The Dynamics of Space Use in Some Lake Malawi Fishes

THESIS

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by

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Abstract

Behaviour and space utilisation of rock-dwelling cichlids were observed at Thumbi East Island, Lake Malawi.

1. Males of five species of the mbuna complex held long-term territories. *Pseudotropheus elongatus* "aggressive" vigorously defended a feeding area and sometimes a spawning site interspecifically, but did not feed in the peripheral part of their territory. Spawning sites of *Pseudotropheus zebra, Pseudotropheus tropheops* "orange chest", *Labeotropheus fuelleborni,* and *Petrotilapia nigra* were interspecifically-defended, while larger mating territories were defended against conspecific neighbours. Feeding areas were shared with many fish and often extended beyond the defended area. There was considerable variation in behaviour and space use within and between species and between times of day.

2. Non-territorial *P. zebra* used larger ranges than territorial conspecifics, and fed more on plankton, but individuals had preferred benthic feeding areas, often in conspecific territories. These 'floaters' were often aggressive. Both size and relative brightness independently predicted the outcome of aggressive interactions between floaters, and a site-specific dominance hierarchy was suggested, with some individuals appearing to be semi-territorial.

3. Males and females of 21 and 13 species respectively were found to establish temporary breeding territories. Overall breeding seasonality was bimodal, but reproductive timing and territory characteristics differed among species. Temporary territories had a considerable impact on the behaviour and habitat use of all resident mbuna species, even causing abandonment of territories.

4. Non-breeding *Protomelas taeniolatus* had limited home ranges, and showed little aggression. During the highly-synchronised reproductive season, males defended spawning sites and females fry-guarding territories. Most chases were directed towards the commonest fish, but predators were chased further and faster. Female behaviour changed over the guarding period. Females generally continued territorial defence after the brood had disappeared. Most broods contained fry of different sizes and species. Significant benefits were found for guarding females with clustered territories, but females did not appear to choose sites adjacent to conspecific parental females.

5. Territoriality in fish is taxonomically widespread and may serve several functions according to species, sex and developmental stage. It also varies according to genotype- and phenotype-limited strategies and short term costs and benefits. Territories may be simultaneously multifunctional.

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Chapter 1. Introduction

Rationale

One of the principal research themes of behavioural ecology has been the study of individual reproductive success and how it is affected by conspecifics. For examples see the literature on aggression and individual contests (e.g. Barlow *et al.* 1986, Huntingford & Turner 1987, Enquist *et al.* 1990, Chase *et al.* 1994, Turner 1994b), and alternative mating strategies (e.g. see Gross 1991, Turner 1993). Few studies have looked at between-species effects on individual reproductive success, except at the level of predation and parasitism.

Ecologists have studied interactions between species primarily by looking at the effects on populations and the implications for community structure (e.g. Buss 1980, Godfray *et al.*, 1994, Huston 1985, Nee & May 1991, Moilanen & Hanski 1995). The study of complexity in biological communities has traditionally been tackled by either the ecosystem approach (looking at the community as a whole without considering individuals in the network), or by studying the population dynamics of a single species or a pair of interacting species (e.g. predator-prey systems). There are exceptions. For example, there are numerous studies on interspecific competition where the effects of one species on the territories of another are documented (fish- Myrberg & Thresher 1974, Robertson & Polunin 1981, Draud *et al.* 1990, Kohda 1991; birds-Orians & Wilson 1964, Cody & Brown 1970, Cimprich & Grubb 1994, Robinson & Terborgh 1995). However, in most cases these studies concentrate on pairs of species, and the behavioural mechanisms by which the effects are mediated have not been examined.

This study focuses on an unusual situation, the cichlid fishes of an area of shallow rocky shore in Lake Malawi, where there is a limited resource (breeding space) which is likely to produce competition between individuals of several different species. However, because these individuals are all males of polygamous species that provide no parental care, this process can lead to individual behavioural competition across species without the population or community effects involved in competition in the ecological sense (Keddy 1989). Sale (1991) suggests that in coral reef fish, for entirely different reasons, interspecific competition is of minimal importance in determining species abundance, but that associated behavioural interactions may govern the local-scale use of habitats. Therefore an alternative approach has been used in this study, which will examine a multispecies mosaic of individual territories. Observations on the

behavioural interactions and individual patterns of space utilisation of component species will be studied.

Most behavioural studies on space utilisation of Malawi fish have concentrated on a single species group (e.g. Holzberg 1978, Marsh 1981, Hert 1990) or collected preliminary data on a vast number of species (Fryer 1959, Ribbink *et al.* 1983a, Konings 1990). Few studies of multispecies interactions have been carried out, and most of these focused on only a small selection of the species in an area (Marsh 1981, Sharp 1981, Hert 1993). The central aim of the present study was to determine how behavioural interactions between rock-dwelling cichlid fishes influenced the ability of a male cichlid fish to control a territory suitable for breeding and feeding.

Lake Malawi and its Fishes

Lake Malawi (9°30'-14°30'S/33°52'-35°20'E) is the third largest of the African lakes after Victoria and Tanganyika, and is the southernmost in the rift valley (see Fig. 1). It is estimated to be between 1 and 2 million years old (Bannister & Clark 1980). It is approximately 600km long and between 28 and 87km wide, with a maximum depth of approximately 700 metres. It is about 450-500 metres above sea level, well to the south of the equator.

Lake Malawi, like the other Great Lakes of Africa, provides an excellent example of intra lacustrine speciation. Although ten families of fish are represented in the lake, the family Cichlidae, amongst which there is estimated to be greater than 99% endemism (Greenwood 1991), are dominant, both numerically and ecologically. The cichlids are represented by two groups-the tilapiines (of which there are five or six species- Trewavas 1983, Turner & Robinson 1991), and the haplochromines, of which there are at least several hundred (Ribbink *et al.* 1983a; Greenwood 1991), and probably greater than a thousand species (Turner 1994a).

The haplochromines, which are considered to have originated from a generalised riverine ancestral form, perhaps like the extant *Astatotilapia calliptera* (Regan 1921, Trewavas 1935, Fryer & Iles 1972, but see Greenwood 1991, Meyer 1993, Eccles & Trewavas 1989), have undergone spectacular adaptive radiation. They show a striking diversity of form and function. There are specialised plankton feeders as well as epiphytic and epilithic algal grazers, but there are also mollusc-eaters, detritivores, lepidophages, paedophages, micropredators specialising on invertebrates, and numerous larger predatory species. Some species are confined to small rocky outcrops whereas others are open water species ranging over large distances. Their adult size varies from a few centimetres to up to 50cm total length (Eccles & Trewavas 1989). This highly speciose cichlid fauna, which has fascinated evolutionary biologists

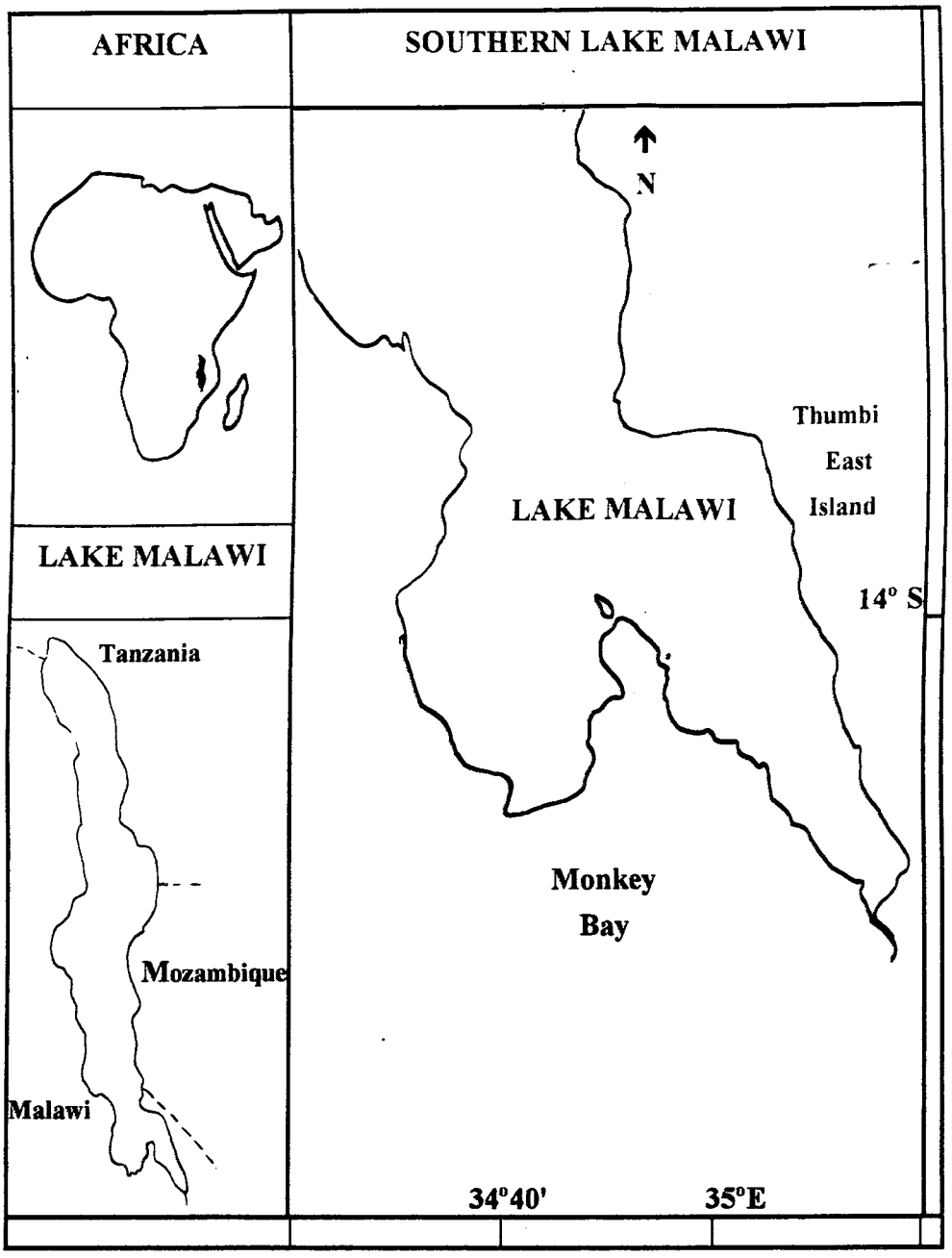


Figure 1. The location of Thumbi East Island, near Monkey Bay, southern Lake Malawi.

since their discovery, is manifested by the coexistence of extremely diverse assemblages of closely-related species. This is very different from the wide taxonomic range represented in coral reef fish communities. In addition, most of the rift lake fish are endemic to a relatively small area, whereas many coral reef fish have a broad, circumtropical distribution (Sale 1991) owing largely to their planktonic larval stages.

The Rocky Littoral Habitat

Many of the Lake Malawi cichlids are confined to the littoral zone. About 70% of the coastline consists of gently sloping sandy beaches, vegetated areas and swamp, and the remaining 30% comprises steep rocky shores (Ribbink *et al.* 1983a). The shallow rocky areas appear to be the most densely populated, and here many species of fish coexist at densities of up to 20 individuals per square metre (Ribbink *et al.* 1983a). Within this community, many species appear to share the same resources (Ribbink *et al.* 1983a, Lowe-McConnell 1991).

Of special interest are the guilds of epilithic algal-grazing fish, frequently composed of over 10 species at one site, collectively referred to by their Chitonga name of mbuna (Fryer 1959). This group of small (adult size usually less than 10cm standard length-Ribbink 1994), colourful, essentially lithophilous cichlids consists of at least 200 species (Ribbink *et al.* 1983a, Ribbink 1994) which appear to be more closely-related to each other than to any other genus in the lake (Trewavas 1935, Fryer 1959, Meyer *et al.* 1989, but see Moran & Kornfield 1993). In addition, most of the mbuna occur in the upper 20 metres of water (Fryer 1959, Ribbink *et al.* 1983a). Many more colour morphs of mbuna are recognised, some of which are seen to represent new species (Holzberg 1978, Ribbink *et al.* 1983, McKaye *et al.* 1982, 1984, Stauffer & Hert 1992, Bowers & Stauffer 1993).

Mbuna lead relatively sedentary lives and many of them are territorial, rather like coral reef fishes (Holzberg 1978, Marsh *et al.* 1981, Ribbink *et al.* 1983a, Sale 1978, Hert 1990, 1992, Konings 1990), but unlike their marine counterparts they do not have a dispersive pelagic phase in their lives (Fryer & Iles 1972, Sale 1991). Many of the mbuna depend on epilithic algal beds for food. This dense mat, often referred to as "aufwuchs", which covers the rocks of shallow littoral areas is composed of firmly-attached filamentous algae and associated epiphytic species, and it acts as a culture medium for bacteria, protozoa and diatoms. It also shelters numerous invertebrates, and traps sediment and organic detritus.

Mbuna species often have territorial males, and more rarely, territorial females (Ribbink *et al.* 1983a). Within populations, the number of sexually mature males is often greater than the number which can hold territories in the space available for

breeding (Holzberg 1978, Ribbink 1990), so in addition to the territorial individuals, there are many non-territorial mbuna (adult females, juveniles and non-territorial male "floaters") which may forage singly or in large groups. They also feed on aufwuchs, often in undefended areas (Marsh & Ribbink 1985). At times these floaters form mixed species shoals feeding in the territories of other fish, gaining entry by swamping the aggression of the tenants, or foraging on plankton blooms in the water column (Marsh and Ribbink 1986). Some mbuna species using the same areas do not appear to defend permanent territories (Ribbink *et al.* 1983a, Hert 1993). Access to the defended feeding areas involves complex patterns of antagonistic interactions, with some fish such as *Melanochromis auratus* (see Appendix 1 for authority of all species in this study) being able to circumvent defences or feed between the territories of other fish (Hert 1993) and others being ignored.

Although the shallow rocky areas appear to be dominated by the mbuna, other non-territorial cichlids are frequently numerous, and of these, *Protomelas taeniolatus* (Trewavas 1935) is the most abundant (Ribbink *et al.* 1983a). This species feeds on aufwuchs and benthic invertebrates, but is only territorial during the reproductive period. The endemic haplochromine cichlids are polygamous and have complex reproductive patterns, involving protracted courtship and mating behaviour. This usually involves the defence of a spawning site by males, and the production of a small number of relatively large, yolky eggs (Fryer & Iles 1972). All species show maternal mouthbrooding. In the mbuna, fry are released into the rocky interstices once they are large enough to be independent, but in many non-mbuna species (e.g. *P. taeniolatus*) females show prolonged parental care, spending days or even weeks guarding their fry after they are first released (Ribbink 1990).

A third group of cichlid fish establish territories in the shallow rocky areas only in their reproductive period, though they are not present in this area at other times of year (e.g. *Copadichromis eucinostomus*- McKaye 1983). Males are not involved in parental care in any haplochromine species and so their territories do not provide resources for females or young (McKaye 1984), but may serve to enhance male fitness by providing food, or a refuge or enhance the males attractiveness to the female (see McKaye 1991).

Competition for Space

At high population densities space could always be a limiting factor. The rocks provide a complex habitat with varying sizes of interstitial space which may buffer competitive interactions between individuals differing in size and mobility. Thus the structural complexity of the area may contribute to the maintenance of species diversity.

A variety of adaptive strategies have evolved among Malawi fish to utilise the gradients in space (e.g. water depth, substrate type, exposure to waves etc.), and some species have a very limited distribution, so consequently, species assemblages vary with location (Ribbink *et al.* 1983a). The whole lake contains many rocky reefs scattered over hundreds of kilometres. These differ in many factors including species assemblage, weather and exposure. On a smaller scale, each reef has its own range of habitat zones and distinctive features. As the spatial area being considered becomes smaller, the gradients are less pronounced and fewer species can coexist in the area. Still, within a small area of the lake, perhaps just a few square metres, there are many closely-related cichlids. Perhaps this can be explained by microhabitat variation (e.g. physical structure and orientation of rocks) since even truly homogeneous space can be exploited in different ways.

Some of the fishes share their space, and others are excluders i.e. they monopolise an area and might therefore be expected to decrease community diversity. However, some territorial animals defend a site only against certain species or individuals and this added complexity may increase community diversity (Marsh 1981).

Territoriality occurs when there is competition for a resource which is economically defendable, not necessarily because space *per se* is limiting. It may be primarily in defence of food, a spawning site, or a refuge from predators (Holzberg 1978, Marsh 1981, Sharp 1981).

Aims and Objectives

The materials and methods used throughout the study are presented in Chapter 2. The aim of the first study (reported in Chapter 3) was to determine how competition, both within and between species, influences the ability of a male cichlid fish to control a territory. This study focussed on the multispecies territory mosaic of all mbuna in one small area. Habitat use by individuals was studied, firstly with the aim of discovering the function and characteristics of territoriality for each species, and describing the home range and defended areas. Defence of a spawning site is essential for many of these fish, but it is not known whether their territories contain all necessary resources or whether fishes forage outside the defended area, since the natural behaviour of territorial fish outside their defended area had not previously been examined in mbuna. Overlap and exclusivity of territories and feeding sites was determined, both within and between species, to investigate the sharing of resources. The implications of behavioural interactions for individuals of different species were discussed.

The second study (reported in Chapter 4), concentrated on the space use and behavioural interactions of one of the commonest, and best studied species,

Pseudotropheus zebra, paying particular attention to the interactions of territorial and non-territorial individuals. The assumption that floaters have limited home ranges was tested. Aggression between non-territorial fish had not previously been recorded, and so their social relationships were evaluated. The behaviour, time budgets and habitat use of the territorial and non-territorial fish were compared.

Many of the mbuna have synchronised reproductive activity with a main peak in August, and for some species, a secondary peak in March (Marsh *et al.* 1986). At these times of year many other species, which are not ordinarily territorial, establish temporary breeding territories in the shallows. In Chapter 5, the results of a preliminary study of these temporarily territorial fish are presented. The number of species and individuals defending temporary breeding territories and the space they occupy were quantified. It is not clear how an apparently densely-packed habitat accommodates these temporary breeding territories. The sites they used were described, to discover whether they compete for space with territorial mbuna. The extent of this competition was estimated, and their impact on resident mbuna assessed.

Protomelas taeniolatus, a species which is abundant in the area but not territorial outside the reproductive period was studied in detail and the results presented in Chapter 6. An attempt was made to find out how the home ranges and feeding sites of non-territorial fish relate to areas defended by mbuna. Individuals were observed during the breeding season, when males defend courtship and spawning sites and females establish fry-guarding territories, to determine how and where territory establishment occurs, the duration occupancy, and the behaviour of territorial fish. Aggressive interactions of breeding fish with other species were recorded. The fry-guarding period was examined to determine how female and fry behaviour changed over time. Although females usually guard fry in isolated territories, they sometimes cooperatively care for offspring in colonies (Ribbink 1990). The behaviour of lone and communally-guarding females was compared, to determine the possible benefits of cooperative care.

The final chapter reviews territoriality in fishes, starting with an examination of the concept of territoriality, in a historical context, and then continuing with a discussion of the diversity of territorial behaviour exhibited by fish. The contribution of the present study to this wider field is discussed.

Chapter 2. Materials and Methods

This study was carried out between August 1990 and November 1992.

The Study Site

SEASONAL CYCLES IN LAKE MALAWI

Although the Lake Malawi is considered to be a relatively stable environment, it experiences marked tropical seasonality (Lowe-McConnell 1987). The hot rainy season is between October and March, when there are usually light north-easterly winds. During this time the lake level can be expected to rise by up to 2.2 metres. In the cooler dry season (March to August), there are strong south-easterly trade winds which generate large waves and strong currents on the lake. At this time the water temperature falls. During the period of this study (October 1990 to August 1992), the water temperature (measured at 5 metres depth) varied from 23°C to 29°C. The lake level varied by a total of 1.8 metres over the 2 year period, but the usual annual cycle was absent, as the country experienced a severe drought in 1991-2. During this time the lake level continued to fall at a time when it was usually rising. There are marked fluctuations in lake level, weather, water temperature, water clarity and food abundance over time.

LOCATION OF STUDY SITE

This study was restricted to a 1km stretch of shore at the island of Thumbi East (14° 03'40s S / 34°55'30s E), in the southern part of the lake (see Fig.2.). This island is just outside Monkey Bay and is part of the Lake Malawi National Park. The chosen area is predominantly rocky, with some intermediate zone, pockets of sand, and patches of macrophytes.

Most of the observations were carried out at less than 10 metres depth, though qualitative observations were made down to 20 metres. Studies focused on individuals in a permanent quadrat, and further observations were carried out in the area around the quadrat and along transects which ran approximately parallel to the coast, to the north and south of the quadrat. The census areas were chosen to cover a range of depths and substrate types.

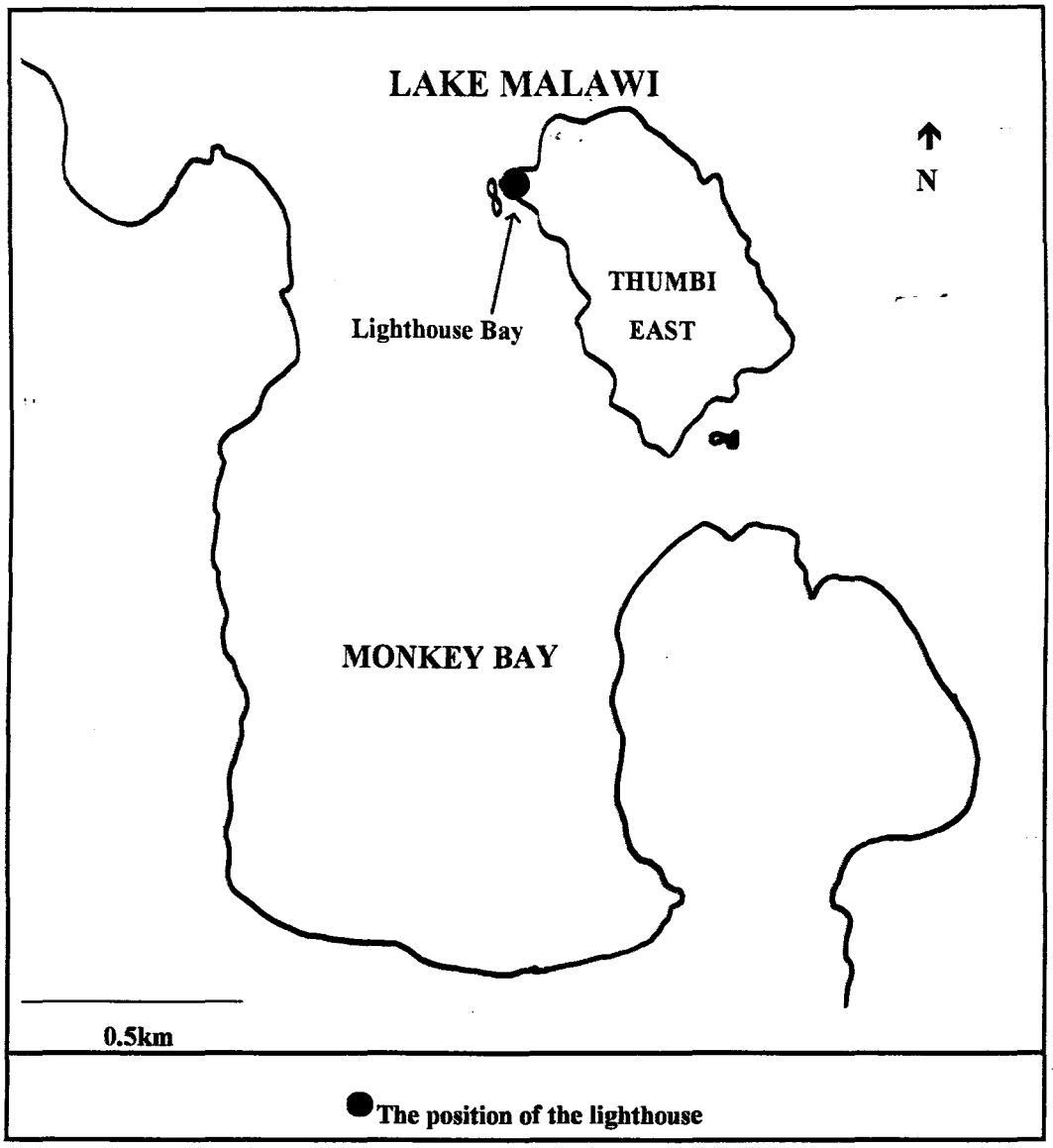


Figure 2. Location of the study site, at the island of East Thumbi, southern Lake Malawi.

DESCRIPTION OF THE STUDY SITES

Area A, Lighthouse Bay.

The name of this area derives from a lighthouse situated on the rocks. This sheltered bay enclosed an area of approximately 700 m^2 and was chosen because casual observation indicated the highest concentration of territories to be located here, and diving could be carried out in all weather conditions. Water depth varied from only a few centimetres at the shore to 12 metres. It was predominantly rocky, but contained a variety of substrate types e.g. pockets of sand and macrophyte beds.

The Quadrat

A permanent study site at one to three metres depth, with a variety of rock sizes, was identified within Lighthouse Bay. A quadrat of 5 x 5 metres was established and a grid of string, forming 1 metre squares, laid across the site. A map of the rocks in the quadrat was drawn, using photographs taken from above. The map was copied onto white perspex sheets, which could be taken underwater and inscribed in pencil. The depth was measured at numerous points in the quadrat, and a contour plot constructed.

Transects

Three transects were used, each along a depth contour parallel to the shore. The census lines were two metres wide and they were chosen to include all rock sizes found at each depth.

The 1 metre depth transect was 300 metres long, in an area dominated by rubble (rocks less than 20 cm) and rocks up to two metres across, which ran southwards and easterly from the lighthouse. Along the same stretch of shoreline, a 5 metre depth transect was carried out where there were mostly rocks of 1 to 3 metres in diameter. A further transect was used which was 400 metres long, leading to the north and east of the lighthouse. Along this transect, depth varied between 5 and 10 metres, as the shore was steeply-sloping, in an area where very large boulders (>3 metres diameter) predominated. For each transect, the type of substrate in each metre of its length was recorded.

The Community

The total number of species recorded in the study area was 74 (see Appendix I), including 10 non-cichlids, though this was probably an underestimate. Within the quadrat, five species of mbuna had territories, namely *Petrotilapa nigra, Pseudotropheus zebra, Pseudotropheus elongatus* 'aggressive', *Labeotropheus fuelleborni* and *Pseudotropheus tropheops* 'orange chest'. Others were territorial in the area, but not the quadrat (*Petrotilapia genalutea, Petrotilapia tridentiger, Pseudotropheus spp.* 'gracilior', 'broadmouth' and 'microstoma'). Additional mbuna species which do not defend a permanent territory, included *Pseudotropheus elongatus* 'yellow tail', *Melanochromis heterochromis, Melanochromis auratus, Melanochromis melanopterus, Genyochromis mento* and *Labidochromis vellicans.* Many non-mbuna were present, the most abundant of which was *Protomelas taeniolatus.* In addition, many fish not normally resident in the area entered this habitat to breed.

Underwater Observations

Underwater observations were carried out by snorkelling or using SCUBA during daylight hours (06.00-18.00 hours). Data were recorded by writing with a pencil on white perspex slates.

Behavioural Observations

TIME BUDGETS

During observation periods of 15 minutes, a focal individual was observed and the apportionment of time to behaviour was recorded. The following behavioural components recorded are shown in Table 1. Time budgets for individual fish were calculated within three time periods between the hours of 06.00-09.59 hours, 10.00-13.59 hours and 14.00-18.00 hours. Replicates were made for each individual, for each time period.

Table 1. Behavioural components recorded for Time Budget analysis.

i.	Time spent swimming
ii.	Time spent motionless (stationary)
iii.	Time spent out of sight in the refuge
iv.	Number of bites at aufwuchs
v.	Time spent feeding on aufwuchs *
vi.	Time spent plankton feeding in midwater
vii.	Time engaged in each type of aggressive interaction
viii.	Frequency and duration of courtship behaviour
ix.	Any other behaviour

*For species that take discrete bites at the aufwuchs, lasting < 1 second (e.g. *P. elongatus* 'aggressive'), this measure included biting and pausing between bites whilst the fish was still orientated in the feeding position. For species that scrape the rocks for longer than 1 second at a time (*L. fuelleborni, P. nigra* and *P. zebra*), the length of each bout (from initial contact of the fishes mouth to the rock surface, to the breaking of contact) was recorded and multiplied by the frequency for that category to give the total time spent feeding, exclusive of any periods of rest.

HABITAT UTILISATION

During the observation periods described above, the movements of the focal fish were recorded on a map, using symbols to denote the type of behaviour being performed at each site (Table 2.).

Table 2. Behavioural components recorded on Habitat Utilisation maps.

i.	Benthic feeding sites
ii.	Plankton feeding sites
iii.	Position of intruders when chased
iv.	Position of focal fish when chase received
v.	Position of participants in other aggressive interactions (e.g. frontal and lateral displays, lunges, bites)
vi.	Courtship sites
vii.	Places where focal fish was seen swimming
viii.	Places where focal fish remained motionless

Analytical Techniques

SPATIAL DATA ANALYSIS

The maps of habitat utilisation were digitised and subsequently analysed using a geographical information system (GIS). This enabled the coordinates of sites used during different focal watches to be combined, and the calculation of areas enclosing particular coordinates (for example feeding sites) to be calculated. Subsequently, the overlap/exclusivity of territories, home ranges and feeding areas within and between species was calculated.

Identification of Fish

INDIVIDUAL RECOGNITION

For individual observations, many fish were distinguishable by site tenacity and colour pattern (e.g. number and position of bars and eggspots). Fish that were not individually identifiable were tagged so that their behaviour could be followed over time. This process involved the capture of fish in a fine-gauge monofilament net, and the suturing of coloured beads to the dorsal musculature of anaesthetised fish. The colour and position of the tags, in combination with the appearance of the fish, allowed individual recognition. These tags remained in place for up to 6 months, with little apparent effect on the behaviour or well-being of the fish

TAXONOMY

Although several hundred Malawian cichlids have been taxonomically described, many more have not, and many closely-related species are morphologically so similar that they are extremely difficult to distinguish from one another except by considering colour patterns and behaviour of live fish (Lewis 1982). Even so, colour is variable with location and motivation, and many species have similar colour patterns. Such problems necessitate the consideration of behavioural and ecological information when deciding what constitutes a species. In this study, fishes have been identified to species level as far as possible. Many cichlids in this study have not been taxonomically described but were formerly assigned descriptive names (Ribbink *et al.* 1983a, Konings 1990). This informal nomenclature is presented in quotation marks to indicate the lack of taxonomic validity.

Where species could not be identified readily, detailed colour notes were made and, if possible, photographs taken and specimens obtained. Samples of unidentified species will be placed in the museum at the JLB Smith Institute of Ichthyology. (see Appendix I for details of the taxonomic status and authority of all fish mentioned in this study, and Appendix II for colour plates).

Chapter 3. Territorial fish.

Introduction

Local monopolization of one or more resources occurs when fish obtain priority of access around a fixed site by social dominance. Defence may be only against conspecifics, or may involve the exclusion of other species, either closely related or taxonomically very distant. Territorial behaviour may occur when space or another resource is limiting *per se*, or it may involve denial of access to a resource that is not in short supply within the territory. The shortage is then relative rather than absolute. The defended resource may be food, a spawning site or a refuge.

Lake Malawi has at least 200 species of fish belonging to the mbuna group, most of which exhibit territorial behaviour (Ribbink *et al.* 1983a). At any one location in the shallow rocky habitat, several of these species coexist in a territorial mosaic defended by males, and more rarely, females (Holzberg 1978; Marsh 1981, Sharp 1981, Ribbink *et al.* 1983a & b). In the present study, the patterns of space utilization and individual interactions of five territorial mbuna species were examined. Previous workers have described different types of mbuna territories. The *P. zebra* species complex (Holzberg 1978) and the *Petrotilapia* complex (Marsh *et al.* 1981) have territories that show no overlap between individuals of one species, but complete overlap between species. In contrast, other studies have shown relatively small interspecifically-defended territories with no overlap between species (Sharp 1981, Hert 1993). This could be a result of different patterns of territoriality between the species studied, but since different methods were employed to measure the defended areas in each case, it may be that the small, interspecifically defended territories are contained in larger, unidentified intraspecific territories or home ranges (Hert pers. comm.). Previous authors have also disagreed about the function of territoriality in mbuna, specifically whether it is primarily in defence of food or not (Holzberg 1978, Marsh *et al.* 1981, Sharp 1981).

Aims and Objectives

This study was aimed at providing a body of quantitative background information from which to erect hypotheses used in the studies outlined in subsequent chapters and to provide information which might enable other workers to do likewise: in other words,

the inductive, rather than the hypothetico-deductive method was employed. However, it was intended that the information collected would also enable the testing of two hypotheses: (i) does interspecific competition affect the habitat use of territorial fish? (ii) are territories primarily established for the defence of food resources, as suggested by Sharp?

The patterns and processes of both inter- and intraspecific competition were described on an individual basis.

For each individual, the home range was determined and related to its intra- and interspecifically-defended areas- few studies have documented space utilization of territorial mbuna outside their defended areas. For some species, it may be that a territory is "an interspecifically defended area which contains the food and shelter resources required by the owner" (Sharp 1981), but other studies (Kornfield *et al.*. in press) and personal observation suggest that many individuals forage outside their territories. If this is the case, then defence of food may not be the primary function of territoriality. By looking at the behaviour of individual fish in different regions, and the overlap or exclusivity of the areas being used, it was possible to determine which resources are being defended and which are shared. Individual differences within species were examined, to determine whether there are different tactics of space utilization, and possibly variation in territory quality.

Territorial interactions and habitat sharing between species were determined. If resource subdivision is by feeding sites used, then overlap of feeding sites between species is not to be expected. It may be that some species share feeding areas whilst others do not. Interspecific aggression was investigated, dominance relationships studied, and competitive abilities assessed. Finally, the territory characteristics in each case were examined.

Methods

TIME BUDGETS

For each species holding territories in the quadrat, four individual fish were studied in detail, although territories of other individuals were also surveyed. In each case the focal fish was observed for periods of 15 minutes, during which individual components of its behaviour were timed and recorded. Time budgets were estimated for 3 different times of day, namely 06.00-10.00 hours, 10.00-14.00 hours and 14.00-18.00 hours respectively (see Chapter 2). A series of 2-way analyses of variance (ANOVA) were performed on the data for individuals nested within species, and with different times of day. Each behaviour in turn was treated as the dependant variable.

HABITAT UTILIZATION

During the above observations period, the position of the focal fish was recorded on a map of the area. The position of any intruders which elicited a chase was also recorded. The maps of habitat use by each fish were digitised and combined using a geographical information system (GIS). Subsequently, the territories and home ranges were analysed using the computer program "Home Range" (Ackerman *et al.* 1989). This allowed calculation of territory sizes using the minimum convex polygon method (Hayne 1949). In this simple and intuitive method (Beckoff & Mech 1984), the peripheral points of the data set (corresponding in this case to the position of intruders eliciting aggression from the territorial fish) are connected in such a way that the internal angles of the polygon thus generated do not exceed 180°. By a similar routine, concentric minimum convex polygons were constructed to encompass only a specified innermost percentage of the data points. These percent convex polygons (Michener 1979, Bowen 1982, Bekoff & Mech 1984) give some indications of the distribution of defence and other activities throughout the territory of each fish.

TERRITORIAL DEFENCE

In order to determine whether the territory is defended against all or only some intruders, details of aggressive interactions were recorded when possible, including the species and relative size of participants and the distance and relative speed of each chase.

INDIVIDUAL SIZE

The size of individual fish was estimated using a ruler placed on the substrate where possible, and in all cases their size relative to each other and was estimated, since to capture and measure all individuals would have caused undue disturbance and possible injury to the fish.

Results

SPECIES PRESENT IN THE STUDY SITE

The following species held territories in the quadrat: *P. zebra*, *L. fuelleborni*, *P. elongatus* 'aggressive', *P. tropheops* 'orange-chest' and *P. nigra*. *Melanochromis heterochromis*, *Pseudotropheus elongatus* 'yellow tail', *Melanochromis auratus*, and

Labidochromis vellicans were also present and frequently aggressive, but seemed to range over large areas and spent long periods under or between rocks.

SPACE UTILISATION

Plots of locations of benthic feeding by territorial fishes (Figs 3.1-3.5) indicate that all species fed principally from the smaller rocks and the sides of larger rocks. Densities of feeding on the upper surfaces of larger rocks were generally low. *P. zebra* tended to avoid feeding on the upper surfaces of large boulders, especially in water depths of 20cm or less. Although the peak densities of feeding by *P. zebra* and *P. elongatus* 'aggressive' showed little overlap, there was little evidence that the other species had spatially segregated feeding areas.

Defended areas for all species

Successive addition of areas of minimum convex polygons enclosing ten percent increments of frequency of chases showed a smooth increase in range size over an area enclosing 80-90% of the chases, indicating an approximately constant density of defence per unit area (Figure 3.6). Further increase in the percentage of chases enclosed resulted in inflection of the curves, indicating a sharp increase in range area, and consequent reduction in the density of defence per unit area. The area up to the inflection point can be regarded as a heavily defended core area, the rest representing a weakly defended peripheral area. There was no indication that the boundaries of the territory were more heavily defended. Core areas of four focal individuals of the five main territorial species are shown on figure 3.7. There was no overlap between core areas of conspecifics of any species, and very little overlap between those of heterospecifics of the three *Pseudotropheus* species. Refuges within core areas were never shared. There was substantially more overlap between core areas of individuals of different genera. The areas used for benthic feeding, estimated as minimum convex polygons, differed significantly among species (Table 3.1). Although there was substantial variation among species in the sizes of total defended and core areas, comparison of four focal fish of each species was not statistically significant, as there were also large individual differences within a species.

Territorial males of all species were seen to leave their defended areas (sometimes up to one metre beyond the territory boundary) to perform courtship displays, but in each case the males alternated the courtship displays with rapid returns to the territory centre, until the female either followed to the spawning site or swam away. Often this behaviour elicited chases from neighbouring territory holders.

Figure 3.1. *L. fuelleborni* feeding areas were broadly spread throughout the quadrat and showed little concentration on the basis of size of rocks or position on the rock surface. Small square symbols represent location of benthic feeding sites (all observation periods combined), thick lines enclose feeding sites of individual territorial fish and thin lines represent rocks in the 5m x 5m quadrat. Feeding area shared by two fish is coloured black and indicated by the arrow.

Figure 3.2. The locations of feeding bouts of territorial *Petrotilapia nigra* were broadly spread throughout the quadrat and were distributed over rocks of all sizes, although there was a tendency to avoid the upper surfaces of the two large rounded boulders on the left. Small square symbols represent location of benthic feeding sites (all observation periods combined), thick lines enclose feeding sites of individual territorial fish and thin lines represent rocks in the 5m x 5m quadrat. Areas of overlap between the feeding areas of two fish are coloured black, and indicated by the arrows

Figure 3.3. The locations of feeding bouts of territorial *P. tropheops* 'orange chest' were distributed over all parts of rocks of all sizes. The higher concentration in the left-hand side of the quadrat is an artifact of the higher number of focal watches on individuals with territories in that area. Small square symbols represent location of benthic feeding sites (all observation periods combined), thick lines enclose feeding sites of individual territorial fish and thin lines represent rocks in the 5m x 5m quadrat. Area of overlap between feeding areas of adjacent fish is coloured black and indicated by the arrow.

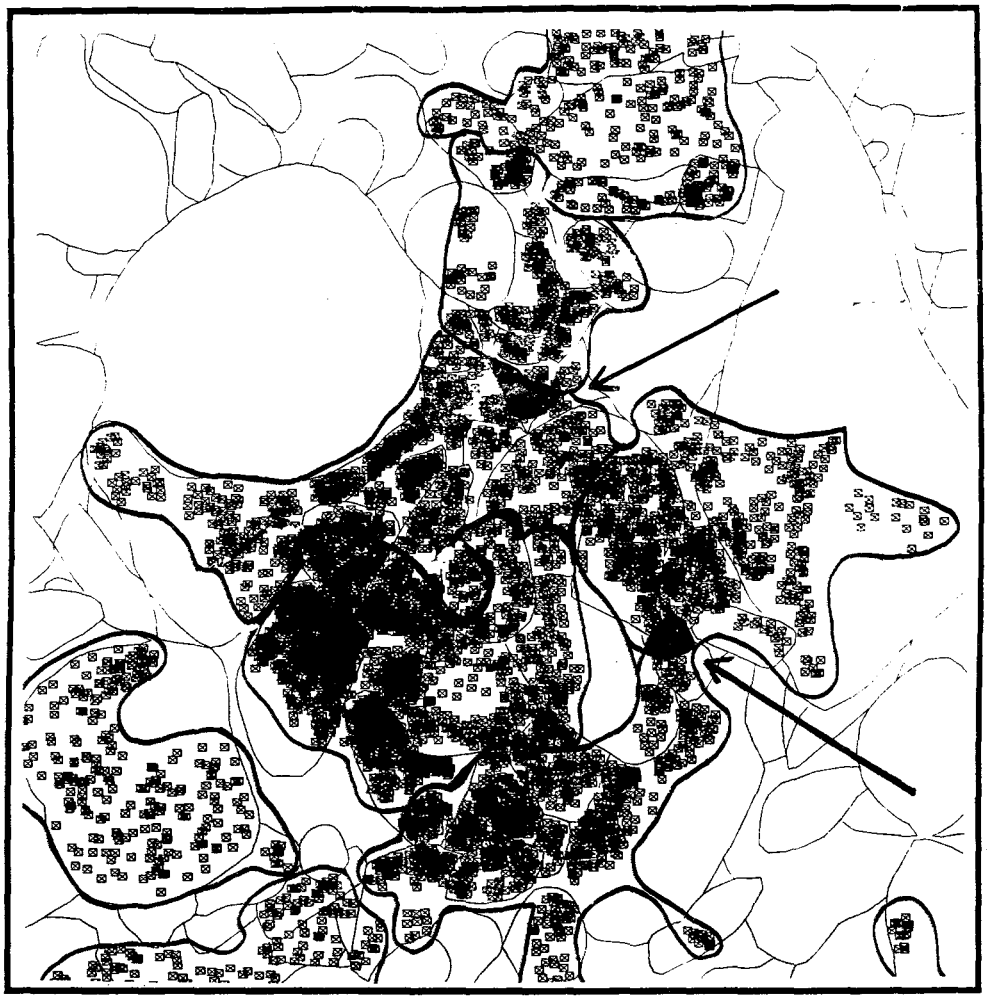


Figure 3.4. *P. zebra* feeding bouts were generally evenly distributed over the area they used, with no gaps between ranges of adjacent individuals. The upper surfaces of large boulders were generally avoided, particularly where the water depth was less than 20 cm. Areas used by *P. elongatus* 'aggressive' were rarely used or avoided. Small square symbols represent location of benthic feeding sites (all observation periods combined), thick lines enclose feeding sites of individual territorial fish and thin lines represent rocks in the 5m x 5m quadrat. Feeding sites shared by two fish are coloured black and indicated by the arrows.

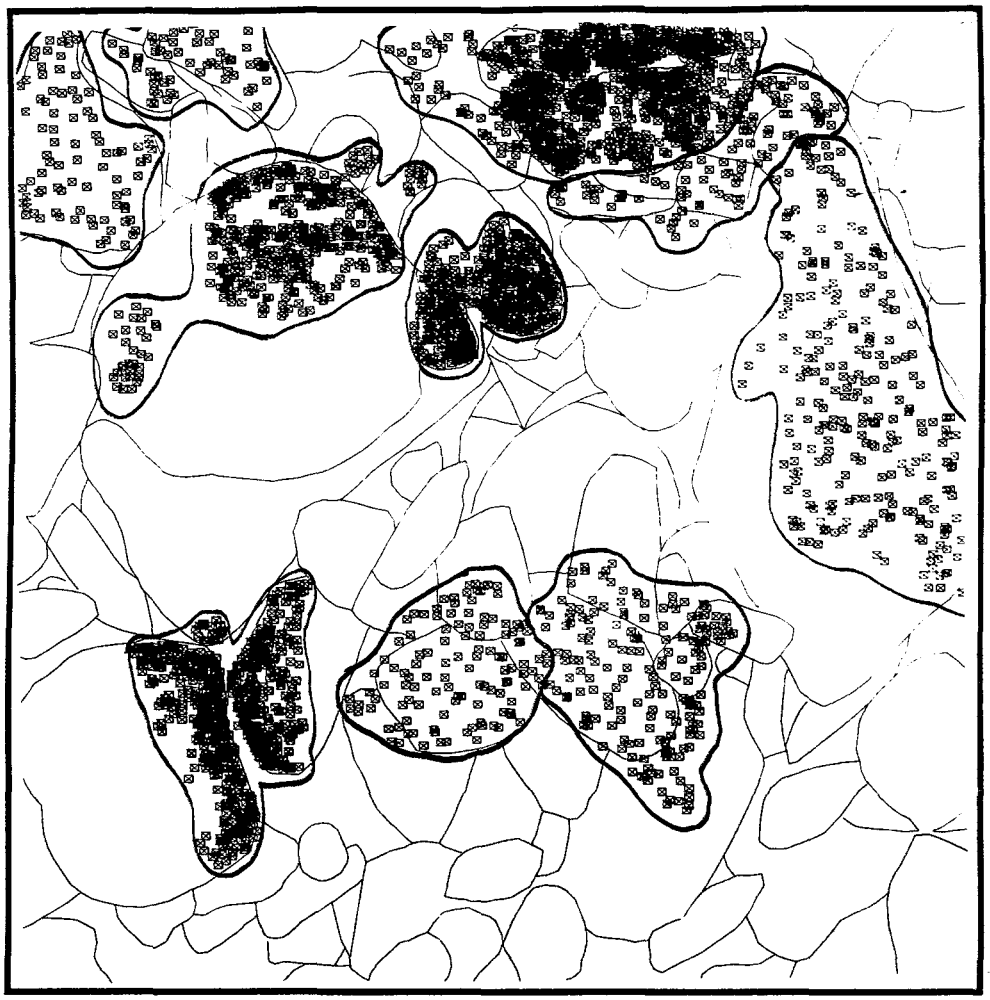
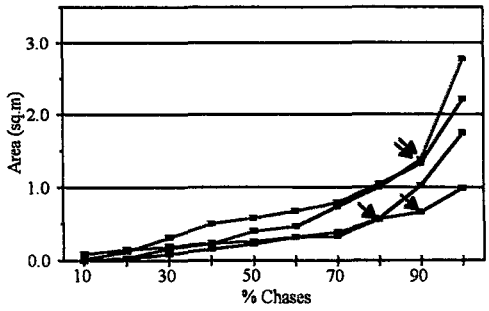
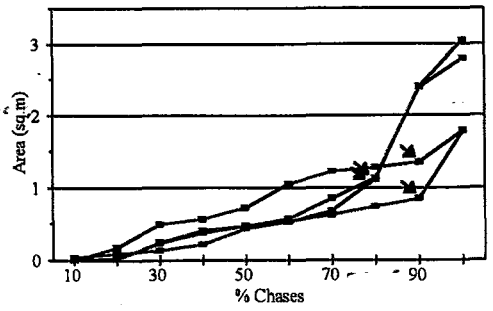


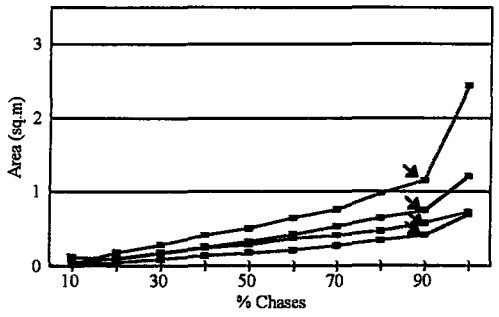
Figure 3.5 *P. elongatus* 'aggressive' feeding bouts were generally concentrated over restricted areas, generally with clear gaps between the areas used by different individuals. There was no avoidance of different sizes of rocks or different portions of larger rocks. Small square symbols represent location of benthic feeding sites (all observation periods combined), thick lines enclose feeding sites of individual territorial fish and thin lines represent rocks in the 5m x 5m quadrat.



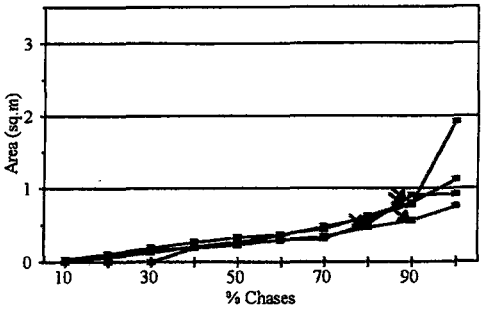
(a) *Labeotropheus fuelleborni*



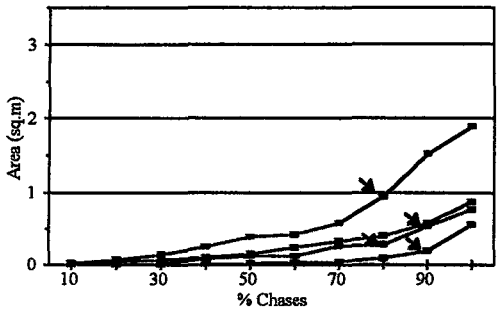
(b) *Petrotilapia nigra*



(c) *Pseudotropheus elongatus* 'aggressive'



(d) *Pseudotropheus tropheops* 'orange chest'



(e) *Pseudotropheus zebra*

Figure 3.6. Total areas of minimum convex polygons enclosed by consecutive 10% increments in numbers of chases by four individual territorial mbuna of five species. Data from all focal watches were combined. Points of inflection of curves (arrowed) indicate core areas beyond which territory area increases rapidly compared to chasing frequency.

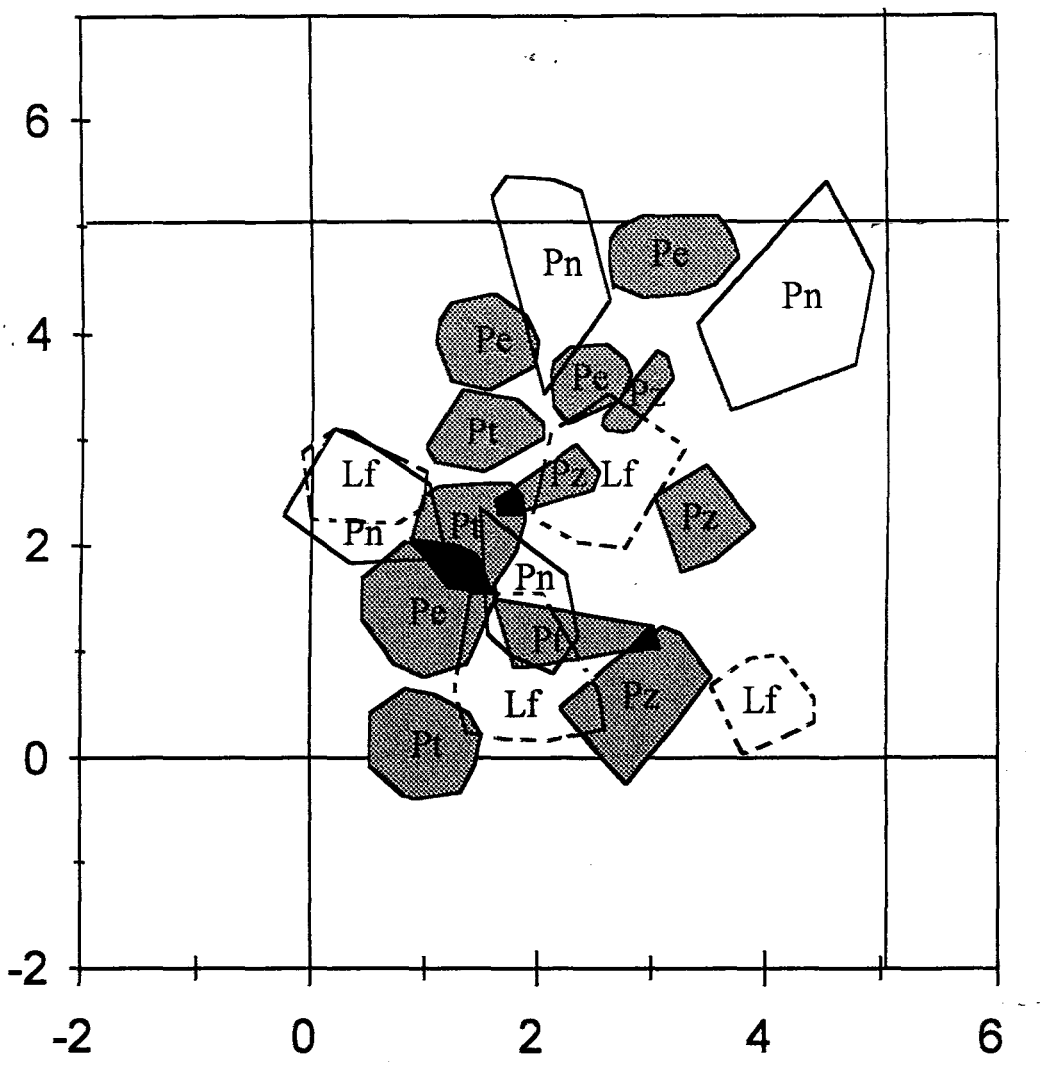


Figure 3.7. Core areas of four focal individuals of five territorial mbuna species, determined from inflection points of plots of minimum convex polygons of ten percentile areas of increments of frequency of chases. Figures along axes represent scale in metres. There was no overlap between core areas of conspecific territorials of any species. Within the genus *Pseudotropheus* (*P. elongatus* 'aggressive'- Pe, *P. tropheops* 'orange chest' - Pt, *P. zebra* -Pz, shaded polygons) there was very little overlap (black areas) between core areas of heterospecifics. Core areas of *Labeotropheus fuelleborni* (open polygons, broken outlines) and *Petrotilapia nigra* (open polygons, solid outlines) overlapped with those of heterospecifics to a considerable extent.

Table 3.1 Comparison of feeding, defended and core areas of five species of territorial mbuna. Based on minimum convex polygons derived from observations of four focal individuals of each species. (Mean values ± standard deviation).

Species	Benthic Feeding Area (m^2)	Defended Area (m^2)	Core Area (m^2)	Feeding/ Defended Area
L. fuelleborni	4.65 ± 2.44	1.93 ± 0.75	0.99 ± 0.43	2.88
P. nigra	4.33 ± 0.98	2.35 ± 0.67	1.12 ± 0.21	1.91
P. elongatus 'agg.'	0.96 ± 0.43	1.26 ± 0.82	0.72 ± 0.31	0.93
P. tropheops 'o-c'	2.40 ± 2.83	1.18 ± 0.52	0.66 ± 0.14	2.39
P. zebra	2.03 ± 0.89	1.02 ± 0.59	0.50 ± 0.34	2.08
Anova, 4,15 df	F=3.11,P<0.05	F=2.77, P=0.07	F=2.73, P=0.07	

Defended areas of most individuals contained a refuge near the centre, to which territorial fish typically fled when alarmed. A few small *P. elongatus* 'aggressive' and at least one *P. tropheops* 'orange chest' lacked these refuges. During courtship bouts, male territorial fish typically attempted to lead females towards these refuges, and most bouts of courtship circling and any spawning observed occurred in these areas. Males without spawning sites/refuges were not seen to receive any response from females. In the absence of females, males frequently rested at this site, occasionally picking up and spitting out mouthfuls of sediment, or slowly circling around. *L. fuelleborni* was seen to spawn on a flat rock surface just inside the cave that served as the male's refuge. Similar sites were found in all core areas of this species. *P. tropheops* 'orange chest' spawning sites were usually visible from above, but were often in a cleft between two vertical rocks, and at approximately 10-45° to the vertical axis, often over a slight hollow in the rock surface. Male *P. zebra* led females deep into their refuge caves and spawning was never seen.

Areas defended by Labeotropheus fuelleborni

Core areas of the territorial *L. fuelleborni* resident in the quadrat were widely spaced (figure 3.8) and at a mean area of $0.99m^2$, were the second largest of the five territorial species in the quadrat. The total defended areas were generally larger (mean $1.93m^2$) and sometimes contiguous. Much of their benthic feeding took place outside the defended area and feeding areas were the largest of the five species, averaging $4.65m^2$ and were almost 3 times as large as the defended areas. Considerable overlap between feeding areas of neighbouring individuals is indicated by plots of minimum convex polygons (fig. 3.8), but a precise representation of feeding sites indicates that

the boundary of the feeding areas forms a complex jigsaw with comparatively little overlap between neighbours (fig. 3.1). Frontal display contests occurred near the boundaries of adjacent ranges, while circling fights in the central areas of territories were invariably contests between pairs of territory holders.

There were no noticeable size differences between territorial males, which were approximately 11-11.5cm total length.

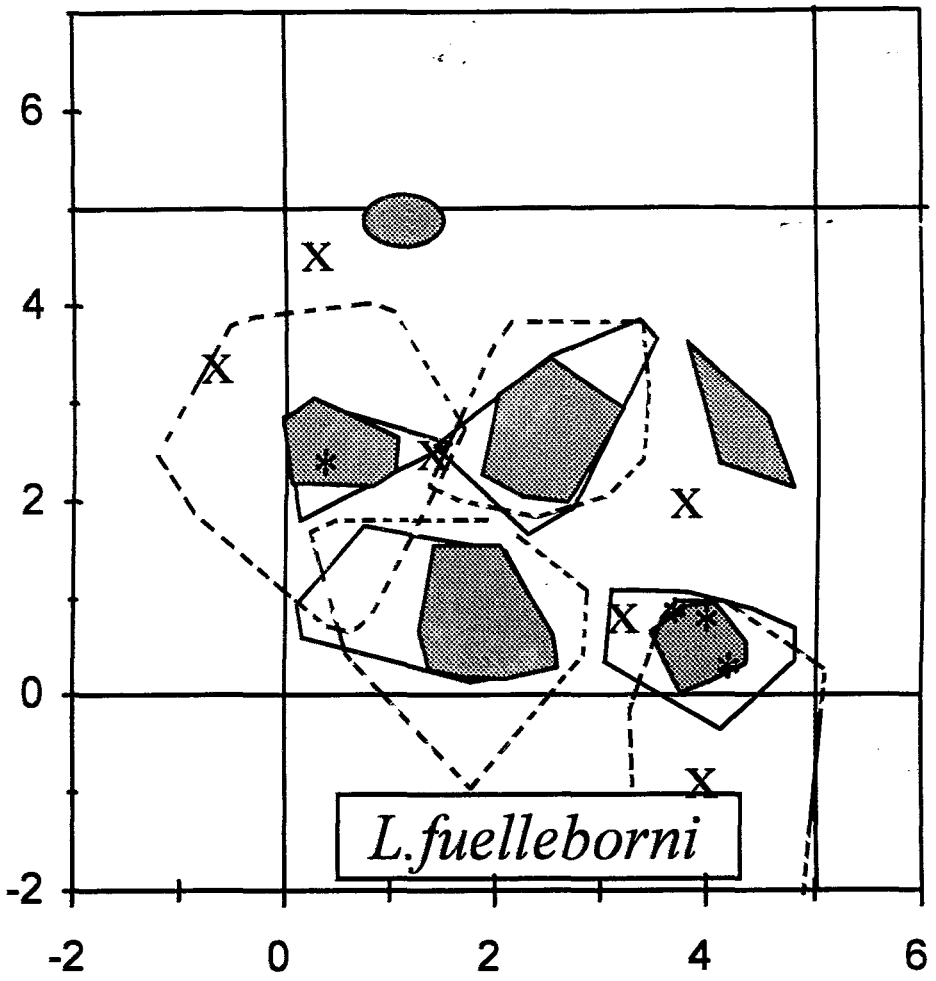


Figure 3.8. Core areas of the six territorial *Labeotropheus fuelleborni* within the quadrat (shaded polygons) were widely spaced. 100% defended areas (open polygons, solid borders) were generally much larger and sometimes contiguous. Feeding areas (open polygons, broken borders) were much larger and partially overlapping, although this is largely an artifact of the use of convex polygons (see figure 3.1 for a more precise representation). Individuals where all three polygons are shown were the focal individuals used in time budget analysis, where only a shaded polygon is shown, the polygon was determined from the locations of chases given during a small number of focal watches, a shaded ellipse indicates that a territorial individual was observed but focal watches were not made. Frontal display contests (x) occurred near the boundaries of adjacent ranges, while circling fights (*) took place in

the central areas of territories and were invariably contests between the resident and another conspecific holding a territory in the quadrat. The individual at the bottom right corner suffered three challenges from the individual holding the territory immediately to its left, while itself invading the territory at the centre of the left side of the quadrat, provoking a circling contest on one occasion and on another being pursued into its own territory by the resident.

