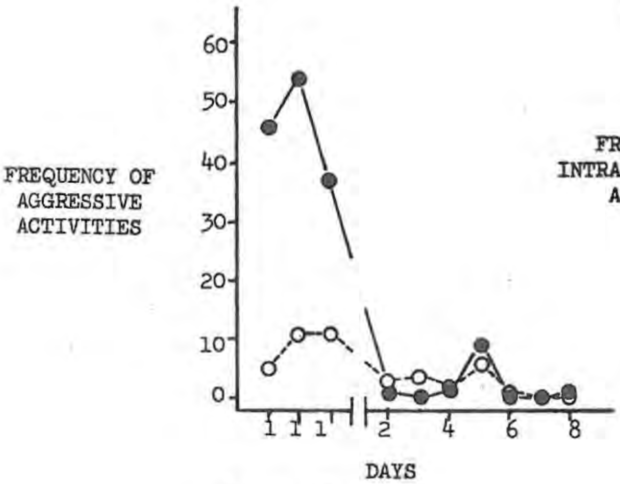


Figure 44

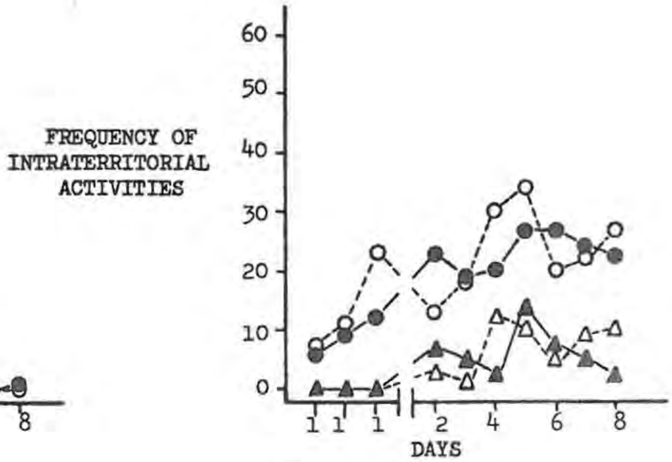


Figure 45

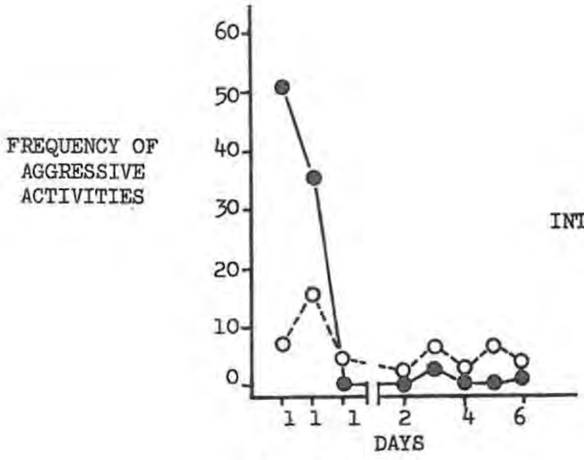


Figure 46

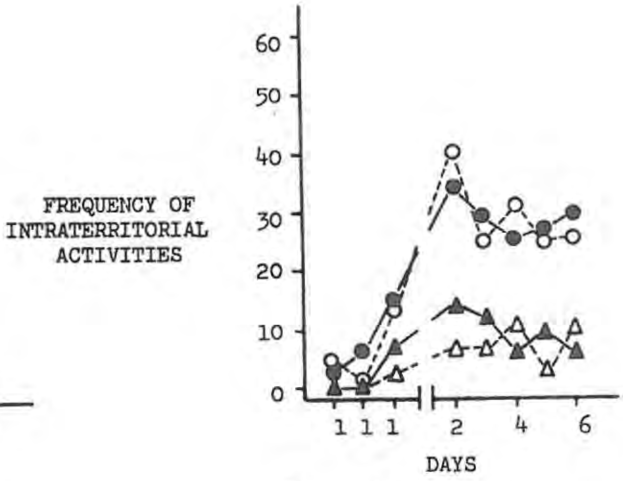


Figure 47

Figures 42, 44, 46

The waning of aggression of two neighbouring territorial S. mossambicus males. Bites and tail-beats●——●, is represented by a single curve for both fish. Frontal display o---o is also represented by a single curve for both fish. Observations were made for three consecutive 10 minute periods on the first day, thereafter for only one 10 minute period each day.

Figures 43, 45, 47

Total number of intraterritorial activities performed by two neighbouring S. mossambicus. Observations were made for three consecutive 10 minute periods on the first day, thereafter one 10 minute observation was made each day.

Total intraterritorial activities performed by the right hand fish (●——●), and by the left hand fish (o----o). Number of nest-building activities for right hand fish (▲——▲), and left hand fish (△----△).

prevented any further interaction between them (fig 42). A decrease of aggressive activities resulted in an increase of intraterritorial activities, with a peak on the second day which was due principally to nest building (fig 43). Removal of the glass partition resulted in little change of the status quo. Though all three fish held their territories, the smaller fish in the centre became submissive when subjected to increased pressures from both sides.

The experiment was repeated using different pairs of males (between 92 and 95mm SL) in even smaller aquaria (66 x 38 x 30cm, figs 44 and 45; 36 x 38 x 30cm, figs 46 and 47). In both cases aggression waned (figs 44 and 46) and the frequency of intraterritorial activities increased after the first set of readings. The fish maintained their positions and ranks when the glass partition was removed. In the smallest aquarium, however, one of the males became dominant after two days.

S. mossambicus appeared far less aggressive than P. philander in the initial 30 minute period, and though all the experiments are not strictly comparable on an absolute basis, table 4 demonstrates the marked difference in the number of activities performed.

TABLE 4

A comparison of the number of aggressive activities performed by S. mossambicus and P. philander during the first 30 minutes of exposure to conspecific territorial neighbours. P. philander appears to be ten times as aggressive as S. mossambicus.

FISH SPECIES	Number of aggressive activities	Number of aggressive activities	Number of aggressive activities	Mean number of aggressive activities
	EXPERIMENT 1	EXPERIMENT 2	EXPERIMENT 3	-
S.mossambicus	137	141	85	121
P.philander in small aquaria	1131	2048	1245	1477
P.philander in larger aquaria	629	1306	1834	1256

It is an error to believe that territory-owning animals are in a state of continuous fighting with their neighbours (Eibl-Eibesfeldt, 1970). Fighting occurs when territories are first established, usually at the beginning of a breeding season, but once a colony is established fighting between neighbours seldom appears.

The initial high level of aggression appears to be necessary to obtain and hold a mating station, thereafter intense aggression is undesirable for it can delay or inhibit mating, and it therefore wanes (Thorpe 1964; Lorenz 1966; Manning 1967).

Both *P. philander* and *S. mossambicus* showed a marked decline of aggressive response. In *P. philander*, however, aggression never disappeared completely and they did not become tolerant of their neighbours. Previous workers (Baenninger 1966; Clayton and Hinde 1968; Peeke 1969; van den Assem and van den Molen 1969; Peeke and Peeke 1970 and Peeke, Herz and Gallagher 1971) attributed the decline in aggressive response to habituation. Habituation implies a tendency to drop out responses to a stimulus, and an animal may become absolutely indifferent to that stimulus (Thorpe 1964). For example, the biting and tail-beating responses between neighbouring *S. mossambicus* disappeared after the initial period of aggression even though the original stimuli were still present. In arenas, however, where territorial fish are sufficiently close to communicate and interact, an absolute indifference to stimuli provided by neighbours would not be achieved. Such total indifference would occur only if the stimulus which an animal habituated was without significance in the life of that animal: the presence of neighbours is charged with significance in the lives of territorial animals of colonies and arenas. In *S. mossambicus* the two aggressive patterns, biting and tail-beating, became fully habituated and frontal display was only partially habituated. Though the number of frontal displays decreased this behaviour was nevertheless retained probably as a communication which maintained the understanding established between neighbours during the early intense encounters.

In *P. philander*, formation of dominant-subordinate hierarchies appeared to be the principal cause of a decrease in aggressive response. The precise role of habituation has still to be established. However, an increased number of intraterritorial activities after the initial bouts of aggression suggests that a partial indifference to the stimuli of neighbours developed, which, in turn, indicates that some habituation occurred. Removal of the boundary always resulted in a domination of one male over the entire aquarium, which illustrates that complete habituation had not occurred. Finally, appetetence for aggression apparent in the larger aquaria indicated that aggression and the need for confrontation were inherent in territorial *P. philander*.

It appears that territories of *P. philander* are maintained by active aggression which keeps neighbours at a distance. The distance appeared to be determined by the area which each male could effectively defend. Successful males with the largest territories would be the more aggressive individuals. There are apparently two categories of cichlid: a) those in which territories are attained and maintained by high levels of aggression such as *P. philander*, and b) those in which aggression is required for the establishment of the territories, thereafter an habituation occurs which enables neighbours to live amicably close to one another, such as *S. mossambicus* and *T. sparrmanii*.

Only one other African cichlid, *Tilapia macrochir*, has been reported to have nests so close together that the rims of tenanted structures actually touch (Fryer & Iles 1972). Possibly in addition to *S. mossambicus*, *T. sparrmanii* and *T. macrochir*, other cichlids which construct relatively large nests live very close to one-another during periods of intense intraspecific competition for space. A prerequisite for all close neighbours is that they habituate to one another.

Those fish in which continued territorialism is dependent upon a maintained high level of aggression have centrally placed nests surrounded by large defended areas. Such territorialism appears common amongst the African cichlids, being especially well represented by *Haplochromis* and *Haplochromis*-like fish which would be unlikely to habituate to their neighbours.

CHAPTER FOUR THE DEVELOPMENT OF A TECHNIQUE FOR COMPARATIVE BEHAVIOURAL STUDIES

The allopatric populations of P. philander had shown clear differences of markings and colour, and since these fish had also come from varied habitats it was possible that they would behave in a dissimilar manner. Indications of a behavioural divergence came from field observations of nest construction: territorial P. philander in Kuruman Eye dug as many as four large nests within a territory whereas the same species in Sibaya limited their nest-building activity to the cleansing of a single centrally placed disc.

It was difficult to establish in the field whether other behavioural differences were present. Therefore, an ethological experimental technique was required to determine if real behavioural divergences between populations had developed.

The populations of P. philander used in the laboratory came from Rhodesia (Lake Kariba), Lake Sibaya, Kuruman Eye and Durban. The specimens from Wondergat were not brought into the laboratory, and those from Otavifontein and Otjikoto arrived too late to be included in most of the analyses, but information from observations of these groups has been included where appropriate.

On arrival in the laboratory all populations were kept apart in separate stock tanks, except when used specifically for experiments which necessitated the mingling of the groups. The progeny of each group was reared apart to retain the integrity of the populations. The fish were kept at temperatures of 21 to 26°C, the water was vigorously aerated and cleansed by subgravel filters. The fish were fed daily upon live or frozen Daphnia, and when Daphnia were unobtainable the commercially prepared fish food, "Tetramin", was used.

For experimental purposes the water temperature was maintained at 25 ± 1°C and overhead banks of flourescent lights provided a 14L - 10D photoperiodicity. All observations were conducted from behind a one way mirror or from behind a screen with a very narrow (1.5cm) viewing aperture. It was important that the observer should be invisible to the fish for they would stop their current behaviour and show a conditioned appetitive feeding response to the appearance of the experimenter.

The experimental conditions peculiar to each specific investigation will be described where appropriate. However, the most commonly employed experimental procedure in the laboratory involved the recording of many different behavioural displays and activities.

A display is a relatively passive behavioural communication which involves very little movement and is analogous to display postures of reptiles, birds and mammals frequently described in ethology texts. Examples of P. philander displays are lateral display, frontal display, hanging, aggressive hanging and aggressive display. An activity refers to a behaviour which is actively performed such as biting, tail-beating and sexual activities. The distinguishing line is not always clear, for example, a side-shake is a sexual activity but it is also an important display. Therefore, such behaviour patterns were recorded as both displays and activities: one side shake was recorded as one sexual activity; the duration of the activity was recorded as the time spent in that courtship display.

Initially a tape recorder was used to record the duration and frequency of displays - as follows: a specific spoken comment would mark the onset of a particular behaviour pattern. It would be recorded that the fish had remained in that pattern until a further comment announced the end of the original display and the initiation of the next. Thus the duration of any display would be the time interval between the announcement marking its onset and that denoting its cessation.

During a particular display, additional activities might be performed. For example, during lateral display, tail-beating might occur. To avoid excessive work from the replay and to decrease the chances of confusion these activities were not recorded on the tape but were counted and written directly into a record book.

This system was extremely time consuming because the replay usually took longer than the recording period due to errors of transcription which required correction. Then the transcribed information needed to be totalled and counted so that the information could be translated into an orthodox form. Thus four hours of experimental work would produce approximately eight hours of paper work before the results of an observation became available.

To avoid the delays inherent in the use of a tape-recorder a 16 channel event recorder, capable of several computations and with direct computer access via a paper tape punch, was designed and built in the Physics Department of this University. This event recorder has several advantages over other recently developed instruments designed to perform similar functions (White, 1971; Dawkins, 1971), but has the disadvantage that it is slightly more expensive and complicated to build. A full description of the circuitry of our event-recorder, its versatility and advantages over other instruments will be published elsewhere (Ribbink and Way-Jones, in preparation), however its principal functions will be described below.

The event recorder was required to record three aspects of behaviour: 1) the number of occasions any specific activity was performed, 2) the time spent in any display or activity, and 3) the sequence of behavioural events.

Sixteen different behaviour patterns, their duration and number of occurrences could be recorded by depression of the appropriate buttons on the 16-channel keyboard.

At the completion of any experiment, or at some other convenient time, a read-out from the memories could be displayed on the screen. The information displayed was a computation of the events during the 300 seconds of the experiment, giving the behaviour pattern, the total number of times it occurred and the total time spent in that behaviour. Experiments could run for any preselected time as the digital clock could be set to record for a specific period of time. In these experiments exactly 300 seconds was the chosen period.

The paper tape punch recorded all the information in the sequence in which it was provided, and punched the computations (total display time and total number of activities for each behaviour) displayed for read-out by the event recorder.

The subsequent handling of the paper tape would depend on what was required: it could be stored as a permanent record, the information could be typed out by a tele-type or it could be run through a computer programmed to perform the desired analyses.

Though the event-recorder was designed specifically for laboratory studies it is portable and may be run from a 12 volt car-battery. It would therefore find a use in the field.

In addition to its verstaility and time and labour saving attributes, a further advantage is that it is possible to have results within a few seconds of the completion of an experiment. An experimenter would therefore be able to keep abreast of events and immediately adjust, alter or cease experiments as expedient. Such a facility is especially important to ethologists who might otherwise lose opportunities to follow behavioural trends because of the unmanageable bulk of their data.

In order to compare the behaviour of different populations of P. philander it was necessary to establish experimental techniques in which as many variables as possible were controlled. Resident males were always placed in aquaria of 38 x 38 x 30cm. This gave them considerably smaller territories than they would have had under natural conditions, which therefore simulated the "inner-territory" and intensified the effect of a stimulus. All aquaria had a sand substrate which appeared to be the preferred substrate under natural conditions. All aquaria were aerated and cleansed by subgravel filters and, except during a drought at the end of 1973, when water was severely restricted, a slow but constant flow of replenishing tap water passed through the aquaria. Overhead flourescent tubes gave 14L - 10D (light from 0600h to 2000h) diurnal illumination of 6000 lux; temperature was maintained at $25 \pm 1^{\circ}C$ and vegetation was limited to one 10cm high aquatic weed (Vallisneria torta) per aquarium. Experimental observations were begun once resident males had become fully territorial. Experience had shown that although the largest male in an aquarium population rapidly assumed dominance, a fully established territory took four to six days to become formed by males which had been removed from stock tanks and placed in their new environment. Consequently six days were always allowed to elapse between placement of fish and the initial exposure to stimuli.

Studies of P. philander diurnal rhythm (page 66) had shown that courtship and aggressive behaviour should be measured between 0900h and 1400h, which was the practice adopted.

The choice of stimuli to be presented to these resident males provided some problem. Even though crude models had been successful as stimuli for aggression and courtship in other fish (Tinbergen,1951; Lissman,1932; Peeke, Wyers and Herz,1969) it was found that even very accurate and detailed models failed to stimulate appropriate responses in P. philander.

An experimental technique which proved successful in stickleback work (Van Iersel,1953; Sevenster,1961; Sevenster-Bol, 1962) and which was used with equal success with P. philander was to house an intruder in a clear glass container. Stimulus P. philander were placed in a 600ml round bottomed flask which was suspended 2cm above the substrate in the centre of a resident males' territory. The responses of territorial males were recorded.

Courtship responses were elicited by enflasked gravid females (see Plate 19). Pilot experiments demonstrated that even spent females and neutrally coloured small males could stimulate courtship. These fish however, failed to show the head-down tendency to follow, consequently resident males then interpolated aggression with sexual invitation behaviour. Provided gravid females were used as the enflasked stimulus, courtship responses of resident males could be quantitatively investigated with accuracy.

Procedural problems arose concerning the use of stimulus males. It is generally accepted amongst ethologists that the relative size of an intruder will influence behavioural responses of territorial individuals. Ribbink (1971) superficially discussed some of the modifications to behavioural responses of territorial male P. philander when confronted with conspecific male intruders which were larger, or smaller, than themselves. On the basis of experience gained in earlier studies it was anticipated that a relatively small enflasked stimulus male would elicit little or no aggression, whereas an 'intruder' substantially larger than the resident might evoke submission. Therefore, to provide a sound basis for the intended comparative study, it was necessary to determine the optimal size of an obligate intruder relative to the territorial males.

The second procedural problem to be solved in preliminary investigations arose because it was considered necessary to subject residents to the challenge of an 'intruder' on ten or more consecutive days. This experiment was required to produce a reliable index of the level of aggression of the subject fish. It was anticipated that the daily number of aggressive responses would settle at a fairly constant measurable plateau. The plateau derived from these quantitative measurements would then form a basis for comparison of behavioural responses of the various races of P. philander. It had been demonstrated, however, that brief or protracted exposure of territorial fish to mirror images (Clayton and Hinde, 1968; van den Assem and van der Molen, 1969), to models (Peeke, Wyers and Herz, 1969) and to live conspecific (Peeke, Herz and Gallagher, 1971) over a period of days resulted in a decrement of aggressive response. It was possible, therefore, that P. philander might show a waning of aggression under these experimental conditions. On the other hand, the short exposure of 300 seconds per day might reinforce territorialism in resident males for a brief fight followed by the removal of the enflasked intruder could be crudely equated to a successful eviction of an unwanted visitor under natural conditions. Such reinforcement could result in a daily increment of the aggressive responses. Three possibilities existed: the aggressive responses might have stabilised at a plateau, they might have increased with time, or they might have waned with time. It was necessary to establish which response would occur.

The third procedural problem to be answered by the preliminary investigations stemmed from the observation that the presence of other fish in an aquarium appeared to promote and maintain territorial behaviour in the dominant male. Much of the experimental work of a similar nature done by previous authors had been on isolated individuals (Clayton and Hinde, 1968; Peeke, Wyers and Herz, 1969; Peeke, 1969 and others). Furthermore Peeke, Herz and Gallagher (1971) comment in justification for the use of isolated fish that,

> "it is a common and easily replicated observation that in a variety of species when a male fish has resided alone, the resident will attack an intruder in defence of his territory".

Another consideration was that although attendant fish might promote territorialism, they might also alter the behaviour which was to be measured. For example, should an attendant fish become gravid then the change in its behaviour would probably affect the responses of the subject male when exposed to a stimulus female, or when exposed to the challenge of an enflasked conspecific male.

This problem required an experimental solution.

Experimental answers to procedural problems

1. An investigation to determine the optimal size of the stimulus male relative to the territorial individual.

I anticipated that the greatest aggressive response would be evoked by a stimulus male which was large enough to present a challenge, but not so large that it inhibited residents. In this experiment enflasked stimulus males of different sizes were placed in each aquarium to determine, from the responses of territorial individuals, the optimal size of obligate intruders.

It was possible that residents might habituate to stimulus males under these experimental conditions, so to guard against this, several precautions were taken.

Firstly, a short exposure period of 300 seconds was chosen not only so that the stimulus fish would maintain its sexual colours throughout the period, but also because van Iersel (1953), Sevenster (1961) and Sevenster-Bol (1962) had made no reference to the waning of aggressive response to the stimulus fish (*Gasterosteus aculeatus*), when using similar methods and time periods as those proposed for *P. philander*. On the other hand, other workers (Peeke 1969; Peeke and Peeke 1970) using identical methods, but a longer exposure duration, demonstrated a waning of aggression.

The second precaution was to expose the males to the stimulus on every other day. Clayton and Hinde (1968) and Peeke *et al.* (1971) had demonstrated that a recovery of the habituated response does occur when given the opportunity. The day between exposure was intended to provide such an opportunity.

In the experiment about to be described, the stimulus males used on each day were either larger or smaller than the stimulus of the previous exposure period (see below). This meant that on each day the stimulus was different. As habituation of a response is stimulus specific (Thorpe 1964) the use of a different sized stimulus for each exposure provided a further precaution against the occurrence of an habituated response.

Finally, to demonstrate that the modifications of behaviour were due to the different sizes of the stimulus males and not to habituation, conditioning or any other factor, the experiment was run twice for each of the five fish. The first sequence began with the smallest stimulus males being exposed to all residents on the first day, and ended with the presentation of the largest stimulus males on the last day. The run was then reversed; the largest stimulus males were presented first and eventually on the last day of the sequence residents were exposed to the smallest stimulus males.

In this preliminary experiment all the subject fish used were 60± 1mm SL and the stimulus males were 50, 55, 60, 65, 70, 75 and 80mm (all ± 1mm) SL. In these and all subsequent experiments in which enflasked males were used as stimuli it was necessary to maintain several stimulus males of a particular size dominant within their own aquaria. Several of these fish were held in reserve in order to provide a replacement stimulus in the event of enflasked fish losing colour.

The experimental procedure was to present a stimulus male to the subject fish, and should the enflasked male retain its colours and fight back then it would be exposed to the next territorial male in subsequent 300 second periods. Should a stimulus fish show signs of submission, then it would be replaced by another male of the same size before exposure to the next subject. Surprisingly few enflasked fish showed submission in this and subsequent experiments, and loss of coloration was generally rectified by a brief sojourn of five to ten minutes in their own aquaria (territories). Presentation of a good stimulus was ensured by using stimulus fish in rotation. Though this procedure required additional manipulations of stimulus fish during the course of an experiment, and also an enormous amount of additional aquarium maintenance, it was found to work very well.

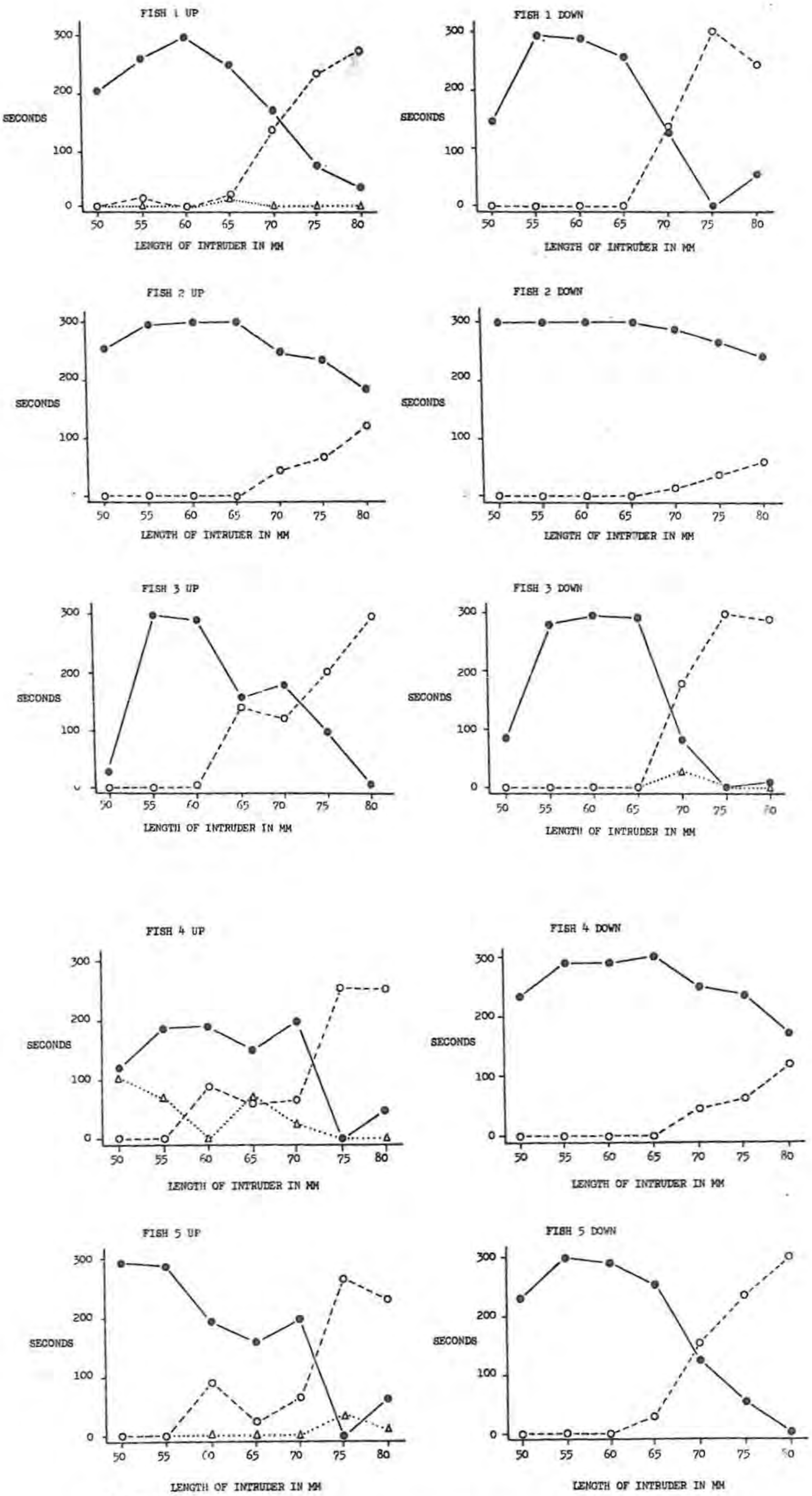


Figure 47

The proportion of 300 seconds each territorial fish spent in aggressive behaviour (●——●), conflict behaviour (O---O) and in hiding or avoidance behaviour (Δ······Δ), when confronted by enflasked intruders of different sizes.

UP - the sequence began with the smallest stimulus fish progressing to the largest.

DOWN - the sequence began with the largest stimulus fish then worked down to the smallest.

Seven attendant fish were placed with the subject male in each aquarium. At this stage it had not been empirically determined whether the presence of attendant fish would be advantageous, but intuitively it was felt that their presence was required. However, to reduce the possibility of the attendant fish affecting the subject male's responses to the stimuli provided, care was taken to ensure that they were either spent females or juvenile males.

Behaviour patterns of particular relevance to this experiment were aggressive responses (lateral display with tail-beating, fighting or alternatively called fins-in with biting), flight responses (hiding and avoidance swimming) and also conflict displays (aggressive hanging and hanging).

The behavioural responses of the individual fish are given by figures 47 and 48 . The mean response is given by figures 49 and 50. A relationship between the aggressive and conflict patterns emerged and this is presented on figures 51 and 52 . From the results obtained it was apparent that 50mm fish evoked relatively little aggression. Occasionally when one of these small stimulus males lost colour on becoming submissive, courtship was elicited. The 55 and 60mm stimulus fish produced the greatest response both in time spent in aggressive displays and in the number of activities (bites and/or tail-beats) directed at these intruders. None of these stimulus males were courted. As the size of the stimulus males was increased there was a progressive decrease in aggressive behaviour accompanied by a steady increase of conflict and submissive behaviour. This trend is discussed more fully below.

The relationship between the four behaviour patterns given on figures 51 and 52 shows that in the presence of small stimulus males the dominant pattern is overt fighting (fins-in and biting). As the relative size of the intruder is increased so overt fighting decreases and lateral display increases. A further increase in the relative size of the intruder results in a decrease in both fighting and lateral display, accompanied by an increase in aggressive hanging and hanging. When challenged by the largest males available aggressive hanging decreased and hanging became the dominant behaviour.

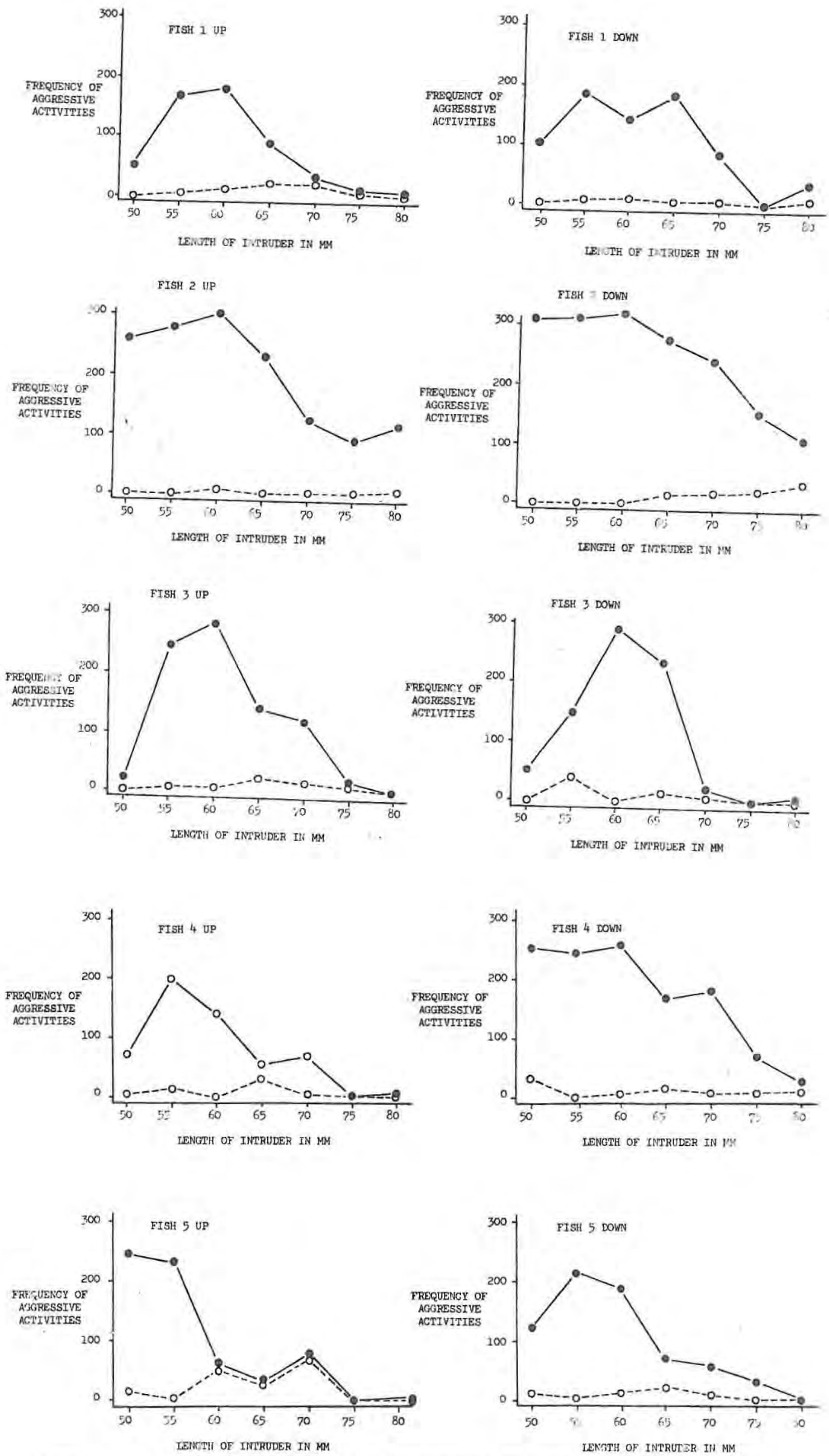


Figure 4 The total number of aggressive activities performed in 300 seconds by each territorial male when confronted with enflasked intruders of different sizes.

●——● TAIL-BEATS AND BITES, ○----○ TAIL-BEATS ONLY.

UP - the sequence began with the smallest stimulus fish progressing up to the largest.
DOWN - the sequence began with the largest stimulus fish progressing down to the smallest.

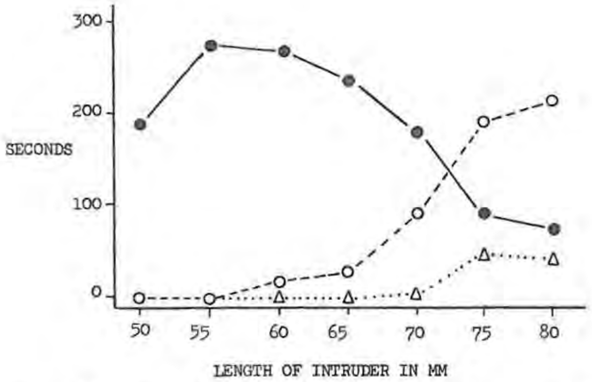


Figure 49 The mean number of seconds spent in aggressive behaviour (●——●), conflict behaviour (O----O), and avoidance behaviour (Δ·····Δ). This figure illustrates that a decrease in aggression is accompanied by an increase in conflict and avoidance behaviour. Maximum aggression was elicited by stimulus males slightly smaller than the 60mm SL resident fish.

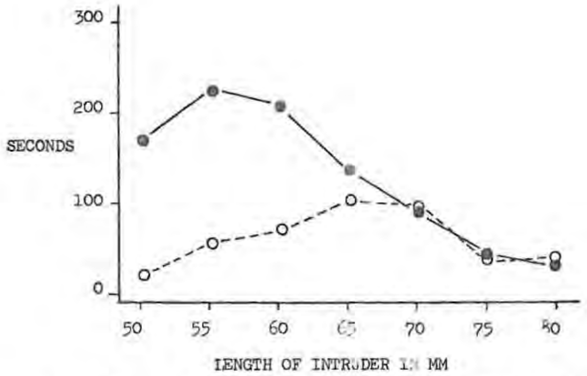


Figure 51 The relationship between fins-in (●——●) and lateral display (O----O). Fins-in is the behaviour which predominates when intruders are relatively small, as the intruders increase in size the proportion of fins-in decreases and lateral-display increases. As the residents are faced by larger challenges they go into conflict (see fig 61).

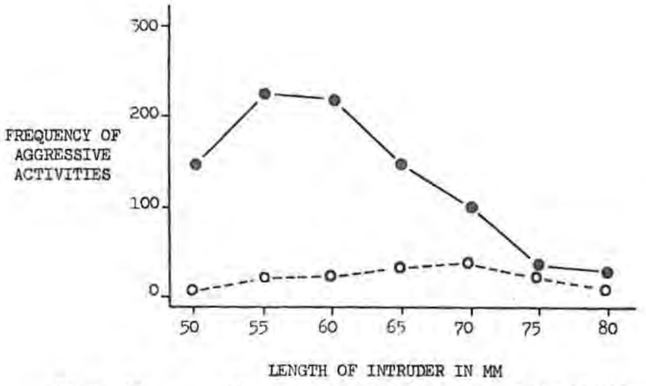


Figure 50 The mean frequency of aggressive activities. Tail-beats and bites (●——●), tail-beats only (O----O). Maximum frequency of aggressive activities was elicited by males slightly smaller than the 60mm SL resident fish.

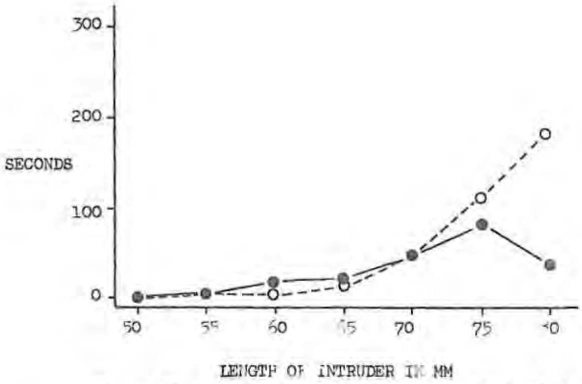


Figure 52 The largest intruders evoked submissive hanging (O----O) more than aggressive hanging (●——●).

It was apparent from these experiments that to elicit a maximum aggressive response from territorial P. philander, a male conspecific slightly smaller than the resident should be used as the stimulus. Since stimulus males were slightly magnified by the flask in which they were housed, the results presented above should not be considered to give an absolute measure of aggression relative to size. Nevertheless a clear relationship between flight and aggressive behaviour in response to stimuli of different sizes was demonstrated. The results also indicate that the fish appear to have a 'knowledge' of their own relative sizes, which confirms an observation made earlier by Baerends & Baerends van Roon (1950).

The present experiment demonstrated that to obtain a maximum aggressive response enflasked stimulus males should be several mm smaller than territorial fish. It is unlikely that one could be more accurate than this for it is well known that motivation and individual variation, in addition to the size of an intruder, will influence a resident's responses. Though all territorial males were 60mm SL in this investigation, in many subsequent experiments resident males were not this size, therefore, sensible adjustments were made in the choice of an enflasked intruder to ensure that it served as an adequate stimulus. In the experiments which follow, stimulus males were between three and seven millimetres (SL) shorter than the residents which ranged from 58 to 78mm SL.

Aggression: its constancy and dependence on attendant fish

2. In preparation for the experiments designed to compare the behaviour of the four allopatric populations of P. philander, two further answers to procedural problems were required. Thus, a preliminary experiment was designed to determine whether the aggressive response of the residents would increase, decrease or remain constant over a minimum period of twelve days. Accommodated within the design of this experiment was an investigation to ascertain whether attendant fish were required for the maintenance of the resident male's territorialism.

Nine aquaria (38 x 38 x 30cm) with a sand substrate and containing a small aquatic plant were used for this preliminary experiment. A 14L - 10D photoperiodicity was provided by overhead

Figure 53

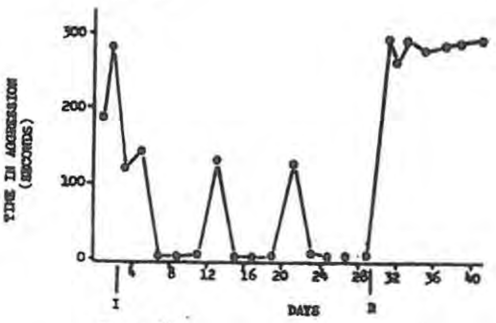


Figure 57

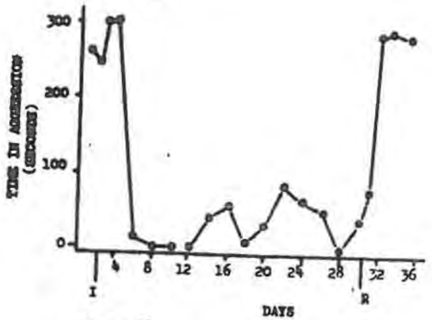


Figure 54

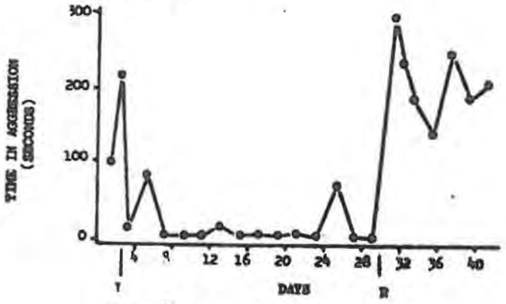


Figure 58

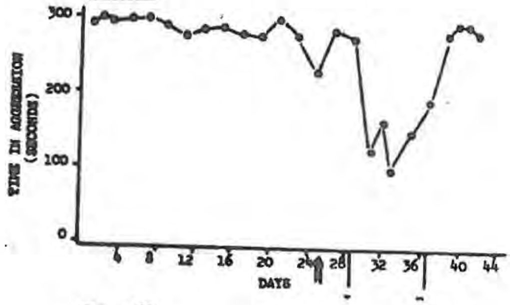


Figure 55

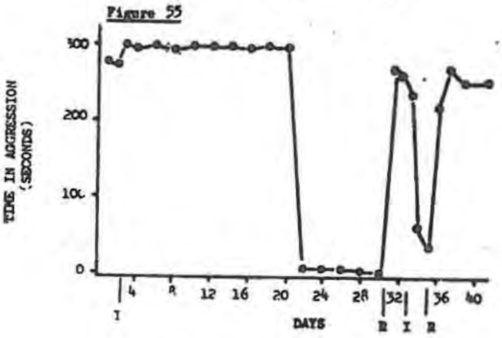


Figure 59

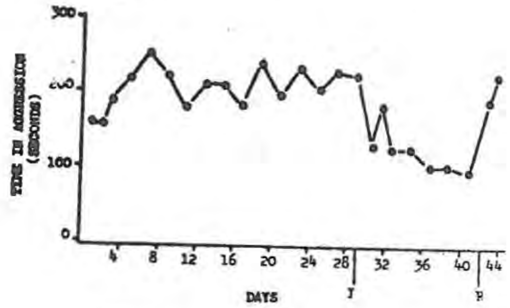


Figure 56

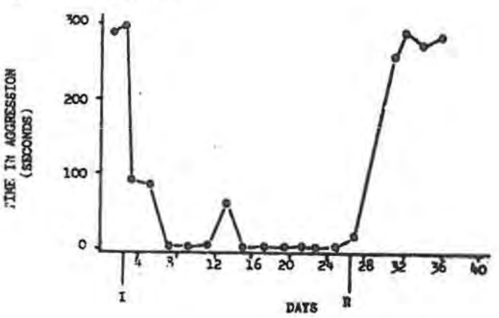


Figure 60

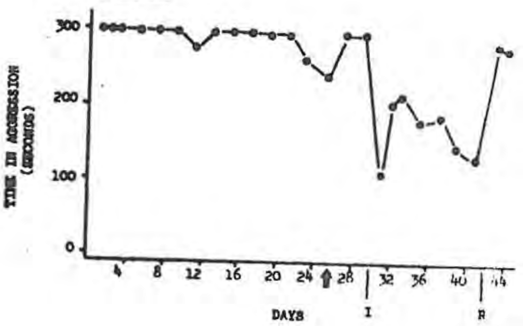
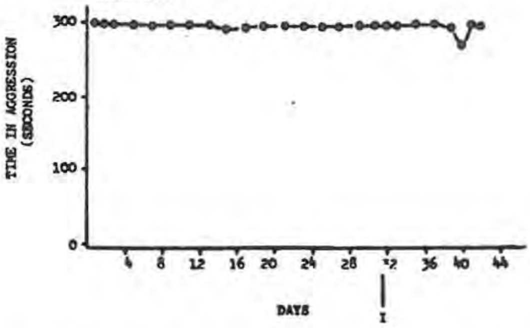


Figure 61



Figures 53 to 61

The time spent in aggression by each fish when presented with a stimulus fish. I = point at which the resident males were isolated (attendant fish removed), R = point at which aggression was reinforced (attendant fish added), and ⇑ = point at which attendant fish were exchanged for others which were new to the aquarium.

When not in aggression the territorial fish were in conflict or avoidance (flight) behaviour patterns.

fluorescent tubes and the water temperature was maintained at 25 ± 1°C. A territorial male (standard length varied from 66 to 68mm), accompanied by seven attendant fish, was placed in each tank. Once the territorial males had become fully dominant (six days were allowed to permit the development of full territorialism), they were exposed to stimulus males for 300 seconds on each day. Though stimuli were presented daily, responses were usually recorded on every alternate day.

For the first few days of the experiment attendant fish were present in all aquaria. Thus the behavioural responses of all territorial males was recorded in the presence of attendant fish. Once this record had been obtained, then attendant fish were removed from five aquaria, leaving isolated males behind. On other occasions during the experiment, attendant fish were taken from or introduced into various territories to investigate the effects of presence (reinforcement), or absence (isolation), of company on the response of residents to stimulus males.

It was apparent from these experiments that isolation resulted in a reduction of the aggressive responses with a corresponding increase in conflict and/or flight responses (figs 53 to 61). Isolation caused an immediate decrement of aggressive response to most fish, but several showed a much longer latency (figs 55 and 61). Addition of attendant fish to aquaria containing isolates resulted in an immediate increase in territorial behaviour which was reflected by an increase of aggressive, and a decrease of conflict and flight behaviour, when the territorial male was exposed to a stimulus male. By addition or removal of attendant fish one could effectively manipulate the behavioural responses of territorial fish to stimulus males.

Those fish which were maintained in the presence of attendant fish showed little waning of aggression. They maintained good sexual coloration throughout the test period and remained active within their aquaria. Nevertheless, it was observed that the attendant fish were driven into the surface waters where they remained in submissive hanging. Under these conditions the aggressive response to the stimulus declined slightly, but could be given a boost if the attendant fish were replaced by individuals which were new to the territory and the subject male (figs 58 and 60).

Isolated males lost virtually all of their sexual coloration and adopted the disruptive pattern. They became inactive and hid on the substrate in a corner or alongside the aquarium wall, the stimulus-response latency increased markedly and in some instances the fish hid and remained motionless for the full duration of the test (figs 53, 54, 55, 56 and 57).

It may be concluded that an enriched stimulus environment is required by territorial P. philander if they are to maintain a high level of intraterritorial activity, and respond in a constant manner to enflasked intruders. In aquaria new visitors cannot continually arrive at the territory, therefore the attendant fish should be renewed each day to prevent a response decrement to stimulus males. It became a practice to replace all attendant fish with individuals new to the aquaria each morning prior to behavioural observations. Experience had shown that seven to ten attendant fish should be placed in the small aquaria (38 x 38 x 30cm) used. Fewer attendant fish would have all of the dominant male's aggression focussed upon them and become severely damaged, and more than this number resulted in overcrowding.

CHAPTER FIVE BEHAVIOURAL DIVERGENCE OF THE ALLOPATRIC POPULATIONS: A PROBLEM IN SPECIATION

It will be recalled that the allopatric populations of P. philander differed from one another with respect to coloration and markings. Attention was drawn (pages 2 and 3) to the possibility that colour acts as a barrier to interspecific hybridisation, and arguments of Greenwood (1965, 1974) and Fryer & Iles (1972) were cited in support of this thesis. It was considered possible that coloration and markings might also serve as a barrier, or deterrent, to interbreeding of the allopatric populations of P. philander.

Though colour is probably not the only aid to recognition of species characteristics it was found that other differences, (differences of morphology and in the execution of behaviour patterns) were less overt. Consequently, the emphasis is placed on colour in the following arguments.

Differences in coloration of the allopatric populations of P. philander suggest an evolutionary divergence of these populations, and it is possible that several, or all, of the populations are incipient species. Experiments were therefore designed to determine to what extent the populations had diverged. Experimental design was based on the following premise: since cichlids select conspecific mates and show a greater aggression towards conspecific intruders, which implies a recognition of species characteristics (Baerends and Baerends van Roon, 1950), it is possible that they would recognise and respond particularly well towards their own population characteristics within the broader spectrum of parameters belonging to the species. It was anticipated that recognition would manifest itself as a difference in the degree of response: for example, it was considered likely that greater sexual and aggressive activity would be elicited from fish confronted with their own colour forms than from fish exposed to the colour forms of other populations.

Field and laboratory observations have shown that although the execution of behaviour patterns might be indistinguishable from one population to the next, the degree to which a behaviour pattern is practised might differ considerably. For example, as regards nest building behaviour, in Kuruman Eye territorial males constructed several large nests, but in Sibaya one small nest was all that ever appeared. Consequently, an adjunct to the principal premise is that quantitative differences of behaviour between populations might provide additional evidence of evolutionary divergence.

As a result of the findings of earlier experiments designed to establish a technique, stimulus males were always slightly smaller than residents, attendant fish were renewed each day and stimulus females were always the most gravid available. Experiments began at 0900h each day, and the exposure to the stimulus fish was for 300 seconds in each case.

Males whose behaviour was to be compared were placed singly, in a row of 12 aquaria (each 38 x 38 x 30cm) in a laboratory in which natural light supplemented the artificial illumination. To compensate for any affect time of day or aquarium location might have had on behaviour, the fish were arranged in a particular sequence which was altered for each experimental run as illustrated by fig 62 . On each day, for 12 days, a single enflasked stimulus female and then a

	Aquarium No	1	2	3	4	5	6	7	8	9	10	11	12
RUN 1	Population	D	S	R	K	D	S	R	K	D	S	R	K
	SL (mm)	64	63	63	63	64	63	64	62	62	63	64	62
	Aquarium No	1	2	3	4	5	6	7	8	9	10	11	12
RUN 1	Population	S	R	K	D	S	R	K	D	S	R	K	D
	SL (mm)	68	68	68	64	63	64	68	73	72	68	68	72
	Aquarium No	1	2	3	4	5	6	7	8	9	10	11	12
RUN 1	Population	K	D	S	R	K	D	S	R	K	D	S	R
	SL (mm)	63	62	62	66	67	67	66	66	67	66	66	66

Figure 62. This figure shows how the fish were arranged in their aquaria for the three experimental runs and also gives their respective sizes in mm SL. Numbers 1 -12 represent the aquarium number; the letters D,R,S,K within the blocks designate the geographical region from which the subject fish had been taken: D = Durban, S = Sibaya, R = Rhodesia (Kariba) and K = Kuruman Eye.

similarly enflasked stimulus male were presented to each of the 12 residents in turn. Over the 12 days the order in which the population of stimulus fish was selected was the same as the linear sequence of territorial males in the aquaria: that is, on day one of the first run the stimulus fish were from Durban, on day two they were from Sibaya and on day three from Rhodesia and so on for 12 days. At the end of 12 days (the end of a run), each of the resident (territorial) male members of the four populations would have been exposed to stimulus fish representing any one of the (4) populations on three occasions. As three experimental runs were completed, the nine resident fish representative of each population would have been exposed to stimulus fish representing any given population on 27 occasions.

A random sequence was not used for the placement of the territorial fish. Such a system, when implemented with the small number of animals available in this experiment, may have placed all the individuals of one population close to or far from a factor, such as window light, which could have influenced the results.

It was originally intended to complete four experimental runs, however, it was considered that the pattern of results established by the three runs would remain unaltered by a forth set of similar experiments. The final run was therefore abandoned.

Baerends and Baerends van Roon (1950) observed that cichlids treat conspecifics differently from other species. Therefore, to serve as a control and to provide a further basis of comparison the stimulus fish on the thirteenth day of each run were male and female Haplochromis darlingi. These stimulus fish were selected on the same criteria of size and ripeness as the P. philander stimulus fish. Though H. darlingi are similar to P. philander in many respects it was anticipated, in view of Baerends and Baerends van Roon's observation above, that they would elicite a lower level of response than any of the P. philander populations.

As in previous experiments, the male P. philander were given six days in which to develop complete dominance and territorialism before being exposed to stimulus conditions.

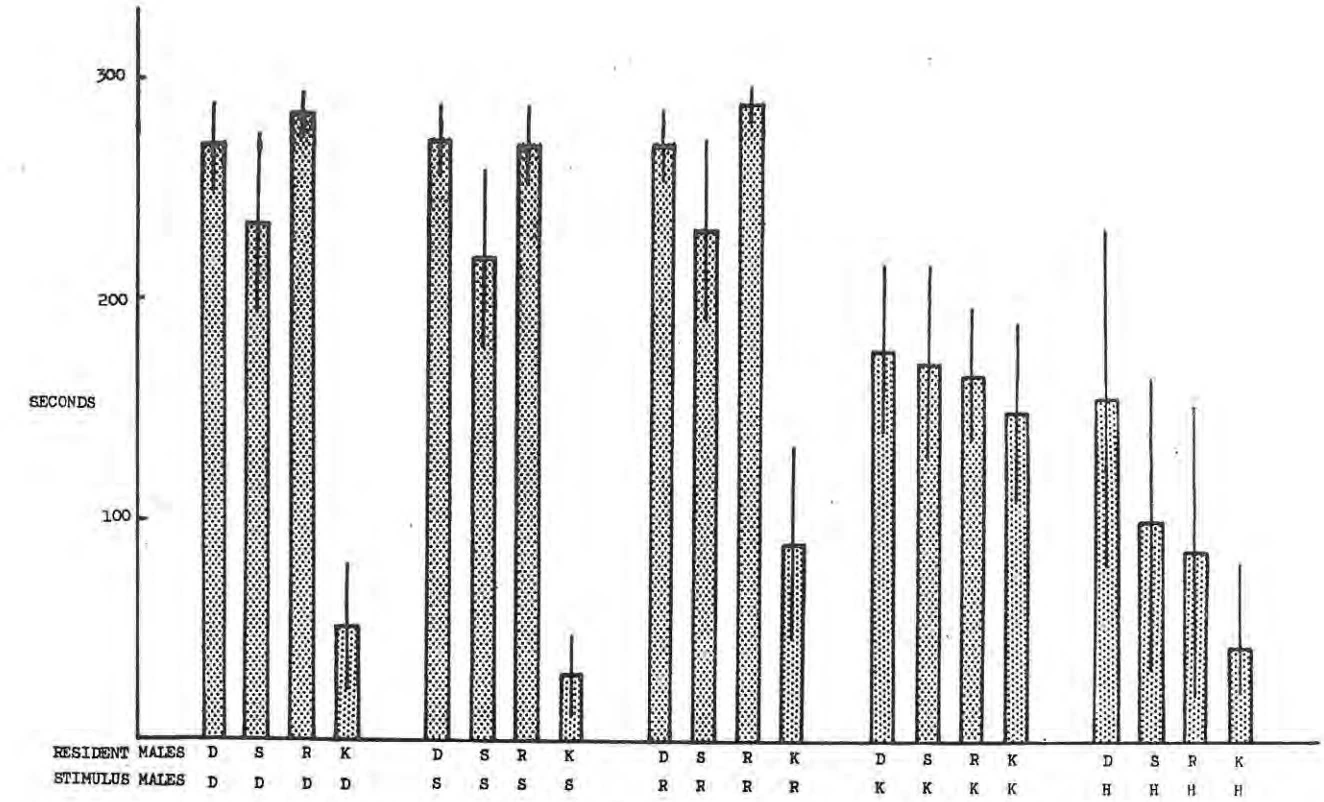


Figure 63 The mean time (in seconds) spent in aggressive display by males drawn from each available population towards stimulus males drawn from the same populations and including H. darlingi (see text).
The 95% confidence interval for each mean is drawn on each column.

D = Durban; S = Sibaya; R = Rhodesian (Kariba); K = Kuruman; H = Haplochromis darlingi

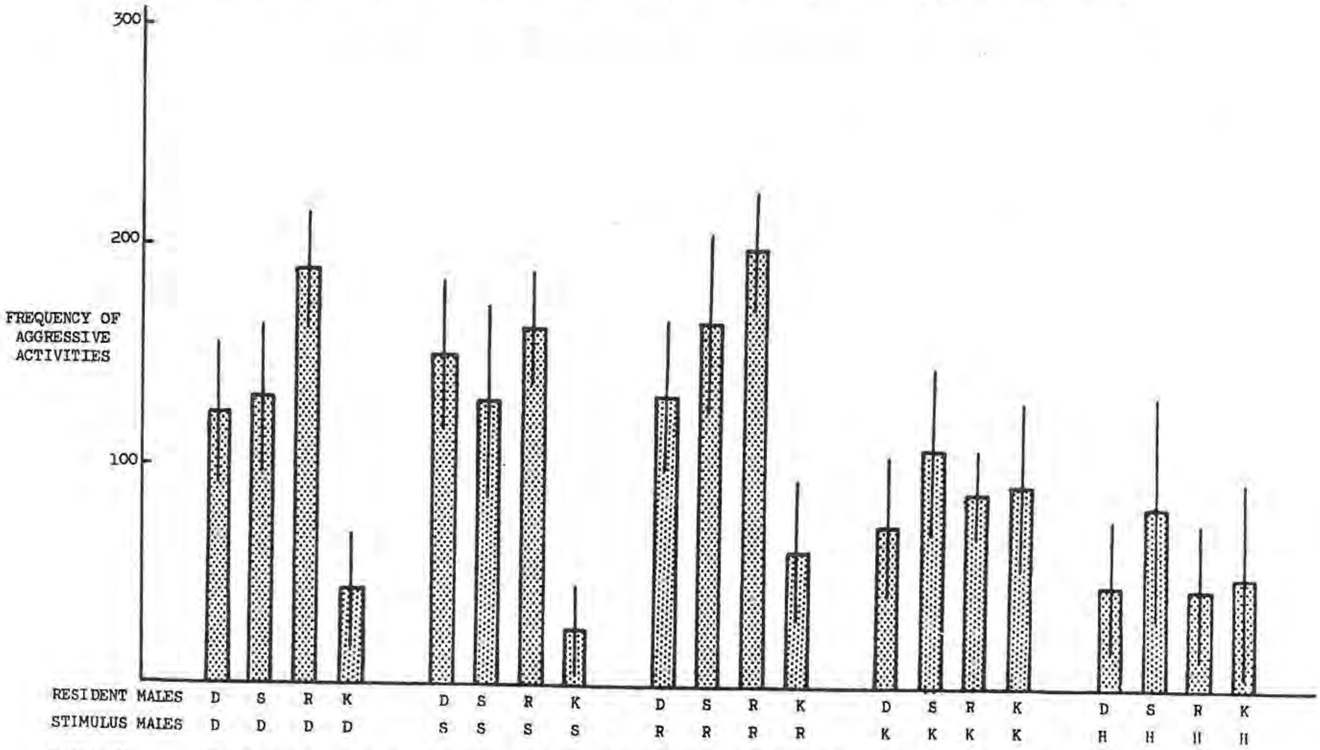


Figure 64 The mean frequency of aggressive activities (tail-beats and bites) by males drawn from each available population towards stimulus males from the same populations and including H. darlingi (see text).

The 95% confidence interval for each mean is drawn on each column.

D = Durban; S = Sibaya; R = Rhodesian (Kariba); K = Kuruman; H = Haplochromis darlingi

During each 300 second period of exposure to the stimulus fish all the resident's displays were recorded as the number of seconds spent in each particular behaviour pattern. In addition, all behavioural activities were counted (the distinction between displays and activities is described on page 117).

The aggressive responses

In fig 63 each group of four columns gives a comparison of the time spent in aggressive display by the resident males representative of the four allopatric populations, when exposed to a particular group of stimulus males. In fig 64 the same comparison between populations is made, but the number of bites and tail-beats (aggressive activities) performed by each group are compared.

From these figures it is apparent that the Kuruman representatives were the least aggressive in all five groups (fig 63), and in three of the groups (fig 64).

To determine whether the resident fish recognise their own population characteristics a comparison of the effect of the various populations of stimulus fish is necessary. This was done by a re-arrangement of data to give figures 65 & 66. In these figures each group of five columns gives a comparison of the aggressive responses (displays fig 65 ; activities fig 66) of a single geographic population of residents to the five different populations of stimulus males.

Though it appeared that the Durban, Sibaya and Rhodesian populations had no difficulty in recognising each other as conspecifics, the stimulus males drawn from the Kuruman population were not easily recognised as conspecifics by these populations of _P. philander_. Indeed the Kuruman stimulus males elicited aggressive responses similar to those evoked by _H. darlingi_ males. When exposed to its own population, however, Kuruman stimulus fish evoked a greater response than any other group of stimulus male which suggests that a recognition of population characteristics may have occurred. An alternative possibility exists and should be borne in mind, that is: the Kuruman resident males may have been less inhibited by their own population of stimulus male than by the others.

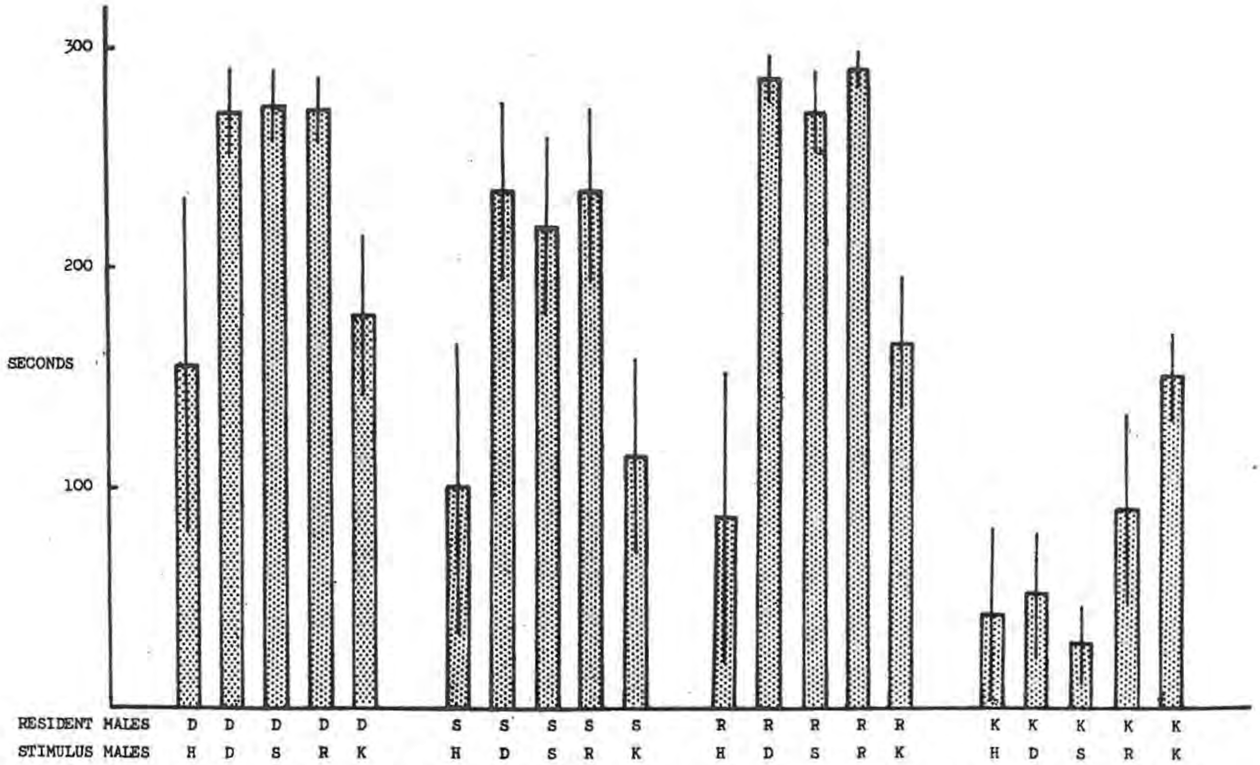


Figure 65 The effect on different populations of stimulus male on the mean time (in seconds) spent in aggression by males drawn from each available population.
The 95% confidence interval for each mean is drawn on each column.

D = Durban; S = Sibaya; R = Rhodesian (Kariba); K = Kuruman; H = *Haplochromis darlingi*

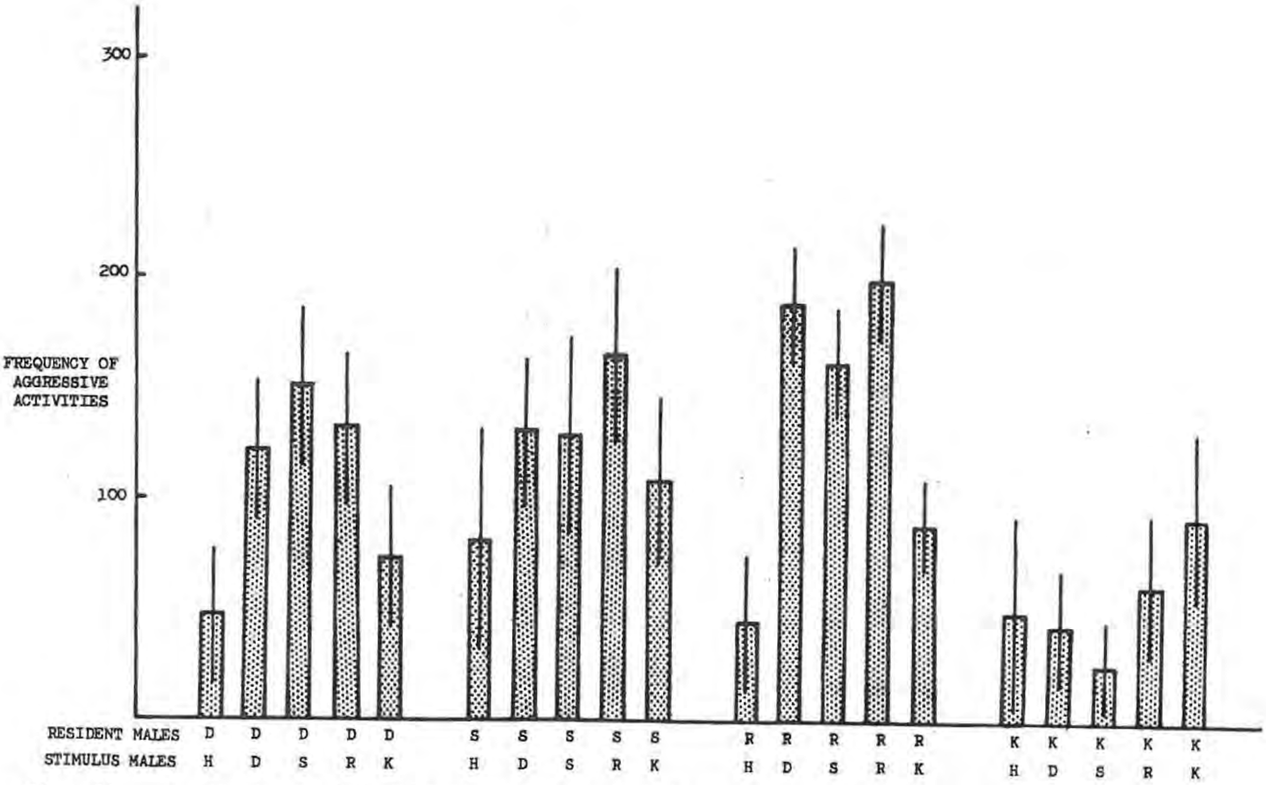


Figure 66 The effect of different populations of stimulus male on the mean frequency of aggressive activities (bites and tail-beats) by males drawn from each available population.
The 95% confidence interval for each mean is drawn on each column.

D = Durban; S = Sibaya; R = Rhodesian (Kariba); K = Kuruman; H = *Haplochromis darlingi*

A more detailed comparison of the aggression of the Durban, Sibaya and Kariba populations was carried out by taking the mean time each group spent in aggression when presented with stimulus males of all groups bar the Kuruman population. The Kuruman population were not considered for this analysis as they proved to be inadequate stimuli for eliciting aggression as has already been indicated by the previous paragraph. Further confirmation of their inadequacy in this respect will be provided by the discussion of courtship errors (see below).

Fig 67 shows that in terms of aggressive display times, the Rhodesian fish were significantly more aggressive than the Durban fish ($P < 0,1$ by analysis of variance), and that both these groups spent considerably more time in aggressive displays than the Sibaya males, the difference being very highly significant ($P < 0,001$ in both instances, by analysis of variance).

A comparison of the mean frequency of bites and tail-beats (aggressive activities) performed by each population (fig 68) shows, once again, that the Rhodesian fish are the most aggressive, however an apparently anomalous result was that the Sibaya population appeared more aggressive than the Durban group, though they had spent less time in aggression (fig 67).

Though this analysis is, in itself, inconsequential (the 95% confidence limits overlap) it does lead to a further analysis. It seemed likely that the Durban population favoured the more time consuming behaviour patterns, lateral display and tail-beats, rather than bites which can be performed rapidly. Table 5 shows that Durban resident males spent considerably more time in lateral display than any other group.

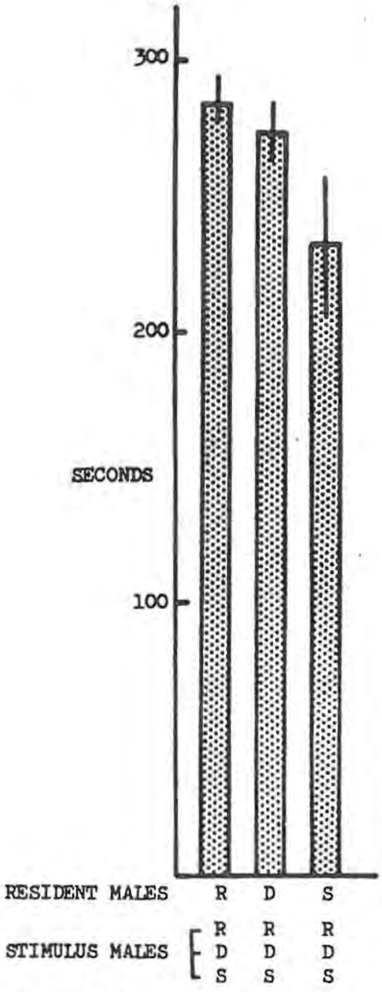


Figure 67

The mean time (in seconds) spent in aggression by the Durban (D), Sibaya (S) and Rhodesian (R) populations towards stimulus males drawn from all three of these populations.

The 95% confidence interval for each mean is drawn on each column.

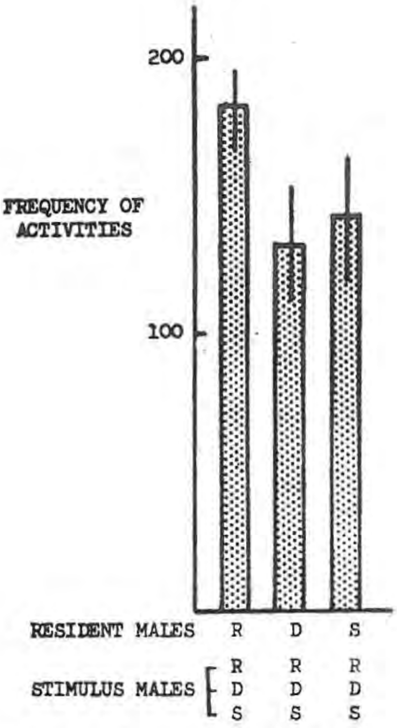


Figure 68

The mean frequency of aggressive activities (bites and tail-beats) by the Durban (D), Sibaya (S) and Rhodesian (R) populations towards stimulus males drawn from all three of these populations.

The 95% confidence interval for each mean is drawn on each column.

Table 5 : The time spent in lateral display, by residents from the four populations in the presence of *P. philander* stimuli from these populations and *H. darlingi* stimuli, expressed as a percentage of the total time spent in aggression. The mean time spent in lateral display towards all the *P. philander* stimulus males is also shown.

		Percentage time spent by the resident fish in lateral display to stimulus males from different populations					
		P. philander					*H. darlingi*
	P. philander	Durban	Sibaya	Rhodesian	Kuruman	Mean	
RESIDENTS	Durban	70	64	70	70	68	73
	Sibaya	53	53	50	40	50	37
	Rhodesian	49	52	44	49	48	74
	Kuruman	46	28	21	48	37	31

An analysis of the number of aggressive activities performed (table 6) shows that the number of tail-beats represents a relatively small percentage of the aggressive activities evoked by the stimulus males.

Table 6 : The number of tail-beats expressed as a percentage of the total number of aggressive activities. This analysis shows that tail-beats are used less frequently than bites and that the Durban population rely more heavily, and the Kuruman population less heavily, upon tail-beat than any other group.

		Percentage number of tail-beats to stimulus males from different populations					
		P. philander					*H. darlingi*
P. philander		Durban	Sibaya	Rhodesian	Kuruman	Mean	
RESIDENTS	Durban	42	29	30	29	32	19
	Sibaya	30	19	23	17	22	6
	Rhodesian	24	27	21	32	25	22
	Kuruman	8	5	13	19	14	8

These analyses show that the tendency for the Durban population to enter into lateral display and tail-beat was greater than any other group. By contrast, the probability that lateral display and tail-beating would be produced by the Kuruman population was less than in any other group.

Lateral display is essentially a signal which conveys information concerning the relative size of two opponents in a fight. Should this signal fail to produce submission in either of the rivals then tail-beating may ensue (Ribbink, 1971). Fish could spend a long time in display and produce very few tail-beats, whereas in the fight (fins-in) behaviour pattern, bites occur very frequently and at short intervals. Therefore those populations which tend to display rather than bite produce fewer aggressive activities than those which utilize fins-in and biting behaviour.

This analysis indicates that the Durban population uses displays more readily than activities, whereas the Sibaya population produces a greater number of aggressive activities per unit time, which explains the apparent anomaly: namely, it accounts for the observation that the Durban population spent more time in aggression but performed fewer activities than the Lake Sibaya population.

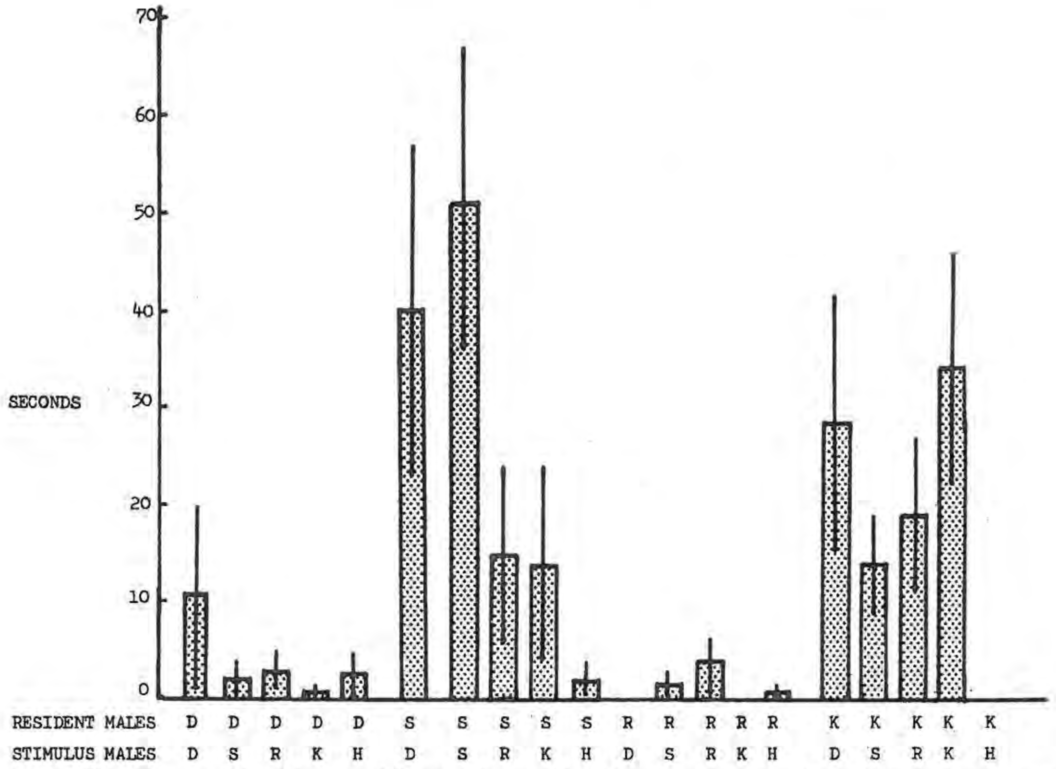


Figure 69 The mean time (in seconds) spent in conflict behaviour by males drawn from each available population in the presence of stimulus males drawn from the same populations and including *H. darlingi* (see text).