Areas defended by Petrotilapia nigra

P. nigra had the largest core area of the territorial species, averaging 1.12 m^2. Core areas neither overlapped nor abutted (fig. 3.9). Total defended areas were larger (mean = 2.35m^2) and sometimes contiguous or partially overlapping. Feeding areas, with an average size of 4.33m^2 frequently overlapped, sometimes even with the core areas of neighbouring conspecifics. Frontal display contests occurred near the boundaries of adjacent ranges.

All males were of approximately the same size, which was estimated to be around 12cm total length.

Areas defended by Pseudotropheus tropheops 'orange chest'

Eleven *P. tropheops* 'orange chest' individuals held territories within the quadrat, the largest number of any species (fig. 3.10). Their core defended areas were small (mean 0.66m^2), closely packed, but neither overlapping nor contiguous. The total defended areas were often contiguous, but showed minimal overlap with those of conspecific neighbours. Feeding areas varied greatly in size between individuals and the larger ranges often overlapped, even with the core areas of conspecifics. Frontal display contests and circling fights generally occurred near the boundaries of adjacent ranges. This species frequently indulged in long and violent fights involving considerable physical contact. Territorial individuals were often badly scarred, with missing scales and split fins.

There were large differences in the size of territorial fish, with the smallest individual being almost three centimeters less in total length than the largest (estimated size range 7.5 to 10.5cm).

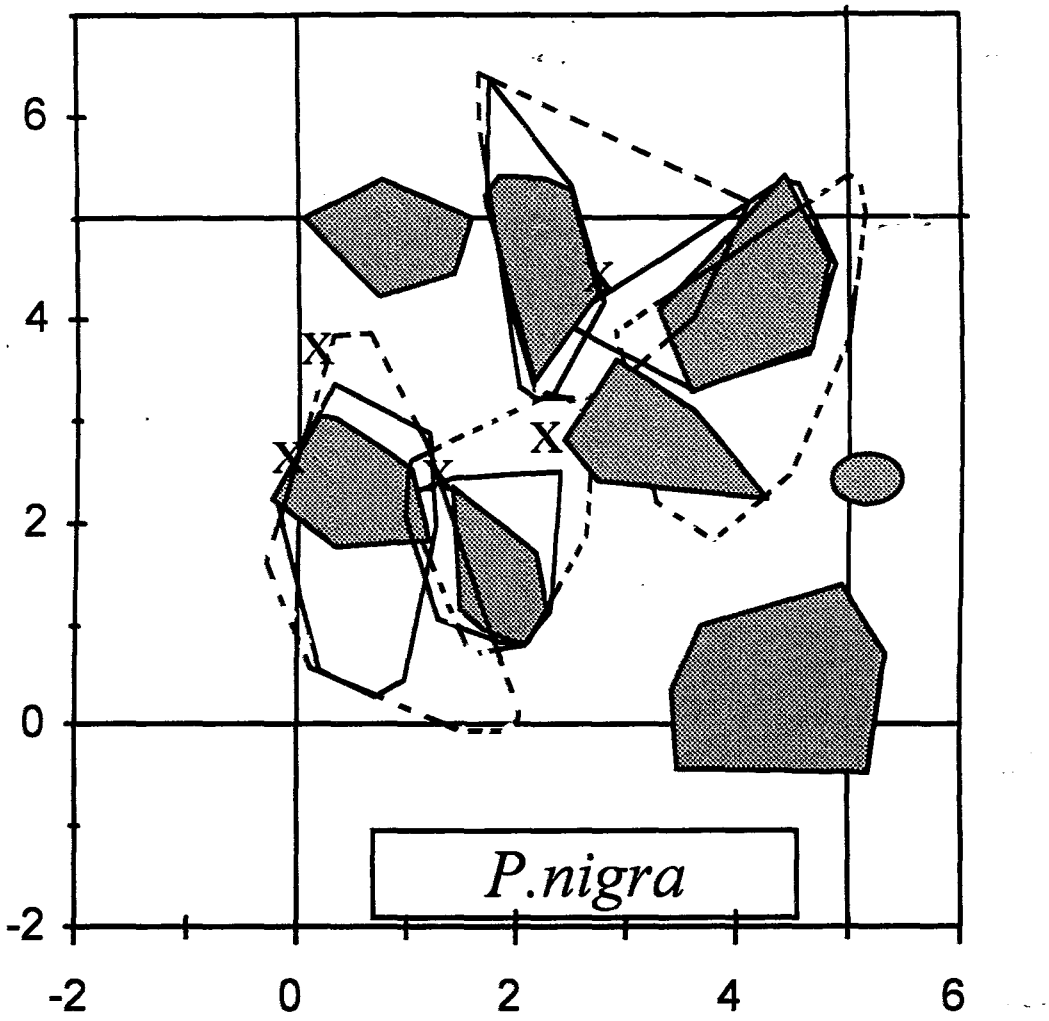


Figure 3.9. Core areas of the eight territorial *Petrotilapia nigra* within the quadrat (shaded polygons) were neither overlapping nor contiguous. 100% defended areas (open polygons, solid borders) were larger and sometimes contiguous or partially overlapping. Feeding areas (open polygons, broken borders) were much larger and frequently overlapped, even partially overlapping the core areas of neighbours. Individuals where all three polygons are shown were the focal individuals used in time budget analysis, where only a shaded polygon is shown, the polygon was determined from the locations of chases given during a small number of focal watches, a shaded ellipse indicates that a territorial individual was observed but focal watches were not made. Frontal display contests (x) occurred near the boundaries of adjacent ranges.

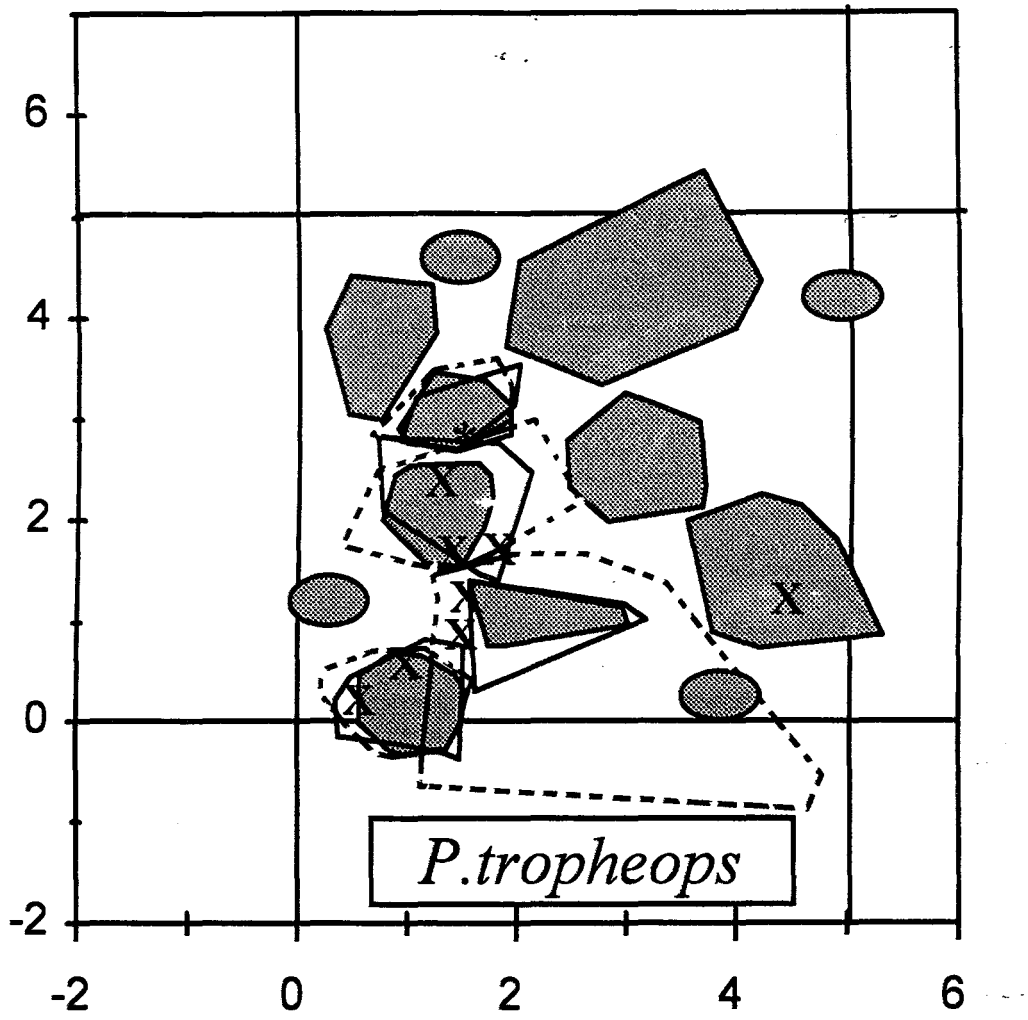


Figure 3.10. Eleven individual *P. tropheops* 'orange chest' held territories within the quadrat. Their core defended area (shaded polygons) were closely packed, but neither overlapping nor contiguous. 100% defended areas (open polygons, solid borders) were often contiguous, but showed minimal overlap with those of their neighbours. Feeding areas (open polygons, broken borders) varied greatly in size between individuals and the larger ranges often overlapped, even with the core areas of conspecifics. Individuals where all three polygons are shown were the focal individuals used in time budget analysis, where only a shaded polygon is shown, the polygon was determined from the locations of chases given during a small number of focal watches, a shaded ellipse indicates that a territorial individual was observed

but focal watches were not made. Frontal display contests (x) and circling fights (*) generally occurred near the boundaries of adjacent ranges.

Areas defended by Pseudotropheus elongatus 'aggressive'

There was no overlap in space use between adjacent conspecific territorial *P. elongatus* (fig 3.11). Feeding areas were very small, averaging less than $\frac{1}{2}m^2$, and were generally smaller than the total defended area (table 3.1). In contrast to all other species, adjacent territorial *P. elongatus* 'aggressive' did not feed right up to their mutual territory boundaries, so that the spatial distribution of total feeding bouts of this species showed discrete clusters, separated by wide gaps (fig. 3.5). Frontal display contests and circling fights generally occurred near the boundaries of adjacent ranges.

Large size differences between individuals were evident with estimated total lengths ranging from 8 to 10cm.

Areas Defended by Pseudotropheus zebra

There was no overlap between the core areas of the ten territorial *P. zebra* individuals within the quadrat (fig. 3.12). Core areas were the smallest of any species, averaging half a square metre. Total defended areas and feeding areas showed minimal overlap with neighbouring conspecifics. Frontal display contests and circling fights generally occurred near the boundaries of adjacent ranges.

There was considerable varation in male size, with total lengths of individuals varying between approximately 8cm and 10cm.

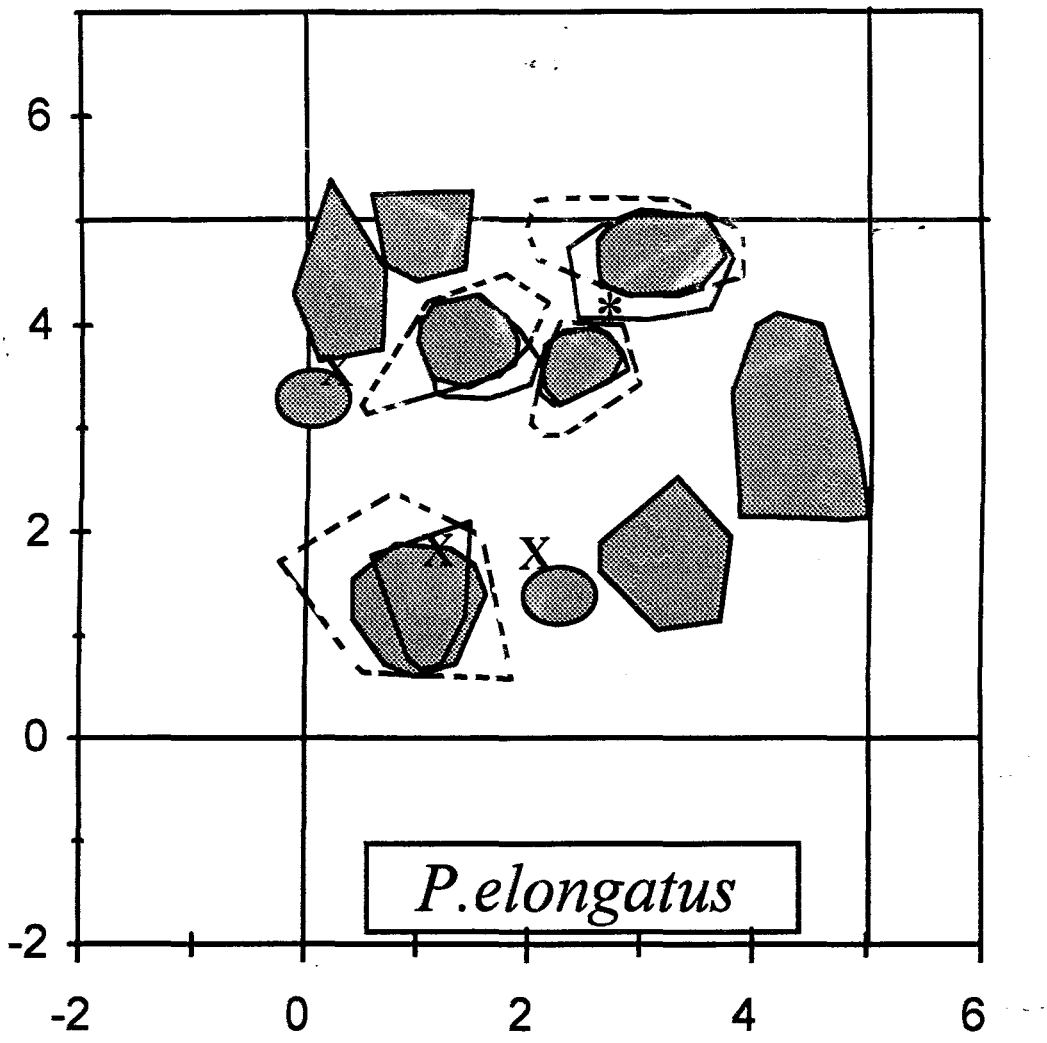


Figure 3.11. Ten *P. elongatus* 'aggressive' individuals held territories within the quadrat. There was no overlap in space use between adjacent conspecifics. Feeding areas (open polygons, solid borders) were frequently scarcely larger than the core defended area (shaded polygons) and were sometimes smaller than the 100% defended areas (open polygons, broken borders). Only the latter were ever contiguous. Frontal display contests (x) and circling fights (*) generally occurred near the boundaries of adjacent ranges.

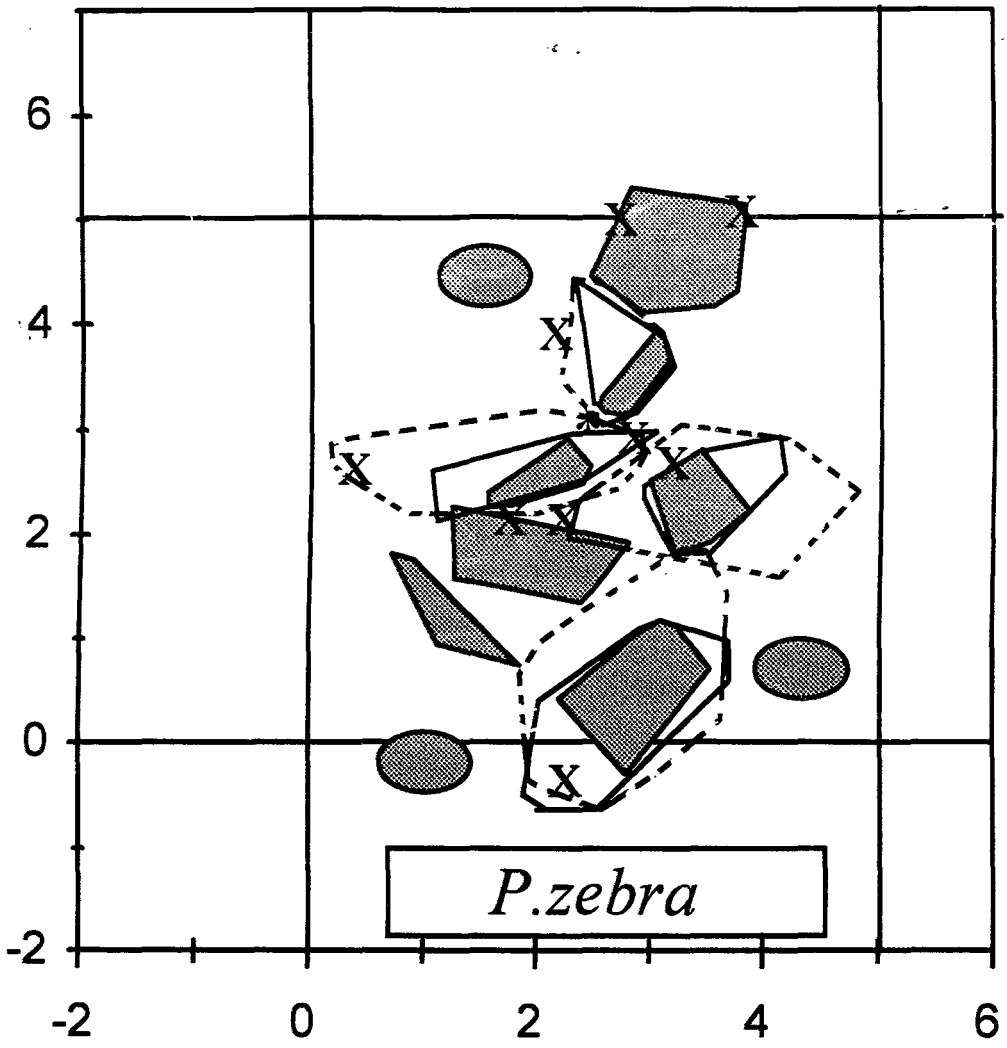


Figure 3.12.. There was no overlap between the core areas (shaded polygons) of the ten territorial *P. zebra* individuals within the quadrat. 100% defended areas (open polygons, solid borders) and feeding areas (open polygons, broken borders) showed minimal overlap. Frontal display contests (x) and circling fights (*) generally occurred near the boundaries of adjacent ranges.

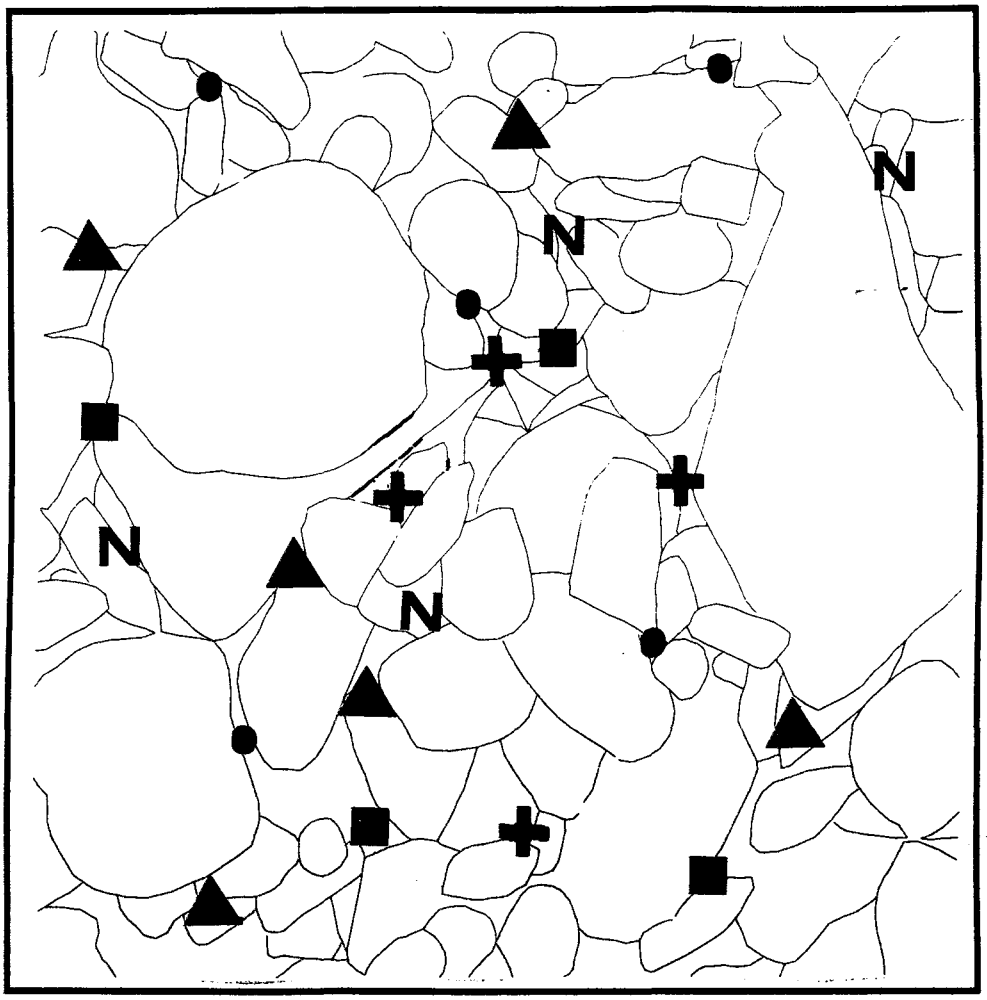


Figure 3.13. Location of spawning sites for all focal territorial individuals in the quadrat, and other fish where possible to determine. ▲ = *P.tropheops* 'orange chest'; ■ = *L. fuelleborni*; N = *P.nigra;* ● = *P. elongatus* 'aggressive'; + = *P.zebra*

DURATION OF TERRITORY OCCUPANCY

The largest individuals of all species, except one *P. elongatus* 'aggressive', maintained their territories throughout the 1½ years of field observation, whereas some of the smaller individual *P. elongatus* 'aggressive', *P. tropheops* 'orange chest' and *P. zebra* left during this time. One *P. tropheops* 'orange chest' territory was inhabited by three different small conspecific individuals during the course of the study. All of the *L. fuelleborni* remained on their territories for the duration of the field work.

No conclusions could be drawn about duration of *P. nigra* territory occupancy. Although individuals could be recognized for a few weeks at a time by torn or bitten fins, it was difficult to determine whether the same individuals were occupying their territories the following year, since body colouration was uniformly dark, all individuals had only one or two eggspots, and there were no distinctive features for long-term identification. The picture was further complicated by the considerable movement of territory boundaries between individuals, which was rarely observed in other species.

TIME BUDGETS

Mean values presented in tables represent either frequency of a particular behaviour or time (in seconds) engaged in a particular activity per 15 minute observation periods (i.e. total 900 seconds). For tables of means, Time 1 = 06.00-10.00 hours, Time 2 = 10.00-14.00 hours and Time 3 = 14.00-18.00 hours. For each table of results for ANOVA, asterisks in the left hand column indicate interactions between factors, for example species by time of day.

Time Spent in Benthic Feeding

Species differed significantly in the time spent feeding from the substrate (Table 3.2a & b; $P<0.001$), ranging from 50.4% for *P. tropheops* 'orange chest' to 17.3% for *L. fuelleborni*. *P. elongatus* 'aggressive' (20.6%), *Petrotilapia nigra* (21.3%) and *P. zebra* (26.7%) were intermediate. Individuals within species also differed significantly in the amount of benthic feeding ($P<0.001$), and there was a significant diurnal pattern ($P<0.001$) which varied among species ($P<0.05$). All species fed least in the morning, but the increase thoughout the day was much more marked in *Labeotropheus fuelleborni* (almost 12-fold between morning and afternoon periods) than in other species (1.5- to 3-fold). Individuals within a species showed very similar diurnal patterns ($P=0.96$).

Number of Benthic Feeding Bites

Species differed significantly in the number of feeding bites directed at the substrate (Table 3.3a & b, P<0.001). *P. tropheops* 'orange chest' consistently performed more feeding bites than any other species, while *Labeotropheus fuelleborni*, *P. zebra* and *Petrotilapia nigra* had much lower scores. This partly reflects the different methods of feeding, since *P. tropheops* 'orange chest' takes discrete bites at the substrate lasting less than a second, whereas the other three species graze the algae in bouts lasting several seconds. Individuals differed significantly (P<0.001), and there was a clear diurnal pattern (P<0.001) which paralleled that of the time measure and also differed between species (P<0.001). (Table 3.3a & b)

Time Spent Feeding in Midwater

During the focal watches, territorials of the five species devoted greatly different amounts of time to feeding in midwater (Table 3.4a & b, P<0.001). *Labeotropheus fuelleborni* and *Petrotilapia nigra* - the two species with the largest benthic feeding ranges- never performed this behaviour, and *P. tropheops* 'orange chest' very rarely (0.1%), while *P. elongatus* 'aggressive' (2.7%) and especially *P. zebra* (6.8%) spent considerable amounts of time on plankton feeding. There were marked differences among individuals (P<0.001), with two *P. elongatus* 'aggressive' and *P. tropheops* 'orange chest' and even one *P. zebra* never feeding in midwater. All individuals fed in midwater much more in the morning than the afternoon, giving rise to a strong diurnal trend (P<0.01). The individual by time, and species by time interactions were rendered significant, not by any deviation from this pattern, but simply by the number of species and individuals which never fed in midwater and therefore showed no diurnal pattern!

Table 3.2a. Mean time spent feeding from substrate (seconds per 15 minute period).

		Individual				
Species	**Time**	**1**	**2**	**3**	**4**	**ALL**
L. fuelleborni	1	0.7	14.3	0.0	79.8	23.7
	2	140.3	206.8	172.0	261.8	195.9
	3	248.4	294.3	278.0	325.8	286.2
***P. t.* 'orange chest'**	1	559.3	304.3	266.0	249.5	330.7
	2	697.0	436.8	494.5	573.8	542.8
	3	594.8	411.6	515.0	617.0	515.4
***P.e.* 'aggressive'**	1	56.7	82.0	120.4	133.3	94.9
	2	209.3	123.8	221.5	279.3	208.4
	3	301.0	264.0	226.8	334.8	279.7
P. zebra	1	268.3	141.0	275.5	88.8	193.4
	2	318.3	304.3	339.8	79.8	260.5
	3	341.3	301.3	304.8	124.0	267.8
P. nigra	1	139.0	205.5	151.0	25.5	130.3
	2	186.5	288.5	197.0	143.5	203.9
	3	235.5	291.0	292.5	139.5	239.6

Table 3.2b. Analysis of variance for time spent feeding from substrate.

Source	**DF**	**Seq SS**	**Adj SS**	**Adj MS**	**F**	**P**
Species	4	2937934	2797451	699363	60.30	0.000
Indiv.(species)	15	1031224	915852	61057	5.26	0.000
Time of day	2	1314467	1028326	514163	44.33	0.000
Species*Time of day	8	234547	238072	29759	2.57	0.011
Time*Individual (species)	30	199131	199131	6638	0.57	0.964
Error	179	2075987	2075987	11598		
Total	238	7793290				

Table 3.3a Mean number of feeding bites directed at substrate (per 15 minute period)

		Individual				
Species	**Time**	**1**	**2**	**3**	**4**	**ALL**
L. fuelleborni	1	0.3	3.2	0.0	14.0	4.4
	2	28.5	42.4	27.3	38.8	34.7
	3	57.4	61.5	46.8	41.0	51.2
***P. t.* 'orange chest'**	1	326.7	189.9	152.8	163.0	200.8
	2	397.0	238.3	281.8	358.4	316.4
	3	422.3	255.4	365.3	416.5	350.7
***P.e.* 'aggressive'**	1	41.1	51.2	86.9	121.0	71.1
	2	139.5	79.5	145.3	229.0	148.3
	3	152.5	164.0	136.5	215.5	166.8
P. zebra	1	62.3	34.5	45.8	20.5	40.8
	2	72.5	73.5	52.0	17.5	53.9
	3	87.3	72.8	60.5	25.5	61.5
P. nigra	1	24.0	38.5	35.0	6.0	25.9
	2	43.5	63.0	47.5	36.5	47.6
	3	47.5	56.0	74.0	42.5	55.0

Table 3.3b Analysis of variance for number of feeding bites directed at substrate.

Source	**DF**	**Seq SS**	**Adj SS**	**Adj MS**	**F**	**P**
Species	4	2177355	2142239	535560	222.26	<0.001
Individual (species)	15	298472	238246	15883	6.59	<0.001
Time of day	2	205000	177796	88898	36.89	<0.001
Species*Time of day	8	73792	95069	11884	4.93	<0.001
Time*Individual (species)	30	75041	75041	2501	1.04	0.421
Error	179	431324	431324	2410		
Total	238	3260985				

Time Spent Stationary

Species differed significantly in the amount of time they spent stationary (Table 3.5a & b, $P<0.001$), which was high in *Petrotilapia nigra* (36.8%) and *Labeotropheus fuelleborni* (29%), intermediate in *P. zebra* (18.6%) and low in *P. tropheops* 'orange chest' (7.0%) and *P. elongatus* 'aggressive' (7.5%). Individuals also differed ($P<0.01$), but there was no significant diurnal pattern ($P=0.7$).

Time Spent Swimming

Species spent different amounts of time swimming (Table 3.6a & b, $P<0.001$), *P. elongatus* 'aggressive' (66.8%) being by far the most active (*Labeotropheus fuelleborni* 47.2%, *P. tropheops* 'orange chest' 40.2%, *Petrotilapia nigra* 37.4% and *P. zebra* 30.2%). Individuals showed significant differences in swimming activity ($P=0.001$) and there was a clear diurnal pattern ($P<0.01$) with all species being most active in the morning.

Table 3.4a. Mean time spent feeding in midwater (seconds per 15 minute period).

		Individual				
Species	**Time**	**1**	**2**	**3**	**4**	**ALL**
L. fuelleborni	1	0.0	0.0	0.0	0.0	0.0
	2	0.0	0.0	0.0	0.0	0.0
	3	0.0	0.0	0.0	0.0	0.0
***P. t.* 'orange chest'**	1	0.0	4.1	0.0	3.5	2.5
	2	0.0	0.0	0.0	0.0	0.0
	3	0.0	0.0	0.0	0.0	0.0
***P.e.* 'aggressive'**	1	0.0	159.4	0.0	131.5	57.5
	2	0.0	7.5	0.0	7.3	3.7
	3	0.0	1.0	0.0	0.0	0.3
P. zebra	1	29.3	400.5	43.0	0.0	118.2
	2	0.0	96.0	58.8	0.0	38.7
	3	0.0	88.5	22.0	0.0	27.6
P. nigra	1	0.0	0.0	0.0	0.0	0.0
	2	0.0	0.0	0.0	0.0	0.0
	3	0.0	0.0	0.0	0.0	0.0

Table 3.4b. Analysis of variance for time spent feeding in midwater.

Source	**DF**	**Seq SS**	**Adj SS**	**Adj MS**	**F**	**P**
Species	4	134830	132974	33244	6.96	<0.001
Indiv(Species)	15	334488	333244	22216	4.65	<0.001
Time	2	59041	46693	23347	4.88	0.009
Species*Time	8	74518	78459	9807	2.05	0.043
Time*Indiv(Species)	30	249758	249758	8325	1.74	0.015
Error	179	855503	855503	4779		
Total	238	1708139				

Table 3.5a. Mean time spent stationary (seconds per 15 minute period).

		Individual				
Species	**Time**	**1**	**2**	**3**	**4**	**ALL**
L. fuelleborni	1	273.2	277.8	591.2	188.7	332.7
	2	216.0	47.2	595.5	135.5	236.7
	3	164.2	155.3	258.6	179.2	191.1
***P. t.* 'orange chest'**	1	0.0	192.3	115.8	85.0	134.5
	2	5.7	37.5	33.5	8.4	21.4
	3	12.5	25.0	21.5	0.0	17.4
***P.e.* 'aggressive'**	1	55.0	82.4	61.6	78.3	67.0
	2	11.8	203.5	21.0	84.8	80.3
	3	48.75	106.3	30.5	16.5	56.7
P. zebra	1	190.0	23.5	46	223.8	120.8
	2	286.8	40.0	161.3	101.3	147.3
	3	301.0	255.8	292.5	84.5	233.4
P. nigra	1	276.0	628.0	96.0	81.5	270.4
	2	683.0	347.5	318.5	349.5	424.6
	3	267.5	0.0	543.5	379.5	297.6

Table 3.5b. Analysis of variance for time spent stationary.

Source	**DF**	**Seq SS**	**Adj SS**	**Adj MS**	**F**	**P**
Species	4	2267182	2283155	570789	15.02	<0.00 1
Individual (species)	15	1386085	1355114	90341	2.38	0.004
Time	2	64527	27552	13776	0.36	0.696
Species*Time of day	8	509628	468380	58547	1.54	0.146
Time*Individual (species)	30	1457623	1457623	48587	1.28	0.166
Error	179	6801661	6801661	37998		
Total	238	12486705				

Table 3.6a. Mean time spent swimming (seconds per 15 minute period).

		Individual				
Species	**Time**	**1**	**2**	**3**	**4**	**ALL**
L. fuelleborni	1	558.2	518.5	254.7	514.3	461.4
	2	503.0	598.4	107.0	367.0	405.9
	3	473.4	441.8	326.8	346.4	394.7
P. t. 'orange chest'	1	330.3	376.6	506.5	534.5	413.3
	2	194.0	404.8	353.8	304.2	321.1
	3	278.5	407.6	346.8	277.5	339.6
P.e. 'aggressive'	1	769.6	543.6	698.3	538.8	658.6
	2	658.3	543.5	638.0	507.0	586.7
	3	531.8	508.3	620.0	516.0	540.1
P. zebra	1	356.5	285.3	443.8	190.0	318.9
	2	275.5	443.5	307.3	156.3	295.6
	3	251.3	239.8	254.0	56.8	200.4
P. nigra	1	441.5	64.5	546.5	594.5	411.8
	2	30.5	260.5	375.0	360.0	256.5
	3	369.0	585.0	47.5	361.5	340.8

Table 3.6b. Analysis of variance for time spent swimming.

Source	**DF**	**Seq SS**	**Adj SS**	**Adj MS**	**F**	**P**
Species	4	3254007	2906570	726643	19.91	<0.001
Individual (species)	15	1607979	1542460	102831	2.82	0.001
Time of day	2	319293	360259	180129	4.94	0.008
Species*Time of day	8	120281	128677	16085	0.44	0.895
Time*Individual (species)	30	1224848	1224848	40828	1.12	0.318
Error	179	6533187	6533187	36498		

Time & Frequency of Chasing

Territorial individuals of the five species spend different amounts of time chasing intruders (Table 3.7a & b, P<0.001). *P. elongatus* 'aggressive' was the most aggressive (2.1%), followed by *P. tropheops* 'orange chest' (1.2%). *P. zebra* (0.5%), *L. fuelleborni* (0.8%) and *P. nigra* (0.9%) spent less time chasing. The species showed different diurnal patterns (P<0.05), with *P. elongatus* 'aggressive' and *P. tropheops* 'orange chest' maintaining a constantly high level of aggression, while *P. zebra* and *Labeotropheus fuelleborni* became progressively less likely to chase throughout the day and *Petrotilapia nigra* exhibiting a lull in the middle of the day. Individuals showed different levels of aggressiveness (P<0.001), particularly in *Petrotilapia nigra.* Frequency of chasing showed an identical pattern (Table 3.8a & b).

Time & Frequency of Receiving Chases

Species differed in the time (Table 3.9a & b, P=0.01) and frequency (Table 3.10a & b, P<0.01) of being chased . The largest species, *Petrotilapia nigra,* and the most aggressive, *P. elongatus* 'aggressive', were rarely chased (0.02% time). *Labeotropheus fuelleborni* (0.11%) and *P. tropheops* 'orange chest' (0.09) spent 4 or 5 times as long fleeing, with *P. zebra* intermediate (0.7%). Individuals within species were chased to different extents (P<0.01), with several individuals, even one *Labeotropheus fuelleborni,* never being chased at all during the focal watches.

Table 3.7a. Mean time spent chasing (seconds per 15 minute period).

		Individual				
Species	**Time**	**1**	**2**	**3**	**4**	**ALL**
L. fuelleborni	1	19.3	4.7	12.2	6.8	10.8
	2	7.3	2.4	9.5	5.8	6.0
	3	1.8	0.3	3.0	7.0	3.2
***P. t.* 'orange chest'**	1	6.7	12.3	8.8	16.5	11.1
	2	3.0	12.8	12.5	9.4	9.8
	3	6.5	18.4	12.8	2.0	11.5
***P.e.* 'aggressive'**	1	17.1	18.0	18.3	17.0	17.7
	2	18.8	18.5	17.5	21.8	19.2
	3	17.3	16.3	18.8	29.0	19.9
P. zebra	1	5.8	7.3	3.3	10.5	6.7
	2	7.8	5.5	5.3	2.5	5.3
	3	3.5	4.5	0.5	0.8	2.3
P. nigra	1	4.0	2.0	7.5	30.5	11.0
	2	0.0	0.0	5.0	13.0	4.5
	3	6.5	16.5	3.5	13.0	9.9

Figure 3.7b. Analysis of variance for time spent chasing.

Source	**DF**	**Seq SS**	**Adj SS**	**Adj MS**	**F**	**P**
Species	4	6317.94	6449.34	1612.33	34.44	<0.001
Individual (species)	15	2131.16	2096.70	139.78	2.99	<0.001
Time of day	2	222.39	275.27	137.63	2.94	0.055
Species*Time of day	8	864.06	786.35	98.29	2.10	0.038
Time*Individual (species)	30	1919.65	1919.65	63.99	1.37	0.111
Error	179	8381.12	8381.12	46.82		
Total	238	19836.31				

Table 3.8a. Mean number of chases (per 15 minute period).

		Individual				
Species	**Time**	**1**	**2**	**3**	**4**	**ALL**
L. fuelleborni	1	10.7	3.8	6.0	3.3	6.0
	2	6.0	2.0	5.8	5.0	4.5
	3	1.8	0.3	3.0	4.8	2.6
***P. t.* 'orange chest'**	1	6.7	9.6	8.0	14.5	9.3
	2	3.0	12.8	12.5	6.6	8.9
	3	5.3	17.2	12.8	2.0	10.8
***P.e.* 'aggressive'**	1	15.8	12.6	13.1	13.0	13.7
	2	18.8	17.0	17.5	19.5	18.2
	3	16.8	14.8	17.8	21.5	17.4
P. zebra	1	3.8	3.5	2.0	4.0	3.3
	2	3.8	3.5	2.5	1.0	2.7
	3	1.8	4.5	0.5	0.8	1.9
P. nigra	1	2.0	2.0	4.0	14.0	5.5
	2	0.0	0.0	2.5	7.0	2.4
	3	2.5	4.5	2.0	7.5	4.1

Table 3.8b. Analysis of variance for number of chases.

Source	**DF**	**Seq SS**	**Adj SS**	**Adj MS**	**F**	**P**
Species	4	6422.86	6506.79	1626.70	80.54	<0.001
Individual (species)	15	924.66	957.10	63.81	3.16	<0.001
Time of day	2	8.99	9.19	4.59	0.23	0.797
Species*Time of day	8	460.04	434.70	54.34	2.69	0.008
Time*Individual (species)	30	691.67	691.67	23.06	1.14	0.290
Error	179	3615.27	3615.27	20.20		
Total	238	12123.49				

Table 3.9a. Mean time receiving chases (seconds per 15 minute period).

		Individual				
Species	**Time**	**1**	**2**	**3**	**4**	**ALL**
L. fuelleborni	1	0.5	1.3	0.7	0.0	0.6
	2	0.0	2.4	0.3	0.0	0.8
	3	3.0	3.0	0.6	0.0	1.6
***P. t.* 'orange chest'**	1	3.7	0.8	0.0	0.0	1.0
	2	0.3	0.8	0.0	1.0	0.6
	3	0.0	1.2	0.0	3.5	0.9
***P.e.* 'aggressive'**	1	0.0	1.2	0.0	0.0	0.3
	2	0.0	0.0	0.0	0.0	0.0
	3	1.3	0.0	0.0	0.0	0.3
P. zebra	1	0.8	0.3	1.0	0.3	0.6
	2	1.3	0.5	0.5	0.5	0.7
	3	0.0	1.0	1.8	0.0	0.7
P. nigra	1	0.0	0.0	0.5	0.0	0.2
	2	0.0	0.0	0.0	1.0	0.3
	3	0.0	0.0	0.5	0.0	0.2

Figure 3.9b. Analysis of variance for time receiving chases.

Source	**DF**	**Seq SS**	**Adj SS**	**Adj MS**	**F**	**P**
Species	4	24.526	26.112	6.528	3.42	0.010
Individual (species)	15	56.897	62.51	4.167	2.18	0.008
Time	2	5.078	4.656	2.328	1.22	0.298
Species*Time	8	11.123	10.933	1.367	0.72	0.677
Time*Individual (species)	30	75.805	75.805	2.527	1.32	0.135
Error	179	341.6	341.6	1.908		
Total	238	515.029				

Table 3.10a. Mean number of chases received (per 15 minute period)

		Individual				
Species	**Time**	**1**	**2**	**3**	**4**	**ALL**
L. fuelleborni	1	0.2	1.3	0.3	0.0	0.5
	2	0.0	2.4	0.3	0.0	0.7
	3	2.8	2.5	0.6	0.0	1.4
***P. t.* 'orange chest'**	1	3.7	0.4	0.0	0.0	0.8
	2	0.3	0.8	0.0	1.0	0.6
	3	0.0	1.2	0.0	3.5	0.9
***P.e.* 'aggressive'**	1	0.0	0.2	0.0	0.0	0.0
	2	0.0	0.0	0.0	0.0	0.0
	3	1.3	0.0	0.0	0.0	0.3
P. zebra	1	0.8	0.3	0.5	0.3	0.4
	2	0.8	0.5	0.5	0.3	0.5
	3	0.0	1.0	1.3	0.0	0.6
P. nigra	1	0.0	0.0	0.5	0.0	0.2
	2	0.0	0.0	0.0	1.0	0.3
	3	0.0	0.0	0.5	0.0	0.2

Figure 3.10b. Analysis of variance for number of chases received.

Source	**DF**	**Seq SS**	**Adj SS**	**Adj MS**	**F**	**P**
Species	4	21.752	24.725	6.181	4.16	0.003
Individual (species)	15	49.9	54.466	3.631	2.44	0.003
Time	2	6.347	4.874	2.437	1.64	0.197
Species*Time	8	8.024	8.257	1.032	0.69	0.697
Time*Individual (species)	30	67.418	67.418	2.247	1.51	0.053
Error	179	266.283	266.283	1.488		
Total	238	419.724				

Time and Frequency of Courtship

Labeotropheus fuelleborni spent far more time courting than any other species (Table 3.11a & b, 1.3%), while *Petrotilapia nigra* spent more than twice as much time (0.5%) in this behaviour as the three *Pseudotropheus* species (0.2%). Analysis of variance of both time and frequency (Table 3.12a & b) of courtship showed significant differences between species at the 1% level. Frequency of courtship showed a significant diurnal pattern ($P<0.05$), being lowest in the middle of the day. *L. fuelleborni* was observed to spawn once during the focal watches, although this took place at 1pm, during the middle time period when courtship was least frequent. Courtship in this case lasted 31 seconds and spawning only 40 seconds.

Territorial *P. zebra, P. tropheops* 'orange chest' and *L. fuelleborni* males in the vicinity of their spawning sites performed courtship displays to non-territorial fish of other species on some occasions, though this behaviour was never reciprocated. The most enthusiastic male courtship displays appear to have been directed at conspecific mouthbrooding females, and occasionally males would leave their territories to court such an individual. Mouthbrooding females reciprocated courtship and followed conspecific males back to the spawning site on some occasions, though the relative frequency of courtship by mouthbrooding and non-mouthbrooding females was not calculated.

Time Spent in Aggressive Displays and Fighting

None of the species spent much time in aggressive displays or fights, ranging from 0.03% in *P. elongatus* 'aggressive' to 0.7% in *P. zebra*. There were no statistically significant differences among species, individuals or times of day (Table 3.13a & b).

Table 3.11a. Time spent in courtship (seconds per 15 minute period).

		Individual				
Species	**Time**	**1**	**2**	**3**	**4**	**ALL**
L. fuelleborni	1	31.0	5.2	18.2	7.3	15.4
	2	11.5	4.0	14.8	2.3	7.9
	3	6.6	1.5	31.0	1.6	10.6
***P. t.* 'orange chest'**	1	0.0	4.8	3.0	2.0	3.4
	2	0.0	2.8	1.5	1.2	1.4
	3	0.0	1.8	3.0	0.0	1.4
***P.e.* 'aggressive'**	1	1.6	4.0	1.0	0.5	1.7
	2	0.0	2.8	2.0	0.0	1.2
	3	0.0	2.3	2.5	1.8	1.7
P. zebra	1	1.8	5.3	0.5	0.0	1.9
	2	0.0	8.0	0.0	0.0	2.0
	3	1.5	6.0	3.0	0.0	2.6
P. nigra	1	5.0	1.5	3.0	2.5	3.0
	2	0.0	0.0	4.5	0.0	1.1
	3	21.0	7.5	12.5	7.0	12.0

Table 3.11b. Analysis of variance for time spent courting.

Source	**DF**	**Seq SS**	**Adj SS**	**Adj MS**	**F**	**P**
Species	4	4192.3	3743.7	935.9	4.06	0.004
Individual (species)	15	4377.2	4109.4	274	1.19	0.283
Time	2	249.9	283.3	141.7	0.62	0.542
Species*Time	8	886.6	903.2	112.9	0.49	0.862
Time*Individual (species)	30	2351.5	2351.5	78.4	0.34	1.000
Error	179	41222.4	41222.4	230.3		
Total	238	53279.9				

Table 3.12a. Mean number of courtships (per 15 minute period).

		Individual				
Species	**Time**	**1**	**2**	**3**	**4**	**ALL**
L. fuelleborni	1	2.2	1.5	2.3	0.5	1.6
	2	1.0	1.4	0.5	0.5	0.9
	3	1.4	0.5	1.8	0.8	1.2
***P. t.* 'orange chest'**	1	0.0	0.5	0.5	1.0	0.5
	2	0.0	0.5	0.5	0.2	0.3
	3	0.0	0.4	0.5	0.0	0.3
***P.e.* 'aggressive'**	1	0.7	0.6	0.1	0.3	0.4
	2	0.0	0.3	0.3	0.0	0.2
	3	0.0	0.5	0.8	0.3	0.4
P. zebra	1	0.3	1.8	0.3	0.0	0.6
	2	0.0	0.5	0.0	0.0	0.1
	3	0.5	2.0	0.3	0.0	0.7
P. nigra	1	1.0	0.5	1.0	0.5	0.8
	2	0.0	0.0	0.5	0.0	0.1
	3	3.0	2.5	1.0	2.0	2.1

Table 3.12b. Analysis of variance for number of courtships.

Source	**DF**	**Seq SS**	**Adj SS**	**Adj MS**	**F**	**P**
Species	4	37.385	32.685	8.171	3.82	0.005
Individual (species)	15	29.266	27.028	1.802	0.84	0.628
Time	2	10.232	13.439	6.72	3.15	0.045
Species*Time	8	16.254	16.749	2.094	0.98	0.453
Time*Individual (species)	30	19.681	19.681	0.656	0.31	1.000
Error	79	382.402	382.402	2.136		
Total	238	495.222				

Table 3.13a. Mean time spent displaying and fighting (seconds per 15 minute period).

		Individual				
Species	**Time**	**1**	**2**	**3**	**4**	**ALL**
L. fuelleborni	1	13.3	5.0	2.8	0.0	5.3
	2	2.0	0.2	0.8	4.0	1.6
	3	0.8	4.0	1.2	0.0	1.4
***P. t.* 'orange chest'**	1	0.0	2.1	0.0	9.0	2.1
	2	0.0	3.8	0.0	2.0	1.6
	3	6.5	21.8	0.0	0.0	9.0
***P.e.* 'aggressive'**	1	0.0	0.0	0.0	0.5	0.1
	2	1.3	0.5	0.0	0.0	0.4
	3	0.0	0.0	1.5	0.0	0.3
P. zebra	1	1.5	4.5	7.3	6.0	4.8
	2	7.0	1.5	3.3	34.5	11.6
	3	1.0	2.8	3.5	6.8	3.5
P. nigra	1	0.0	2.0	0.0	6.0	2.0
	2	0.0	0.0	0.0	0.0	0.0
	3	0.0	0.0	0.0	7.5	1.9

Table 3.13b. Analysis of variance for time spent in aggressive displays and fights.

Source	**DF**	**Seq SS**	**Adj SS**	**Adj MS**	**F**	**P**
Species	4	1172.7	1118.4	279.6	2.03	0.092
Individual (species)	5	2135.5	2254.5	150.3	1.09	0.366
Time	2	12.4	1.1	0.5	0	0.996
Species*Time	8	1447.5	1041.5	130.2	0.95	0.479
Time*Individual (species)	30	3092.8	3092.8	103.1	0.75	0.823
Error	179	24609	24609	137.5		
Total	238	32469.9				

Aggressive Interactions

The majority of aggression involved the chasing of intruders by territorial fish. This usually lasted less than one second as the intruder immediately fled. Sometimes on rapid approach of the territory owner, intruders would perform a submissive display or move away a short distance. Often they continued to feed undisturbed in some parts of the territory, although not in the core area. Occasionally, territorial fish pursued an intruder, usually a large conspecific floater or territorial neighbour, for distances of several metres. Lateral displays by territorial fish and side-tilt submissive displays by intruders were also common, and usually brief, with one fish submitting almost instantly as another individual, usually conspecific, approached.

Aggression between conspecific territorial neighbours was less frequent but more protracted. Usually, frontal displays were performed near the territorial boundary, often taking the form of a series of mutual displays, each lasting several seconds. If neither fish retreated, an escalated fight could result. Lunges and bites, both on the mouth and flanks often led to obvious injuries, such as loss of scales on the flanks. Circling fights usually occurred when one territorial fish swam into the core area of a neighbour. Bites were sometimes exchanged on these occasions, which terminated when the intruder was chased back into its own territory.

The generally non-territorial *Melanochromis heterochromis* was frequently observed to chase *P. tropheops* 'orange chest' or *P. zebra* from underneath, so that the two individuals rose through the water column in a spiralling movement lasting several seconds.

The type and targets of aggression displayed by territorial males differed between species, although for all except *P. elongatus* 'aggressive', the majority of aggression was directed at conspecific floaters. (figs. 3.14a-f). *P. elongatus* 'aggressive' chased all intruders, rarely bothering with the subtlety of displays, and contact fights between territorial neighbours were never seen. This species was dominant in the vast majority of interactions with other species, though occasionally small individuals were dominated by large *P. tropheops* 'orange chest', or *P. nigra*. Escalated aggression was rarely seen but is summarised in Table 3.14. *P. nigra*, the largest species was dominant over all other species, and although several individuals of other species might have territories and feeding areas within its range, on the approach of a territorial male *P. nigra*, these fish would usually swim away or perform submissive displays. Only *P. elongatus* 'aggressive' attempted to chase *P. nigra* males away. *L. fuelleborni* and *P. zebra* males were dominant in most encounters, but *P. tropheops* 'orange chest' seemed to receive a large amount of aggression from *M. heterochromis*, to which it was frequently subordinate.

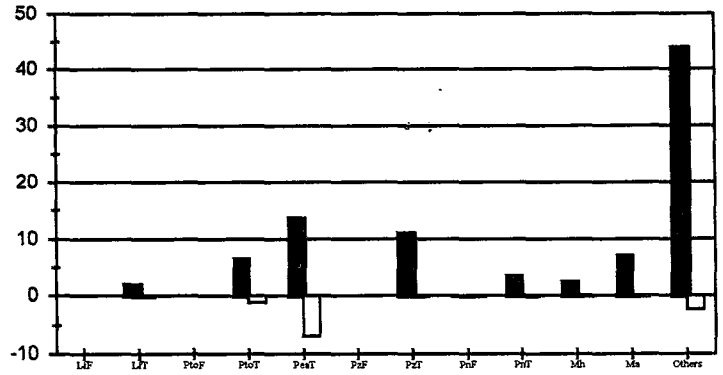


Figure 3.14. (a) *Pseudotropheus elongatus* 'aggressive' (mean number of chases given = 65.7 per hour)

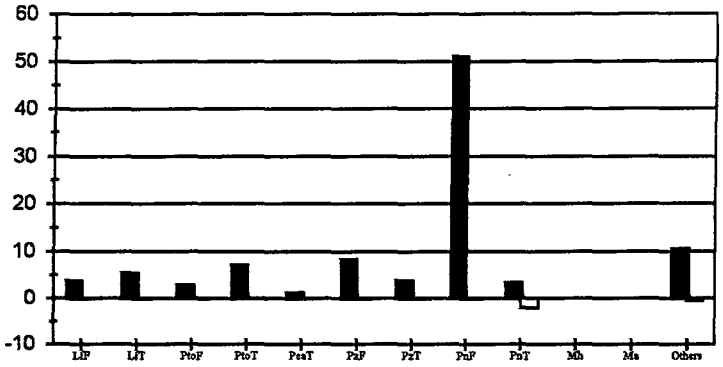


Figure 3.14. (b) *Petrotilapia nigra* (mean number of chases given = 16 per hour)

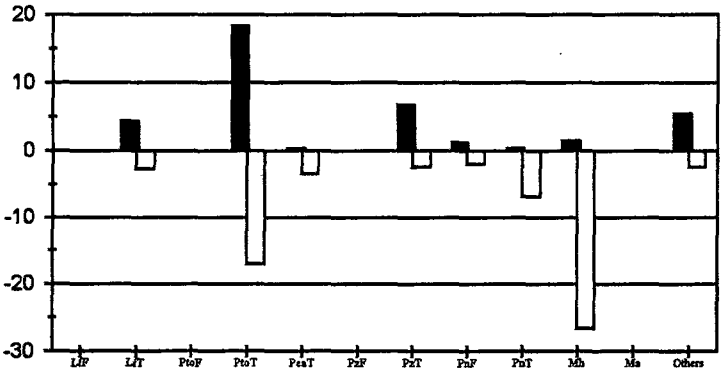


Figure 3.14. (c) *Pseudotropheus tropheops* 'orange chest' (mean number of chases given = 38.6 per hour)

Figure 3.14a-c. Aggressive interactions of territorial males of three mbuna species. Positive values on y-axis (filled bars) correspond to aggression given, negative values (open bars) to aggression received or submissive displays given. Abbreviations: Lf: *L. fuelleborni*; Pto: *P. tropheops* 'orange chest'; Pea: *P. elongatus* 'aggressive'; Pz: *P.zebra*; Pn: *P. nigra*; Mh: *M. heterochromis*; Ma: *Melanochromis auratus*. Suffix 'T': territorial; 'F': floater.

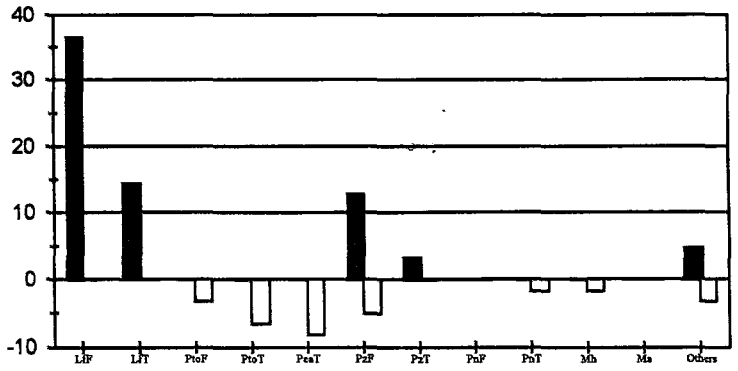


Figure 3.14. (d) *Labeotropheus fuelleborni* (mean number of chases given = 17.5 per hour)

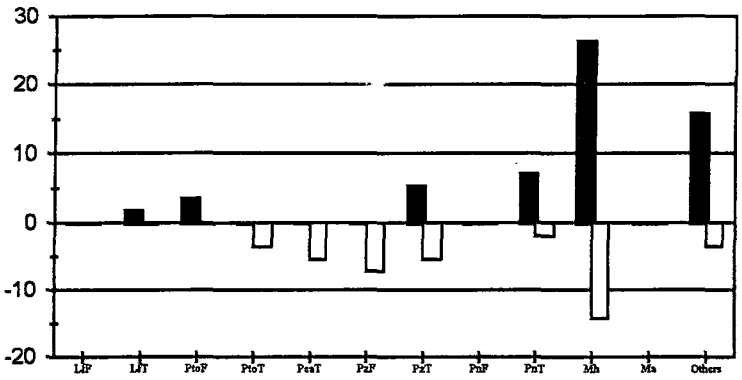


Figure 3.14. (e) *Melanochromis heterochromis*

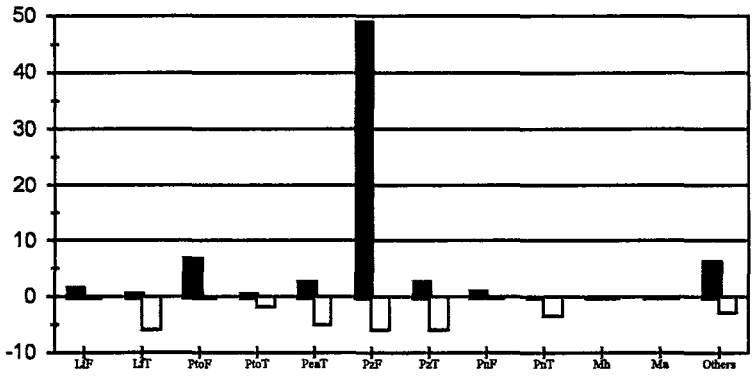


Figure 3.14. (f) *Pseudotropheus zebra* (mean number of chases given = 10.5 per hour)

Figure 3.14d-f. Aggressive interactions of territorial males of two mbuna species and non-territorial, but aggressive *Melanochromis heterochromis*. Positive values correspond to aggression given, negative to aggression received or submissive displays given. Abbreviations: Lf: *L. fuelleborni*; Pto: *P. tropheops* 'orange chest'; Pea: *P. elongatus* 'aggressive'; Pz: *P.zebra*; Pn: *P. nigra*; Mh: *M. heterochromis*; Ma: *M. auratus*. Suffix 'T': territorial; 'F': floater.

Table 3 14. Frequency and type of escalated aggressive interactions in which focal territorial individuals were involved, and the territorial status of the opponent (T=territorial, F=non-territorial). Bracketed figures indicate duration of the interaction, in seconds, or range of values when more than one interaction of a type was seen. For mutual displays, initials indicate the type of interaction x frequency (where FD = Bilateral frontal display, CA = Bilateral circle around and SP = Spiralling).