D = Durban; S = Sibaya; R = Rhodesian; K = Kuruman; H = *Haplochromis darlingi*

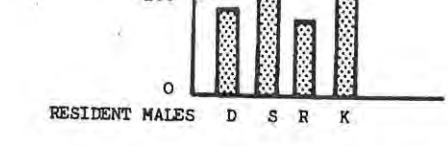


Figure 70 The total number of occasions on which conflict patterns were stimulated in each population.

In the earlier figures (figs 63, 64, 65 and 66) it was apparent that Sibaya males responded less aggressively towards stimulus males drawn from the Sibaya population than towards Kariba and Durban stimulus males. Furthermore, from these figures, and also from figure 67, it is apparent that the time spent in aggression by Sibaya males was less than that of Rhodesian and Durban residents. It was found that one of the principal reasons for this reduced response of the Sibaya resident males, when presented with stimulus males from Sibaya, was that under these stimulus circumstances they tended to enter more easily into conflict behaviour. Similarly, figure 69 shows that representatives of other allopatric populations of P. philander also entered into conflict most readily when presented with stimulus males from their own population.

This observation implies that these fish recognise their population characteristics. It appears, therefore, that conflict behaviour provides the patterns most indicative of recognition. This in no way contradicts the observation that cichlids show more aggression towards conspecifics (Baerends & Baerends van Roon 1950), but adds to it: both aggression and submission are more likely to be stimulated by conspecifics than fish of another similar species.

The fish most likely to enter into conflict behaviour under these experimental conditions were the Kuruman males, followed in order by the Sibaya, Durban and Rhodesian populations (fig 70). This sequence is the complete reverse of the aggressive trends and therefore tends to confirm those observations.

Courtship errors

The fact that territorial fish from Rhodesia, Durban and Sibaya directed less aggression at Kuruman stimulus males (figs 63 to 66) may be partially explained by the observation that Kuruman males were frequently mistaken for females and courted. These errors occurred in the presence of stimulus males from all populations, but were most frequent when enflasked Kuruman males were presented (fig 71).

Usually errors were made within the initial few seconds of exposure to the stimulus and then rectified, though in some instances a large proportion of the 300 seconds was spent in misguided courtship. Resident fish had been courting enflasked females immediately prior to the presentation of the male stimuli and it

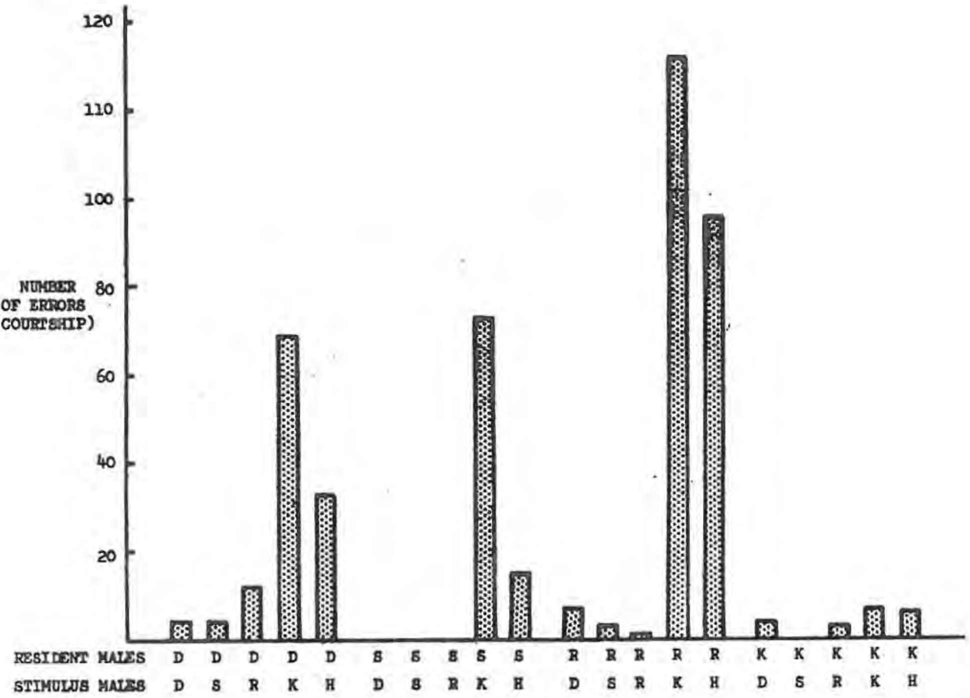


Figure 71 The number of courtship activities towards various stimulus males, in error. Since resident fish were exposed nine (not 27) times to the H. darlingi stimuli, the column for H. darlingi has been increased three-fold to facilitate comparison.

D = Durban; S = Sibaya; R = Rhodesian (Kariba); H = Haplochromis darlingi

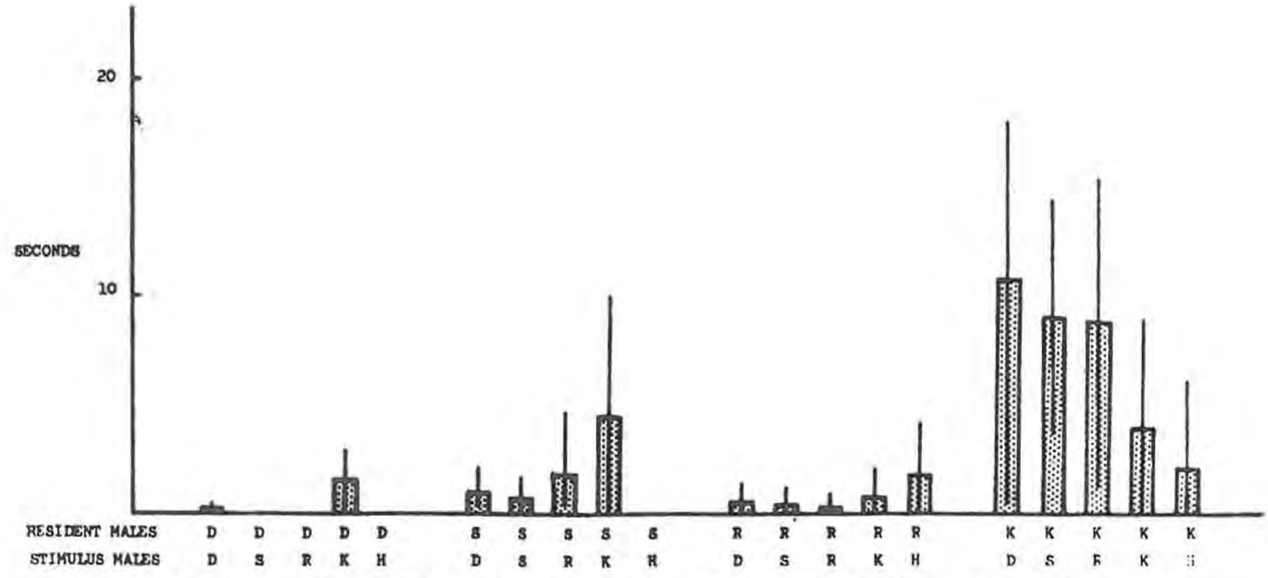


Figure 72 The mean time (in seconds) spent in foraging by males drawn from each available population in the presence of stimulus males drawn from the same populations and including H. darlingi (see text).
The 95% confidence interval for each mean is drawn on each column.
D = Durban; S = Sibaya; R = Rhodesian; K = Kuruman; H = Haplochromis darlingi

appeared that the Kuruman males were, therefore, not recognised for what they were.

H. darlingi males also elicited numerous courtship errors, but not as many as the Kuruman males. Probably due to their lack of vivid coloration H. darlingi were not easily recognised as male challengers, but they also lacked the species characteristics of the female P. philander.

Redirected, displacement and avoidance behaviour

A territorial fish might respond to a male conspecific intruder by overt aggression, in a manner indicative of conflict, or by submissive and avoidance behaviour. Overt aggression has been discussed. The conflict situation in which the enflasked intruder cannot be chased from the territory, yet also fails to attack the resident, has been outlined (page 125). Such a conflict situation may result in aggressive and submissive hanging. This same conflict situation might also release redirected aggression and displacement activities.

The most common form of displacement activity of P. philander is displaced feeding. All foraging activities (both real and displacement) were recorded, and figure 72 shows that within the experimental situations the Kuruman fish foraged more than any other group. Their foraging was especially marked when in the presence of the Durban, Sibaya and Rhodesian stimulus fish. By contrast, the other three groups foraged very little, and when they did it was most prevalent in the presence of the Kuruman and H. darlingi stimulus males.

Increased foraging in response to a stimulus unrelated to feeding is a displacement activity. To establish whether the foraging shown by Kuruman males was displaced, the amount of foraging in the 300 seconds before the stimulus fish were presented (absence of stimuli) was recorded on several occasions. A comparison of these results with those taken in the presence of a stimulus shows (table 7) that the additional foraging was a displacement activity.

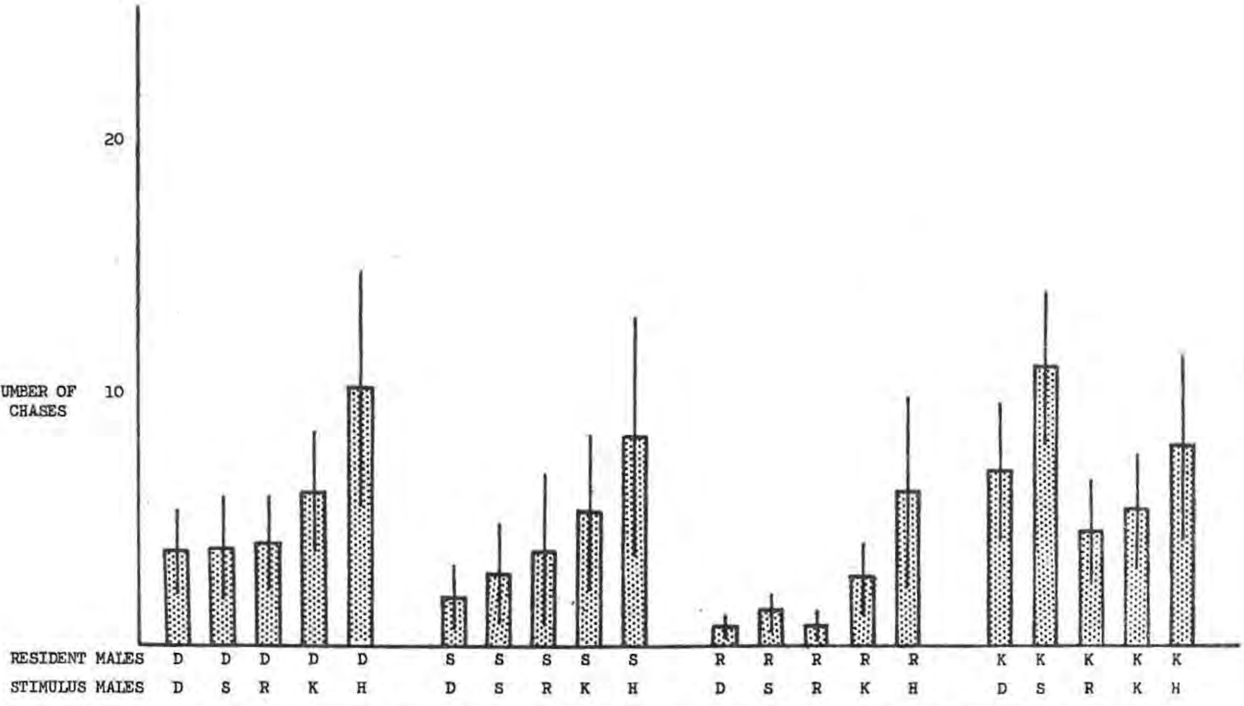


Figure 73 The mean frequency of chases by males drawn from each available population when exposed to stimulus males from the same populations and including H. darlingi (see text).

The 95% confidence interval for each mean is drawn on each column.

D = Durban; S = Sibaya; R = Rhodesian; K = Kuruman; H = Haplochromis darlingi

Table 7 : A comparison of the foraging performed in 300 seconds in the absence and then the presence of enflasked stimuli. All readings were taken from the first experimental run.

FORAGING RESPONSE STIMULUS ABSENT		FORAGING RESPONSE STIMULUS PRESENT		AQUARIUM NUMBER	DAY	STIMULUS TYPE
Number of foraging activities performed	Time spent in foraging (seconds)	Number of foraging activities performed	Time spent in foraging - (seconds)			
0	0	7	30	4	5	DURBAN
0	0	3	16	8	5	DURBAN
0	0	4	13	12	5	DURBAN
2	8	11	71	4	7	RHODESIAN
0	0	2	8	8	7	RHODESIAN
1	3	6	31	12	7	RHODESIAN

When confronted with enflasked stimulus males, resident fish spent a proportion of their time chasing attendant fish. It was found (fig 73) that the Kuruman males spent more time chasing than any other population of territorial fish. Kuruman males chased most frequently when challenged by enflasked Lake Sibaya, Durban and H. darlingi males. The Rhodesian, Durban and Lake Sibaya resident males chased attendant fish most often when in the presence of Kuruman and H. darlingi stimulus males.

Chasing may result from either the expression of genuine drives, or as redirected aggression arising from conflict situations provided by the introduced stimuli. A chase resulting from a genuine drive would occur (a) if the challenge of the stimulus male was insufficient to hold the attention of the resident, as may have occurred when the relatively light coloured Kuruman and H. darlingi stimulus males were placed in the territories of Durban, Lake Sibaya and Rhodesian fish, and (b) in the event of an attendant fish interfering in any way with the resident.

The apparently excessive chasing of the Kuruman males may be explained as follows: 1) In the presence of the light coloured H. darlingi the lack of challenge was such that they failed to hold the attention of the resident males, and 2) in the presence of the other population of P. philander chasing was the result of redirected aggression. Redirected aggression would occur in situations where the challenge of an intruder was great enough to promote partial submission in the resident. Aggression in the Kuruman males may have been inhibited by the other populations of P. philander which are more vividly coloured. It is, however, difficult to be certain of an underlying cause of behaviour, so to determine whether the apparently additional chasing of the Kuruman males was a redirected aggression, or a genuine response to the attendant fish, chases were counted on several occasions immediately before presentation of the stimulus fish from Rhodesia , Durban and Sibaya.

The findings (table 8) strongly suggest that the additional chases were redirected activities performed as a response to the challenge of the enflasked intruders.

Table 8 : The number of chases performed in 300 seconds in the absence and then in the presence of enflasked stimuli

THE NUMBER OF CHASES IN THE ABSENCE OF ENFLASKED STIMULI	THE NUMBER OF CHASES IN THE PRESENCE OF ENFLASKED STIMULI	AQUARIUM NUMBER	EXPERIMENTAL RUN	DAY	STIMULUS TYPE
9*[1]	34	4	1	5	DURBAN
8	18	11	2	2	SIBAYA
8	14	3	2	6	RHODESIA
6	18	7	2	5	SIBAYA
6	37	11	2	5	SIBAYA
10	13	7	2	9	SIBAYA

It will be recalled from earlier behavioural discussions that a response to a male intruder is the balance of two drives: to

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*[1] The number of chases recorded in this column was slightly higher than anticipated from the diurnal rhythm studies (page 157). In the present experiment the attendant fish were renewed each morning which would have promoted chasing. In the diurnal rhythm studies no renewal of attendant fish was made on the days of observation.

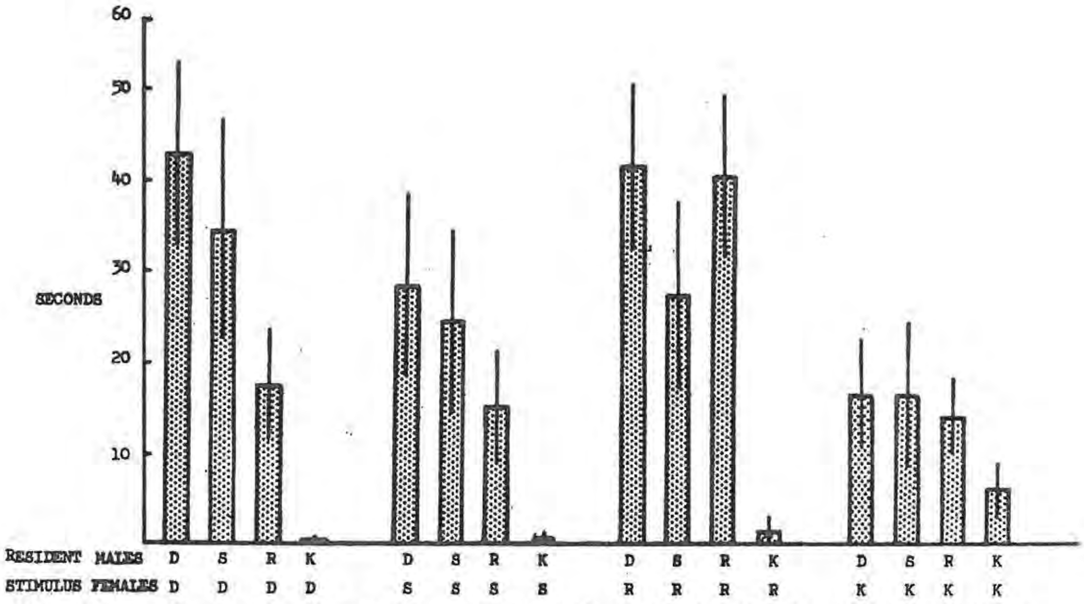

Figure 74 The mean time (in seconds) spent in courtship displays by males drawn from each available population towards stimulus females drawn from the same populations.
The 95% confidence interval for each mean is drawn on each column.

D = Durban; S = Sibaya; R = Rhodesian; K = Kuruman.

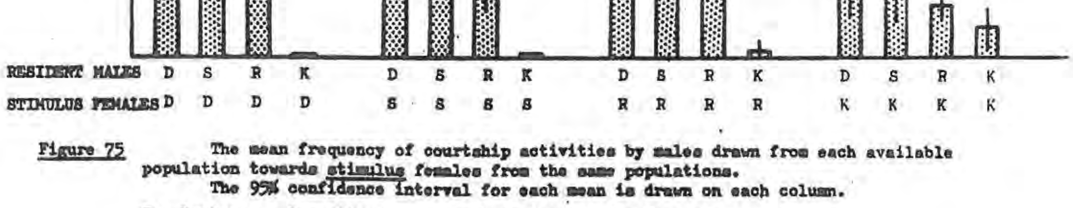

Figure 75 The mean frequency of courtship activities by males drawn from each available population towards stimulus females from the same populations.
The 95% confidence interval for each mean is drawn on each column.

D = Durban; S = Sibaya; R = Rhodesian; K = Kuruman.

attack or to flee. Where the territorial fish flees, but the intruder cannot chase because it is enflasked, then the resident shows avoidance behaviour. Avoidance behaviour may be easily recognised in fish which adopt a disruptive pattern and hide from the intruder. Alternatively avoidance may be very difficult to distinguish from normal behaviour, especially if a fish sheds little of its sexual coloration and continues with its daily behaviour in a manner which suggests that it has not seen the intruder. Careful observation under these circumstances would however, show that the resident was studiously ignoring the intruder. Though anthropomorphic, this behaviour can best be described as "pretence avoidence". As is the case with pretence generally, it was difficult to be sure that this was a response to the presence of the intruder. Where this 'pretence avoidance' was coupled with the increased number of displaced and redirected activities, which occurred under these experimental conditions, there was little doubt as to its authenticity.

The courtship responses

The responses of the allopatric populations of resident males to stimulus females drawn from the available populations was compared to determine (a) whether any population of male courted more than the others, and (b) whether males recognised their own population of stimulus females.

Each group of four columns (fig 74) gives a comparison of the mean time spent in courtship by male representatives of the four allopatric populations, when exposed to a particular population of stimulus females. In figure 75 the number of courtship activities performed in response to particular female stimuli, by each population of males, is compared. It is apparent from these figures that the Kuruman males courted all groups less, and the Kuruman stimulus females elicited less courtship, than any other population of P. philander.

To compare the courtship responses of the other three populations of P. philander, the mean time spent in sexual behaviour in response to all four populations of stimulus female was determined. It was found (table 9) that the Durban males were the most active in courtship, followed by the Sibaya and Rhodesian residents in that order.

Table 9 : A comparison of the courtship responses of the Durban, Sibaya and Kariba males to stimulus females from all four populations of P. philander. (N = 108 in all cases)

POPULATION	DURBAN	SIBAYA	RHODESIAN
mean time (in seconds) spent in courtship	65.4 secs	51.4 secs	43.7 secs
S.E.	± 4.9	± 5.1	± 3.0

In an analysis to determine the ability of Rhodesian, Durban and Sibaya stimulus females to elicit courtship, the mean of the combined responses of all three population of male to each of the three different populations of female was taken. (The Kuruman population was not included in this analysis as it was so clearly different). A comparison of the results shows that the Rhodesian stimulus females released the most courtship (table 10).

Table 10 : A comparison of the courtship response (in seconds) stimulated by three different populations of stimulus female. In all cases N is 81 as the mean was taken from the combined responses of the Rhodesian, Durban and Sibaya males, each of which was exposed to the appropriate population of stimulus females on 27 occasions.

	COURTSHIP RESPONSES TO		
	RHODESIAN FEMALES	DURBAN FEMALES	SIBAYA FEMALES
MEAN	74.1 secs	64.0 secs	45.9 secs
S.E.	± 5.7 secs	± 5.8 secs	± 5.1 secs

That the Durban males are the most active in courtship is confirmed by figures 76 and 77. These figures also show that the Rhodesian males and Kuruman males entered into courtship most readily

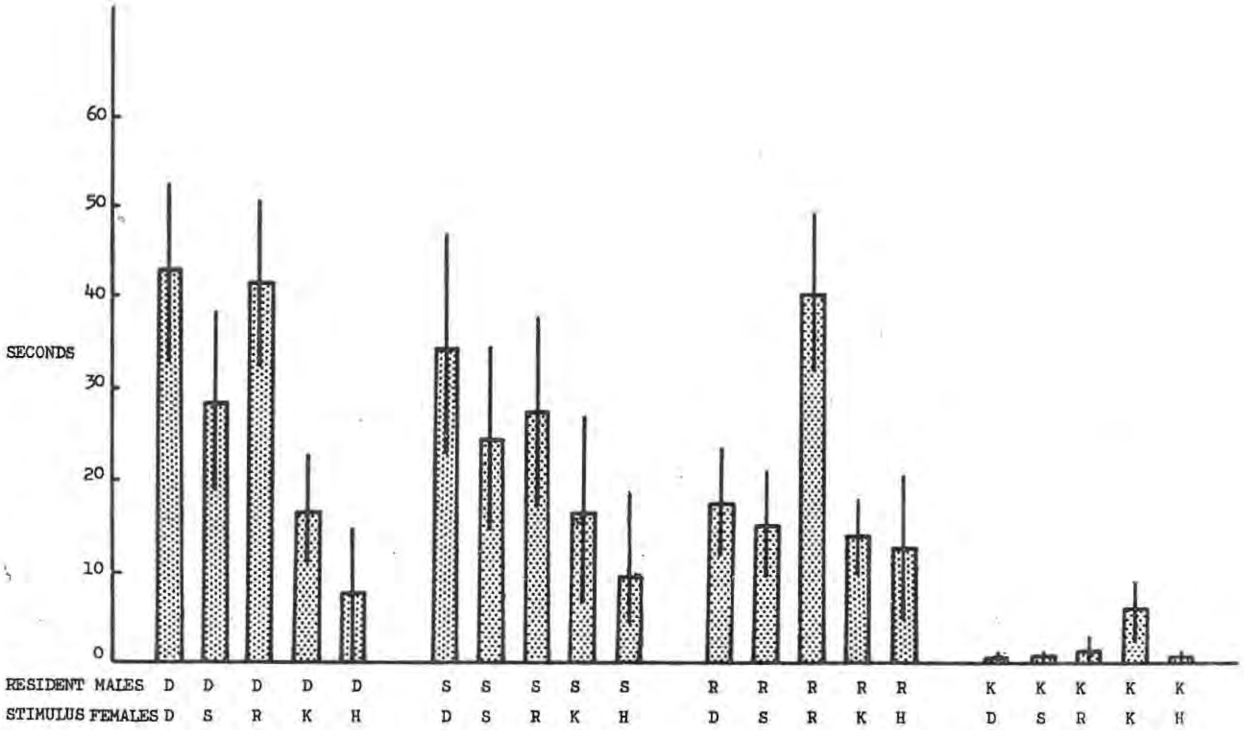

Figure 76

The effect of different populations of stimulus female, including H. darlingi, on the mean time (in seconds) spent in courtship by males drawn from each available population.
The 95% confidence interval for each mean is drawn on each column.

D = Durban; S = Sibaya; R = Rhodesian; K = Kuruman; H = Haplochromis darlingi

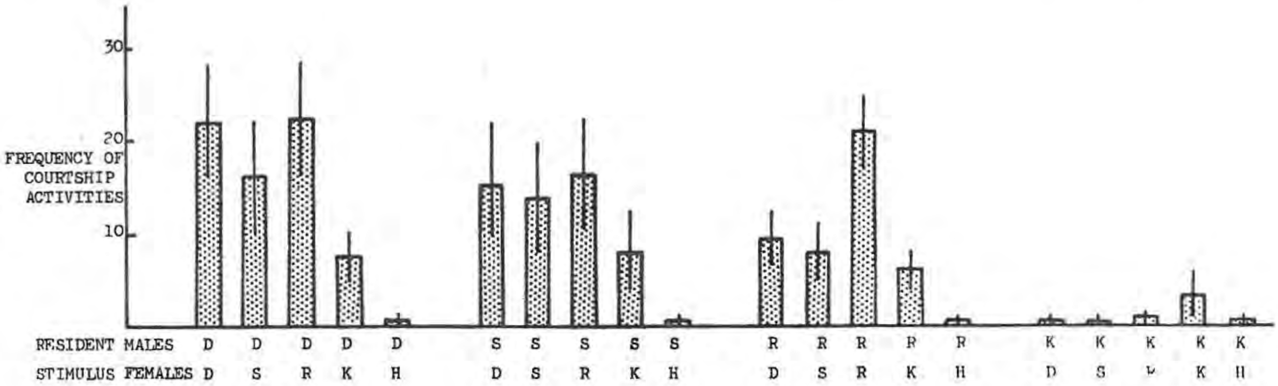

Figure 77

The effect of different populations of stimulus female, including H. darlingi, on the mean frequency of courtship activities by males drawn from each available population.
The 95% confidence interval for each mean is drawn on each column.

D = Durban; S = Sibaya; R = Rhodesian; K = Kuruman; H = Haplochromis darlingi

when stimulated by females drawn from their own respective populations. The fact that Rhodesian males responded well to their own population of females and not to the others accounts for the apparently enhanced stimulus effectiveness of the Kariba females shown in table 10 above. The increased response of the Rhodesian and Kuruman males to their own populations of females indicates a response to releasers characteristic of, or specific to, those populations - i.e., a recognition. The recognition may have been mutual, or by only one member of a pair: a positive recognition response from an enflasked female to a male of its own population, would release greater sexual activity from the male, <u>or</u> a male which recognised a female would respond to a greater extent. A mutual recognition would, of course, stimulate a greater sexual response.

Durban and Sibaya males courted the entire spectrum of stimulus females. Though they responded less to the Kuruman females than to any other population of stimulus fish.

Sibaya females evoked less courtship from Durban, Rhodesian and Sibaya males than either the Durban or Rhodesian stimulus females. This finds partial explanation in the observation that many Sibaya stimulus females became hyperactive and relatively unreceptive to courtship activities when placed within the flasks. This was not true of other populations of stimulus fish.

<u>H. darlingi</u> females elicited very little courtship activity. Indeed less sexual activity was evoked by <u>H. darlingi</u> females than by males of this species. So ineffectual were the stimuli profferred by <u>H. darlingi</u>, and sometimes by Kuruman <u>P. philander</u> females, that on many occasions the territorial males of Durban, Sibaya and Kariba populations preferentially courted attendant fish, which were neither gravid nor receptive, rather than the enflasked <u>H. darlingi</u> or Kuruman stimulus females.

When not involved in sexual displays in the presence of stimulus females, the territorial males would chase attendant fish, attack the enflasked female when it failed to follow, and for the same reason (failure to elicite following) embark upon displacement nest-building and/or displaced foraging.

The analyses of aggressive, courtship and other responses, recorded in the experiments outlined above, suggest that the various populations of P. philander have a "knowledge" of their population characteristics. If this is true, then the greater colour intensity of the more vividly coloured populations may have inhibited the behavioural responses of the Kuruman population. The Kuruman P. philander are much paler[1] than any of the other available populations and the results (figs 65 and 66) show that the aggression of Kuruman males was least when challenged by the darkest and most vivid fish (Sibaya males) and increased as the colour intensity of the challengers decreased through Durban, Kariba to Kuruman stimulus fish. If territorialism is inhibited by the more vivid releasers, as the above correlation suggests, then the inhibition would need to be carried over (remembered) from day to day. Fish do have the ability to learn and remember (Hale,1956; Aronson & Herberman,1960; Kaplan and Aronson,1967; Ribbink 1972), and amongst other things fish do remember their hierarchical positions, and also experiences such as unsuccessful confrontations (Peeke, Herz and Gallagher, 1971).

To determine whether the behaviour of territorial Kuruman P. philander had, in reality, been inhibited by the other populations of stimulus male the experiments were repeated as follows: six males from each population, which had not previously been used in these experiments, were placed individually in aquaria as described before. Once they had become fully territorial they were presented with enflasked stimulus females followed by enflasked males from their own populations only. That is Kuruman males received stimulus fish from the Kuruman population and no others, similarly Durban fish received only Durban stimuli and so forth. Attendant fish were renewed each morning prior to the experimental observation period, and the experiment was repeated daily for six days, so that 36 exposures to male and female stimulus fish were made.

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[1] This relatively light coloration of the Kuruman population may be a consequence of selection due to their inhabitation of a shallow, clear water body and breeding over sand where vivid fish would be conspicuous to predators.

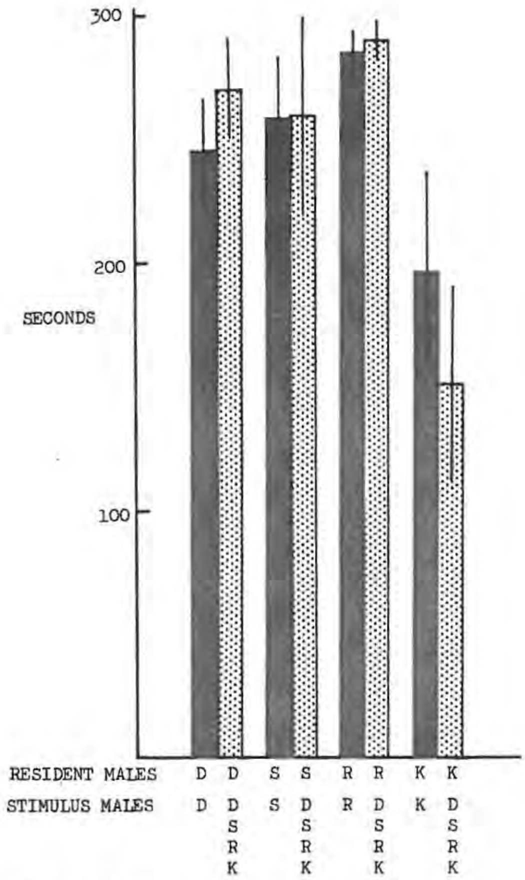


Figure 78

The mean time (in seconds) spent in aggression by males drawn from each available population towards stimulus males of all four populations of P. philander (lightly stippled), and towards males drawn from their own respective populations only (darkly stippled).

The 95% confidence interval for each mean is drawn on each column.

D = Durban; S = Sibaya; R = Rhodesian; K = Kuruman.

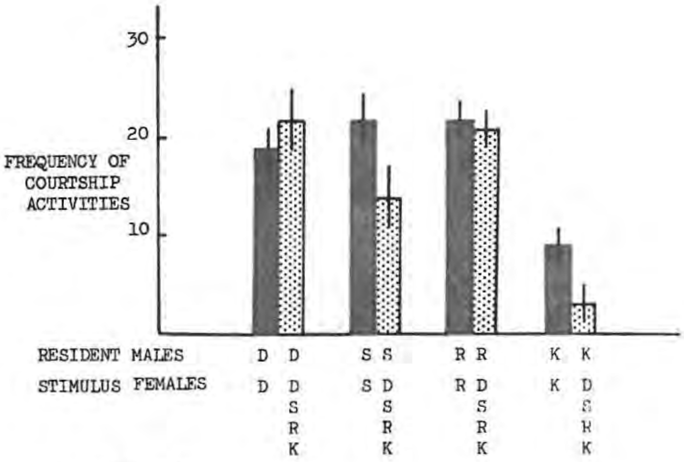


Figure 79

The mean frequency of courtship activities by males drawn from each available population towards stimulus females of all four populations of P. philander (lightly stippled), and towards females drawn from their own respective populations only (darkly stippled).

The 95% confidence interval for each mean is drawn on each column.

D = Durban; S = Sibaya; R = Rhodesian; K = Kuruman.

A comparison of the behaviour elicited in this experiment with that of previous findings (fig 78 shows that an increase in the aggressive behaviour of Kuruman males did occur. Furthermore, fig 79 shows that the number of courtship activities increased three-fold relative to the earlier experiment (earlier result, right hand column fig 79).

The most serious criticisms of this experiment are that 1) only six fish from each population were used, and 2) each investigation lasted a mere six days. As a consequence sampling errors may have had an effect on the results. For example, the relative increase of sexual activity of the Sibaya males is attributed to the fact that two of the Lake Sibaya stimulus females were exceptionally receptive (one eventually laid eggs in the flask) and initiated a greater amount of courtship than was usual. The explanation for the decrease in aggressive behaviour of the Durban population is not readily apparent. Had the number of experiments been increased and included more representatives from each population then extreme reactions, which are not uncommon in behavioural investigations, would probably have had a less marked effect. I am, however, confident that the three-fold increase in courtship and the greatly enhanced aggressive response of the Kuruman population reflects a response to the removal of an inhibition. Possibly the vivid coloration of the other populations of male P. philander acts as a super-releaser which inhibits the relatively palid Kuruman populations.

Though the Kuruman males responded more readily to the stimulus fish in the experiment (figs 78 and 79), their response level was nevertheless considerably lower than any other population of P. philander. This suggests that either their response levels are inherently different, or aquarium conditions per se inhibit Kuruman fish more than other populations. There is some evidence (see pages 158 and 160) which indicates that laboratory induced inhibitions of the Kuruman population occurred, but as no comparable field studies have been carried out on the other populations one should consider this evidence to be no more than inferential. Simple field experiments could give an accurate indication of the effects of the laboratory on behavioural responses. For example, if one used the arenas as natural laboratories, enflasked stimulus fish could be placed in the inner territories of the males of each population and the responses recorded for comparisons with other populations and with laboratory experiments. At present only activities could be recorded, but an underwater extension cable attached to the event recorder would enable display times to receive consideration.

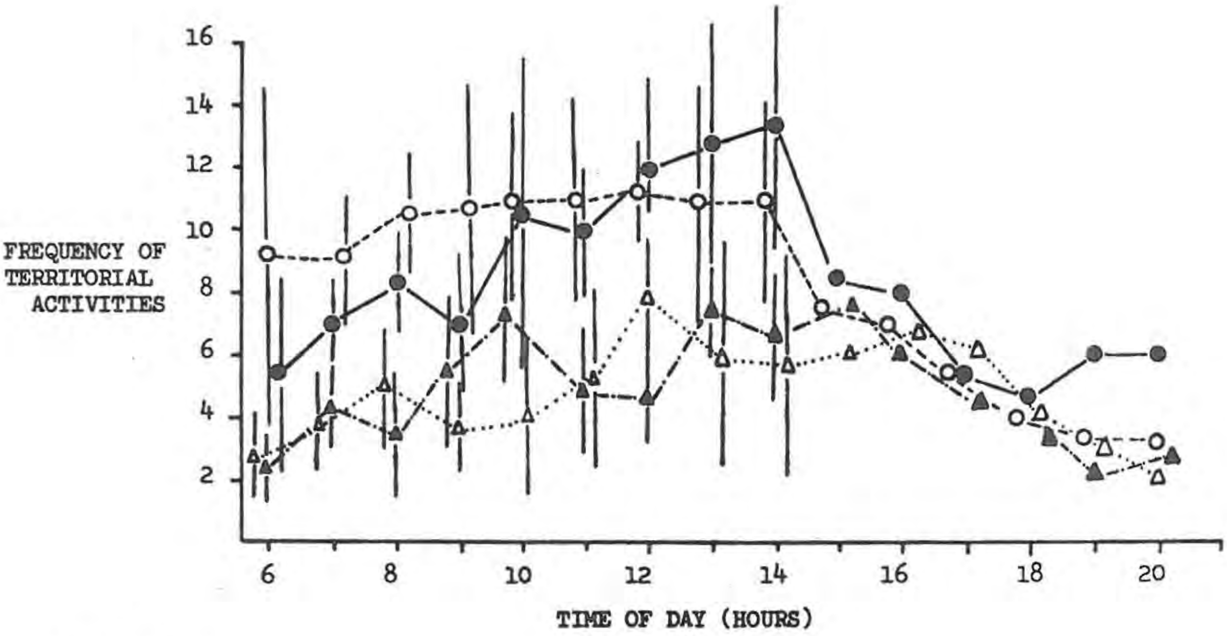


Figure 80

The diurnal rhythm of the four populations of P. philander. The 95% confidence interval for each mean is drawn on the figures, except after 14h00 where considerable overlap occurred.

Additional evidence of a behavioural divergence of the populations

To determine whether additional behavioural differences between the populations had developed, a comparison of the behaviour of the four allopatric populations of the territorial male in the absence of enflasked stimuli was conducted.

Observations of activity of territorial males when in the presence of the attendant fish only, were made from 06h00 to 20h00 hourly on the fourteenth day of each run. Territorial behaviour predominated in the mornings reaching a peak in the early afternoon and then declined (fig 80)

Fish from Durban and Lake Sibaya were more active in the mornings than those from Kariba and Kuruman Eye. All groups behaved in a similar manner after 14h00.

Little foraging occurred during the day, but increased in the evenings (table 11). The Kuruman population foraged less than any other group.

Table 11 : Total number of foraging activities performed by the various populations of <u>P. philander</u>, at different times of the day.

	TOTAL NUMBER OF FORAGING ACTIVITIES AT DIFFERENT TIMES														
DURBAN	4	3	2	2	1	3	0	13	3	6	6	8	17	27	31
SIBAYA	0	2	3	5	4	0	0	3	5	4	0	9	5	16	18
RHODESIAN	2	2	7	1	3	8	4	3	5	5	1	7	13	6	10
KURUMAN	0	7	0	6	1	2	0	0	0	1	1	3	5	8	8
TIME HOURS OF DAY	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20

The Kuruman males in aquaria were approximately one third as active as the territorial males in Kuruman Eye. This reduction finds partial explanation in that the major aquarium induced artefact, for all populations, was that the residents were not continually visited by intruders and gravid females, nor challenged by neighbours. The daily replacement of attendant fish would help to counter, but never entirely alleviate this artefact. Another possibility is that the physical conditions of the aquaria reduced territorial activity.

It was found that the Durban males built more nests and spent more time in nest-construction than any other group. The number of nests present in each territory were counted on the final day of each experimental run. The total number of nests built by the nine representatives of each population is given by table 12.

Table 12 : The total number of nests constructed by the nine representatives of each population during the three experimental runs.

POPULATION	NUMBER OF NESTS BUILT
DURBAN	41
SIBAYA	13
RHODESIAN	8
KURUMAN	4

Confirmation of the Durban population's tendency to indulge in nest-building behaviour came from observations of diurnal activity (14th day of each run) in the absence of stimulus fish (table 13).

Table 13 : The total number of nest-building activities performed by each population during the diurnal observation periods.

POPULATION	NUMBER OF NEST-BUILDING ACTIVITIES
DURBAN	115
SIBAYA	18
RHODESIAN	4
KURUMAN	0

So prevalent was the nest-building of the Durban males that one could identify them by this behaviour. Their established territories could also be distinguished from those of any other population by an examination of the substratum which would always have several large nests and numerous signs of nest-building activity.

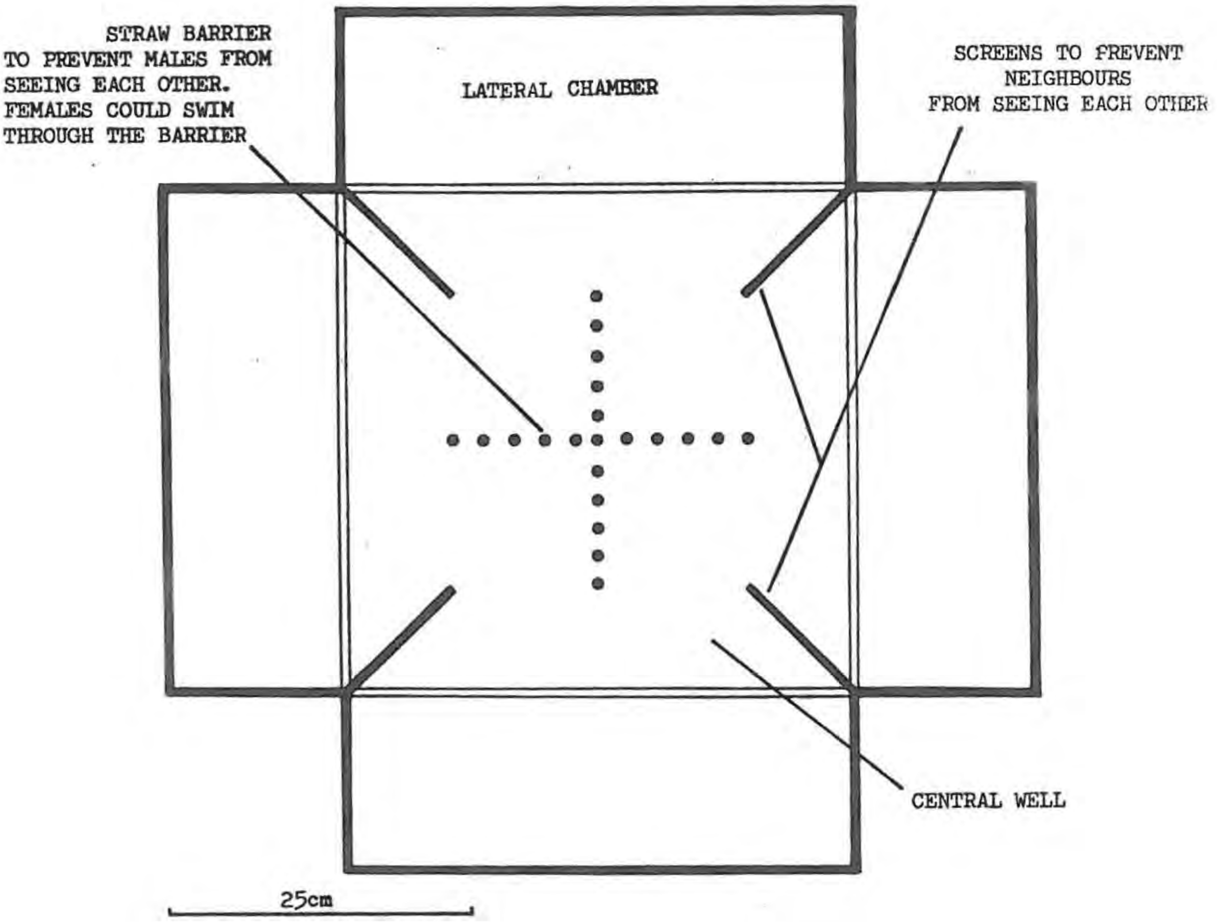
Nests constructed by Sibaya males in aquaria were shallow plaques similar to those found in Lake Sibaya. Although in the lake no territories were observed to have more than a single nest, during these experiments in four of the aquaria housing Sibaya males, two nests were constructed.

The Rhodesian (Kariba) population, in stock tanks, readily excavated nests as large as 12.5cm in diameter and 3.5cm deep. These nests were usually closely associated with weed cover. Under experimental conditions in which only a single aquatic plant was provided nest construction was less marked, but those constructed (not more than one per aquarium) were relatively large.

Seldom in their laboratory existence did any Kuruman male embark upon nest-building activity on a scale comparable to that in Kuruman Eye. During the course of the experiments described above, the Kuruman males dug very few nests (table 12).

Nest characteristics appear species specific among cichlids, and also amongst the sticklebacks (Morris 1952). Within a species it is conceivable that female cichlids are particular as to the type of nest in which they spawn. Thus, nest size, location and construction may influence the final choice of a mate as a female visits the nest of one male and then another. Such preferences would be one of the factors that might select for a particular nest-type and nest-building behaviour. The nests, and the manner in which nests are constructed, are similar in the populations of P. philander studied, but the differences which exist provide evidence of an incipient divergence. The divergence has progressed much further in the allopatric populations of S. macrochir, in which the nests and their associated nest-building behaviour are so distinctive that the two forms can be told apart using these criteria only (Audenaerde 1964, in Fryer and Iles 1972). When the two forms interbreed the progeny construct intermediate types of nest. There is little doubt that these two forms, which diverged in terms of nest-building behaviour, are genetically distinct, and at present there is some confusion as to their taxonomic status (Fryer and Iles 1972).

Figure 81 **A plan view of the choice chamber.**



Single dark lines represent opaque walls, double lines indicate clear glass walls. The depth of the aquarium was 40cm.

Choice of a partner

The initial premise on which these experiments were based, was that the allopatric populations of P. philander may have diverged behaviourally as well as in coloration. In addition it was anticipated that they might show varied responses to different stimulus fish indicative of a recognition of their own population characteristics. Evidence to support both premises emerged. Differences were found from one population to the next in the levels of aggressive, nest-building, courtship, conflict, redirected, displacement, lateral-display and tail-beating behaviour. Kuruman stimulus fish were not treated as conspecifics by the Durban, Sibaya and Rhodesian males. The responses elicited by the Kuruman stimulus fish resembled that evoked by H. darlingi most closely. Kuruman males, however, appeared to recognise members of their own population. Rhodesian P. philander also indicated a recognition of their own population characteristics. Further evidence which suggests that certain populations have a "knowledge" of their population characteristics, came from observations of free-swimming females in large aquaria. These fish tended to mate with males drawn from their own populations in preference to any other. Experiments were almost invariably complicated by the development of dominant-subordinant hierarchies. Under such conditions the dominant male always won the right to spawn with receptive females, regardless of the population from which they had been drawn. It therefore became necessary to construct a choice chamber to determine whether females preferentially chose their own population of males.

The design of the choice chamber was such that territorial males were physically, visually and olfactoraly separated each within its lateral compartment in such a way that hierarchies were not possible (fig 81). Attendant fish were placed within the central well and periodically renewed. Males chosen for choice chamber experiments were always of the same standard length so that the effect of size on the choice would be eliminated. The choice was effected by placing a ready to spawn female in the central well, allowing it to find and court the partner of its choosing. That such courtships through glass are possible is shown by this work and that of others (Aronson 1949, Tinbergen 1951, Van Iersel 1953). On several occasions gravid enflasked female P. philander laid eggs in the flasks in response to courtship of resident males. Consequently it was anticipated that females would respond to the appropriate males and eventually lay eggs at the glass wall.

To score positively females had to indicate, behaviourally, a full acceptance of the chosen male. Initially the criterion for a positive result was oviposition at the glass wall. This proved to be impracticable because several days were required for the threshold of spawning to be lowered sufficiently to permit egg-laying. Continuous observation over periods of this duration were unproductive, consequently gravid females were placed in the choice chamber for probe periods of 30 minutes. If no choice (the criteria for a positive choice are described below) had been made by the end of this period the female was returned to the female stock tanks until the next trial period in the choice chamber. During each session in the choice chamber females would be sexually stimulated by male courtship displays, which probably enhanced progressively their receptivity. A positive response was recorded when females consistently returned to a particular partner, responsed to its courtship displays and showed a defence of the area alongside the partitioning wall.

In order to prevent any bias of results due to extraneous factors the experiment was conducted in a small dark-room with black walls. The aquarium was illuminated by a centrally placed 100watt electric bulb on a 14L - 10D time-switch and the territorial males were moved to another compartment after each successful trial. The glass walls were kept clean so that the choice would not be affected by poor visibility. To prevent undue disturbance of the fish I lay on my back on the floor in the shadow beneath the choice chamber and noted the activities reflected in a mirror placed alongside the light-bulb.

Relatively few of the gravid females placed in the choice chamber scored positively. The results shown on table 14 must thus be considered no more than a preliminary indication that Rhodesian and Kuruman females selected mates from their own population in preference to those of any other. By contrast, the Durban and Sibaya females responded to all but the Kuruman males, possibly showing a preference for the yellow forms (Sibaya and Durban males have a yellow ground colour).

Table 14 : This table records the number of occasions on which gravid females of the different populations responded positively to male representatives of the four populations.

TERRITORIAL MALES

	DURBAN	SIBAYA	RHODESIAN	KURUMAN
DURBAN FEMALE	4	7	3	0
SIBAYA FEMALE	5	5	4	0
RHODESIAN FEMALE	0	0	11	0
KURUMAN FEMALE	0	0	1	4

Several experiments were conducted to determine whether the various populations would interbreed. As a general rule, males of any population would readily court all forms of female. The females, however, frequently showed a reluctance to 'hybridise' which suggests, once again, that it is the female which selects its mate. Crosses between Sibaya and Durban populations occurred very easily. Hybridisation of Durban and Sibaya females with Rhodesian males occurred frequently and readily, but Rhodesian females did not cross-breed quite as readily. It appeared as though these females had to wait considerably longer for their threshold of response to be lowered before they would spawn. Both sexes of the P. philander from Otavifontein, and the single male from Otjikoto also bred with the Rhodesian, Sibaya and Durban populations.

Crosses between the Kuruman population and the others were not readily achieved, though they were obtained at least once with members of the other populations, Otjikoto excepted. In these hybridisations, Kuruman males spawned with females of the other populations. Only once was a Kuruman female induced to spawn with a male from another population (Durban).

The coloration of the off-spring (F1 generation) of the crosses at sexual maturity was usually intermediate between, and often a blending of, the parental forms. Several of these hybridisations produced extremely beautiful fish, especially the Sibaya-Rhodesian cross. The hybrids were found to be viable. To keep the parental stocks pure all hybrid forms were destroyed when not required.

In aquaria the threshold of response can be so lowered that hybridisation between similar species (Fryer & Iles 1972), and even similar genera (Jubb pers.comm.), is possible. Therefore a "reluctance" to interbreed on the part of the Kuruman fish, and the apparent spawning preferences of the Kariba and Kuruman fish for their own respective populations suggests that any of the three foreign populations placed in Kuruman Eye would not hybridise with the Kuruman population. Similarly, foreign populations (drawn from those available in this work) placed in Kariba might remain distinct.

The overall indications, from the behavioural investigations and observations outlined in this chapter, are that distinctive behavioural differences have developed between populations. Further, the ethology of the species has shown that male coloration and possibly population specific traits of behaviour, do affect both the choice of a mate and the dominance and level of aggression of territorial males. All these factors could prevent interbreeding between certain of the populations, should they ever become sympatric.

CHAPTER SIX FURTHER DIFFERENCES BETWEEN THE ALLOPATRIC POPULATIONS

Rather late in the course of this project it was discovered that the allopatric populations of P. philander differed from one another in several respects which have not yet received consideration. The data collected are as yet incomplete. Nevertheless the differences found point to a further evolutionary divergence of the available populations of P. philander, and, as they are pertinent to the investigation, they are described in this chapter.

The eggs and fry

Casual observation indicated that the Rhodesian population were the most fecund: they appeared to breed most frequently and produce the greatest number of eggs and fry. Further investigation revealed that the eggs of the Rhodesian population were smaller than those of any other group, and that the eggs of each allopatric form were different in colour as well as size (table 15).

Table 15 : This table records the colour, mean length, mean diameter and the variation in egg-size of the different populations of P. philander. At least thirty eggs of each population were measured from females of different standard lengths. A sample of at least 10 eggs was taken from females less than 35mm SL, 10 eggs from females between 36 and 50mm SL and 10 eggs from females greater than 50mm SL.

POPULATION	MEAN EGG-LENGTH	MEAN EGG-DIAMETER	EGG-COLOUR	N eggs
RHODESIA	1.6 ± 0.1mm	1.4 + 0.1mm	Reddish-orange	38
OTAVIFONTEIN	1.7 ± 0.1mm	1.5 ± 0.1mm	Orange-yellow	30
DURBAN	2.5 ± 0.2mm	1.8 ± 0.15mm	Beige	30
KURUMAN	2.6 ± 0.15mm	1.8 ± 0.15mm	Cream	30
SIBAYA	2.7 ± 0.2mm	1.86 + 0.15mm	Beige	30

All measurements were made using a measuring graticule (eyepiece) placed in a Wild binocular microscope.

Eggs from small and large females within a particular population were found to be of the same size and are, therefore, a constant distinguishing feature of each population.

Fry from different populations were also found to be different in size (table 16). All fry measured for this comparison were in their final developmental stage, that is when the yolk-sac was fully absorbed (see Evans 1974, fig 17). Samples of eight to twelve fry from several females of each population were taken.

Table 16 : The lengths of different populations of P. philander fry, measured in their final developmental stage.

POPULATION	TOTAL LENGTH IN MM	NUMBER OF FRY MEASURED
RHODESIAN	8.05 ± 0.15	48
OTAVIFONTEIN	8.62 ± 0.20	31
DURBAN	8.95 ± 0.25	33
KURUMAN	8.96 ± 0.26	38
SIBAYA	9.05 ± 0.24	41

Wickler (1963) suggested that the eggs of P. philander might be larger than those of P. multicolor, because, in his opinion, the egg-dummies of P. philander are larger than those of their northern counterpart. Though the basis for this assumption is incorrect - egg-dummies of P. philander are variable in size and may be very small or absent - the eggs of P. multicolor are small. They are slightly larger than the smallest philander eggs, namely those of the Rhodesian form. Welcomme (1969) found that P. multicolor eggs are 2.0mm in length, and the fry are 8mm total length, which is smaller than any P. philander fry. P. ventralis, however, appears more like the Sibaya population in this respect as its eggs are 2.5mm in length and the fry 7mm SL (Loiselle, pers.comm.), which would probably give a total length of 8.5 to 9.0mm.

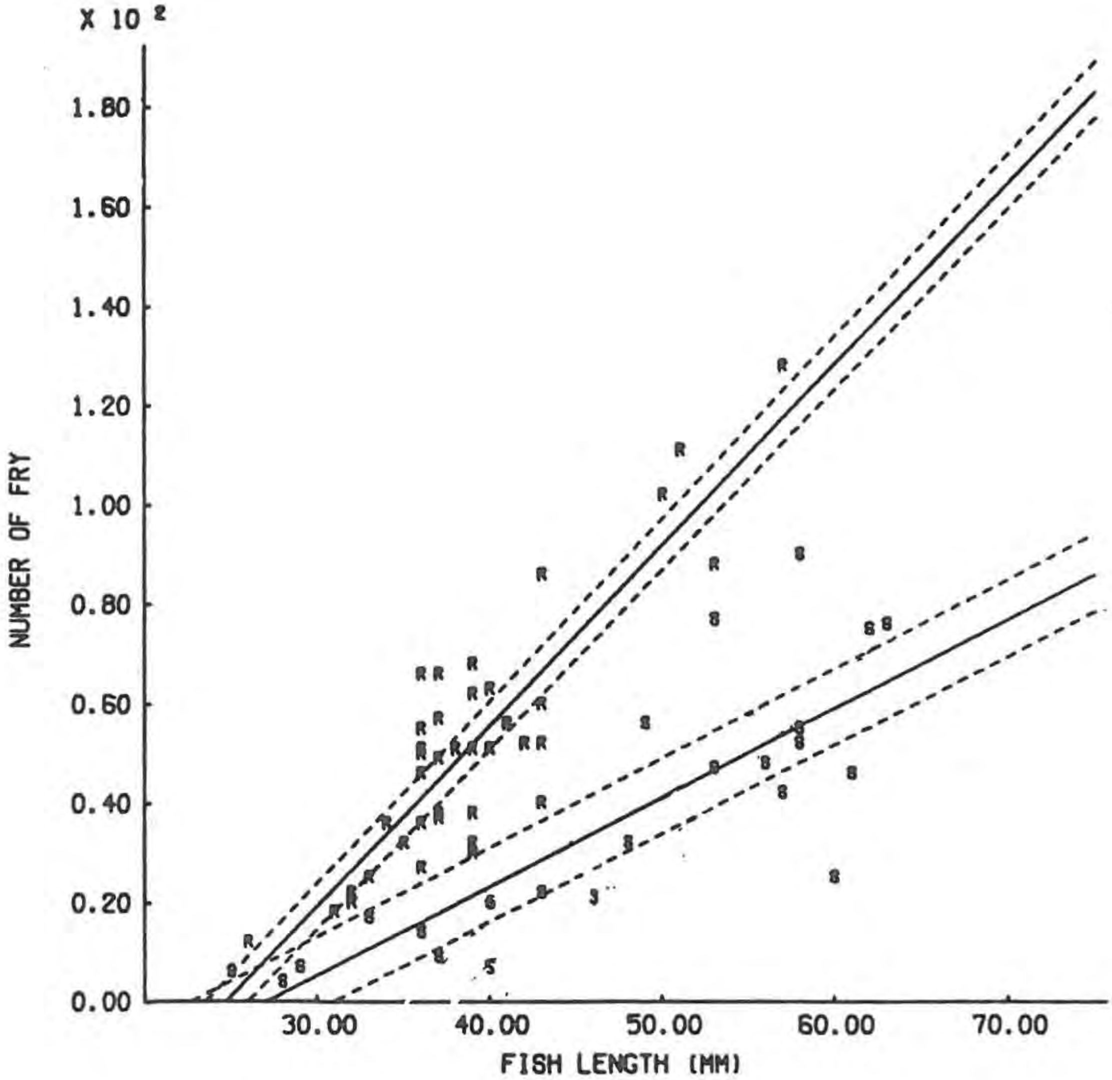


Figure 82 A plot of linear regression lines of fry produced by different lengths of fish using data obtained from the Rhodesian (R) and the Lake Sibaya (S) populations, at the 95% confidence limits for regression analyses.

In mouthbrooders, and indeed in other fish too, the number of eggs and fry produced is a function of the size of the parent (Liebman 1933, Lowe 1955, Welcomme 1967, 1969, Fryer & Iles 1972). P. philander also produce more progeny as their size increases which is indicated by fig 82 Furthermore the figure suggested that the Rhodesian population, which lays the smallest eggs, produced the greatest number of progeny per unit fish (length). Using these data a linear regression was performed for Lake Sibaya and Rhodesian populations. Insufficient data were available for regression analyses of the Kuruman, Otavifontein and Durban groups. The regressions were examined by analysis of variance (Sokal and Rohlf 1969, page 423) to determine if the slopes were significantly different from zero. Both were found to be significant at the 99.9% level.

The 95% confidence intervals were fitted to the regression slopes (Sokal and Rohlf 1969, page 423). It was found that the slope for the Lake Sibaya population differs significantly from that of the Rhodesian population.

It is apparent that those fish which produce small eggs and fry, produce numerically more off-spring per unit fish length than those populations which produce physically larger eggs. This demonstrates another difference between populations.

Preliminary investigations indicated that the number of eggs deposited was greater than the number of fry produced. Clearly some eggs or fry are lost during incubation. Other workers have frequently found that the number of fry produced were fewer than the number of eggs laid by mouthbrooders (Liebman 1933; Lowe-McConnell 1955; Welcomme 1967, 1969). The loss of progeny by mouthbrooders has also been discussed by Fryer and Iles (1972) and Greenwood (1974), who drew attention to those fish adapted for predation on eggs, embryo and larval fish which apparently steal from mouthbrooders. Possibly this stealing, by paedophagic predators, evolved from cannibalistic egg-robbing behaviour described earlier (page 98). Fryer and Iles (1972) also report cases in which fry or eggs were jettisoned by parents and not retrieved. In my laboratory P. philander were observed to jettison fry only once: a large Sibaya female (71.0mm SL) deposited 135 eggs, held them for several hours and then, apparently being unable to cope with the large number of eggs spat them out. Welcomme (1969), however, found that brooding efficiency of P. multicolor fell as length increased, which indicated that "the larger fish seemingly produce more eggs than they can brood."

Usually extra-eggs are not jettisoned, but swallowed. Liebman (1933) suggested that those fish which swallowed eggs did so only where the eggs deposited were too many to find room in the buccal cavity, a view supported by Welcomme (1967). Thus, egg-loss due to over deposition is one of the reasons for the discrepancy between fecundity (egg-production) and fertility (young produced).

It has also been noted that the number of progeny carried in the mouth diminishes during the period of incubation. Liebman (1933) suggested that developing embryos and young were swallowed to serve as additional food for the parent during the period of incubation. Welcomme (1967) suggested that some ova escape fertilization and are therefore wasted due to the relatively inefficient mechanisms of fertilization. It is argued by Loiselle (pers.comm.), however, that given the combination of extra-and intrabuccal fertilization no eggs should escape the spermatozoa. True though this may appear, examination of broods of P. philander at different stages during the incubation period revealed that quite frequently a number of eggs failed to develop (escaped the spermatozoa or water hardened before they were fertilized), and a small proportion of embryos developed partially and then died. Probably mouthbrooders are able to detect and swallow those eggs which fail to develop, which is a behaviour practised by substrate-spawners (Baerends & Baerends van Roon 1950). Eggs deposited and then picked up by a P. philander female in the absence of a male (vacuum activity) failed to develop and were all swallowed (Ribbink 1971). Removal of dead eggs and embryos, by swallowing, would be advantageous. It would provide an additional food source for the parent, and remove the substrate most susceptible to potentially infectious bacterial and fungal attack, thus safeguarding the healthy embryos.

A further variable among the different populations of P. philander was the incubation period. Evans (1974) reared P. philander fry and found that the Rhodesian population of fry passed through their stages of development more rapidly than the others. Her results are summarised in table 17.

Table 17 : The number of days taken for the development of fry from fertilization to the wriggler stage ready for release at 22°C, for the various populations of P. philander.

	RHODESIAN	DURBAN	KURUMAN	SIBAYA	OTAVIFONTEIN
DAYS	17/18	19/20	20	19/20	19

The interbrood period was found to be shorter for Rhodesian females than for other populations. Females which had just released their broods were placed in aquaria in which an abundance of Daphnia was always available. These fish rapidly became gravid and responsive to courtship. Where necessary the females were fin-clipped for identification purposes. Once spawning occurred the lapse in days from the release of the previous brood to the laying of the newest batch of eggs was calculated and recorded. The results in table 18 show that the Rhodesian (Kariba) fish have the shortest period between broods and the Kuruman fish the longest.

Table 18 : The mean number of days between the release of one brood and the next spawning. Total variation and the number of samples are given in columns three and four respectively.

POPULATION	MEAN NUMBER OF DAYS	VARIATION IN DAYS	N
RHODESIAN	14	11 to 19	17
OTAVIFONTEIN	17	13 to 24	4
DURBAN	18	16 to 22	11
SIBAYA	24	18 to 31	9
KURUMAN	37	28 to 51	8

Should these laboratory studies accurately reflect the situation under natural conditions then without doubt the Rhodesian (Kariba) population would be the most fecund. They lay the most eggs, produce the most fry in the shortest time and have the shortest interval between broods. By contrast, the Kuruman P. philander would be the least fecund. One can make an interesting, and probably totally unjustified extrapolation of these observations. Lake Kariba has only recently been formed. Vast new areas must inevitably have been made available for arenas. The population of P. philander in Kariba might conceivably be undergoing a massive expansion to fill the space available. Kuruman Eye, however, is all that remains of what was the large Kuruman River. The remnants of the Kuruman population are now concentrated in the small "Eye" and it is probable that population growth is relatively static. So, on the one hand no intraspecific social restrictions are imposed upon reproductive behaviour (Kariba), whereas on the other a social inhibition does exist. Should these effects be fairly long lasting then the fish when subject to the constraints of the laboratory system may continue in their inhibited or uninhibited ways. Regrettably this interesting correlation is probably no more than a co-incidence and what is more likely is that the aquarium conditions suited the Kariba fish, but were relatively unsuitable for the Kuruman population which performed poorly in all spheres of behaviour.

Juvenile behaviour and growth

The behavioural relationship between cichlid parents and their off-spring has received much attention (Baerends and Baerends van Roon 1950; Tinbergen 1951; Shaw and Aronson 1954; Myrberg 1964; Noakes and Barlow 1968; Iles and Holden 1969; Weber 1970; Oppenheimer 1970; and Audenaerde 1970 amongst others). Several authors have shown that imprinting of the parent on the fry does not occur in the classical manner found in birds and mammals (Greenberg 1963; Sjölander and Ferno 1973; and Ribbink 1971). Indeed the fry of maternal mouthbrooding cichlids are notoriously bad at recognising their parent and will follow models which have no resemblance to the parent in colour, shape, size or markings (Baerends & Baerends van Roon 1950; Ribbink 1971). Virtually all that is required to induce following is that the model be moved in a manner which simulates calling movements (Ribbink 1971). Consequently fry cannot be used as indicators of further differences between populations as they would readily accept any foster parent. Parents, however, may be more selective, especially since it has been established that various populations of fry were of different sizes at release. This investigation was furthered by Evans (1974) who found that the fry of different populations could be swapped provided they were of approximately the same age. Presumably the parents did not detect size discrepancies between fry if their behaviour and, possibly, smell* were normal. Apparently the parents were not able to distinguish between their own fry and those of another population of the same age. If, however, an age discrepancy of two or more days existed then the foreign fry were eaten.

A full comparative analysis of parent-fry and juvenile behaviour has not been attempted. Observations indicated that all groups appeared to behave in a very similar manner. In the laboratory growing fish spent their lives feeding in groups which formed schools when frightened. Initially they fed primarily upon algal growths on the aquarium walls and substrate, but at four to six weeks foraging in the substratum began. Occasionally, from the age

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* Kümme (1964) demonstrated that smell (chemical releasers) is of importance in parent fry relationships of some cichlids.

of four weeks, the young fish would perform adult movements such as lateral-display and tail-beating for brief periods, and then resume their foraging. Kirchshofer (1953) suggested that these behaviour patterns in young cichlids formed the same maturation and co-ordination functions as play does in mammals.

Rearing the fish with an abundance of food available at all times, it was found that sexual maturity and reproduction occurred from as early as twelve weeks in all but the Kuruman populations. The Kuruman fish bred for the first time at 21 weeks of age. In the early stages of sexual maturity the males outgrew the females, became territorial and courted. Lake Sibaya, Rhodesian and Durban females as small as 24, 25 and 28mm SL respectively produced and cared for fry. The smallest female from the Kuruman population to produce eggs was 36mm SL. Loiselle (pers.comm.) reports that sexual activity commences as early as eight weeks post release in P. ventralis, and that females as small as 20mm SL have carried broods successfully. P. ventralis appear to breed earlier and at a smaller size than P. philander. Welcomme (1969) found that P. multicolor under natural conditions grow slowly to reach sexual maturity at seven months and a size of 28mm SL (males) and 26mm SL (females).

Comparison of growth rates of the different populations of P. philander were carried out at 25°C, in aquaria of 25 x 25 x 30cm. Daphnia, the plant material were supplied ad libitum. The conditions under which Loiselle reared his Pseudocrenilabrus were, however, not communicated, and the validity of the comparison has still to be established.

An advantage of laboratory studies is that the influence of uncontrolled variation in environmental conditions is eliminated, thus facilitating direct comparisons. Important in this respect is the finding that fish bred and reared in the laboratory (FI & F2 generations) produced eggs and fry with the same meristic characters as fish, representing the same populations, which had been caught in the field.

Differences in egg-size, egg-colour, clutch size and interbrood periods may be considered indicative of a divergence of the populations. Before attaching importance to such criteria one should be certain that the differences are not due to temporary ecophenotypic affects. For example, populations of the *Sarotherodon* group may become stunted if confined to small waterbodies. It is well established that many stunted populations of *Sarotherodon* produce eggs which may be two to three times smaller than those produced by the "normal" (non-stunted) form (Iles 1973).

Stunting, as it is known in *Sarotherodon*, is probably not a characteristic of *P. philander*. Firstly, the size of the water body apparently does not affect the fecundity of this species. The Rhodesian population of *P. philander* is the most fecund: its members lay the smallest eggs in the greatest number and at the highest frequency yet they were drawn from the largest water body included in the present study (Lake Kariba), the least fecund were those from Kuruman Eye which is an extremely small water body. The Durban population came from a very small water body (Happy Valley) and those in Lake Sibaya live in a relatively large lake, yet only slight differences exist between these two populations (table 15 and 16). Though *P. philander* parallel the *Sarotherodon* group in that their eurytopic nature permits them to successfully occupy many different habitats, the data does not provide evidence to suggest that *P. philander* have the ability to adjust fecundity by "stunting" or "dwarfing" under different conditions.

Evidence accumulated regarding the differences in male reproductive coloration (chapter one), behavioural differences and the reluctance to interbreed (chapter five) and the differences of fecundity reported in this chapter, suggest that the allopatric *P. philander* populations under consideration may have diverged sufficiently to warrant a re-appraisal of their taxonomic status.

This taxonomic question, and its related problems of speciation, will be discussed in the following chapter after a brief comment on field ethology.

CHAPTER SEVEN DISCUSSION

A comment on the ethological approach to field studies

The ethological approach to this study differs from the methods generally followed in the investigation of freshwater fish biology. Consequently several interesting and unusual aspects of problems associated with cichlid biology were exposed. Underwater observational techniques, widely used in this study, have already proved invaludable to marine biologists.

There is little doubt that this approach, which enables one to actually see the species interrelations, observe natural behaviour and determine the population structure and the distribution of its components will uncover a vast, as yet relatively untapped source of information in freshwaters. It is true that in many fresh waters the turbidity, flow rate, pollution, parasites, hidden dangers and depths are such that underwater observation is impossible or unattractive. The Great Lakes of Africa, however, lend themselves admirably to direct ethological study and the work presented in this thesis demonstrates that an ethological approach, albeit in relatively small southern African water bodies, provides an extremely valuable tool for freshwater fisheries biologists. By an application of underwater ethological techniques to the Great Lakes it is probable that many of the questions asked by Fryer & Iles (1972), might be answered. Some of these questions are concerned with species interrelationships, the distribution and utilization of available resources, polymorph relationships and, possibly, even those questions concerning cichlid speciation.

A recommendation for further ethological field studies would be that two prerequisites are satisfied 1) a sound laboratory knowledge of the behaviour of the fish be obtained prior to field observations (in this work the earlier studies of Ribbink (1971) provided such a basis), and 2) that the classical groundwork involving estimates of population density, morphological measurement and examination of the specimens (state of gonads, fecundity estimates, gut contents, condition factors, sex and age determination and so forth) in the field be used to form the foundation on which the ethological springboard may be soundly constructed. The groundwork based upon such measurements and dissections was inadequate in this work and therefore useful information from such quantitative studies was not available to augment many of the arguments which were based almost entirely upon behavioural observation.

The polytypic nature of P. philander

The wide and varied distribution of P. philander demonstrates the adaptability of this species which, together with T. sparrmanii and S. mossambicus, is amongst the most eurytopic of southern Africa's cichlids. Indeed their distribution and apparently varied niche utilization markedly contrasts the limitations placed on those stenotypic cichlids endemic to the Great Lakes of Africa, which appear to be restricted by their specialisations to their particular, often very narrow, niches.

Any gene pool isolated from its parent population will differ from the original stock, genetically at least (no two gene pools, even though they come from the same stock with unrestricted gene flow, will be identical, Mayr /1963/). The differences between the populations will increase as each population is progressively selected for adaptations to the specific environment in which it lives. Thus a eurytopic species, such as P. philander, will become extremely polytypic in time. Eurytopism and retarded gene flow in a widely distributed species, leading to polytypism, also provides a fertile field for speciation. Each population of P. philander might ultimately become uniquely adapted to its local environment. Indeed, a clinal variation appears to exist which links the Zambian, Rhodesian, Malawian, Natal, Zululand and Mozambique populations of P. philander, and there is little doubt that the resistance to gene flow between distant populations is sufficiently great to make terminal populations appear different.

Where terminal populations become distinct from one another, it is likely that they might also have speciated as a result of the development of isolating mechanisms through a very long chain of populations, Mayr (1963) cites many examples of such speciating mechanisms.

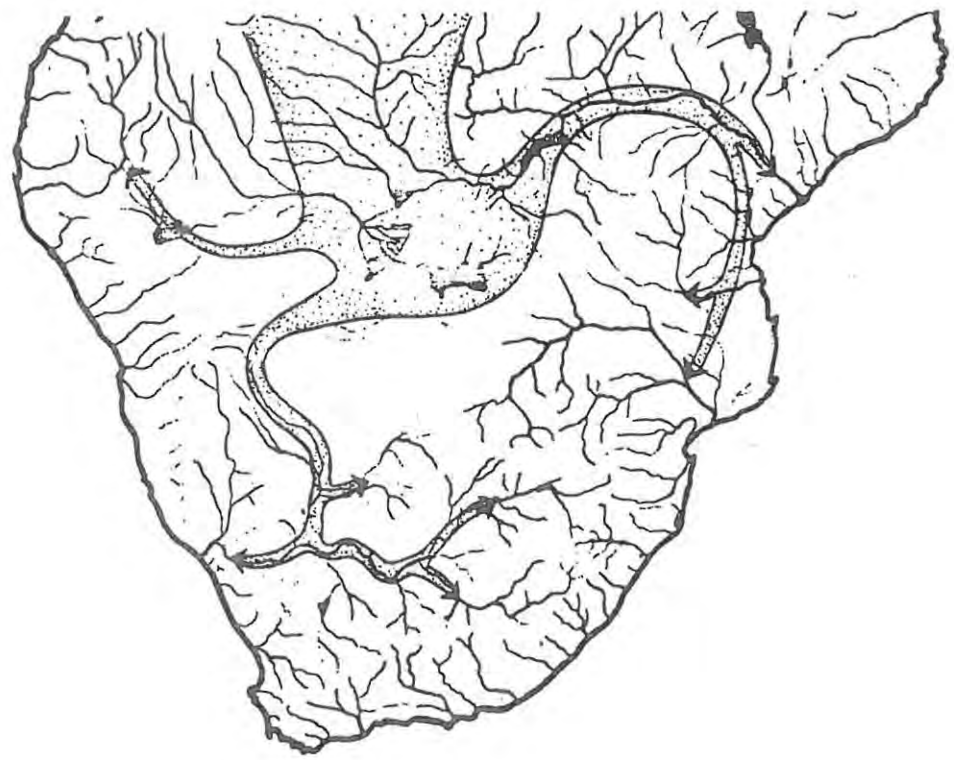

Figure 83 The invasion of southern Africa by *P. philander* (after Jubb and Farquharson 1965).