Territorial species	**Fights with conspecifics**	**Mutual Displays with conspecifics**	**Fights with different species**	**Mutual Displays with different species**
P.tropheops **"orange chest"**	Territorial: x 4 * (7-317 secs)	Territorial: 35 x FD (4 -25 secs.)		*P.zebra* (T): 2 x FD (4 secs) *P.taeniolatus* (T): 4 x FD (3-11 secs) *M.heterochromis*: 21 x SP (1-20 secs.)
P.elongatus **"aggressive"**		Territorial: 1 x FD (1 sec.) Territorial: 1 x CA (3 secs.)	*P.taeniolatus* (T): x 1 (9 secs) Crab: Lunge x 2 given, Nip x 2 received (2 sec.)	*P.zebra* (T): 1 x FD (5secs.) *Petrotilapa* (F): FD x 1 (6 secs.) *P.taeniolatus* (T): 1 x FD (3secs)
P.zebra	Territorial: x 1 (131 secs.)	Territorial: 6 x FD (3-27secs) Floater: 1 x FD (2 secs.)		*T.macrostoma* (larger): 1 x FD (4 secs.)
P.nigra		Territorial: 6 x FD (6-42 secs.)		*P.zebra* (T): 1 x FD (15 secs.) *L.fuelleborni* (T): 2 x FD (15 & 42 secs.)
L.fuelleborni	Territorial: x 7 (5-40 secs.) Floater: x 1 (4 secs.)			
M.heterochromis	2 (9 & 11 secs.)	1 x CA (4 secs.)		*P.zebra* (T): 1 x FD (4 secs.)

* Fight with territorial conspecific neighbour lasting 317 seconds involved the focal fish giving 2 mouthbites, receiving 2 mouthbites and 99 flank bites being exchanged.

Time Spent Away from Territory

Three of the focal *L. fuelleborni* individuals spent considerable times away from their territories, mainly in the afternoon, although one was also absent for a period in the middle of the day (Table 3.15). One individual was observed to swim a distance of 50 metres to feed on the surface of two large rocks, one a boulder approximately 3 metres across and the other a large vertical rocky slab. On these long excursions, the bright colouration was lost and the fish usually behaved in a subordinate manner. Occasionally, courtship attempts, in bright colouration, were observed. In each case the wandering fish was immediately chased by a large, brightly coloured conspecific in the area. Overall, this meant *L. fuelleborni* territories were vacant for an average of 3% of the daylight period and during this time were often occupied by other *L. fuelleborni* individuals, which fed in, and occasionally aggressively defended the territory against floaters, adopting bright colouration in the process. These aggressive intruders were not neighbouring territorial individuals, and would immediately become submissive upon the return of the territory owner. None of the other individuals of other species left their territories during the focal watches.

Table 3.15. Mean time spent away from territory (seconds per 15 minute period).

		Individual				
Species	**Time**	**1**	**2**	**3**	**4**	**ALL**
L. fuelleborni	1	0.0	0.0	0.0	0.0	0.0
	2	0.0	9.6	0.0	0.0	9.3
	3	252.0	45.3	19.2	0.0	80.9
***P. t.* 'orange chest'**	1	0.0	0.0	0.0	0.0	0.0
	2	0.0	0.0	0.0	0.0	0.0
	3	0.0	0.0	0.0	0.0	0.0
***P.e.* 'aggressive'**	1	0.0	0.0	0.0	0.0	0.0
	2	0.0	0.0	0.0	0.0	0.0
	3	0.0	0.0	0.0	0.0	0.0
P. zebra	1	0.0	0.0	0.0	0.0	0.0
	2	0.0	0.0	0.0	0.0	0.0
	3	0.0	0.0	0.0	0.0	0.0
P. nigra	1	0.0	0.0	0.0	0.0	0.0
	2	0.0	0.0	0.0	0.0	0.0
	3	0.0	0.0	0.0	0.0	0.0

Discussion

SPAWNING SITES

Spawning was rarely seen. Most previous studies on mbuna have not recorded spawning in the field (Holzberg 1978, Ribbink *et al.* 1983a, Marsh *et al.* 1986, Hert 1993, Kornfield *et al.* in press) and in many species takes place under rocks, where it is difficult or impossible to observe. Spawning was seen in *L. fuelleborni* and *P. t.* 'orange chest', but spawning sites were recognisable from the behaviour of males, both during courtship and when alone. The vigorous defence of the spawning site is presumably against egg predators which are numerous in the lake (McKaye 1984) or against sneaking conspecifics, though the latter have not been reported in mbuna (Chan & Ribbink 1990). Intrusions of other fish, even to feed in the area, may lead to the female leaving the male's territory and spawning elsewhere.

DEFENDED AREAS AND FEEDING RANGES

Male mbuna require a spawning site to breed. The males in the study site have a core area containing a spawning site which is defended against all individuals of all species. Although the core areas of some species overlap, the central spawning site is never shared, demonstrating that interspecific competition for space is important. Males may remain on their territories for at least 18 months (see also Hert 1990, Kornfield *et al.* in press). In other cichlid groups, individuals which are territorial for short periods may abandon feeding during the breeding season (McKaye 1977, Turner & Robinson 1991), but while a male mbuna must continue to control the spawning site, acquisition of sufficient food is essential to maintain condition over such a protracted period. Different species and individuals within a species achieve this in a variety of ways.

Two main types of territorial defence are practised. *P. elongatus* 'aggressive' vigorously defends a feeding area against all intruders, and the feeding areas of conspecifics never overlap. The core area is surrounded by a less well defended perimeter in which it does not feed. Sharp (1981) found that the territories *P. elongatus* 'aggressive' contained a higher standing crop of algae than surrounding rocks. This has been referred to as 'algal garden' (Ribbink *et al.* 1983a). A similar phenomenon is seen in the large dusky damselfish, *Stegastes dorsopunicans*, which defends an area containing a higher biomass of algae than that of other, smaller damselfish, since it is more aggressive and therefore able to inhibit blue tang surgeon fish, *Acanthurus coeruleus*, from cropping the algal mat (Foster 1985a). Although all *P. elongatus* 'aggressive' greater than 6 cm are territorial (Ribbink *et al.* 1983a), the

smallest individuals in the quadrat, identified as males by their active courtship, sometimes defended territories on large rocks with no obvious refuge or spawning site. These were the only individuals seen to receive any aggression. No female territories were identified in the quadrat. Hence, it seems that in this species a feeding territory is essential, and suboptimal sites have no refuge.

All of the other species have a core area, containing a spawning site, which is heavily defended against intruders of all species, but feeding areas are much larger and are shared with other fish. The prime function of territoriality is defence of the spawning site. Although there is very little overlap of feeding sites between territorial individuals of one species, floaters frequently feed in the territories of conspecifics, using all except the core area. Within a species, territories are often contiguous. At the periphery, very little chasing was performed, and it is defended principally against conspecific territorial neighbours, generally through frontal display contests. Although Sharp (1981) found a higher standing crop of algae on the near-vertical rock faces in *P. tropheops* 'orange chest' territories, the present study does not support his conclusion that the main function of territoriality is defence of food. The luxuriant algal growth around the spawning site would seem to be a side-effect of the defence of the refuge. Heavy algal growth was also observed in the temporary breeding territories of male *P. taeniolatus* (chapter 6). One *P. tropheops* 'orange chest' territory in the quadrat apparently did not have a refuge, but no individual remained on this territory for more than a few months, suggesting it was a suboptimal site. Other authors have concluded that within the *P. zebra* and *Petrotilapia* species complexes, territoriality is not in defence of feeding sites and, either species do not compete for food, food is not a limiting factor, or resource subdivision occurs on a finer scale (Holzberg 1978, Marsh & Ribbink 1985).

Petrotilapia nigra and *L. fuelleborni* were the largest permanently territorial fish in the quadrat and their extensive feeding ranges may be explained by their energetic demands. They also have the most specialized feeding apparatus (Ribbink *et al.* 1983a), perhaps allowing them to share feeding areas with other species, although both species avoided the territories of large *P. elongatus* 'aggressive'. This had been previously shown for *P. nigra* by Marsh & Ribbink (1985). Unlike the *Pseudotropheus* species, territorial males of these two large species were never observed to feed on plankton, during focal watches, though according to Reinthal (1990), these two species had the widest feeding resource breadths of the mbuna in the present study. Plankton may provide an important supplement to the diets of fish with smaller benthic feeding ranges, and more generalised trophic morphology. The fish that fed on plankton usually did so in midwater above their territory. Not only did the frequency of plankton feeding vary between species but also within species.

Some fish are apparently unable to find sufficient benthic algae in the vicinity of the spawning site. Three of the focal *L. fuelleborni* spent considerable times feeding away from their defended areas, usually in the afternoon. During these forays, their appearance and behaviour was generally indistinguishable from those of conspecific floaters. Although these distant feeding sites did not appear to be optimal mbuna territories, they did appear to be defended by conspecifics. When these territorial fish vacated their territories, conspecific floaters sometimes temporarily replaced the residents and looked and acted like territorials. This indicates that floaters can rapidly assume the territorial role and suggests that a dominance hierarchy among floaters may determine succession to vacated territories.

Intraspecific variation of feeding areas was most marked in *P. zebra.* The largest of the focal individuals (#4) had the smallest feeding area, spent the least time benthic feeding, and was the only individual never seen to feed in midwater. It was also the second least active, the second least aggressive, and received the least aggression. As it remained in this territory for more than a year, its small territory must have met all its requirements. The small individual with the largest territory and feeding range (#2), spent the second least time benthic feeding, was the most active and performed the most chases. It spent almost five times as much time plankton feeding as any of the others.

The territorial boundaries of *P. nigra, L. fuelleborni* and *P. tropheops* 'orange chest' appear to be determined by behaviour of conspecifics, since peripheral zones of neighbours often abutted. In contrast, peripheral zones of territories of *P. zebra* and *P. elongatus* 'aggressive' were rarely abutting, and large areas of the quadrat appear to be unused by territorial fish.

INDIVIDUAL SIZE AND DURATION OF TERRITORY OCCUPANCY

Individual territorial *Pseudotropheus* were more variable in size than those of the other genera. This seemed to be related to duration of territory ownership, with larger individuals maintaining their territories throughout the study period (18 months). Small *P. tropheops* 'orange chest' and *P. elongatus* 'aggressive' often controlled territories without a refuge, but tenure of these territories was often for only a few months. Some of the smaller *P. zebra* were considered to be 'semi-territorial' (see Chapter 4). On Thumbi West Island, Kornfield *et al.* (in press) also found that smaller male *P. zebra* remained on their territories for shorter periods.

AGGRESSIVE INTERACTIONS

P. elongatus 'aggressive' was the most aggressive species, and a higher proportion of its aggression was chasing rather than displays and fights. All of the space used by territorial fish of this species was defended interspecifically. For the other species, defence of the territory appears to operate at two scales. In the core area, no intruders are tolerated, perhaps to prevent incursions in the event of successful courtship. This represents an interspecifically-defended spawning site. A larger area is defended principally against conspecific territorial neighbours, and this will be referred to as a mating territory. In this area large conspecific floaters which did not behave submissively and territorial neighbours were attacked, possibly as they may present a threat of territory take-over or compression of boundaries. Numerous floaters, including conspecifics, fed in the peripheral zones (the mating territory) of all species except *P. elongatus* 'aggressive', and were apparently tolerated. In addition, all territorial fish maintained an 'individual space' within their feeding range, occasionally chasing floaters feeding close by. Floaters of many territorial species, and non-territorial species such as *Melanochromis auratus* (Hert 1993) show similar behaviour.

Circling fights initiated as one territorial *L. fuelleborni* swam into a neighbour's spawning cave may function as assessments of the neighbour's fighting ability and perhaps territory quality, since the intruder never attempted to feed in the area, and swam directly into the core area.

INTRASPECIFIC TERRITORIALITY

Wilson (1975) stated that territorial displays involve conspicuous and elaborate behaviour aimed to increase the apparent size of the performer, that the resident usually wins contests, and contests are mostly limited to bluffing, with serious injuries being rare. All of the mbuna described in this study display typical intraspecific territoriality of this nature. In mbuna, as in birds, aggression usually increases towards the centre of the territory, where a male is usually invincible (Tinbergen 1939). The centre may be the spawning site or the most concentrated feeding site, depending on the species. The gradient of aggressiveness and dominance from the territory centre also varies between species, with *P. elongatus*' aggressive' defending the perimeter almost as much as the core. The other species showed concentric zones of outwardly decreasing dominance, which is also seen in Stellar's Jays,*Cyanocitta stelleri* (Brown 1963). Like many mbuna, some territorial birds, such as savannah sparrows, *Passerculus sandwichensis,* also forage mostly outside the defended area (McLaren 1972), and Orians (1969) considers that polygynous birds are particularly likely to

occur in places where food is plentiful but numbers of breeding sites are restricted.

In *L. fuelleborni, P. tropheops* 'orange chest' and *P. nigra* where mating territories of conspecific males are frequently abutting, but rarely overlapping, spacing between males of each species may be an important factor in determining territory size and therefore the number of territories available. If this is the case, then the behaviour of conspecifc neighbours is more important than that of other species. This type of spacing behaviour is seen in many animals, but in fish it has been most dramatically demonstrated in *Oreochromis mossambicus,* where males defend hexagonal territories in a homogeneous habitat (Barlow 1974a). The topographic heterogeneity of the rocky shores of Lake Malawi may explain why mbuna territories are not so regular in shape.

POPULATION REGULATION

As territories cannot be indefinitely compressible without becoming uneconomical to defend, they may have the effect of limiting the size of the breeding population, although this is not their function. There may be a large proportion of males that are prevented from breeding, but female mbuna can mate at will and there is no evidence that the number of female mbuna is affected by territorial behaviour. The mating system is polygamous and males can mate repeatedly, so territoriality cannot lead to population regulation by limiting reproduction. In some butterflies, males are territorial but all females are inseminated regardless of whether all or only a small percentage of males obtain territories (Shapiro 1975). A similar system may operate in the mbuna, since multiple paternity has recently been demonstrated (Parker and Kornfield pers comm.). Indeed, intermale competition may result in the largest and strongest individuals holding the best sites, and receiving the most mating opportunities, and if this has a genetic basis, this could improve the fitness of the population. Territoriality could limit populations if floaters were unable to find adequate food resources, but neither behavioural observations (*P. zebra*: chapter 4) nor studies of body condition (*P. zebra, Cynotilapia afra:* Munthali, in press) support this contention. *P. elongatus* 'aggressive' may be an exception in being limited by availability of feeding territories. Population size may not be affected by territoriality at all. There is little evidence in fish that recruitment of juveniles is related to adult population size, but ample evidence that adult population sizes are principally determined by juvenile mortality (Pitcher & Hart 1982, Wootton 1990). Competition between fry for refuge sites may be the critical process (Trendall 1988), but survival of young stages may also be heavily influenced by stochastic events.

The present study demonstrates interspecific territoriality between five species of mbuna. The interactions between individuals depend on the species and size as well as individual aggression. Although Murray (1971, 1976) suggested that interspecific territoriality was an accident of misidentification, and therefore maladaptive, it seems unlikely that animals such as cichlids, which rely so heavily on pattern and colouration in communication (Baerends & Baerends van Roon 1950) would be unable to differentiate between conspecifics and other species. It is now generally considered that interspecific territoriality results from competition between sympatric species (Catchpole & Leisler 1988). Adaptive convergence between similar species may produce mutually exclusive territories, since there are advantages to excluding any species competing for the same resource (Cody 1969). So, for Malawi mbuna, coexistence may be facilitated by social dominance and the complex suite of cichlid behaviour.

Interspecific territoriality has been documented in several other fish communities. In Lake Tanganyika, a size-based dominance hierarchy exists between three coexisting herbivorous cichlid species which were found to maintain discrete intra- and interspecific territories, though the feeding areas of some overlapped (Kohda 1991). Territoral fish attacked small intruders but exhibited displays towards larger neighbours irrespective of species. A different system was found to operate in the three spot damselfish, *Eupomacentrus planifrons,* which was found to attack intruders presented in a jar at a critical distance for the species, though in this case size was insignificant, and conspecifics were attacked at a greater distance (Myrberg & Thresher 1974). In some reef fishes, aggressive defence of a territory is directed at species with similar feeding habits (Sale 1991), and this was interpreted by Robertson and Gaines (1986) as evidence of limited resource availability. Selective defence is also seen in *Pomacentrus flavicauda* which evicts 38 species from its territory, 35 of them food competitors, but allows access to another 6 species that are not food competitors (Low 1971). In other cases, aggression in reef fish does not appear to be directed at feeding competitors (Bellwood and Choat 1990).

Interspecific territoriality is considered to be an important spacing mechanism in birds (Catchpole & Leisler 1988, Robinson & Terborgh 1995). In contrast to the present study, interspecific defence in birds is often highly directed, with only particular species being excluded. In a large number of closely-related Amazonian birds most interspecific territoriality was shown to be asymmetrical, in that one species in each interacting pair generally dominates the other, resulting in non-overlapping territories (Robinson & Terborgh 1995). Birds with overlapping territories tended not

to interact aggressively, or to act with reduced intensity when they did interact. The authors concluded that aggression led to spatial segregation

In Fretwell & Lucas' (1970) model, interspecific aggression determines priority of access to high quality habitats, so that the dominant partner in a species pair would exclude the other from some habitats, but by virtue of its larger size, would be obliged to feed at a higher rate. Thus, some patches in a habitat would be unable to support the dominant species. A similar phenomenon may be occurring between *P. zebra* and *P. elongatus* 'aggressive', whose feeding areas rarely overlap. Large *P. elongatus* 'aggressive' are able to exclude *P. zebra* from their territories by 'despotism' not because of their absolute size, but relative size and aggression. Smaller individuals, though equally aggressive, are less able to exclude *P. zebra.* Large areas of the quadrat are unused by *P. elongatus* 'aggressive', which may be a reflection of the energetic demands of its extremely aggressive behaviour.

Studies of space use by the component species in different assemblages might shed some light on whether any of the species are being excluded from their preferred habitat by dominant species. The yellow-headed blackbird *Xanthocephalus xanthocephalus* is dominant over the red-winged blackbird *Agelaius phoeniceus.* When they both nest in their preferred marshy habitat, the redwings are forced out of their most favoured sites by the yellow-headed blackbirds (Orians & Wilson 1964). Carolina Chickadees (*Parus carolinensis*) expanded their feeding ranges when their socially dominant congener the Tufted Titmouse(*Parus bicolor*) was artificially removed (Cimprich & Grubb 1994). In some animals territory size also varies with the number of competitor species present at a particular site. This has been demonstrated in song sparrows (*Melospiza melodia*) where territory size increases with the number of small nesting bird species (Cody 1974).

Chapter 4. Territorial and non-territorial *P. zebra*.

Introduction

The rocky shores of Lake Malawi are inhabited by a variety of species of endemic haplochromine cichlids. The most conspicuous and well-studied are the mbuna, a group of 10 morphologically similar and probably closely related genera (Ribbink *et al.* 1983a). Some species appear to be non-territorial (Ribbink *et al.* 1983a). In others adult males may hold breeding and feeding territories for several years (Kornfield *et al.*, in press). In most such species, juveniles, females and many males are non-territorial, and these non-territorial individuals are collectively referred to as 'floaters' (Holzberg 1978, Ribbink *et al.* 1983a). These fish can be seen in large numbers in any rocky habitat of Lake Malawi, often feeding a few metres above the rocks, on plankton (Ribbink *et al.* 1983a). Previous studies have documented the existence of floaters, but their behaviour and patterns of space use have not previously been investigated. This chapter reports behavioural observations of floaters of *Pseudotropheus zebra* at Thumbi East Island in southern Lake Malawi, and compares them with those of territorial conspecifics.

P. zebra is among the most numerous, widespread and best-studied of the mbuna (Holzberg 1978, Ribbink *et al.* 1983a, Munthali in press, Kornfield *et al.* in press). Formerly thought to be a single polymorphic species (Fryer & Iles 1972), it is now known to comprise more than twenty distinct populations, many of which represent biological species (Ribbink *et al.* 1983a, Stauffer & Hert 1992). The most widespread form is characterised by the strongly-barred blue and black (BB-morph) territorial and courtship colour of the males (Ribbink *et al.* 1983a). Females and non-territorial males of the BB-morph are typically dull blue-grey with faint bars, although females may also be bright orange (O-morph) or orange with black blotches (OB-morph).

Up to 20-28 mm standard length, juvenile *P. zebra* and other mbuna live cryptically under rocks and have restricted home ranges and defended refuges (Trendall 1988). Larger fish of both sexes live in the open and sometimes feed in midwater (Ribbink *et al.* 1983a). Females of the related *Pseudotropheus aurora* frequently return to favoured 'sleeping places' each night and appear to have restricted home ranges (Hert 1992). Some sexually mature males defend territories which include a cave serving as a refuge and spawning site, as well as a feeding site, but may leave their territories to forage elsewhere either benthically or in midwater (Kornfield *et al.*

in press, Munthali in press). Other mature males are reported to be non-territorial floaters. At Nkhata Bay, Holzberg (1978) estimated that 43% of the mature males were floaters, while Munthali (in press) found between 76% and 80% at Thumbi West island.

Aims and Objectives

The aims of the present study were firstly to determine whether floaters of *P. zebra* occupy limited home ranges. Secondly, to compare the time budgets, including diurnal patterns of territorial and non-territorial *P. zebra* to determine, for example, whether floaters spend more time feeding on plankton than territorial fish. Aggressive interactions within the floater community and between floaters and territorials were investigated to determine whether floaters are able to control access to resources such as benthic feeding sites. The possible roles of coloration and size in the outcome of aggressive interactions were investigated, as was the possibility that floaters might have the opportunity to court and mate. Finally, the differences between individuals in space utilisation and aggression was examined and compared.

Methods

IDENTIFICATION OF INDIVIDUALS

Fourteen individual *P. zebra* floaters of undetermined sex were caught in a monofilament net, tagged and their total length (TL) measured before being released. Five individual *P.tropheops 'orange chest'* were tagged and observed, and their behaviour compared qualitatively with that of territorial conspecifics and floaters of different species.

SPACE UTILISATION AND TIME BUDGETS

Colour-coded markers were placed at known intervals along the lake bed to form a grid around the site of capture and subsequent release. Using these markers and the main features of the area, a map was drawn and transcribed onto perspex slates for use underwater.

For observation periods of 15 minutes, focal individuals were followed and the amount of time spent in each behavioural activity recorded. Behavioural interactions were also recorded, noting the relative size and colour of both the focal tagged fish and individuals with which they interacted in each encounter, at the same time their

position on the map was marked. In addition, whenever a tagged fish was seen, its position and behaviour was entered onto the map. Home range areas were calculated as minimum convex polygons, using the program 'Home Range' (see chapter 3).

Some of the tagged individuals were recaptured at the end of the study so that their sex could be determined, but logistic difficulties prevented this in the majority of cases.

Results

HOME RANGES OF FLOATERS

Floaters, which were followed over periods of between 1 and 61 days, were repeatedly observed over restricted home ranges, which varied in size from 1.1 to 101 m^2 (Table 4.1). Smaller fish tended to have larger home ranges, but this was not statistically significant (Pearson's correlation, r = -0.27, 11 df, P = 0.31). The main axis of the larger ranges was invariably parallel to the shore, along an approximate depth contour. This might suggest that they remain in the depth zone to which their swimbladders were equilibrated. Individuals thus occupied very narrow depth distributions- far narrower than that of the species as a whole. Floater ranges overlapped with each other and with numerous conspecific territories. Within their ranges, individual floaters had preferred areas for benthic feeding, where they were frquently seen, and often several widely spaced areas. These preferred areas differed between individuals. The ranges and feeding sites of floaters encompassed territories of both conspecific and non-conspecific males, to which floaters wer subordinate, but floaters did not feed in the areas defended by *Pseudotropheus elongatus* 'aggressive'.

TIME BUDGETS

Time Spent on Benthic Feeding

Both territorial and floater *P. zebra* spent considerable amounts of time feeding from the substrate (means of 29 and 16% respectively). Territorial *P. zebra* spent significantly more time feeding from the substrate than floaters (Table 4.2a & b, $P<0.001$). Both floaters and territorial fish tended to feed more later in the day ($P<0.001$). Although the increase was more marked for floaters (mean of 102 to 216 seconds compared to 234 to 295 for territorials), there was no significant type/time interaction (P=0.41). There were significant differences between individuals, irrespective of whether they were floaters or territorials, in both the overall feeding

time (P<0.001) and in the distribution of feeding throughout the day (P=0.01). Six floaters fed little in the morning or in the middle of the day, while two maintained a high feeding rate all day.

Table 4.1. Summary of *P. zebra* floaters tagged and observed.

Indiv Code #	Period of Observed (days)	Number of Focal Watches	TL (cm)	Range size (m^2)	Mean Number. of Dominant Acts/hr	Mean Number of Subordinate Acts/hr	Notes
6	61	26	9.2	28.17	1.6	4.8	
11	13	14	8.4	78.53	7.6	10.9	**Female.** Dominant over #14.
12	34	26	7.3	101.0	0.9	12.4	
13	9	17	9.9	36.13	2.7	3.6	Occasionally strongly barred and bright blue.
14	18	21	6.5	30.1	3.6	8.8	Darks bars, 2 eggspots. Sexually immature. Submissive to #11
17	16	11	7.7	19.1	5.3	6.7	3 egg-spots. Submissive to #15
18	13	13	9.5	22.72	2.5	7.5	Occasionally strongly blue & barred..
21	38	12	8.6	34.26	0.0	8.0	OB **female.** Plankton feeds alone
5*	2	2	8.9	37.14	0.0	4.0	
9*	6	7	9.3	3.12	2.0	12.0	
3*	1	1	8.5	4.77	0.0	8.0	
15*	16	3	8.5	1.12	-	-	Dominant over No.17
10*	2	4	7.9	13.07	-	-	

* Individuals #3, 5, 9, 10 & 15 were excluded from the time budget analysis as insufficient replicates were obtained for all observation periods.

Number of Benthic Feeding Bites

The total number of feeding bites did not differ between floaters and territorials, a reflection of the greater interval between bites by territorial fish (mean = 5) than floaters (3.3). Individual fish differed significantly in the numbers of feeding bites (Table 4.3a & b, P<0.001). As with time spent feeding, there was a strong diurnal

effect, most fish feeding more later in the day (P<0.001). Floaters and territorials differed in the distribution of feeding bites throughout the day (P=0.001)- the increase from the earliest to latest observational periods being much greater in floaters (mean = 161%) than territorials (23%). There were significant differences between the diurnal patterns of individual fish (P=0.001).

Table 4.2a. Mean time spent feeding from substrate (seconds per 15 minute period).

	Time[1]	1	2	3	4	5	6	7	8	ALL
Territorial	**1**	315.5	141.0	275.5	88.8	119.0	268.3	231.0	416.8	234.1
Territorial	**2**	258.7	304.3	339.8	79.8	147.0	318.3	383.3	223.5	264.3
Territorial	**3**	490.0	301.3	304.8	124.0	153.0	341.3	361.8	309.0	294.8
Floater	**1**	338.0	20.4	294.8	0.0	57.8	158.5	45.8	38.8	101.8
Floater	**2**	315.8	60.4	261.5	6.2	77.0	183.0	116.3	74.0	129.8
Floater	**3**	323.0	96.5	284.8	132.0	195.5	197.0	296.3	219.5	215.5

Table 4.2b. Analysis of variance for time spent feeding from subatrate.

Source	**DF**	**Seq SS**	**Adj SS**	**Adj MS**	**F**	**P** [2]
type[3]	1	689452	492402	492402	66.90	0.000 ***
indiv(type)	14	1615691	1554430	111031	15.09	0.000 ***
time	2	234924	217161	108581	14.75	0.000 ***
type*time[4]	2	21486	13351	6676	0.91	0.406
time*indiv(type)	28	383988	383988	13714	1.86	0.010 *
Error	148	1089302	1089302	7360		
Total	195	4034842				

[1]. For all time budget analyses Time 1 = 06.00-10.00 hours; Time 2 = 10.00-14.00 hours and Time 3 = 14.00-18.00 hours.

[2]. Asterisks to the right of tables of results for ANOVA indicate significance level, where *** = 99.9%, ** = 99% and * = 95%.

[3] 'type' means whether individuals were floaters or territorials.

[4] Asterisks in the left hand column indicate interactions which were tested. For example 'type*time' represents the test for different behaviour with time of day **between** floaters and territorials.

Table 4.3a. Mean number of feeding bites directed at the substrate (per 15 minute period).

	Time	1	2	3	4	5	6	7	8	ALL
Territorial	1	35.5	34.5	45.8	20.5	43.0	62.3	59.8	64.0	46.6
Territorial	2	93.0	9.5	63.2	0.0	18.0	49.3	12.2	13.6	27.7
Territorial	1	62.0	73.5	52.0	17.5	46.0	72.5	51.8	45.5	52.7
Floater	2	92.5	26.2	64.0	6.2	25.0	60.8	29.5	34.8	40.2
Floater	1	43.0	72.8	60.5	25.5	46.5	87.3	52.0	63.3	58.0
Floater	2	94.8	35.5	77	109.4	47.5	68.3	62.8	79.3	72.9

Table 4.3b. Analysis of Variance for feeding bites directed at the substrate.

Source	DF	Seq SS	Adj SS	Adj MS	F	P
type	1	2527.5	329.2	329.2	0.66	0.417
indiv(type)	14	73600.1	67826.6	4844.8	9.74	0.000 ***
time	2	27635.3	19301.3	9650.7	19.40	0.000 ***
type*time	2	8697.8	7357.4	3678.7	7.40	0.001 **
time*indiv(type)	28	32569.0	32569.0	1163.2	2.34	0.001 **
Error	148	73607.6	73607.6	497.3		
Total	195	218637.4				

Time Spent Feeding in Midwater

Floaters spent more time feeding in midwater (36%) than any other activity. On average, territorial fish spent 7% of their time on midwater feeding. Floaters spent significantly more time feeding in midwater than did territorial fishes (Table 4.4a & b, $P<0.001$), although there were significant differences between individuals ($P<0.001$)- two territorials and one floater were never observed to feed in midwater. There was a strong diurnal pattern ($P<0.001$), with the incidence of midwater feeding declining during the day, the reverse of the trend for benthic feeding. The diurnal trend varied between individuals ($P<0.001$) and between floaters and territorials ($P<0.001$), being much more marked in floaters (mean decline of 96%) than in territorials (52%).

Table 4.4a. Mean time spent feeding in midwater (seconds per 15 minute period).

	Time	1	2	3	4	5	6	7	8	ALL
Territorial	**1**	0.0	400.5	43.0	0.0	0.0	29.3	24.8	107.3	86.4
Territorial	**2**	0.0	96.0	58.8	0.0	22.5	0.0	0.0	237.8	55.7
Territorial	**3**	0.0	88.5	22.0	0.0	88.0	0.0	13.0	122.0	41.4
Floater	**1**	58.8	719.8	205.8	899.7	477.0	0.0	752.0	713.8	537.1
Floater	**2**	15.0	433.0	0.0	765.8	307.5	0.0	704.2	238.5	346.2
Floater	**3**	37.0	3.8	0.0	101.4	0.0	0.0	0.0	0.0	20.3

Table 4.4b. Analysis of variance for time feeding in midwater

Source	DF	Seq SS	Adj SS	Adj MS	F	P
type	1	3265366	2028892	2028892	60.50	0.000 ***
indiv(type)	14	6087272	5069874	362134	10.80	0.000 ***
time	2	2839160	1845841	922920	27.52	0.000 ***
type*time	2	1602163	1394642	697321	20.79	0.000 ***
time*indiv(type)	28	2596311	2596311	92725	2.76	0.000 ***
Error	148	4963467	4963467	33537		
Total	195	21353738				

Time Stationary

Territorial and floating individuals did not differ in the amount of time spent stationary (mean values 19 and 21% respectively), but there was a significant difference between individual fish (Table 4.5a & b, $P<0.001$). There was a significant diurnal pattern ($P<0.01$), with most fish generally spending longer periods motionless later in the day. The diurnal patterns of floaters and territorials were different ($P<0.05$), with floaters showing a more marked increase in time stationary throughout the day (floater mean increase =235%, territorials =43%)

Table 4.5a. Mean time spent stationary (seconds per 15 minute period).

	Time	1	2	3	4	5	6	7	8	ALL
Territorial	**1**	278.5	23.5	46.0	223.8	209.0	190.0	309.3	3.5	148.5
Territorial	**2**	71.3	40.0	161.3	101.3	260.5	286.8	282.8	26.5	149.3
Territorial	**3**	174.5	255.8	292.5	84.5	6.0	301.0	334.0	125.8	212.0
Floater	**1**	137.3	17.3	182.4	0.0	117.5	380.3	10.8	49.8	92.7
Floater	**2**	44.8	122.2	320.8	1.4	139.8	664.3	10.3	392.8	192.5
Floater	**3**	17.8	284.0	561.5	226.2	138.0	603.8	55.0	619.3	310.6

Table 4.5b. Analysis of variance for time spent stationary

Source	DF	Seq SS	Adj SS	Adj MS	F	P	
type	1	19521	80059	80059	2.46	0.119	
indiv(type)	14	3671712	3658617	261330	8.04	0.000	***
time	2	689497	426021	213010	6.55	0.002	**
type*time	2	175305	210957	105478	3.24	0.042	*
time*indiv(type)	28	1282830	1282830	45815	1.41	0.100	
Error	148	4811791	4811791	32512			
Total	195	10650656					

Time Swimming

In general territorial fish spent more time swimming than floaters (Table 4.6a & b, $P<0.001$), although there were marked differences between individuals ($P<0.001$). Territorial fish spent on average 34% of their time swimming- more than any other activity- compared to 23% for floaters. There was no overall diurnal trend, but significant differences ($P<0.05$) between the diurnal patterns of territorials, which were least active late in the day, and floaters which were most active in the afternoon.

Table 4.6a. Mean time spent swimming (seconds per 15 minute period).

	Time	1	2	3	4	5	6	7	8	ALL
Territorial	**1**	303.0	285.3	443.8	190.0	561.5	356.5	265.3	331.3	329.2
Territorial	**2**	567.7	443.5	307.3	156.3	405.0	275.5	210.8	370.8	330.0
Territorial	**3**	233.5	239.8	254.0	56.8	614.0	251.3	185.0	325.5	248.0
Floater	**1**	361.0	141.5	209.2	0.0	229.0	346.8	90.8	94.6	163.1
Floater	**2**	519.0	209.4	247.3	121.6	334.5	50.5	59.8	65.0	191.1
Floater	**3**	511.0	357.8	49.3	331.4	476.3	84.0	368.5	18.8	276.3

Table 4.6b. Analysis of variance for time spent swimming

	DF	Seq SS	Adj SS	Adj MS	F	P
type	1	451529	36483	436483	13.18	0.000 ***
indiv(type)	14	2298670	2213481	158106	4.77	0.000 ***
time	2	17574	3176	1588	0.05	0.953
type*time	2	317292	235846	117923	3.56	0.031 *
time*indiv(type)	28	1323030	1323030	47251	1.43	0.092
Error	148	4901894	4901894	33121		
Total	195	9309990				

Time Spent Chasing

Neither territorial (0.5%) nor floater (0.06%) fish spent much time chasing. Territorial fish spent significantly more time chasing (Table 4.7a & b, $P<0.001$). The overall frequency of chasing declined during the day ($P<0.05$). This was an effect of the 56% decline in chasing by territorials. Floaters showed a different diurnal pattern ($P<0.05$), chasing more later in the afternoon.

Table 4.7a. Mean time spent chasing (seconds per 15 minute period).

	Time	1	2	3	4	5	6	7	8	ALL
Territorial	**1**	2.5	7.3	3.3	10.5	8.5	5.8	7.3	8.0	6.8
Territorial	**2**	0.7	5.5	5.3	2.5	4.0	7.8	2.3	10.3	5.0
Territorial	**3**	1.0	4.5	0.5	0.8	3.0	3.5	3.5	6.3	3.0
Floater	**1**	3.0	0.0	0.0	0.1	0.0	1.0	0.0	0.0	0.4
Floater	**2**	1.3	0.0	0.3	0.0	2.3	0.0	0.0	0.0	0.4
Floater	**3**	1.0	0.5	0.5	1.6	0.0	0.0	1.5	0.5	0.7

Table 4.7b. Analysis of variance for time spent chasing

Source	DF	Seq SS	Adj SS	Adj MS	F	P
type	**1**	937.52	796.93	796.93	57.08	0.000 ***
indiv(type)	**14**	308.98	299.40	21.39	1.53	0.106
time	**2**	72.26	95.45	47.72	3.42	0.035 *
type*time	**2**	130.94	115.57	57.78	4.14	0.018 *
time*indiv(type)	**28**	277.52	277.52	9.91	0.71	0.855
Error	**148**	2066.47	2066.47	13.96		
Total	**195**	3793.69				

Number of Chases

Territorial fish performed more chases (Table 4.8a & b $P<0.001$), but there were significant differences between individuals ($P<0.01$). Again there was a difference in the diurnal patterns of the two types of *P. zebra* ($P<0.05$), with territorial fish being less aggressive in the afternoon. Neither territorials nor floaters were observed to chase during periods of midwater feeding.

Table 4.8a. Mean number of chases (per 15 minute period).

	Time	1	2	3	4	5	6	7	8	ALL
Territorial	**1**	1.0	3.5	2.0	4.0	6.5	3.8	2.8	3.3	3.3
Territorial	**2**	0.7	3.5	2.5	1.0	3.5	3.8	1.0	3.5	2.4
Territorial	**3**	0.5	4.5	0.5	0.8	2.0	1.8	1.5	3.3	1.9
Floater	**1**	3.0	0.0	0.0	0.1	0.0	1.0	0.0	0.0	0.4
Floater	**2**	1.3	0.0	0.3	0.0	0.5	0.0	0.0	0.0	0.2
Floater	**3**	1.0	0.5	0.5	1.6	0.0	0.0	1.0	0.5	0.7

Table 4.8b. Analysis of variance for number of chases

Source	DF	Seq SS	Adj SS	Adj MS	F	P
type	1	215.892	194.018	194.018	61.10	0.000 ***
indiv(type)	14	114.176	112.250	8.018	2.52	0.003 **
time	2	9.284	16.996	8.498	2.68	0.072
type*time	2	19.950	19.766	9.883	3.11	0.047 *
time*indiv(type)	28	72.821	72.821	2.601	0.82	0.726
Error	148	469.974	469.974	3.175		
Total	195	902.097				

Time & Frequency of Being Chased.

Territorial males and floaters did not differ in the amount of time they spent being chased (mean 0.1%), but there were significant differences among individuals in both time (Table 4.9a & b, $P<0.05$) and frequency (Table 4.10a & b, $P=0.001$) of being chased. There was no overall diurnal pattern, although floaters and territorials differed in the pattern of frequency of being chased, as did individuals ($P<0.05$).

Table 4.9a. Mean time spent being chased (seconds per 15 minute period).

	Time	1	2	3	4	5	6	7	8	ALL
Territorial	**1**	0.0	0.3	1.0	0.3	2.0	0.8	2.0	2.8	1.1
Territorial	**2**	0.7	0.5	0.5	0.5	1.5	1.3	1.8	0.8	0.9
Territorial	**3**	0.0	1.0	1.8	0.0	0.0	0.0	1.5	1.3	0.8
Floater	**1**	0.3	1.1	0.6	0.1	0.8	7.8	0.2	0.2	1.2
Floater	**2**	1.0	0.8	1.0	2.4	0.3	1.5	0.0	1.3	1.0
Floater	**3**	3.5	1.8	0.8	0.8	3.0	2.3	0.3	0.8	1.6

Table 4.9b. Analysis of Variance for time spent being chased

Source	DF	Seq SS	Adj SS	Adj MS	F	P
type	1	4.658	8.425	8.425	1.62	0.205
indiv(type)	14	132.933	130.515	9.322	1.79	0.045 *
time	2	2.065	2.423	1.212	0.23	0.793
type*time	2	4.823	5.982	2.991	0.57	0.564
time*indiv(type)	28	169.072	169.072	6.038	1.16	0.281
Error	148	770.749	770.749	5.208		
Total	195	1084.301				

Table 4.10a. Mean number of chases received (per 15 minute period).

	Time	1	2	3	4	5	6	7	8	ALL
Territorial	**1**	0.0	0.3	0.5	0.3	2.0	0.8	0.5	1.8	0.7
Territorial	**2**	0.7	0.5	0.5	0.3	1.5	0.8	1.0	0.5	0.7
Territorial	**3**	0.0	1.0	1.3	0.0	0.0	0.0	0.5	1.0	0.5
Floater	**1**	0.3	1.1	0.2	0.1	0.8	3.0	0.2	0.2	0.7
Floater	**2**	1.0	0.4	0.3	1.2	0.3	1.0	0.0	0.3	0.5
Floater	**3**	2.8	1.0	0.5	0.8	3.0	1.5	0.3	0.8	1.3

Table 4.10b. Analysis of variance for number of chases received

Source	**DF**	**Seq SS**	**Adj SS**	**Adj MS**	**F**	**P**	
type	1	1.639	2.252	2.252	2.20	0.140	
indiv(type)	14	40.185	39.208	2.801	2.74	0.001	***
time	2	3.844	2.141	1.070	1.05	0.354	
type*time	2	6.867	8.852	4.426	4.33	0.015	*
time*indiv(type)	28	47.845	47.845	1.709	1.67	0.027	*
Error	148	151.349	151.349	1.023			
Total	195	251.730					

Courtship

Courtship was rare, only being observed in 5 territorial and 4 floater individuals. Territorial *P. zebra* were involved in a greater number of bouts of courtship (Table 4.12a & b, $P<0.01$), but there was also great variation between individuals ($P<0.001$). No statistical differences were found in the time spent in courtship, which was very small (Table 4.11a & b, 0.17% in territorials, 0.12% in floaters). In all cases territorial *P. zebra* performed active courtship displays, while all floaters were passive recipients of displays.

Table 4.11a. Mean time spent courting/ being courted (seconds per 15 minute period).

	Time	1	2	3	4	5	6	7	8	ALL
Territorial	1	0.0	5.3	0.5	0.0	0.0	1.8	0.0	0.0	1.1
Territorial	2	0.0	8.0	0.0	0.0	2.0	0.0	0.0	2.0	1.5
Territorial	3	0.0	6.0	3.0	0.0	6.5	1.5	0.0	0.0	2.0
Floater	1	0.0	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.1
Floater	2	0.0	0.8	4.5	0.0	0.8	0.0	0.0	0.0	0.7
Floater	3	0.0	0.0	0.0	0.0	0.5	0.0	22.0	0.0	2.7

Table 4.11b. Analysis of variance for time spent courting/ being courted

Source	DF	Seq SS	Adj SS	Adj MS	F	P
type	1	9.17	3.53	3.53	0.07	0.785
indiv(type)	14	802.96	1023.05	73.07	1.55	0.102
time	2	118.77	115.14	57.57	1.22	0.299
type*time	2	33.88	20.66	10.33	0.22	0.804
time*indiv(type)	28	1425.58	1425.58	50.91	1.08	0.374
Error	148	6998.30	6998.30	47.29		
Total	195	9388.67				

Table 4.12a. Mean number of courtships given/received (per 15 minute period).

	Time	1	2	3	4	5	6	7	8	ALL
Territorial	1	0.0	1.8	0.3	0.0	0.0	0.3	0.0	0.0	0.3
Territorial	2	0.0	0.5	0.0	0.0	1.0	0.0	0.0	0.3	0.2
Territorial	3	0.0	2.0	0.3	0.0	1.0	0.5	0.0	0.0	0.5
Floater	1	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0
Floater	2	0.0	0.2	0.5	0.0	0.3	0.0	0.0	0.0	0.1
Floater	3	0.0	1.0	0.1	0.0	0.5	0.3	0.1	0.0	0.1

Table 4.12b. Analysis of variance for number of courtships given/received

Source	DF	Seq SS	Adj SS	Adj MS	F	P	
type	1	2.9030	2.6451	2.6451	7.71	0.006	**
indiv(type)	14	20.5301	20.5258	1.4661	4.27	0.000	***
time	2	0.3268	0.3571	0.1786	0.52	0.595	
type*time	2	0.8762	0.7066	0.3533	1.03	0.360	
time*indiv(type)	28	7.3138	7.3138	0.2612	0.76	0.799	
Error	148	50.8000	50.8000	0.3432			
Total	195	82.7500					

Time Spent in Aggressive Display and Fighting

Neither territorial (mean 0.7%) nor floater (0.5%) fish spent much time in aggressive display or fighting. Territorials and floaters did not differ statistically in the amount of time spent in aggressive contests (Table 4.13a & b, P=0.62), but they showed different diurnal patterns (P<0.05), with territorial fish more aggressive in the middle of the day, and floaters in the afternoon. There was no significant difference between individuals (P=0.45).

Table 4.13a. Mean time spent displaying and fighting (seconds per 15 minute period).

	Time	1	2	3	4	5	6	7	8	ALL
Territorial	1	0.0	4.5	7.3	6.0	0.0	1.5	6.0	2.8	4.0
Territorial	2	0.7	1.5	3.3	34.5	5.5	7.0	18.5	8.5	10.6
Territorial	3	1.0	2.8	3.5	6.8	0.0	1.0	1.3	5.8	3.1
Floater	1	1.8	0.0	0.8	0.0	0.3	5.8	0.4	2.6	1.2
Floater	2	3.3	0.2	9.0	2.6	9.8	0.5	0.3	3.8	3.4
Floater	3	6.3	12.8	2.0	9.4	1.5	8.0	23.0	5.0	8.5

Table 4.13b. Analysis of variance for time displaying and fighting

Source	DF	Seq SS	Adj SS	Adj MS	F	P
type	1	166.1	33.3	33.3	0.24	0.624
indiv(type)	14	1878.9	1955.3	139.7	1.01	0.447
time	2	684.4	618.6	309.3	2.24	0.111
type*time	2	1333.2	1095.9	548.0	3.96	0.021 *
time*indiv(type)	28	3793.4	3793.4	135.5	0.98	0.502
Error	148	20475.2	20475.2	138.3		
Total	195	28331.1				

Aggressive interactions of floaters.

A detailed breakdown of aggressive interactions of *P. zebra* floaters is presented in Table 4.14. Three hundred aggressive interactions were observed over 23 hours of focal watches- a rate of 13 per hour. Floaters were not always submissive, but were dominant in almost 25% of all encounters, sometimes even over territorial fish including conspecifics. This is probably an underestimate of the proportion of dominant encounters, because submissive displays by focal individuals were more readily observed than were those exhibited by other fish, especially other floaters, towards the focal fish. Floaters were observed to bite and chase territorial fish on occasion, although not to displace them from their territories. More than 75% of all aggression took place with conspecifics, and most of this with other floaters. All display contests and the single escalated fight observed were between pairs of *P. zebra* floaters. Focal individual floaters were significantly more likely to dominate duller coloured conspecific floaters than those which were more brightly coloured (Table 4.15) and less likely to dominate floaters larger than themselves ($P<0.05$, Table 4.16). These effects were independent of each other, as larger non-focal fish were less likely to be brightly coloured than smaller ones. This may be because the proportion of females is higher among larger fish,= (since many large males are territorial), or because focal fish avoided interactions with bright conspecifics larger than themselves. The range size of floaters was independent of the mean frequency of performing dominant ($r = 0.23$, 9 df, $P = 0.50$) or subordinate ($r = 0.36$, 9 df, $P = 0.28$) activities (data from Table 4.1).

Table 4.14. Aggressive interactions shown by *P. zebra* floaters in 23h of observations. Submissive interactions include avoiding and being bitten by other fish and giving a submissive display. Dominant actions were biting, chasing, lateral displaying at opponent and receiving a submissive display. Fighting includes mutual lateral display and circling fights.

	Percentage Submissive	Percentage Dominant	Percentage Fighting	Frequency	% Total
Floaters of territorial species					
***Petrotilapia/P. tropheops* floaters**	28.6	71.4	0.0	7	2.3
***P. zebra* floaters**	57.2	34.0	4.4	159	53.0
Non-territorial species					
Genyochromis	100.0	0.0	0.0	7	2.3
Labidochromis vellicans	100.0	0.0	0.0	4	1.3
Melanochromis auratus	80.0	20.0	0.0	5	1.7
Melanochromis heteropictus	100.0	0.0	0.0	5	1.7
Non-mbuna	100.0	0.0	0.0	4	1.3
Territorial individuals					
Labeotropheus fuelleborni	100.0	0.0	0.0	8	2.7
***P. elongatus* 'aggressive'**	91.7	8.3	0.0	12	4.0
***P. elongatus* 'yellowtail'**	80.0	20.0	0.0	5	1.7
Petrotilapia nigra	50.0	50.0	0.0	2	0.7
P. tropheops	92.9	7.1	0.0	14	4.7
P. zebra	94.1	5.9	0.0	68	22.7
TOTALS	74.2	23.7	2.0	300	100.0

Table 4.15. Focal floater *P.zebra* were significantly less likely to dominate more brightly coloured conspecific floaters. The colour of the opponent was recorded prior to the interaction. .

Opponent Colour	Dominant	Submissive	Total	Percentage Focal Fish Dominant
Brighter	3	28	31	9.7%
Duller	54	67	121	44.6%
Total	57	95	152	

G-test with Williams' correction, 1df, G=14.79, P<0.001

Table 4.16. Focal floater *P.zebra* were significantly less likely to dominate larger conspecifics. Opponent's colour (see Table 4.15) was not responsible for this difference, as larger fish were less likely (12.2%) to be brightly coloured than smaller ones (24.3%).

Size of Opponent Relative to Focal Fish	Dominant	Submissive	Total	Percentage Focal Fish Dominant
Larger	12	45	57	24.5%
Smaller	37	58	95	43.7%
Total	49	103	152	

G-test with Williams' correction, 1df, G=5.35, P<0.05

Semi-territorial Fish

Three focal fish were considered to show behaviour intermediate between typical territorial and floater individuals. These semi-territorial fish spent part of their time in bright colours aggressively defending a small area of substrate. Defended areas, calculated as minimum convex polygons of 0.77, 0.85 and 1.04 m^2, were more or less

the same size as those of typical territorial conspecifics. At least two of these fish appeared to defend a refuge which might have served as a spawning site. However, their core areas overlapped with those of other territorial conspecifics and they frequently could not be located in their defended area. During 6 out of 25 focal watches, individuals were observed to leave their core areas and feed from the substrate in other places. Total feeding area convex polygons were 5.15 and 4.57m^2, very much larger than those of typical territorial *P. zebra*. The third individual fed over an area of 1.34m^2 centred around its defended area, but also used another, distant area of approximately 1m^2. The total ranges of these fishes were 4.6, 6.7 and 11.4m^2. During the time they were away from their defended areas they were generally dull-coloured and non-aggressive. This behaviour is much like that of typical territorial *Labeotropheus*, but was never observed in other *P. zebra* territorials, which only occasionally left their territory for short distances to feed in midwater. As they could often not be located and were not consistently observed outside their defended areas, the total time budgets of semi-territorials could not be quantified accurately and so they have not been compared statistically with those of floaters and territorials. However, percentage time budgets were calculated from periods where they were initially observed in their core area. These semi-territorial fish spent a longer time (35.9%) feeding on the substrate than either floater or territorial fish. They fed in midwater for a far smaller proportion of their time (9%) than did floaters, but slightly more than territorials. Stationary periods (20%) did not differ from other conspecifics, but the time spent swimming (31%) was similar to that of territorials and longer than that of floaters. They spent more time chasing (7%), being chased (0.2%) and displaying (0.8%) than either of the other two groups, but participated in less courtship (0.03%).

Feeding Bout Lengths

Time budget analysis indicated that territorial and floater fish differed in the amount of time spent feeding from the substrate, but not in the number of feeding bites. This suggests a difference in the duration of bout lengths between the different types of *P. zebra*. The lengths of all bouts of benthic feeding were recorded for all focal individual *P. zebra*, territorials, semi-territorials and floaters. This was a larger number of individuals than used for the time budget analysis. The durations of 3,386 feeding bouts by territorial *P. zebra*, 1,426 by semi-territorials and 4,986 by floaters were recorded. The frequency distributions were right-skewed (Fig. 4.1) and so were compared statistically with a Kolmogorov-Smirnov test, which does not assume a normal distribution. The bout length distributions differed significantly between all

three groups of fish (territorials and floaters, D=0.200; territorials and semi-territorials, D=0.138; semi-territorials and floaters, D=0.265; for all, P<0.001). Semi-territorial fish generally had greater feeding bout lengths, and floaters the shortest.

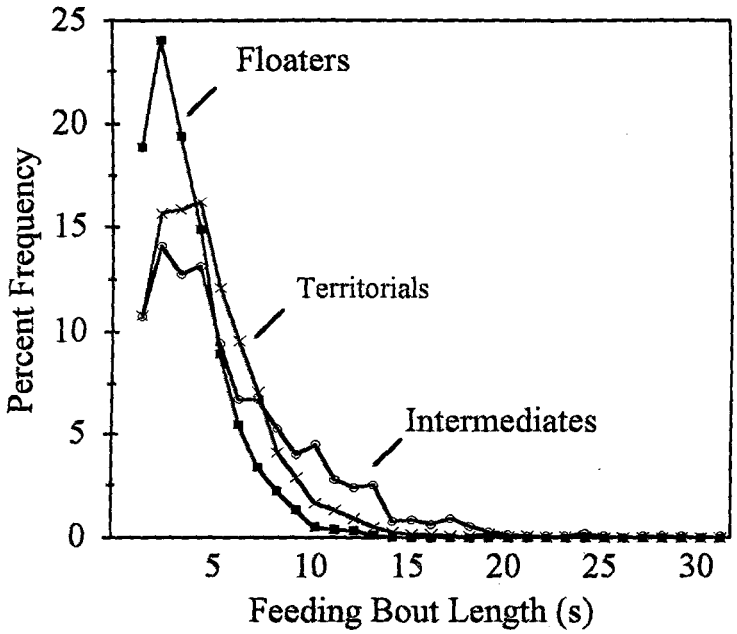


Figure 4.1. Comparison of distributions of benthic feeding bout lengths by territorial, floater and semi-territorial *P. zebra.*

Floaters of Other Species

All other species, apart from *Pseudotropheus elongatus* 'aggressive', included floaters. It appears that many, if not all, of these individuals also occupied limited home ranges, like those of *P. zebra.* Tagged individual *Pseudotropheus tropheops* 'orange chest' observed over periods of up to 33 days, occupied total ranges calculated as minimum convex polygons of 7.3, 7.5, 11.5 and 12.0m^2, although one individual was observed to join a school of plankton feeding fish 90m away from its original capture site in its normal range. It appeared that some individual *P. tropheops* 'orange chest' showed semi-territorial behaviour similar to that recorded for *P. zebra.*

Discussion

Early studies of fish behaviour underestimated individual variability and flexibility (Magurran 1994). Fish schools, once seen as homogenous aggregations for mutual

benefit, are now regarded as dynamic aggregations of distinct individuals, which may even have preferred partners for undertaking risky activities such as investigating a predator (Pitcher & Parrish 1994). What were once regarded as species-specific mating systems are now known to comprise a complex interaction of alternative male and female reproductive strategies (Turner 1986a). Individual variability is now one of the most active areas of study in fish ethology (Magurran 1994). Individual differences may result from three processes: (i) spatial and temporal variability in the environment, (ii) phenotypic variation among individuals, (iii) the behaviour of other individuals. Territorial defence may not be advantageous when feeding in the water column, as plankton is not a defensible resource. Large male individuals may be better able to control breeding and feeding sites than smaller individuals. The switch from floater to territorial depends critically on how many other males are already occupying available territory sites, and on their relative competitive abilities. All of these factors promote the evolution of the ability of individuals to assess the environmental and social situation and respond flexibly. Where a behavioural change requires a complex and costly physiological and anatomical change, such as a change of sex, the switch is likely to be made rarely in an animal's lifetime and may be irreversible. There is no particular reason to suppose that it is costly to switch between territorial and floater strategies and the results of the present study indicate not only that *P. zebra* makes such a switch on a regular short term basis, but that there is continuous variation among individuals in the degrees of territorial and floater behaviour they exhibit.

TIME BUDGETS OF TERRITORIAL AND FLOATER *P. ZEBRA*

In the field, *P. zebra* has never been observed to spawn in the open, and a spawning cave is essential to the breeding success of an adult male. Vacated spawning sites are rapidly colonised by floater or other territorial males (Kornfield *et al.* in press) and costly, escalated fights may be required to decide ownership if a newcomer is allowed a long period to establish itself. The amount of time a male is absent from its territory is inversely related to the number of times it courts with females (Kornfield *et al.* in press), indicating that absence from the territory may lead to reduced reproductive opportunity. Territorial males, in possession of a spawning site, spent much less time feeding in midwater and more time feeding benthically than floaters. Both territorial and floater individuals ranged more widely when feeding on plankton, perhaps as a result of the patchy distribution of crustacean or algal aggregations. Floaters, although spending less time feeding benthically than territorial fish, frequently fed in the territories of other fish. The residents of most species, apart from *P. elongatus* 'aggressive' did not attempt to exclude them from their territories, usually only chasing

floaters when they are at very close range, in the core area of the territory or if the floaters are brightly coloured. *P. zebra* floaters associate with other non-territorial fish (of the same and different species) most frequently when they are feeding on plankton. When feeding benthically, they usually feed alone, though sometimes shoals of floaters are seen invading the territories of other fish (Marsh & Ribbink 1986), especially just before sundown (personal observation). The greater length of feeding bouts in territorial fish is probably a reflection of their dominant status. Floaters may need to be vigilant against attacks from residents, and feeding is often interrupted when they are forced to flee by the approach of a dominant fish.

Aggression between plankton feeding fish was never seen, perhaps because plankton patches are mobile and not a defensible resource. Individuals feeding on plankton are subject primarily to scramble competition, since the resource is patchy, unpredictable and subject to huge fluctuations of abundance (FAO 1993). In contrast, benthic algae is a more reliable resource that can be defended, and is thus subject to contest competition. In times of low plankton availability, individuals with priority of access to benthic feeding areas may be at an advantage. Individuals defending a territory do not relinquish their opportunity to feed on plankton and some take advantage of plankton blooms more than others (see Chapter 3).

The time budgets of semi-territorial fish were intermediate in most respects between those of territorial and floater fish. The higher proportion of benthic feeding may be an artefact. It is likely that often when these fishes were feeding on plankton, they travelled long distances from their benthic 'territory'. Unlike the focal floater individuals they were not tagged and could not be recognised outside the quadrat. They were involved in more aggressive interactions than either floaters or territorials, perhaps because they were attempting to establish dominance in the area.

HOME RANGES OF *P. ZEBRA* FLOATERS

Though it is possible that the home ranges of floaters may tend to drift over longer periods of time, they were constant for the duration of the study. It is possible to imagine a number of advantages to site fidelity, although they remain to be tested for mbuna. Familiarity with topography might facilitate predator evasion, and perhaps this may explain Hert's (1992) observation that female *P. aurora* regularly re-use favoured sleeping sites, and that artificially displaced fish would swim up to 2.5km to return to their usual home ranges. Individuals may learn the location of good feeding sites, particularly those lying between the core defended areas of neighbouring territorial fish and thus avoid the attacks of residents. Males may become familiar with their breeding territory before they are able to take possession of it, and they may also be continually

assessing their chances of being able to displace a current resident and may establish dominance over floaters with overlapping ranges which might compete for a vacant territory. Females may learn the location of preferred males, minimising the costs of searching for mates during the breeding season, as well as suitable places to release fry.

AGGRESSION IN TERRITORIAL AND NON-TERRITORIAL *P. ZEBRA*

It is evident from this study that *P. zebra* floaters are not merely passive wanderers. They spent as much time in aggressive displays and fights as did territorial conspecifics and although they performed less chasing than territorial individuals, they did not receive more chases. The majority of aggressive interactions were with conspecifics, and most of these between floaters. Large and colourful floaters were more likely to be dominant than small and dull ones. Thus, there were dominance hierarchies amongst *P. zebra* floaters. Aggression was largely site-specific and occurred more often in parts of the preferred benthic feeding range of the floaters. The result is that individual floaters had areas in which they dominate many, though not necessarily all, other floaters, and outside these areas they behaved in a subordinate manner, as when feeding in the core areas of territorial fish, of their own or other species.