Gene flow may also be severely restricted, or completely stopped, by the geographic or physical isolation of one or more populations from their parent and sister populations. Probably, the populations of P. philander confined to the sinkholes, Kuruman Eye and possibly the Orange River, are completely isolated from their nearest neighbours. Mayr (1963), however, considers that isolation is never complete, and argues that the isolated regions could not have been colonized originally if gene flow were impossible. Such an argument may find applicability to species isolated on Pacific islands, such as Darwin's finches, but is without sufficient regard for the physiographic and climatic changes which might isolate populations of fish. As examples, the Lake Nabugabo populations of Haplochromis have become physically isolated from the parent species in Lake Victoria (Greenwood 1965); the crater lake populations of Tilapia (T. vulcani) have become totally isolated from Lake Rudolph populations (Trewavas 1933) by physiographic developments. Various groups of Cyprinodonts of Death Valley have become completely cut off from one another by climatic changes (Miller 1950, Brown 1971). All these isolated populations have been unable to interbreed with the original populations for so long that they are now recognised as separate species.

Against this background, it appears necessary to ask whether the terminal clinal populations of P. philander, and those geographically isolated populations, are merely races of a polytypic species or already different species. This problem receives consideration below.

Geological and geographical information

It has been suggested (Jubb and Farquharson 1965) that P. philander entered southern Africa from the north of present day Zambia, a little to the west of Rhodesia. From this central invasionary route the species spread to the east coast down the Zambezi drainage basin and then worked its way southwards into the drainage basins of the Limpopo and the numerous rivers and streams of present day Zululand and Natal (fig 83). (The Malawian populations were not given consideration by Farquharson & Jubb /1965/). The species also spread westwards through the Okavango to the Cunene, and south-west through the present day Kalahari where they came to inhabit the Orange River. Though the headwaters of the Limpopo/Olifants rivers lie close to those of the Vaal/Orange rivers Jubb and Farquharson (1965) argue convincingly that an exchange of fish fauna across the mountains which separates the systems is impossible.

In recent times the aridity of the country between the Okovango, the Cunene and Orange systems would preclude a migration across these wastes. Thus, on the western half of the continent the P. philander populations have become fragmented, and so isolated that interbreeding appears unlikely, if not impossible.

The waterless desert of the Kalahari is such an impenetrable extrinsic barrier that one immediately wonders how the fish arrived in the first place to inhabit Kuruman Eye, the sinkholes and Orange River. It seems that the climactic changes which occurred in the desert region of southern California and Nevada and isolated the Cyprinodonts (Miller 1950), also occurred in southern Africa (Jubb & Farquharson 1965, Butzer, Fock, Struckenrath and Zilch 1973) and isolated P. philander on several occasions. The climate during the Pleistocene was apparently cooler and considerably wetter than at present. Lakes and flowing rivers were fed principally by underground upwellings. It was during these Pluvial periods about 30 000 to 40 000 years ago that P. philander is considered to have entered these regions (Jubb and Farquharson 1965). The warming and desiccation of the postglacial times disrupted the drainage and fragmented what were probably continuous populations, until only those fish in permanent springs, perennial rivers and sinkholes remained.

It appears difficult, if not impossible, to determine precisely when the sinkholes, which house P. philander, were formed. Rusk (pers.comm.) has pointed out that sinkholes will not develop in a purely desert environment because their development requires a copious supply of rainwater. Furthermore sufficient drainage is required to remove the carbonates permanently in solution, which suggests that large scale sinkhole formation might be correlated with one or more of the rainy Pleistocene epochs.

The evidence indicates that the species invaded the Kalahari regions 30 000 to 40 000 years ago and that the sinkholes, rivers and springs, such as Kuruman Eye, were present or formed during those periods.

Probably, gene flow from faunal exchanges continued until more recently than 30 000 years ago as had originally been suggested by Jubb & Farquharson (1965). Butzer and his co-workers (1973) have produced evidence indicating that wet, slightly cooler conditions may have continued until as recently as 16 000 years ago. Thereafter drying and warming occurred which probably fragmented the continuous populations and eventually only those fish in natural springs, perennial rivers and sinkholes survived. As the desiccation was fairly gradual it is probable that gene flow continued, sporadically at least, until even more recent times. This implies that the populations of P. philander have probably been isolated for less than 16 000 years.

The evidence of Greenwood (1965) and Miller (1950) suggests that speciation of fish in 16 000 years may take place, especially in small isolated populations where genetic homeostasis has minimal effect. The haplochromid-like fish usually show a remarkable ability to speciate rapidly (Greenwood 1965, 1974; Lowe-McConnell 1969; Fryer & Iles 1972). Indeed if the conclusions of Greenwood (1965) are correct, they may speciate in as little as 4 000 years. Yet the Kalahari-South West African populations of P. philander (Kuruman, Otavifontein, Otjikoto and also Wondergat) are very similar to one another in view of the evidence which suggests that each of the populations has been isolated for about 16 000 years. Morphologically they are virtually indistinguishable (Trewavas 1936; Trewavas in a personal communication to Jubb, 1967). These populations of P. philander do, however, show differences in male coloration which Greenwood (1965, 1974) considers to be of importance (the role of coloration will be discussed more fully below). The indications are that the populations of P. philander might reasonably be expected to have diverged more than they have in the time apparently available.

It is possible that P. philander speciate more slowly than any other haplochromid-like fish. Lowe-McConnell (1969) and Jubb & Farquharson (1965) drew attention to the observation that the rate of speciation in the tropics, where the Nabugabo species developed (see Greenwood, 1965), is more rapid than in the more temperate regions. P. philander populations of the Kalahari were isolated in cool regions relative to those of Nabugabo.

That the isolated cyprinodonts of the Nevada should have speciated more rapidly than P. philander, under what were apparently similar climatic conditions, may be accounted for by the rapid time rate of generations shown by the Cyprinodontidae. Miller (1950) found that in some species only four to six weeks were required for the newly hatched fish to reach breeding condition, so eight to ten generations could be produced per annum. A further contributory factor to the rate of development of Cyprinodon was that the selection pressures placed upon these fish were severe in terms of the varied temperature conditions and chemical composition characteristic of these various springs (Brown 1971).

Another explanation may be advanced for the apparently slow rate of speciation of P. philander on the western half of the continent. Though it is most likely that P. philander came to inhabit the sinkholes in the wet Pleistocene periods, it is not impossible that more recent invasions of some of the sinkholes were made, and that gene flow between sinkholes might still persist. It is known that underground passages link the sinkholes Otjikoto and Guinas (Rust pers. comm.), and that Wondergat and Molopo-Oog are confluent (these two sinkholes are only eleven kilometres apart). Jubb (1971b) presents evidence which suggests that subterranean dispersal occurs over short distances, though one doubts its effectiveness over vast distances. Sheet floods, which periodically appear in the desert regions, might also on rare occasions inject alien genes into otherwise isolated populations. Dispersion by both sheet floods and underground passage appear unlikely routes for gene flow over the vast Kalahari tracts, but the possibility that such an exchange might exist should not be entirely discarded.

Finally, though P. philander is a haplochromid-type of cichlid, which is considered to be plastic and capable of rapid speciation (Lowe-McConnell 1969), it is probable that the plasticity of P. philander lies in its ability to utilize many and varied environs without having to change in itself. In other words P. philander is so generalized that it is capable of, and possibly preadapted to, successfully occupying numerous habitats. These attributes would retard the rate of speciation of isolated groups since most selection pressures would be attenuated by the apparently inherent eurytopism. Such attributes would also enable the species to survive sudden changes which might kill more specialized species. It is possible that *P. philander* has been successful because it has remained generalized and plastic in its ecological requirements.

It is believed (Trewavas 1949; Lowe-McConnell 1969; Greenwood 1974 and others) that the *Haplochromis* species flocks of the Great Lakes evolved from a generalized riverine species, such as an *H. callipterus*-like ancestor in Lake Malawi (Trewavas 1949) and an *H. bloyeti*-like ancestor in Lake Victoria (Greenwood 1974), and that the speciation occurred fairly rapidly. One wonders why the apparently successful generalized ancestors should have given rise to many specialized species. Much speculation, (and indeed Beadle (1974) is of the opinion that too much speculation and too little established information exists) has given rise to many interesting papers and books in an endeavour to answer this and other problems associated with cichlid speciation in the Great Lakes (see Lowe-McConnell 1969; Fryer & Iles 1972; Greenwood 1974 and the relevant references they cite). I can add little to these works except the observation that *P. philander* throughout the area which has been studied appears to have been troubled little by competitors and predators. The effect of certain predators on the rate of speciation has been hotly debated by Jackson on the one hand and Fryer on the other (Jackson 1961, 1965, 1973; Fryer 1965; Fryer & Iles 1972). It has been suggested (Lowe-McConnell 1969; Beadle 1974) that the answer to this dispute probably lies somewhere between the two schools of thought. Little is known about the effect of predators on the rate of speciation of *P. philander*.

Where competitors are present, such as in Lake Malawi, *P. philander* is absent. In Rhodesia and Zambia *H. darlingi* competes with *P. philander* and appears on occasion to exclude it from the edges of large rivers which would otherwise appear to be typically *P. philander* habitats (Jackson pers.comm.). As the ecological requirements of the two species are somewhat different (Jackson pers.comm.), this interspecific competition is not intense.

Except for the evidence of Jubb and Farquharson (1965), which indicates species of fish with which *P. philander* shared its habitat, there is no evidence to indicate whether the pressure of predators and competitors has changed significantly over the past 16 000 years. Nevertheless it is possible that due to what appears to have been a relative lack of predators and competitors throughout most of its range, evolutionary changes have occurred slowly in P. philander. By contrast, in the Great Lakes of Africa, once speciation had begun in the haplochromids, intense competition developed and increased its rate.

P. philander populations confined to Kuruman Eye and the sinkholes are self-contained small populations showing all the characteristics of peripheral isolates as defined by Mayr (1963). Because they carry such a small reservoir of genetic diversity peripheral isolates are usually highly vulnerable to the dangers of homozygosity, and are usually ephemoral (Mayr 1963). Should peripheral isolates successfully resist extinction then they are usually destined to form new species. There are many examples of small populations of animals which have apparently maintained themselves successfully for thousands of years. The most remarkable on record is a population of cyprinodonts in Mexican Spring, Death Valley. Between 20-40 fish have lived in this minute water body, of just over 300 litres, for possibly thousands of years (Brown 1971). Many other cyprinodonts isolated in small bodies of water in Death Valley are now recognised as separate species (Miller 1950; Brown 1971).

Those populations of P. philander which have survived for thousands of years in the sinkholes and springs are more likely to form new species than become extinct.[1] Evidence of their divergences is apparent from the colour and fecundity differences described in the text of the thesis. These isolated populations are probably incipient species.

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[1] Present day environmental pressures exerted by man may, unhappily change the fate of any of these populations. Already Otavifontein has been converted into a recreational resort, with the result that the only surviving fish from the spring are in aquaria (Penrith, pers.comm.)

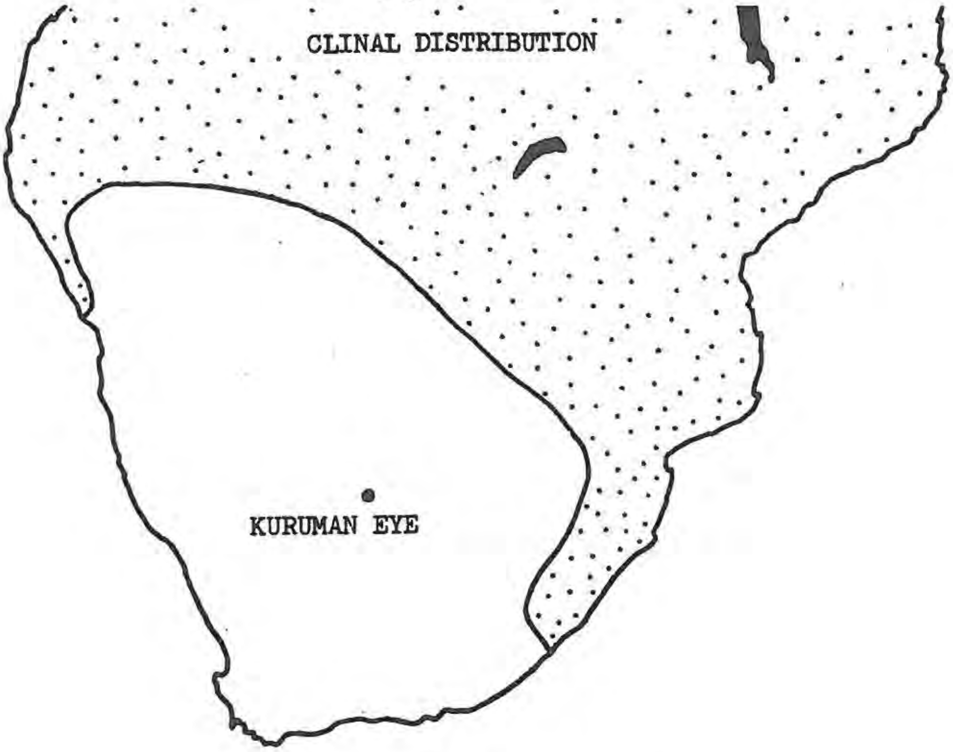

Figure 84 **The suggested clinal distribution of *P. philander* (stippled), and the relative isolation of the Kuruman population.**

Figure 85 **The suggested invasion of Natal and Zululand** by the "yellow-form" of *P. philander*, and subsequent spread northwards and southwards (darkened arrows). A region where the yellow and blue forms of *P. philander* might co-exist has been encircled.

The evidence of Jubb and Farquharson (1965) indicates that the P. philander which came to inhabit the drainage basins of the eastward-flowing rivers invaded these regions about 30 000 to 40 000 years ago. Though the period during which the invasion occurred is the same as that which saw colonisation of the western half of the continent, those populations in the eastern drainage basin were not fragmented and isolated. The populations of P. philander in Zambia, Malawi, Rhodesia, Mozambique, Zululand and Natal have probably been contiguous to the present day. Indications of gene flow came from the observations of Bell-Cross (pers.comm.), in Rhodesia. He observed active faunal exchange in the headwaters of adjoining drainage basins during a "wet season". A likely consequence of this continued gene flow, even though drastically retarded by distance, is that the Rhodesian (Kariba), Durban and Sibaya populations would have retained more in common with each other than with the isolated populations in Kuruman Eye (fig 84). This evidence may to some extent account for the behavioural differences which distinguished the Kuruman population from the others. (See chapters four and five).

Some evidence indicates that the clinal variation is such that there exists a region of circular overlap of the blue and yellow forms. Sterba (1962) reports that both the blue and yellow forms of P. philander appear in Beira. Assuming that P. philander founder populations originated in the central part of southern Africa, as suggested by Jubb and Farquharson (1965), then, in addition to the dispersion route shown by those authors, it is necessary to postulate an additional route to account for the appearance of the blue and yellow forms in Beira. Such a route may be postulated as follows: in addition to coming coastwards down the Zambezi, the species probably also travelled down the Limpopo/Olifants basins (fig 85). The fish in the Limpopo/Olifants basins were probably the progenitors of the yellow-gold forms. These forms then spread to the southern limit of their distribution, and northwards as well to overlap with the easternmost populations of the blue Zambezi-forms in Beira. It has not yet been established whether the two populations within this region of "terminal overlap" behave as non-interbreeding species, for Sterba (1962) did not unambiguously state whether these two colour forms co-existed sympatrically. It would be of value to ascertain whether or not the Beira populations are effectively two different taxa.

The geological evidence adds to the behavioural findings which suggest that within P. philander there are several incipient species, and possibly even fully fledged species.

The role of colour differences in speciation

The most overt differences between the populations of P. philander are those of male breeding coloration and markings. In the following section consideration will be given to colour as an isolating mechanism.

Colour differences of the various populations of P. philander reflect differences in the genotypes of these groups: cross-breeding experiments produced forms with intermediate coloration, the colours characteristic of each population remained true under laboratory conditions when bred through several generations, and the differences in colour were not due to changes in colour intensity associated with the different phases of the reproductive cycle, or changes in the emotional state of the fish, or changes resulting from freaks of feeding or transient environmental conditions.

Within each population there were slight colour differences amongst the individuals. Observation of any group of animals will show that the individuals within an interbreeding population will vary, but also that the variation is limited, and that the average characteristics of the population are monotypic (polymorphism excepted). With respect to colour, the average characteristics of the sexually active male P. philander of each population were distinguishable from those of other populations: the males in breeding dress were clearly and easily recognised by the colours and markings characteristic of their population.

In P. philander there is some laboratory evidence which suggested that the females may exhibit colour polymorphism: a dark gold and a light yellow form are described in chapter one.

The observation that polychromatism is sex-linked (Fryer 1959; Greenwood 1974) to the females in most of the cichlids which exhibit it, suggests that the males are endowed with a relative constancy of epigamic releasers which facilitate species recognition and male selection by females. There are species in which male polymorphism occurs: the best known examples are those of Pseudotropheus zebra, which exhibits at least three forms of polychromatism common to both sexes which co-exist in a single population (Fryer 1959), and the piebald forms of Macropleurodus bicolor in Lake Victoria (Greenwood 1974). The proportion of male polymorphs in any population is much lower than that of the females, which suggests (Greenwood 1974) that this rarity may be attributable to adverse selection pressures on those individuals possessing them. That is, the chances of such males being recognised and chosen by females for the purpose of spawning are greatly reduced and it is possible that polymorphic males do not breed at all. Fryer & Iles (1972) are, however, of the opinion that the occurrence of male polymorphs, especially those of P. zebra, violates the hypothesis which suggests that female sex-limited polychromatism confers sanctity on the male coloration. It seems that the correctness of this assertion could only be ascertained by determining in the field whether the colour polymorphs of P. zebra confine their breeding activities to their conmorph partners, or whether they breed equally well with the other polymorphs. It nevertheless appears that, in general, males of the maternal mouthbrooding group of cichlids do maintain a relative constancy of epigamic releasers to facilitate species recognition and mate selection by females.

An awareness of the importance of colour in species recognition has been in evidence for some time and it has been suggested (Greenwood 1965, 1974; Fryer & Iles 1972) that male coloration was one of the factors involved in the dramatic and often rapid speciation of the cichlids in the African Great Lakes. Greenwood (1965, 1974) in particular has laid emphasis on the role of male colour. He described several species of Haplochromis from Lake Nabugabo which had been separated from Lake Victoria by a sand bar some 4 000 years ago. Five of the six species of Haplochromis endemic to Lake Nabugabo were obviously closely related to species still living in Lake Victoria. Anatomically the Nabugabo species were little different from their Victoria "parent" species. However, the colour differences of the breeding males were so "trenchant" that the Nabugabo fish could easily be distinguished from their closest Victoria relatives on this basis alone. Greenwood (1965) believes that the anatomically nearest species of Lakes Nabugabo and Victoria would behave as biological species should they ever become sympatic, the marked differences of male coloration providing the interspecific barriers isolating mechanisms). It would be extremely interesting to determine experimentally the accuracy of this premise, which is at present based on inferential evidence. The experimental procedure should probably follow the lines of the behavioural investigations I conducted on the allopatric populations of P. philander.

It cannot be certain, until demonstrated, that the species named by Greenwood (1965), and that by Trewavas (1933) are more than phenotypic variations. Greenwood (1965) points out that the hydrology of Lake Nabugabo differs from that of Lake Victoria, and that adaptations of physiological characters concerned with respiration and osmoregulation would have to be made. It is possible too, that the colour changes are ecophenotypic differences which occurred as a response to the differences in hydrology and water clarity, and should the Nabugabo species be returned to Lake Victoria they might quickly re-assume the patterns of the Lake Victoria forms. A similar argument has been raised concerning T. vulcani described by Trewavas (1933), since the hydrology of the crater lake differs considerably from Lake Rudolf (Fryer and Iles, 1972). This question, however, remains unresolved.

Until experimental work has confirmed or modified his conclusions, Greenwood's experience and authority in these matters must be accepted. It appears therefore that Lake Nabugabo provides a classical example of geographic isolation resulting in speciation, and it demonstrates that male breeding colours can evolve rapidly in the haplochromids. Relative to the Tilapia - Sarotherodon groups the haplochromids and haplochromid-like fish appear to be genetically plastic. The reorganisation of the genotype of any population is prone to include colour changes, which are likely eventually to influence courtship behaviour as male coloration and markings are important epigamic releasers.

The male breeding colours of the geographically separated groups of P. philander have been found to be distinctive. In this respect the populations of P. philander parallel the Nabugabo - Victoria species. The question then is whether some or all of the populations of P. philander should also be given a new nomenclatural status, or whether speciation in this species is still incipient.

Colour as an aid to species identification has been convincingly discussed by Fryer and Iles (1972). Colour may also act as an ethological barrier which results in speciation - as the inferential evidence of Greenwood (1965) suggests. The behavioural evidence of this work on P. philander, and also that of Burchard and Wickler (1965), who found that two colour forms of Hemichromis fasciatus, would not interbreed when placed together, suggests, in support of Greenwood (1965), that colour differences may prevent population hybridisation.

Ethological barriers: their role in taxonomy and speciation

Ethological barriers are probably the most important isolating mechanisms in animals. There is little evidence of the existence of such barriers between geographical races. This evidence is not easily obtained because differences observed might indicate incipient barriers, but not the existence of barriers. Furthermore, in fish under laboratory conditions the threshold of reproductive behaviour may be so lowered that races which would not normally interbreed may be induced to spawn. Indeed, Jubb (pers.comm.) reports that under artificial conditions transgeneric interbreeding may occur in cichlids. It is quite possible, indeed probable, that the Nabugabo species would not interbreed with their closest relatives in Lake Victoria. Similarly the colours and behaviour of the Kuruman males suggests that they would not interbreed with P. philander from Lake Sibaya, Kariba, or Durban if placed in Kuruman Eye. It is difficult under these circumstances, to distinguish between the effects of colour and those of behaviour.

Recently, however, behavioural criteria have been used for taxonomic purposes. Trewavas (1973) split the genus Tilapia into two genera: Tilapia for the stout-toothed substratum-spawning fish, and Sarotherodon for the brush toothed mouth-brooding species. The division appears to have been based principally upon the contrasting behaviour of the two groups.

More pertinent to this discussion was the naming of the genus Hemihaplochromis by Wickler in 1963. Wickler observed that the markings and behaviour of Haplochromis multicolor were intermediate between those of the Hemichromis-type and the[1] Haplochromis-type. His evidence has been summarised in table 19 below.

Table 19 after Wickler, (1963) p. 90-91

Hemichromis	Hemihaplochromis	Haplochromis
Special marks on the anal fin absent.	Anal fin of male with egg-coloured border (trailing edge).	Anal fin of male with egg-dummies.
Substrate breeder.	Mouth breeder.	Mouth breeder.
Male and female with strong pair bonds.	During each egg-laying the female keeps to one particular male.	For each spawning the female takes a different male.
Male and female defend the spawning site.	Male defends the spawning site strongly, while female defends only for a short time and not very vigorously.	Only male defends spawning site.
Both parents fan the nest which is attached to a rock.	The female fans an imaginary nest beneath her, and this is in spite of the fact that the eggs are in her mouth.	Neither male nor female fan the eggs.

When Wickler erected the genus Hemihaplochromis he assumed that Haplochromis philander, as P. philander was called at that stage, was sufficiently closely related to H. multicolor to be one of the same genus. Such an assumption was justified for though Wickler had not owrked on philander both species had a conspicuously coloured trailing edge to their anal fins and lacked the 'egg-dummies' characteristic of the haplochromids. The behaviour, he believed, was also very similar.

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1. The realization that all Haplochromis species show very similar courtship behaviour tends to convince one of the importance of species specific markings.

However, recent work (Ribbink 1971 and chapter two above) has shown that though the behaviour of the two species is similar, several important differences do exist. In particular, the female *philander* do not keep to one male during the breeding season but consort with several males. Indeed on one occasion a female *philander* which had been disturbed whilst spawning with one male laid her remaining eggs with another in a manner reminiscent of the polyandry practiced by many female *Haplochromis*. Secondly, female *philander* do not fan an imaginary nest, and finally the female participation in the defence of the nest-site during spawning appeared similar to that of *Haplochromis darlingi* (which indicates that not all haplochromid females are polyandrous), and different from that of the substratum-spawner, *T. sparrmanii*.

Though one might agree that behaviourally *P. philander* and *P. multicolor* should be placed between the *Hemichromis* and *Haplochromis*-types it is apparent that *philander* has the closer haplochromid affinities, whereas *multicolor* has stronger ties with the substratum spawners. The behaviour of these two species is by no means as similar as Wickler assumed.

Jubb (1971 suggested that a behavioural investigation might serve to distinguish *multicolor* from *philander* in the hope, it seems, that *philander*, at least, might be returned to the genus *Haplochromis*. A comparison of two species within a genus could illustrate that the behavioural characteristics of one of the species were such that it should be placed in another genus. The comparison outlined above, however, merely highlights specific differences within the genus. There is no doubt that Wickler's generic name, *Hemihaplochromis*, derived logically from ethological comparisons, has greater biological value than the error of Fowler (*Pseudocrenilabus*), nevertheless *Pseudocrenilabrus* has priority over subsequent names and must be accepted as such. A case could be made to spare *multicolor* from the consequence of Fowler's misjudgment, since behavioural evidence points to a distinctness between the two species. Such an approach would be unrealistic. It would be a pity to see Wickler's excellent and valuable deductions buried by the earlier mistake, but this may be inevitable.

Clearly behavioural differences may be used effectively to establish the existence of specific or generic differences between closely related species. The power of ethological tools in the hands of obsessed "splitters" is frightening because there appears to be no end to the distinctions which may be found. Already Loiselle (pers.comm.) has indicated that in his opinion Trewavas (1973) did not split the original genus Tilapia sufficiently far. In his opinion Sarotherodon is subdivisible into at least two further groups based upon courtship behaviour of males. In one group, characterised by Sarotherodon (oreochromis) mossambica, the male displays to the female head down, body at a 45 to 60 degree angle to the substratum, with dorsal and anal fins folded and caudal spread wide. In the second group, characterised by Sarotherodon (nilotilapia) leucosticta and Sarotherodon (n.) aurea, males court with the body held at a five degree or smaller angle to the substratum, with all fins spread wide. Loiselle argues that these are very real differences, and any generic taxon that groups species whose courtship behaviour is as different as this is as artificial as one that groups substratum-spawning and buccal-incubating species together. Without doubt additional behavioural distinctions could be found which might provide the basis for further sub-division, and then for subdivisions of the subdivisions.

It may be argued that at each taxonomic cleavage biologically significant information is added to the name, for example, Sarotherodon are essentially maternal mouthbrooders which have relatively transient associations with their mates, the males may mate several times a day and only they hold territories. The Tilapia (sensu Trewavas 1973) are substrate spawners which form long-lasting stable pair bonds and both members of the pair defend the territory. Before Trewavas separated Sarotherodon and Tilapia, one unfamiliar with the group would not have known from the name whether the Tilapia was a mouthbrooder or a guarder. A further subdivision of the genus Sarotherodon into those fish which court at one angle with fins extended and those which court at another angle with fins folded would add further information to the name, and so one could continue in this vein splitting the groups on behavioural, morphological, colour, physiological and ecological criteria. To affi information to the name is not the role of taxonomy. Indeed, naming in this manner would eventually make a full understanding of the nuances of all behaviour (and the other criteria) an essential prerequisite to cichlid classification. This rather puts the cart before the horse and will indubitably make classification difficult to those who have not developed in this generation of innumerable subdivisions based upon subtle distinctions. The classification of cichlids will become an impenetrable jungle for the non-specialist if the "splitters" have free rein.

In the same way that morphological, physiological and other characteristics may engender name changes, so ethological differences between groups may be sufficiently great to justify nomenclatural recognition of local species or regional races. As a guide and a restriction to "splitters", subdivisions based on behavioural differences should be shown conclusively to provide ethological barriers which prevent hybridization. Several difficulties face a biologist in dealing with this problem. Firstly, it may be argued that species specific behaviour is stereotyped and easily recognised by conspecifics. Indeed it is remarkable at first sight that the populations of P. philander behave qualitatively in such a similar manner despite slight morphological and marked colour differences. It seems that the stereotypy of courtship and spawning behaviour resists change. Any fish which behaved incorrectly would be selected against. Very small changes might nevertheless creep in and slowly accrue. Therefore one could conclude that any population which showed reproductive behaviour atypical of the species would probably be behaviourally isolated from other populations, and would probably have been physically separated from the other populations for a long time.

Behaviour patterns should be weighted in an assessment of their importance as an isolating mechanism. For example, differences in the initial invitation patterns (such as those highlighted in Loiselle's comparison, see above) would be of relatively little consequence, whereas disharmony in the spawning activities would lead to a cessation of courtship. It has been observed in the field and laboratory that small S. mossambicus have followed P. philander to the nest in a response to the invitation patterns, but once the behavioural exchanges within the nest became discordant the Sarotherodon were chased away. Therefore differences in angle and the display of the invitation patterns such as those described for the two groups of Sarotherodon (see above) are real, but need not necessarily provide an ethological barrier. Differences in spawning behaviour and bond formation, such as the differences which separate Tilapia from Sarotherodon probably form very effective ethological barriers.

A further problem associated with investigation of the reality of ethological barriers is that under experimental conditions it has been found that fish which would not normally hybridize do interbreed (outlined above). A free choice of partners should be provided to obviate the pressures which induce hybridization. Should there be a free gene flow between laboratory held populations when given a choice of partners, including their own population group, and without hybridisation pressures (such as behavioural dominance of one group over another), then one could be fairly certain that the variation between populations was insufficient to isolate these races. On the other hand, an unwillingness of two populations to interbreed in an aquarium should not be taken as conclusive proof that the two populations are so different that gene flow between them is no longer possible for reasons explained below.

Two factors appear to affect the choice of a mate: firstly, there is an innate response to the species specific characteristics (releases) of the conspecific partner, and secondly, the sexual characteristics of a cichlid appear to become imprinted upon the conspecific members of the population. Cichlids reared in the exclusive company of another species until adulthood have shown an initial tendency, which may last up to three months (Sjölander and Ferno, 1973), to choose the imprinted species in preference to conspecifics (Sjölander and Ferno, 1973; Evans,1974). These workers have indicated that sexual imprinting does occur in cichlids. It seems likely that imprinting upon conspecifics would be strongly reinforced by the experience of one or more matings with members of the opposite sex. The conspecific characteristics thus learned would facilitate subsequent mate selections and militate against errors. Substratum spawners which form strong pair bonds during protracted relationships conceivably imprint more powerfully on the species specific releasers of their mates, than would mouthbrooders which have brief relationships with their spawning partners. Thus, fish which have experienced previous matings with conspecifics of their own particular race, in the field or laborabory, would be more likely to choose these in preference to those of another race. Therefore, when faced with the results of a choice chamber experiment in which the "own population" was chosen, one would need to differentiate between the innate and imprinted responses. Failure to do so would cast doubt upon conclusions drawn. For example, Voss (1972) considered that the unwillingness of two forms of T. sparrmanii to interbreed indicated the occurrence of sibling species, and Loiselle (communicated results of his M.Sc. Thesis) considered that because he was unable to induce hybridisation between four geographical races of the west African substratum spawner, Hemichromis bimaculatus, he was therefore dealing with four distinct species. As yet the role of imprinting in cichlid speciation has not been explored, and some writers (Greenwood 1974) doubt that imprinting occurs in certain cichlids (Haplochromis). Sexual imprinting may have played a role in the speciation and the rate of speciation in the cichlids of the Great Lakes. It is difficult to appreciate its mode of action: imprinting could prevent gene flow between races which had come together again after a relatively short period of separation, but imprinted characteristics would not keep the progeny of these mixed populations apart.

Given a choice, P. philander females chose partners of their own population. Where no choice was given population hybridisation occurred. To determine the respective roles of learned and innate responses fry should be reared and then maintained in adulthood in mixed populations. Under these conditions they would learn species, but not necessarily population, characteristics. Should they still show a preference for their own population this may then be taken as an inherited trait. The work of this thesis will eventually be extended to test this hypothesis.

If treated cautiously, and paying due regard to the problems inherent in behavioural analyses, then behavioural criteria may be used successfully to differentiate between taxa. It is recommended, though, that a tight rein be held to prevent the dissection of polytypic species. There is no doubt that ethological barriers play an important role in speciation.

There are sufficient colour and behavioural differences between the populations of P. philander to cause the "splitters" to clamour for nomenclatural recognition of these races. The grounds for such clamour would increase if the information concerning differences of eggsize, egg-colour, incubation and interbrood periods is added to the list. Furthermore, the inferential evidence of laboratory experiments suggests that were Sibaya fish placed in Kuruman Eye, or Kuruman fish placed in Sibaya, then hybridization would be unlikely to occur. Interbreeding amongst the Sibaya, Durban and Kariba populations is more likely. Though complete ethological separation has not yet been proven the foregoing evidence suggests that serious consideration should be given to nomenclatural changes of some races of P. philander.

As far as the Durban, Sibaya and Kariba populations are concerned, information depicting clinal variation, principally the distribution of the intergrades, is not yet available. Without this information it would be premature and unnecessary to seek subdivision. Further information might show that the yellow and blue forms are indeed very different and that they maintain their distinctness in the Beira region of overlap. Until this is confirmed it is recommended that there should be no nomenclatural division, or subdivision of the species.

Thus all the populations in the eastern drainage basins should retain the sub-specific status originally suggested by Trewavas (1936): P. philander philander (Weber).

Since her description of Pseudocrenilabrus philander dispersus in 1936, Trewavas has decided that the sub-species is no longer definable, and that Pseudocrenilabrus philander philander probably dominates the whole distribution of the species, except in Otavifontein where Pseudocrenilabrus philander luebberti resides (Trewavas, unpublished personal communication to Jubb in 1967). This view has appeal in that it doesn't unwarrantedly subdivide a widely distributed polytypic species. Trewavas' suggestion for a regrouping of P. philander wins my support in respect of those populations between which gene exchange is possible.

The peripheral isolates in the sinkholes, springs and possibly the Orange River System appear so isolated that an exchange of genes with other populations is highly unlikely. Of these populations only that of Kuruman Eye was studied in detail and the discussion which follows is accordingly confined to this geographical group.

The behavioural evidence presented, and the colour differences described in this thesis appear to indicate that the Kuruman population is distinct from the clinal populations with which it was compared (Durban, Sibaya and Rhodesian populations). Further, the laboratory experiments indicated that the Kuruman population was reluctant to hybridise with the clinal populations. Though these factors may suggest that the Kuruman population should be set apart from the other populations and given its own taxonomic status. I, however, have an objection: the behavioural tests were sensitive. Should any sensitive test be applied to any two populations of a species, differences will be found. If more tests are applied,more differences will emerge. Yet the populations need not necessarily be taxonomically different. The reluctance of the Kuruman fish to hybridise may perhaps be accounted for by imprinting and the effects of geographical variation within the taxon.

Another objection to elevating the Kuruman population to subspecific status is that, if this were done, then in all the innumerable other sinkholes, springs and small permanent waterbodies of the Kalahari, Transvaal and South West Africa, one would probably find populations of P. philander differing slightly from one another and meriting a sub-specific status. Morphologically the populations are extremely difficult to tell apart, and apparently represent a single taxon. Thus, to give sub-specific status to each of these populations, on the basis of colour differences and differences in the response to sensitive behavioural tests, would merely be to append locality tags to their names. This is of doubtful benefit: it would not add an orderliness to the classification of P. philander, but would make it a taxonomically unwieldy group. Latinized locality tags appear unnecessary in biology since experimental biologists always tacitly acknowledge the polytypic nature of a species by citing the location from which their material was drawn.

I am aware of the tendency of many taxonomists, the "splitters", to sieze upon small differences which exist between populations. Then, forgetting that geographical variation exists within a species, they taxonomically redefine populations, on what frequently appears to be extremely slender evidence.

The present sinkhole and Kuruman Eye populations are probably what Greenwood (1974) would have referred to as a "cradle of a species". Should these peripheral isolates survive then an inevitable consequence of their isolation would be speciation, in a manner analogous to the cyprinodonts in Death Valley (Miller 1950; Brown 1971). Until then, however, let us hope that reason prevails and that hasty taxonomists do not snatch these populations of _P. philander_ prematurely from the "cradle" during their incipient stages of speciation.

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APPENDIX 1

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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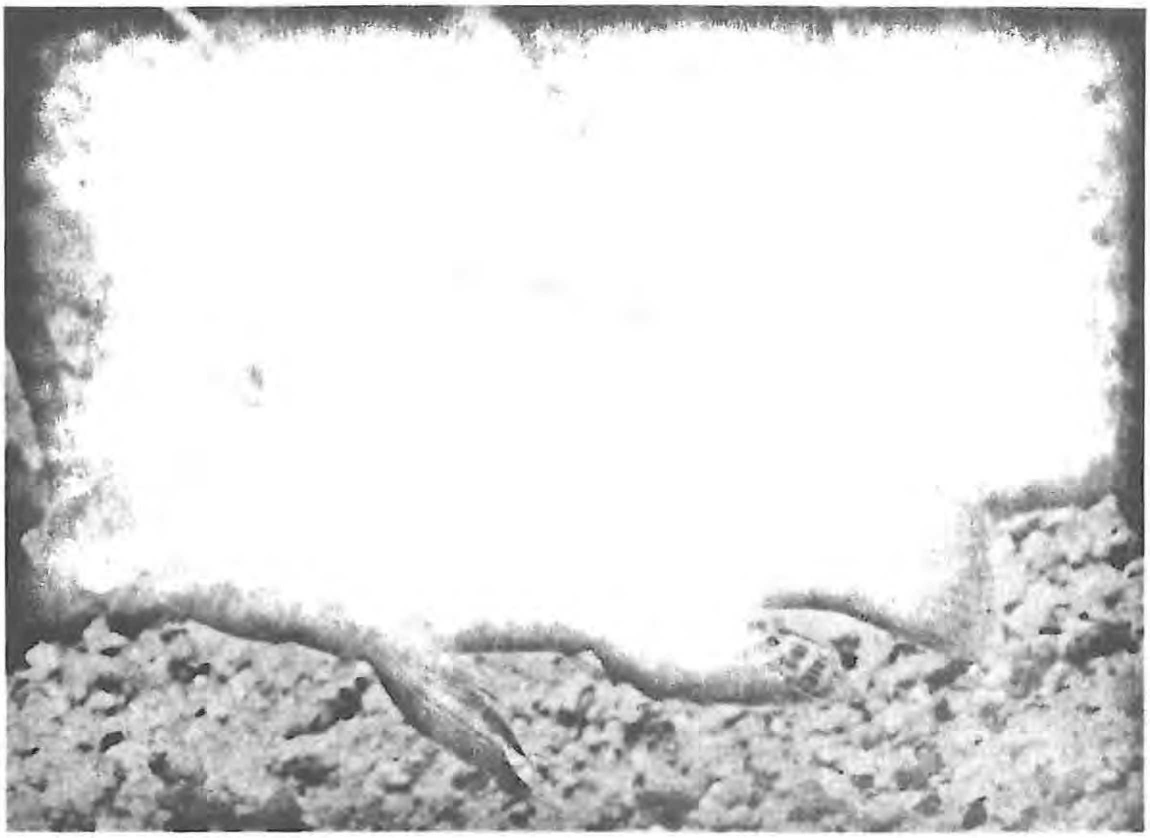


PLATE 1

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,

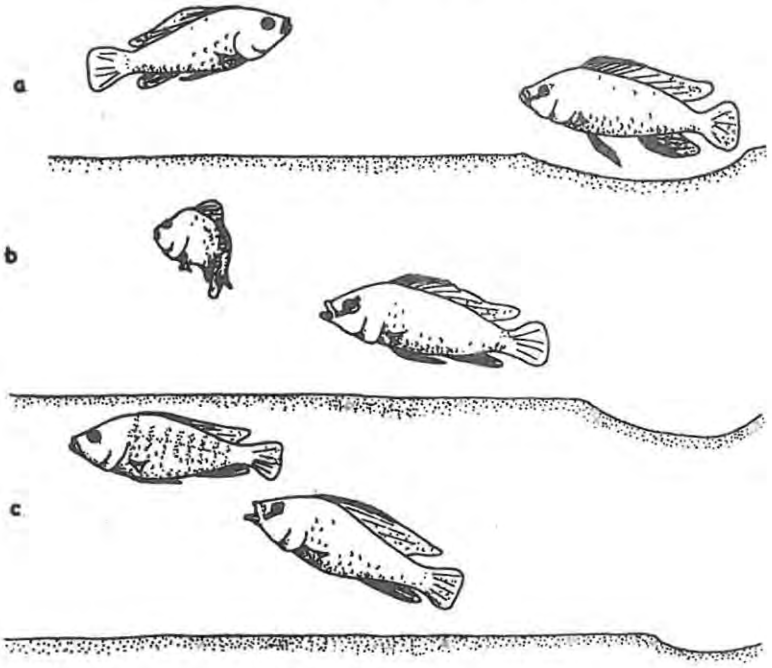


FIGURE 1

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

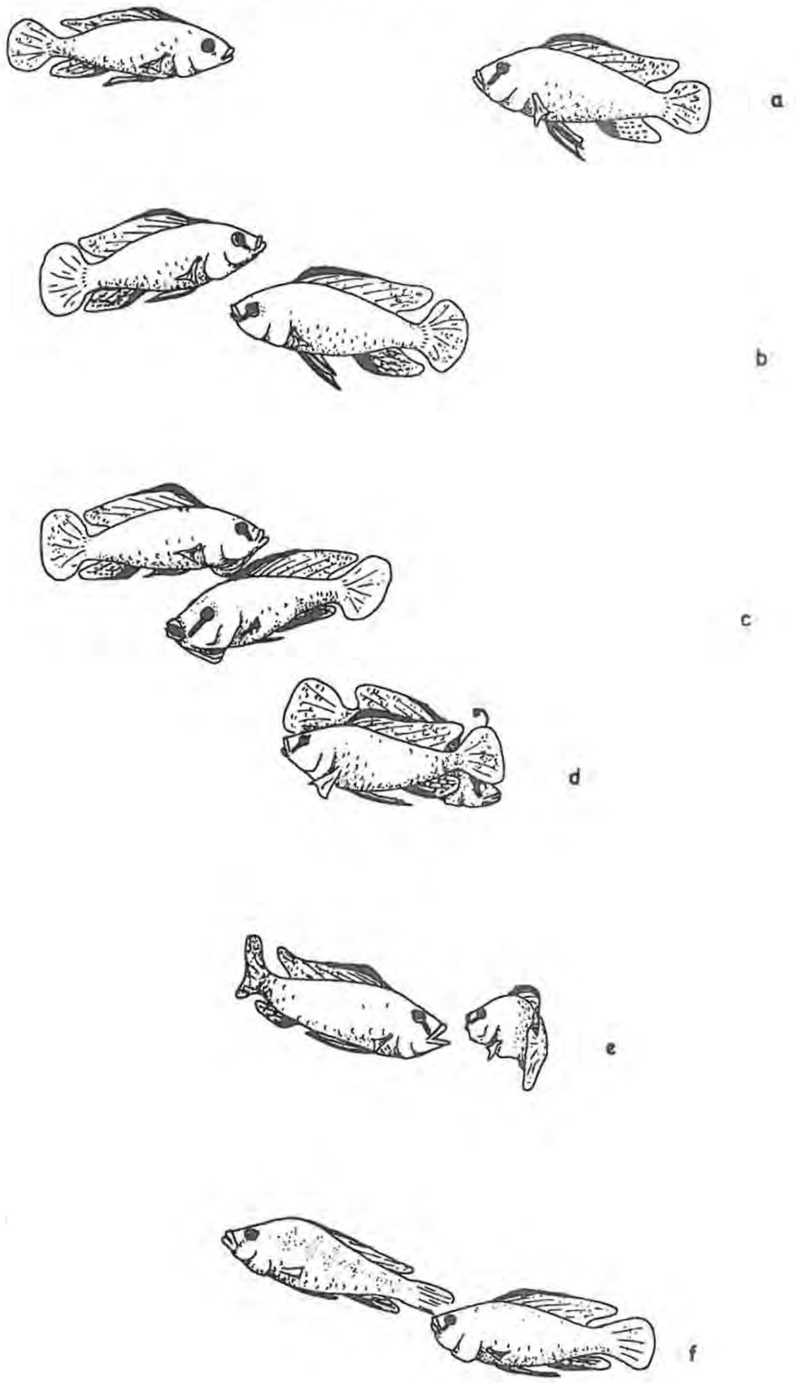


FIGURE 2

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,

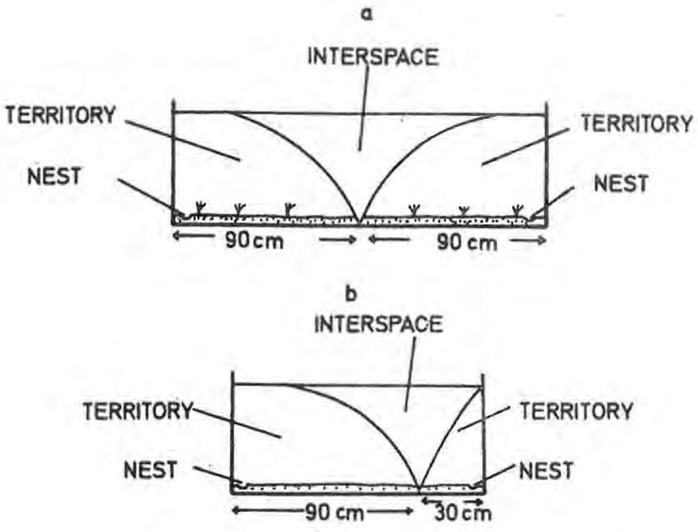


FIGURE 3
(*a*) The two dominant males have territories in which the boundaries are 90 cm from their nests. The non-territorial fish are confined to the interspace. (*b*) In aquaria which cannot accommodate two 90 cm territories, one male will have a territory with a 90 cm radius and another male may, 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

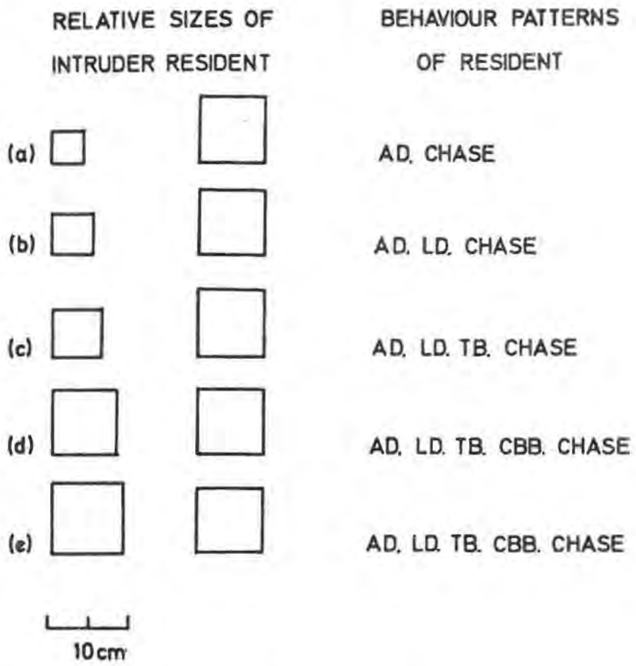


FIGURE 4

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

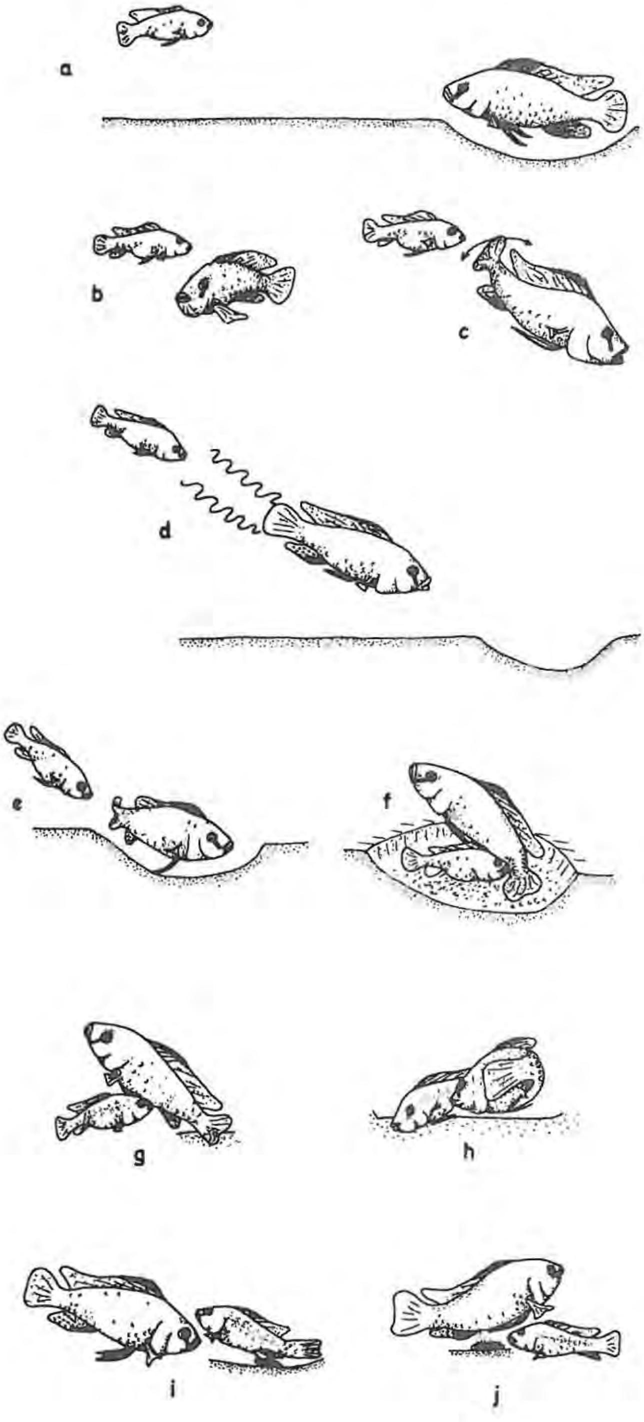
The female's entry into the nest releases the "vertical nest-shake" in which the male raises his head into an almost vertical position, while the caudal region of the body is kept on the substrate by means of a body-flexure in the region of the anal fin (Fig. 5f). As the male rises up from the horizontal 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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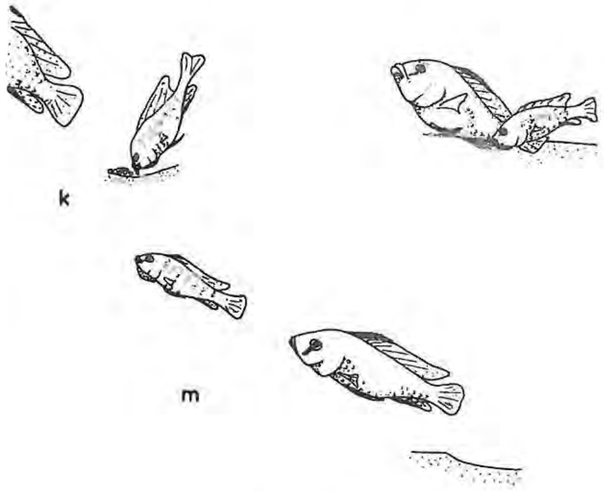

FIGURE 5

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.

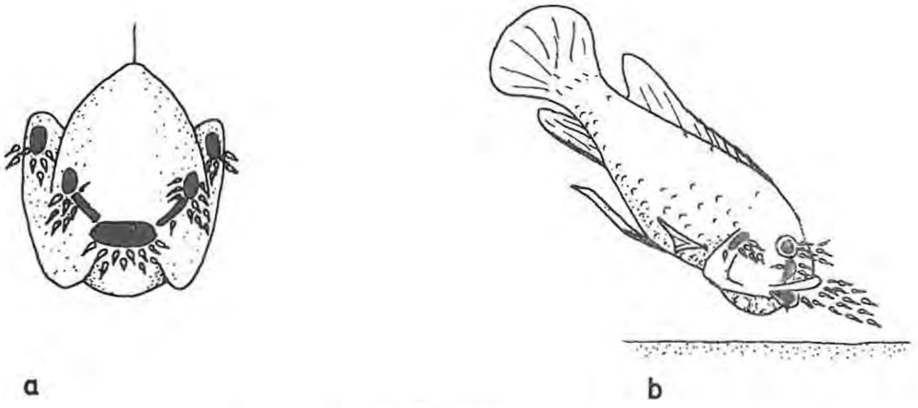

FIGURE 6
(*a*) The facial pattern of the maternal fish showing the markings which attract the fry. (*b*) A female gathering her brood.

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 swarming. 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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APPENDIX 2

THE BEHAVIOUR AND BRAIN FUNCTION OF THE CICHLID FISH *HEMIHAPLOCHROMIS PHILANDER*

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ABSTRACT

Forebrain extirpations from *Hemihaplochromis philander* (Pisces: Cichlidae) resulted in a decrease of aggressive (territorial), courtship, and spontaneous behaviour. The stimulus-response latency was found to be increased by the extirpations. Forebrainless males were unable to distinguish between male and female conspecifics on a visual basis. Abnormal responses to certain stimuli occasionally resulted in accidents suggesting a failure of neural feedback mechanisms.

It was suggested that the teleost forebrain houses a primitive limbic system the main functions of which would be general arousal and the selection of appropriate responses to the incoming external and endogenous (motivational) stimuli.

KEYWORDS:
Brain Function, Teleost, telencephalon, Cichlid fish behaviour, limbic system, hippocampus.

The anatomy and location of the teleost forebrain led earlier workers to assume that the function of this part of the brain was exclusively one of integration and correlation of olfactory information. This error is perpetuated in current textbooks despite a good deal of evidence to the contrary from Janzen (1933), Noble (1937), Hale (1956a and b), Segaar and Nieuwenhuys (1963) and others, who have shown that the forebrain is involved in non-olfactory behaviour.

This paper draws attention to several of the more important non-olfactory behavioural changes which occurred as a result of the surgical removal of the forebrain of a small cichlid fish, *Hemihaplochromis philander* (Wickler).

PROCEDURE

The experimental fish were caught by netting in lakes of Natal and Zululand, from where they were transferred to the laboratory. The males, which were to be used in the experiment were maintained in a cold water aquarium (at 17 ± 1°C) for fourteen days prior to the commencement of the investigation, in order to obtain a degree of pre-experimental conformity of the behaviour and physiology of the fish.

Each male was then placed in a separate aquarium where its behaviour could be observed from behind a one-way mirror. All these aquaria were of the same size (40 cm x 30 cm x 35 cm); had equal artificial illumination for 14 hours per day, a sand substrate, two small aquatic plants, and contained two spent female and three juvenile male conspecifics. The water temperature was then raised over a twelve hour period to 25 ± 1°C, and maintained at that temperature throughout the experiment.

These conditions were known to promote territorial and reproductively oriented behaviour in *H. philander* (Ribbink 1971).

The ensuing aggressive and courtship behaviour of the subject fish was assessed every day for fifteen days, commencing approximately 36 hours after the fish had been placed in the experimental aquaria. The 36 hour period was considered to be a necessary recovery period for those fish which had undergone surgery.

Three categories of experimental fish were used. Each group or category contained seven adult males, between six and eight centimetres in length. The categories were as follows:

(i) Normal males, which served as normal controls.

(ii) Sham operated controls, in which the surgical procedure went as far as the severing of the choroid tela.

(iii) Experimental males from which the forebrain had been surgically removed.

Surgical Procedure

The fish were anaesthetised with Sandoz MS 222, the concentration of which was adjusted so that respiratory movements were maintained but other movements were suppressed. The bodies of the fish were held in a foam rubber lined clamp and the heads were secured by two "V"-clamps into which the supra-orbitals were fitted. The mouth and gills were submerged but the top of the head was exposed. A longitudinal incision was made on either side of the supra-occipitals, the hypaxial muscles were then parted and held by retractors in order to expose the roof of the cranium. A dental burr was used to drill through the skull to expose the choroid tela. In the sham operated controls the tela was severed and the wounds were closed. In the experimental fish the forebrain was removed by separating the telencephalon from the diencephalon with a LM_4 Lesion Maker (Grass Instrument Company), and removed from the cranial vault by means of suction. The wounds were sewn closed with ophthalmic needles and silk, and treated with aureomycin cream to prevent infection.

Measurements of aggressive behaviour

Under natural conditions aggressive behaviour is elicited by a male conspecific entering the territory of the resident male. The normal patterns are active aggressive display, lateral display, and circling (Ribbink 1971).

Aggression was induced by lowering a round-bottomed flask, which contained a sexually coloured male conspecific, into the aquarium/territory of the subject fish. The object fish was always 5-10 mm smaller than the resident male. On all occasions the flask was lowered into the centre of the aquarium, and suspended between three and five centimetres above the substrate.

After a 60 second pause had been allowed for the subject fish to recover from any disturbance caused by the flask, all the behavioural displays were recorded verbally by the observer on a tape-recorder for exactly 300 seconds. The total time spent in each display pattern was then determined from the playback of the recording.

Aggressive activities such as tail-beating and biting, which are performed during the behavioural displays, were also enumerated during the 300 seconds.

Measurements of sexual behaviour

Under normal conditions a gravid female is invited to the male's nest by a series of invitation behaviour patterns, and once there the nest activities which lead to spawning are elicited (Ribbink 1971).

Courtship behaviour was evoked experimentally by lowering a flask which contained a gravid female into the aquarium. The time spent in courtship was recorded and transcribed by the methods described earlier. The number of courtship activities performed during the 300 seconds was also counted.

RESULTS

Results of surgery

After the experiment every fish was sacrificed and a microscopic examination and measurement of the brains of the forebrainless and sham operated fish was made to determine whether the operations for this experiment had been performed as intended.

Aggressive behaviour

(a) *Time*

The measurements of aggressive behaviour revealed that the fish from which the telencephalon had been removed spent very little time in aggression during the course of the investigation (Fig. 1). By contrast, the two control groups increased their aggressive behaviour until 255 or more of the 300 seconds were spent in aggression.

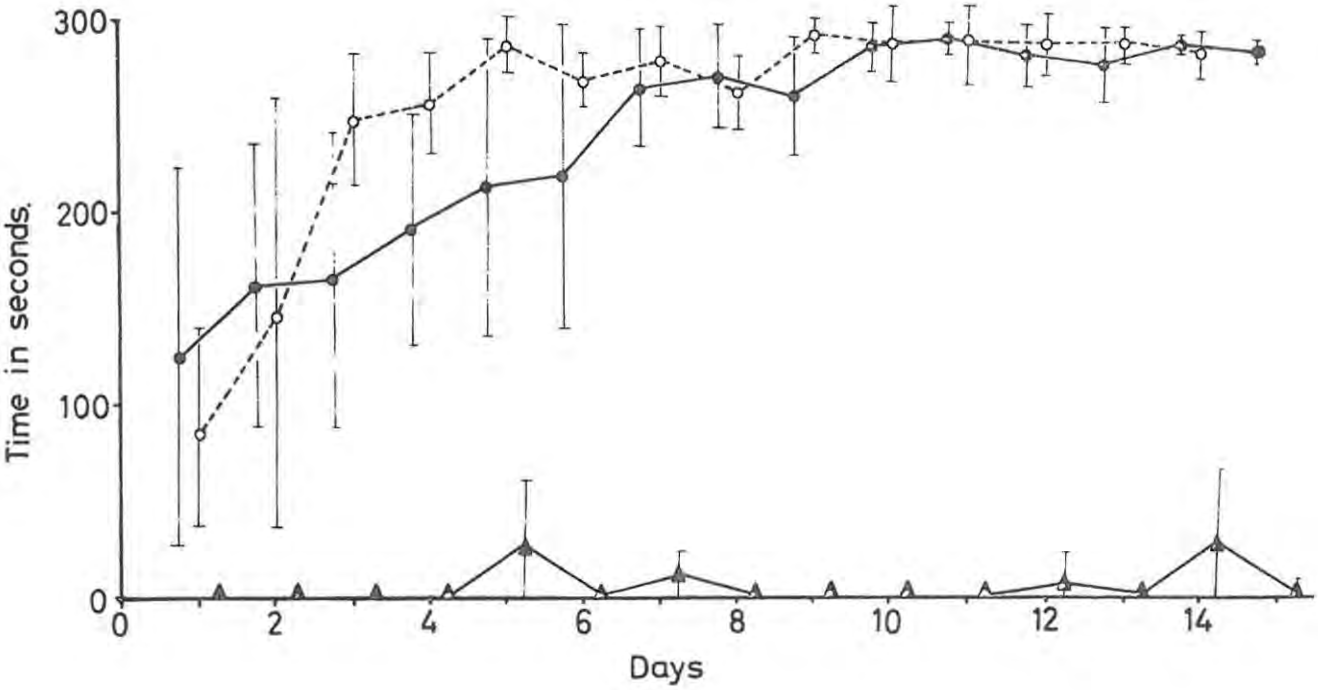

FIGURE 1
The time *H. philander* spent in aggression during each experimental period. The measurements of behaviour were taken on successive days. The points on the graph represent the mean values (N=7). and the variation is expressed as two standard errors.
Normal controls (●); sham operated controls (○); forebrainless fish (▲).

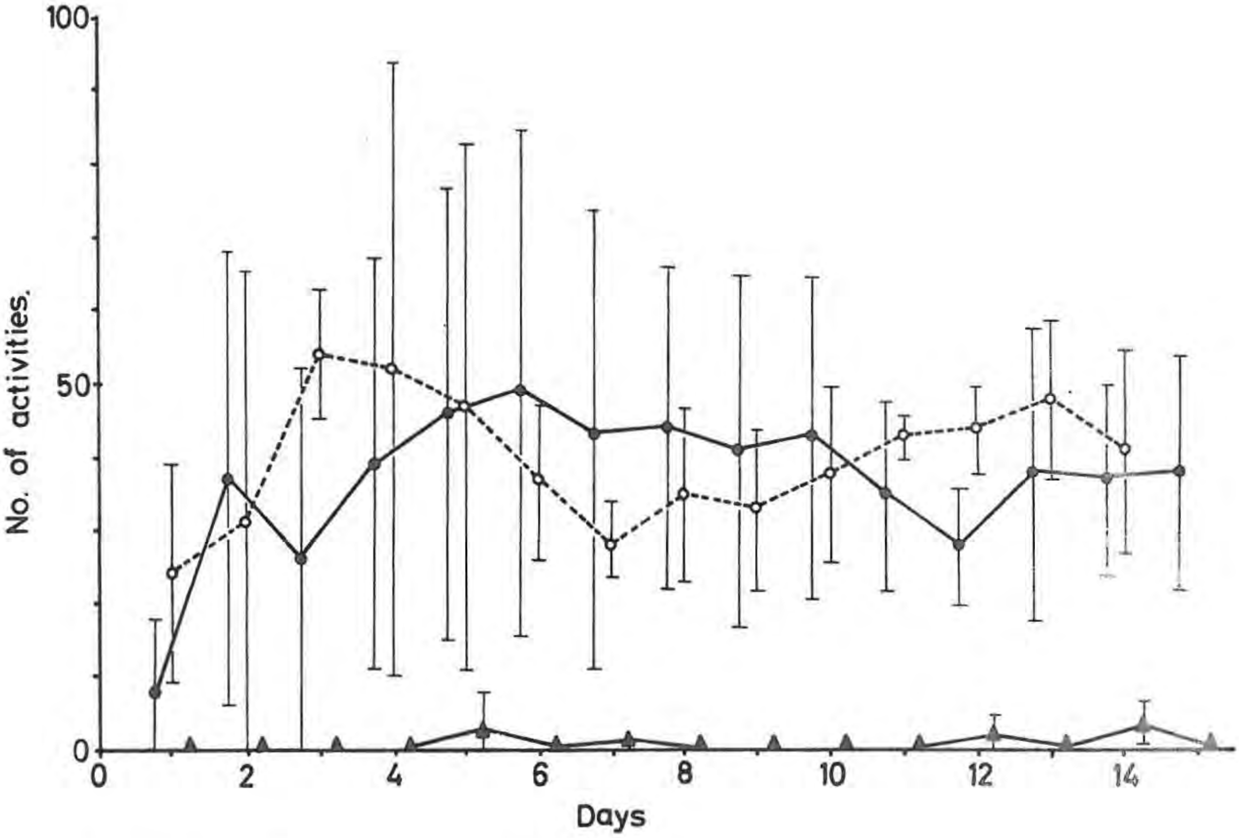

FIGURE 2

The number of aggressive activities *H. philander* performed during each experimental period, on successive days. The points on the graph represent the mean values (N=7), and the variation is expressed as two standard errors.

Normal controls (●); sham operated controls (○); forebrainless fish (▲).

The amount of variation in the behaviour of the normal and sham operated fish was remarkably small after the sixth day. It is suggested that the more variable behaviour during the first six days may be attributed to the "uncertainty" which exists during the establishment of a territory.

(b) *Aggressive activities*

The form of the curves which illustrate the number of aggressive activities performed was found to be similar to those curves depicting the time spent in active aggression (Fig. 2).

(c) *Other behaviour in the presence of a male conspecific*

The remaining periods of the 300 seconds were occupied either in passive displays or by swimming. The passive displays (Fig. 3) took two forms; the fish either did not do anything, or

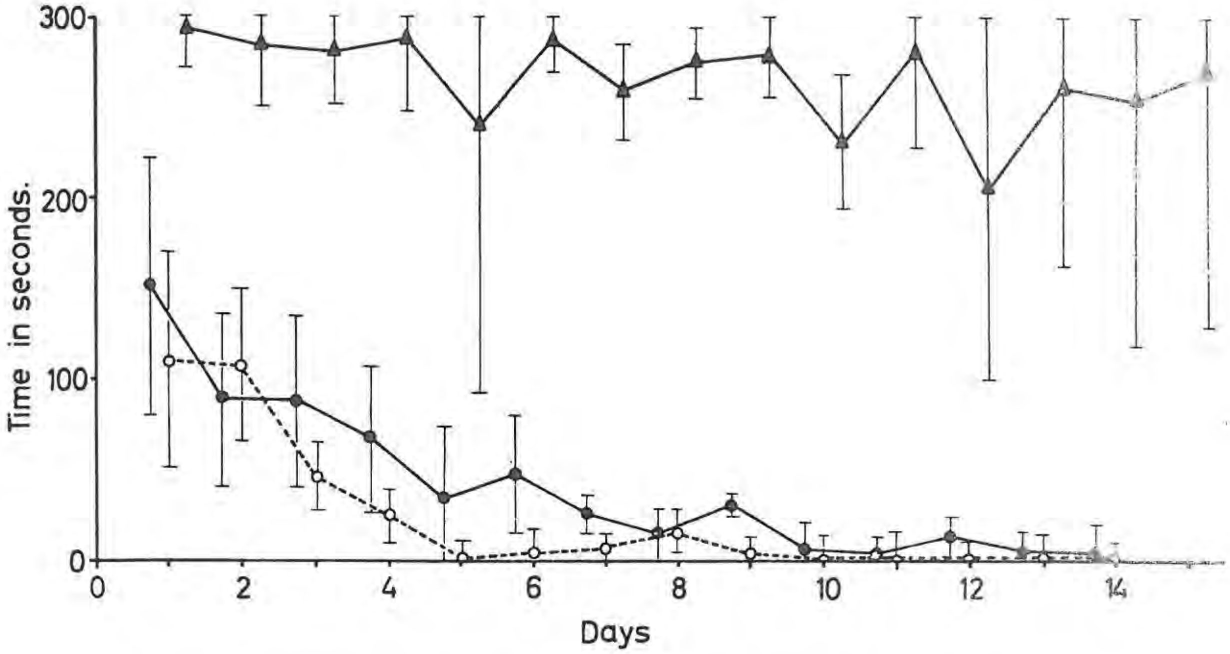

FIGURE 3
The time *H. philander* spent in passive behaviour during measurements of aggression in each experimental period, on successive days. The points on the graph represent the mean values (N=7), and the variation is expressed as two standard errors.
Normal controls (●); sham operated controls (○); forebrainless fish (▲).

exhibited a passive aggressive display during which it remained motionless with fins fully extended. The swimming also occurred in two behavioural forms, either swimming to the flask to initiate or resume aggressive behaviour, or the chasing of other fish in the aquarium. This chasing of other fish appeared to be redirected aggression, since this activity could be increased markedly by placing a larger object fish in the flask.

The two control groups were found to chase frequently during the initial stages of the investigation, but the number of chases decreased later in the experiment (Table 1). These findings indicate that the proportion of redirected activity is high during establishment of the territory, but once territoriality reaches a maximum the aggression becomes more appropriately directed, which may account for the decrease in the number of chases.

An unexpected behaviour pattern appeared in the fish from which the telencephalon had been removed. These fish were found to court male conspecifics which were presented in the usual manner. This suggests that they were unable to distinguish between males and females on a visual basis. This aspect of their behaviour will be dealt with more fully later in this paper.

TABLE 1

THE TOTAL NUMBER OF CHASES PERFORMED BY *H. philander* MALES DURING THE EXPERIMENTAL PERIODS IN WHICH AGGRESSIVE BEHAVIOUR WAS MEASURED. THE MEASUREMENTS WERE TAKEN ON SUCCESSIVE DAYS

Day	*Control*	*Sham*	*Forebrainless*
1	13	14	0
2	30	17	1
3	32	22	0
4	21	14	3
5	17	17	0
6	14	14	10
7	16	21	3
8	19	10	2
9	11	9	1
10	13	10	0
11	9	8	14
12	5	14	7
13	13	3	4
14	12	4	5
15	10	4	1

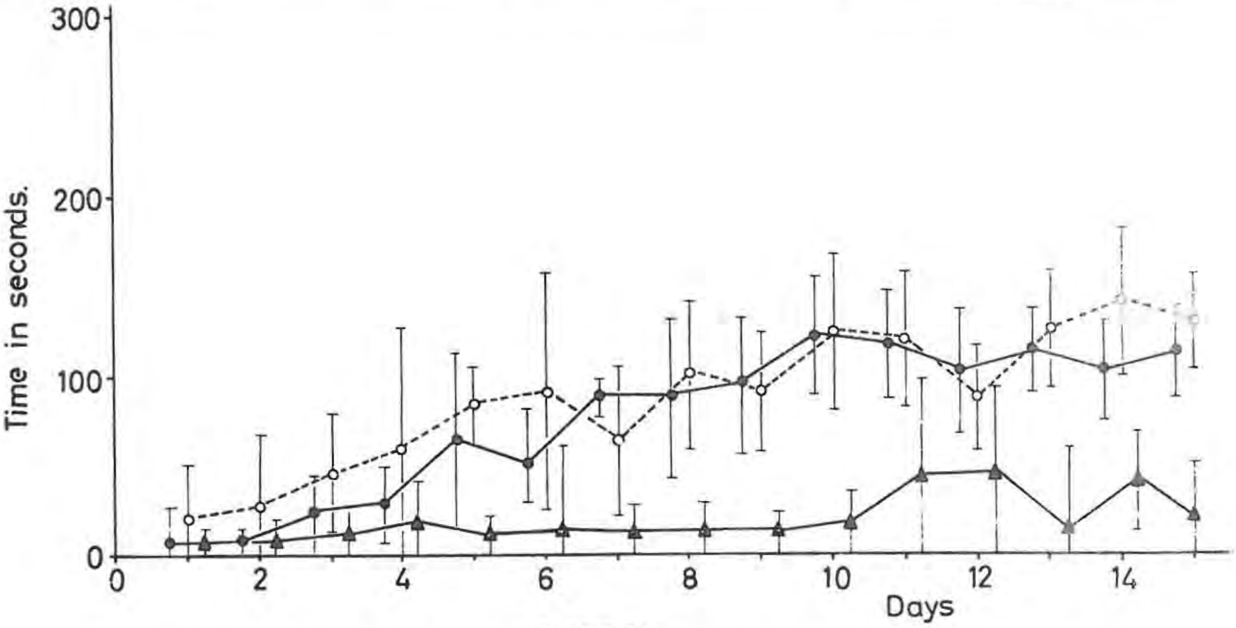

FIGURE 4

The time *H. philander* spent in courtship during each experimental period, on successive days. The points on the graph represent the mean values (N=7), and the variation is expressed as two standard errors.

Normal controls (●); sham operated controls (○); forebrainless fish (▲).

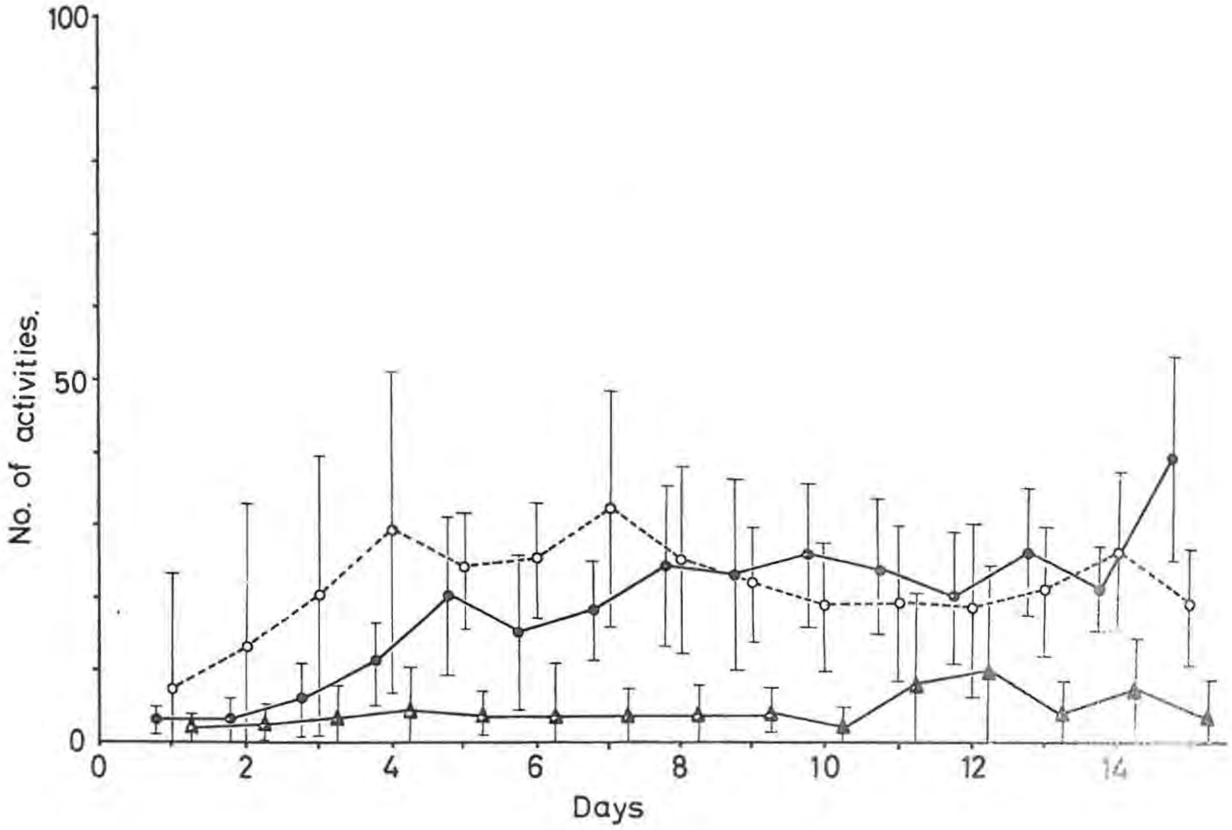

FIGURE 5
The number of courtship activities performed by *H. philander* during each experimental period, on successive days. The points on the graph represent the mean values (N=7), and the variation is expressed as two standard errors.
Normal controls (●); sham operated controls (○); forebrainless fish (▲).