The presence of semi-territorial fish was initially confusing. These individuals were thought to be territorial but their frequent absence from the site and the overlap with conspecific territories suggested that this species was not so clearly divided into territorial and non-territorial individuals. Holzberg (1978) observed that some floaters attempted to hold small territories between those of dominant males, hiding to avoid aggression, although the behaviour of these individuals was not documented in detail. Kornfield *et al.* (in press) noted that some territorial fish spent long periods out of their territories, that these were generally smaller individuals, and that smaller individuals usually retained their territories for shorter periods than larger fish. Holzberg's territorial floaters, Kornfield *et al.*'s floating territorials and the semi-territorials described in the present chapter may all be different views of the same phenomenon, leading to the idea of site specific dominance hierarchies. It appears that there is a continuum of site-specific dominance behaviour, at one end of which are immature floaters, ranging over large areas, often feeding in the territories of conspecifics and showing submissive behaviour in most interactions. At the other end of the spectrum are territorial males which defend territories containing all the resources they need-food and a cave serving as a spawning site and refuge. In between these two extremes are fish that have priority of access over other individuals in certain areas, though these sites do not provide all the needs of the individual fish, which forage over larger areas.

The tolerance of floaters by territorial fish depends on the costs and benefits of

excluding them. Territorial fish may benefit from a dominance hierarchy since the beta fish, by excluding other subordinates, may share the cost of territorial defence. The trade-off between this possible benefit and the sharing of resources with the semi-territorial fish has not been quantified. The increased aggression seen in semi-territorials suggests that these fish are less inclined to share their resources, or may be a consequence of their unfamiliarity and thus reduced avoidance by other floaters.

DIFFERENCES BETWEEN THE SEXES

It is unfortunate that it was not possible to recapture the majority of tagged fish, since sex differences in behaviour could not be quantified for an adequate sample of floaters. However some differences were apparent. Female fish were never found to be territorial in this or in previous studies (Holzberg 1978, Ribbink *et al.* 1983a, Kornfield *et al.* in press). Though previous workers have not recorded ritualised aggression amongst females (Holzberg 1978), it is clear from this study that they are aggressive on some occasions- the most aggressive of the focal floaters (#11: Table 4.1) was a known female. Aggression by females may establish priority of access to good feeding sites, a refuge, fry release sites and high quality mates. Although male mbuna provide no resources for the female or young, recent studies have demonstrated that females mating with preferred males have more vigorous or viable offspring than those experimentally compelled to mate with less attractive males (peacocks: Petrie 1994; guppies: Reynolds & Gross 1992). Female *Melanochromis auratus* are aggressive to both males and females in the field (Hert 1993) and laboratory (Nelissen 1985). In the laboratory, female *P. zebra* are aggressive to each other (personal observation), and female *Oreochromis mossambicus* have dominance hierarchies which are correlated with their food intake rate (K. Wyatt & G.F. Turner, unpublished data). In aquarium conditions, female mbuna may defend temporary territories in the vicinity of fry release sites, perhaps allowing the fry time to find their way to refuges (*P. tropheops*, J. C. Deutsch pers.comm.; *P. livingstonii*, personal observation). It is not known if this behaviour occurs in the field or is a laboratory artefact. It would certainly seem adaptive, and might easily have been overlooked in the field.

During the focal watches, the floaters studied never performed the courtship displays typical of territorial males, though they were seen to receive the attention of courting males. Territorial males sometimes courted dull-coloured males (personal observation), and none of the floaters was seen to respond to courtship attempts, so their sex could not be determined by these interactions. Although some of the floaters were juveniles and females, some were larger individuals that appeared to be males. Courtship by male floaters was seen, very rarely, outside the focal fish watches but no

response was seen. On such occasions, the courting floater, which had become brightly coloured, was chased away by a neighbouring territorial fish. From observations of territorial fish, it seems that successful courtship in this species involves leading the female to a safe spawning site in a cave. Spawning of *P. zebra* has never been recorded in the wild, and is assumed to occur within the male's refuge (Holzberg 1978, Kornfield *et al.* in press) and so a male without a spawning site will not be able to breed. For male floaters, the main factor in choosing a home range should be prospects of a good breeding territory in future but not at the cost of feeding opportunities.

THE USE OF COLOUR IN STATUS SIGNALLING

Colouration of sexually mature male cichlids is considered to be one of the most important components of the specific mate recognition system (Paterson 1993), an incidental effect of which is to prevent hybridisation (Ribbink 1986, 1994). It is also considered likely to play a major role in mate choice within a species (McKaye 1991, Turner 1994a) which some authors believe may in turn sometimes have an effect on species recognition (see discussions of this subject by Endler 1989, Ryan 1990, Paterson 1993, Andersson 1994). It is less likely that female colour is important in mate recognition, not only because females are generally more discriminating about their mates, but because females in many mbuna species often exist as two or more abundant colour morphs, often markedly different in appearance (Ribbink *et al.* 1983a). Male appearance is most likely to be the first cue to initiate a courtship response in a ripe female and courtship behaviour appears to be more or less the same in all mbuna species (Ribbink *et al.* 1983a, McElroy & Kornfield 1990).

Floaters generally appear to have much duller coloration than territorial males, except when courting or performing aggressive acts. It is not known whether females ever adopt the bright blue-black colour pattern. Holzberg (1978) suggested they do not, but females of other mouthbrooding cichlids may adopt a colour pattern similar to territorial males (Nelissen 1985, Turner & Falter 1989) but intensely coloured floaters rapidly become dull in the presence of a dominant fish. In the present study some floaters, including one very small, sexually immature individual, were brightly coloured in sites where they were aggressive, but dull in other areas. All semi-territorial fish were brightly coloured within their territories and dull when they ventured outside their sphere of dominance. A similar situation is seen in territorial *P. zebra, P. nigra* and *L. fuelleborni* whose bright colour fades when they forage outside their territories. Thus, colour is correlated with dominance and aggressive motivation. Although initially regarded as controversial by theoretical biologists, it is now generally accepted that animals can signal levels of aggressiveness using low cost badges of status and thus

win contests over resources of low value (Maynard Smith & Harper 1988).

Brightly coloured floaters were significantly more likely to win aggressive interactions, so the advantage of such a signal would be avoidance of challenges by subordinate fish. Feeding territories held by floaters for a few minutes are low value resources. Colour is a low cost signal, since although it may provoke attacks from territorial fish, it can be switched off relatively quickly, unlike the bright colours of birds or coral reef fish. Breeding territories held for more than a year are of high value, but most intruders are not intent on displacing the resident, merely in feeding. Escalated circling fights occurred in response to intrusions by other territorial conspecifics (chapter 3) which may be more of threat to long-term territorial tenure. Colour is not used to settle these contests over high-value resources.

The drab colour pattern of floaters and male territorials outside their territories, is unlikely to be as provocative to resident males, but may be costly in that it is not attractive to females and may result in lost mating opportunities.

TERRITORIAL AND NON-TERRITORIAL MALES

In general, the presence of floater or supernumerary males has been used as evidence of habitat saturation but avoidance of low quality territories may give the same results. In either case, supernumerary males must either wait until they are able to acquire a territory to breed or else they may adopt an alternative tactic (Ribbink 1990). Sneaking has been documented for many fish species (Gross 1984, Kodric-Brown 1986, Taborsky *et al.* 1987, Magnhagen 1994), and though it may have been seen in the field (Hert, pers. comm) it has not been documented for mbuna, and so it seems likely that non-territorial male *P. zebra* have no opportunity to mate.

It is not clear whether non-territorial male mbuna are unable to hold a territory because they are smaller or poorer competitors. When territorial male *P. aurora* were removed by Hert (1990), 23 out of 34 vacated territories were re-occupied by floaters, and 10 by males which had previously occupied other (possibly suboptimal) territories in the vicinity. The males occupying the vacated territories were not significantly different in length from the original owners, while Munthali (in press) found the same for mature non-territorial and territorial males of *P. zebra* and *Cynotilapia afra*. Although Kornfield *et al.* (in press) found that territorial males were of greater mean size than non-territorial male *P. zebra*, size distributions showed considerable overlap. Laboratory experiments with *Oreochromis mossambicus* have demonstrated that if a number of males are simultaneously introduced into an aquarium only the largest males can control territories (Turner 1986b). However, non-territorial males grew faster and eventually exceeded territorial males in size. Non-territorial fish did not have reduced

access to food, and generally had higher food conversion efficiencies than territorial males (Turner, Wyatt & Seow, unpublished data). Field studies by Munthali (in press) showed that non-territorial males of *P. zebra* and *C. afra* were in better condition than territorial males. Only when non-resident *O. mossambicus* had attained much greater weights than territorial males were they able to successfully compete for territories (Turner 1986b, 1994b). There are four possible explanations why, at a given size, some males are territorial, while others are not:

(i) individuals differ in aggressiveness and some are better at competing for territories;

(ii) individuals are adopting a frequency dependent conditional strategy. Once a certain number of males of a given size are territorial, it is no longer beneficial for other males of that size to become territorial;

(iii) males are unable to assess their own relative size or the costs and benefits of territoriality until they hold a territory. If they are unsuccessful at securing mates or begin to lose condition through lack of feeding opportunity or frequent fighting and chasing, they can return to being floaters;

(iv) since males have restricted home ranges and are probably unaware of territorial vacancies outside this range, some small males may simply find vacant territories within their range, while others do not, or are excluded by larger floaters whose range also overlaps the vacant territory.

Although floaters were seen to be aggressive to territorial males on some occasions, they were never oberved to engage in escalated fights with territorial fish or displace them from their territories. Some fish were seen to abandon their territories when they were in poor condition, and others disappeared over a short period of time, perhaps taken by predators. Kornfield *et al.* (in press) and Sharp (1981) found that smaller territorial fish were more likely to leave their territories than larger males. Site-specific dominance hierarchies among floaters may mean that there is an ordered queue of inheritors waiting for a territorial vacancy in any particular area. This may influence the optimal range size for floaters. A larger range may allow more territories to be monitored, increasing the chance of finding a vacancy, but it is likely to be less costly to maintain dominance over a small area. Thus large males, which are more likely to be at a stage when they might benefit from switching from floater to territorial, might be expected to have smaller ranges than immature fish. In the present study floater size was negatively related to range size. The lack of statistical significance may be due to the fact that male and female floaters were not distinguished.

The behavioural strategies adopted by floater and territorial *P. zebra* are not confined to Malawian cichlid fishes. Zack & Stutchbury (1992) have emphasised that the idea that floaters are simply randomly drifting individuals is largely erroneous for birds. They cite numerous studies carried out since 1978 which have demonstrated that non-breeding individuals of many species have restricted home ranges that encompass more than one breeding territory. As floaters range over several territories they are members of several dominance hierarchies (Smith 1978). The home range of floaters can be considered as an "assessment sphere" (Zack 1990). For this term to be used there should be (i) site-specificity as a non-breeder, (ii) owner tolerance of non-breeders to some degree, (iii) competition among floaters for sites and (iv) benefits of delayed breeding resulting in acquisition of higher quality territories. The first three conditions have been demonstrated in *P. zebra*, while circumstantial evidence make the fourth seem probable. In birds, high dominance status among non-breeders increases the likelihood of territory acquisition when a vacancy occurs (Baeyens 1981, Birkhead & Clarkson 1985), as does previous experience of the area (Porter 1988, Wegger & Larson 1987). Familiarity with nearby territories and establishment of site dominance are important in territory acquisition (Zack 1990). Floaters prefer high quality territories and delay breeding rather than take an inferior territory when it arises (Zack & Rabenold 1989, Zack 1991). Zack & Stutchbury (1992) argue that a clear distinction in plumage between territorials and non-territorial individuals permits subadults to avoid aggression of territorials and gain access to, and assess high quality territories. This again has parallels with *P. zebra*.

Zack & Stutchbury (1992) developed a model in which future acquisition of a high quality territory in birds was a direct benefit of delayed breeding. The prerequisites for the evolution of delayed breeding were (i) differences in territory quality, (ii) differences in resource-holding potential of individuals and (iii) long-term site tenacity by territorial individuals, making it difficult for them to switch territories later in life. Kornfield *et al.* (in press) and Hert (1992) have demonstrated long-term territorial tenure in mbuna (see also chapter 3). Larger male mbuna consistently defeated smaller ones in territorial contests staged in ponds (Kornfield *et al.* in press), indicating differential resource holding ability. It has still not been convincingly demonstrated that there are differences in territory quality, although the findings of Hert (1990) and the results of chapter 3 point in that direction.

To test Zack & Stutchbury's hypotheses, it will be necessary to determine whether there really are differences in the quality of *P. zebra* territories. Future studies should investigate differences between territorial males in condition, growth rate, survival and mating success. Simultaneously removing males from putative high-quality and low-quality territories should lead to greater competition for the best territories. This could be manifested either through better territories being filled faster or by larger males. Observation of the frequency of challenges faced by the incoming territorials would also be informative. Long term studies of the replacement males might indicate whether those males occupying the supposedly better territories also reaped their benefits. If not, it would suggest that the differences in male growth, condition or reproductive success might be more due to male quality than to territory quality.

If Zack and Stutchbury's hypotheses are not applicable to mbuna, the reason may be that birds are unable to test territory quality and their own capabilities by spending short periods as territorials. Transition from floater to territorial is sometimes accompanied by a change in plumage which cannot be reversed during the whole of the breeding season. Birds invest heavily in their territories, building nests, laying eggs and rearing young. Thus they must pay a large part of the cost of territoriality early in the season. By contrast, mbuna males could spend a few days or weeks as territorial fish and easily revert to a floater strategy if they were unsuccessful.

Chapter 5. Temporary breeding territories and their impact on the resident community.

Introduction

The rocky shores of Lake Malawi are inhabited by a great density of fish- there may be as many as 20 adult cichlid fishes per square metre (Ribbink *et al.* 1983a). In addition to fishes of the families Characidae, Cyprinidae, Cyprinodontidae, Mormyridae, Mochokidae, Clariidae, Bagridae, Mastacembelidae, as well as five species of tilapiine cichlids, Ribbink *et al.* (1983a) recorded 60 species of haplochromine cichlids in the vicinity of Monkey Bay in the south of the lake. On the shores of Thumbi East Island, at the edge of Monkey Bay, ten species of mbuna maintain permanent territories (i.e. throughout the year, rather than on a seasonal basis) in shallow water, resulting in a complex mosaic of intra- and interspecifically defended territories. Non-territorial fish of these and several other species use the same habitat (chapter 3, see also Holzberg 1978, Marsh & Ribbink 1985 & 1986, Hert 1990). When a territory is vacated it is rapidly filled, usually within days or even hours (Sharp 1981, Hert 1990, 1992, Kornfield *et al.* in press). Despite this apparently intense competition for space, at particular times of the year further territories are established in the area (Ribbink 1990, Konings 1990) by fishes normally inhabiting open waters or sandy shores, such as the openwater zooplanktivorous species known as "utaka" (Iles 1960) e.g. *Copadichromis* spp. (Lowe-McConnell 1991, Konings 1990), or by species normally present in the rocky areas but not normally territorial, such as *Protomelas taeniolatus* (Ribbink *et al.* 1983). Although this phenomenon has been reported, the numbers of species, density of individuals, and seasonality of these temporarily territorial fishes have not yet been studied, nor have the effects on the resident community been investigated.

Aims and Objectives

The aims of the present study were to carry out a preliminary survey of the temporarily territorial species on a small area of rocky habitat at Thumbi East Island. By observing the locations of temporary territories, and the behaviour of these 'transient territorial' fish as well as that of neighbouring permanent residents, the possible impact on the species which maintain long-term territories in the same habitat was investigated.

Methods

This study was carried out between January 1991 and November 1992.

SEASONALITY OF TEMPORARY BREEDING TERRITORIES

The number, species and sex of fish on temporary breeding territories was estimated twice monthly between August 1991and August 1992. Counts were made whilst swimming along three transects, and all territories within 1 metre either side of the diver were counted. The transects corresponded approximately to depth contours parallel to the shore, and the details are given below.

> 1m-transect. Length: ca 300 m. Location: immediately south of the lighthouse, following the shore south- and eastwards (see Chapter 3). Habitat: rubble and small rocks up to two metres across predominated. Total area: ≙ 600m^2.
>
> 5m-transect 1. Length: ca 300 m. Location: immediately south of the lighthouse, following the coast south- and eastwards. Habitat: largely rocks between one and three metres high. Total area: ≙ 600m^2.
>
> 5m-transect 2. Depth varied from 5-10 m as parts of the transect included sheer rock faces where the the bottom dropped sharply. Length: 400 m. Location: immediately north of the lighthouse, following the shore north and east. Habitat: mostly very large boulders. Total area: ≙ 800m^2.

Additional qualitative observations were made to a depth of 15 metres.

HABITAT PREFERENCES

To determine whether site preferences differ between species, a description of the sites used by transient territorials was recorded whilst swimming along the transects. The water depth, type of substratum/size of rock, and angle of the rock face being used were noted for each species. The duration of territorial occupation was recorded for individuals of each species and sex.

OVERLAPS IN SPACE USE

Territories of all resident mbuna had been mapped in the 5 m x 5 m quadrat described in chapter 3. During a six-week period from early September to mid-October, territories of transient territorial fish were mapped each day, Monday to Friday. The number and species of residents affected was determined. It was possible to classify overlaps according to whether they were with the core defended areas, total defended areas or feeding ranges of the residents. Changes in space use were determined and any cases of expulsion from territories noted.

AGGRESSIVE BEHAVIOUR OF BREEDING FISH

Five- to 15-minute focal watches were made for individual transient territorial fish and the species, sex and relative sizes of any territorial individuals chased from the territory were recorded.

EFFECTS ON BEHAVIOUR OF RESIDENT FISH

Fifteen minute focal watches of resident fishes with territories adjacent to those of transient territorials were carried out and time budgets and habitat use compared with observations made before and after the tenure of the transient fish.

Results

SPECIES ESTABLISHING TEMPORARY BREEDING TERRITORIES

Male courtship and spawning territories were established by 21 species of cichlids. As the behaviour and colour of courting males makes them highly conspicuous, this is likely to be a relatively complete inventory. Females of 13 species were found to establish transient territories in which they guarded free-swimming fry (Table 5.1), but as guarding females and their fry are well camouflaged and their behaviour is often cryptic further species, particularly those guarding fry under or between rocks, may be present. Biparental territories were held by the non-endemic cichlid *Tilapia rendalli* and the catfish *Bagrus meridionalis*. Neither was common in the study area.

Table 5.1. Species establishing transient breeding territories on the shallow rocky areas of Thumbi Island East. Jan. 1991-Nov. 1992, all transects. Asterisks indicate whether the territories are established by males, females or biparentally (BIPAR.).

	MALE	FEMALE	BIPAR.
Buccochromis heterotaenia		*	
Copadichromis cf. azureus	*		
Copadichromis "blue streamer"	*		
Copadichromis borleyi	*	*	
Copadichromis chrysonotus	*		
Copadichromis cf. eucinostomus	*		
Copadichromis "eucinostomus big blue"	*		
Copadichromis "eucinostomus big spot"	*		
Copadichromis jacksoni	*		
Copadichromis cf. prostoma	*	*	
Ctenopharynx cf. intermedius	*		
Dimidiochromis kiwinge	*	*	
Hemitaeniochromis urotaenia		*	
Lethrinops spp.	*		
Mylochromis anaphyrmus	*		
Nyassachromis cf. breviceps		*	
Nyassachromis nigritaeniatus	*		
Otopharynx sp. "heterodon Nankhumba"	*	*	
Oreochromis karongae	*		
Oreochromis squamipinnis	*		
Protomelas fenestratus	*	*	
Protomelas sp. "spilonotus Likoma"	*	*	
Protomelas taeniolatus	*	*	
Serranochromis robustus		*	
Taeniolethrinops laticeps		*	
Tilapia rendalli			*
Tyrannochromis macrostoma	*	*	
Bagrus meridonalis			*

The small benthic feeding rock-dweller *P. taeniolatus* was by far the most common temporary territorial in the area. The remainder belong mostly to the utaka, small zooplankton feeding species, mainly *C.* cf. eucinostomus, *C.* cf. prostoma, *C. jacksoni*

and *C. borleyi.* Other commonly-seen breeding territories belonged to *P.* "spilonotus Likoma"- a species similar to *P. taeniolatus*, *D. kiwinge*- a predator of midwater schooling fish, the mollusc feeding *M. anaphyrmus* and the large algal feeder *O. karongae*.

REPRODUCTIVE SEASONALITY

The total number of transient breeding territories was highest from the end of the cold season to the beginning of the rainy season (August to November), with a smaller peak during the rainy season from January to March (Fig 5.1). There was a similar bimodal pattern for the total number of species controlling temporary territories (Fig. 5.2). Throughout the year there were never fewer than 4 species of temporary residents in the area. Many species showed a bimodal breeeding seasonality very similar to the overall pattern: these included the small sediment feeder *P. fenestratus* (Fig. 5.3), the zooplanktivores *C. borleyi*, *C. cf eucinostomus* and *C. cf. prostoma* (Figs. 5.4-5.5), and perhaps also the large sand-dwellers *N. nigritaeniatus*, *M. anaphyrmus* and *H. urotaenia* (Figs. 5.6-5.8). Unimodal breeders included three benthic feeders permanently resident on rocky shores *P. taeniolatus*, *P.* "spilonotus Likoma" and *O.* "heterodon Nankhumba" (Figs. 5.9, 5.10 & 5.13), and three zooplanktivores *C. jacksoni*, *C. chrysonotus*, and C. 'eucinostomus bigspot' (Figs. 5.11, 5.12, & 5.14). The large algal feeder *O. karongae* (Fig. 5.15) and another zooplanktivore *C.* 'blue streamer' (Fig. 5.16) had long breeding seasons, with relatively short lulls during April to August and July to September respectively. The midwater piscivore *Dimidiochromis kiwinge* also apparently breeds throughout the year with possible peaks in April to June and September to October (Fig. 5.17). *Tyrannochromis macrostoma*, a major predator of mbuna, bred in small numbers for much of the year (Fig. 5.18).

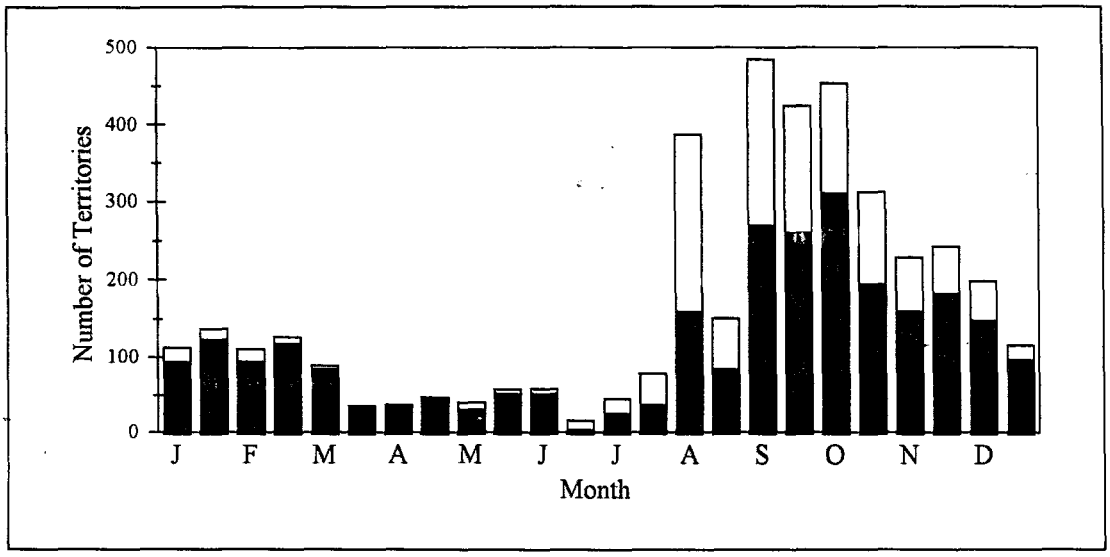


Figure 5.1. The number of transient territorial fish on the rocky shore at Thumbi East Island shows a bimodal distribution with the main peak at the end of the cold season and a secondary peak during the rainy season. *Protomelas taeniolatus* (□); all other species (■). Data are twice-monthly counts from three transects, August 1991-August 1992.

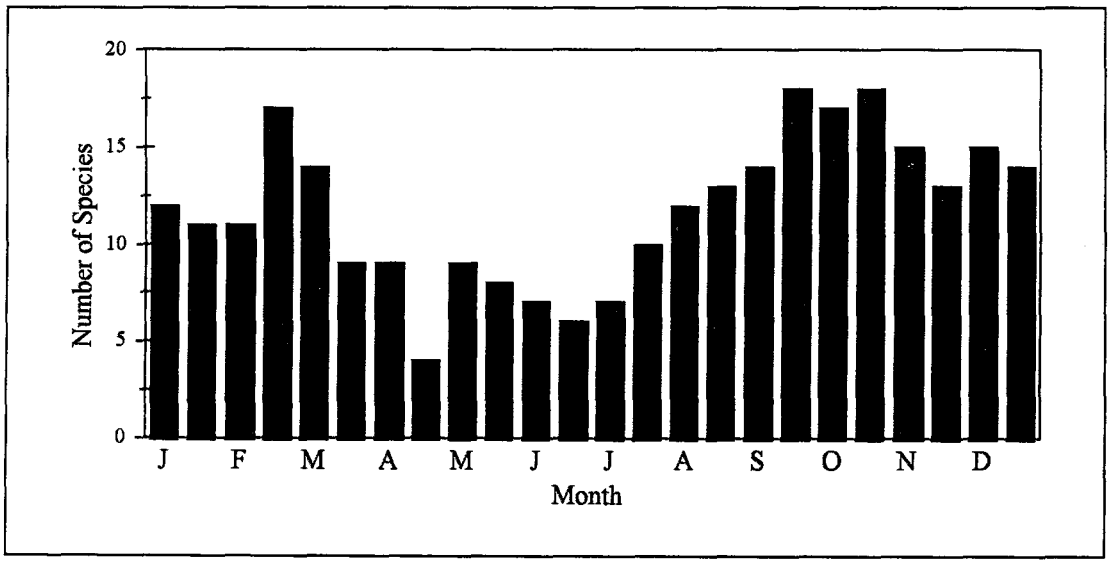


Figure 5.2. The number of species of transient territorials on the rocky shore at Thumbi East Island is bimodally distributed, but the peaks are much less marked than those of the distribution of number of individuals. Data are twice-monthly counts from three transects, between August 1991-August 1992.

Figures 5.3-5.18 show the number of territorial individuals of each species throughout the year.

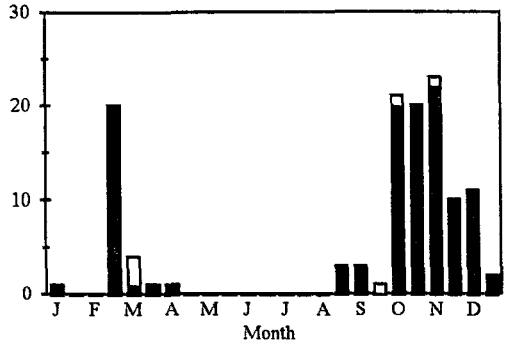


Figure 5.3. *Protomelas fenestratus* shows a bimodal breeding pattern at Thumbi East Island: males (■); females (□).

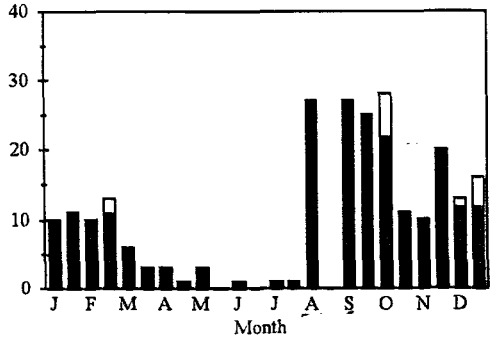


Figure 5.4. *Copadichromis borleyi* breeds for most of the year, but has a bimodal peaked pattern: males (■); females (□).

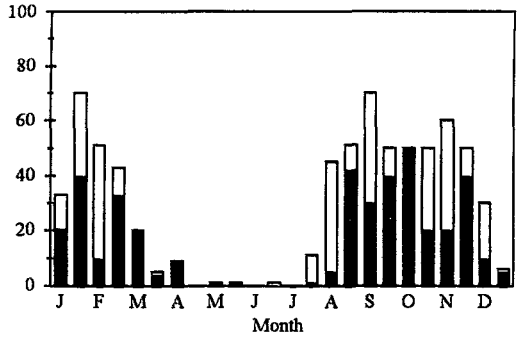


Figure 5.5. *Copadichromis cf eucinostomus* (■) and *C. cf prostoma* (□) have similar bimodal breeding seasons.

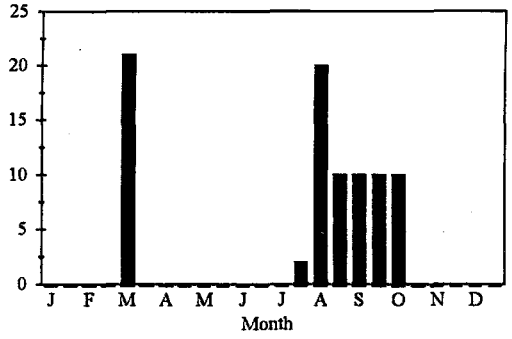


Figure 5.6. *Nyassachromis nigritaeniatus* males aggregate in leks of approximately 10 fish.

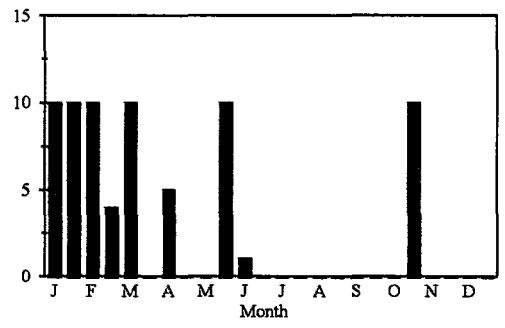


Figure 5.7. Leks of male *Mylochromis anaphyrmus* appear intermittently, but seem to be bimodally distributed.

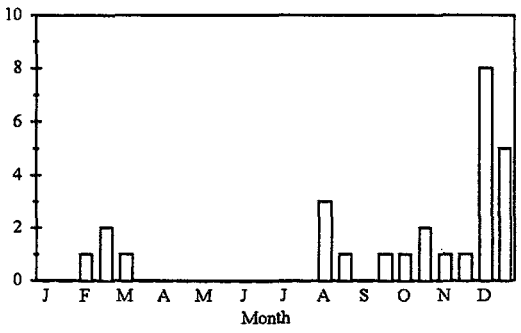


Figure 5.8. Female *Hemitaeniochromis urotaenia* were found throughout the main breeding season, with the main peak in December.

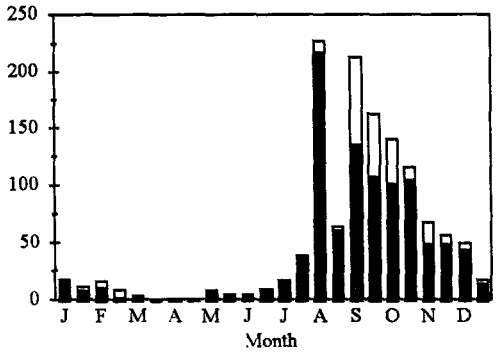


Figure 5.9. *Protomelas taeniolatus* has a strongly unimodal breeding pattern at Thumbi East Island: males (■); females (□).

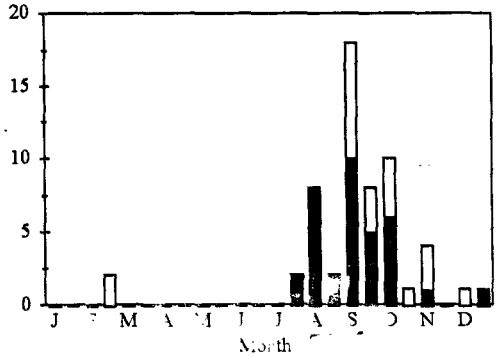


Figure 5.10. *Protomelas* spilonotus 'Likoma' has a largely unimodal breeding season: males (■); females (□).

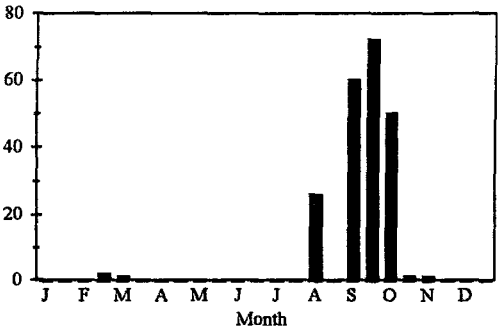


Figure 5.11. *Copadichromis jacksoni* males are mostly present from August to October.

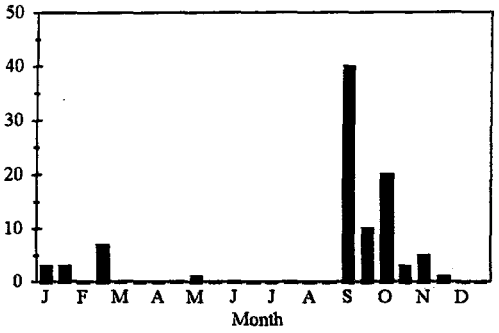


Figure 5.12. *Copadichromis chrysonotus* males appear in large numbers in September and decrease in abundance throughout the breeding season.

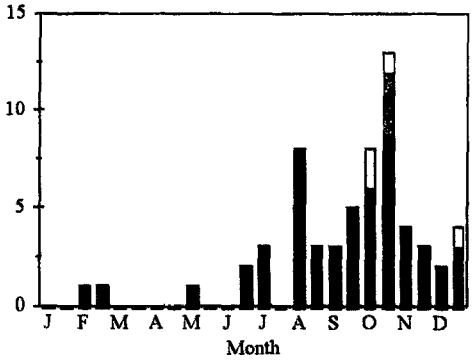


Figure 5.13. *Otopharnyx* 'heterodon Nankhumba' breeds sporadically throughout the year, but the a main peak is from August to October: males (■); females (□)

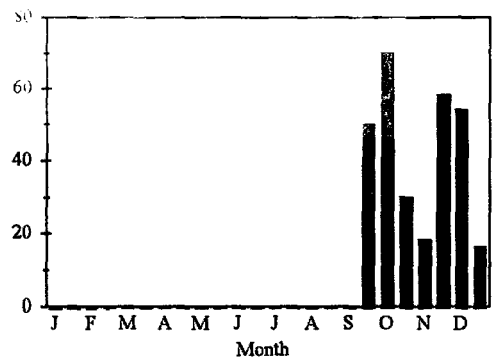


Figure 5.14. *Copadichromis* 'eucinostomus big spot' has a single short breeding season.

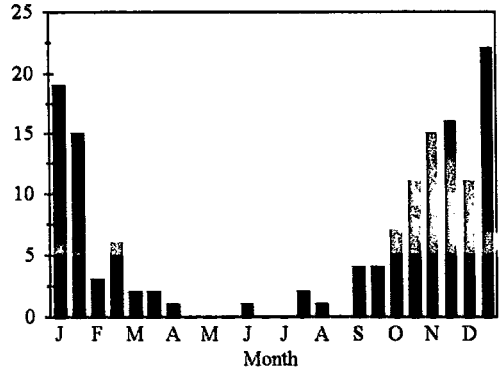


Figure 5.15. *Oreochromis karongae* has a long breeding season, but a strong peak from November to January

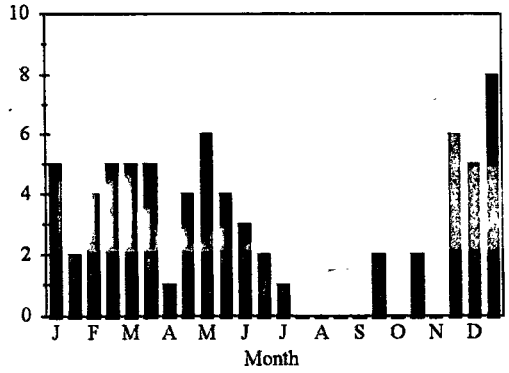


Figure 5.16. *Copadichromis* 'blue streamer' breeds throughout the year, although there appears to be a lull from July to October.

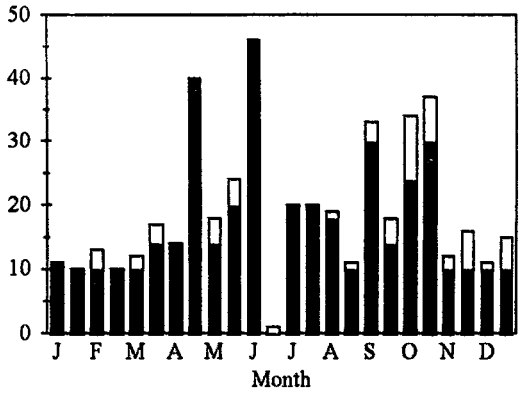


Figure 5.17. *Dimidiochromis kiwinge* breeds throughout the year: males (■) females (□).

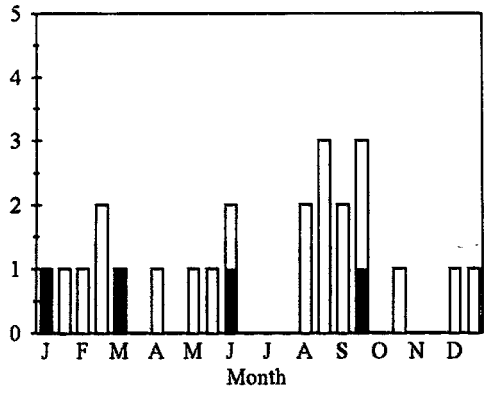


Figure 5.18. *Tyrannochromis macrostoma* was present in small numbers throughout the year: males (■) were seen less often than females (□).

ABUNDANCE AND DEPTH DISTRIBUTION OF TRANSIENT TERRITORIAL FISH

There was a higher proportion of female fry-guarding territories at 1 m than at 5 m (Table 5.2). *P. taeniolatus* was the dominant species at both depths with the similar *Protomelas* "spilonotus Likoma" the second most numerous species on the shallow transect. The large predator *Dimidiochromis kiwinge* was also numerous at both depths for all three species, both sexes defend territories in the breeding season, either as spawning sites or female fry-guarding sites. Many of the same species were found at both depths, but the relative abundances varied. Qualitative observations indicated that the density of breeding territories at 10 metres depth and beyond was much lower than in shallow water.

MICROHABITAT PREFERENCES

The preferred rock size and orientation differs between species to some extent, although there is a large overlap in sites used, with the majority of species in the rocky areas defending breeding territories on the top of rocks (Table 5.3). None of the male transients occupied caves under rocks, although almost all resident male mbuna did so. Female *C. borleyi* occupied caves, in one case deep within the core refuge of a male *L. fuelleborni.* The latter normally courts and spawns in the outer part of its refuge.

In the majority of species, the mean water depth of female territories was less than that of males. Larger species, such as *T. macrostoma, O. karongae, T. laticeps, D. kiwinge, B. heterotaenia, M. anaphyrmus* and *H. urotaenia* generally ranged into deeper water. Particular large boulders were occupied by several transients simultaneously and successively (see Figure 5.19).

Table 5.2. Bathymetric distribution of breeding territories (Figures show percentage frequency of transient territories on each transect).

	Male	Female	TOTAL for species
1m depth transect:			
P. taeniolatus	22.[illegible]	38.5	60.8
P. "spilonotus Likoma"	9.3	5.3	14.6
D. kiwinge	10.6	3.7	14.3
M. anaphyrmus	3.3	-	3.3
C. borleyi	1.3	1.7	3.0
C. cf. eucinostomus	1.3	-	1.3
Others	1	1.7	2.7
Totals	**49.1**	**50.9**	
5m depth transect:			
P. taeniolatus	23.1	1.2	24.3
D. kiwinge	11.0	1.4	12.4
C. cf. eucinostomus	11.6	-	11.6
C. cf. prostoma	9.4	0.0	9.4
C. 'eucinostomus big spot'	8.7	-	8.7
C. jacksoni	6.2	-	6.2
C. borleyi	6.7	0.2	6.9
O. karongae	4.2	-	4.2
P. fenestratus	3.4	-	3.4
Others	12.2	0.8	12.9
Totals	**96.5**	**3.6**	

Table 5.3. Description of sites used for transient breeding territories in the study site (0-12 metres depth).

N	Species	Sex	Depth Range (mean)	Substrate	Characteristics
2	*B. heterotaenia*	F	5-7m (6)	Mixed rocks & sand.	>100 fry on sand or ledge of rock slab
1	*C. cf. azureus*	M	6m	Mixed rocks & sand.	Lopsided sand nest, 20 cm diameter, adjacent to 20 cm rock
22	*C. borleyi*	F	1-5m (3.5)	Rock	Under rocks of 1-3 m. Females and fry rarely appear above rock.
40	*C. borleyi*	M	1-9m (4.7)	Rock	Small sand nest on outer hump of rock, 1.5-3 m, or occasionally larger.
58	*C. eucinostomus* complex.	M	4-8m	Rocks, sand or rocks sand.	Defend sand nest or rock, often in leks.
21	*C. jacksoni*	M	2-4m (2.9)	Rocks	Usually on hump of rock 2-4 m across, often in lek
27	*C.* 'blue streamer'	M	5-12m (8.5)	Rocks	Hump on rock 1.5-3 m.
12	*Ct. cf. intermedius*	M	10m	Rocks on sand	Small sand nest on rock of 0.5-3 m.
48	*D. kiwinge*	F	1-10m (5)	Rock or sand	13-100 fry. Usually hollow in large rock (>3 x 3m), or rarely sand nest.
103	*D. kiwinge*	M	5-10m (5.6)	Rocks, sand or rocks on sand.	Often on top of large boulder, 2 m below surface or large sand nest. Leks of 2-20.

Table 5.3 (continued).

N	Species	Sex	Depth Range (mean)	Substrate	Characteristics
30	*H. urotaenia*	F	0.5-11m (5.9)	Rocks on sand or slab.	16-60 fry, on rock or sand
17	*M. anaphyrmus*	M	6-8m (6.8)	Rocks on sand	Lopsided sand nest 45cm across, sometimes on rock. May be in leks of up to 10.
2	*N. cf. breviceps*	F	2-12m	Rock	ca 60 fry, on top of rocks, 1-2 m across
30	*N. nigritaeniatus*	M	4-6m (4.4)	Rock or rock on sand.	Sand nest on top of large rocks (4 x 3 m), just below water surface. Leks up to 14, sometimes with male *D. kiwinge*
1	*N. polystigma*	F	2m	Rock slab	≤ 50 fry. Hollow in slab.
1	*C.* cf. prostoma	F	3m	Rock slab	On flat surface of rock
31	*C. cf. prostoma*	M	3-8m (4.3)	Rock or rocks on sand.	Rocks 1-5m , sometimes rocks on sand. May be in leks >10.
10	*O.* "heterodon Nankhumba"	F	3-7m (4.6)	Rocks on sand.	On sand near rock, on slab, or in cave.
9	*O.* "heterodon Nankhumba"	M	5-8m (5.8)	Rocks on sand.	Between, on or under rocks.
30	*O. karongae*	M	4-10m (5.9)	Rocks on sand.	Sand nest, often adjacent to rock, may be in leks.
12	*P. fenestratus*	F	1-5m (2.6)	Rocks on sand, macrophyte beds	6-12 fry. On sand or rocks of 0.1- 5 m, often near macrophytes

Table 5.3 (continued).

N	Species	Sex	Depth Range (mean)	Substrate	Characteristics
28	*P. fenestratus*	M	5-10m (7.5)	Rocks on sand.	Rocks 0.3-2 m, occas. on large slab.
15	*P.* "spilonotus Likoma"	F	0.5-6m (1.6)	Rock	≤ 23 fry. Top or side of rocks of 0.5-1m across, or spaces between them. Occasionally on rubble or larger rocks
10	*P.* "spilonotus Likoma"	M	1m	Rock	Rocks of 0.5-2 m across. Flat to 45° Sometimes with small deposit of sand on rock.
87	*P. taeniolatus*	F	0.3-9m (2.9)	Rock	Top of rock 0.5-2 m, occasionally in a hollow on slab.
76	*P. taeniolatus*	M	2-7m (4.8)	Rock	Small sand deposit on rocks of 1-5 m.
1	*S. robustus*	F	12m	Rock.	Hollow in slab.
2	*T. laticeps*	F	5-9m	Rock slab or rocks on sand.	50-100 fry. Between rocks or in hollow of slab.
2	*T. rendalli*	Pair	5m	Sand, rocks on sand. or rock.	One on sand near macrophytes, one on purely rocky area, rock of size 3 x 1.5m
23	*T. macrostoma*	F	3-11m (5.2)	Rock	30-100 fry. Large rocks, 1.5-10 m across, often in hollow.
2	*T. macrostoma*	M	3.5-5m	Rock	Large rock >3m. Flat to 40°.

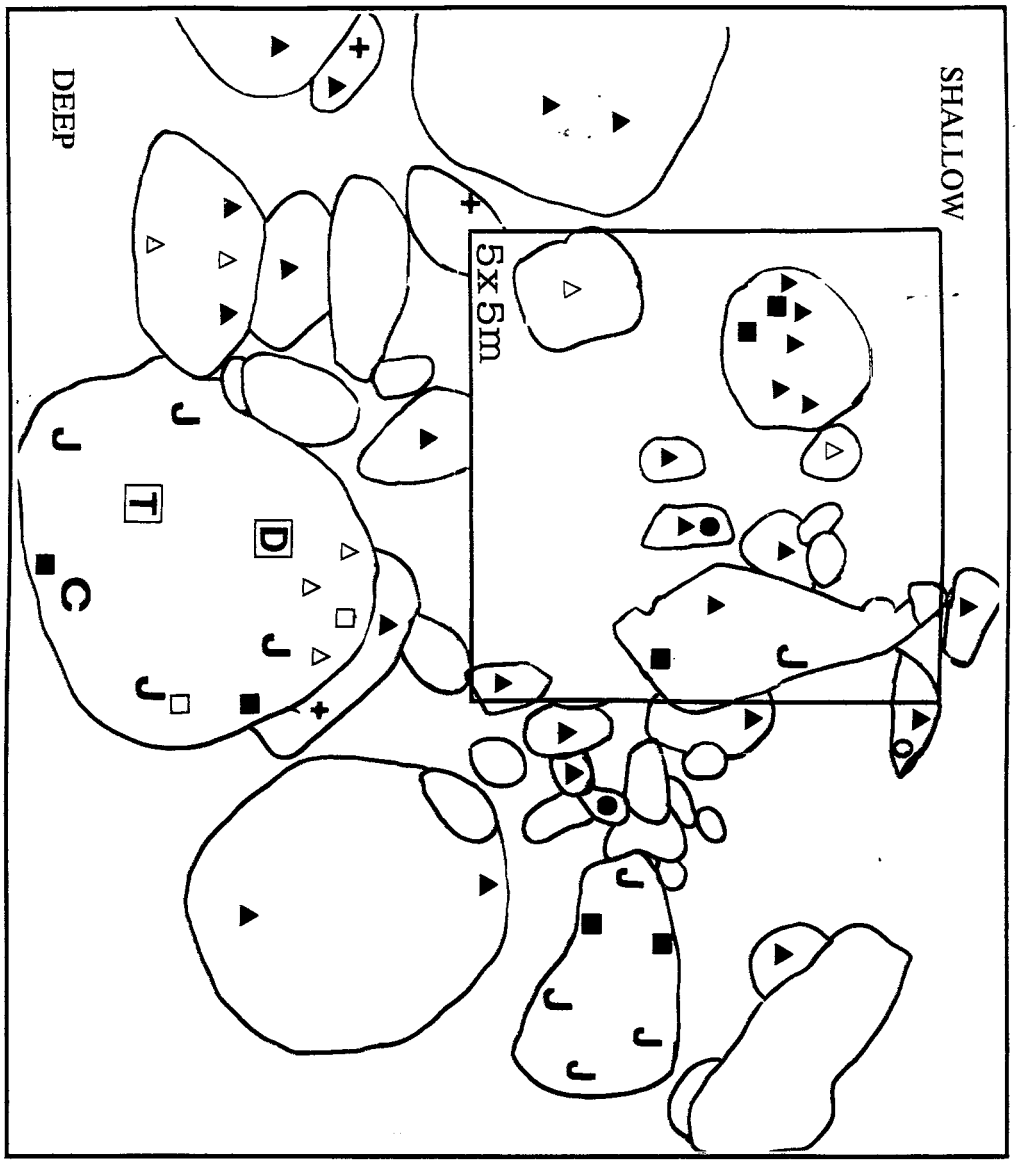


Figure 5.19. Location of transient breeding territories established in and around the quadrat (enclosed by a square) between 4th September and 9th October 1991.
▲ = *P.taeniolatus* female; Δ = *P.taeniolatus* male; ■ = *C.borleyi* female; □ = *C.borleyi* male; ● = *P.* 'spilonotus Likoma' female; ○ = *P.* 'spilonotus Likoma' male; **J** = *C. jacksoni* male; **C** = *C.chrysonotus* male; **D** = *D. kiwinge female*; **T** = *T.macrostoma female*.
The substratum in the whole area was rocky, but for this diagram, only major landmarks and rocks used by transients are drawn.

DURATION OF TERRITORY OCCUPATION

Male *C. jacksoni* and *P. taeniolatus* remained on their territories for up to 2 or 3 months (Table 5.4). They often seemed to be 'semi-territorial' for part of their tenure, being pale coloured and not fully able to monopolise a spawning site. Even when fully controlling a territory, they often left the area completely, particularly during the afternoon, perhaps to feed.

Females of most species occupied territories for relatively short periods, generally around 10-12 days and never more than 30 days. While incubating eggs and yolk-sac fry most females were non-aggressive and mobile. Shortly before releasing fry for the first time, they generally became more aggressive and less mobile. After fry became free-swimming, females were generally highly aggressive and remained in a limited territory throughout the day and night for the full fry guarding period. Fry were retrieved before dusk and kept in the buccal cavity overnight. An exception to the pattern was *D. kiwinge*. Females of this species often retrieved their fry and left their territory in the late afternoon. It is not known where they spent the night. The following day they returned to the site or defended their brood at a different location. Females of some smaller species sometimes retrieved their brood and temporarily left their territories during invasions of large feeding shoals of mbuna in the late afternoon. These females usually remained close to their territory, generally remaining stationary and without releasing their brood returning after the feeding shoals had passed. Females of *P. taeniolatus*, *P.* 'spilonotus Likoma', *C. borleyi* and *T. macrostoma* were rarely observed to change their territories once the fry had been released, although prior to this, females often spent short period of time being aggressive in several localities, as if attempting to establish territories.

Table 5.4. Duration of territory occupation by individual transient territorial fish (days).

Species	Males	Females
C. borleyi	5+, 16+, 17	2, 8,8,10, 10+, 11, 11, 12, 15
C. jacksoni	2, 9, 24, 24, 30, 39, 58	
C. 'eucinostomus big-spot'	8+	
N.cf. breviceps		4
O. karongae	1, 4	
O. 'heterodon Nankumba'		9, 10+, 25, 29, 30
P. 'spilonotus Likoma'		13
P. taeniolatus	8, 50, 52, 65, 76, 91	up to 21 days (see chapter 6)
T. macrostoma		8+

OVERLAP BETWEEN TRANSIENT AND PERMANENT TERRITORIES

During the six weeks of observations in the quadrat, sixteen territories were held by transient territorials: 10 female *Protomelas taeniolatus*, 1 female *P.* 'spilonotus Likoma; 2 female *Copadichromis borleyi*, 1 male *C. jacksoni* and 2 male *P. taeniolatus* (Figure 5.20). Each of these transient territories overlapped with a number of defended areas or feeding ranges previously held by a permanent resident (table 5.5). The majority of overlaps with core defended areas were with *P. elongatus* 'aggressive' and *P. tropheops* 'orange chest', but these were among the most numerous species, and the distribution of overlaps between species was not significantly different from the frequency distribution of species in the quadrat (G-test, G=3.05, 4 df, P>0.50). Comparison with feeding ranges and total defended areas would be of less value, as there was much more inter- and intraspecific variation in the sizes of these ranges while core areas were comparatively uniform.

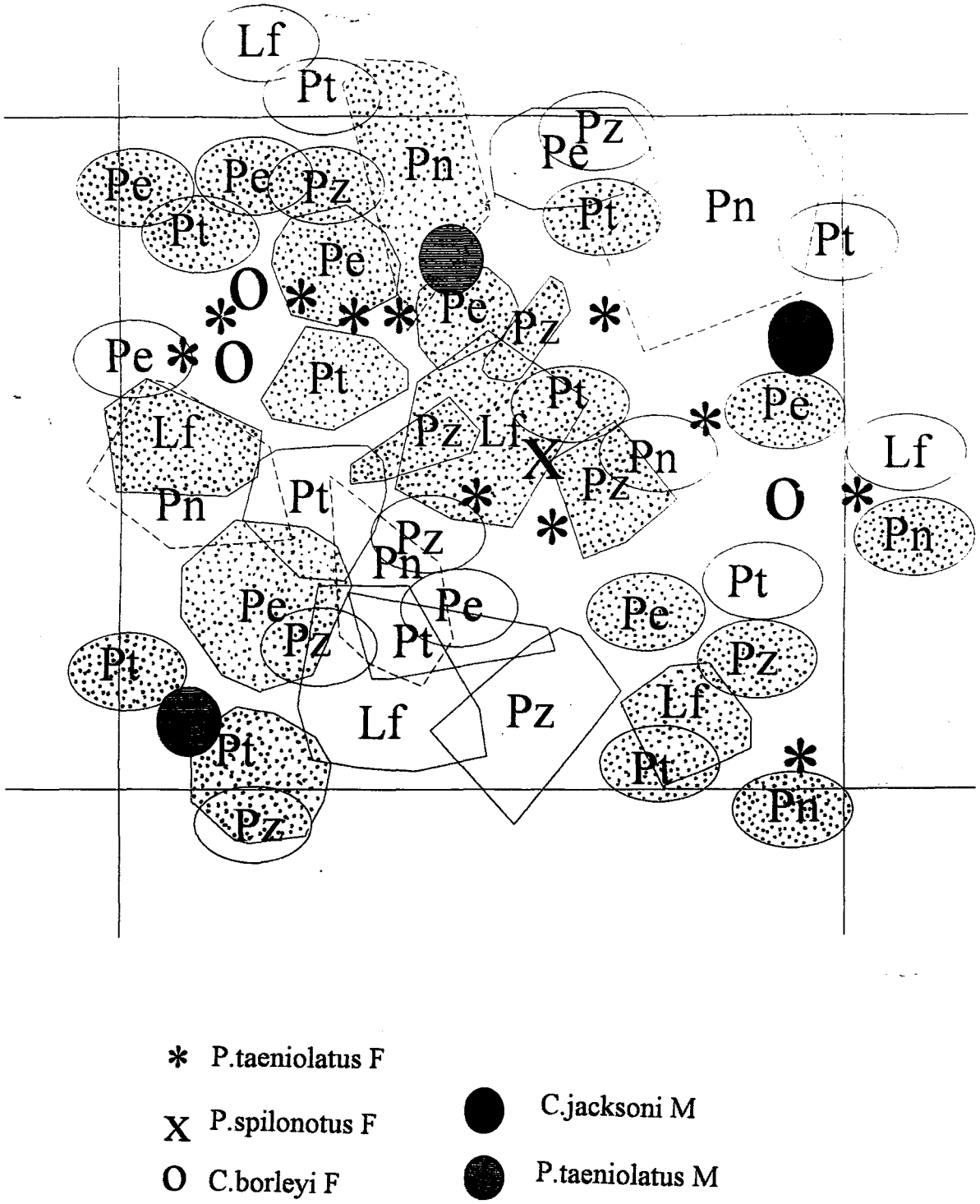


Figure 5.20. Transients territories established in the study quadrat in relation to the territorial mbuna. Symbols for the transients are shown above. Stippled areas indicate territories of resident mbuna that were seen to receive aggression from the transients. The core areas of residents subject to focal watches are indicated by open polygons, and for other residents the approximate centre of the territory is indicated by an ellipse. Abbreviations: Lf: *L. fuelleborni*; Pn: *P. nigra*; Pt: *P. tropheops* 'orange chest'; Pe: *P. elongatus* 'aggressive'; Pz: *P. zebra*.

Table 5.5. Frequency of overlap between territories of transient territorial fish and permanent residents of a 5 x 5 m quadrat. Particular permanent residents may have overlapped with several transient territories and vice versa. Figures in brackets are the numbers of territorial residents whose core areas were within the quadrat

	Core Area	Defended Area	Feeding Area
P. tropheops 'orange chest' (8)	14	16	20
L. fuelleborni (6)	6	7	16
P. zebra (9)	9	10	16
P. elongatus 'aggressive' (10)	15	15	15
P. nigra (7)	7	13	19
Totals	51	61	86

Establishment of transient territories resulted in three possible outcomes: (i) expulsion of transients; (ii) expulsion of residents; (iii) partial overlap and compaction of resident ranges.

(i) Neither male *P. taeniolatus* stayed in the quadrat for more than a few days. Their colours remained subdued throughout, although conspicuously brighter than those of non-territorial conspecifics. Their attempts to establish themselves appear to have been unsuccessful and they abandoned their territories. Likewise, one female *P. taeniolatus* was observed to leave the quadrat, with its brood, after a single day guarding its free-swimming fry. The large boulder on the top left of the quadrat was often simultaneously occupied by several mouthbrooding *P. taeniolatus,* which were initially passive but became aggressive as the fry appproached the free-swimming stage. Although several were successful at establishing a territory on this rock, others moved elsewhere, after receiving frequent attacks from territorial mbuna or conspecific guarding females.

(ii) Within the quadrat, a single *P. elongatus* 'aggressive' (# 2) territory was overlapped by a succession of fry-guarding female *P. taeniolatus* territories, over a period of 5 weeks, and was eventually abandoned by the *P. elongatus* 'aggressive'. (Fig. 5.23). Outside the quadrat, two other *P. elongatus* 'aggressive's were observed to abandon their territories, and establish defended sites some 2-3 m away. Prior to their moves, each individual's territory had overlapped with that of a much larger male *P.*

taeniolatus. Aggressive interactions occurred frequently in the overlap area. (Fig. 5.24). As the territories in this area had not been mapped it was not known if the displaced *P. elongatus* 'aggressive' themselves displaced other residents.

(iii) Establishment of temporary breeding territories usually led to overlapping space use between transient and territorial fish, with frequent aggression in the zones of overlap. Some territorial mbuna thus affected decreased their range size, or spent more time in areas used by other permanent territorial residents. (Figs. 5.21-5.23).

AGGRESSION BY BREEDING TRANSIENT TERRITORIAL FISH

Qualitative observations indicate that many transient territorial fish chased most of the species which were permanently resident in the area (Table 5.6). Focal watches on the most abundant transient species, *Protomelas taeniolatus,* indicate that most of the overt aggression is directed towards non-territorial fish (Table 5.7). Males rarely attacked territorial mbuna, perhaps because transient male territories were usually at the top of tall boulders and well away from territorial mbuna refuges. Most attacks were directed at conspecific males. Conspecific males might compete for the same territories and on several occasions males adopting the dark colour of ripe female *C. borleyi* were observed to rush in beside circling pairs either to eat eggs or sneak fertilisation. Other attacks were on territorial non-mbuna, such as *Labeo cylindricis* and *Tyrannochromis macrostoma.* By contrast 75% of female attacks on territorial fish were directed towards mbuna, principally *Pseudotropheus* spp. Qualitative observations and a few focal watches indicated that similar patterns were demonstrated by other *Protomelas* and *Copadochromis* species.

Table 5.6. Aggression shown by Transient Territorials towards resident fish. T= territorial resident, F= non-territorial resident, ✓= non-territorial residents.