Courtship behaviour

(a) *Time and activities*

Fish without their forebrain spent less time in courtship (Fig. 4) and performed fewer courtship activities (Fig. 5) than the sham operated and normal males.

(b) *Aggression during courtship measurements*

Aggressive behaviour in the presence of a gravid female also occurred. This aggression was evident in the two control groups, but was virtually absent from the forebrainless fishes (Figs. 6 & 7). Aggression in the former groups was especially marked during the establishment of the territories, when intruders were treated aggressively regardless of sex. In the later stages of the investigation, aggression was also evoked when the female in the flask failed to follow the courting male. This

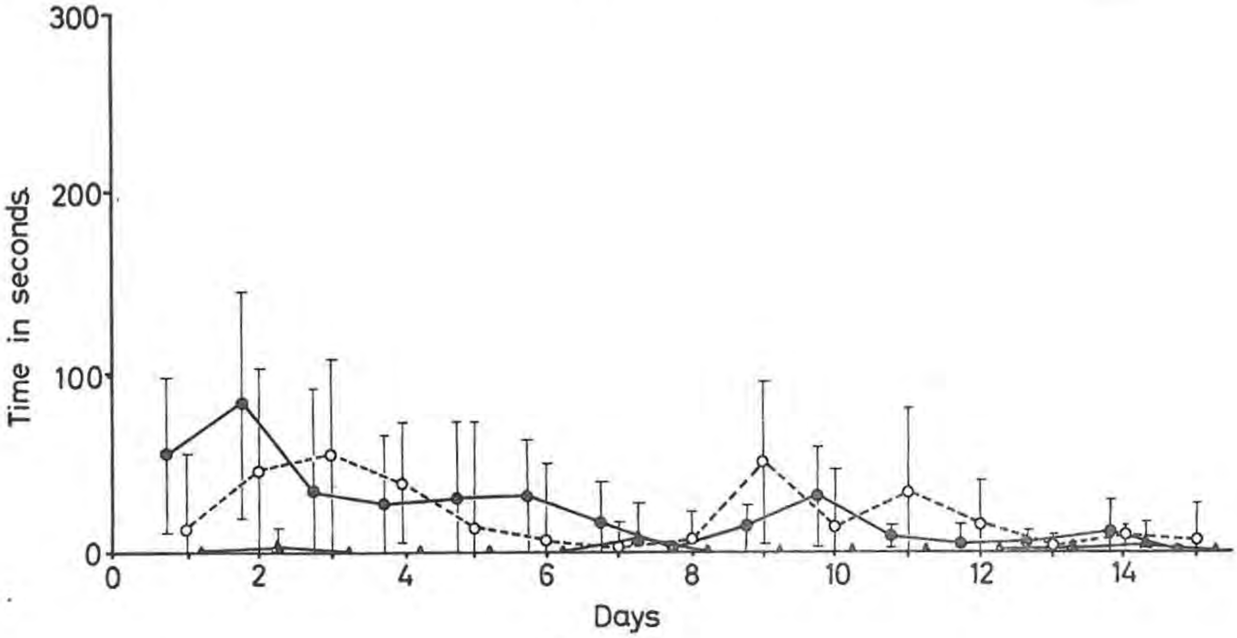

FIGURE 6

The time *H. philander* spent in aggressive behaviour during courtship in each experimental period, on successive days. The points on the graph represent the mean values (N=7), and the variation is expressed as two standard errors.
Normal controls (●); sham operated controls (○) and forebrainless fish (▲).

TABLE 2

THE TOTAL NUMBER OF CHASES PERFORMED BY *H. philander* MALES DURING THE EXPERIMENTAL PERIODS IN WHICH COURTSHIP BEHAVIOUR WAS MEASURED. THE MEASUREMENTS WERE TAKEN ON SUCCESSIVE DAYS

Day	*Control*	*Sham*	*Forebrainless*
1	15	26	2
2	35	22	0
3	17	31	0
4	31	25	4
5	38	36	3
6	35	42	2
7	35	21	1
8	37	43	0
9	28	43	1
10	36	38	2
11	28	24	12
12	25	36	2
13	29	23	8
14	45	29	0
15	36	31	0

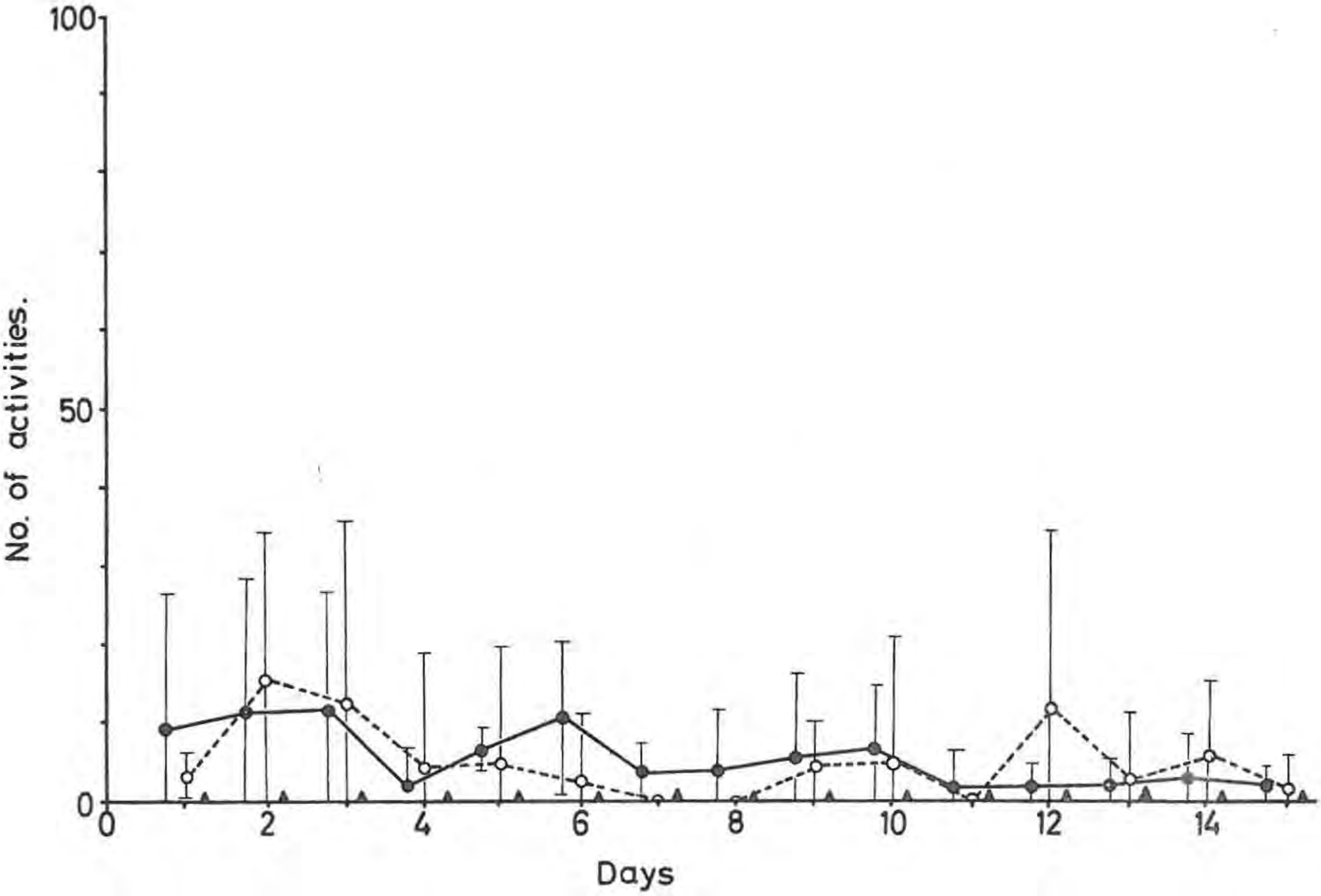

FIGURE 7
The number of aggressive activities performed by *H. philander* during courtship in each experimental period, on successive days. The points on the graph represent the mean values (N=7), and the variation is expressed as two standard errors.
Normal controls (●); sham operated controls (○); forebrainless fish (▲).

aggression was often directed at the female in the flask but it was more commonly redirected, as manifested by an increased number of chases (Table 2).

The number of chases in the presence of a gravid female is greater than when in the presence of male conspecifics (Table 1), probably due to the aggression being more appropriately directed in the latter instance.

(c) *Passive performances*

When in the presence of a gravid female the two control groups spent less time in passive behaviour than the forebrainless fish (Fig. 8). A comparison of the time spent in inactivity when in the presence of a male conspecific (Fig. 3), with that when in the presence of a female conspecific (Fig. 8), shows that the time spent by the forebrainless fish in passive behaviour was similar in both instances. However, the two control groups were found to spend more time in inactivity

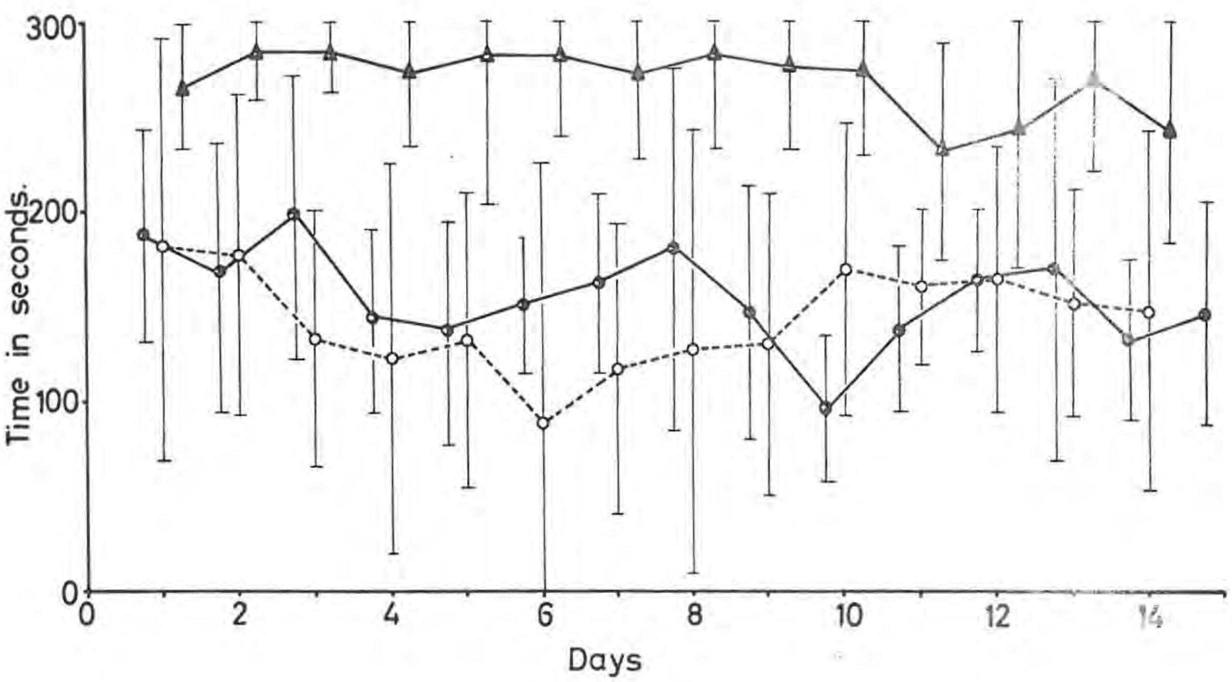

FIGURE 8
The time *H. philander* males spent in passive behaviour during each experimental period, when in the presence of female conspecifics. Measurements of behaviour were taken on successive days. The points on the graph represent the mean values (N=7), and the variation is expressed as two standard errors. Normal controls (●); sham operated controls (○); forebrainless fish (▲).

when presented with a gravid female. This increased inactivity of the sham operated and normal males could be partly attributed to the time spent in waiting for the females to either turn towards them, or waiting for the females to follow them to the nest.

(d) *Courtship sequences*

Thus far, the total number of courtship activities and the total time spent in courtship have been considered. This overlooks the fact that the courtship sequences are composed of a number of behavioural components. By considering each component of the courtship behaviour as a percentage of the total courtship pattern (Figs 9a and 9b) it is clear that the forebrainless fish spent the greater proportion of time in sideshake (SS). The forebrainless fish showed no nest-shake activity (NS) and the time spent in vertical-nest-shake (V) was increased. During the course of the experiment, the forebrainless fish spent 79 seconds in vertical-nest-shake whilst the normal fish spent five, and the sham operated fish spent four seconds in vertical-nest-shake.

This indicates that the relative occurrence of components of the courtship sequence was disproportionately altered by the ablations.

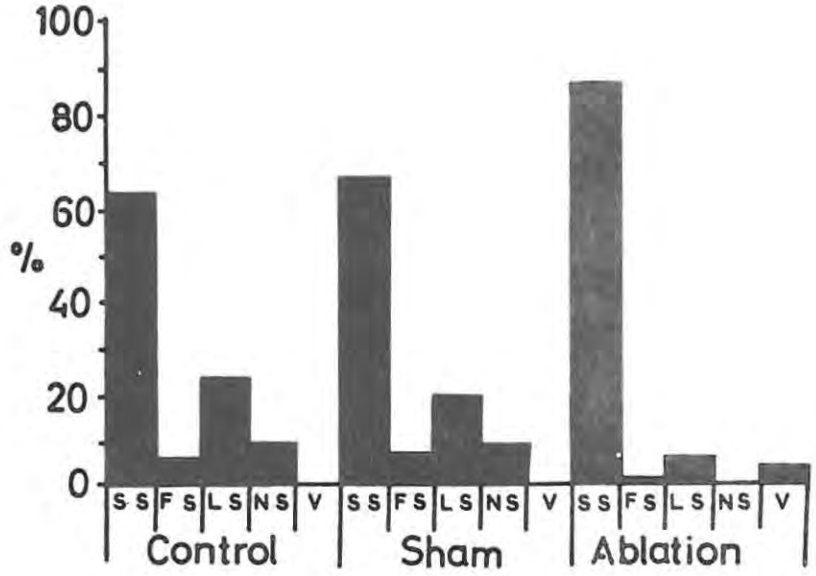

FIGURE 9a
The number of performances of each courtship component by *H. philander*, expressed as a percentage of the total number of courtship activities.
SS = side-shake; FS = follow-shake; LS = lead-swim; NS = nest-shake; V = vertical-nest-shake.

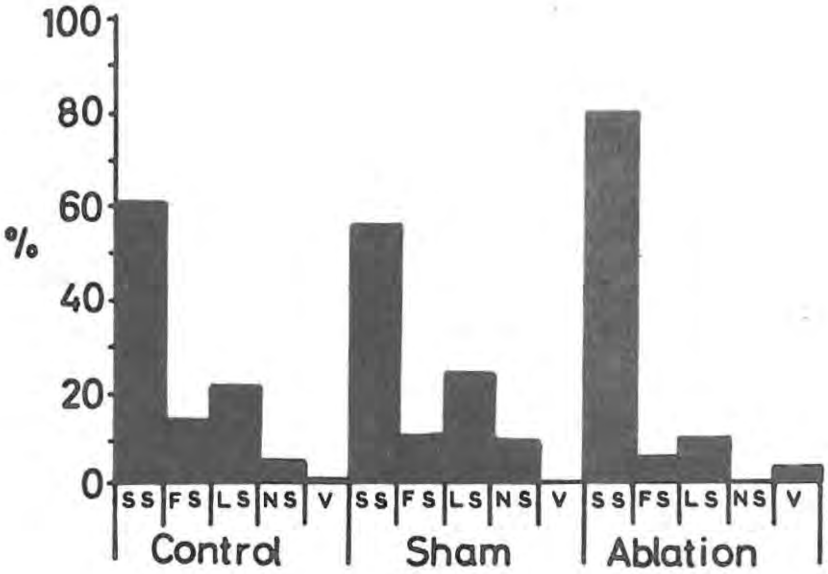

FIGURE 9b
The time *H. philander* spent in each component of courtship expressed as a percentage of the total time spent in courtship.
SS = side-shake; FS = follow-shake; LS = lead-swim; NS = nest-shake; V = vertical-nest-shake.

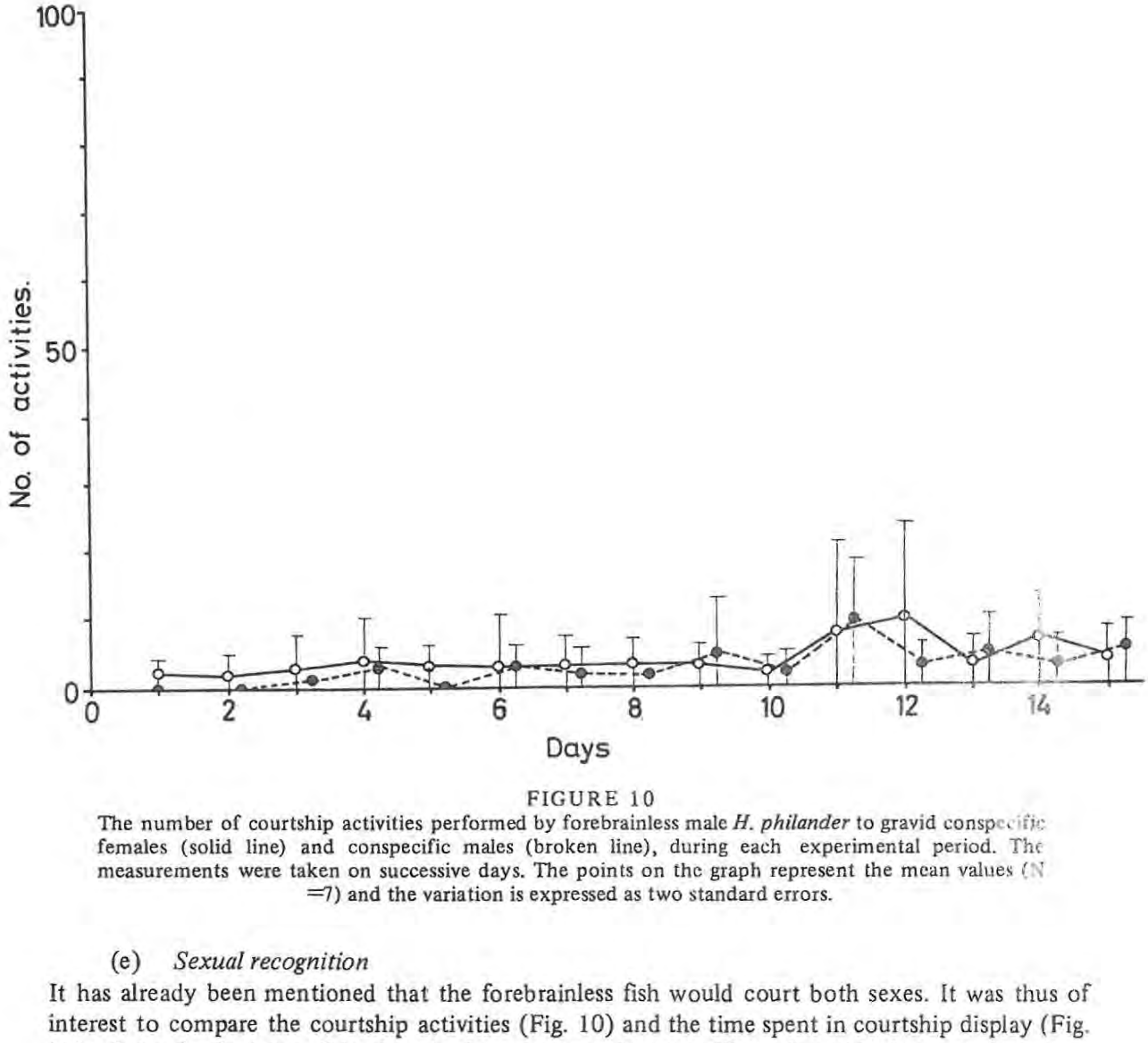

FIGURE 10
The number of courtship activities performed by forebrainless male *H. philander* to gravid conspecific females (solid line) and conspecific males (broken line), during each experimental period. The measurements were taken on successive days. The points on the graph represent the mean values (N =7) and the variation is expressed as two standard errors.

(e) *Sexual recognition*

It has already been mentioned that the forebrainless fish would court both sexes. It was thus of interest to compare the courtship activities (Fig. 10) and the time spent in courtship display (Fig. 11) of the forebrainless fish when in the presence of conspecific males with those performances when in the presence of conspecific females. These results show a striking similarity which demonstrates that the forebrainless fish were unable to distinguish between males and females, using the visual information provided under the conditions of this experiment.

The behaviour of the forebrainless fish under less restrictive conditions was investigated. On twenty-eight different occasions during the course of the experiment, a free-swimming conspecific male was released into the aquaria of the forebrainless fish. A normal male would not tolerate the

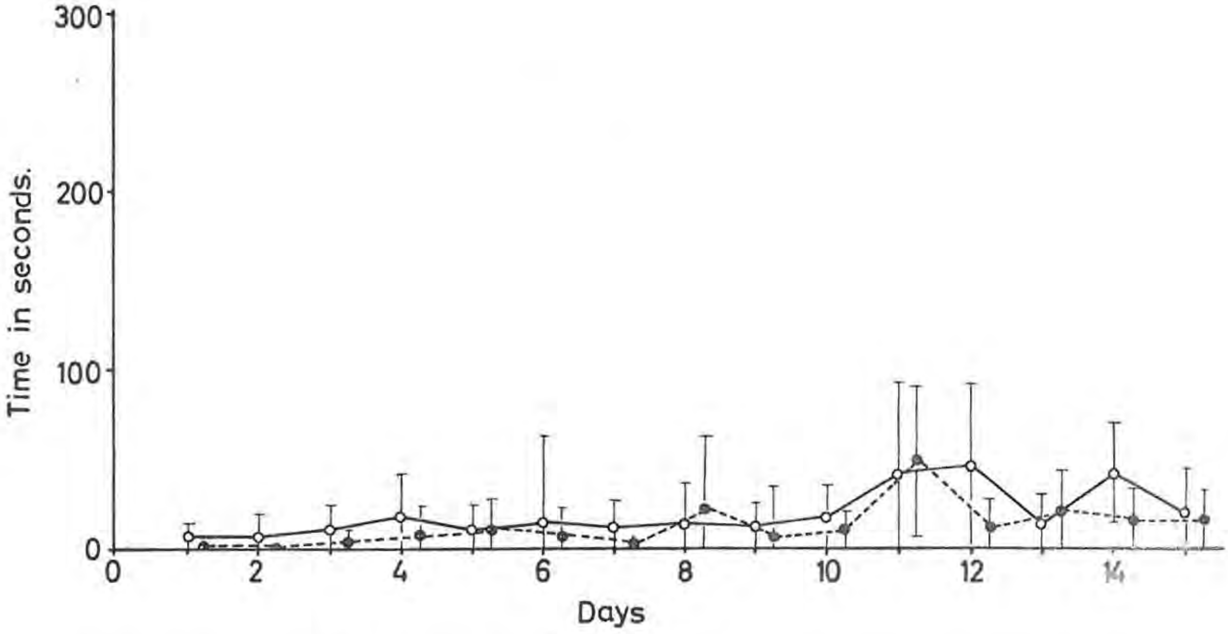

FIGURE 11
The time forebrainless *H. philander* males spent in the courtship of conspecific males (broken line) and conspecific females (solid line), during each experimental period. The points on the graph represent the mean values (N=7) and the variation is expressed as two standard errors.

presence of the intruder (Ribbink 1971) but the forebrainless males were found to court the intruding males.

The general pattern of behaviour, under these conditions, was as follows. The free-swimming normal male would begin to explore the aquarium. The forebrainless male would remain in inactivity from twenty to three hundred and sixty seconds, after which delay it might swim towards the intruding male. More frequently however, the exploring normal male would find the forebrainless fish. The approach of the normal male would elicit courtship in the forebrainless fish, to which the intruder would respond in an aggressive manner with bites and tail-beats. The forebrainless males usually continued with their unsuccessful sexual overtures for some time after the assault from the normal male had begun. Thereafter, a brief show of lateral display and possibly one or two tail-beats would appear, and then on every occasion the forebrainless fish was easily and rapidly defeated.

These results indicate that aggressive behaviour was inhibited by the forebrain ablation, and could only be elicited by repeated tactile assaults. Further, it would appear that males from which the telencephalon had been removed could not distinguish between the sexes on a visual basis, and it is doubtful if they can do so on a tactile basis, since the response to the tactile assault may be considered to be one of self defence and not sexual recognition.

TABLE 3

THE TOTAL NUMBER OF NESTS CONSTRUCTED BY EACH GROUP (N = 7) OF FISH DURING THE COURSE OF THE EXPERIMENT

Day	*Control*	*Sham*	*Forebrainless*
1	0	0	0
2	0	0	0
3	3	5	0
4	6	7	0
5	8	7	0
6	8	9	0
7	13	11	0
8	14	12	0
9	16	15	0
10	16	18	0
11	17	18	0
12	19	18	0
13	22	18	0
14	25	18	0
15	25	18	0

Additional results

Forebrainless fish failed to explore their environment and new objects, and failed also to dominate aquaria even when they were substantially larger than the other fishes. Furthermore, forebrainless males would allow themselves to be dominated by females.

Feeding behaviour was normal in execution, but the stimulus-response lag was considerably greater than that of normal and sham operated males. Nest building behaviour was entirely absent (Table 3).

On many occasions the response to a stimulus was abnormally powerful, which sometimes resulted in accidents. For example, the normal escape response elicited by a movement of a hand over the water surface is for the fish to dive down to settle on the substrate. It was not unusual for a forebrainless fish to dive into the sand substrate and become buried. Similarly the forebrainless fish often swam forcibly into or past the flask which contained the object fish. This did not occur in the control groups.

DISCUSSION

(i) Decreased activity

The most apparent alteration to the behaviour of *H. philander* resulting from the extirpation of the forebrain, was that these fish became less active than those in the control groups. The forebrainless fish spent most of their time motionless just above the substrate, usually in a corner or near a plant. They only occasionally showed any spontaneous activity, and exploratory behaviour appeared to be completely absent. By contrast, the fish in the control groups initially explored their aquaria, and later they readily investigated new objects placed within the aquaria. They were perpetually employed in some form of activity; when presented with object fish the behaviour of the fish in the control groups was directed at these. At other times the males occupied themselves by establishing or maintaining their dominance, by digging or enlarging their nests and by chasing and foraging.

Telencephalic ablations in other fish have also been reported to result in severe decrements or loss of spontaneous and exploratory behaviour (Janzen 1933; Hosch 1936; Hale 1956a). It seems probable that the decreased activity of forebrainless fish is due to a decrease of spontaneous behaviour. A further contributing factor would be the increased stimulus-response latency found during measurements of feeding, courtship and aggressive behaviour of *H. philander.* This effect is not confined to *H. philander,* but has also been found by Aronson (1967), Aronson and Herberman (1960), Aronson and Kaplan (1963; 1965; 1968) and Hale (1956a) in other fish. Thus, in *H. philander,* and presumably in other teleosts, the decreased activity which results from telencephalic ablations can be partly explained by the apparent decrease or loss of spontaneous and exploratory behaviour, and by the increased stimulus-response lag period.

The observed decrements of all forms of territorial behaviour may be due to direct inhibition of such behaviours, or they may represent 'artifacts' of an increased stimulus-response latency.

(ii) *Aggressive behaviour*

With few exceptions it appears as though removal of the entire forebrain from teleosts results in a marked depletion of aggressive behaviour, accompanied by a loss of social status and other dependent territorial behaviours. Segaar (1961) also found that certain forebrain lesions in *Gasterosteus aculeatus* males resulted in a decrease of aggression so that they were unable to protect their territories. Similar reductions of aggressive, territorial and social behaviour were also found by Aronson (1948) using *Tilapia macrocephala,* and Hale (1956b) working on *Lepomis cyanellus.* Noble and Borne (1941), however, found no apparent reduction in vigour in the fighting of *Betta splendens, Hemichromis bimaculatus* and *Xiphophorus helleri* after partial or complete forebrain destruction. An assessment of their work is difficult, since it appeared only as a brief abstract.

It is not clear whether the loss or decrease of nest-building behaviour in *H. philander, G. aculeatus* and *T. macrocephala* can be linked with the apparent inhibition of aggression, or whether this represents a separate inhibitory phenomenon. Certainly the loss of social status and the inability to form and hold a territory can be partly ascribed to the decrease of aggressive behaviour after forebrain ablation.

One aspect of territorial behaviour which could be evoked by visual stimuli in forebrainless *H. philander* was that of chasing. The forebrainless fish chased on relatively few occasions (Table 1), and the chases differed from those of the normal fish insofar as they were incomplete. The forebrainless fish appeared to be unable to pursue a fleeing intruder which changed direction during the course of its flight. As a result of this the duration of the individual swimming pursuits was shorter in the forebrainless fish than in the control groups. A similar observation was recorded by Noble (1936) using other cichlids from which the forebrain had been removed. These fish were "unable to follow the school through rapid turnings". It seems likely that the lag period between stimulus and response was too great for the deprived fish to maintain the stimulus-response communication.

(iii) *Courtship Behaviour*

As early as 1936/37 Noble reported that lesions in the corpus striatum (=forebrain) resulted in permanent defects in the sexual behaviour of some cichlid fish. Later, Noble and Borne (1941) found that forebrain extirpation from *H. bimaculatus* and *B. splendens* resulted in the complete loss of sexual activity in these fish, whereas in *X. helleri* all elements of sexual activity persisted after forebrain lesions. They claim that in *H. bimaculatus* and *B. splendens* both partners play an active role in courtship, while in *X. helleri* the female is the passive partner. They therefore concluded that the forebrain of *H. bimaculatus* and *B. splendens* regulates sexual activity by co-ordinating and synchronizing the behaviour patterns of the partners, whereas it is implied that in *X. helleri* the forebrain plays little or no part in the mediation of sexual behaviour.

In a more detailed study by Aronson (1948) it was found that the early courtship patterns of *T. macrocephala* were not reduced by "total decerebration" (forebrain ablation), whilst the later patterns, which were more directly associated with spawning, suffered a reduction in frequency of occurrence. Work on *Xiphophorus maculatus* (Kamrin and Aronson, 1954) showed that all sexual acts, except gonopodial swinging, decreased in frequency as a result of forebrain lesions. Segaar (1961) and also Segaar and Nieuwenhuys (1963) using *G. aculeatus*, demonstrated that sexual, aggressive and parental behaviour are in some form of balance in normal males. A series of different telencephalic ablations altered the normal balance of these drives in different ways, depending on the size and position of the ablation. They concluded that the function of the telencephalon of the stickleback is to regulate the timing and strength of expression of the components of aggressive, sexual and parental behaviour.

In *H. philander* the forebrain extirpations reduced the amount of invitation (early) courtship behaviour, and also changed the percentage occurrence of side-shake and other courtship behavioural components in a disproportionate manner. Furthermore, the ablations resulted in the inability of these fish to distinguish between male and female conspecifics on a visual basis.

(iv) *The execution of motor-patterns*

Both agonistic and courtship behaviour were drastically reduced by the ablations. However by means of visual stimuli courtship behaviour could be evoked, and a combination of visual and tactile stimuli could provoke intraterritorial aggressive behaviour. In both cases it appeared as though the behavioural motor-patterns were normal in execution. Because the execution of these patterns appears to be normal in fish without the forebrain it is likely that the organization of the execution of these motor-patterns takes place in brain centres posterior to the telencephalon. Since the motor-patterns appear to be organised elsewhere in the brain, the role of the forebrain in the mediation of these non-olfactory behaviours requires an explanation.

(v) *Interpretation of forebrain function*

There are at present two opposing schools of thought concerned with the non-olfactory functions of the telencephalon of bony fish. On the one hand, it is considered (Noble 1936; 1937; Noble & Borne 1941; Segaar 1961; Segaar & Nieuwenhuys 1963) that the integration of agonistic (territorial), sexual and parental behaviour takes place in the forebrain. Those holding this opinion do not necessarily attribute the control of the behavioural motor-patterns to the telencephalon, but they suggest that the forebrain provides the necessary integration (co-ordination, synchronisation and adjustments to drives) of incoming information, thereby producing the correct responses in normal fish. It therefore seems, that although the control of the execution of the motor-patterns is seated in lower brain centres, it is the forebrain which is partially responsible for the translation of sensory input into the behavioural output.

The second school are of the opinion that integration of non-olfactory behaviour does not take place in the telencephalon, and suggest that the forebrain acts as an "activator", "facilitator" or "arouser" of these behaviour patterns. These ideas originated from the work of Janzen (1933) who observed that goldfish without their forebrains showed a decreased response to external stimuli, and very little endogenous activity such as exploration. He therefore suggested that the telencephalon is responsible for "initiative" and "spontaneity". Support for these suggestions comes from Herrick (1933) who suggested that one of the functions of the cerebral hemispheres of all vertebrates, including fish, is to serve as a "non-specific activator". Experimental work on *T. macrocephala* led Aronson (1948) to conclude that the telencephalon – "does not integrate any behaviour patterns, but rather facilitates the functioning of other parts of the brain which more precisely control these activities". Aronson's contentions were reinforced by Hale (1956b) who suggested that the behaviour patterns of the sunfish, *Lepomis cyanellus,* are organised in lower brain levels and that the telencephalon acts by facilitating these patterns. More recently Aronson and Kaplan (Aronson 1967; Aronson & Kaplan 1968; Kaplan & Aronson 1963) furthered their hypothesis by means of avoidance conditioning experiments, in which it was demonstrated that the stimulus-response latency of *T. macrocephala* was markedly increased by forebrain extirpations. Although Hale (1956a) found that all previously established associations were lost as a result of forebrain extirpations, Aronson and Kaplan (1968) found that previously conditioned responses were not obliterated by the operations, and therefore concluded that forebrain ablations cause a decline or change of behaviour patterns, but not the elimination of these patterns. Aronson and Kaplan (1968) suggested that the forebrain does not organise behaviour but exerts a strong influence over almost every behaviour pattern studied. They suggested that the forebrain functions are (1), non-specific and (2) facilitative i.e. the forebrain functions as a "non-specific arousal system". They drew support for their hypothesis from the electro-encephalographic (EEG) recordings of Enger (1957), and Schadé and Wieler (1959), in which the EEG activation was associated with reduced reaction time (=arousal). Furthermore, an anatomical examination of the brain of *T. macrocephala* revealed major fibre tracts running from the telencephalon to the di- and mesencephalon, which suggested to Aronson and Kaplan (1967) that the forebrain might exert a "dynamic influence on the midbrain". Probably it is the midbrain which organises the behavioural motor-patterns.

On the basis of this hypothesis Aronson (1967) prefers to interpret his own work, and the decrements and alterations to behaviour reported by other workers, as a failure of the "arousal system" rather than the removal of excitatory or inhibitory systems as interpreted by Segaar, Nieuwenhuys, Noble and others.

The effects of forebrain ablations on the behaviour of *H. philander* cannot be satisfactorily explained by the interpretations of one school of thought to the exclusion of the other, but requires both interpretations to account for the behavioural modifications found. This suggests that an interpretation of the function of the forebrain of teleosts should incorporate both of these views.

The conversion of the endogenous and exogenous sensory input into a behavioural output must be considered as a process involving neural integration, and the resultant behavioural response would represent the final balance of the incoming information. The elucidation of the role of the telencephalon in the mediation of non-olfactory behavioural responses cannot be fully explained in terms of adjustments to the balance of the excitatory and inhibitory nuclei. In fact, were it not for the experimental evidence to the contrary, the involvement of the telencephalon in these behaviours would seem unnecessary, because with the possible exception of nest-building behaviour, it has been shown that the non-olfactory behaviour patterns are organized in lower brain levels.

The non-specific arousal hypothesis could explain (incorporating neural integration) the involvement of the telencephalon in visually oriented behaviour. It could also account for the increased stimulus-response latencies, the loss of spontaneous behaviour (exploratory), and partially account for the decreased frequency of occurrence of aggressive/territorial, courtship and swimming behaviour which resulted from telencephalic extirpations. This hypothesis, however, is too general to yield much information about the precise mechanisms involved. Furthermore; (1) the inability of forebrainless *H. philander* to distinguish between males and females; (2) the disproportionate relative decrements to the frequency of the occurrence of the components of courtship behaviour and (3) the abnormal escape response cannot be explained in terms of a failure of an arousal mechanism, but rather as a disruption of the balance between excitatory and inhibitory nuclei.

Although Enger (1957), Schadé and Wieler (1959), and Gusel'nikov *et al.* (1964) have shown that electrical patterns associated with 'arousal' occur infrequently in the telencephalon of fish, Timkina (1965) and Zagorul'ko (1965) have shown that some electrical transfers do take place between the telencephalon and mesencephalon. It therefore seems possible that the arousal system is present in certain teleosts, but it is poorly developed.

Arousal is one of the functions of the limbic system of higher vertebrates, and several authors (Aronson & Kaplan 1968; Gusel'nikov *et al.* 1964; and Segaar & Nieuwenhuys 1963) have drawn attention to the similarity of function of the limbic system of mammals and the teleost forebrain. Other important functions of the limbic system, and particularly the hippocampus, are those associated with the focussing of attention, motivationally oriented behaviour (drives) and the selection of the appropriate behavioural response to a situation (total stimulus input).

Anatomical evidence (Ariens Kappers, 1921; Nieuwenhuys, 1959) indicates that much of the limbic system of mammals is represented by precursors in the teleost telencephalon. In addition Ariens Kappers (1921) and Gusel'nikov *et al.* (1964) (by implication) are of the opinion that the epistriatum of teleosts is an analogue of the primordium hippocampi of amphibians and other vertebrates.

The presence of a limbic system, albeit primitive, in the teleost forebrain could account for most behavioural modifications resulting from telencephalic ablations. Those behaviour patterns which cannot be explained in terms of the arousal system, could be accounted for by other limbic systems. For example, the ability to distinguish between male and female conspecifics would depend upon an evaluation of the incoming information, and upon the selection and initiation of an appropriate behavioural response. If the teleost epistriatum is the analogue of the hippocampus of higher vertebrates, then the fish forebrain would be expected to house the neural apparatus for the assessment of sensory input and for the selection of appropriate behavioural output. The inability of forebrainless *H. philander* to distinguish between the sexes could then be explained in terms of an alteration or removal of such a selection mechanism.

The arousal hypothesis has been used to explain the increased stimulus response latency. An alternative suggestion is that the removal of the usual mechanism for response selection makes it necessary to use compensatory selection routes where possible. These compensatory mechanisms would take more time to select the appropriate, or in *H. philander* some inappropriate, behavioural responses. Aronson and Kaplan (1964) have evidence for the presence of long term compensatory mechanism in the cerebellum.

Since the regulation of motivationally directed behaviour is partly attributed to the limbic system in mammals (Guyton 1966), it may also be possible to account for the alterations to the balance of drives, described by Segaar (1961) and Segaar and Nieuwenhuys (1963), in terms of an interference with the limbic system. Should limbic structures be present in fish then it is probable that they would influence each other, and thus the final behavioural response would represent an integration of numerous centres.

It is suggested that the forebrain of *H. philander* functions not only to provide a general excitation (arousal) of non-olfactory behaviour patterns, but also functions in a more specific manner by which it selects the behavioural response(s) appropriate to a given situation. This not only indicates that a limbic system may be present, but also suggests that a partial organisation of non-olfactory behaviour occurs in the forebrain.

Finally, Gusel'nikov *et al.* (1964) found good EEG responses in the forebrain of amphibia and reptiles to photic and acoustic/lateral line stimuli, but very poor responses in the forebrain of the goldfish. They therefore concluded that the conduction of all forms of sensation to the telencephalon begins in the amphibia, and that this has been the basis of telencephalic development in the vertebrates. In view of the involvement of the teleost forebrain in behavioural responses to visual and tactile stimuli, it would appear that sensations, even if modified by the tectum, are transferred to the telencephalon. Thus it seems possible that the progressive development of the vertebrate forebrain began in early fishes.

ACKNOWLEDGEMENT

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APPENDIX 3

THE NATURAL SEPARATION OF THE BREEDING ARENAS OF THREE SPECIES OF CICHLID WHICH BREED CONCURRENTLY

(A PAPER READ TO THE SYMPOSIUM ON HERPETOLOGY AND
ICHTHYOLOGY, ZOOLOGICAL SOCIETY OF SOUTHERN AFRICA,
4th SEPTEMBER 1975)

INTRODUCTION

During the course of behavioural studies of Pseudocrenilabrus philander in its natural environment, it became apparent that the breeding[1] arenas of this species were separated from those of Tilapia sparrmanii and Sarotherodon mossambicus. Though all three species bred at essentially the same time of the year (summer months) an equitable division of the natural resources was achieved by the territorial fish. In this paper I shall describe how the territories of these fish are distributed and provide an explanation for the horizontal and vertical separation of the three species.

P. philander was studied in three water bodies. In Kuruman Eye and Wondergat (described below) it shared the environment with T. sparrmanii; S. mossambicus being absent. In Lake Sibaya all three species were present.

The Distribution in Kuruman Eye

Kuruman Eye, situated on the edge of the Kalahari, is a small, shallow spring or fountain which flows into what Jubb (1971) descriptively calls a miniature lake (see plate 23, main text of thesis). It is roughly rectangular in shape, approximately 122m long and 22m wide (fig 15 main text). Water entering the "Eye" is clear and suitable for behavioural observation, its temperature is 21.9°C in summer and winter. Water flow is such (± 22 million litres per day, Jubb 1971) that ambient temperatures affect water temperature very little.

Kuruman Eye is so shallow (1.65m maximum depth) that a vertical separation of the species due to depth is impossible. A horizontal distribution of the territories of the two species occurred. To determine the distribution of P. philander territories nests were marked by floats (fig 4, main text) and the distances between each nest measured. Distribution was then plotted (fig 16, main text).

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[1] Breeding arenas were described and equated with colonies of nesting birds.

T. sparrmanii construct substantially larger nests, and the distances between these were measured directly (fig 16, main text).

It was apparent that *T. sparrmanii* occupied the more sheltered regions amongst the macrophytes and under the excavated embankment, while *P. philander* were confined to the relatively exposed regions on the periphery of the weedbeds. *T. sparrmanii* appeared to competitively exclude *P. philander* from the covered regions. Eivdence suggestive of competitive exclusion comes from winter observations. *T. sparrmanii* do not breed in winter in Kuruman Eye, whereas *P. philander* bred all the year. Therefore, in winter, *P. philander* were found in many of the regions which had been occupied by territorial *T. sparrmanii* in summer. Behavioural evidence also supports this suggestion: a newly formed pair of *T. sparrmanii* moved beneath a rocky overhang occupied by a tagged territorial *P. philander*. Active aggression between the two species was not overt, but the encroachment was such that the territorial *P. philander* moved off to establish itself at a site two metres away.

In Kuruman Eye, horizontal distribution occurs in which territorial *T. sparrmanii* occupied regions of cover and *P. philander* nest sites were more exposed.

Distribution in Wondergat

Wondergat, near Mafeking, is a sinkhole of 60m depth with sheer, rocky walls (plate 26, main text). The initial interest in Wondergat was to investigate the behavioural adaptations which enabled *P. philander* to breed in a region which lacked a sand substratum. It is usual for this species to form territories on sandy-substrata, in shallow water. The answer to this initial problem was what one might have anticipated: namely, the males form their nests on rocky ledges and outcrops.

It was also found that territorial *P. philander* occurred to 26m depth, whereas *T. sparrmanii* pairs were not found below 14m depth. It appeared that *P. philander* utilized greater depths.

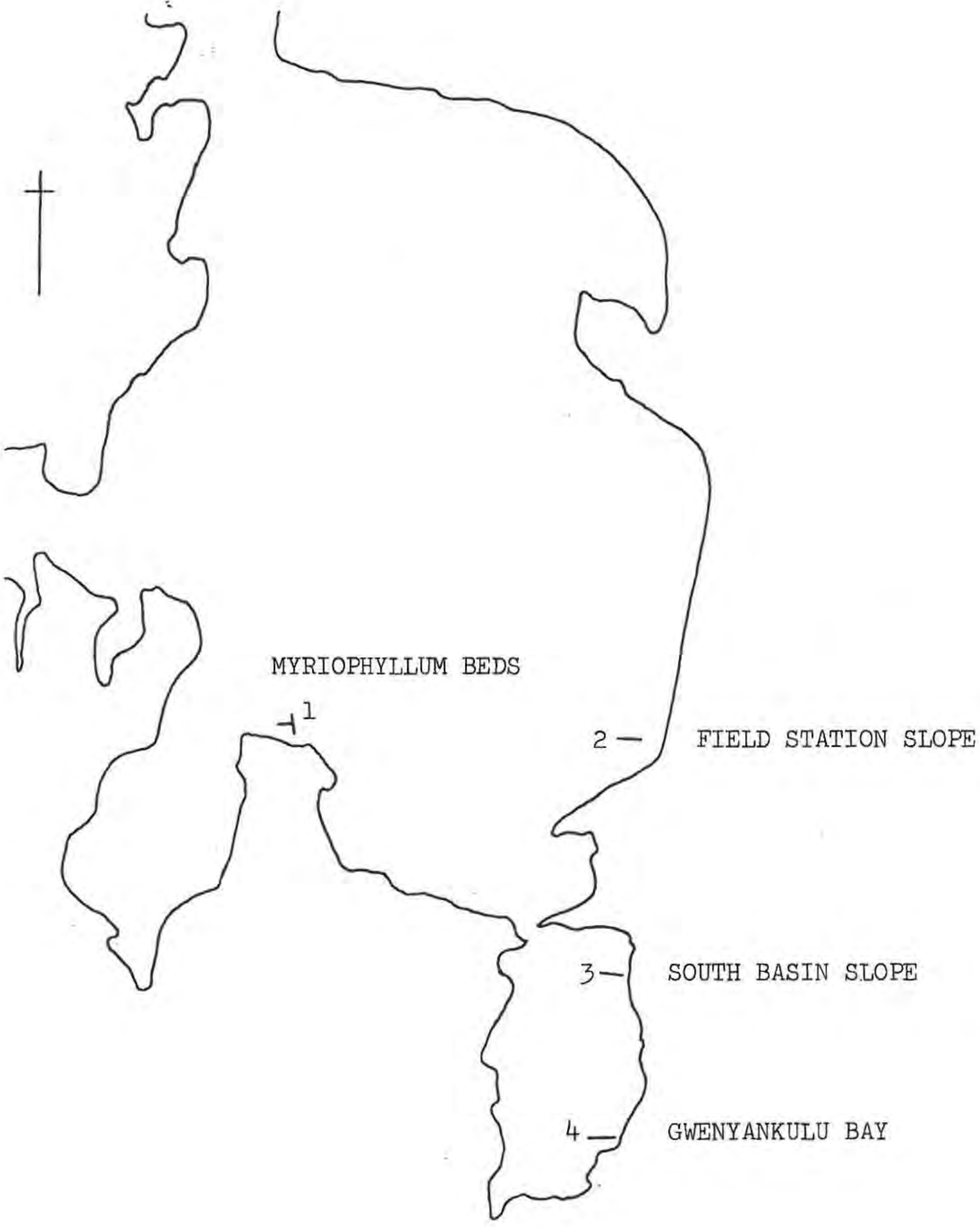

Figure 1 Four diving stations in Lake Sibaya.

Lake Sibaya

Lake Sibaya of northern Zululand is a land locked freshwater coastal lake of 65 sq.km. in area, and has a mean depth of 13m (Hill 1969). Several different habitats are to be found in the lake. These have been described by Boltt, Hill and Forbes (1969) and also Allanson, Bruton and Hart (1974).

The distribution and behaviour of cichlids in the lake was investigated by swimming compass course transects at several diving stations over different habitats (Appendix figure 1).

Three different compass course transects were swum from the boat's anchor in the Myriophyllum spicatum beds (station 1), at five metres depth, over a gently sloping sand substratum. The distribution of the macrophytes and nests of the three species of cichlid was measured using an underwater plastic tape, recorded on writing slates and subsequently plotted to provide appendix figure 2. The horizontal distribution shows T. sparrmanii within the macrophyte clumps, the single S. mossambicus nest was also associated with the Myriophyllum and P. philander were in the open with little or no plant cover.

At station 2 (Appendix figure 3), T. sparrmanii were found in the relative shallows with their nests associated with plant cover. P. philander were found from 12m to 22m depth in the open, though frequently nests were constructed beneath submerged twigs (see fig 17, in main text). Though S. mossambicus nests were not found in this transect, at a similar site one hundred metres to the north, nests of this species were common on the upper slope and edge of the terrace.

In the south basin, several transects at each of two diving stations (3 and 4) produced data to give a composite picture (Appendix figure 4). The depths and vegetation density correspond most closely to those of station four (Gwenyankulu Bay). Station 3 was very similar to station two, except that S. mossambicus were numerous on the upper slope and edge of the terrace (see Bruton 1973).

Figure 4 illustrates that S. mossambicus was found in the shallows, their nests were constructed amongst the Scirpus littoralis and Potamogeton pectinatus on the edge of the terrace and upper slope,

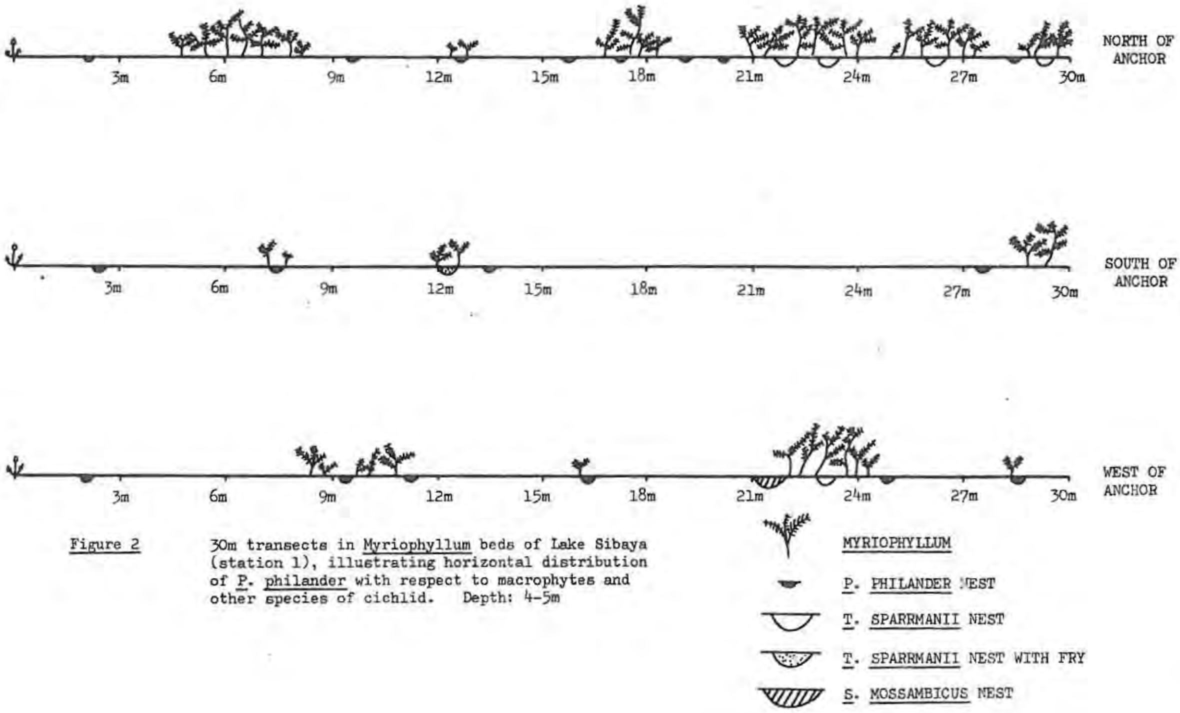

Figure 2 30m transects in *Myriophyllum* beds of Lake Sibaya (station 1), illustrating horizontal distribution of *P. philander* with respect to macrophytes and other species of cichlid. Depth: 4-5m

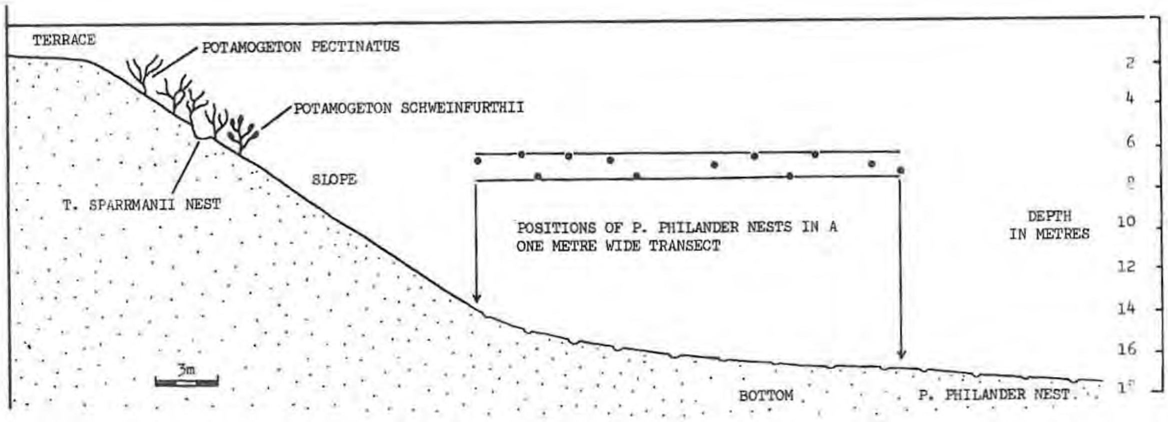

Figure 3 The bottom of Lake Sibaya in front of Rhodes University field station.

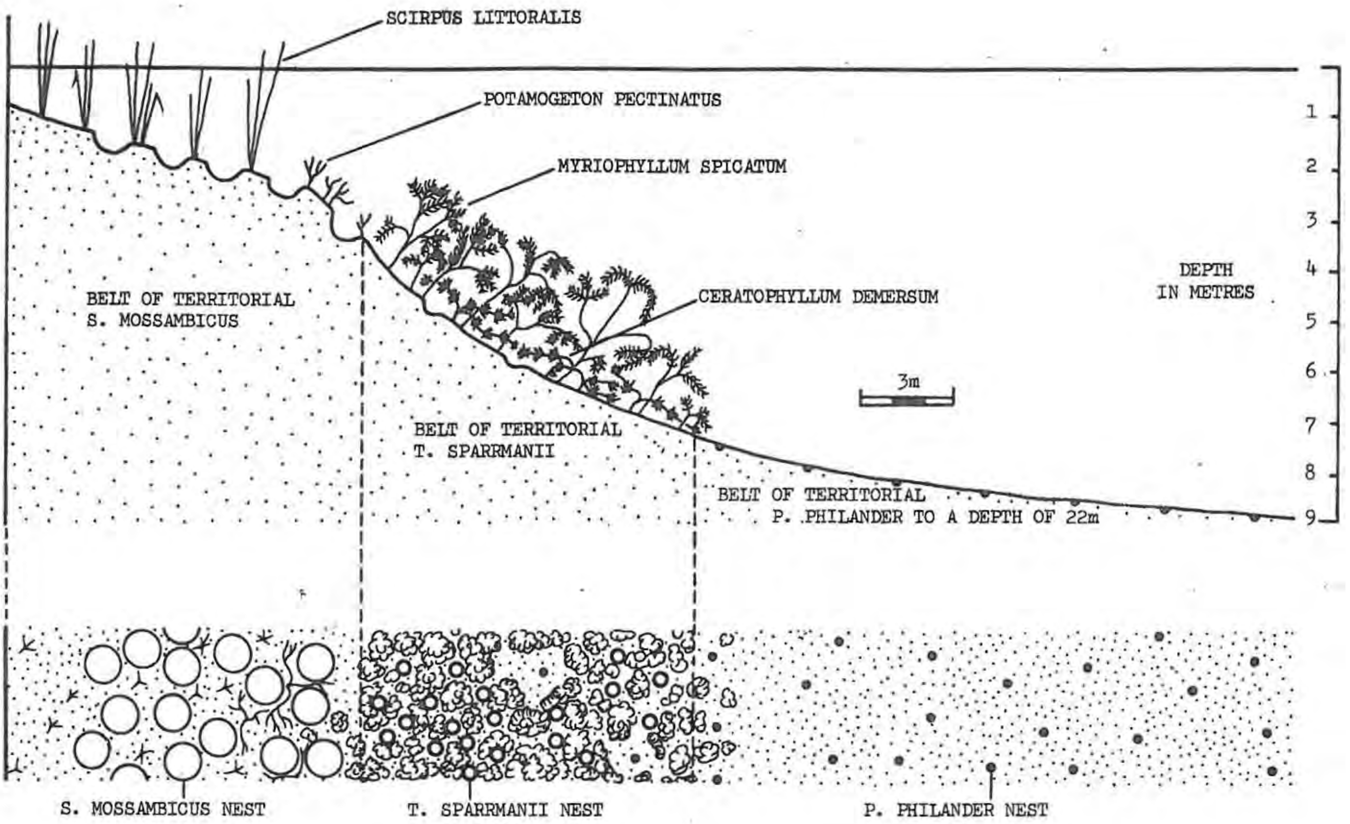

Figure 4 Horizontal and vertical distribution of territories of *S. mossambicus*, *T. sparrmanii* and *P. philander*, with respect to each other and to macrophytes. Represented as a vertical section through the lake (upper diagram), and a plan view to show the horizontal distribution (lower diagram).

in water of one to four metres depth (occasionally their nests were in water of 8m depth, Bruton 1973). *T. sparrmanii* nests were in the dense cover of the *Myriophyllum spicatum* and *Ceratophyllum demersum* from three metres to seven metres depth. *P. philander* territories occupied the relatively exposed bottom of the lake below seven metres depth.

A possible explanation of the distribution of the three species

Depth Considerations

Bruton (1973) found, by means of echosounding, that *S. mossambicus* did not penetrate into the deeper water of Lake Sibaya. As a result of this finding Caulton (1973) placed species of cichlid in a pressure chamber to simulate depth and found that adult pressure compensation was limited to :

11.5 m	at 22°C	*S. mossambicus*
15.0 m	at 22°C	*T. sparrmanii*
16.0 m	at 22°C	*P. philander*

Though I found ***P. philander* territories below these depths, Caulton's work does demonstrate that the ability to penetrate depth can limit the vertical distribution of the three species.

Feeding

P. philander remain in their territories all day and feeding is therefore confined to their defended areas. M.N. Bruton's observations of *S. mossambicus* in Lake Sibaya suggest that these fish also remain in their territories to feed (Bruton, pers.comm.) *T. sparrmanii* are not restricted to the nest for feeding, but wander around in the close vicinity, browsing from plants (epiphytic growths in Kuruman Eye and Lake Sibaya), and growths on the rock surfaces (*aufwuchs*) of Wondergat.

S. Bowen (unpublished data) has found that *S. mossambicus* feed upon epilithic diatoms and algae, and that these food sources are richest in the shallows of the terrace and upper slope, i.e. where *S. mossambicus* hold their territories.

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* Caulton (1973) worked on *P. philander* from Happy Valley, Durban which is very shallow, (less than one metre). In Sibaya and Wondergat I found *P. philander* territories at depths greater than 16m.

T. sparrmanii are essentially epiphytic browsers. Macrophytes provide a large surface area from which they can nip the microflora and fauna. They feed mostly in the evenings moving up and down the plants, turning on their sides and nipping off the growths. In Wondergat there are no macrophytes and the feeding is on *aufwuchs*.

Food sources of both *T. sparrmanii* and *S. mossambicus* are dependent upon photosynthesis, consequently there is little need, from a nutritional point of view, for these species to penetrate to depths beyond which photosynthesis can occur.

P. philander are predators which forage in the substratum for benthic fauna. In his study of the benthos of Lake Sibaya, the late Dr R.E. Boltt found that the greatest abundance of benthic crustacea and polychaeta, on which *P. philander* feeds, were to be found in the gently sloping sandy substratum from the base of the slopes, and in the *Myriophyllum* beds (Boltt 1969). Namely, the regions where *P. philander* hold their territories.

Thus, the territories of all three species are found where their particular food resources are richest.

Breeding Requirements

Though *T. sparrmanii* can go down to depths of 15m they did not nest beyond the limits of the macrophytes, which Boltt, Hill and Forbes (1969) found to be at about seven metres in Lake Sibaya. Furthermore, the tendency of *T. sparrmanii* to be more cryptic in its behaviour than the other two species was noted, and it seemed that different requirements for breeding might serve to separate the species and reduce interspecific competition.

T. sparrmanii form pairs and once paired remain together in a long lasting association typical of substrate spawners. The partners were found to hide (preferentially) in dense vegetation, between rocks or under embankments where they made and defended their nests. The breeding dress of the pair is always one of disruptive coloration which is consistent with their cryptic tendencies.

P. philander and *S. mossambicus* are maternal mouthbreeders. Territorial males have to attract gravid females and pairs are formed only for the short duration of courtship and spawning, after which the female leaves with the eggs in her mouth. Males may spawn with several females in a day. To entice females, territorial fish need to be conspicuous. Consequently the males have vivid breeding colours and their territories are more open than those of T. sparrmanii.

The principal difference is that the association between the members of a pair of [1] substrate spawners is such that they can advantageously hide away in dense cover, whereas the mouthbrooders need to advertise and successfully lead passing gravid females to their nests. Dense vegetation would complicate matters for mouthbrooders, but some cover in which to hide, if necessary, and to provide privacy during spawning may be used to advantage.

Though the three species do not compete overtly for food or feeding grounds, some competition does occur for space and protective cover. It has been mentioned already, that T. sparrmanii in Kuruman Eye exclude P. philander from the covered regions. This was also found, though less markedly, in Lake Sibaya. It is suggested that an increase of intraspecific competition, within one species, would have ripple effects within and between other species. For example, an increase in the number of breeding T. sparrmanii in Kuruman Eye would exclude a greater number of P. philander from breeding sites. This would result in increased competition within each species and between the two species for space. Where a greater number of species are involved the ripple effects would probably be widespread.

In conclusion, these preliminary observations indicate the separation of the breeding arenas of the three species of cichlid (S. mossambicus, T. sparrmanii and P. philander) is effected by the distribution of their preferred food sources, ability to penetrate depth, behavioural adaptations and interspecific competition.

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1. Not all substrate spawners are cryptically coloured, indeed Hemichromis bimaculatus is amongst the most brightly and conspicuously coloured of cichlids. T. sparrmanii, however, are cryptic in behaviour and colouration.

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APPENDIX FOUR

A MODIFICATION OF THE LORENZIAN HYDRAULIC MODEL TO EXPLAIN TERRITORIAL BEHAVIOUR OF P. PHILANDER

Finally, I would like to develop arguments which point to a self reinforcement of behavioural drives. This appears at first to be a contradiction of Lorenz's theories on loss of drive as a result of consummatory acts. My ideas developed as a result of the experiments which demonstrated that attendant fish are required for the maintenance of the territorial drive (chapter four above), and from field and laboratory observations which indicated that territorial drives increased with increasing intraterritorial activity.

Certain fish do maintain a high level of aggression when isolated (Gallagher *et.al*. 1972). Apparently, in the damsel fish, *Microspathodon crysurus*, aggression increases gradually over a period of days when their tendency to fight has been frustrated by isolation (Rasa 1971).

By contrast, aggression of *P. philander* decreased on isolation. A response decrement also occurs in other species of fish: Welty (1934), Greenberg (1947) and Hale (1956) reported that isolated fish had a lower level of behavioural performance than those fish which had company. Isolated fish became relatively inactive, were more darkly pigmented and tended to remain in contact with the wall or floor of the aquarium. Hale (1956) suggested that much of the 'group advantage' could be attributed to a decreased disturbance by outside stimuli and a mutual reassurance. In addition to these effects, which probably also apply to *P. philander*, observations of the behaviour of this species indicated that attendant fish stimulated and reinforced the territorial drive (see chapter four above).

The physical environment may stimulate or inhibit drives governing groups of behaviour common to those drives. For example, by decreasing water temperature to 17°C, sexual and territorial activities of P. philander were inhibited; by raising the temperature to above 20°C these activities were stimulated. Equally, components of the biotic environment are important. For example, Aronson (1949) found that female Tilapia macrocephala failed to prepare nests when alone. If they were able to see a male, even through glass in the next tank, their ovaries developed and nests were dug. In the last instance physical conditions remained the same, but the drive would not develop in the absence of a conspecific male. Similarly, P. philander males under constant physical conditions require the reinforcement given by other fish to maintain territorialism.

In the field, territorial males are continually visited by conspecifics. Therefore, by providing company for a male in an aquarium one stimulates more accurately the natural condition. Arrival of visitors would elicit either courtship or aggression. During periods when visits were infrequent, as occurred in peripheral territories of Kuruman Eye, then nest-building and/or appetitive aggression and sexual behaviour resulted. It seemed that the energy* associated with the territorial drive was maintained by the expression of one or more of the component territorial behaviour patterns, each of which acted as a positive feedback to reinforce the principal drive. In the absence of adequate stimuli from visitors, appetitive behaviour and nest-building arising from endogenous energy would probably be insufficient to support the drive. The benefit of a system such as this is that a territory established at a locus which was not visited by conspecifics, especially females, nor surrounded by neighbours, would not be maintained. Indeed, it would be maladaptive to do so under such unrewarding conditions. In essence, territorialism needs to be practised to be maintained, and to these ends visitors and neighbourly confrontations are necessary stimuli for the reinforcement of the drive.

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* The term 'energy' is used in the behavioural sense as envisaged by Lorenz (1937, 1950), Tinbergen (1951), Thorpe (1964) and others. It is not intended that this behavioural energy should be considered as a form of physical energy. The ambiguity of the use of a physical term for imprecise behavioural descriptions is clear, but the value of the term in the bheavioural sense has been most instructive. Hinde (1960, 1970) gives greater consideration to this terminology.

Thorpe (1964) takes the attitude that most behaviour is directive in that variable means are used to a constant end. Applied to territorial P. philander it appears that all intraterritorial behaviour may be grouped as having a common drive: all serve to maintain a high level of intraterritorial activity typical of territorial males and without which reproduction would be severely restricted. This may be taken to imply that both the stimulus and the response promote territorial activity. For an energy model to fit this proposal, it would require that both stimulation and performance increase energy, and thus a decrease in activity would be related to a decrease in energy. This concept appears to have been illustrated by a comparison of P. philander males which had company with those which were isolated. Such a model would have been completely unacceptable to Lorenz when he proposed his 'reaction specific energy' model in 1937 and later (1950) his 'psycho-hydraulic' model. Firstly, Lorenz held that the reservoirs for functionally related activities were not fed from a common source and he emphatically opposed McDougall's view (1923) that superordinated instincts employ motor mechanisms as a means to an end. In viewing territoriality of P. philander, McDougall's suggestion appears the more applicable: all subservient behaviour reinforces the principal drive. Hinde (1960) observed that Lorenz was concerned primarily with limited sequences of behaviour, and not with a synthesizing model of the whole organism. It was therefore sufficient for Lorenz to talk about an 'action specific energy' as he emphasized the individuality of each type of response and ascribed to the external situation the integration of discrete responses into functional units. In the development of his energy model, Lorenz (1950) suggested that the co-ordination mechanism of each fixed pattern tends to build up a kind of specific tension in the central nervous system, and if the animal does not find itself in the appropriate situation for the reaction pattern to be released, this specific action potential is, as it were, dammed up. The damming up process results in a lowering of threshold for stimuli effective in releasing that particular action pattern. If continued long enough, the tension may accumulate to the point at which the action pattern goes off without any external stimulus at all: a vacuum or overflow activity. This system proposes a build up of behavioural energy and consequent release of that energy. Animals show appetitive behaviour and increased activity prior to consummatory acts. After a response, an animal typically becomes more quiescent, as if satisfied, until once again the drive develops and the sequence is repeated. Many examples to which this model can be applied are to be found in the texts of ethology: the drives to feed, to drink and for sex, since illustrate the principle most clearly.

True to the Lorenzian proposal, isolated gravid female P. philander will show appetitive tendencies and eventually embark upon courtship, lay and pick up her eggs all in the absence of a spawning partner. By contrast, a territorial male P. philander will not perform as predicted by this model, but will become progressively less active when isolated. In all behavioural energy models the energy is supposed to build up and subsequently be released, and the cessation of activity is ascribed to the discharge of energy that flows away as a consequence of performance (Hinde,1960). However, the energy discharge of previously territorial P. philander when isolated was not achieved by performance, but rather by the lack of performance (displacement and redirected activities were seldom observed). This favours the suggestion that attendant fish will increase activity and sexual coloration of males as a consequence of both stimulus and response. As males become aroused, the stimulus-response latency decreases, and it appears to an observer that with each successive intraterritorial activity its "confidence" grows and alertness develops. The arousal of activity appears to be non-specific in that any of the behaviours grouped by the common drive may be performed; that which is performed appears to be dictated by the stimulus situation and is apparently without regard to sequence. A particular stimulus, a male intruder, will suddenly promote the drive to chase, the chase will be consummatory and the energy of chase will decrease true to the Lorenzian thesis of action specific energy. It appeared, however, as though the behavioural energy was not entirely dissipated, but in some way, probably the performance of the activity, fed back to increase the general arousal. The continual positive feedback makes P. philander extremely active within their territories.

Others have also noted that certain cichlids are apparently hyperactive within their territories (Fryer & Iles,1972; Axelrod pers.comm.). Lowe-McConnell (1956) provides further evidence in support of a positive feedback. She noted that the act of spawning in S. karomo appeared to incite the male to greater female leading activity. In other words, and contrary to the Lorenzian thesis, the sexual consummatory act resulted in increased sexual activity.

Thus the overall view of territorialism in P. philander and possibly S. karomo, can accommodate the Lorenzian energy model when applied to component behaviour patterns, with the rider that behavioural energy may be returned to positively reinforce the drive. Because of the general arousal of an established territorial P. philander, the time interval between two similar patterns may be very short if two stimuli follow closely upon one another, for example, chase and chase again. Such a sequence may be interpreted as a mere reflex stimulus-response situation without regard to the appetitive, consummatory and quiescent phases of behaviour. This is inaccurate, however, for a territorial male is appetitive in that it is aroused, and a stimulus to court or to chase will evoke the consummatory act followed by a brief decline of that particular response (quiescent phase), but not a diminuition of the principal drive.

If, to explain the territorial-drive of P. philander, one were to propose a Lorenzian-type energy model based on hydraulics, then the reservoir would be leaky so that the endogenous energy by itself would be insufficient to maintain the drive. Constant reinforcement from external stimuli and behavioural activities would top-up the reservoir and be depicted as several inlet taps. This model would be similar to that proposed by McDougall (1923) in which some of the consummatory energy could flow back to the reservoirs or a general source. Without stimulation from conspecifics the energy of the territorial drive would leak away.

Positive feedback systems, such as this proposed behavioural activation system, would require controlling mechanisms to prevent runaway hyperactivity. The inherent diurnal rhythm may moderate the system. Factors most likely to inhibit the territorial drive would be fatigue and the requirement for food.

Rasa (1971) working on juvenile damsel fish, also found that a non-specific arousal or excitement associated with territorialism appeared responsible for the maintenance of a high level of activity. In contrast to P. philander, the territorial drive of the damsel fish appeared to be largely endogenous in origin, and behavioural performance was required to dissipate energy. This difference may be accounted for by the observation that the drive of juvenile damsel fish of both sexes was directed at the maintenance of a feeding territory; their territories under natural conditions are essential for survival. In P. philander, territorialism was stimulated at maturity by the environmental factors which favoured reproduction. Although these fish fed in their territories, a territory was not a prerequisite for feeding. Thus the damsel fish were, of necessity, more dependent upon their internal drive. The inherent aggression, and the performance of motivated behaviour was a way in which behavioural energy accumulated within the damsel fish could be dissipated. Thus, though, the Lorenzian view may hold true for the damsel fish, it is less applicable to P. philander.

Though behavioural energy models might be informative, they are not necessary. Furthermore, physiological evidence in support of such models is not being produced. On the other hand, an increasing amount of physiological and behavioural evidence is accumulating which suggests that non-specific arousal systems are both real and of behavioural importance. The role of the ascending reticular system, for example, in the 'awakening' behaviour of mammals is well known. It is also encouraging for those who propose arousal systems that although Lorenz initially opposed such suggestions on the grounds that "to justify the term general arousal or general excitement, it should be demonstrated that all the thresholds of the animal's responses are lowered simultaneously", he (Lorenz, 1971) now believes that general arousal is an integral part of the mechanisms underlying behaviour, and points out that arousal fluctuates considerably and does so under the influence of stimulus situations. This view is in keeping with the observations of the differences of behaviour of P. philander under conditions of high (attendant fish present) and low (attendant fish absent) environmental stimulation.

The concept of an arousal system for promotion of general behavioural activity in fish is not new from a physiological viewpoint, for Janzen proposed just such a system in 1933 as a result of his work on the brains of goldfish. Work on fish brains and behaviour has been furthered by several biologists, and on the basis of their work and my own on *P. philander*, Ribbink (1972) suggested that 'the teleost forebrain houses a primitive limbic system, the main functions of which would be general arousal and the selection of appropriate responses to the incoming external and endogenous (motivational) stimuli'.

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