	Transient Territorial *:					
Territorial Resident:	**Pt (M)**	**Pt (F)**	**PsL (F)**	**Cb (F)**	**Nb (F)**	**Tren (pr)**
P. e."aggressive"	FT	FT	FT	FT	F	F
P. zebra	FT	FT	FT	F	FT	F
L. fuelleborni	FT	FT	FT		FT	
P. t."orange chest"	FT	FT	FT		FT	
P. nigra	FT	FT	T		F	F
Aggressive residents, non-territorial:						
Melanochromis auratus	✓	✓	✓	✓		✓
Melanochromis heterochromis	✓	✓	✓	✓	✓	
Labidochromis vellicans	✓	✓				

* Pt= *P.taeniolatus,* PsL= *P.*"spilonotus Likoma", Cb= *C.borleyi,* Nb= *N.breviceps,* Tren= *T.rendalli.* (F) = Fry-guarding female, (M) = male, (pr) = fry-guarding pair.

Table 5.7. Aggressive interactions between transient territorial *Protomelas taeniolatus* and other territorial fish.

	Frequency of Chasing		Frequency of Being Chased	
	Male	**Female**	**Male**	**Female**
Mbuna:				
Labeotropheus fuelleborni	0	19	0	8
Melanochromis auratus	0	2	0	0
Petrotilapia nigra	0	5	0	0
Pseudotropheus elongatus 'aggressive'	1	90	0	10
Pseudotropheus tropheops 'orange chest'	2	38	0	17
Pseudotropheus tropheops, others	0	12	0	3
Pseudotropheus zebra	16	28	0	11
Total Mbuna	**19**	**194**	**0**	**49**
Non-mbuna:				
Copadichromis spp.	1	5	0	0
Labeo cylindricus	13	0	0	0
Protomelas taeniolatus	28	24	0	0
Tyrannochromis macrostoma	14	1	0	0
Total Non-Mbuna	**56**	**30**	**0**	**0**
Total Territorials	**75**	**224**	**0**	**49**
Total Chases in Focal Watches	**720**	**3195**	**0**	**75**

EFFECTS ON THE BEHAVIOUR OF RESIDENT FISH.

During the peak breeding season, focal watches indicated significant changes in the behaviour of resident mbuna which held territories adjacent to those of transients (Table 5.8). The behaviour of some residents tended to return to previous levels after the transients had left, while in others behavioural changes were maintained. The most

consistent trend was a significant reduction in the time spent motionless which occurred in all four fish which had been observed prior to the establishment of transient territories (Table 5.9). Reduced feeding time was seen in only one fish (Table 5.8; *P. elongatus* 'aggressive' #5), which displaced its feeding and defended areas downwards while a transient territorial female *P. taeniolatus* occupied the part of its range nearer to the top of the quadrat, in shallower water (Figure 5.21). Two of the residents were also chased more often than before, and both of these spent less time courting females (Table 5.9). Two individuals became more aggressive, and in each case the resident and transient fish did not co-exist for long. One *P. elongatus* 'aggressive' shared the lower right part of its feeding and defended area with a guarding female *P. taeniolatus*. The two fish avoided each other, and the *P. elongatus* became more aggressive and expanded the upper and left borders of its range before disappearing from its territory (*P. elongatus* 'aggressive' #2: Table 5.8, Fig 5.23). It is not known whether it died or re-established its territory elsewhere. A male *P. tropheops* 'orange chest' (*P. tropheops* 'orange chest' #3) which had a large male *P. taeniolatus* on the upper boundary of its territory (Fig 5.22), expanded its lower and right boundaries, and increasingly confronted the male conspecific on its left boundary in frontal display contests. It also increased its total rate of chasing. The male *P. taeniolatus* departed after a few days and the *P. tropheops* immediately expanded its range upwards again, while continuing to use the new areas on the lower and left borders of the old territory.

Other territorials changed their patterns of space use. The *Labeotropheus* male (# 4) contracted its upper and lower defended borders after *P. taeniolatus* females had settled on both. Having previously fed mainly within its defended area, this fish now spent a lot of time feeding outside its territory to both left and right (Fig. 5.21). It was chased more often and decreased its own frequency of chasing (Table 5.8). After the departure of the transient territorials, it not only maintained its new feeding range, but now defended it all, increasing its rate of chasing and of displaying and fighting. The *P. tropheops* 'orange chest' male (#10) which had not been the subject of focal watches before the breeding season greatly contracted its feeding range after its transient neighbour departed (Fig. 5.23), having foraged more on a large boulder near by when the transient was present.

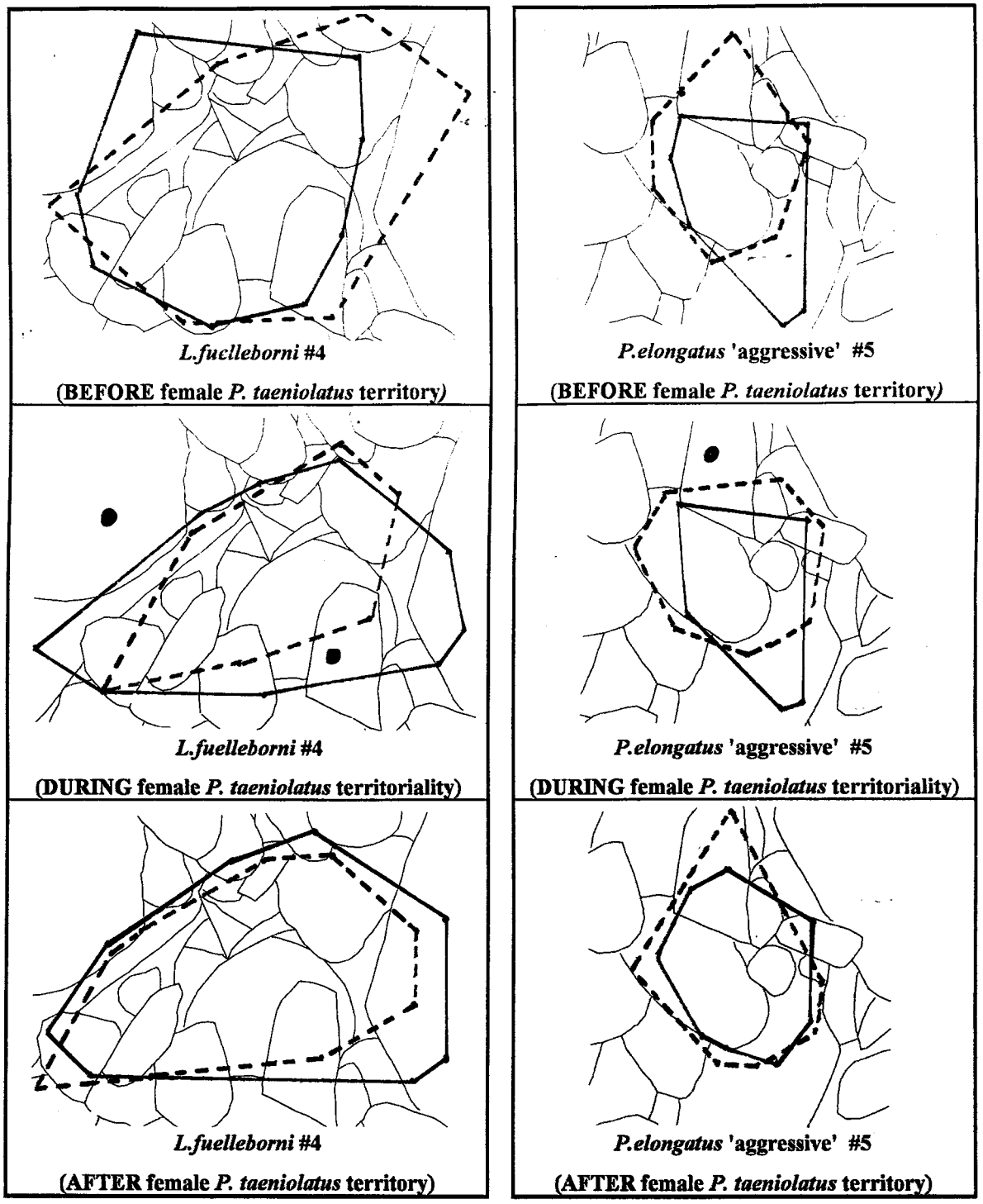


Figure 5.21 The effects of transient territorial neighbours on the space utilization of *L.fuelleborni* #4 and *P. elongatus* 'aggressive' #5. Each map is based on 3¾ hours observation for *L. fuelleborni* #4, and 1 hours observation for *P.elongatus* 'aggressive' #35. Solid lines indicate total feeding area used and dashed lines indicate total defended area used. Thin lines represent rocks. ● indicates centre of transient territory in each case.

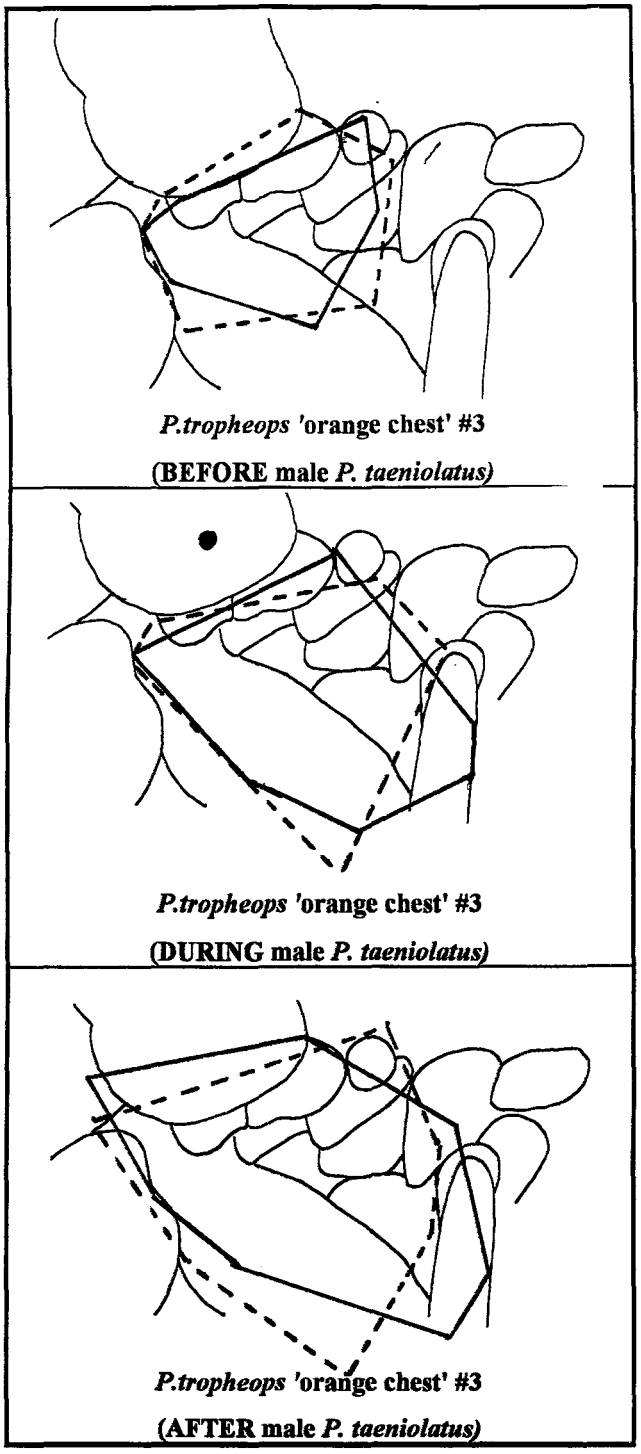


Figure 5.22 The effects of transient territorial neighbours on the space utilization of *P.tropheops* 'orange chest' #3 Each map is based on 3 hours observation. Solid lines indicate total feeding area used and dashed lines indicate total defended area used. Thin lines represent rocks. ● indicates centre of transient territory.

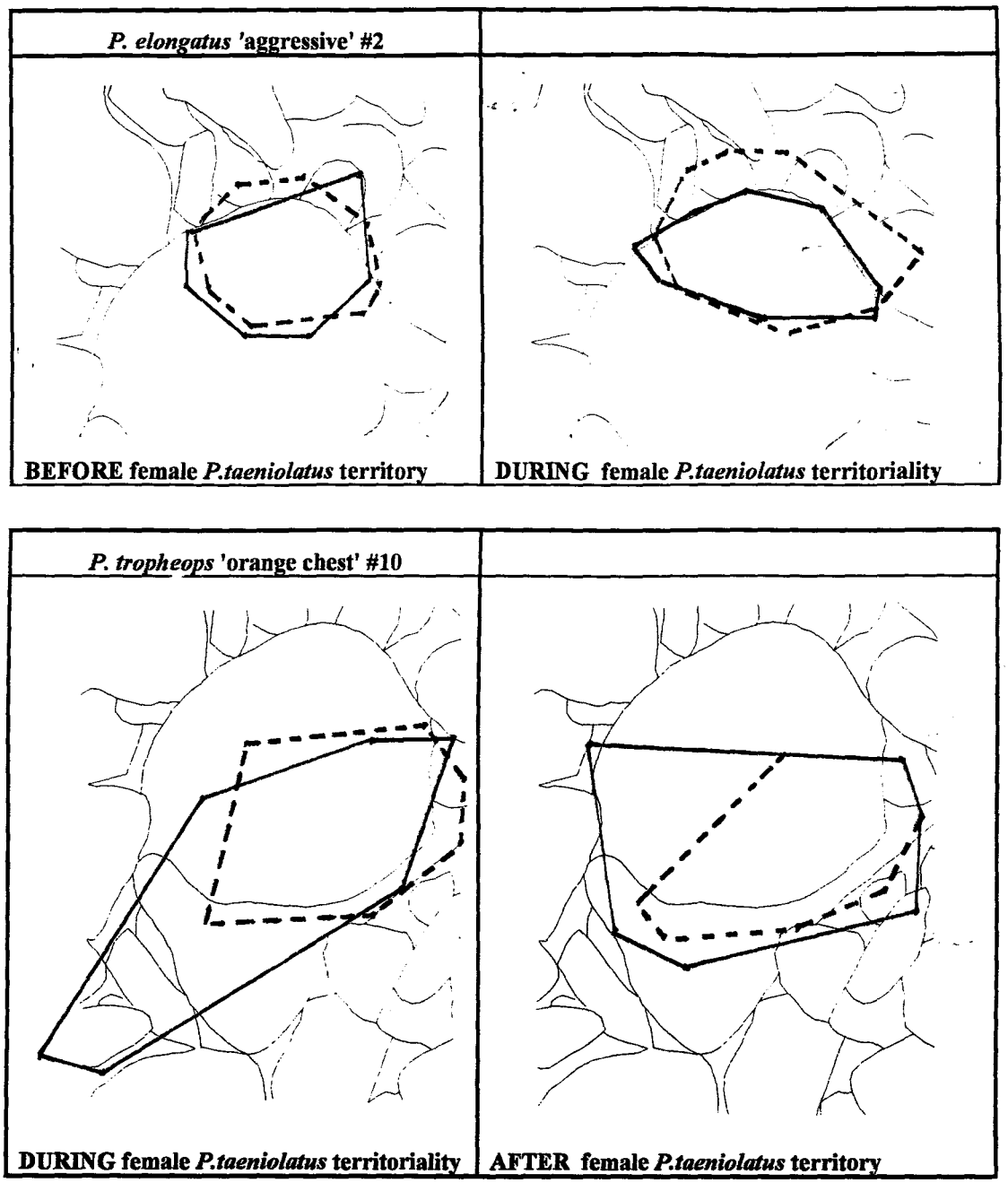


Figure 5.23. Territories of *P.elongatus* 'aggressive'#2 and *P. tropheops* 'orange chest' #10, both of which were affected by the same *P.taeniolatus* fry-guarding territory, which was established on top of the large rock. Solid lines indicate total feeding areas used and dashed lines indicate total defended areas. Thin lines represent rocks. Each *P. elongatus* 'agressive' #2 map is based on 3¾ hours observation and each *P. tropheops* 'orange chest' #10 map is basedon 10 hours observation.

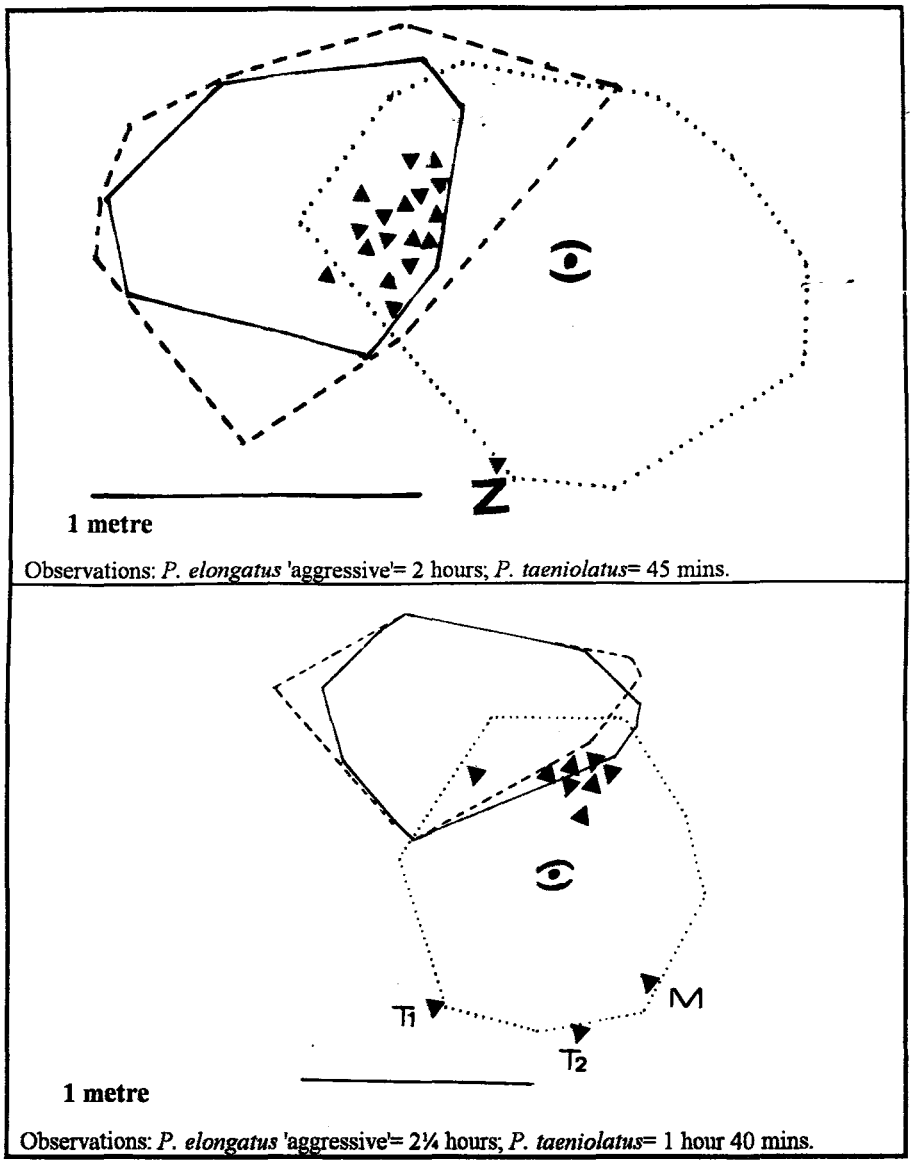


Figure 5.24. Positions of two territorial *P. elongatus* 'aggressive' on separate boulders with newly-established transient territorial (male *P. taeniolatus*) neighbours, which subsequently displaced them. Solid lines indicate feeding areas and dashed lines show defended areas of *P. elongatus* 'aggressive', whilst dotted lines show defended areas and 👁 show spawning sites of male *P. taeniolatus.*

Triangles indicate sites of mutual frontal displays. Where these displays involved the transient territorial and residents other than the focal *P. elongatus* 'aggressive', this is denoted by a letter, where M = *Melanochromis auratus,* T1 & T2 = 2 territorial *P. tropheops* 'orange chest' individuals and Z = territorial *P.zebra.*

Table 5.8. Comparison of the behaviour of five territorial mbuna before, during and after the presence of a neighbouring transient territorial fish (PT = *P.taeniolatus*). Means are frequencies or total durations in seconds during a 15-minute focal watch. Statistical analysis is with oneway parametric analysis of variance (F value shown), or where the data are not normally distributed, Kruskal-Wallis non-parametric test (H value shown).

Individual/ Behaviour	**Time Relative to Transient**			**Statistical Significance**			
***P. elongatus* 'aggressive' (#2)**							
[transient=PT female]	**Before**	**During**	**After**		**df**		
Time Benthic Feeding	380.3	328.0		F=2.24	1,52	P=0.141	ns
Number of Bites	186.9	190.9		F=0.07	1,52	P=0.794	ns
Time Still	17.5	4.6		H=14.5	1	P<0.001	***
Time Swimming	489.1	538.9		F=2.08	1,52	P=0.155	ns
Time Chasing	12.3	25.2		F=31.09	1,52	P<0.001	***
Number of Chases	11.9	25.1		F=32.0	1,52	P<0.001	***
Time Being Chased	0.2	0.2		H=0.04	1	P=0.84	ns
Freq. Being Chased	0.2	0.2		H=0.04	1	P=0.84	ns
Time Courting	0.0	2.3		H=1.09	1	P=0.30	ns
Freq. Courting	0.0	0.1		H=1.09	1	P=0.30	ns
Chafe	0.6	0.4		H=1.23	1	P=0.27	ns
T. Displaying/Fighting	0.0	0.4		H=1.48	1	P=0.22	ns
***P. elongatus* 'aggressive' (#5)**							
[transient=PT females]	**Before**	**During**	**After**		**df**		
Time Benthic Feeding	117.8	71.1	187.3	F=48.07	2,77	P<0.001	***
Number of Bites	79.8	69.6	144.4	F=25.0	2,77	P<0.001	***
Time Plankton Feeding	206.3	0.0	0.0	H=9.45	2	P=0.009	**
Time Still	14.8	5.7	80.3	H=57.1	2	P<0.001	***
Time Swimming	348.5	789.0	598.3	F=80.8	2,77	P<0.001	***
Time Chasing	19.5	21.2	24.5	F=1.0	2,77	P=0.37	ns
Number of Chases	14.5	20.1	17.5	F=1.48	2,77	P=0.23	ns
Time Being Chased	0.0	0.1	0.0	H=1.94	2	P=0.379	ns
Freq. Being Chased	0.0	0.1	0.0	H=1.94	2	P=0.379	ns
Time Courting	0.8	3.7	0.5	H=1.93	2	P=0.382	ns
Freq. Courting	0.3	0.4	0.2	H=1.49	2	P=0.475	ns
Time in Refuge	192.5	8.9	7.6	H=0.13	2	P=0.939	ns
Chafe	0.0	0.2	1.3	H=23.3	2	P<0.001	***
T. Displaying/Fighting	0.0	0.1	0.1	H=0.24	2	P=0.89	ns

Table 5.8.(continued).

L. fuelleborni (#4)

[transient=PT female]	Before	During	After		df		
Time Benthic Feeding	210.3	262.9	306.9	F=2.06	2,77	P=0.14	ns
Number of Bites	29.6	45.4	55.7	F=5.48	2,77	P=0.006	**
Time Still	171.3	34.5	52.9	F=7.52	2,77	P=0.001	**
Time Swimming	419.0	566.5	509.1	F=7.35	2,77	P=0.001	**
Time Chasing	6.6	4.6	7.5	H=9.96	2	P=0.007	**
Number of Chases	4.3	3.8	5.3	H=9.48	2	P=0.009	**
Time Being Chased	0.0	0.5	0.2	H=7.99	2	P=0.019	*
Freq. Being Chased	0.0	0.5	0.2	H=7.99	2	P=0.019	*
Time Courting	4.1	3.3	7.1	H=6.09	2	P=0.048	*
Freq. Courting	0.6	0.7	1.3	H=7.15	2	P=0.028	*
Time in Refuge	87.3	25.9	10.8	H=3.12	2	P=0.212	ns
Chafe	0.3	0.7	0.6	H=2.73	2	P=0.256	ns
T. Displaying/Fighting	1.1	1.1	4.8	H=11.58	2	P=0.003	**

P. tropheops 'orange chest' (#10)

[transient=PT female]	Before	During	After		df		
Time Benthic Feeding		694.9	671.1	F=2.31	1,78	P=0.13	ns
Number of Bites		435.5	465.1	F=3.05	1,78	P=0.09	ns
Time Still		6.0	2.4	H=2.67	1	P=0.103	ns
Time Swimming		185.0	213.5	F=4.35	1,78	P=0.04	*
Time Chasing		8.2	10.0	H=3.97	1	P=0.047	*
Number of Chases		4.1	5.2	H=1.55	1	P=0.21	ns
Time Being Chased		1.4	1.3	H=1.59	1	P=0.21	ns
Freq. Being Chased		1.4	0.8	H=3.44	1	P=0.06	ns
Time Courting		0.5	0.4	H=0.58	1	P=0.45	ns
Freq. Courting		0.5	0.1	H=0.71	1	P=0.40	ns
Chafe		0.7	0.6	H=0.41	1	P=0.52	ns
T. Displaying/Fighting		3.4	0.9	H=0.65	1	P=0.42	ns

Table 5.8.(continued).

P. tropheops 'orange chest' (#3)					df		
[transient=PT male]	**Before**	**During**	**After**				
Time Benthic Feeding	425.2	443.0	441.5	F=0.11	2,80	P=0.89	ns
Number of Bites	266.6	282.8	293.2	F=0.44	2,80	P=0.65	ns
Time Still	56.9	7.6	12.7	H=13.4	2	P=0.001	**
Time Swimming	402.3	412.5	412.9	F=0.05	2,80	P=0.95	ns
Time Chasing	11.3	16.5	23.5	F=10.7	2,80	P<0.001	***
Number of Chases	11.1	13.4	17.9	F=7.12	2,80	P=0.001	**
Time Being Chased	0.0	1.2	0.0	H=16.9	2	P<0.001	***
Freq. Being Chased	0.0	0.8	0.0	H=16.7	2	P<0.001	***
Time Courting	2.5	0.4	0.3	H=13.9	2	P=0.001	**
Freq. Courting	0.5	0.1	0.1	H=13.2	2	P=0.001	**
Chafe	1.3	1.4	2.0	H=2.16	2	P=0.34	ns
Peck	0.5	0.1	0.0	H=2.51	2	P=0.29	ns
T. Displaying/Fighting	0.0	17.1	7.1	H=16.4	2	P<0.001	***

Table 5.9 Summary of behavioural effects of transient territorials on five resident mbuna territorials.
(D=during territory tenure of transient; A= after departure of transient)

Behaviour	**Pea #2**	**Pea #5**	**Lf #4**	**Pto #10**	**Pto #3**
Benthic Feeding	-	Down D	-	-	-
Plankton Feeding	-	Down D	-	-	-
Motionless	Down D	Down D	Down D	-	Down D
Swimming	-	Up D	Up D	Up A	-
Chasing	Up D	-	Down D	Up A	Up D & A
Being Chased	-	-	Up D	-	Up D
Courting	-	-	Down D	-	Down D & A
Displaying & Fighting	-	-	Up A	-	Up D

Discussion

Many, but not all, of the Lake Malawi fish have definite breeding seasons which seem to coincide with times of food abundance (Lowe-McConnell 1979, 1987, Marsh *et al.* 1986). The main peak in reproductive activity for many species is August to October (Marsh *et al.* 1986) which follows a seasonal plankton bloom resulting from increased primary productivity caused by the release of nutrients caused by wind-driven upwelling (FAO 1982). Some species have a secondary peak in February to March when epilithic algae is most abundant, perhaps as a result of nutrient enrichment of shallow waters by run-off during the reainy season (Ribbink *et al.* 1983a, Marsh *et al.* 1986). The bimodal peaks in breeding activity for the transient territorial fish coincide with those of the resident mbuna (Marsh *et al.* 1986), as well as other groups, such as the *Oreochromis* spp. (Turner & Mwanyama 1992). It is likely that this overall pattern of reproductive seasonality is driven by food availability (Marsh *et al.* 1986).

The fishes establishing temporary territories in the rocky habitat have considerable impact on the permanent residents. All species of permanent residents may change their behaviour and alter their spatial patterns of habitat use. In extreme cases, they may abandon their territories and move elsewhere.

Although there are peaks in the numbers of breeding territories, some are to be found throughout the year. A large number of species defend temporary breeding territories and the sites chosen by each species have fairly predictable characteristics. Many of the smaller species breed in shallow water, where the density of permanent resident is highest (Ribbink *et al.* 1983a). It does not appear that sites are superabundant and all transient territorials appear to come into conflict with resident fish.

Transient territorials defend their sites against territorial individuals of several mbuna species, against other transient territorials as well as against many non-territorial fish. When a fish attempts to establish a breeding territory, it often does so in an area wholly or partly within the home ranges of one or more territorial mbuna or other breeding fish. The most common breeding territories were those of *P. taeniolatus,* which competed with all five mbuna species holding territories in the quadrat, as well as several of the other aggressive but non-territorial species resident in the area. It appeared that both males and females of this species were sometimes unable to maintain their territories, perhaps as a result of competition from permanent residents.

Alteration of residents' behaviour and habitat use take a variety of forms. Individual residents were affected in different ways, but it was not possible to test for differences in the effect on different species, owing to the small sample size. It was

notable that only *P. elongatus* 'aggressive' was actually expelled from its territory. Although highly aggressive, this is the smallest territorial mbuna in the area, and it appears not to feed outside its defended area (chapter 3). Perhaps the territories of this species cannot be greatly compressed while still providing enough food to support their owner. Unlike the other mbuna species, all *P. elongatus* 'aggressive' individuals above 6 cm (including perhaps immature males and females) defend territories (Ribbink *et al.* 1983a). Many smaller individuals lacked a spawning refuge (chapter 3) and their ranges probably are not breeding territories. For this reason, it may be easier for these individuals to find alternative territory sites and this may be preferable to attempting to defend a territory which provides insufficient food. For other species of mbuna, the critical resource is the spawning refuge and these are likely to be in limited supply. Since the peak breeding season for the transient species is also the peak breeding season for the mbuna, males are likely to lose reproductive opportunities if they abandon their territories at this time. Most of these species feed outside their defended areas anyway, and appear to respond to loss of territory by feeding further from their core areas. They seem to be able to achieve this without a reduction in feeding rate, but often with an increase in aggressive interactions. The only focal fish to suffer a reduction in its feeding rate was the *P. elongatus* 'aggressive' (#5) which maintained its territory throughout the transient breeding season. This large individual possessed a spawning refuge and appeared to be a male and so perhaps traded off reduced foraging in favour of maintaining reproductive opportunity.

Varying degrees of reproductive competition are reported for other cichlid communities. In Sri Lanka, two species of cichlids which are territorial during their reproductive phase (*Etroplus maculatus* and *E. suratensis*) apparently do not compete for habitat, and reproduce synchronously (Ward & Wyman 1977). In Lake Tanganyika there is also a high density of territorial algal feeders in the shallow rocky areas (Kawanabe 1981, Takamura 1983). In a study of 10 species of the genus *Lamprologus* which are territorial only in their reproductive period (Yanagisawa & Nshombo 1983), Nagoshi (1983) reported that the ecological requirements of each species are distinct and concluded that their spawning and breeding sites never overlap. However, In Lake Jiloa, Nicaragua, there is intense competition for breeding sites in the rocky habitat, 90% of attempts at territorial establishment being unsuccessful (McKaye 1977). In addition to competition between conspecifics, *Neetroplus nematopus* was observed to expel the less aggressive *Cichlasoma nicaraguense*, and during the peak breeding season of the large and numerous rocky shore species *Cichlasoma citrinellum*, all other large species are excluded from the optimal breeding areas and either breed in suboptimal habitats or later in the year. The two small rocky shore species *Cichlasoma nigrofasciatum* and *N. nematopus* do not compete with *C. citrinellum* for breeding

sites and breed simultaneously.

The present study also indicates that guarding of free-swimming fry is more widespread among Lake Malawi cichlids than had been previously thought. Ribbink (1990) reported that many large haplochromines guard large numbers of free-swimming fry, specifically mentioning *T. macrostoma* and *D.kiwinge*. In addition to these species, other large predators observed fry guarding were *B. heterotaenia, H. urotaenia, N. polystigma, S. robustus*, as well as the large benthic invertebrate feeder *T. laticeps*. In addition, it was believed that females of most small haplochromines, (mbuna, *Copadichromis* and *Aulonocara*) which usually produce a few relatively large fry in each brood, did not take fry back into their mouths after first release. Some *Copadichromis* leave the young to be guarded by other fish (Ribbink 1977), while *Protomelas taeniolatus* was thought to be exceptional in being a small species providing prolonged fry-guarding by the female. Konings (1990) reported fry-guarding in a species of *Copadichromis*. To this list can now be added *P. fenestratus, P.* 'spilonotus Likoma', *O.* 'heterodon Nankumba', *C. cf prostoma, N. cf. breviceps* and *C. borleyi*. Females of the small pelagic zooplankton feeder *Diplotaxodon limnothrissa* have also been collected brooding fry which had been feeding on exogeneous material (Turner 1994c). This suggests that fry guarding among small species is not confined to the rocky coast but also occurs in the open pelagic zone.

Chapter 6. *Protomelas taeniolatus* (Trewavas, 1935).

Introduction

Protomelas taeniolatus is a common haplochromine cichlid in the rocky littoral zone between depths of 0 to 28 metres (Ribbink *et al.* 1983). Though it is not an 'mbuna', it is a member of the same community, being of a similar size (maximum standard length 90-102 mm- Sharp 1981) and lithophilous habit. It is the most abundant non-mbuna cichlid on the rocky shore at Monkey Bay, reaching densities of 120 individuals per 100 m^2 in places (Sharp 1981). In the aquarium trade, *P.taeniolatus* is the non-mbuna most frequently exported from the lake (Konings 1990).

Throughout most of the year this species is not territorial and the sexes are indistinguishable. Although they do not defend a territory, the extent of their home range is not known, and their inter- and intraspecific relationships have not been examined in any depth.

Cichlid fishes have well developed parental behaviour and along with the other cichlids endemic to the lake, this species is a maternal mouthbrooder (Fryer & Iles, 1972; Ribbink *et al.* 1983). In the highly synchronised breeding season (Marsh *et al.*, 1986) both sexes defend territories, and *P. taeniolatus* has been shown to compete for sites with resident territorial fish (Chapter 5). The process of territory acquisition has not previously been studied in either sex. Male *P. taeniolatus* become bright blue in the reproductive phase, and establish a courtship and mating territory on a rock, which they defend for several weeks or possibly even months (Ribbink 1990), during which time they court, and presumably spawn, with many females. The behaviour of territorial male *P. taeniolatus* has not been examined and it is not known whether the territory is defended throughout the day or whether males feed during the reproductive phase. Other Malawi cichlids using temporary breeding territories have been found to have empty guts throughout this period (Turner *et al.* 1991). If this is the case then the duration of territorial occupancy will be determined by the ability of the male to endure starvation.

During spawning, the female takes the eggs into her mouth and immediately afterwards she swims away, leaving the male free to court other females.The incubation period, including hatching and resorption of the yolksac, lasts between 22-30 days until the fry are free-swimming (Fryer & Iles 1972). In the mbuna, once this stage is reached, fry are released into the rocky interstices and abandoned by the female. There is no further parental care (Holzberg 1978; Ribbink *et al.* 1983a).

However, in *P. taeniolatus* and many other Malawi fish, the female establishes a fry-guarding territory where she releases and defends her fry for days or even weeks (Ribbink 1990).

Predation pressure on eggs and juveniles is intense (Fryer & Iles 1972; Holzberg 1978; Ribbink *et al.* 1980, 1983a). Not only are there many specialised predators, but most fish in the rocky areas are opportunistic predators on the eggs and juveniles of their own and other species, thus fry-guarding is energetically very costly. Usually a single female *P. taeniolatus* guards her brood against all other fish, but neighbouring territories may be in close proximity. Adoption of fry from other broods and even other species is commonplace, usually as a result of accidental mixing (Ribbink *et al.* 1980). In some places, at certain times of year, very high densities of *P. taeniolatus* fry-guarding territories are seen. Sometimes adjacent territories are so close that the broods of several females coalesce and are guarded communally. The present study is carried out in such a location. Here the females apparently practice co-operative care, in protective stations, and collectively chase away predators (Ribbink, 1990).

For the guarding female there is a trade-off between foraging opportunity and parental care, (i.e. current and future reproductive investments), and according to parental investment theory predictions (Trivers, 1972), the balance might be expected to change with the age of the fry, as the offspring become more valuable (Sargent 1990). Female *P. taeniolatus* present an ideal model for testing these predictions in the field.

Aims and Objectives

The aims of this study were to examine the behaviour, intra and interspecific relationships and space utilization of *P. taeniolatus*, of both sexes, both in the breeding season and in the non-reproductive period.

For non-breeding fish, the assumption that they have a limited home range, constant over a period of time, was tested, and the extent of their movements determined. Their feeding sites in relation to the territorial mbuna species were determined, and their interspecific relationships examined, to discover whether feeding is limited by the behaviour of territorial fish of other species. Intraspecific relationships were examined to determine if there is a dominance hierarchy in *P. taeniolatus*.

Estimates of breeding fish abundance were determined throughout the year to establish the extent of reproductive synchrony. The type of sites chosen by each sex was examined to determine if the site characteristics are predictable. The process of territory acquisition was studied, by observing both mouthbrooding females and males

that had begun to assume their breeding colouration. By examining the aggressive interactions of fish attempting to establish territories, the success and failure of particular individuals was related to other territorial fish in the vicinity. The duration of territory occupancy was quantified. Territorial *P.taeniolatus* of both sexes were examined and their time budgets compared to non-breeding conspecifics, to estimate the costs of reproduction.

Studies on parental care were carried out with particular regard to territorial defence, and how it changes throughout the phase of parental care, to test the predictions of Trivers (1972).

The distribution of female territories was studied to determine whether they are spread evenly through the available habitat. The abundance of the types of sites used by females was estimated, to assess whether they are in short supply, since this may lead to intense intraspecific competition during the breeding season, and aggregation by chance. Clusters of fry-guarding females were examined to determine whether or not females within a group are aggressive to one another. Parental behaviour of colonial guarders was compared to that of females guarding in isolation, by examining the duration of guarding period, amount of time spent feeding and time spent in territorial defence. The costs and benefits of communal guarding were considered.

Since individual utilization of time and space may be a critical determinant of reproductive success, differences in territorial behaviour within the sexes were examined.

Methods

The study site was a stretch of shore, approximately 700 metres long, on the relatively sheltered southwestern side of Thumbi East island, near Monkey Bay, southern Lake Malawi (14°3' 30s south and 34° 55' 30s east of Greenwich). See Figure 2. This stretch of shoreline is predominantly rocky, shelving steeply and reaching sand in less than 40 metres depth (Ribbink *et al.*, 1983). Field studies were carried out between October 1990 and August 1992, by SCUBA diving and snorkelling between the daylight hours of 06.00 and 18.00 hours, at depths of 0 to 15 metres.

TAGGING

Non-breeding fish were tagged by suturing coloured beads to the dorsal musculature, anterior to the dorsal fin. The colour and position of the tags, in combination with the appearance of the fish, allowed individual identification.

HABITAT USE AND TIME BUDGETS

During observation periods of 15 minutes, the movements of individual fish were noted on a map, using different symbols to denote different activities. Each individual was observed during the periods 6-10.00 hours, 10-14.00 hours and 14-18.00 hours. At the same time, activities of the focal fish were timed using a stopwatch and recorded. Time Budgets were calculated for breeding and non-breeding fish by combining the data from several individuals.

BREEDING SEASONALITY

Four census areas were chosen to cover a range of depths and substrate types. The abundance of male and female territories in each of these areas was counted at least twice monthly, between October 1990 and August 1992. The area was chosen because casual observation indicated that it contained the highest concentration of territories. The transects corresponded approximately to depth contours parallel to the shore, and all territories within 1 metre on either side of the diver were counted.

Area A: ≙ 700 m^2. Location: lighthouse bay. Habitat: Predominantly rocky, gravel to large rock slabs (>10m), many boulders, occasional pockets of sand and macrophytes. Depth 0-10 metres. A subsection of this area (100 $m^{2)}$ was surveyed separately for guarding sites.

1m-transect. Length: ≙ 300 m. Location: immediately south of the lighthouse, following the shore south- and eastwards. Habitat: rubble and small rocks up to two metres across predominated. Total area: ≙ 600m^2.

5m-transect 1. Length: ≙ 300 m. Location: immediately south of the lighthouse, following the coast south- and eastwards. Habitat: largely rocks between one and three metres high. Total area: ≙ 600m^2.

5m-transect 2. Depth varied from 5-10 m as parts of the transect included sheer rock faces where the the bottom dropped sharply. Length: ≙400 m Location: immediately north of the lighthouse, following the shore north and east. Habitat: mostly very large boulders. Total area: ≙ 800m^2

Additional qualitative observations were made to a depth of 15 metres.

SITE PREFERENCE

The characteristics of sites used by territorial fish of both sexes were recorded, considering: depth, physical characteristics of the substratum, and proximity of nearest territorial neighbour (both of the same and different species)

AGGRESSIVE INTERACTIONS AND TERRITORIAL DEFENCE

For both breeding and non-breeding individuals, interactions with other fish were recorded. For territorial fish, additional information on the approximate distance and relative speed of chases (score 1 to 4, where 1= slow following, and 4= rapid lunge) was recorded, along with the species and relative size of recipients. To determine whether some species were responded to more ferociously than others, an index of aggression was calculated, by adding distance (in units of approximately 30cm) and relative speed of each chase performed, and calculating a mean value for each species

BROOD CARE

The behaviour of females and their offspring was recorded throughout the brood-care period, until final parental separation from juveniles, for both females guarding communally and those guarding in isolation. In addition to the time budget data described in Chapter 2, and aggressive interactions described above, the following observations were recorded:

i. retrieval of fry into buccal cavity.
ii. attacks on fry.
iii. horizontal and vertical distance of female from site focus (i.e. position where female usually rests, and fry most often congregate).
iv. position and number of fry in the brood.
v. brood mixing, species and relative size of alien fry.
vi. whether females were guarding fry communally (defined as two-way movement of fry between females during observation period) or in isolation.
vii. fry swarming (defined as cohesive swimming in groups and streaming up to female)

Results

NON-BREEDING FISH

Tagged non-breeding *P.taeniolatus* used limited home ranges (up to 112m$^{2)}$ during the 45 days of observation. They fed throughout the range, mostly on rocks of 30-100 cm diameter (52%), though also on smaller (17.4%) and larger rocks (30.6%). They were rarely seen to feed on plankton, in macrophyte beds or in soft sediment, and never during focal watches. Their main feeding areas were sites where mbuna are abundant, and many of them were in mbuna territories. They spent approximately 20.3% of their time feeding, 37.6% swimming and a large amount of time stationary (40.6%).

Aggressive interactions were rare, and mostly involved *P.taeniolatus* being chased by territorial mbuna or conspecifics (Table 6.1). No aggression was received from non-territorial mbuna, except *Genyochromis mento*, the fin-biter and scale eater. *P.taeniolatus* was only aggressive towards conspecifics, and never to territorial individuals.

Table 6.1. Details of all aggressive interactions in which non-breeding focal *P.taeniolatus* were involved, during 1 hour 45 minutes of focal fish watches (T indicates territorial individuals).

	Focal fish subordinate		**Focal fish dominant**	
Details of fish interacting with focal individual:	**Chase received**	**Submissive display to**	**Chase given**	**Lateral display given**
Small conspecific	**1**		**2**	**2**
Similar conspecific	**6**	**1**	**3**	**3**
Larger conspecific	**1**		**1**	**1**
Mouthbrooding conspecific	**4**		**1**	
Territorial conspecific (T)	**6**			
***P. tropheops* spp. (T)**	**5**			
***P.elongatus* 'aggressive' (T)**	**5**			
***P.nigra* (T)**	**2**			
***P.zebra* (T)**	**1**			
***P.*'spilonotus Likoma' (T)**	**1**			
G.mento	**1**			

The synchronization of reproductive activity in *P.taeniolatus* is unimodal and very finely tuned. Territorial males peak in August, though some are partly blue all year round. The abundance of female mouthbrooders peaks at the same time, and fry-guarding was most commonly seen in September (fig. 6.1). Males are highly conspicuous so estimated numbers are likely to be fairly accurate, but females and fry may be cryptic in behaviour as well as colour, so abundance may have been underestimated.

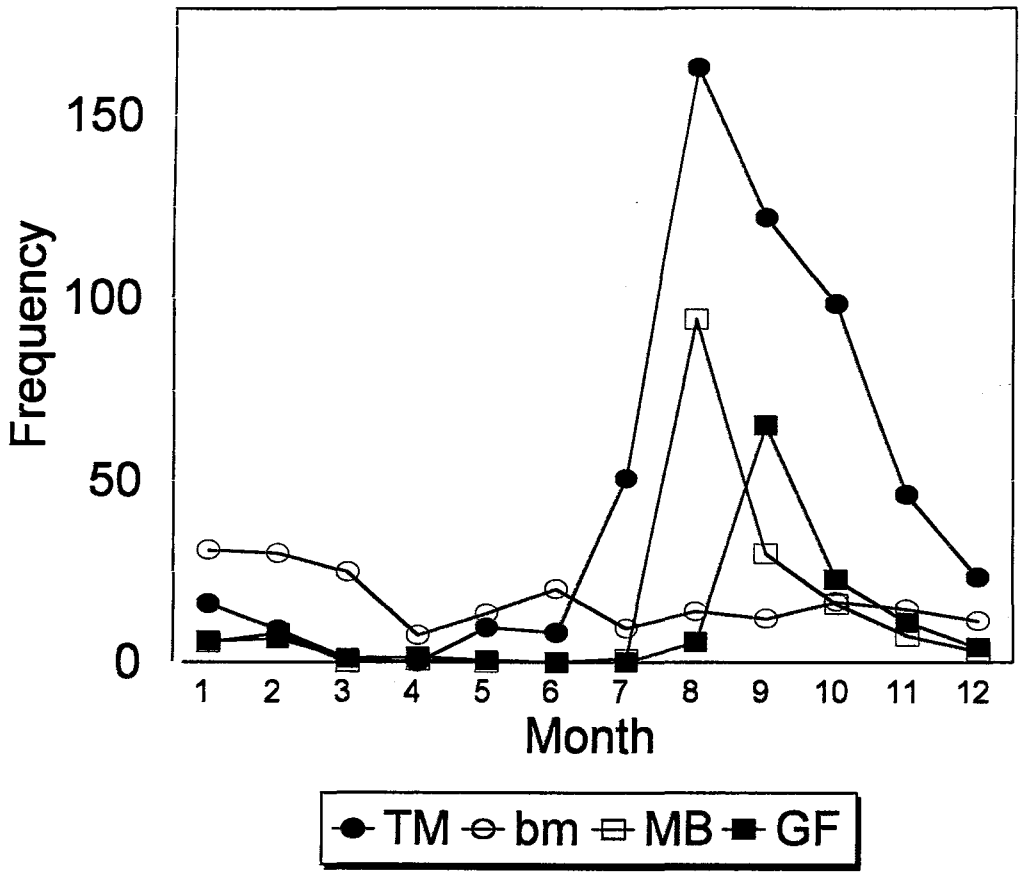


Fig. 6.1. Abundance of reproductively active of *P.taeniolatus* in all census areas, throughout the year. (TM= territorial males, bm= partially blue males, MB= mouthbrooding females, GF= guarding females).

Within the breeding season, peak breeding activity is between mid-September to mid October (fig. 6.2).

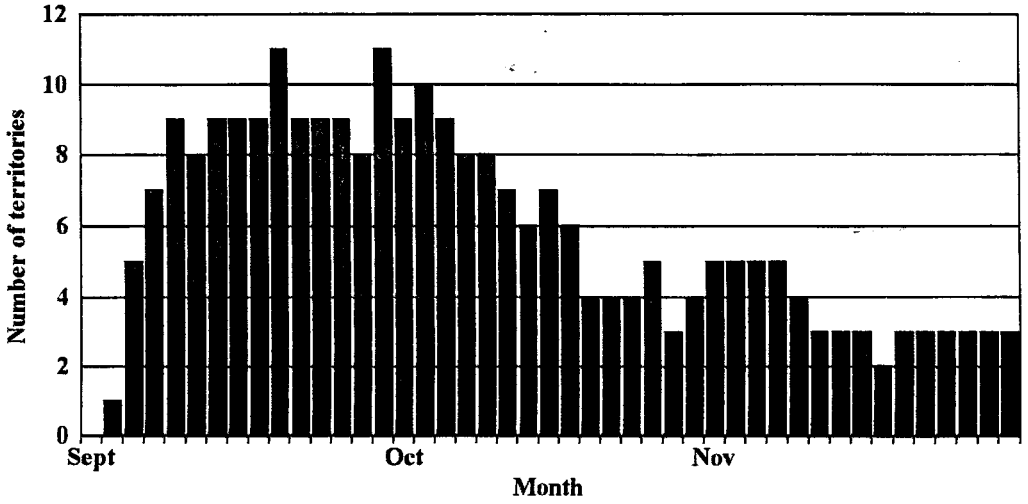


Fig.6.2. Abundance of fry-guarding territories in area of approximately $100m^2$, in lighthouse bay, during the breeding season.

SITE PREFERENCE

Marked site preferences were evident both in territorial males and females, with males tending to use larger rocks in deeper water than females.

Male Courtship and Spawning territories.

The mean depth of male territories was 4.8 metres, with the mode between 5-6 metres (Fig. 6.3).

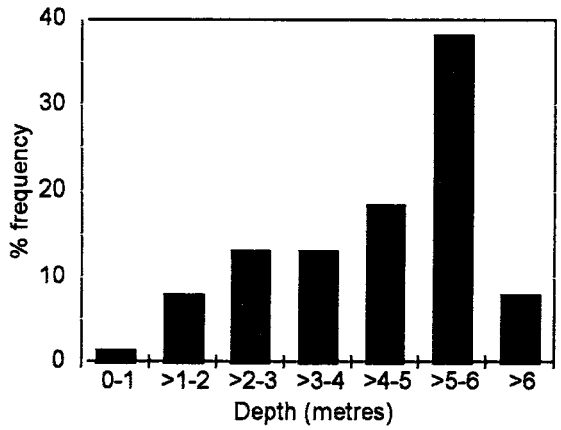


Fig. 6.3 Depth distribution of male *P.taeniolatus* spawning territories.

Males appear to prefer fairly large rocks (> 0.5m^2 surface area) which are raised above the surrounding terrain, and a variety of different sized rocks were used (Fig. 6.4) Average dimensions were 2.3 x 2.8 metres. These sites are apparently not in short supply, though frequently several fish defend temporary breeding territories on one rock, and territorial mbuna use the same sites.

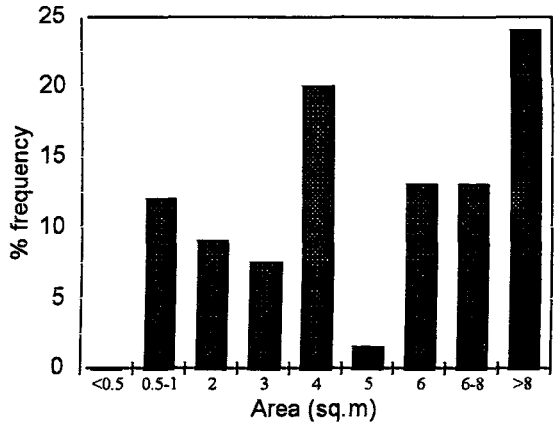


Fig.6.4. Size of rocks used by territorial male *P.taeniolatus.* (N=76).

Unlike mbuna, male *P.taeniolatus* do not defend refuges, and the spawning site is exposed. It is usually located in a very slight indentation, on the upper outer surface of a sloping rock face, with mean angle of 42.5° to the horizontal (fig. 6.5). They are most frequently seen to rest at the spawning site, where they often pick up and spit out mouthfuls of sediment, which leads to this area being visibly different from the surrounding rock (see photograph in appendix 2.1). Algal growth around the spawning site also appears to be more luxuriant than in peripheral areas, after several weeks of territorial defence, though this is not apparent when the territories are first established.

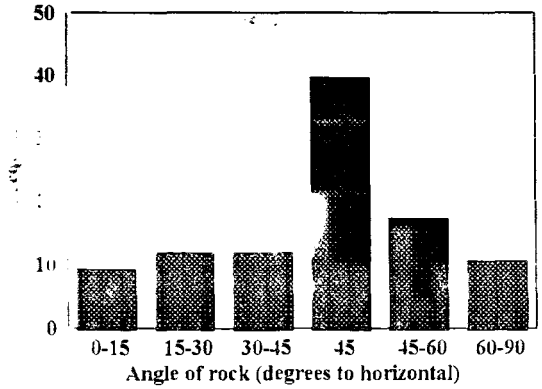


Fig. 6.5. Inclination of rock faces used as spawning site in the territories of male *P.taeniolatus*.

Fry-guarding Territories

Fry-guarding territories were usually in very shallow water and were most abundant on the 1 metre transect and in the shallow portion of Area A. The mean depth of female territories was 2.8m (N=100), but the mode was between 0-2 metres (Fig. 6.6).

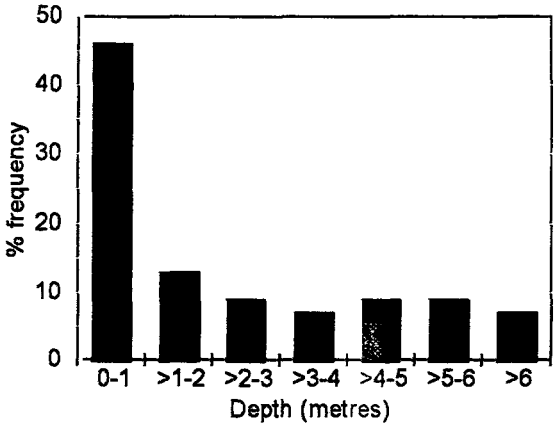


Fig.6.6 Depth of *P.taeniolatus* female fry guarding territories.

Guarding females also used sites on single large rocks, though they preferred smaller rocks than those used by males. Mean dimensions of rocks used for fry-guarding were 1.9 x 2.4m, with the modal area around $1m^2$ (Fig.6.7).

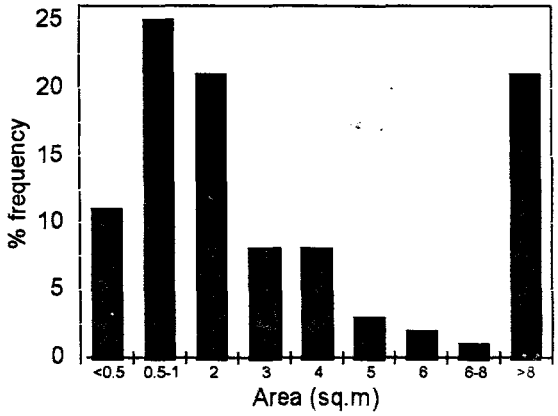


Fig. 6.7. Size of rocks used by females as fry-guarding territories.

Females showed a preference for the top of flat or gently -sloping rocks that were raised above the surrounding terrain (Fig.6.8) . The mean angle of inclination of rocks used by females was 12.4-26.3°. Territories on more steeply shelving rock faces were usually on very large rock slabs, and the females used a ledge, or hollow in the rock, as the focus of their territory. There was no evidence of increased algal growth in female territories.

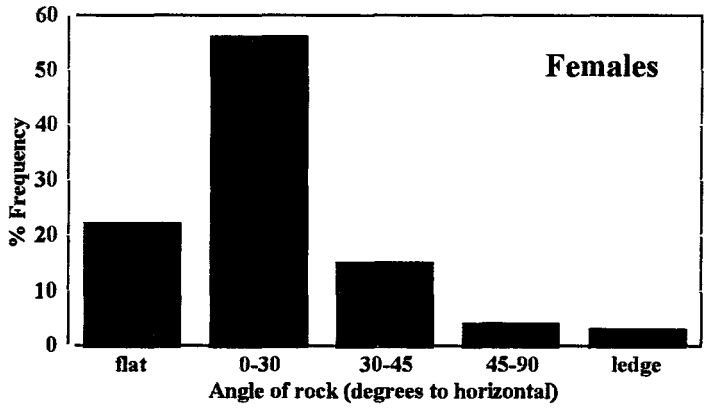


Fig. 6.8. Inclination of rocks used as fry-guarding territories.

DISTRIBUTION OF TERRITORIES

Although territorial males were apparently evenly distributed over all suitable rocks at 5 metres depth, males in partial breeding dress were more abundant at 1 metres depth,

and most particularly in area A. (Table 6.2). Mouthbrooding females were more abundant in the shallow portions of Area A than at similar sites along the 1 metre transect.

Table 6.2 Distribution of Breeding *P.taeniolatus* in different census areas. Figures show percent occurrence per unit area

	1 metre depth transect	5 metre depth transect	Area A
Mouthbrooding females	28.2	20.1	51.7
Guarding females	55.7	15.7	29.1
Males in partial breeding dress	39.8	20.9	39.2
Territorial males	9.4	74.4	16.2

Fry-guarding females also appeared to be non-randomly distributed amongst rocks of suitable size, at 1 metres depth. Along the 1 metre depth transect, 56% of the substratum was composed of rocks that were apparently suitable for female territories and 34% was rocks that may or may not have been appropriate. Only 10% of the census line was unsuitable substratum (sand or reedy areas), thus rocks which appear to be suitable are not in short supply. The distribution of territories along this line shows that female territories were concentrated around bays, which may be more sheltered areas (Fig. 6.9).

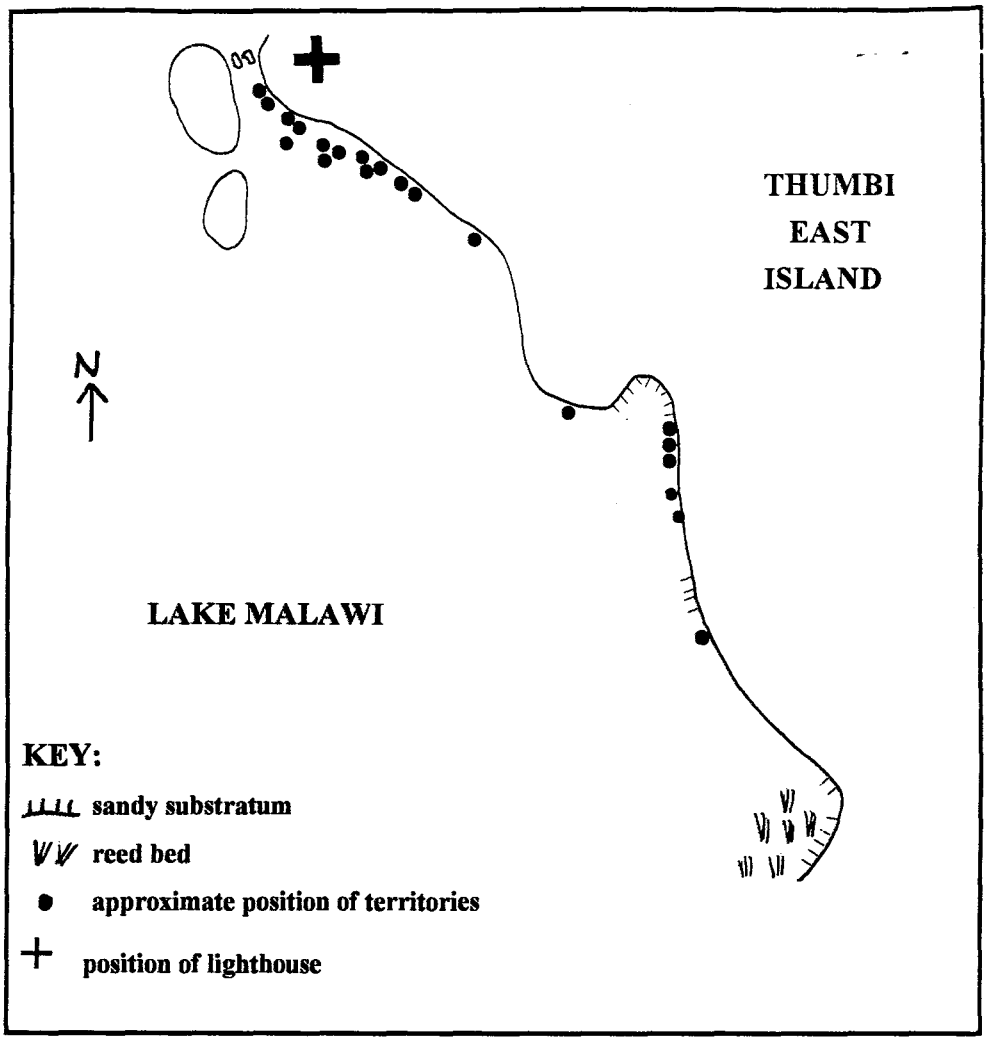


Figure 6.9. Approximate distribution of *P.taeniolatus* fry-guarding territories along a transect, 300 metres long, at one metres depth, to the south of the lighthouse. August 1991.

Distance Between Fry-guarding Territories

Despite the high concentration of guarding territories in certain areas, in the majority of cases, females used territorial sites greater than two metres away from conspecific guarding females, (Table 6.3), so they do not appear to aggregate by choice. All but two of the females with neighbours up to 2m away were in 1m of water (the preferred depth) and all but one were in the peak breeding season, when the density of territories was highest. The two females with neighbours 1-2m away were in deeper water.

Table 6.3. Distance to nearest guarding female conspecific (N=100).

Nearest guarding female	**Frequency**
≤1m	15 %
>1≤2m	14 %
>2m	71 %

TERRITORY ACQUISITION AND DURATION OF OCCUPANCY

Males

None of the tagged fish established spawning territories during this study so it was impossible to determine whether males choose sites in their home range. On numerous occasions, males in partial breeding dress were seen to behave aggressively at a particular site for periods of days or even weeks, but spend some of the time wandering around the area, being non-aggressive and feeding several metres away. Some of these males subsequently took on full breeding colouration and fully defended a spawning site, but on other occasions males abandoned the site without ever achieving their full reproductive appearance, though remained in the general vicinity and were seen to revert to non-breeding colouration. Males in partial breeding dress showed aggression to other territorial fish in the area, and received aggression from them. These territorial neighbours were mbuna, conspecifics and other species with temporary breeding territories.

Males in full breeding dress defended territories for between 10 and 91 days, though they often spent periods of up to 40 days (both before and after this time) in partial breeding colouration.

Females

Several of the tagged fish subsequently spawned and established fry-guarding sites, frequently in their original home range, though some moved to different areas. Females often chose sites that were already defended by territorial individuals of other species, usually male mbuna and guarding females, of their own and other species. Brooding females were sometimes seen singly, but frequently they occur in groups of 5 to 50 individuals. These aggregations occurred in rocky areas at a maximum depth of 5 metres, though most frequently in shallower regions. Maximum densities occurred in Area A (lighthouse bay). Initially they spent most of their time stationary, usually between rocks (ranging in size from a few centimetres to slabs of several metres length), or commonly underneath rocky overhangs, where they avoided much of the aggression of territorial mbuna i.e. they tended to aggregate where they were chased least. They were often forced to move on by the aggression of territorial mbuna in the vicinity, and in the early stages of mouthbrooding, females showed no aggression.

Females in the later stages of brooding became increasingly aggressive, returning the chases of other fish. These females moved away from the mouthbrooding aggregations and attempted to establish territories. At this stage females chased away all approaching fish, including territorial mbuna and mouth-brooding conspecifics. Aggressive interactions between the mouthbrooding females and resident fish were common. Sometimes the females were chased away by a territorial resident, and moved to another site where they continued to be aggressive, but at other times the contest ended with the establishment of a fry-guarding territory. Females occasionally attempted to establish territory at several sites in the few days preceding first release of fry, but after this stage had been reached females only changed the focus of parental care in exceptional circumstances.

The territorial period lasted between one and 21 days in female *P.taeniolatus* (Fig. 6.10) and surprisingly, frequently continued for one or two days after the fry had dispersed. Of 14 broods in which termination of the guarding phase was observed, 8 females remained to guard the site after her brood had dispersed, and 3 females abandoned their brood, leaving them in the care of another female. In another 3 cases the female left with her brood (possibly to a territory at another site). Duration of guarding period was not significantly different between females guarding in the early part of the breeding season, and those guarding towards the end of the breeding season (Anova $p>0.05$.)

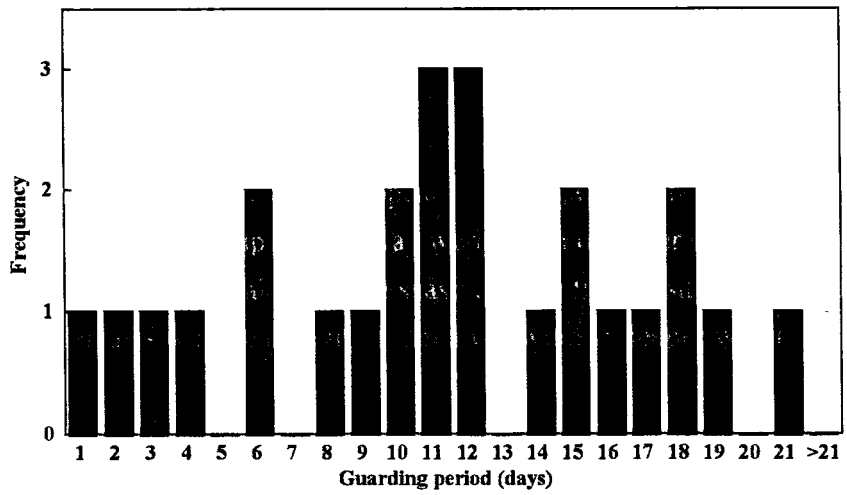


Fig .6.10. Duration of the fry-guarding period for 25 female *P.taeniolatus.*

AGGRESSIVE INTERACTIONS

Territorial Males

Once a male had adopted full breeding colouration, the spawning site was defended against all intruders. The majority of interactions were chases by the male followed by flight of the intruder. Twenty eight species were chased by male *P.taeniolatus*, and those chased most frequently were the most numerous in the area, namely conspecifics and members of the mbuna species, especially *Pseudotropheus zebra*. Details of the recipients are given in Table 6.4.

The ferocity (in terms of both distance and relative speed) of chases performed by territorial male *P.taeniolatus* differed dramatically between the species of fish being chased (Table 6.5). The species to elicit the most aggressive response was *Protomelas insignis*, a congeneric fish specialized as an egg predator. Other fish scoring highly on the index of aggression were predators and conspecifics.

Table 6.4. Aggression shown by territorial male *P.taeniolatus*. (total of 9 hours and 10 minutes of observations during territorial defence)

SPECIES	% chases received	Diet
Conspecifics	28.6	invertebrates
Pseudotropheus zebra	22.5	herbivore
Copadichromis spp.	8.6	zooplankton
Melanochromis auratus	6.8	herbivore
P. tropheops "orange chest"	5.7	herbivore
Petrotilapia spp.	5.7	herbivore
Labeotropheus fuelleborni	3.1	herbivore
Labeo cylindricus	2.9	herbivore
P. tropheops spp.	2.4	herbivore
Protomelas fenestratus	2.1	invertebrates
Genyochromis mento	1.9	scale eater
P. elongatus "aggressive"	1.9	herbivore

Each of the species below accounted for < 1% of chases by territorial male *P.taeniolatus*:

Predators: *T. macrostoma, Buccochromis heterotaenia, Dimidiochromis kiwinge, Nimbochromis polystigma, Protomelas insignis, Champsochromis spilorynchus*, Unidentified predator.

Non-predators: *Barbus johnstoni, Ctenopharynx pictus, Copadichromis borleyi, Placidichromis johnstoni, Labidochromis vellicans, Otopharynx lithobates,* Alien fry, *Melanochromis heterochromis, Protomelas* "spilonotus Likoma".

Table 6.5. Index of aggression shown by territorial male *P. taeniolatus* towards different species (score = mean distance of chase in feet + relative speed of chase). This, therefore, is a measure of vigour of chase, and not related at all to frequency.

SPECIES	Aggression	Diet
Protomelas insignis		Egg predator
Unidentified [illegible] cichlid		[illegible]
Dimidiochromis kiwinge		[illegible]
Conspecifics	6.67	
Buccochromis heterotaenia	6.50	Predator
Champsochromis spilorhynchus	6.29	Predator
Protomelas fenestratus	5.73	
Copadichromis borleyi	5.67	
Melanochromis heterochromis	5.29	
P. tropheops "orange chest"	5.24	
P. elongatus "aggressive"	5.21	
Tyrannochromis macrostoma	5.17	Predator
Genyochromis mento	5.14	
Copadichromis spp.	5.03	
Unidentified juvenile	5.00	
Ctenopharynx pictus	5.00	
Labidochromis vellicans	5.00	
Melanochromis auratus	4.94	
Labeotropheus fuelleborni	4.91	
Pseudotropheus zebra	4.80	
Labeo cylindricus	4.67	
Petrotilapia spp.	4.63	
Barbus johnstonii	4.60	
Nimbochromis polystigma	4.50	Predator
Pseudotropheus tropheops spp.	4.47	
Placidochromis johnstoni	4.33	
Otopharynx lithobates	4.00	
Protomelas "spilonotus Likoma"	4.00	

Territorial male *P.taeniolatus* rarely received chases, and most of these were from territorial members of the mbuna group (*P.nigra*, *P.tropheops* "orange chest", *P. elongatus* "aggressive"), *Melanochromis auratus* males (aggressive, though non-

territorial mbuna) and *Genyochromis mento*. In all of these species except *G.mento*, mutual frontal displays and lunges were exchanged between the opponents. Males also received occasional chases from other temporarily territorial fish, defending adjacent sites, namely male *C. borleyi* and fry-guarding females of the large predatory species *T. macrostoma.*

Guarding females

All approaching fish were chased from female territories. As for males, territorial females chased *P.zebra* and conspecifics (the two most abundant species) most frequently (Table 6.6). Overall they chased a greater number of species (≥45) than did territorial male conspecifics. Most chases (90.4%) were directed at non-territorial individuals. Smaller fish were chased 53.9% of the time, similar-sized fish 33.4% and larger fish 12.7% of the time.

Table 6.6. Aggression shown by guarding female *P.taeniolatus*.
(analysis of over 48 hours focal fish watches, 3196 chases)

SPECIES	% chases received	Diet
Pseudotropheus zebra	22.2	herbivore
Conspecifics	20.8	invertebtrates
Pseudotropheus tropheops 'orange-chest'	7.0	herbivore
Protomelas fenestratus	6.3	invertebtrates
Petrotilapia spp.	5.5	herbivore
Tyrannochromis macrostoma	4.3	Predator
Copadichromis spp.	3.6	zooplankton
Pseudotropheus tropheops spp.	3.2	herbivore
Pseudotropheus elongatus 'aggressive'	2.9	herbivore
Nyassachromis prostoma	2.7	zooplankton
Buccochromis sp.	2.5	Predator
Alien fry	2.0	herbivore
Melanochromis auratus	1.9	herbivore
Labeotropheus fuelleborni	1.8	herbivore
Protomelas sp. 'broodstealer'	1.7	Predator
Genyochromis mento	1.3	scale eater
Melanochromis heterochromis	1.2	herbivore
Dimidiochromis kiwinge	1.0	Predator
Nimbochromis polystigma	1.0	Predator

Each of the species below accounted for <1% of chases by guarding females:
(within two groups, shown in order of decreasing frequency of chases)

Predators: *Melanochromis melanopterus, Dimidiochromis compressiceps, Protomelas insignis,* Unidentified predator, *Champsochromis spilorhynchus, Hemitaeniochromis urotaenia, Nimbochromis livingstonii, Rhamphochromis* spp., *Taeniochromis holotaenia, Nimbochromis linni.*

Non-predators: *Labidochromis vellicans, Ctenopharynx pictus, Otopharynx* 'Heterodon nankhumba', *Otopharynx lithobates, Pseudotropheus elongatus* 'yellowtail', *Lethrinops* spp., *Barbus johnstoni, Petrotilapia nigra, Oreochromis* spp., *Labeo cylindricus, Placidochromis johnstoni, Protomelas* 'spilonotus Likoma', *Barbus arcislongae, Lichnochromis acuticeps, Protomelas kirkii, Mylochromis anaphyrmus.*

The degree of aggression shown by females (measured by distance and relative speed of chasing) differed greatly between species, with the most aggressive responses elicited by obligate predatory fish of numerous species (Table 6.7). The least aggressive responses were to mbuna, planktivores and omnivorous fish. Their reaction to conspecifics was intermediate between the two. The chase distance also varied with intruder size, with mean distance of chase being 2.10' for smaller fish, 2.14' for similar-sized fish and 2.34' for larger fish.

This territorial defence is extremely effective. In most observation periods no other fish were in the defended area, though occasionally mbuna (territorial in 41 cases and non-territorial in 57 cases) fed on the rocks at the guarded site. (Table 6.8). In most of these cases the intruder ignored or returned the female's chases or threats and continued feeding in the territory. In some cases the female tolerated this intrusion, but moved a short distance away from the intruder, still within her territory. In the case of the territorial *P. tropheops* 'orange chest', and invasions by a group of floaters on the site focus, the female eventually retrieved her brood and moved a short distance away from the site, to return when the intruders left. Occasionally intruders were feeding while the female was involved in interactions with other fish, or while she was away foraging. Intrusions were more common in the late afternoon period. Between the hours of 09.00-12.00, fish were seen feeding in guarding territories in 14.7% of observation periods. Between the hours of 15.00-17.00 this rose to 37.2%.

Table 6.7. Index of aggression shown by female *P.taeniolatus* towards intruders of different species.

SPECIES	Aggression score	Diet
C. spilorhynchus	10.33	Predator
Buccochromis spp.	9.81	Predator
T. macrostoma	8.64	Predator
Unidentified predator	7.91	Predator
Protomelas sp. 'broodstealer'	7.08	Predator
N. livingstoni	7.00	Predator
D. compressiceps	6.94	Predator
P. insignis	6.36	Predator
N. polystigma	6.31	Predator
L. cylindricus	6.14	
N. linni	6.00	Predator
Protomelas 'spilonotus Likoma'	5.75	
Alien fry	5.71	
O. lithobates	5.46	
Conspecifics	5.43	
M. melanopterus	5.35	Predator
H. urotaenia	5.33	Predator
P. nigra	5.25	
Lethrinops spp.	5.25	
B. johnstonii	5.22	
P. fenestratus	5.09	
P. elongatus 'yellowtail'	5.08	
P. kirkii	5.00	
C. pictus	4.95	
Otopharynx 'heterodon Nankhumba'	4.79	
D. kiwinge	4.78	Predator
M. heterochromis	4.75	
P. tropheops spp.	4.70	
L. vellicans	4.70	
M. auratus	4.70	
B. arcislongae	4.67	
P. elongatus 'aggressive'	4.63	
P. tropheops 'orange chest'	4.56	
P. johnstoni	4.50	
G. mento	4.42	
N. prostoma	4.41	
Petrotilapia spp.	4.38	
L. fuelleborni	4.32	
P. zebra	4.31	
Copadichromis species	4.13	
L. acuticeps	4.00	
C. borleyi	3.66	
Oreochromis spp.	3.60	
Mylochromis anaphyrmus	3.00	

Table 6.8. Number of observation periods during which herbivorous fish were seen feeding in the fry-guarding territory (L=larger than female, M=similar size, S=smaller than guarding female). The site focus was considered to be the part of the rock in which the fry were positioned, and which the female used as a resting place.

Species	Territorial status & Relative size	Frequency of intrusion on site focus	Frequency of intrusion on guarded rock, 0.2-0.6m from site focus.	Total frequency for species
P. tropheops **'orange chest'**	L Territorial	14		21
	M Floater	4	1	
	S Floater	0	2	
Other *tropheops* spp.	L Territorial	8	2	27
	M Floater	4	8	
	S Floater	1	4	
P. zebra	L Territorial	3	4	23
	L Floater	3	5	
	M Floater	3	5	
P. **'elongatus aggressive'**	S/L Territorial	5	3	8
P. nigra	L Territorial	1		1
other *Petrotilapia* spp.	L Floater	2		3
	S Floater		1	
P. elongatus **'yellowtail'**	M Aggressive	1		1
Conspecific	L Floater	3		3
Multiple floaters	S/L Floater	5	6	11

Guarding females rarely received chases from other fish. Throughout focal fish watches (total 48 hours 20 minutes) when guarders gave chase 3196 times, only 69

chases were received (Table 6.9). Most of these (60 chases) were from territorial mbuna and very few from floaters (9 chases).

Table 6.9. Chases received by guarding female *P.taeniolatus.*

Chases received from:	**Total number for species**	**Type of individuals**		**Relative size of attacker**
Conspecifics	**16**	13	Guarding female	Similar
		2	Non-territorial	Larger
		1	" "	Smaller
M. heterochromis	**1**		Territorial male	Smaller
***P. tropheops* 'orange chest'**	**17**	15	Territorial	Similar & Larger
		2	Floaters	Similar & Smaller
P. tropheops* other species	**6**	3	Territorial	Larger
		3	Floaters	Similar
P. zebra	**14**	13	Territorial	Similar & Larger
		1	Floater	Similar
L. fuelleborni	**7**		All territorial	Similar & Larger
***P.elongatus* 'aggressive'**	**8**		All territorial	All sizes

* The other *P. tropheops* species include *P.t.*'broadmouth' and *P.t.* 'gracilior'.

Escalated aggressive interactions (frontal displays, either unilateral or mutual, and lunges) were rare and only occurred between conspecific guarding females (a total of two mouthbites and one frontal display during focal watches) and between guarding females and *Protomelas* 'brood stealer'.This is an undescribed species, of a similar size to *P.taeniolatus,* which was seen to attack a brooding female only once, by ramming her in the mouth, but was frequently seen in the area, when it elicited a ferocious chase from the guarding female. Guarding females responded to this species at a distance of

several metres by rising up in the water column and remaining motionless, then chasing if the fish continued to advance. On one occasion a guarding female with no fry in her mouth was seen to lunge at the fish and ram it head-on, whilst it was still over a metre away from the territory.

Despite the attempts of females to defend their brood, attacks on fry were occasionally seen. These attacks were rare, and most commonly carried out by specialized predators, although opportunistic mbuna were also seen to attack fry (Table 6.10).

Table 6.10. Attacks on fry during a total of 48 hours 20 minutes of focal fish watches.

Species of attacker	Relative size	Frequency
T. macrostoma	S	13
	L	2
Buccochromis sp.	SM	2
	L	2
P. elongatus 'aggressive'	S	2
P. nigra	L	1
M. auratus	S	1
P. elongatus 'yellow tail'	SM	1
G. mento	SM	1
Conspecific	S	2

TIME BUDGETS

The time budgets of territorial *P. taeniolatus* were markedly different from non-breeding conspecifics (Table 6.11). Much less time was spent on feeding by territorial fish, and females performed hardly any feeding. Guarding females spent the majority of time stationary whilst territorial males were never motionless during the day. Territorial males and females performed a similar amount of aggression, but males also spent more time in fights and aggressive displays, whereas guarding females and non-breeding fish rarely engaged in these activities. Partially blue males were much less aggressive than fully territorial conspecifics, and were never seen to fight or perform aggressive displays. Territorial fish received less aggression than non-territorial conspecifics, and males in partial breeding dress were intermediate.

Table 6.11. Time budgets of breeding and non-breeding *P.taeniolatus.* (Figures show mean ± standard deviation, per 15 minute period).

	N	No. of feeding bites	Time stationary (secs.)	Time spent swimming (secs.)
Non-breeding fish	29	183.1 ± 162.0	365.7 ± 266.6	338.6 ± 241.8
Mouthbrooding females	19	0.5 ± 2.0	682.1 ± 305.0	203.5 ± 297.6
Guarding females	380	9.2 ± 22.0	666.9 ± 306.4	194.9 ± 297.4
Territorial males	34	82.4 ± 72.2	0.0 ± 0.0	757.1 ± 69.0
Partially-blue males	7	413.4 ± 181.7	38.9 ± 37.9	440.1 ± 157.5

	N	No. of chases given	No. of chases received	Number of fights and displays given.
Non-breeding fish	29	0.6 ± 1.4	3.2 ± 4.2	0.6 ± 1.4
Mouthbrooding females	19	2.4 ± 4.5	0.6 ± 1.2	0.6 ± 1.6
Guarding females	380	21.0 ± 15.6	0.4 ± 1.4	0.7 ± 1.79
Territorial males	34	22.1 ± 7.6	0.5 ± 1.1	5.2 ± 8.8
Partially-blue males	7	0.4 ± 1.0	1.5 ± 2.1	0.0 ± 0.0

BROOD CARE

No significant differences were found in the number of chases performed by females over the guarding period, or of displays given or received (Fig. 6.11). However, the behaviour of the females and fry changed over the guarding period in a number of ways.

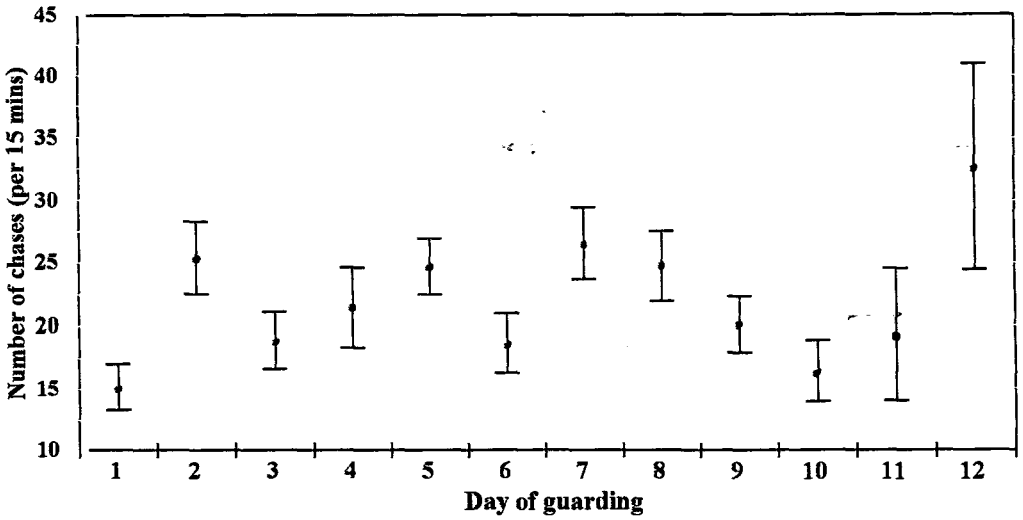


Fig.6.11. Number of chases performed by guarding females during each observation period, for each day of guarding. (mean and standard error).

In the early stages of fry-guarding, females do not feed at all, but feeding increases steadily over the guarding period (Fig. 6.12; Anova: 13,368 df, F= 23.28 $p<0.001$).

r

Fig. 6.12. Mean and standard error for number of feeding bites per 5 minute period, performed by guarding female *P. taeniolatus* throughout the period of parental care.

The amount of time that females spend away from the guarding site increases with time (Fig. 6.13; Anova: 13,369 df, F=4.05, $P<0.001$). Initially fry are very cohesive, but gradually they increase the time spent foraging individually. They usually remain on the guarded rock unless chased by larger fish.

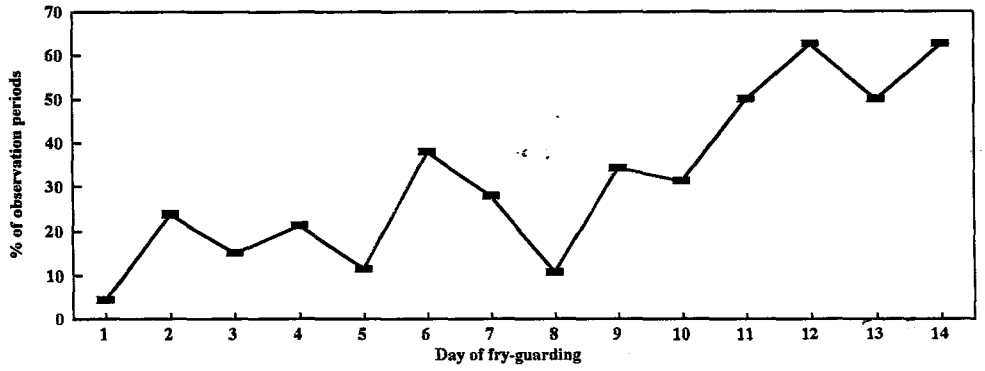


Fig.6.13 .Percentage of observation periods during which guarding females left their territory, for different days in the guarding period.

The maximum horizontal distance that females moved from their territories during focal watches increased over the guarding period (Fig 6.14).

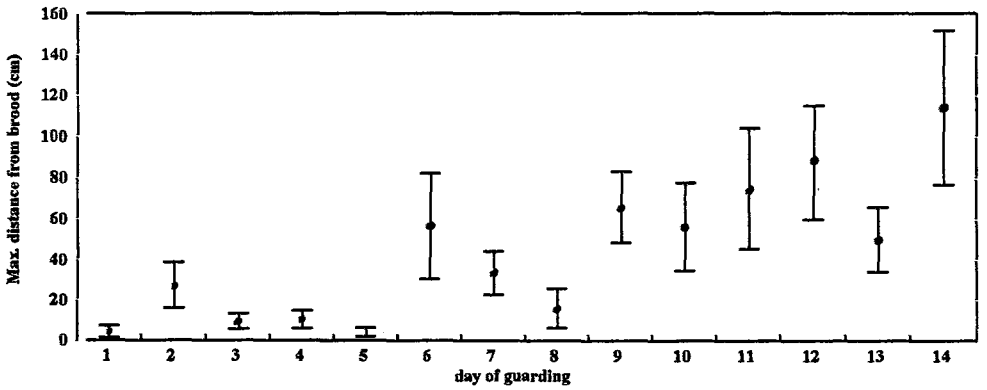


Fig. 6.14. Maximum distance of female from fry during each observation period, for each day of guarding. (mean and standard error).

In addition, when the female was in the territory with her fry, her mean height above the rock for each observation period increased with day of guarding. (Fig 6.15)

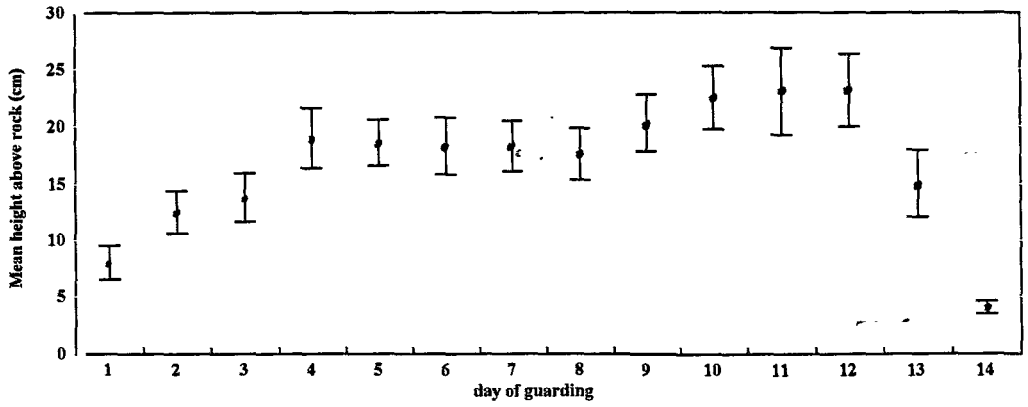


Fig.6.15. Mean height of guarding female above rock, in centimetres, for each observation period, over day of guarding.(mean and standard error).

In the early days of guarding, females were mouthbrooding at least some of the time in all observation periods, but the percentage of observation periods where focal females were seen with fry in their mouth decreased steadily as brood age increased. Fry perform 'swarming' behaviour by streaming up to the females mouth and attempting to gain entry. Sometimes a female will respond by retrieving her brood, but on many occasions this swarming behaviour is ignored and the fry are refused entry to her mouth. At these times females keep their mouth closed, often shake their head and swim away from the offspring. Swarming behaviour met with decreasing success over the guarding period. The performance of this swarming behaviour decreased over the guarding period, but more slowly than the tendency of females to brood their fry. (Fig. 6.16).

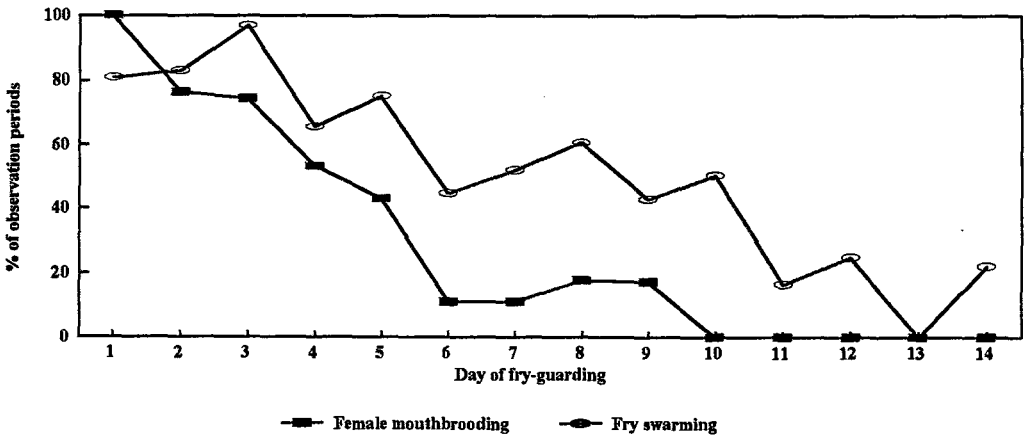
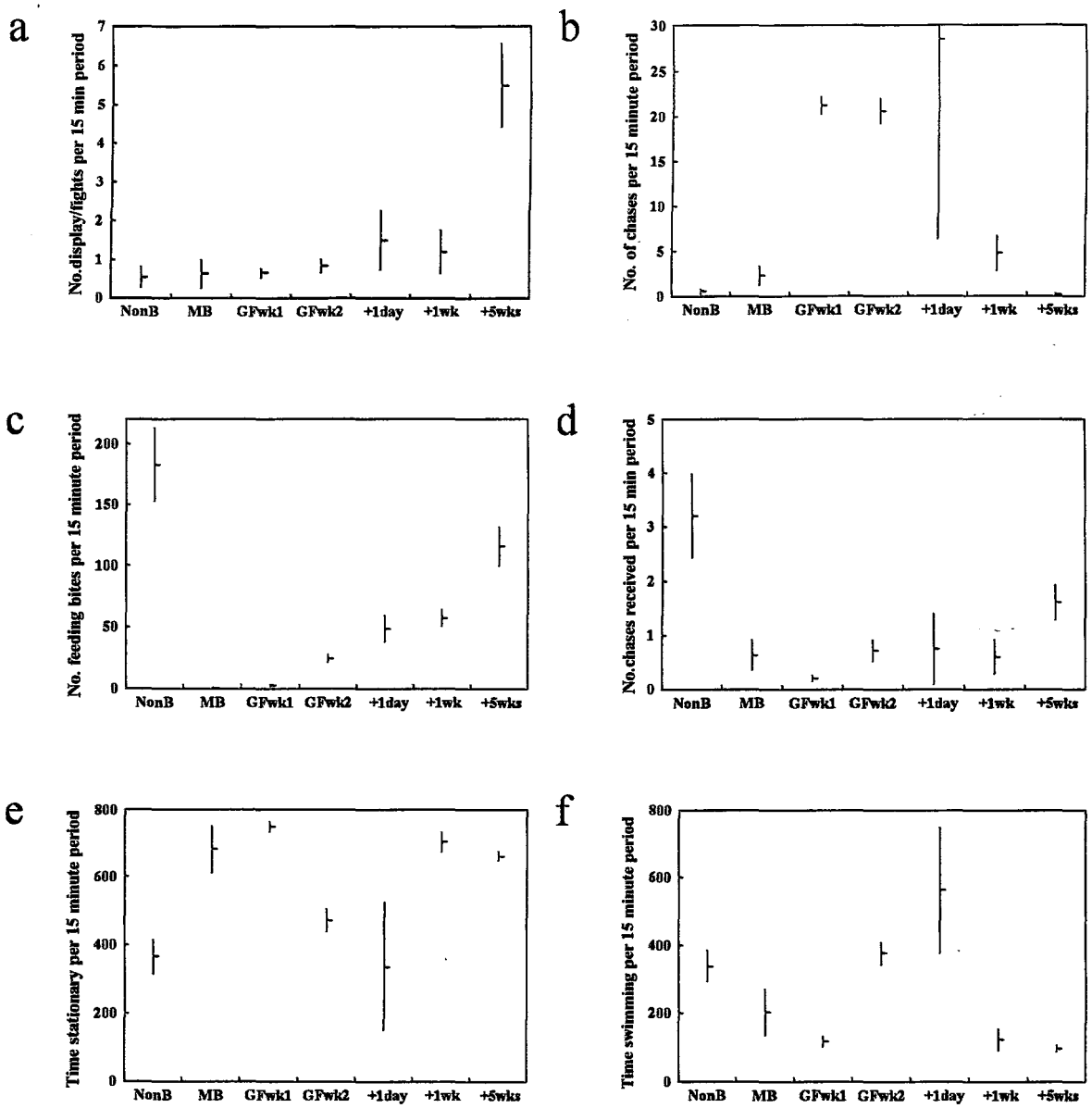


Fig. 6.16. Percentage of observation periods during which females were brooding fry and fry performed swarming behaviour.

Rather surprisingly, females remained aggressive after their fry had dispersed, and in several cases remained to defend the territory after their fry had gone. Even one week after fry-guarding had ended, females continued to be aggressive (Fig 6.17a-f). Five weeks after guarding had ceased, the number of chases performed was not significantly different from non-breeding fish, but the number of aggressive displays performed was still much higher than pre-breeding levels.



Figs. 6.17a-f. Behaviour of *P.taeniolatus* females during and after breeding in comparison to non-breeding conspecifics (where NonB= non-breeding fish, MB= mouthbrooding females,

GFwk1= females in the first week of guarding, GFwk2= females in the second week of guarding, +1day= females after 1 days separation from fry, +1wk= females 1week after guarding has ceased, +5wks=females 5 weeks after fry guarding has ended).

BROOD MIXING

Brood mixing was common. Of the 17 broods that were observed daily throughout the guarding period, 15 showed evidence of brood mixing. One of the broods remaining pure, disappeared two days after the fry were first released. Many of the alien offspring were conspecifics, both larger and smaller than members of the original brood, though fry of other species were commonly involved. Often broods contained several species of fry, both larger and smaller than the original offspring. The other fry mixed in *P.taeniolatus* broods were offspring of species with guarding females in the vicinity, namely *Protomelas* 'spilonotus Likoma' (which often used similar guarding sites to *P.taeniolatus*) the planktivore *Copadichromis borleyi* (which defends fry underneath rocks in the same habitat) and the undescribed species *Otopharynx* 'heterodon Nankhumba' (which held territories on sandy areas between rocks). Guarding females of these species were also frequently seen to have broods containing *P.taeniolatus* fry. The number of *P.taeniolatus* broods containing alien fry increased over the duration of the guarding period (Fig. 6.18).

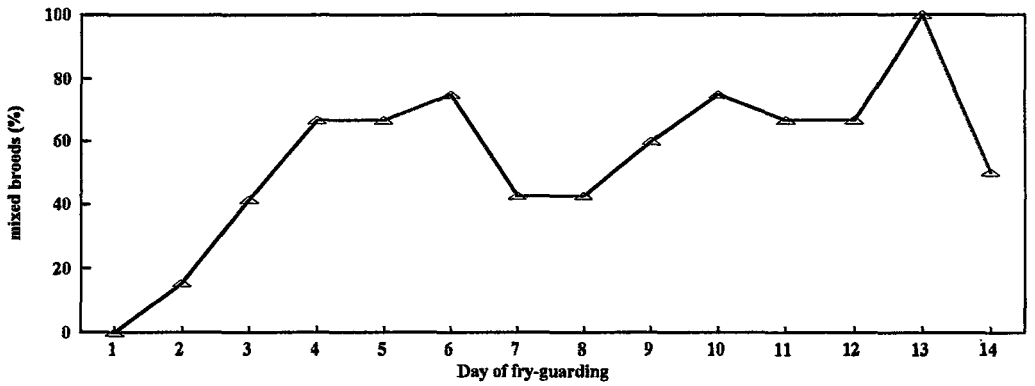


Fig.6.18. Percentage of broods containing alien fry, with day of guarding.

On numerous occasions fry were seen to approach mouthbrooding or guarding females other than their parents, but sometimes they followed *P. taeniolatus* that were not parental. Occasionally they were chased by a mouthbrooding or non-parental adult

and immediately scattered. On several occasions, guarding females were seen to approach their fry slowly, head down, and then dart rapidly at the gathering offspring. This occurred infrequently, but even when the brood was apparently unmixed.

COMMUNAL FRY-GUARDING

Nearest neighbour distance

The proximity of guarding female neighbours was found to have a significant effect upon female behaviour. Females with neighbours less than one metre away performed siginificantly fewer chases than females with neighbours between 1 and 2 metres away (Kolmogorov-Smirnov test: A v B, $p < 0.05$; A v C $p < 0.05$). Inter-neighbour distances greater than 2 metres were not significantly different from those in the 1-2 metre range. i.e. any benefits of clumping are only apparent if female territories are less than one metre apart (Fig 6.19a-c).

Lone guarders were thus defined as females whose nearest guarding neighbour was over 1 metre away, and whose fry were being guarded in isolation. Communal guarders were defined as females whose nearest guarding neighbour was less than 1 metre away, and whose fry move back and forth between the protective spheres of at least two females. Communal guarding was seen on several occasions, commonly also involving *P.* 'spilonotus Likoma' and more rarely *O.* 'heterodon Nankhumba'. Between two and four broods were involved on each occasion, and often, after one or two days of brood sharing, a newly arriving female would find herself with a larger brood which had been abandoned. The females in these cases were always aggressive to one another.

On one occasion, four females (three *P.taeniolatus* and one *P.*'spilonotus Likoma') established territories in a line, over a period of several days, with each less than one metre from its neighbour. Fry moved readily between the protective umbrellas of all four females. As the longer-standing guarders wandered away to forage, the remaining females were left to guard the fry. This ended when one female was left guarding a brood of approximately 48 young, the other females having ceased guarding. This brood also included three *C.borleyi* fry, which had strayed from their parental site, found to be situated underneath a rock in the vicinity.

There was only one group of communally-guarding fish in this study for any length of time. This group consisted of 4 female *P.taeniolatus* that began guarding on the same day, sharing a rock of approximately $1m^2$ surface area. One female was seen to leave the group after one day, taking her brood with her, after receiving aggression from the other guarders. Two females abandoned their fry at the site after 6 and 11

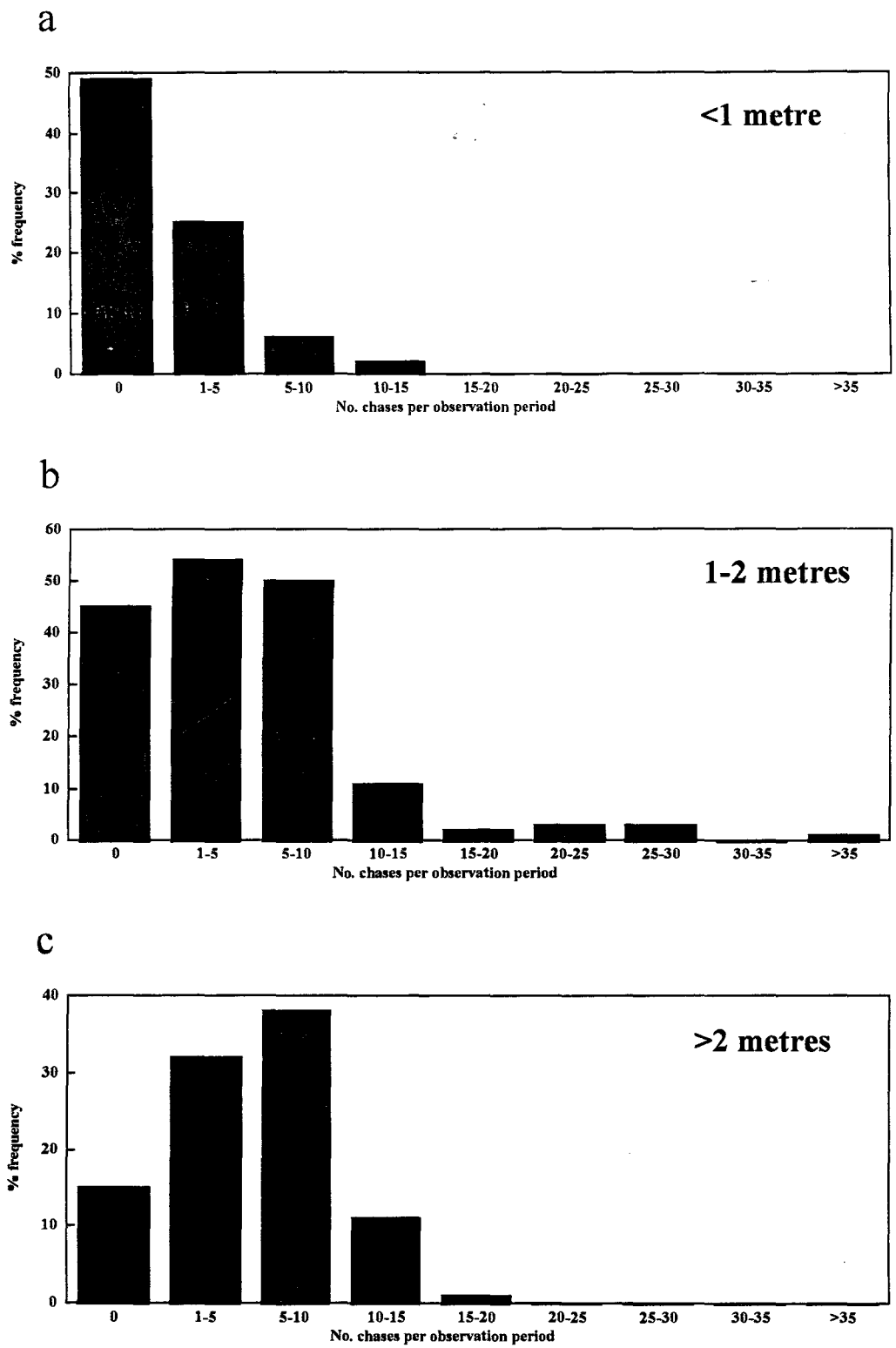


Fig.6. 19a-c. Frequency distribution of number of chases performed per observation period, by females with guarding neighbours at different distances.

days respectively, and the other female, guarding the remains of several broods, left after 14 days. This group of females was used to collect data on communal guarding.

In this group, one of the females was performing most of the aggression during any observation period, the others being predominantly motionless. All of the females took turns at defending the fry. The fry tended to follow the most active female.

COMPARISON OF LONE AND COMMUNAL GUARDERS

The amount of time spent feeding was significantly different between the lone and communal guarders when days 1-6, 7-11, and 12-14 were compared for the two types (Table 6.12). In the first 6 days, lone females performed more feeding (mean =3.12 ± 9.87 standard deviation) than communal guarders (0.27 ± 1.42), whereas in the next 5 days communal guarders performed much more feeding (23.23 ± 37.30) than isolated females (9.75 ± 17.33). In the last few days, only one female remained from the commune and there was no significant difference between the amount of feeding by this fish and other lone females.

Table 6.12 Results of Analysis of Variance for time spent feeding by lone versus communally-guarding females, for each phase of guarding.

phase of guarding		**F**	**P**		**df**
day 1-6	3 communal guarders	4.54	<0.05	*	227
day 7-11	2 communal guarders	7.49	<0.01	**	122
day 12-14	1 female remaining from commune	0.18	0.68	NS	26

Territorial defence

Communally-guarding females were found to perform significantly fewer chases than lone females, when days 1-6 and 7-11 were compared for the two types, and there was no difference between the number of chases performed by the female remaining from the commune and other lone guarders (Table 6.13, Fig. 6.20).

Table 6.13 Results of Analysis of Variance for number of chases performed by lone versus communally-guarding females, for each phase of guarding.

phase of guarding		F	P		df
day 1-6	3 communal guarders	130.14	<0.001	***	223
day 7-11	2 communal guarders	31.92	<0.001	***	122
day 12-14	1 female remaining from commune	1.25	0.28	NS	25

The duration of fry-guarding was not significantly different for lone (1-21 days) and communally-guarding females (1-16 days).

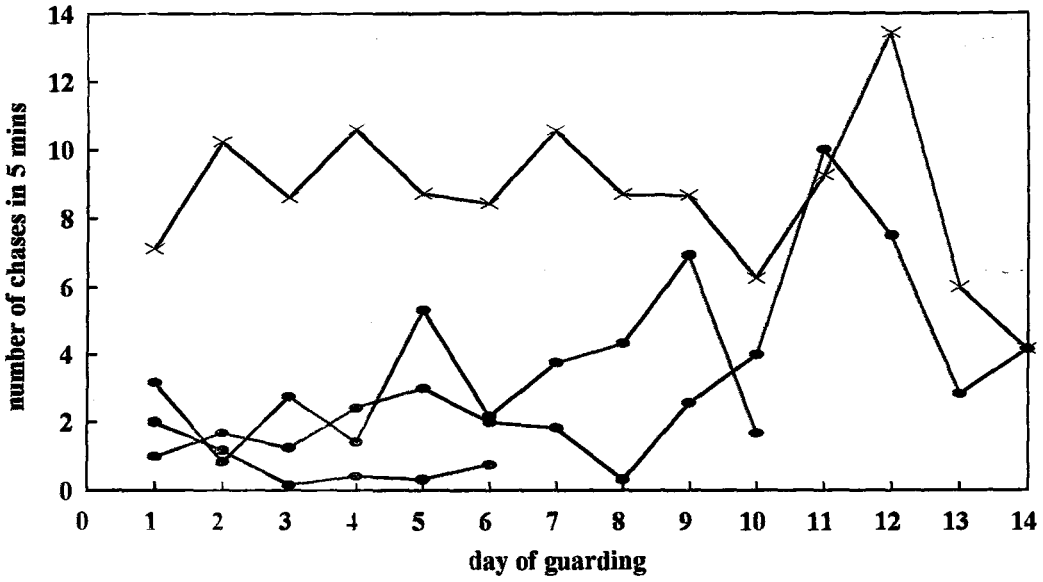


Fig. 6.20. Differences in mean number of chases performed per 5 minute period for lone and communally-guarding females. (Filled ellipses show mean values for each of the females that had been guarding communally, crosses represent mean values for several females guarding in isolation). One of the communal guarders left after day 6, another after day 10, therefore from day 11 onwards, only one female remained, guarding alone.

The total amount of aggression shown by females in the communal territory,

regardless of the number of guarders involved, was approximately equal to that for a female guarding an isolated territory. Thus, when 3 females were guarding communally (on days 1-6), the number of chases each performed was approximately 1/3 of that for lone females at a similar stage. When 2 females guarded communally (days 7-11) each performed approximately half the chases of lone females at the equivalent stage (Table 6.14).

Table 6.14. Comparison of territorial defence by lone and communal fry-guarders. (Figures show mean ± standard deviation, per 5 minute period)

Phase of guarding	No. of chases in isolated territories	No. of chases in communal territories	No.of females in commune
day 1-6	8.95 ± 1.17	5.31 ±1.70	3
day 7-10	8.69 ± 1.40	7.08 ± 2.21	2
day 11-14	7.87 ± 4.01	4.83 ± 1.96	1

In observation periods where chasing occurred, an average of 23.4% of chases were directed towards conspecifics by lone females compared to only 17.5% by communal guarders, (3.2% to other females in the cluster).

Discussion

NON-BREEDING FISH

Outside of their reproductive period, *P. taeniolatus* are non-territorial and very rarely show or receive any aggression, despite the fact that they frequently feed within the territories of mbuna (Sharp 1981). The large amount of time spent stationary (in comparison to both territorial and non-territorial mbuna) may be a result of vigilance behaviour, and avoidance of aggression by territory owners. Although there were few aggressive interactions with conspecifics, the interactions recorded suggest that there may be a dominance hierarchy among non-breeding individuals, though this is probably diffuse rather than linear, considering the home range size and large number of individuals occurring in any particular area.

REPRODUCTIVE SEASONALITY

The reproductive seasonality of this species appears to be very finely tuned, with little year to year variation, since the results of the present survey agree closely with previous studies (Marsh *et al.* 1986). This is not surprising since the peak in breeding activity coincides with that of many other species studied (Marsh *et al.* 1986, see also Chapter 5). Synchronised breeding may be a response to predation pressure on fry, since it carries the benefits of predator swamping, and the dilution effect (Darling 1938 but see Ims 1990). For fry-guarding females, there is the additional benefit of increased vigilance and collective defence by parents in surrounding areas (Dominey 1981). However, the highly synchronised breeding activity most probably results from increased availability of food allowing the fish to reach breeding condition, since in aquarium conditions, when food is not limited, *P. taeniolatus* and mbuna will breed all year round (personal observation). The strong winds during the cool, dry season (April to August) cause upwelling of cold, nutrient-rich water in the lake (Eccles, 1974) which stimulates plankton blooms. Although *P. taeniolatus* was rarely seen to feed on plankton, this dietary supplement may be sufficient to stimulate ripening of the gonads.

LOCATION OF TERRITORIES

The depth distribution of territorial *P. taeniolatus* may be explained by predation on adult fish. The main piscine threat to adult cichlids would appear to be the large nocturnal catfish *Bagrus meridonalis*, which moves in from deeper water at night. In some Lake Malawi cichlids, these predators are thought to determine the lower depth limit of temporary male breeding territories (McKaye 1983), and this may also be true for *P. taeniolatus*. The extreme shallows (where fry-guarding is concentrated) are the safest refuge from this threat. However, fish in this habitat are especially vulnerable to avian predators (Kingfishers, cormorants and fisheagles), and otters (personal observation), which hunt by vision, and the most conspicuous fish are likely to be the most vulnerable. Thus, whilst cryptic females may be less at risk from visual-hunting predators than the mbuna with which they share the habitat, males are conspicuous in colouration and larger than most mbuna, and do not have the benefit of a refuge in their territory. For them, the extreme shallows may be too risky, and the balance between the predation threats leads them to choose sites at 5 metres depth. Furthermore, fry may grow faster in shallow water, either because productivity and food abundance are greater and/or because the temperature is higher. This could be of benefit to both parent and offspring.

Males appeared to choose sites that were already defended by mbuna or other temporarily territorial fish, and for which the competition was intense. They appeared to spend a considerable amount of time in a potential territory before taking on full breeding dress or establishing exclusivity of the site, during which time they still fed. During this period, they may be assessing the quality of the site, in relation to the abundance of gravid females or the costs of defence. On some occasions, they apparently decide that the territory is not economically defensible, and they abandon it for other reasons. Some of these males were then seen to revert to non-breeding colouration and remain in the region of the abandoned territory. It is possible that these males were assessing their own ability to defend a reproductive territory.

On other occasions males in partial breeding dress proceeded to fully establish a spawning territory and take on full breeding colouration. Once a spawning territory was established it could be defended for several months, during which time the male would perform very little feeding, hence there are considerable costs to breeding, with respect to lost feeding opportunities. The majority of territorial defence (71.4%) was directed at non-conspecifics. A similar result was found for *Copadichromis eucinostomus* with temporary breeding territories in monospecific leks (McKaye 1983).

Although the most frequent attacks by *P. taeniolatus* were on species competing for space (mbuna), the most aggressive attacks were carried out on conspecifics (which are potential sneakers) and egg-predators. Sneaking has not previously been documented for Lake Malawi fish, though casual observations suggest that it may occur in some species (*Pseudotropheus aurora*-Hert pers. comm., *Copadichromis borleyi*- personal observation). On the other hand, there are several specialised egg predators in the lake which present a very real and well-documented threat (McKaye & McKenzie 1982, & Kocher 1983, Stauffer & McKaye 1986). In a study of sand-dwelling haplochromines in leks, courting pairs were approached approximately once every 3 minutes by egg predators of several species, though 95% of the time they were driven off by the focal male or a territorial neighbour (McKaye 1983). In McKaye's (1983) study, *C. eucinostomus* males performed an average of 22 attacks every 15 minutes during morning courtship periods, which is very similar to the present findings for *P. taeniolatus.* The present study showed that specialised paedaophages were encountered less frequently by breeding fish at the study site than by the sand-dwelling fish in leks studied by McKaye. However, the similar attack rates of *P. taeniolatus* to *C. eucinostomus* may reflect the abundance of opportunistc egg predators in rocky habitats.

The varation in duration of territorial defence, which is also seen in other temporary breeders (McKaye 1983, Chapter 5) may reflect the differences in condition of the males, and therefore their ability to withstand protracted periods without food. Some males in partial breeding dress were present throughout the year, but the number declined in the peak breeding season. This supports the idea of a territorial "assessment phase" and suggests that some males are ready to reproduce at all times of year, but that few proceed to full territoriality outside the peak reproductive period, perhaps because of the lack of gravid females.

In order to breed, females must not only be able to withstand a fast of several weeks, during the incubation and early fry guarding phase, but they must also bear the energetic costs of egg production, which may be considerably higher than the cost of spermatogenesis. Thus females may be more dependent on annual cycles of food abundance to reach breeding condition, than males, and more constrained in their reproductive activity. Parental care may also be affected by food availability, as demonstrated in *Cichlasoma nigrofasciatum* which devote a greater proportion of their time to foraging when food availability is low, at the expense of care for the current brood (Townsend & Wootton, 1985). Thus, by breeding when food is abundant, parental fish may be able to devote relatively more time to brood care. However, comparisons between female *P. taeniolatus* guarding in the early and late breeding season showed no significant differences in behaviour. In this species, it may be the condition of the female at spawning that is the critical factor, rather than the abundance of food in the fry-guarding phase, when little feeding is performed.

Since some females establish a fry-guarding territory in their home range, it may be possible for them to assess potential fry-guarding sites (and possibly even potential mates) long before the breeding season. For them, rapid establishment of a territory is imperative for fry survival, once the brood approaches the free-swimming phase. If females can identify less heavily-defended sites, then their chances of establishing a territory at the first attempt will be increased. If they are unsuccessful, they may be forced to release their fry at a site where they have not established dominance. The aggression received by guarding females was mostly from territorial neighbours, but aggressive interactions of this kind distracted the female from caring for her offspring, making them more vulnerable.

Females attacked fish competing for space most often, but displayed the most intense aggression towards brood predators, as has been recorded for other parental cichlids (Cichocki 1977, Townsend & Wootton 1985, Keenleyside *et al.* 1990). The undescribed *P.* 'broodstealer' was assumed to be a brood predator. Head ramming behaviour (as a broodstealing tactic) has been reported for other paedophagous Lake Malawi cichlids (McKaye & Kocher 1983). In most cases, predators retreated when chased by a parental fish. On one occasion, a large *N. polystigma* refused to be chased away by the female, and positioned itself at the edge of the rock about 20cm from the brood. The female diplayed at it by swimming circles over it, until it finally retreated.

After several weeks of fasting during the incubation period, a parental female must balance the benefits of fry guarding and feeding. The costs of continued parental care may include reduced parental growth rate and survivorship, fecundity and future reproduction (Rangely & Godin 1992, Smith & Wootton 1994), but the value of offspring increases with approaching independence. Thus the female must make a trade-off between parental investment in the current brood and lifetime reproductive success (Williams 1966, Trivers 1972, Dawkins & Carlisle 1976, Sargent & Gross 1993, Smith & Wootton 1994). The present study did not show increased parental care with brood age, as predicted by the age-investment hypothesis (Dawkins & Carlisle 1976). Laboratory studies on *Cichlasoma nigrofasciatum* showed similar findings, though the authors suggest that habituation effects may have dampened parental responses, or behavioural changes may not have been statistically detectable (Rangely & Godin 1992). There may be several reasons why the results did not support the parental investment theory of Trivers (1972). Firstly, this study measured parental care and not the costs of this care to the female, which are not the same thing, although this distinction is seldom made in empirical studies (Evans 1990).

Studies on fish showing increased nest defence with brood age (eg. *Cichlasoma cyanoguttatum*, Itzkowitz 1985, *Cichlasoma nigrofasciatum*, Lavery & Colgan 1991) were in substrate-spawning species, and compared parental care in the egg, wriggler and free-swimming fry-guarding stages. The rise in aggressive parental defence seen in these fish may be a response to the increased mobility of the young at the free-swimming stage which makes them more vulnerable to predation (Keenleyside 1979, McKaye 1977), but there must be a point beyond which parental care no longer increases. Some studies have shown an initial increase in parental care followed by a later decrease as offspring approach independence (van Iersel 1953, Barlow 1964, Colgan & Gross 1977, Huntingford 1977, Sargent & Gebler 1980, Sargent 1981). In mouthbrooding species, the vulnerability of free-swimming fry is likely to decrease with offspring age as their anti-predator responses develop, and so increased parental defence is not required. Comparable studies of substrate-spawning fish which examine parental care over the free-swimming fry stage do not show increases in parental care (Lavery & Colgan 1991).

In *P.taeniolatus*, feeding increases over the guarding cycle and brood retrieval diminishes, which is to be expected since increasing female hunger inhibits brood care motivation (Mrowka, 1986). Although continued parental care will be beneficial to fry, at a certain stage, the conflicting demands on the female mean that she will gradually decrease parental investment and might eventually be expected to abandon the brood

(Sargent & Gross 1993). The most surprising finding of the present study was that rather than fry remaining at the guarding site after abandonment by the female, the commonest scenario was of females continuing to defend a site after all fry had apparently dispersed. This led to the discovery that female behaviour takes several weeks to return to normal after fry-guarding had ceased. This would seem to be maladaptive, since post-guarding females need to increase their physical condition after the considerable energetic expense of parental care. It is suggested that female behaviour is physiologically constrained, perhaps by hormonal effects.

BROOD MIXING

Although rocks of appropriate dimensions for fry-guarding are abundant at a depth of one metre, the preferred sites for female territories are sheltered bays, where there is intense competition for sites, from mbuna and other fry-guarding females, of their own and less frequently, other species. This leads to many territories being clustered in certain areas, which Getty (1981) suggests may be advantageous even when it is not necessitated by initial densities. The high incidence of fry-guarding territories in certain areas leads to the accidental mixing of fry between broods, both in Lake Malawi and elsewhere (McKaye & McKaye 1977). It is suggested that brood mixing occurs after fry have become accidentally separated from their parent (perhaps after an attack by a predator), and their tendency to follow other parental fish leads them to join the brood of the next guarding female they encounter.

The number of mixed broods was higher than previously recorded (Ribbink *et al.* 1980), because individual broods were followed throughout the parental care period, and the chance of mixing increased with the duration of guarding. Mixing appears to result from the high degree of reproductive synchronisation in a densely-packed habitat, and the poor parental recognition by fry, which has been remarked upon by other authors (Baerends & Baerends van Roon 1950, Ribbink 1971, but see Vives 1988). The ability of females to discriminate between their own offspring and intruders is uncertain (Myrberg 1966, Noakes & Barlow 1977, McKaye & McKaye 1977, Mrowka 1987), but even if they are able to do so, separating unwelcome fry could be more problematical. On the occasions when females chased their own fry, the ensuing chaos provided the chance for opportunists to attack the scattering brood, putting all fry at risk. In experimental situations, cichlid fry apparently prefer the more active of two fish presented (Lavery *et al.* 1990), regardless of which is the parent (DeGannes & Keenleyside 1992).

Although there may be costs to fostering fry in mouthbrooding species, all species which show prolonged parental care are likely to have foreign fry accidentally

mixed with their broods on occasions (Ribbink *et al.* 1980), and casual observation suggested this was the case. It has also been suggested that a wide variety of fish, including utaka, have other species care for their offspring in a cuckoo-like fashion, deliberately dumping their fry into broods of other species (Ribbink 1977). In this study, all alien fry in *P.taeniolatus* broods were found to originate from species that were fry-guarding in the region, some of which were not previously thought to exhibit protracted parental behaviour. Of particular importance is the discovery that some utaka (*Copadichromis borleyi* and *Copadichromis prostoma*) care for their free-swimming fry, in the same habitat as *P.taeniolatus*, though often in more cryptic locations beneath rocks.

COMMUNAL CARE

Communal care is seen in several fish, including *T. rendalli*, (Ribbink *et al.* 1981), the Sri Lankan species *Etroplus maculatus* (Ward & Wyman1976, 1977) and some Nicaraguan cichlids (McKaye & McKaye 1977). It would appear to be an adaptive behavioural trait to decrease predation on offspring. In colonial nesting bluegill sunfish (*Lepomis macrochirus*) isolated nests were found to be more vulnerable to predators than clustered nests (Dominey 1981).

In *P.taeniolatus*, there are several potential benefits and costs to communal care. Any possible benefits on fry survivorship were not detectable, because brood mixing was so common, but females were shown to benefit by sharing the costs of territorial defence. Although there was no discernible difference in length of guarding period between lone and communally-guarding females, the only times that females were seen to leave the guarding site before fry had dispersed was when the fry were being guarded by another female. Thus for some fish, communal guarding may allow brood desertion whilst ensuring that offspring continue to be protected by another female. There seem to be no demonstrable costs to communal care. Food competition between females or between fry are unlikely to be important. Initially, guarding females feed very little, if at all, and then they forage outside the guarding site. The area guarded by females appears to be constant regardless of the proximity of neighbours, so the amount of food available to the fry should be unaffected. Predation of fry by other guarders also seems unlikely. Firstly because parental females may be inhibited from consuming fry by internal parental motivation, and in any case may be unable to distinguish their own offspring (Mrowka 1987, but see Baerends & Baerends van Roon 1950), but also because in approximately 1000 hours of underwater observation, *P. taeniolatus* were never seen to eat or attempt to eat fry of any species. This is surprising since they are obviously capable of accomodating juvenile fish in

their buccal cavity and most cichlids, regardless of trophic specialisation, will feed opportunistically on eggs and young (Fryer 1959; Fryer & Iles 1972; Holzberg 1978; Ribbink *et al.*, 1980, 1981, 1983a). However, this suggests that predation of fry is an unlikely cost of communal guarding, and the approach of fry to non-parental conspecifics is not so risky in *P.taeniolatus* as in other cichlids (Ward & Samarakoon 1981, Mrowka 1987). The relative sizes of fry in early and late stages of parental care are not sufficiently different to make predation of fry by fry a possibility.

Despite proven advantages to communal fry-guarding in *P.taeniolatus*, females do not appear to be actively choosing sites adjacent to conspecific parental females, and considerable aggression is seen between conspecific guarders in close proximity. The lower percentage of attacks on conspecifics by communally-guarding females may result from decreased intraspecific aggression in order to facilitate cooperative parental care, but another explanation is more likely. Male *C.eucinostomus,* on arenas where only conspecifics hold territories, chase conspecific intruders (floaters as well as territorials) less frequently than do territorial males on multispecies arenas. (McKaye 1983). Since a cluster of territorial fish would be more conspicuous than an isolated territory, non-territorial conspecifics would be more likely to avoid the area and therefore receive less aggression. In addition, neighbouring territorial conspecifics are often likely to repel intruders before they approach the focal fish, particularly those presenting a threatening stimulus, such as conspecifics. This could apply whether the territorial fish were males defending spawning sites or females defending fry.

In communal guarders, an average of 3.2% of all chases were directed at other females in the cluster. Only one female in the cluster was active at one time and the other females avoided aggression by remaining motionless. The fry followed the most active female, regardless of whether it was their parent, which has been documented in other cichlids (DeGannes & Keenleyside 1992). So, although the temporal and spatial patterns of breeding sites can be expected to evolve to maximise reproductive success (Krebs & Davies 81), and although the benefits of communal care are apparent, aggregation seems to be a chance occurrence, and *P.taeniolatus* does not appear to be fully exploiting the possibilities.

Chapter 7. Territoriality in Fishes

Definitions of Territoriality

Territoriality is a form of interference competition where one individual denies competitors access to a resource, which may in itself not be limiting. In some cases the resource may actually be in excess in the territory. Early definitions of territoriality include "any defended area" (Noble 1939) and "a topographically localised defended area" (Hinde 1956). Hinde's definition will be used here since it distinguishes territoriality from the defence of personal space (which is seen in *Melanochromis auratus*- Hert 1993) or of a moving resource, and emphasises site-dependent aggressive behaviour. Thus, important components of territoriality are agonistic behaviour and exclusivity, with regard to a given set of individuals. Aggression without exclusivity occurs in dominance hierarchies, and exclusivity without aggression may occur purely because of low population density. Although aggressive contests must be present, the results of these contests may be more easily seen than the aggressive acts themselves, which may be rare. One characteristic of a territory is that at the boundary, an owner's behaviour changes from attack to retreat (Huntingford & Turner 1987).

Historical Perspectives

The earliest publications on territoriality related to the behaviour of birds, and Bernard Altum (1868) was the first to provide a general theory of this subject. His work (in German) was largely unknown in the English-speaking world until it was translated some time later by Mayr (1935). In the early part of the 20th century, several amateur naturalists produced classical studies on territoriality (Moffat 1903, Howard 1920, Nice 1937), all based on comprehensive ornithological observation in the field. The early studies were all species-orientated, but in the 1930's, the concept of territoriality became more widely known, and its importance amongst vertebrates and arthropods was recognised. By the next decade there were many studies on territoriality, and the search for a unifying theory began.

The earliest work on territoriality in fish concentrated on three-spined sticklebacks (*Gasterosteus aculeatus*), with the publications of ter Pelkwijk & Tinbergen (1937), van Iersel (1953) and Van den Assem (1967) being the most significant, and Baerends and Baerends van Roon's (1950) classical study of cichlid ethology contributed greatly to the understanding of territoriality in other species.

Reviews on territoriality in fish have been provided by Noble (1939) and Gerking (1953).

Territoriality in Fishes

Although male lampreys (Malmquist 1983) and grey reef sharks (Johnson & Nelson 1973, Barlow 1974b, Nelson 1981) are known to be territorial, the vast majority of observations on territorial fish relate to Osteichthyans, especially teleosts. The teleosts are the most speciose vertebrate group (Nelson 1976), so it is not surprising that they display a huge variety of territorial and non-territorial behaviour. For this reason, and because they can easily be maintained in laboratory conditions, they are excellent subjects for the study of territoriality. Most field studies have concentrated on fish of coral reefs, or other clear water bodies, since turbidity makes direct observation difficult.

Some fish families, such as lophiids, are not known to be territorial, whereas all known pomacentrids are territorial, either permanently or only in their reproductive period. Others like the cichlids display many forms of territoriality. Within some lineages, e.g. the darters, (*Etheostomatinidae*), there is a progression from primitive species (e.g. *Percina caprodes*) which show little aggression, to others (e.g.*Etheostoma caeruleum*) which defend individual females in a limited area, to species (e.g. *Etheostoma blennoides*) which are highly aggressive around a fixed territory (Winn 1954).

Whether a fish is territorial or not depends on its lifestyle, especially reproductive and feeding biology, which affects the economic defensibility of a territory. When the benefits gained from exclusive access to limited resources exceed the cost of defence, territoriality occurs (Brown 1964). The resources being defended in a territory may be food, a spawning site, mates, offspring or a shelter and will affect the animals fitness (in terms of survival or reproductive output). Territorial defence may involve aggressive displays and even fighting, especially at the early stages of acquisition, and the costs of territoriality may be high, in terms of both energy and time. Severe damage resulting from fights is rare in nature, but injuries may affect the fishes' ability to feed or attract mates.

Defensibility is largely determined by resource dispersion. If resources are fairly evenly distributed then they may not be worth defending, but if they are very clumped, defence may be too costly. When resource concentrations are moderate then territories are often economically defensible. Fish that forage over huge areas and scatter their eggs in very large numbers to counteract predation would be unable to defend either their food supply or their offspring, so fish with this kind of lifestyle (e.g. offshore

marine species such as herring, *Clupea harengus*, and some freshwater fish such as grass carps *Ctenopharyngdon idella*) do not display territoriality.

Alternatively, many species lay demersal eggs and defence of a spawning site is the commonest form of territoriality in fish. Some species defend separate spawning and parental care sites, but often one territory serves both functions. Benthic food may also be defensible. For example, the distribution of corals upon a reef has promoted territorial social systems among corallivorous reef fishes (Tricas 1985). In some areas of coral reefs, 70% of the substrate is defended by territorial fish (Klummp *et al.* 1987).

The same cost-benefit analysis may also determine the size of a territory. As long ago as 1934, Huxley recognised that territories are compressible only up to a certain point, when he put forward the "elastic disc" theory, and since a territory is a defended area, it must also have an upper size limit. The minimum size will be determined by the provision of the resource, and the maximum by the costs of defence, since a fish is unlikely to defend an area larger than it needs. Hence the optimal size is a compromise determined by the individual owner. If a territory serves more than one function, then several factors will interact to determine the size of the defended area.

Characteristics and Functions of Territoriality

Territories can be classified according to the resource being defended, but in practise the function is often a combination of several factors. In some fish the whole range is defended as a multipurpose territory, whilst in others a core area containing shelter or spawning site is defended but feeding is carried out in a larger home range, which is not defended. The main functions of territoriality will be discussed below.

MATING TERRITORIES AND PARENTAL CARE SITES

The most common form of territoriality involves male defence of a spawning site, often around a particular structure. The stable focus may be a rock (*Copadichromis borleyi*, Lake Malawi), a cave (*Pseudotropheus zebra*), a gastropod shell (*Pseudotropheus livingstoni* in Lake Malawi and *Lamprologus callipterus* and *L. multifasciatus* in Lake Tanganyika) or a nest (*G. aculeatus*). Rarely fish defend spawning sites in midwater (e.g. the Malawian haplochromine cichlid *Copadichromis chrysonotus* -Eccles & Lewis 1981). External fertilization with male parental care is usual in fish, and consequently, a high quality territory (offering cover, food, protection from predators, a good location, or being large in size) may enable a fish to acquire more mates (van den Assem 1967, Unger & Sargent 1988, Sargent 1988, McKaye *et al.* 1990).

Many fish (most freshwater species and many inshore marine species) have demersal eggs, and territoriality is often involved with minimizing the risks to which they might be vulnerable, by modifying a spawning site to avoid turbulence (e.g. blennies and gobies) or siltation (e.g.salmon), constructing a nest (e.g.*G.aculeatus*) or actively defending offspring against predators (many cichlids). In freshwater fish, 57.4% of families show some parental care, whilst in marine fish 15.4% of families have parental care (Baylis 1981), and in many cases, territoriality is involved. Territoriality is not related to parental care in viviparous species (e.g. swordtails, guppies and mollies) or in species where the offspring are protected in the parent's brood pouch (pipefish and seahorses). (For reviews on parental care in fishes see Blumer 1979, Perrone & Zaret 1979, Baylis 1981, Blumer 1982, Potts 1984, Gross & Sargent 1985).

Often a territory serves no function other than a spawning site, and the male either does not feed in the reproductive period (e.g.*Oreochromis karongae*-Turner *et al.* 1991) or he must abandon the territory to feed. McKaye (1983) described huge mating arenas of *Copadichromis eucinostomus* in Lake Malawi where thousands of males defend spawning bowers and compete for females each morning. They leave the arenas in the afternoon to feed on plankton.

In many Lake Malawi fish, and some Lake Tanganyika cichlids (e.g. *Pseudosimochromis cuvifrons*) the males defend courtship and spawning sites, for periods of weeks or even months (Chapter 5, Kuwamara 1991) during which they court, and presumably spawn with, many females. The system is polygamous, and after fertilization, the female swims away for a period of oral incubation of the eggs. In some species the female goes on to establish a fry-guarding territory, where she guards her free-swimming offspring (see Chapter 6), though in others the free-swimming young are abandoned after first release (Holzberg 1978).

In many fish, the spawning site is also the focus of parental care (e.g. the territories of biparental substrate guarders of South & Central America e.g. *Cichlasoma* species), and the provision of food for adults or their offspring may be important. In *Lamprologous brichardi* of Lake Tanganyika, helpers are involved in the rearing of young (Taborsky 1984, 1985).

The establishment of temporary breeding territories is often accompanied by the appearance of secondary sexual characteristics, (such as the vivid breeding dress of Malawian haplochromines, the epidermal tubercles of bream, or the kype of salmonids which is used for fighting), which may also be energetically costly (both in production and increased conspicuousness). For some individuals, the costs may be too high and they may be unable to establish a territory. Many fish lose condition during their reproductive cycle (e.g. sticklebacks -Stanley 1983, *Oreochromis mossambicus* Turner

1986b) and they may be unable to withstand challenges for ownership from other fish (see Chapter 5). A study of fathead minnows (*Pimephales promelas)* revealed that males guarding isolated territories lose weight during the reproductive cycle, whereas those on group territories do not. The dry weight of these group-living fish decreases but they apparently maintain their weight by increasing body water content, presumably to maintain their apparent size to competitors (Unger 1983).

FEEDING TERRITORIES

To maintain a feeding territory a fish must be able to aquire all of its nutritional needs in an area which is economically defensible. Certain food types lend themselves to defence, in particular corals (defended by the butterflyfish *Chaetodon multicinctus* - Tricas 1985) and benthic algae (defended by *Pseudotropheus elongatus* "aggressive"- Ribbink *et al.* 1983a, Chapter 3), and aggression is often focussed on feeding competitors (Myrberg & Thresher 1974). Feeding territories may be defended by mature and immature fish of both sexes in some fish (Wyman & Ward 1973, Tooker & Miller 1980, Sharp 1981, Ribbink *et al.* 1983a).

Territorial behaviour may alter the composition of algae and associated organisms within an area. For example, a distinctive algal turf with a higher standing crop and higher productivity is seen in the territories of some coral reef fish (Russ 1987, Klummp *et al.* 1987). In Lake Malawi, the territories of *P.elongatus* "aggressive" may have more than twice as much algae as surrounding areas (Sharp 1981).

It may be expected that fish will defend areas containing sufficient food for their short term needs, and that territory size should be adjusted as an inverse function of local food abundance. Studies in rainbow trout (*Oncorynchus mykiss*) and the butterflyfish (*C.multicinctus*) support this hypothesis (Slaney & Northcote 1974, Tricas 1986), but experimental manipulations of the food supply in other species have yielded conflicting results (Salmon- Symonds 1971, Reef fish- Ebersole 1980). Some fish are apparently able to assess the abundance of food and alter their territory size accordingly, contracting it in times of plenty and expanding it in times of need. Other species may employ long-term bet-hedging, so that territory size reflects long-term needs, and short-term fluctuations in food abundance have little effect on size of the defended area. In salmon, the abundance of food only affects territory size at the time of initial establishment (Dill *et al.* 1981).

An alternative hypothesis is that territory area is restricted by food competitors. The prediction of this model is that territory size will be adjusted as an inverse function of competitor abundance, and therefore defence costs (Krebs 1971, Norton *et al.*

1982). Increased density of food may mean that intruder pressure becomes too great and defence too costly (eg Brook char- McNicol & Noakes 1984) or it may mean that a feeding territory is no longer worth defending once food is abundant.

Hixon (1980) developed a model for an animal attempting to maximise food consumption (ie. foraging limited by available time) that takes account of both food supply and competitor density. This model was tested in a field study of the butterflyfish *C.multicinctus* (Tricas 1989) in which both sexes invest more than 90% of their time in feeding, and territory size was shown to be adjusted according to defence costs rather than to food abundance. Unfortunately, few field studies consider intrusion pressure and food abundance independently (but see Ebersole 1980).

In many cases territories are not solely defended as feeding sites, and so territory size may be determined by factors other than abundance of food. If a fish is also breeding in its territory (e.g. Lake Malawi mbuna) it may not be able to spare the time or energy to expand its territory when food is scarce, and it may feed outside the defended area (Chapter 3). Also, the territory size may be determined by the distance to the nearest breeding conspecific, so that at times it is larger than would be necessary solely in defence of food. Sexual selection for larger territories may produce a similar effect.

In practise, territories often serve several functions which may be difficult to determine, and which may vary between individuals within a species. Some individuals of the Lake Malawi mbuna *Pseudotropheus zebra* may defend a territory which provides a spawning site, food, shelter and all necessary resources, whilst others defend a spawning site/refuge but forage outside the defended area (Chapter 4). Some species defend separate feeding and mating territories (Ochi 1993).

Territorial Defence and Exclusivity

Although most territories are defended by single individuals or mated pairs, group territoriality is occasionally seen. For example unrelated females of the herbivorous Caribbean striped parrotfish (*Scarus iserti*) defend group feeding territories in some cases (Clifton 1989). Each individual moves freely through the territory which is defended by all. Group-living territorials spend significantly less time defending their territory than lone territorial fish, and the author suggests that sharing the costs of territorial defence allows more time for individual feeding. In *Lamprologous brichardi* related individuals jointly defend breeding territories (Taborsky & Limberger 1981, Taborsky 1984, 1985).

In some cases the costs of defence are thought to be shared between species. Mutualism apparently occurs between some acanthurids and pomacentrids which share

territories (Robertson & Polunin 1981), and in Lake Tanganyika, *Tropheus moorii* benefits from the presence of *Petrochromis trewavasae* in the maintenance of borders against the larger species *Petrochromis orthognathus* (Kohda 1991). The interaction between the acanthurids *Ctenochaetus striatus* and *Acanthurus lineatus* varies both locally and geographically, and it is suggested that they may be interacting competitively or synergistically (Choat & Bellwood 1985, Robertson & Gaines 1986, Sale 1991).

Territorial defence may involve the exclusion of all intruders or only certain individuals or certain species. Intruders may be ignored or chased away depending on the perceived threat they present to the owner. Intruders may be able to circumvent defences by virtue of their size, aggressive dominance or grouping. Examples of the latter are seen in many species (Jones 1968, Vine 1974, Robertson *et al.* 1976, Marsh & Ribbink 1986, Reinthal & Lewis 1986, Foster 1985, 1987).

INTRASPECIFIC TERRITORIALITY

Usually, the fishes with the highest degree of resource overlap will receive the most aggression from territorial fish, and often these are conspecifics. Not all conspecifics are treated equally, however. For example, males holding spawning territories will attempt to attract gravid females, but exclude mature males, whilst juveniles may present no threat. One mechanism by which individuals can minimize defence costs is to reduce aggression towards familiar neighbours, (the dear enemy phenomenon-Wilson 1975, Krebs 1982), which present less of a threat than strange rivals, and aggression towards these individuals is relatively rare (Thresher 1976, 1979, Tricas 1989).

Since spawning territories may primarily involve defence against sneak fertilizations by conspecific males, distance between spawning sites is important in some cases (Barlow 1974a). This differential aggression towards conspecifics of the same sex may lead to large territories including several smaller territories or home ranges of the opposite sex, the haremic system. This is seen in South American species such as *Apistogramma trifasciatum*, *Crenicara* sp., *Nannacara* sp.and some of the Tanganyikan Lamprologines (Limberger 1983, Sato 1994). In other fish mature males are territorial and females and immature fish are non-territorial (e.g.some Malawian mbuna), and these "floaters" may be allowed access to the territory if they show submissive behaviour (Chapter 3).

Intraspecific territoriality often results in increasing niche breadth to avoid overlap of resource use (Huntingford & Turner 1987), with subordinate fish using different sites (e.g. for feeding) as a result of exclusion from preferred sites by

dominant territory owners. If males are dominant, females may be forced to forage elsewhere, using different techniques or more widespread sites. Thus conflict can affect the distribution of the population, with some sections being forced to move to different areas.

INTERSPECIFIC TERRITORIALITY

Although many studies on territoriality only report interactions between conspecifics, the exclusion of other species from fish territories is commonplace (Chapters 3 & 6, Zumpe 1965, Low 1971, Myrberg & Thresher 1974, Barlow 1975, Thresher 1976, Losey 1982, Neil 1984, De Martini 1985, Breitburg 1987, Petersen 1988, Clifton 1989, Hert 1990, McKaye *et al.* 1990, Karino 1991, Kuwamara 1991, Fitzsimons *et al.* 1993). Interspecific territoriality is likely to be most frequent and intense between closely-related species using similar, limited resources, but it also occurs in distantly-related species.

Territories for spawning and/or parental care usually involve the exclusion of all fish which may be brood predators. For example, brooding pairs of *Amphiprion clarkii* in Japanese waters attacked 19 species of fish, with 58% of chases directed at the cardinal fish *Apogon notata*, numerically the most abundant species in the area (Yanagisawa & Ochi 1986). Male *Protomelas taeniolatus* chased 28 species from spawning territories and fry-guarding females of the same species attacked 45 species (Chapter 6). The most frequent attacks were directed at the species which were most numerous in the area, but the most rapid chases, and the longest attack distances were elicited by predatory species. Observations on parental care in other fish yield similar results (Meral 1973, Cichocki 1977, Nagoshi 1983, Keenleyside *et al.* 1990).

Interspecific territoriality between feeding competitors has also been demonstrated, and the intensity of defence and the distance at which the owner reacts to an intruder may be greater for species with more dietary overlap (Ebersole 1977, Myrberg & Thresher 1974). For example, the banded butterflyfish *C. multicinctus* feeds upon the polyps and surface tissues of hard coral (Hobson 1974, Reese 1975, Motta 1988), and adult pairs aggressively defend permanent contiguous feeding territories from both conspecifics and other corallivorous species (Tricas 1985). In Lake Malawi *P.elongatus* "aggressive" attempts to exclude all fish from its defended area, though much larger species such as *Petrotilapia* spp. are able to circumvent these defences (Sharp 1981, Ribbink *et al.* 1983a, Chapter 3).

Territory Geometry and Complexity

Although for this review a territory was defined as "a topographically localised defended area" (Hinde 1956), it is apparent that in many cases the behaviour of a fish within the territory is not uniform. Recent field studies have demonstrated the importance of differential responses to intruders of different species and sizes (Kohda 1991), and location with respect to territory geometry (Chapter 3, Kuwamara 1991).

Often aggression is most intense in the focal point of a territory which contains the key resource (which may be a refuge, spawning site, or a food patch). This has been referred to as the "invincible centre" (Tinbergen 1939, Nice 1941, Krebs 1971). The steepness of the slope describing the relationship between the distance from the territory centre and the amount of defence will vary between species, depending on the resource being defended and the number of competitors in the area. For example, *P.elongatus* "aggressive" defend their feeding territories almost uniformly against all intruders, whereas *P. zebra, Pseudotropheus tropheops*"orange chest", *Labeotropheus fuelleborni* and *Petrotilapia nigra* show a steep decline in territorial defence from the spawning site to the outer defended area. Similar results have been found by other authors (Kuwamara 1991, Kohda 1987, Chapter 3, Thresher 1976, 1979).

There may be several different territories defended by an individual, against different intruders. For example, in Lake Tanganyika cichlids, male *Gnathochromis pfefferi* defend feeding sites over sandy or rocky areas and separate mating territories near vegetation (Ochi 1993), and male *Telmatochromis bifrenatus* often expand their feeding territories in the reproductive season to include suitable holes for spawning (Mboko 1991). The mudskipper *Periophthalmus sobrinus* defends a burrow as a refuge on the upper banks of a mangrove swamp at high tide, and a feeding territory on the lower shore at low tide (Brillet 1975). More commonly, fish defend central areas of their territory against some intruders and outer areas against only a subsection of these. For example, males of three algal feeding Tanganyikan cichlids (*Petrochromis* spp.) defend three types of territory: all intruders are excluded from the central spawning site, algal feeding species are chased from a larger area and conspecific males are chased from the farthest border (Kohda 1987). Similar concentric territories are seen in the three-spot damselfish (Thresher 1976, 1979) and other Tanganyikan fish (Kuwamara 1991).

Some Lake Malawi mbuna have an interspecifically-defended core area containing a refuge/spawning site, and a larger area defended principally against conspecific males, and sometimes there is an undefended feeding range which is even larger (Chapter 3). This leads to the formation of a complex multispecies territorial mosaic. When all species in an area are considered together, there is little overlap

between the interspecifically-defended core areas which contain spawning sites, but almost total overlap of outer peripheral zones. For many mbuna species, when all individuals are considered together, a jigsaw of abutting, rarely-overlapping conspecific mating territories is apparent, and all of the area is used (Holzberg 1978, Marsh 1981, Chapter 3). The jigsaw of one species is overlaid on the jigsaws of other species (Chapter 3).

This complexity makes the interpretation of removal experiments somewhat difficult. Several authors have reported the replacement of artificially-vacated territories by conspecific fish in multi-species communities (Marsh 1981, Sharp 1981, Yanagisawa & Ochi 1986, Kuwamara 1991), and interpreted this as site-specific territoriality, which suggests that species do not compete for space, since they all have distinct, non-overlapping requirements. However, an alternative explanation is possible. Site-specificity may be less important than the effects of territorial fish in adjacent regions. The removal of one individual will only leave a gap in the jigsaw of its own species, the area remaining full with respect to other species. The vacated area is likely to be part of the diffusely-defended peripheral zones of several individuals of other species, which may not have been recorded. To overcome any possible neighbour effects, Sharp (1981) removed all territorial fish in a small area, and found similar results. However, the behaviour of non-territorial males in the area may affect recolonization. Studies on *P. zebra* and *L. fuelleborni* (Chapter 3 & 4) show that some mbuna are semi-territorial and others show site-specific dominance, though they wander over large ranges. It is suggested that dominant, non-territorial individuals (previously beta fish in an area) are able to rapidly fill vacated territories in their range. Prior residence effects (Turner 1994b) and knowledge of territorial boundaries before removals, means that newly established territories would be likely to cover similar, though not identical, areas. This hypothesis remains to be tested. Hert (1990) suggested that female use of traditional spawning sites could lead to competition between males for these areas, and that knowledge of territory boundaries could be socially transmitted. The effect of neighbours, particularly conspecifics, was also considered to play a major role in the recolonization of vacated territories, but species-specific habitat requirements were considered unlikely.

Intraspecific Variation in Social Systems

Within a species, the social system may be highly variable according to both genetic and environmental factors, so that the propensity for territoriality varies temporally, spatially and between individuals. Some fish may be territorial at certain times of their reproductive cycle (many species establishing temporary breeding territories have

already been discussed), but others alter their social system as they grow, being territorial at some times of life but not others (Helfman 1978). Young blue gouramis (*Trichogaster trichopterus*) show most aggression in the presence of food, and later they concentrate their aggression around food patches, which they abandon when food is scarce. Eventually, at the age of 7-8 weeks, they defend a territory even when food is temporarily absent (Tooker & Miller 1980). The progression from schooling behaviour to territoriality also occurs in French grunts, *Haemulon flavolineatum*, (McFarland & Kotchian 1982, Helfman & Schulz 1984), and some Lake Malawi mbuna (Ribbink *et al.* 1983a, Chapter 4).

Some fish, especially protogynous reef fish, have very complex patterns of behaviour related to ontogeny. Females and primary males of the parrotfish, *Scarus iserti*, form groups when small (Ogden & Buckman 1973) but establish territories when larger, either alone (Buckman & Ogden 1973) or in groups (Clifton 1989). Newly transformed males repeat this sequence and eventually defend mating territories, usually encompassing several female territories (Clifton 1989). Secondary males form static groups when small, then form roving groups when larger and eventually they become territorial (Warner & Downs 1977, Clifton 1989). A similar pattern is seen in redband parrotfish, *Sparisoma aurofrenatum* (Clavijo 1982).

Polymorphic mating tactics within a species, where some males show territorial behaviour and others do not, are widely documented in fish (Gross 1980, 1984, 1985, 1991, Dominey 1980, Warner 1982, Feldmeth 1983, Thresher 1984, Aldenhoven 1986,Taborsky *et al.* 1986, 1987, Kodric-Brown 1986, Kuwamara 1987, Sigurjonsdottir & Gunnarsson 1989, Buxton & Garrat 1990, Chan & Ribbink 1990, Magnhagen 1994). For example, in the Gasterosteid *Hypoptychus dybowskii*, some males in bright nuptial colouration defend eggmasses and spawning sites in weed beds, whereas other non-territorial males shoaling in the area apparently obtained fertilizations by "sneaking". In laboratory conditions, individual males were able to rapidly switch between the two tactics (Akagawa & Okiyama 1993).

The social system adopted by fish may be determined by environmental factors. Greenberg (1947) demonstrated that in the aquarium, sunfish (*Lepomis cyanellus*) formed territories or dominance hierarchies depending on density. The significance of this discovery, for natural populations, was not fully recognised (Stokes 1974) until later work on house mice was presented in a more theoretical framework (Anderson 1961). In dominance hierarchies the direction of aggression between freely-mixing individuals is determined by properties of the participants, such as size and aggressiveness (e.g. Damselfish, *Dascyllus aruanus*,-Forrester 1991). It is now recognised that territoriality and dominance hierarchies represent two ends of a continuum of social organisation, and intermediate forms of social system exist.

In *Thalassoma bifasciatum*, large males defend mating sites and smaller males in large aggregations occupy other spawning sites. On small reefs all spawning sites of this species are defended by territorial fish, whereas on large reefs, where population densities are much higher, most spawning sites are used by aggregations. This is because at high densities, large numbers of females congregate at spawning sites, which then are not economically defensible (Warner & Hoffman 1980). However, the cost-benefit analysis will differ between individuals, and within a population there may be both dominance hierarchies and territorial individuals, and individuals may switch between the two states (e.g. *P. zebra*-Chapter 4). Factors other than density may affect an individuals decision. For example, food abundance, population density and presence of vegetation are all important factors which determine whether male sticklebacks are territorial, and whether they nest singly or in groups (van den Assem 1967, FitzGerald 1983, Stanley & Wootton 1986).

Some individuals are simultaneously territorial and belong to a dominance hierarchy. The anemone fish, *Amphiprion akallopisos*, and the Caribbean striped parrotfish, *Scarus iserti*, defend territories in groups within which size-based dominance hierchies are established (Fricke 1979, Clifton 1989). Hierarchies may exist between fish holding individual territories, with dominant fish acquiring better sites (McKaye *et al.* 1990). There may also be site-related dominance without exclusivity in an area, where fish feed as mobile groups but individuals alter their status with location (*P.zebra*-Chapter 3).

The behaviour of each individual, in any particular situation will be determined by the cost-benefit analysis of territoriality at that time (Milinski & Parker 1991). Environmental factors and genetic constraints will affect an individual's decision about whether or not to defend a territory. Competition for high quality territories has been documented in some fish (Bisazza & Marconato 1988, Hoelzer 1990). If dominant fish deny subordinates access to good quality sites, then the costs of territoriality may outweigh the benefits for individuals which are forced into suboptimal areas. Alternatively, it may simply be that there is insufficient space for all fish which are physiologically capable of holding territories to do so. Fish may be unable to defend a territory because they are phenotypically unsuited or because the environment is unfavourable.

Territorial Spacing and Population Limitation

Territorial behaviour can influence the distribution of animals both within and between habitats (Fretwell 1972), and the spacing of territories depends very much on the particular purposes they serve. Fairly evenly spaced territories should occur within a suitable habitat when defended sites provide all resources. When territories serve as courtship or nesting sites, distributions are frequently clumped.

Spacing may vary both within and between species, depending on environmental factors. For example, male Pacific sergent majors (*Abudefduf troschelii*) nest in dense colonies, and fish in centrally-placed nests are more likely to spawn and rear offspring succesfully than males on peripheral nests, which are more vulnerable to predatory wrasses (*Thalassoma lucasanum*). Their Caribbean counterparts (*A. saxatilis*) form colonies of much lower densities, probably because they are not exposed to similar predation on embryos (Foster 1989).

A clumped pattern of territories may result from cooperation among individuals (e.g. colonial nesting sunfish-Dominey 1981, Gross & MacMillan 1981, Bietz 1981) or from "preemptive behaviour" in newly-settling fish (Getty 1981). The "preemptive" model suggests that fish with compressible territories should settle closer to existing territories than initial density requires. This prevents subsequent settlers from trying to establish a territory between those already existing, which might force the territory to be compressed. This means that preempting individuals may ultimately end up with larger territories than individuals that initially spaced their territories widely and subsequently were forced to contract them.

Interspecific effects will also vary with the community under consideration. In a study of three damselfish species with similar patterns of resource use, all holding both intra-and interspecifically-defended territories, Sale (1977, 1978, 1980) found that space was limited but vacated territories were not always filled by conspecifics. He called this a "lottery for living space". In other reef fish, space may not be limiting and the species composition depends on the number of fish larvae over the reef at the time, with number and species of settlers being unrelated to local density (Sale 1978, Doherty 1983). In Lake Malawi mbuna, although spawning sites are interspecifically defended, larger mating territories are defended against conspecific neighbours. Thus, intraspecific competition for breeding sites would appear to be more important than interspecific competition, in determining the relative number of territories of each species. Territoriality may affect the relative abundance and distribution of component species, or alternatively it may play no part in the determination of the community structure.

The role of territoriality in limiting population size remains controversial, though the debate is longstanding. Huxley's (1934) "elastic disc" theory suggested a limit to the compressibility of a territory which could eventually limit population density. Kluyver & Tinbergen (1953) presented an alternative theory, the "buffer mechanism", in an attempt to explain the relatively stable densities of breeding birds in the most favourable habitats. This theory suggests that animals attempt to settle in the preferred habitat and only when that is crowded will they use less favourable habitats. Wynne-Edwards (1962) postulated that territoriality not only reflects the size of populations but that it evolved specifically as a mechanism of population control. Lack (1954) argued that territoriality is only important in spacing within populations, not in limiting them. The debate has continued, largely with reference to bird populations (Fretwell & Lucas 1969, Brown 1969, Orians 1971, Krebs 1971, Sibley & Smith 1985, Sutherland & Parker 1985, Patterson 1980, 1985), though it is also relevant to fish.

The basis of the argument is whether resources, such as food, limit population size or whether territorial behaviour restricts population levels below those at which the supply of resources becomes critical. The answer may differ between species and populations. In some fish, territoriality breaks down at high population densities, so population limitation is by other factors. In other species population size may be limited in a density-dependent manner by territoriality. For example, gymnotoids, catfish of South Americal streams, trout and fish of the Great Barrier Reef (Lowe-McConnell 1991). Territorial behaviour does not affect the number of young damselfish that are able to settle (Doherty 1983). It is also unlikely to limit populations of Malawian haplochromines, since in this case the territorial fish are males of polygamous species which do not exhibit parental care, and shared paternity has recently been demonstrated for several of these species (Parker & Kornfield unpublished data, Kellogg *et al.*. unpublished data). It is possible that the behaviour of territorial fish affects the abundance and composition of non-territorial fish in the area, which in turn affects population size, for example, by limiting access of non-territorial fish to defended sites which may contain better feeding areas. Growth rate and survival of some reef fish may be inversely related to density of their own and other species (Thresher 1983), and some species show social inhibition of growth (Farr 1980, Metcalfe 1980, Metcalfe *et al.* 1992) or maturation (Borowsky 1987).

Experimental Manipulations

Few field studies involve more than direct observation of territorial behaviour, and many ignore interspecific effects. Manipulative experiments to extricate important factors and processes are rare, but there are exceptions. For example, removal

experiments in the bluehead wrasse (*Thalassoma bifasciatum*), showed that breeding sites which are defended by males, are determined by female preference (Warner 1988, 1990). However, reliable direct evidence about the functions of territoriality is scarce.

Fish are ideal subjects for laboratory studies on territoriality, since they can be kept in more or less natural conditions and their relatively short reproductive cycle makes it possible to gather a large amount of data in a relatively short period of time. Experimental studies on the pumpkinseed sunfish (*Lepomis gibbosus*), in aquarium conditions, examined asymmetries in resource holding power (body size) and resource expectation (prior feeding) on attack behaviour and dominance. Results suggested that value expectation was a good predictor of first attack, but not of victory (Dugatkin & Ohlsen 1990).

There have been many excellent studies of parental territoriality, especially in convict cichlids (Fitzgerald & Keenleyside 1978, Colgan & Salmon 1986, Russock 1986, Rogers 1988, Raadik *et al.* 1990, Lavery *et al.* 1990, Lavery & Colgan 1991, DeGannes & Keenleyside 1992), but also much work on fighting behaviour (Enquist & Leimar 1983, Enquist 1985, Keenleyside *et al.* 1985, Barlow *et al.* 1986, Turner 1986b, 1994b, Turner & Huntingford 1986, Getty 1987, Bakker 1988), territory size and the ideal despotic distribution (Fretwell & Lucas 1970, Fretwell 1972, Davies 1978, Parker & Knowlton 1980, Davies & Houston 1984, May & Harvey 1988) and signalling (Colgan & Gross 1977, Stacey & Chiszar 1978), all of which may be relevant to our understanding of territorial behaviour.

Caution must be exercised in the interpretation of behavioural observation in aquarium conditions, however, especially when attempting to extrapolate results to understanding territoriality in natural conditions. Fish behaviour may be quite different in the field and the laboratory (e.g. sticklebacks-FitzGerald & Kedney 1987, Dufresne *et al.* 1990, Malawian haplochromine cichlids-Robinson & Turner 1990), and it is important to tease out the factors (e.g.density, food distribution) which affect behaviour in any particular situation.

Conclusions

The literature on fishes shows that territoriality is taxonomically widespread. There are many descriptions of territorial behaviour but there are far fewer studies of causality, function and evolution, which require controlled experiments where environmental and social factors can be independently manipulated. A thorough understanding of territoriality must begin with a description of its occurrence in nature. Then, relationships between function and causality can be explored. In many cases, the critical resource targets of territorial fish are unknown, and this might be a fruitful area

of investigation, especially for coral reef fish and Malawian mbuna, which feed on epilithic algae and associated matter. For these animals it is difficult to know whether different individuals feeding on the algal mat are using the same resource or are selecting certain components.

It is fruitless to seek a single function for territoriality, since it may serve several functions, according to species, sex, and developmental stage. It also varies according to genotype and phenotype-limited strategies and short term costs and benefits. Territories may be simultaneously multifunctional. More importantly, environmental factors play a large part in determining the social structure within a species, which may be highly variable. Whilst simplifying the questions that are asked in studies of territoriality may assist in the determine of underlying principles, overlooking the complexity of this subject may give misleading results.

Chapter 8. General Discussion

In this section, the contribution of the present study to the understanding of Lake Malawi cichlids is briefly assessed, limitations of the work discussed and suggestions for future research are made.

For behavioural ecologists, like population geneticists, evolution is the change in frequencies of genes within a population and the material on which selective processes operate is genetically-based individual variability. Selective advantages at the level of group and species are not considered to operate at a time scale which can compensate for disadvantages at an individual level. Thus, group selection is rejected. Processes operating at the levels of community or ecosystem are considered to be the consequence of the interaction of many processes operating at the level of the individual in many species. Different components of a community or ecosystem can only influence one another through the medium of individuals. Thus, a principal theme of behavioural ecology is the variability among conspecific individuals. Consequently, a major emphasis of the present work is the study of individuals.

Previous studies on the territorial behaviour of Lake Malawi fishes can be divided into two groups: (i) detailed studies of the behaviour of single species (Hert 1990, 1992, Kornfield *et al.* in press), or a group of sibling species within an area (Holzberg 1978, Marsh 1981) and (ii) broad descriptive studies of numerous species (Ribbink *et al.* 1983). A striking feature of the rocky shore fish community in Lake Malawi is the coexistence of many closely-related cichlid species within the same habitat. Many of these species have been said to exploit very similar resources, both in diet and space (Fryer & Iles 1972). Males of many of these species are territorial throughout the year and so competition is not avoided by differing seasonality. The present work is the first detailed quantitative field study of all species coexisting within an area of the lake and as such it provides new insight into this multispecific community, particularly in terms of consequences for individual fish.

This simultaneous emphasis on covering all species, as well as repeated sampling of individuals is not without its disadvantages. Principal among these are the restricted area of the lake which could be investigated and the small number of individuals of each species examined.

The study was principally concentrated within a single 5 x 5 m quadrat. It would be unwise to make many broad generalisations from such a small area. The rocky habitat is diverse in many respects, and any two quadrats within this habitat, even in close proximity, would contain different topographic features. Rock size is

likely to strongly influence not only the species composition of the community, but also the behaviour of individuals: for example, on substrates of large slabs or bedrock, there will be few refuges and territories may be considerably larger than in the present study. The ratio of territorial to non-territorial individuals is also likely to vary, perhaps altering the costs of resource defence. A similar effect may hold for areas where large rocks lie directly on a sandy substrate ('intermediate' habitat). The present study was focused on an area in a sheltered bay, in which the sediment levels, water movements and possibly even temperature regimes would differ from other sites on the same island. The patterns of light and shadow may be different from that on other shores. In addition, the rocky substratum extends to a much greater depth than that studied in the present work and different depths are populated by different species (Ribbink *et al.* 1983). Finally, each island and patch of rocky coastline is inhabited by a different community of species. Some of the species in the present study will find themselves co-existing with others not covered herein, at different locations. It is noteworthy that each of the permanently territorial species in the study was a member of a different species complex. It is known that territories of sibling species (members of the same species complex) can co-exist in the same habitat and their territories may overlap (Holzberg 1978, Marsh 1981). This may lead to higher degrees of interspecific competition than those described in the present work.

In any quantitative study, there is a limit to the number of samples which can be taken and thus a trade-off between the numbers of categories analysed and the number of replicates per category. The categories in the present study were: species, territorial/ floater, individual, time of day and replicate observation. The approach outlined above necessitated concentration of effort on the two extremes: species on the one hand and within-individual sampling (time of day and replicate observation) on the other. This meant reduction in the other categories. Floaters were studied for a single species (*P. zebra*) only, while four individuals were chosen from each of the territorial species for intensive quantitative analysis. The nested analysis of variance design allows for the partitioning of hypothesis testing into an 'individual-within-species' component and a 'between-species' component. It should be stressed that the between-species component is representative only of the range of individual variability recorded in the present study conditions. For example, conspecific territorial males may behave rather differently on different substrate types, or at different depths. Larger or smaller males may hold territories in other areas and these may behave differently from those sampled in the present work. The between-species component should, at most, be interpreted as referring to a difference between species within the particular habitat studied. However, this in no way invalidates the results of comparisons of behaviour between individuals.

One clear outcome of the study has been the demonstration of striking differences in the behaviour of individuals within species. Many of these, such as being territorial, semi-territorial or floater, are clearly dependent on the context within which the individual is located in space and time and with particular regard to the presence and behaviour of other individuals of the same and different species. Individuals were found to exhibit great flexibility in their behaviour, and much of the variation among individuals is almost certainly representative of variation within an individual at different stages in its life, as it grows in size and strength, acquires more familiarity with its local habitat and increases its position in the local social hierarchy.

Territoriality in the mbuna was found to be more complex than had previously been reported (Marsh 1981, Sharp 1981, Hert 1990), and often involved an interspecifically defended core area containing a spawning site, and a larger mating territory defended principally against conspecific territorial neighbours, with individuals also apparently defending personal space, as reported for other species by Hert (1993). The removal experiments on territorial fish by other workers (Marsh 1981, Sharp 1981, Hert 1990) did not take account of this complexity, and merely recorded which individuals occupied the artificially-vacated sites. A possibly fruitful future study would be to assess the effects of the vacated site on the behaviour of neighbouring territory holders of all species, and to record the interactions of the new territory occupant with these fish.

The study of transient breeding territories was a very preliminary survey but clearly both the number of species involved, and the demands which the transient territorial fish make on space in the rocky area are substantial. There was also wide variation in the duration of territorial defence among the individuals of each species and sex, and evidence that some species attempt to establish a breeding territory and fail. The present study is the first to report competition for space between the permanent residents in an area and cichlids which establish territories only during their reproductive phase. Previous work on temporary breeding territories (McKaye 1983, McKaye *et al.* 1990, Turner & Robinson 1991) has focused on species of sandy habitats where there is no resident territorial community. This study suggests that transient territorial fish may play an important role in structuring the mbuna assemblages in the rocky shore, which had not previously been considered. A particularly interesting result was the displacement of three *P. elongatus* 'aggressive' individuals by territorial *P. taeniolatus.* Perhaps the territories of this mbuna species are relatively incompressible in comparison to others, and displacement is a frequent outcome of these contests. However, the samples in this study were particularly small and so general conclusions about the differential effects of transient species on the different mbuna species could not be determined. Future studies involving larger

samples of transient/mbuna interactions would be needed to draw conclusions on differences between species, since interactions have already been shown to depend on individual size and aggression, as well as the species involved.

The study on fry-guarding behaviour of *P. taeniolatus* highlighted the frequency of brood mixing which has previously been documented (Ribbink *et al.* 1980), but unlike previous studies (Ribbink 1977), the fry in mixed broods were all found to originate from species which perform fry-guarding in the area. In addition, a greater number of species appear to guard free-swimming fry than had previously been recognised.

Communal fry-guarding in *P. taeniolatus* is a phenomenon that deserves more attention. If the results of this study are true for larger sample sizes, then there are benefits to communal care (reduced defence costs and increased feeding opportunities for females) but no apparent disadvantages. In addition, the only time that females were seen to desert their broods was when their offspring were being protected by another female. This is a form of intraspecific brood parasitism. There was no evidence that females actively sought to aggregate with conspecifics, or that they reduced their aggressive behaviour in an appropriate fashion. This may indicate that although communal guarding may be an optimal evolutionary strategy for the species, the genetic variation necessary to allow the females to exploit it fully is absent.

The general review of territoriality in fishes has served to indicate that the complexity and individual variability shown by the Malawian mbuna in the present study can be integrated into the general framework of the conclusions drawn by behavioural ecologists from studies of other species. Territories in fishes are often simultaneously multifunctional and territorial individuals use different parts of their territories for different purposes: feeding, courting, hiding. Different parts of the territory are often defended to different degrees and against different individuals of various species. Interspecific territoriality is widespread. Territoriality is often dependent on phenotype- and genotype-limited behavioural strategies within a species.

In the terminology of behavioural ecology, individuals assess the costs and benefits of territoriality and choose accordingly between territorial and non-territorial behaviour, but this is not an all or nothing choice, intermediate conditions exist and animals modify their behaviour continuously according to environmental and social conditions. It is probable that this, rather than genetic differences among individuals, is the main cause of variability among conspecific individuals observed in the present study.

REFERENCES

Ackerman, B.B., Leban, F.A., Garton, E.O. Samuel, M.D. (1989) *Home Range computer programe*. Department of Fish and Wildlife Resources, Idaho.

Akagawa, I. & Okiyama, M. (1993) Alternative mating tactics in *Hypoptychus dybowskii* (Gasterosteiformes): Territoriality, body size and nuptial colouration. *Japanese Journal of Ichthyology* **40** (3), 343-350.

Aldenhoven, J. M. (1986) Different reproductive strategies in a sex-changing coral reef fish *Centropyge bicolor* (Pomacanthidae) *Australian Journal of Marine and Freshwater Research* **37**, 353-60.

Altum, J.B.T. (1868) *Der Vogel und sein Leben.* Munster.

Anderson, P.K. (1961) Density, social structure, and nonsocial environment in house-mouse populations and the implications for regulation of numbers. *Transactions of the New York Academy of Science* **23**, 447-451.

Andersson, M. (1994) *Sexual Selection.* Princeton University Press, Princeton, New Jersey. pp. 599.

Assem, J. van den (1967) Territory in the three-spined stickleback, *Gasterosteus aculeatus* L. An experimental study in intraspecific competition. *Behaviour (Supplement)* **16,** 1-167.

Baerends, G. P. & Baerends van Roon, J. M. (1950) An introduction to the ethology of cichlid fishes. *Behaviour Supplement* **1**, 1-243.

Baeyens, G. (1981) Functional aspects of serial monogamy: the magpie pair-bond in relation to its territorial system. *Ardea* **69,** 145-166.

Bakker, T.C.M., Feuthy-de-Bruijn, E. & Svenster, P. (1988) Asymmetrical effects of prior winning and losing on dominance on sticklebacks (*Gasterosteus aculeatus*) *Ethology* **82**, 224-229.

Banister, K.E. & Clark, M.A. (1980) A revision of large *Barbus* (Pisces, Cyprinindae) of Lake Malawi with a reconstruction of the history of the southern African Rift Valley lakes. *Journal of Natural History, London* **14**, 483-542.

Barlow, G. W. (1964) Ethology of the Asian teleost *Badis badis.* V. Dynamics of fanning and other parental activities, with comments on the behavioour of the

larvae and postlarvae. *Zeitschrift für Tierspsychologie* **21**, 99-123.

Barlow, G.W. (1974a) Derivation of threat display in the grey reef shark. *Marine Behavioural Physiology* **3,** 71-81.

Barlow, G. W. (1974b) Hexagonal territories. *Animal Behaviour* **22**, 876-878.

Barlow, G. W. (1975) On the sociobiology of four Puerto Rican parrotfishes (Scaridae) *Marine Biology* **33**, 281-293.

Barlow, G.W. Rogers, W. & Fraley, N. (1986) Do midas cichlids win through prowess or daring? It depends. *Behavioural Ecology & Sociobiology* **19**, 1-8.

Baylis, J. R. (1981) The evolution of parental care in fishes, with reference to Darwin's rule of male sexual selection. *Environmental Biology of Fishes* **6**, 223-251.

Beckoff, M. & Mech, L. D. (1984) Simulation analyses of space use: home range estimates, variability and sample size. *Behaviour research methods, instruments and computers* **16**(1), 32-37.

Bellwood, D.R., & Choat, J.H. (1990) A functional analysis of grazing in parrotfishes (family Scaridae): the ecological implications. *Environmental Biology of Fishes* **28,** 189-214.

Bietz, B.F. (1981) Habitat availability, social attraction and nest distribution patterns in longear sunfish (*Lepomis megalotis peltastes*) *Environmental Biology of Fishes* **6(2),** 3-200.

Birkhead, T.R. & Clarkson, K. (1985) Ceremonial gatherings of the magpie *Pica pica*: territory probing and acquisition. *Behaviour* **94,** 324-332.

Bisazza, A. & Marconato, A. (1988) Female mate choice, male-male competition and parental care in the river bullhead, *Cottus gobio* L. (Pisces: cottidae) *Animal Behaviour* **36**, 1352-1360.

Blumer, L.S. (1979) Male parental care in the bony fishes. *The quarterly review of biology*, **34**, 149-161.

Blumer, L.S. (1982) A bibliography and categorization of bony fishes exhibiting parental care. *Zoolological Journal of the Linnean Society* **76,** 1-22.

Borowsky, R.L. (1987) Agonistic behaviour and social inhibition of maturation in

fishes of the genus *Xiphorus* (poeciliidae) .*Copeia* **3**, 792-796.

Bowen, W.D. (1982) Home range and spatial organization of coyotes in Jasper National Park, Alberta. *Journal of Wildlife Management* **46**(1), 201-216.

Bowers, N.J. & Stauffer, J.R. (1993) New species of rock-dwelling cichllid (Pisces: Cichlidae) from Lake Malawi, Africa, with comments on *Melanochromis vermivorous* Trewavas. *Copeia* **3**, 715-722.

Breitburg, D.L. (1987) Interspecific competition and the abundance of nest sites: factors affecting sexual selection., *Ecology* **68** (6) : 1844-1855.

Brillet, C. (1975) Relations entre territoire et comportment aggressif chez *Periophthalmus sobrinus* Eggert (Pisces, Periophthalmidae) au laboritoire et en millieu natural. *Zeitschrift für Tierpsychologie* **39**, 283-331.

Brown, J.L. (1963) Social organization and behaviour of the Mexican jay. *Condor* **65**, 126-153.

Brown, J.L. (1964) The evolution of diversity in avian territorial systems. *Wilson Bulletin* **76**.

Brown, J.L. (1969) Territorial behaviour and population regulation in birds. *Wilson Bulletin* **81**, 293-329.

Buckman, N.S. & Ogden, J.C. (1973) Territorial behaviour of the striped parrotfish *Scarus croicensis* Bloch (Scaridae) *Ecology* **54**, 1377-1382.

Buss, L.W. (1980) Competitive intransitivity and size-frequency distributions of interacting populations. *Proceedings of the National Academy of Science, USA.* **77**, 5355-5359.

Buxton, C.D. & Garratt, P.A. (1990) Alternative repreoductive styles in seabreams (Pisces: sparidae). *Environmental Biology of Fishes* **28**, 113-124.

Catchpole, C.K. & Leisler, B. (1988) Interspecific territorialism in *Acrocephalus*: a reply to Murray's critical review. *Ornis Scandinavica* **19**, 314-316.

Chan, T.-Y. & Ribbink, A.J. (1990) Alternative reproductive behaviour in fishes, with particular reference to *Lepomis macrochira* and *Pseudocrenilabrus philander. Environmental Biology of Fishes* **28**, 249-256.

Chase, I.D., Bartolomeo, C & Dugatkin, L.A. (1994) Aggressive interactions and

inter-contest in.erval: how long do winners keep winning? *Animal Behaviour* **48,** 393-400.

Choat, J.H., & Bellwood, D.R. (1985) Interactions amongst herbivorous fishes on a coral reef: influence of spatial variation. *Marine Biology* **89,** 221-234.

Cichocki, F.P. (1977) Tidal cycling and parental behaviour of the cichlid fish, Biotodoma cupido. *Environmental Biology of Fishes* **1**(2), 159-169.

Cimprich, D.A. & Grubb, T.C. (1994) Consequences for Carolina chickadees of foraging with tufted titmice in winter. *Ecology* **75** (6), 1615-1625.

Clavijo, I. (1982) *Aspects of the reproductive biology of the redband parrotfish Sparisoma aurofrenatum*. PhD thesis, University of Puerto Rico, Mayaguez, Puerto Rico.

Clifton, K.E. (1989) Territory sharing by the Caribbean striped parrotfish, *Scarus iserti*: patterns of resource abundance, group size and behaviour. *Animal Behaviour* **37**, 90-103.

Cody, M.L. (1969) Convergent characteristics in sympatric species: a possible relation to interspecific competition and aggression. *Condor* **71**, 223-239.

Cody, M.L. & Brown, J.H. (1970) Character convergence in Mexican finches. *Evolution* **24**, 304-310.

Colgan, P.W. & Gross, M.R. (1977) Dynamics of aggression in male pumpkinseed sunfish (*Lepomis gibbosus*) over the reproductive phase. *Zeitschrift fur Tierpsychologie* **43**, 139-151.

Colgan, P.W. & Salmon, A.B. (1986) Breeding experience and parental behaviour in convict cichlids (*Cichlasoma nigrofasciatum*) *Behavioural processes*, **13,** 101-118.

Darling, F. (1938) *Bird flocks and the breeding cycle. A contribution to the study of avian sociality.* Cambridge.

Davies, N.B. (1978) Territorial defence in the speckled wood butterfly (*Pararge aegea*): the resident always wins. *Animal Behaviour* **26, 138-147**.

Davies, N.B., & Houston, A.I. (1984) Territory economics. In J.R.Krebs & N.B.Davies (eds), *Behavioural Ecology* 2nd edn. Blackwell Scientific

Publications, Oxford. pp. 148-169.

Dawkins, R. & Carlisle, T.R. (1976) Parental investment, mate desertion and a fallacy. *Nature* **262**, 131-133.

DeGannes, G.C. & Keenleyside, M.H.A. (1992) Convict cichlid fry prefer the more maternally active of two parental females. *Animal Behaviour* **44**, 525-532.

De Martini, E.E. (1985) Social behaviour and coloration changes in painted greenling, *Oxylebius pictus* (Pisces: Hexagrammidae) *Copeia* **4**, 966-975.

Dill, L.M., Ydenburg, R.C. & Fraser, A.H.G. (1981) Food abundance and territory size in juvenile coho salmon (*Onchorynchus kissutch*) *Canadian Journal of Zoology* **59**, 1801-1809.

Doherty, P.J. (1983) Tropical territorial damsel fishes: is density limited by aggression or recruitment? *Ecology* **64**, 176-190.

Dominey, W.J. (1980) Female mimicry in male bluegill sunfish- a genetic polymorphism? *Nature* 284, 546-548.

Dominey, W.J. (1981) Anti-predator function of bluegill sunfish nesting colonies. *Nature*. **290**, 586-588.

Draud, M., Itzkowitz, D.E & Itzkowitz M. (1990) Co-defence of territory space by two species of coral reef fishes. *Bulletin of Marine Science* **47**(3), 721-724.

Dugatkin, L.D. & Ohlsen, S. (1990) Contrasting asymmetries in value expaectation and resource holding power: effects of attack behaviour and dominance in the pumpkinseed sunfish (*Lepomis gibbosus*) *Animal Behaviour* **39**, 802-804.

Dufresne, F., FitzGerald, G. J. & Lachance, S. (1990) Age and size related differences in reproductive success and reproductive costs in threespine sticklebacks. *Behavioural Ecology* **1**, 140-147.

Ebersole, J.P. (1977) The adaptive significance of interspecific territoriality in the reef fish *Eupomacentrus leucosticus. Ecology* **58**, 914-920.

Ebersole, J.P. (1980) Food density and territory size: An alternative model and a test on the reef fish *Eupomacentrus leucostictus. American Naturalist* **115**, 492-509.

Eccles, D.H. (1974) An outline of the physical limnology of Lake Malawi (L.Nyasa)

Limnology & Oceanography, **19**, 730-742.

Eccles, D.H. & Lewis, D.S.C. (1981) Midwater spawning in *Haplochromis chrysonotus* (Boulenger) (Teleostei: cichlidae) in Lake Malawi. *Environmental Biology of Fishes* **6** (2) : 201-202.

Eccles, D.H. & Trewavas, E. (1989) *Malawian cichlid fishes. The classification of some Haplochromine genera.* Herten (W. Germany), Lake Fish Movies.

Endler, J.A. (1989) Conceptual and other problems in speciation. In Otte, D. & Endler, J.A. (eds) *Speciation and its consequences.* Sinauer, Sunderland, Mass. pp. 628-648.

Enquist, M. & Leimar, O. (1983) Evolution fo fighting behaviour: decision rules and assessment of relative strength. *Journal of Theoretical Biology* **102**, 387-410.

Enquist, M. (1985) Communication during aggressive interactions with particular reference to variation in choice of behaviour. *Animal Behaviour* **33**, 1152-1161.

Enquist, M., Leimar, O. Ljundberg, T., Mallner, Y. & Segerdahl, N. (1990) A test of the sequential assessment game: fighting in *Nannacara anomola. Animal Behaviour* **40,** 1-4.

Evans, M. (1990) The relationship between parental input and investment. *Animal Behaviour* **39**, 797 pp.

FAO (1982) Fishery expansion project, Malawi. Biological studies on the pelagic ecosystem of L.Malawi. FAO, FI:DP/MLW/75/019, Technical Report no. 1, 182 pp.

FAO (1993). Fisheries management in south-east Lake Malawi, the Upper Shire River and Lake Malombe. CIFA Technical Paper 17 106pp. FAO, Rome.

Farr, J.A. (1980) The effects of juvenile social interaction on growth rate, size and age at maturity, and adult social behaviour in *Girardinus metallicus* Poey (Pisces: poeciliidae) *Zeitschrift fur Tierpsychologie* **52**: 247-268.

Feldmeth, C.R. (1983) Costs of aggression in trout and pupfish. In W.P.Asprey & S.I.Lustick (eds), *Behavioural Energetics: The cost of survival in vertebrates.* Ohio State University Press, Columbus. pp.117-138.

FitzGerald, G. J. (1983) The reproductive ecology and behaviour of three sympatric sticklebacks (Gasterosteidae) in a saltmarsh. *Biology of Behaviour* **8**, 67-79.

FitzGerald, G. J. & Keenleyside, M. H. A. (1978) The effects of numerical density of adult fish on reproduction and parental behaviour in the convict cichlid fish *Cichlasoma nigrofasciatum* (Gunther) *Canadian Journal of Zoology* **56,** 1367-1371.

FitzGerald, G. J. & Kedney, G. I. (1987) Aggression, fighting and territoriality in sticklebacks: three different phenomena. *Biology of Behaviour* **12**, 186-195.

Fitzsimons, J. M., Nishimoto, R. T. & Yuen, A. R. (1993) Courtship and territorial behaviour in the native Hawaiian stream goby, *Sicyopterus stimpsoni. Ichthyological Exploration of Freshwaters* **4**(1), 1-10.

Forrester, G.E. (1991) Social rank, individual size and group compostition as determinants of food consumption by humbug damselfish, *Dascyllus aruanus. Animal Behaviour* **42**, 701-712.

Foster, S.A. (1985a) Size-dependent territory defence by a damselfish. *Oecologia* **67**, 499-505.

Foster, S.A. (1985b) Group foraging by a coral reef fish: a mechanism for gaining access to defended resources. *Animal Behaviour* **33**, 782-792.

Foster, S.A. (1987) Aquisition of a defended resource: a benefit of group foraging for the neotropical wrasse, *Thalassoma lucasanum. Environmental Biology of Fishes* **19**(3) : 215-222.

Foster, S.A. (1989) The implications of divergence in spatial nesting patterns in the geminate Caribbean and Pacific sergeant major damselfishes. *Animal Behaviour* **37**, 465-476.

Fretwell, S.D. (1972) *Populations in a seasonal environmnent.* Princeton University Press, Princeton, New Jersey.

Fretwell, S.D. & Lucas, J.R. (1970) On territorial behaviour and other factors influencing habitat distribution in birds. I. Theoretical developments. *Acta Biotheoretica* **19**, 16-36.

Fricke, H.W. (1979) Mating system, resource defence and sex change in the anemonefish *Amphiprion akallopisos. Zeitschrift fur Tierpsychologie* **50**, 313-

326.

Fryer, G. (1959) The trophic interrelationships and ecology of some littoral communities of L.Nyasa with special reference to the fishes, and a discussion of the evolution of a group of rock-frequenting Cichlidae. *Proceedings of the Zoological Society, London* **132**, 153-281.

Fryer, G., & Iles, T.D. (1972) *The cichlid fishes of the Great Lakes of Africa. Their Biology and evolution.* TFH Publications. Hong Kong.

Gerking, S.D. (1953) Evidence for the concepts of home range and territory in stream fishes. *Ecology* **34**, 347-365.

Getty, T. (1981) Competitive collusion: The preemption of competition during the sequential establishment of territories. *American Naturalist* **118**, 426-431.

Getty, T. (1987) Dear enemies and the prisoner's dilemma: Why should territorial neighbours form defensive coalitions? *American Zoologist* **27,** 327-336.

Godfray, H.C.J., Hassel, M.P. & Holt, R.D. (1994) The population dynamic consequences of phenological asynchrony between parasitoids and their hosts. *Journal of Animal Ecology* **63,** 1-10.

Goulet, D. & Green, J. M. (1988) Reproductive success of the male lumpfish (*Cyclopterus lumpus* L.) (Pisces, Cyclopteridae): evidence against female mate choice. *Canadian Journal of Zoology* **66**, 2513-2519.

Greenburg, B. (1947) Some relations between territory, social hierarchy and leadership in the green sunfish (*Lepomis cyanellus*) *Physiological Zoology* **20**, 269-299.

Greenwood, P.H. (1991) Speciation. In M.H.A. Keenleyside (ed) *Cichlid Fishes-Behaviour Ecology & Evolution.* 86-102 pp. Chapman & Hall, London.

Gross, M. R. (1980) *Sexual selection and the evolution of reproductive strategies in sunfishes* (*Lepomis*: Centrarchidae) Unpublished PhD dissertation, University of Utah.

Gross, M.R. (1984) Sunfish, salmon and the evolution of alternative reproductive strategies and tactics. in G.W.Potts & R.J.Wootton (eds) *Fish Reproduction: strategies and tactics.* Academic Press, London, 55-75.

Gross, M.R. (1985) Disruptive selection for alternative life histories in salmon. *Nature*

313, 47-48.

Gross, M.R. (1991) Evolution of alternative reproductive strategies, frequency-dependent sexual selection in male blue-gill sunfish. *Philosophical Transaction of the Royal Society Series Bulletin* **332,** 59-66.

Gross, M.R. & MacMillan, A.M. (1981) Predation and the evolution of colonial nesting in bluegill sunfish (*Lepomis macrochirus*) *Behavioural Ecology & Sociobiology* **8,** 163-174.

Gross, M.R. & Sargent, R.C. (1985) The evolution of male and female parental care in fishes. *American Zoologist* **25,** 807-822.

Hayne, D.W. (1949) Calculation of size of home range. *Journal of Mammalogy* **30,** 1-18.

Helfman, G.S. (1978) Patterns of community structure in fishes: summary and overview. *Environmental Biology of Fishes* **3**, 129-148.

Helfman, G.S. & Schulz, E.T. (1984) Social transmission of behavioural traditions in a coral fish. *Animal Behaviour* **32**, 379-384.

Hert, E. (1990) Factors in habitat partitioning in *Pseudotropheus aurora* (Pisces: cichlidae) , an introduced species to a species-rich community in Lake Malawi. *Journal of Fish Biology* **36**: 853-865.

Hert, E. (1992) Homing and home-site fidelity in rock-dwelling cichlids (Pisces: Teleostei) of Lake Malawi, Africa. *Environmental Biology of Fishes* **33**, 229-237.

Hert, E. (1993) Time sharing, a strategy of habitat utilization in *Melanochromis auratus*, a rock-dwelling cichlid of Lake Malawi, Africa. *Ichthyological Exploration of Freshwaters*, **4** (1), 61-64.

Hinde, R.A. (1956) The biological significance of territories in birds. *Ibis* **98**, 340-369.

Hixon, M.A. (1980) Food production and competitor density as the determinants of feeding territory size. *American Naturalist* **115**, 510-530.

Hobson, E.S. (1974) Feeding relationships of teleost fishes on coral reefs in Kona, Hawaii. *Fishery Bulletin, U.S.Fish & Wildlife Service* **72**, 915-1031.

Hoelzer, G.A. (1990) Male-male competition and female choice in the Cortez

damselfish, *Stegastes rectifraenum*. *Animal Behaviour* **40**, 339-349.

Holzberg, S. (1978) A field and laboratory study of the behaviour and ecology of *Pseudotropheus zebra* (Boulenger), an endemic cichlid of Lake Malawi (Pisces: cichlidae) *Z. Zool. Syst. Evolot.-forsch.* **16,** 171-187.

Howard, F. (1920) *Territory in bird life.* Atheneum, London.

Huntingford, F. A. (1977) Inter- and intraspecific aggression in male sticklebacks. *Copeia* 1977, 158-159.

Huntingford, F.A. & Turner, A.K. (1987) *Animal Conflict.* Chapman & Hall.

Huston, N. (1985) Patterns of species diversity on coral reefs. *Annual Review of Ecology & Systematics* **16,** 149-177.

Huxley, J.S. (1934) A natural experiment on the territorial instinct. *British Birds* **27**, 270-277.

Iersel, J.J.A. van (1953) An analysis of the parental behaviour of the male three-spined stickleback (*Gasterosteus aculeatus* L.) *Behaviour Supplement* **3**, 159 pp.

Iles, T.D. (1960) A group of zooplankton feeders of the genus Haplochromis (Cichlidae) *Annals & Magazine of Natural History* **17**, 257-280.

Ims, R.A. (1990) On the adaptive value of reproductive synchrony as a predator-swamping strategy. *American Naturalist* **136** (4), 485 -498.

Itzkowitz, M. (1985) Sexual differences in offspring defense in a monogamous cichlid fish. *Zeitschrift fur Tierpsychologie* **70,** 247-255.

Johnson, R.H. & Nelson, D.R. (1973) Agonistic displays in the gray reef shark, *Carcharhinus menisorrah,* and its relationship to attacks on man. *Copeia* 76-84.

Jones, R.S. (1968) Ecological relationships in Hawaiian and Johnston Island Acanthuridae (surgeonfishes) *Micronesia* **4,** 309-361.

Karino, K. (1991) Interspecific interactions and territoriality of an algal feeding cichlid, *Neolamprologus moorii*, at Kasenga. In Kawanabe, H. & M.Nagoshi (eds) *Ecological and Limnological Study on Lake Tanganyika and its Adjacent Regions VII,* 29- pp.

Kawanabe, H. (1981) Territorial behaviour of *Tropheus moorei* (Osteichthyes: Cichlidae) with a preliminary consideration on the territorial forms in animals. *African Study Monographs*, Kyoto, **1**, 101-108.

Keddy. P.A. (1989) *Competition. 2nd edn.* Chapman & Hall.

Keenleyside, M.H.A. (1979) *Diversity and Adaptation in Fish Behaviour* Springer Verlag, Berlin.

Keenleyside, M.H.A., Rangely, R.W. & Kuppers, B.U. (1985) Female mate choice and male parental defence behaviour in the cichlid fish *Cichlasoma nigrofasciatum. Canadian Journal of Zoology* 2489-2493.

Keenleyside, M.H.A, Bailey R.C. & Young, V.H. (1990) Variation in the mating system and associated parental behaviour of captive and free-living *Cichlasoma nigrofasciatum* (Pisces, Cichlidae) *Behaviour* **112**, 202-221.

Klummp, D.W., McKinnon, D. & Daniel, P. (1987) Damselfish territories: Zones of high productivity on coral reefs. *Marine Ecology Progress Series* **40**, 41-51.

Kluyver, H.N. & Tinbergen, N. (1953) Territory and the regulation of density in titmice. *Arch.neerl Zoology* **10**, 265-287.

Kodric-Brown, A. (1986) Satellites and sneakers: opportunistic male breeding tactics in pupfish (*Cyprinodon pecosensis*) *Behavioural Ecology & Sociobiology* **19**: 425-432.

Kohda, M. (1987) Preliminary report on the intra- and interspecific social interactions among three aufwuchs eating cichlid species. *Ibid* **4**, 22-23.

Kohda, M. (1991) Intra- and interspecific social organization among three herbivorous cichlid fishes in Lake Tanganyika. *Japanese Journal of Ichthyology* **38** (2), 147-163.

Konings, A. (1992) *Cichlids and all the other fishes of Lake Malawi.* TFH Publications, Neptune City, New Jersey.

Kornfield, I., Taylor, J.N. & Brown, J.A. (in press) Territoriality and behaviour of *Pseudotropheus zebra* (Cichlidae) in Lake Malawi: Potential for intermale sexual selection. *Copeia.*

Krebs, J.R. (1971) Territory and breeding density in the great tit, *Parus major* L.

Ecology **52**, 2-22.

Krebs, J.R. (1982) Territorial defence in great tits: do residents always win? *Behavioural Ecology & Sociobiology* **4**, 185-194.

Krebs, J.R. & Davies, N.B. (1981) *An introduction to behavioural ecology.* Blackwell, Oxford.

Kuwamara, T. (1987) Male mating territory and sneaking in a maternal mouthbrooder, *Pseudosimochromis curvifrons* (Pisces: cichlidae) *Journal of Ethology* **5**, 203-206.

Kuwamara, T. (1991) Territory structure of *Pseudosimmochromis curvifrons* males in relation to mating and competition with other algal feeders. In Kawanabe, H. & M.Nagoshi (eds) *Ecological and Limnological Study on Lake Tanganyika and its Adjacent Regions.* **VII**, 27-28 pp.

Lack, D. (1954) *The Natural Regulation of Animal Numbers.* Clarendon Press, Oxford. pp.343.

Lack, D. (1964) A long-term study of the great tit (*Parus major*) *Journal of Animal Ecology* **33** (supplement), 159-173.

Lavery, R.J., Mackereth, R.W., Robilliard, D.R.C & Keenleyside, M.H.A. (1990) Factors determining parental preference of convict cichlid fry, *Cichlasoma nigrofasciatum* (Pisces: Cichlidae) *Animal Behaviour* **39** (3) 573-581.

Lavery, R.J. & Colgan, P.W. (1991) Brood age and parental defence in the convict cichlid, *Cichlasoma nigrofasciatum* (Pisces: Cichlidae) *Animal Behaviour* 41 (6), 945-952.

Lewis, D.S.C. (1982) Problems of species definition in Lake Malawi cichlid fishes (Pisces: Cichlidae) *J.L.B.Smith Institute of Ichthyology Special Publication* **23**, 1-5.

Losey, G.S. (1982) Intra- and interspecific aggression by the Central American midas cichlid fish, *Cichlasoma citrinellum. Behaviour* **79**, 39-80.

Low, R.M. (1971) Interspecific territoriality in a pomacentrid reef fish, *Pomacentrus flavicauda* Whitley. *Ecology* **52**, 648-654.

Lowe-McConnell, R.H. (1979) Ecological aspects of seasonality in fishes of tropical

waters. *Symposia of the Zoological Society of London* **44**, 219-241.

Lowe-McConnell, R.H. (1987) *Ecological studies in tropical fish communities.* Cambridge University Press, Cambridge.

Magnhagen, C. (1994) Sneak or challenge: alternative spawning tactics in non-territorial male common gobies. *Animal Behaviour* **47** (5), 1212-1215.

Magurran, A.E. (1994) Individual differences and alternative behaviours. In T.J.Pitcher (ed) *Behaviour of teleost fishes.* 2nd edn. Chapman & Hall, London. pp. 441-477.

Malmquist, B. (1983) Breeding behaviour of brook lampreys *Lampetra planeri:* experiments on mate choice. *Oikos* **41,** 143-148.

Marsh, A.C. (1981) *A contribution to the ecology and systematics of the genus Petrotilapia (Pisces: Cichlidae) in Lake Malawi, Africa.* MSc thesis, Rhodes University, Republic of South Africa.

Marsh, A.C., Ribbink A.J. & Marsh, B.A. (1981) Sibling species complexes in sympatric populations of *Petrotilapia,* Trewavas (Cichlidae, L.Malawi) *Zoological Journal of the Linnean Society* **71,** 253-264.

Marsh, A.C. & Ribbink, A.J. (1985) Feeding site specialization in three sympatric species of *Petrotilapia* from Lake Malawi. *Biological Journal of the Linnean Society* **25**, 331-338.

Marsh, A.C. & Ribbink, A.J. (1986) Feeding schools among L.Malawi cichlid fishes. *Environmental Biology of Fishes* **15**, 75-79.

Marsh, B.A., Marsh, A.C. & Ribbink, A.J. (1986) Reproductive seasonality in a group of rock-frequenting cichlid fishes in Lake Malawi. *Journal of Zoology, London.* (A) **209**: 9-20.

May, R.M. & Harvey, P.H. (1988) Tampering with territories. *Nature* **335,** 668-669.

Maynard Smith, J. & Harper, D.C.G. (1988) The evolution of aggression:can selection generate variabilty? *Philosophical Transactions of the Royal Society, London.* **B 319**, 557-570.

Mayr, E. (1935) Bernard Altum and the territory thoery. *Proceedings of the Linnean Society of New York*, **45 & 46,** 24-38.

Mboko, S.K. (1991) Some notes on the social behaviour of *Telmatochromis bifrenatus* in Lake Tanganyika. In Kawanabe, H. & M.Nagoshi (eds) *Ecological and Limnological Study on Lake Tanganyika and its Adjacent Regions* **VII,** 89 pp.

McElroy, D.M. & Kornfield, I (1990) Sexual selection, reproductive behaviour, and speciation in the mbuna species flock of Lake Malawi (Pisces: Cichlidae) *Environmental Biology of Fishes* **28**, 285-294.

McFarland, W.N. & Kotchian, N.M. (1982) Interaction between schools of fish and mysids. *Behavioural Ecology and Sociobiology* **11**, 71-76.

McKaye, K.R. (1977) Competition for breeding sites in the cichlid fishes of L.Jiloa, Nicaragua. *Ecology* **58,** 291-302.

McKaye, K.R. (1983) Ecology and breeding behaviour of a cichlid fish *Cyrtocara eucinostomus,* on a large lek in L.Malawi, Africa. *Environmental Biology of Fishes* **8**, 81-96.

McKaye, K.R. (1984) Behavioural aspects of cichlid reproductive strategies: patterns of territoriality and brood defence in Central American substratum spawners and African mouthbrooders., In G.W. Potts & R.J.Wootton (eds) *Fish reproduction: Strategies and tactics.* Academic Press (London)

McKaye, K.R. (1991) Sexual selection and the evolution of the cichlid fishes of Lake Malawi, Africa. In M.H.A.Keenleyside (ed) *Cichlid fishes: behaviour, ecology and evolution.* Chapman & Hall, London. 241-257 pp. mate ch

McKaye, K.R. & McKaye, N.M. (1977) Communal care and kidnapping of young by parental cichlids. *Evolution* **31**, 674-681.

McKaye, K.R. & MacKenzie, C. (1982) *Cyrtocara liemi*: a previously undescribed paedophagous cichlid fish (Teleostei, cichlidae) from Lake Malawi, Africa. *Proceedings of the Biological Soceity of Washington* **95** (2), 3398-402.

McKaye, K.R., Kocher, T.D., Reinthal, P.N. & Kornfield, I. (1982b) A sympatric sibling species complex of *Petrotilapia* Trewavas from Lake Malawi analyzed by enzyme electrophoresis (Pisces, Cichlidae) *Zoological Journal of the Linnean Society* **76,** 91-96.

McKaye, K.R. & Kocher, T. (1983) Head ramming behaviour by three paedophagous cichlids of Lake Malawi, Africa. *Animal Behaviour* **31**, 206-210.

McKaye, K.R., Kocher, T., Reinthal, P.N., Harrison, R. & Kornfield, I. (1981) Genetic evidence for allopatric and sympatric differentiation among colour morphs of a Lake Malawi cichlid fish. *Evolution* **38,** 215-219.

McKaye, K.R., Louda, S.M. & Stauffer, J.R. (1990) Bower size and male reproductive success in a cichlid fish lek. *American Naturalist* **135,** 597-613.

McLaren, W.D. (1972) Further data on interspecific competition at a joint bufflehead-goldeneye nest site. *Canadian Field Naturalist* **83**, 59-60.

McNicol, R. G. & Noakes, D. L. G. (1984) Environmental influences on territoriality of juvenile brook char *Salvelinus fontinalis* in a stream environment. *Environmental Biology of Fishes* **10**, 29-42.

Meral, G.H. (1973) *The adaptive significance of territoriality in New World Cichlidae.* PhD thesis. University of California, Berkeley.

Metcalfe, N.B.(1986) Intraspecific variation in competitive ability and food intake in salmonids: consequences for energy budgets and growth rates. *Journal of Fish Biology* **28,** 525-531.

Metcalfe, N.B., Wright, P.J. & Thorpe, J.E. (1992) Relationship between social status, otolith size at first feeding and subsequent growth in Atlantic salmon (*Salmo salar* L.) *Journal of Animal Ecology* **61, 585-589.**

Meyer, A. (1993) Phylogenetic relationships and evolutionary processes in east African cichlid fishes. *Trends in Ecology and Evolution* **8,** 279-284.

Meyer, A., Kocher, T.D. & Wilson, A.C. (1989) Speciation rates and evolutionary relationships of East African cichlid fishes inferred from mt-DNA sequences. *American Zoologist* **29 A,** 32.

Michener, G.R. (1979) Spatial relationships and social organisation of adult Richardsons ground squirrels. *Canadian Journal of Zoology* **57,** 125-139.

Milinski, M. & Parker, G.A. (1991) Competition for resources. In J.R.Krebs & N.B.Davies (eds) *Behavioural Ecology: An Evolutionary Approach.* 3rd edn. 137-168 pp. Blackwell Scientific Publications, Oxford..

Moffatt, C.B. (1903) *The spring rivalry of birds.* Irish Naturalist 12, 152-166.

Moilanen, A. & Hanski, I. (1995) Habitat destruction and coexistence of competitiors

in a spatially realistic metapopulation model. *Journal of Animal Ecology* **64,** 141-144.

Moran, P. & Kornfield, I. (1993) Retention of an ancestral polymorphism in the mbuna species flock (Telesostei: cichlidae) of Lake Malawi. *Molecular Biology and Evolution* **10,** 1015-1029.

Motta, P.J. (1988) Functional morphology of the feeding apparatus of ten species of Pacific butterflyfishes (Perciformes, Chaetodontidae): An ecomorphological approach. *Environmental Biology of Fishes* **22**, 39-67.

Mrowka, W. (1986) Satiation restores brood care motivation in the female mouthbrooder Pseudocrenilabrus multicolor (Cichlidae) *Physiology and Behaviour* **38,** 153-156.

Mrowka, W. (1987) Brood adoption in a mouthbrooding cichlid fish:experiments and a hypothesis. *Animal Behaviour* **35**, 922-923.

Munthali, S.M. (in press) Territoriality and nutritional condition in *Cynotilapia afra* Gunther and *Pseudotropheus zebra* Boulenger, Cichlidae in Lake Malawi National Park, Malawi. *Journal of Ichthyology.*

Murray, B.G. (1971) The ecological consequence of interspecific territorial behaviour in birds. *Ecology* **52,** 414-423.

Murray, B.G. (1976) A critique of interspecific territoriality and character convergence. *Condor* **78,** 518-525.

Myrberg, A.A., (1966), Parental recognition of young in cichlid fishes. *Animal Behaviour* **14** (4), 565-571.

Myrberg, A.A. & Thresher, R.E. (1974) Interspecific aggression and its relevence to the concept of territoriality in fishes. *American Zoologist* **14,** 81-96.

Nagoshi, M. (1983) Distribution, abundance and parental care of the genus *Lamprologus* (Cichlidae) in Lake Tanganyika. *African study monographs* **3,** 39-47.

Nee, S. & May, R.M. (1992) Dynamics of metapopulations: habitat destruction and competitive coexistence. *Journal of Animal Ecology* **61,** 37-40.

Neil, S.J. (1984) Field studies on the behavioural ecology and agonistic behaviour of

Cichlasoma meeki (Pisces: Cichlidae) *Environmental Biology of Fishes* **10,** 59-68.

Nelissen, M., (1985) Structure of the dominance hierarchy and dominance determining 'group factors' in *Melanochromis auratus* (Pisces , Cichlidae) *Behaviour* **94**, 85-107.

Nelson, J.S. (1976) *Fishes of the world.* Wiley Inter-Science. New York 416 pp.

Nelson, D.R. (1981) Aggression in sharks: is the grey reef shark different? *Oceanus* **24**, 45-55

Nice, M.M., (1937) Studies in the life history of the song sparrow I. *Transactions of the Linnean Society fo New York* **4,** 57-83.

Nice, M.M. (1941) The role of territory in bird life. *American Midland Naturalist* **26,** 441-487.

Noakes, D.L.G. & Barlow, G.W. (1973) Cross-fostering and parent -offspring responses in *Cichlasoma citrinellum* (Pisces, cichlidae) *Zeitschrift fur Tierpsychologie* **33,** 147-152.

Noble, G.K. (1938) Sexual selection among fishes. *Biological Reviews* **13,** 133-158.

Noble, G.K. (1939) The role of dominance in the social life of birds. *Auk* **56,** 263-273.

Norton, M.E., Arcese, P., & Ewald, P.W. (1982) Effect of intrusion pressure on territory size in black-chinned hummingbirds (*Archilochus alexandri*) *Auk* **99**, 761-764.

Ochi, H. (1993) Maintenance of separate territories for mating and feeding by males of a maternal mouthbrooding cichlid, *Gnathochromis pfefferi*, in Lake Tanganyika. *Japanese Journal of Ichthyology* **40,**(2), 173-182.

Ogden, J.C. & Buckman, N.S. (1973) Movements, foraging groups, and diurnal migrations of the striped parrotfish *Scarus croicensis* Bloch (Scaridae) *Ecology* **54,** 589-596.

Orians, G.H. (1969) On the evolution of mating systems in birds and mammals. *American Naturalist* **103,** 589-603.

Orians, G.H. (1971) Ecological aspects of behaviour. In D.S. Farner & J.R. King (eds) *Avian Biology* **1,** 513-546. Academic Press, New York. 586 pp.

Orians, G.H. & Wilson, M.F. (1964) Interspecific territories in birds. *Ecology* **45,** 736-745.

Parker, G.A., & Knowlton, N. (1980) The evolution of territory size- some ESS models. *Journal of Theoretical Biology* **84,** 445-476.

Paterson, H.E.H. (1993) Animal species and sexual selection. pp.209-228 in D.R.Lees & D.Edwards (eds) *Evolutionary patterns and processes.* Academic press, London.

Patterson, I.J. (1980) Territorial behaviour and the limitation of population density. *Ardea* **68,** 53-62.

Patterson, I.J. (1985) Limitation of breeding density through territorial behaviour: experiments with convict cichlids, *Cichlasoma nigrofasciatum.* In R.M.Sibly & R.H.Smith (eds) *Behavioural Ecology,* Blackwell Scientific Publications, Oxford pp. 393-407.

Pelkwijk, J.J. ter, & Tinbergen, N. (1937) Eine reizbiologische Analyse einiger Verhaltensweisen von *Gasterosteus aculeatus* L. *Zeitschrift fur Tierpsychologie* **1,** 193-200.

Perrone, M. & Zaret, T.M., 1979, Parental care patterns of fishes. *American Naturalist* **113**(3), 351-363.

Pitcher, T.J. & Hart, P.J.B. (1982) *Fisheries Ecology.* Croom Helm, London.

Pitcher, T.J. & Parrish, J.K. (1994) Functions of shoaling behaviour in teleosts. in T.J.Pitcher (ed) *Behaviour in teleost fishes.* 2nd edn. pp. 363-439. Chapman & Hall, London.

Porter, J,M, (1988) Prerequisites of recruitment of kittiwakes *Rissa tridactyla. ibis* **130,** 204-215.

Potts, G.W. (1984) Parental behaviour in temperate marine teleosts with special reference to the development of nest structures. In G.W.Potts & R.J.Wootton (eds) *Fish Reproduction: Strategies and Tactics.* Academic Press, London. pp.223-244.

Raadik, T.A., Bourke, D.W., Clarke, M.F. & Martin, A.A. (1990) Behaviour and reproductive success of pairs and lone parents in the convict cichlid, *Heros nigrofasciatus. Animal Behaviour* **39** (3), 594-595.

Rangely, R.W. & Godin, J-G. J. (1992) The effects of a trade-off between foraging and brood defence on parental behaviour in the convict cichlid fish, *Cichlasoma nigrofasciatum. Behaviour* **120,** 1-2.

Reese, E.S. (1975) A comparative field study of the social behaviour and related ecology of reef fishes of the family Chaetodontidae. *Zeitschrift fur Tierpsychologie* **37,** 937-948.

Regan, C.T. (1921) The cichlid fishes of Lake Nyasa. *Proceedings of the Royal Society, London* 1921, 675-727.

Reinthal, P.N. (1990) The feeding habits of a group of herbivorous rock-dwelling cichlid fishes (Cichlidae:Perciformes) from Lake Malawi, Africa. *Environmental Biology of Fishes* **27**, 215-233.

Reinthal, P.N. & Lewis, S.M. (1986) Social behaviour, foraging efficiency and habitat utilization in a group of tropical herbivorous fish. *Animal Behaviour* **34**, 1687-1693.

Reynolds, J.D. & Gross, M.R. (1992) Female mate preference enhances offspring growth and reproduction in a fish, *Poecilia reticulata. Proceedings of the Royal Society of London* **B 250**, 57-62.

Ribbink, A.J., (1971) The behaviour of *Hemihaplochromis philander,* a South African cichlid fish. *Zoologica Africana* **6** (2), 263-288.

Ribbink, A.J., (1977) Cuckoo among Lake malawi cichlid fish. *Nature* **267,** 243-244.

Ribbink, A.J., (1986) The species concept, sibling species and speciation. *Annals of the Musee Royal de L'Afrique Centrale, Tervuren* **251**, 109-116.

Ribbink, A.J., (1990) Alternative life-history styles of some African cichlid fishes. *Environmental Biology of Fishes* **28,** 87-100.

Ribbink, A.J. (1994) Biodiversity and speciation of freshwater fishes with particular reference to African cichlids. In P.S.Giller, A.G.Hildrew and D.G.Raffaelli (eds) *Aquatic ecology: scale, pattern and process.* Blackwell.

Ribbink, A.J., Marsh, A.C., Marsh, B. & Sharp, B.J. (1980) Parental behaviour and mixed broods among cichlid fish of Lake Malawi. *South African Journal of Zoology* **15** (1) 1-6.

Ribbink, A.J., Marsh, B.A., Marsh, A C., Ribbink, A.C. & Sharp, B.J. (1983a) A preliminary survey of the cichlid fishes of rocky habitats in Lake Malawi. *South African Journal of Zoology* **18** (3) 155-309.

Ribbink, A.J., Marsh, A.C., Marsh, B.A. & Sharp, B.B. (1983b) The zoogeography, ecology and taxonomy of the genus *Labeotropheus* Ahl, 1927, of Lake Malawi (Pisces: cichlidae) *Zoological Journal of the Linnean Society* **79,** 223-243.

Robertson, D.R., Sweatman, H.P.A., Fletcher, E.A. & Cleland, M.G. (1976) Schooling as a mechanism for circumventing the territoriality of competitors. *Ecology* **57,**1208-1220.

Robertson, D.R., & Sheldon, J.M. (1979) Competitive interactions and the availability of sleeping sites for a diurnal coral reef fish. *Journal of Experimental Marine Biology & Ecology* **40,** 285-298.

Robertson, D.R., & Polunin, N.V.C. (1981) Coexistence: symbiotic sharing of feeding territories and algal food by some coral reef fishes from the western Indian *Oceanography & Marine Biology* **62,**185-195.

Robertson, D.R. & Gaines, S.D. (1986) Interference competition structures habitat use in a local assemblage of coral reef surgeon fishes. *Ecology* **67,** 1372-1383.

Robinson, S.K. & Terburgh, J. (1995) Interspecific aggression and habitat selection by Amazonian birds. *Journal of Animal Ecology* **64,** 1-11.

Robinson, R.L. & Turner, G.F. (1990) Comparison of the social behaviour of an endemic Lake Malawi cichlid in the field and laboratory *Journal of Fish Biology.* **36,** 615-616.

Rogers, W. (1988) Parental investment and division of labor in the midas cichlid (*Cichlasoma citrinellum*) *Ethology* **79,** 126-142.

Rowland, W. J. (1989) The effect of body size, aggression and nuptial colouration on competition for territories in male three-spined sticklebacks, *Gasterosteus aculeatus. Animal Behaviour* **37,** 282-289.

Russ, G.R. (1987) Is the rate of removal of algae by grazers reduced inside territories of tropical damselfishes? *Journal of Experimental Marine Biology and Ecology* **110,** 1-17.

Russock, M. (1986) Preferential behaviour of *Sarotherodon (Oreochromis) mossambicus* (Pisces: cichlidae) fry to maternal models and its relevance to the concept of imprinting. *Behaviour* **96** (3/4) : 304-321.

Ryan, M.J. (1990) Signals, species and sexual selection. *American Science* **78,** 46-52.

Sale, P.F. (1977) Maintenance of high diversity in coral reef fish communities. *American Naturalist* **111,**337-359.

Sale, P.F. (1978) Coexistence of coral reef fishes- a lottery for living space. *Environmental Biology of Fishes* **3,** 85-102.

Sale, P.F. (1980) The ecology of fishes on coral reefs. *Oceanography and Marine Biology* **18,** 367-421.

Sale, P.F. (1991) *The ecology of fishes on coral reefs.* Academic Press.

Sargent, R. C. (1981) *Sexual selection and reproductive effort in the stickleback, Gasterosteus aculeatus.* Unpublished PhD dissertation, SUNY, Stony Brook.

Sargent, R. C. (1988) Parental care and egg survival both increase with clutch size in the fathead minnow, *Pimephales promelas. Behavioural Ecology and Sociobiology* **23**, 33-38.

Sargent, R.C. (1990) Behavioural and evolutionary ecology in fishes: conflicting demands during the breeding season. *Ann. Zool. Fenni.*, **27,** 101-118.

Sargent, R. C. & Gebler, J. B. (1980) Effects of nest concealment on hatching success, reproductive success, and parental behaviour of the threespine stickleback, *Gasterosteus aculeatus. Behavioural Ecology and Sociobiology* **71**, 137-142.

Sargent, R.C. & Gross, M.R. (1983) Parental investment decision rules and the concorde fallacy. *Behavioural Ecology and Sociobiology* **17,** 43-45.

Sato, T. (1994) Active accumulation of spawning substrate: a determinant of extreme polygyny in a shell-brooding cichlid fish. *Animal Behaviour*, **48**, 669-678.

Shapiro, A.M.(1975) The temporal component of butterfly species diversity. In M.L.Cody & J.M.Diamond (eds) *Ecology and evolution of communities.* 187 pp. Belknap Press, Harvard University Press, Cambridge.

Shapiro, D.Y. (1989) Inapplicability of the size-advantage model to coral reef fishes., *Trends in Ecology and Evolution* **4** (9) : 272-273.

Sharp, B.J. (1981) *An ecological study of territoriality in four cichlid species resident on rocky shores near Monkey Bay, Lake Malawi.* MSc thesis, Rhodes University, Republic of South Africa.

Sibly, R.M., & Smith, R.H. (1985) Behavioural ecology and population dynamics: towards a synthesis. In R.M.Sibly & R.H.Smith (eds) *Behavioural Ecology*. Blackwell Scientific Publications, Oxford. pp. 577-591.

Sigurjonsdottir, H. & Gunnarsson, K. (1989) Alternative mating tactics of arctic charr, *Salvelinus alpinus*, in Thingvallavatn, Iceland. *Environmental Biology of Fishes* **26**, 159-176.

Slaney, P.A. & Northcote, T.G. (1974) Effects of prey abundance on density and territorial behaviour of young rainbow trout (*Salmo gairdneri*) in laboratory stream channels. *Journal of the Fisheries Research Board of Canada* **31,** 1201-1209.

Smith, S.M. (1978) The underworld in a territorial sparrow: adaptive strategy for floaters. *American Naturalist* **113,** 571-582.

Smith, C. & Wootton, R.J. (in press) The cost of parental care in teleost fishes. *Reviews in Fish Biology & Fisheries.*

Stacey, P.B., & Chiszar, D. (1978) Body colour pattern and aggressive behaviour of male pumpkinseed sunfish (*Lepomis gibbosus*) *Behaviour* **64**, 271-304.

Stanley, B.V. (1983) *Effect of food supply on reproductive behaviour of male Gasterosteus aculeatus,* PhD thesis, University of Wales.

Stanley, B.V. & Wootton, R.J. (1986) Effects of ration and male density on the territoriality and nest-building of male three-spined sticklebacks (*Gasterosteus aculeatus* L.) *Animal Behaviour* **34**, 527-535.

Stauffer, J.R (1993) A new species of *Protomelas* (Teleostei: Cichlidae) from Lake Malawi, Africa. *Ichthyological Exploration of Freshwaters* **4** (4), 343-350.

Stauffer, J.R. & McKaye, K.R. (1986) Description of a paedophagous deepwater cichlid (Teleostei, Cichlidae) from Lake Malawi, Africa. *Proceedings of the Biological Society of Washington* **9**, 29-33.

Stauffer, J.R. & Hert, E, (1992) *Pseudotropheus callanois*, a new species of mbuna (Cichlidae), with analyses of changes associated with two intra-lacustrine

transplantations in Lake Malawi, Africa. *Ichthyological Exploration of Freshwaters* **3,**, 253-264.

Stokes, A.W. (1974) Territory. *Benchmark Papers in Animal Behaviour, 2.* Dowden, Hutchinson & Ross Inc., Stroudsberg, Pennsylvania.

Sutherland, W.A., & Parker, G.A. (1985) Distribution of unequal competitors. In R.M.Sibly & R.H.Smith (eds) *Behavioural Ecology.* Blackwell Scientific Publications, Oxford. pp.255-273.

Taborsky, M. & Limberger, D. (1981) Helpers in fish. *Behavioural Ecology and Sociobiology* **8,** 143-145.

Taborsky, M. (1984) Broodcare helpers in the cichlid fish *Lamprologus brichardi:* their costs and benefits. *Animal Behaviour* **32,** 1236-1252.

Taborsky, M. (1985) Breeder-helper conflict in a cichlid fish with broodcare helpers: an experimental analysis. *Behaviour* **95,** (1/2) : 45-75.

Taborsky, M. Hert, E. Siemens, M. & Stoerig, P. (1986) Social behaviour in *Lamprologous* species: functions and mechanisms. *Annals Musee Royal de L'Afrique Centrale, Tervuren* **251,** 7-11.

Taborsky, M., Hudde, B. & Wirtz, P. (1987) Reproductive behaviour and ecology of *Symphodus (Crenilabrus) ocellatus.* A European wrasse with four types of male behaviour. *Behaviour* **102** (1/2), 82-118.

Takamura, K. (1983) Interspecific relationship between two aufwuchs eaters *Petrochromis polyodon* and *Tropheus moorii* (Pisces, Cichlidae) of Lake Tanganyika, with a discussion on the evolution and functions of a symbiotic relationship. *Physiological Ecology of Japan* **20,** 59-69.

Thresher, R.E. (1976) Field analysis of the territoriality of the threespot damselfish, *Eupomacentrus planifrons* (Pomacentridae) *Copeia*, 266-276.

Thresher, R.E. (1978) Territoriality and aggression in the threespot damselfish (Pisces ,Pomacentridae): an experimental study of causation. *Zeitschrift fur Tierpsychologie* **46**, 401-434.

Thresher, R.E. (1979) Social behaviour and ecology of two sympatric wrasses (Labridae: *Halichoeres* spp.) off the coast of Florida. *Marine Biology* **53,** 161-172.

Thresher, R.E. (1983) Habitat effects on reproductive success in the coral reef fish, *Acanthochromis polyacanthus* (Pomacentridae) *Ecology* **66,** 1139-1150.

Thresher, R.E. (1984) *Reproduction in reef fishes.* Neptune, N.J.:TFH Publications.

Tinbergen, N. (1939) Field observations of East Greenland birds. II. The behaviour of the snow bunting (*Plectrophenax nivalis subnivalis* (Brehm)) in spring. *Transactions of the Linnean Society of New York* **5,** 1-94.

Tooker, C.P & Miller, R.J. (1980) The ontogeny of agonistic behaviour in the blue gourami *(Trichogaster trichogaster) Animal Behaviour* **28,** 973-988.

Townsend, T.J. & Wootton, R.J. (1985a) Effects of food supply on the reproduction of the convict cichlid, *Cichlasoma nigrofasciatum. Journal of Fish Biology* **2,** 91-104.

Townsend , T.J. & Wootton, R.J. (1985b) Adjusting parental investment to changing environmental conditions: the effect of food ration on parental behaviour of the convict cichlid, *Cichlasoma nigrofasciatum, Animal Behaviour* **33**, 494-501.

Trendall, J. (1988) Recruitment of juvenile mbuna (Pisces: Cichlidae) to experimental rock shelters in Lake Malawi, Africa. *Environmental Biology of Fishes* **22**, 117-131.

Trewavas, E. (1935) A synopsis of the cichlid fishes of Lake Nyasa. *Annals and Magazine of the Natural History Service* **10**(16), 65-118.

Trewavas, E. (1983) *Tilapiine fishes of the genera Sarotherodon, Oreochromis and Danakilia.* British Museum (Natural History), London.

Tricas, T.C. (1985) The economics of foraging in coral-feeding butterflyfishes of Hawaii. *Proceedings of the 5th International Coral Reef Congress* **5,** 409-414.

Tricas, T.C. (1986) *Life history, foraging ecology, and territorial behaviour of the Hawaiian butterflyfish, Chaetodon multicinctus.* PhD thesis, University of Hawaii.

Tricas, T.C. (1989) Determinants of feeding territory size in the corallivorous butterflyfish, *Chaetodon multicinctus. Animal Behaviour* **37**, 830-841.

Trivers, R.L. (1972) Parental investment and sexual selection. In B.Campbell (ed) *Sexual selection and the descent of man.* pp. 136-176. London: Heinemann.

Turner, G.F. (1986a) Teleost mating systems and strategies, in T.J.Pitcher (ed) *Behaviour in teleost fishes*, pp. 253-274. Chapman & Hall. London.

Turner, G.F. (1986b) Territory dynamics and the cost of reproduction in a captive population of the colonial nesting mouthbrooder *Oreochromis mossambicus* (Peters) Journal of Fish Biology **29**, 573-587.

Turner, G.F. (1993) Teleost mating behaviour.In T.J.Pitcher (ed) *Behaviour of Teleost Fishes, 2nd edn.* Chapman & Hall. pp.307-332.

Turner, G.F. (1994a) Speciation mechanisms in Lake Malawi cichlids: a critical review. *Advances in Limnology* **44,** 139-160.

Turner, G.F. (1994b) The fighting tactics of male mouthbrooding cichlids: the effects of size & residency. *Animal Behaviour* **47**, 655-662.

Turner, G.F. (1994c) A description of a commercially important new pelagic species of the genus *Diplotaxodon* (Pisces: Cichlidae) from Lake Malawi, Africa. *Journal of Fish Biology.* **44**, 799-807.

Turner, G.F. & Huntingford, F.A. (1986) A problem for game theory analysis: assessment and intention in male mouthbrooder contests. *Animal Behaviour* **34**, 961-970.

Turner, G.F. & Falter, U. (1989) On the adoption of "male typical" colouration by female mouthbrooding cichlids. *Journal of Fish Biology* **34,** 805-806.

Turner, G.F. & Robinson, R.L. (1991) Ecology, morphology and taxonomy of the Lake Malawi Oreochromis (Nyasalapia) species flock. *Annals Musee Royal de l'Afrique Centrale, Tervuren* **262,** 23-28.

Turner, G.F., Grimm, A.S., Mhone, O.K., Robinson, R.L. & Pitcher, T.J. (1991) The diet of *Oreochromis lidole* (Trewavas) and other chambo species in Lakes Malawi & Malombe. *Journal of Fish Biology* **39,** 15-24.

Turner, G.F. & Mwanyama, N.C. (1992) Distribution and biology of chambo (*Oreochromis* spp.) in Lakes Malawi and Malombe. FI:DP/MLW/86/013. Field Document 21. 23pp

Unger, L. M. (1983) Nest defence by deceit in the fathead minnow, *Pimephales promelas. Behavioural Ecology and Sociobiology* **13**, 125-130.

Unger, L. M. & Sargent, R. C. (1988) Allopaternal care in the fathead minnow,

Pimephales promelas: females prefer males with eggs. *Behavioural Ecology and Sociobiology* **23**, 27-32.

Vine, P.J. (1974) Effecs of algal grazing and aggressive behaviour of the fishes *Pomacentrus lividus* and *Acanthurus sohal* on coral reef ecology. *Marine Biology* **24,** 131-136.

Vives, S.P. (1988) Parent choice by larval convict cichlids, *Cichlasoma nigrofasciatum* (Pisces: Cichlidae) *Animal Behaviour* **36,** 11-19.

Ward, J.A. & Wyman, R.L. (1977) Ethology and ecology of cichlid fishes of the genus *Etroplus* in Sri Lanka: preliminary findings. *Environmental Biology of Fishes* **2,** 137-145.

Ward, J.A. & Samarakoon, J.I. (1981) Reproductive tactics of the Asian cichlids of the genus *Etroplus* in Sri Lanka. *Environmental Biology of Fishes* **6**(1) 95-103.

Warner, R.R. (1982) Mating systems, sex change and sexual demography in the rainbow wrasse, *Thalassoma lucasanum. Copeia* 653-661.

Warner, R.R. (1987) Female choice of sites versus mates in a coral reef fish, *Thalassoma bifasciatum. Animal Behaviour* **35**, 1470-1478.

Warner, R.R. (1988) Traditionality of mating site-preferences in a coral reef fish. *Nature* **335,** 719-721.

Warner, R.R. (1990) Resource assessment versus traditionality in mating site determination. *American Naturalist* **135,** 205-217.

Warner, R.R. & Downs, I.F. (1977) Comparative life histories: growth vs. reproduction in normal males and sex-changing hermaphrodites of the striped parrotfish, *Scarus croicensis, Proceedings of the Third International Coral Reef Symposium*, 275-281.

Warner, R.R. & Hoffman, S.G. (1980) Population density and the economics of territory defence in a coral reef fish. *Ecology* **61,** 772-780.

Wegge, P. & Larson, B.B. (1987) Spacing of adult and subadult male common capercaillie during the breeding season. *Auk* **104,** 481-490.

Williams, G.C. (1966a) Natural selection, the costs of reproductopn and a refinement of Lack's principle. *American Naturalist* **100**, 687-690.

Williams, G.C. (1966b) *Adaptation and natural selection.* Princeton University Press, Princeton, New Jersey, 308 pp.

Wilson, E.O. (1975) *Sociobiology- The new synthesis*, Harvard University Press.

Winn, H.E. (1954) Comparative reproductive behaviour of 14 species of darter. *Ecological monographs* **28**, 151-191.

Winn, H.E., Marshall, J.A.& Hazlett, B. (1964) Behaviour, diel activities and stimuli that elicit sound production and reactions to sounds in the longspine squirrelfish. *Copeia* 413-425.

Wootton, R. J. (1990) *The Ecology of Teleost Fishes.* Chapman & Hall, London.

Wyman, R.L. & Ward, J.A. (1973) The development of behaviour in the cichlid fish *Etroplus maculatus* (Bloch) *Zeitschrift fur Tierpsychologie* **33,** 461-491.

Wynne-Edwards, V.C. (1962) *Animal dispersion in relation to social behaviour.* Edinburgh: Oliver & Boyd.

Yanagisawa, Y. & Nshombo, M. (1983) Reproduction and parental care of the scale-eating cichlid fish *Perissodus microlepis* in Lake Tanganyika. *Physiological Ecology of Japan* **20,** 23-31.

Yanagisawa, Y. & Ochi, H. (1986) Step-fathering in the anemonefish *Amphiprion clarkii*: a removal study. *Animal Behaviour* **35,** 1769-1780.

Zack, S. (1990) Coupling delayed breeding with short-distance dispersal in cooperatively breeding birds. *Ethology* **86,** 265-286.

Zack, S. (1991) Manipulating dispersal options in cooperatively breeding birds: can stripe-backed wrens count and divide? *Acta XX International Ornithological Congress,* 1301-1308.

Zack, S. & Rabenold, K.N. (1989) Assessment, age and proximity in dispersal contests among cooperative wrens: field experiments. *Animal Behaviour* **38**, 235-247.

Zack, S. & Stutchbury, B.J. (1993) Delayed breeding in avian social systems: the role of territory quality and "floater" tactics. *Behaviour* 194-219.

Zumpe, D. (1965) Laboratory observations on the aggressive behaviour of some butterfly fishes (Chaetodontidae) *Zeitschrift für Tierpsychologie* **22**, 226-236.

APPENDIX 1: SPECIES IN THE STUDY AREA.

NB: [M] = mbuna, * = non-cichlid species

	SPECIES	Illustration	AUTHORITY
	*Aethiomastecembalus shiranus**		(Günther, 1896)
	*Anguilla bengalensis labiata**		Peters, 1852
	*Aplocheilichthys johnstoni**		Günther, 1893
	Astatotilapia calliptera		(Günther, 1893)
	Aulonocara sp.		Regan, 1921
	*Bagrus meridionalis**		Günther, 1893
	*Barbus arcislongae**		Keilhack, 1908
	*Barbus johnstonii**		Boulenger, 1907
	Buccochromis heterotaenia		(Trewavas, 1935)
	Champsochromis spilorhynchus		(Regan, 1922)
	Cheilochromis euchilus		(Trewavas, 1935)
	*Clarias gariepinus**		Burchell, 1822
	Copadichromis cf. azureus	Fig, 8.2‡	see Konings 1990
	Copadichromis "blue streamer"	Fig. 8.3‡	undescribed
	Copadichromis borleyi		(Iles, 1960)
	Copadichromis chrysonotus		(Boulenger, 1908)
	Copadichromis eucinostomus		(Regan, 1922)
	Copadichromis "*eucinostomus* big blue"		undescribed
	Copadichromis "*eucinostomus* big spot"		undescribed
	Copadichromis cf. prostoma	Fig, 8.8‡	(Trewavas, 1935)
	Copadichromis jacksoni		(Iles, 1961)
	Ctenopharynx cf. intermedius	Fig, 8.4‡	(Günther, 1864)
	Ctenopharynx pictus		(Trewavas, 1935)
	Dimidiochromis compressiceps		(Boulenger, 1908)
	Dimidioochromis kiwinge		(Ahl, 1927)
	Dimidioochromis strigatus		(Regan, 1922)
	*Engraulicypris sardella**		(Günther, 1868)
	Genyochromis mento		Trewavas, 1935
	Hemitaeniochromis urotaenia		(Regan, 1922)
	*Labeo cylindricus**		Peters, 1852
	Lethrinops sp.		undetermined
[M]	*Labeotropheus fuelleborni*		Ahl, 1927
[M]	*Labidochromis vellicans*		Trewavas, 1935
	Lichnochromis acuticeps		Trewavas, 1935
[M]	*Melanochromis melanopterus*		Trewavas, 1935
[M]	*Melanochromis auratus*		(Boulenger, 1899)
[M]	*Melanochromis heterochromis*		Bowers & Stauffer, 1993
	*Mormyrops deliciosus**		(Leach, 1818)
	Mylochromis anaphyrmus		(Burgess & Axelrod, 1973)
	Nimbochromis linni		(Burgess & Axelrod, 1975)
	Nimbochromis livingstoni		(Günther, 1893)
	Nimbochromis polystigma		(Regan, 1922)
	Nyassachromis cf. breviceps	Fig, 8.5‡	(Regan, 1922)
	Nyassachromis nigritaeniatus		(Trewavas, 1935)
	Nyassachromis prostoma		(Trewavas, 1935)
	Oreochromis karongae		(Trewavas, 1941)
	Oreochromis lidole		(Trewavas, 1941)
	Oreochromis squamipinnis		(Günther, 1864)
	Otopharynx sp. 'heterodon Nankhumba'	Fig, 8.6‡	see Konings, 1990
	Otopharynx lithobates		(Oliver, 1989)

[M]	*Petrotilapia genalutea*		Marsh, 1983
[M]	*Petrotilapia nigra*		Marsh, 1983
[M]	*Petrotilapia tridentiger*		Trewavas, 1935
	Placidochromis johnstoni		(Günther, 1893)
	Protomelas 'broodstealer'		undescribed
	Protomelas fenestratus		(Trewavas, 1935)
	Protomelas insignis		(Trewavas, 1935)
	Protomelas kirkii		(Günther, 1893)
	Protomelas 'spilonotus Likoma'	Fig, 8.7‡	see Konings 1990#
	Protomelas similis		(Regan, 1922)
	Protomelas taeniolatus	Fig, 8.1	(Trewavas, 1935)
[M]	*Pseudotropheus elongatus* sp. 'aggressive'		see Ribbink *et al.*, 1983
[M]	*Pseudotropheus elongatus* sp. 'yellowtail'		see Ribbink *et al.*, 1983
[M]	*Pseudotropheus tropheops* sp. 'broadmouth'		see Ribbink *et al.*, 1983
[M]	*Pseudotropheus tropheops* sp. 'gracilior'		see Ribbink *et al.*, 1983
[M]	*Pseudotropheus tropheops* sp. 'microstoma'		see Ribbink *et al.*, 1983
[M]	*Pseudotropheus tropheops* sp. 'orange-chest'		see Ribbink *et al.*, 1983
[M]	*Pseudotropheus zebra*		(Boulenger, 1899)
	Rhamphochromis spp.		undetermined species
	Serranochromis robustus		(Günther, 1864)
	Taeniochromis holotaenia		(Regan, 1922)
	Taeniolethrinops laticeps		(Trewavas, 1931)
	Tilapia rendalli		(Boulenger, 1896)
	Tyrannochromis macrostoma		(Regan, 1922)

NB: For other species present at Thumbi East but not recorded during this study, see Ribbink *et el.* 1983a, and Konings 1990.

‡ Specimen placed at the JLB Smith Institute of Ichthyology, Grahamstown, S.Africa.

This species may be the same as that described as *P.dejunctus* by Stauffer 1993. It appeared rather similar to *P.taeniolatus* but was usually larger, with male breeding colouration more intensely blue, with a bright yellow gular region. The ground colour of non-breeding fish was less white than that of *P.taeniolatus.*

Figure 8.1. *Protomelas taeniolatus* (Male in breeding dress at spawning site, live fish). Thumbi East Island, Lighthouse Bay, at 3 metres depth. September 1991. Spawning territory: around hollow on outer face of rock (3.5m x 3.5m across, 3m high).

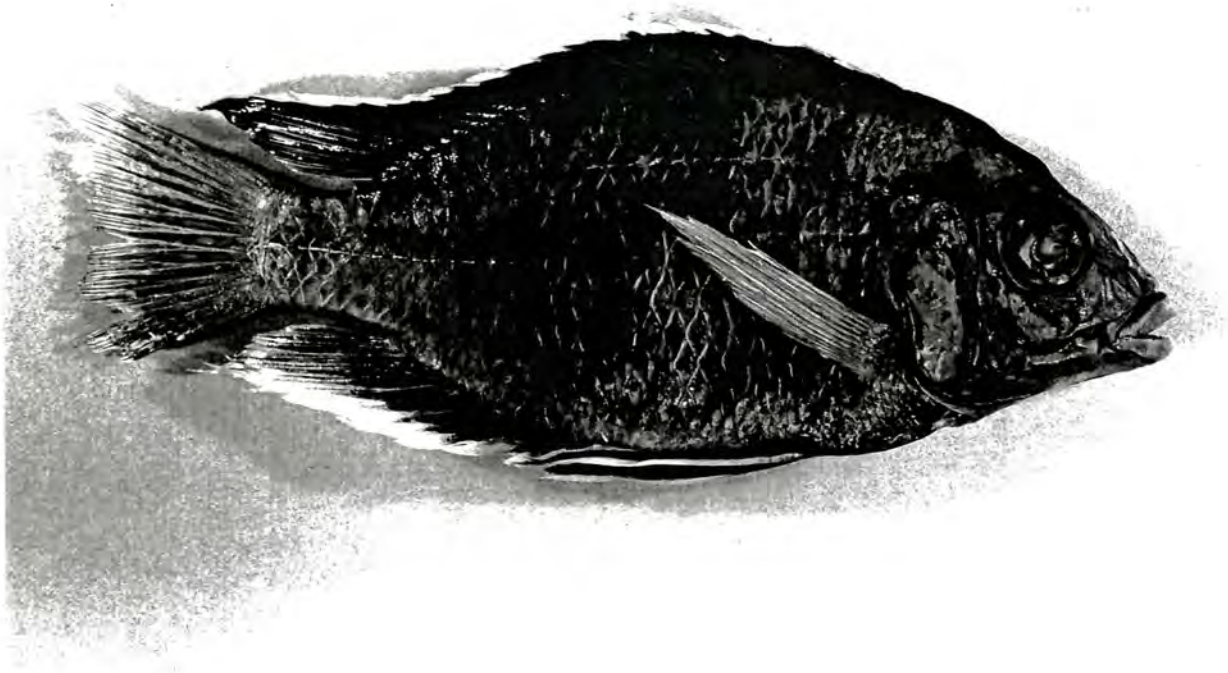
Figure 8.2. *Copadichromis cf. azureus* (Male in breeding dress, freshly caught specimen). Total Length = 122mm. Caught at Thumbi East Island, 100m south of lighthouse, 6m depth. May 1992. Spawning territory: lopsided sand nest, approx. 20cm diameter, adjacent to rock of 20cm diameter, near macrophyte bed. Specimen at JLB Smith Institute of Ichthyology.

Figure 8.3. *Copadichromis* 'bluestreamer' (Male in breeding dress, freshly caught specimen). Total Length = 145mm. Caught at Thumbi East Island, 50m West of Lighthouse Bay, 12m depth. May 1992. Spawning territory: sand deposited on upper, outer hump of a rock, (approx. 2m x 1m across, 1m high). Named after overall blue coloration and long pelvic fins, the tips of which sometimes reach past the posterior insertion of the anal fin. Specimen at JLB Smith Institute of Ichthyology.

Figure 8.4. *Ctenopharynx cf. intermedius* (Male in breeding dress, freshly caught specimen). Total Length = 125mm. Caught at Thumbi East Island, 50m West of lighthouse, 12m depth. May 1992. Spawning territory on rock (2m x 1m across, 1m high), surrounded by sand. Eleven conspecific territorial males on adjacent rocks. Specimen at JLB Smith Institute of Ichthyology.

Figure 8.5. *Nyassachromis cf. breviceps* (Guarding female, freshly caught). Total Length =115mm. Caught at Thumbi East Island, 50m south of lighthouse, 2m depth. May 1992. Fry-guarding territory: on top of rock (3m x 3m across, approx. 2m high). Approx. 60 fry. Specimen at JLB Smith Institute of Ichthyology.

Figure 8.6. *Otopharynx* sp. 'heterodon Nankhumba' (Non-breeding female above T.L. = 82mm, male in breeding dress below, T.L. = 122mm, freshly caught specimens). Caught at Thumbi East Island, Lighthouse Bay, 12m depth. May 1992. Spawning territory: on sand between or under rocks. Fry-guarding territory: on sand or rock, often under rocky overhang. Specimens at JLB Smith Institute of Ichthyology.



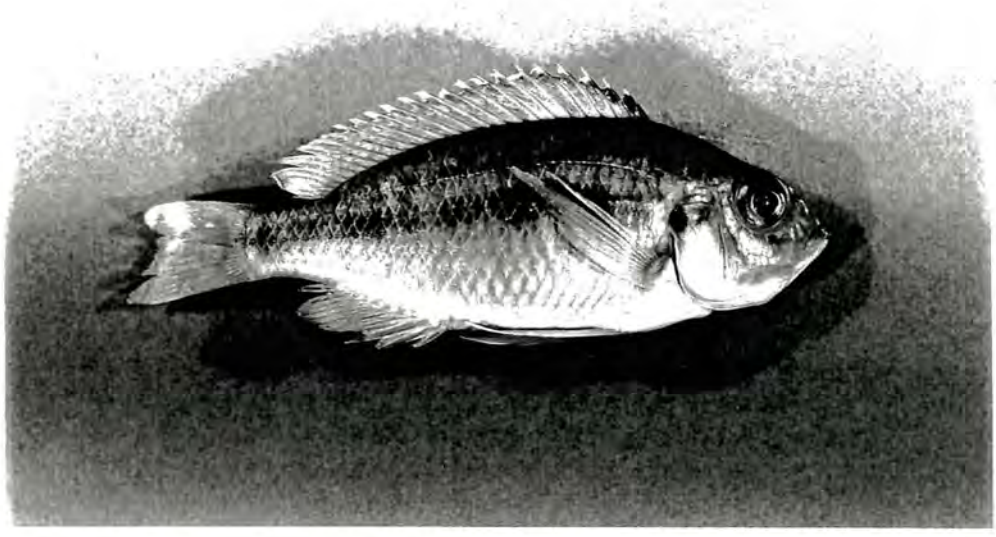


Figure 8.7.(upper): *Protomelas* 'spilonotus Likoma' (Male in breeding dress, preserved specimen). Total Length = 14.6cm. Caught at Thumbi East Island, Lighthouse Bay, 1m depth, August 1991. Territory: between rocks (size 0.5-1m across).

Figure 8.8.(lower): *Copadichromis cf prostoma* (Guarding female, preserved specimen). Total Length = 11.5 cm. Caught at Thumbi East Island, 50m north of lighthouse, 5m depth. September 1991. Fry-guarding territory: on top of rock slab (>10m x 5m).