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Territoriality and the Coexistence between the Introduced and the Native *Mbuna* of the Lake Malaŵi National Park

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Abstract: The rock-dwelling cichlids, mbuna, of the Lake Malaŵi National Park are astoundingly rich and diverse, and globally represent the most splendid examples of adaptive radiation. They include introduced mbuna, endemic to other parts of the lake. The elucidation of factors, which have sustained the coexistence of the native and the introduced species for well over 30 years, has been and continues to be a major challenge to contemporary aquatic ecologists. A study was carried out at Thumbi West Island near Mitande Point (S14′ 01.444; E034′49.380), to examine the extent to which intra-and interspecific rock-size preference, territoriality and feeding site specifity, combined to promote the coexistence of four native species: Labeotropheus fuelleborni, Melanonchromis auratus, Pseudotropheus tropheops "intermediate" and Petrotilapia "mumbo blue", and two introduced species: Metriaclima callinos, and Tropheops sp. "red cheek".

An underwater substrate configuration of an area of 25 m × 5 m was mapped using underwater semi- transparent A_2 graphed tracing films, an A_2 graphed plastic board, and two 1m x 1m steel quadrats with the aid of mask and snorkel, and SCUBA. Mapping of territories relied on marking attack points and outermost points of a foraging territorial fish on an A_2 underwater semi-transparent sheet corresponding to the mapped substrate configuration.

Males and females of both *Pseudotropheus* species defend territories, which do not overlap mostly. Territory characteristics exist among the species. *Tropheops* "intermediate" males and females established territories with dense algal growth; males and females of *Tropheops* "red cheek" the established territories with little algal growth. There were no distinct feeding sites in the territories of the natives, while the territories of the introduced species had distinct feeding sites. Introduced individuals also established larger territories compared to the native species. The mean territory sizes of 0.40 m^2 ± 0.03, n = 72, and 0.17 m^2 ± 0.02, n = 32 for the introduced and the natives respectively, were statistically different (t = 5.2, P >.05). Intraspecific territory sizes were not different. For the introduced species, the mean territory sizes of 0.240 m^2 ± 0.04, n = 24, and 0.40 m^2 ± 0.04, n = 48, for the males and the females respectively, were not statistically different (t = 1.03, P > .05). Similarly, the mean territory sizes of 0.20 m^2± 0.02, n = 18, and 0.25 m^2± 0.02, n = 14, for the males and the females respectively, of the native species were also not statistically different (t = 1.9, p > .05).

Tropheops "intermediate" males established territories used for both feeding and mating. *Tropheops* "intermediate" females established territories, which they used for feeding and brood guarding. *Tropehops* "red cheek" established territories used for feeding only. *Labeotropheus fuelleborni* and most of the male *M. callinos* did not defend territories but established distinct feeding sites. *M. auratus* and *Petrotilapia mumboensis* neither defended territories nor established prominent feeding sites.

The distribution and arrangement of mostly non-overlapping territories and feeding sites suggest spatial segregation, which potentially promotes the coexistence of the introduced and the native species at Thumbi West Island.

Key words: coexistence, resource partitioning, interspecific competition, intraspecific competition, conspecifics, consexual, trophic specialization, food-switching

1. Introduction and Literature Review

1.1 Introduction

Lake Malaŵi (09 30′-14 30′S; 33 52′-35 20′E) is about 2 million years old [1, 2]. The fish faunas of the lake are dominated by the teleost family Cichlidae [3, 4]. Over 450 species have been described with an estimated 850 species inhabiting the lake. Such an explosive speciation and adaptive radiation within a single vertebrate family in such a short geological time scale is astounding, and has consequently attracted considerable ecological, evolutionary, and behavioural research [5].

The littoral zone of the lake supports the most diverse assemblages [6-8]. This zone is predominantly home to small colourful rock-dwelling haplochromine cichlids called mbuna in Chi Tonga. The mbuna comprise greater than 200 species [9], representing an estimated 50% of the described cichlids of Lake Malaŵi.

1.2 Research Justification

In the Lake Malaŵi National Park, over twenty **mbuna** species endemic to other parts of the lake, were introduced [10]. These introductions were a consequence of ornamental fish trade [9]. Fishes from different parts of the lake were brought to Cape Maclear alive for export. Not all the fishes could however be exported. The rest were released alive in the lake locally. While specific locations of releases were not recorded, Mitande Point, at Thumbi West Island, harbours most of the introduced species and is in this regard strongly implicated. The introduced species at Thumbi West Island have coexisted with indigenous species for over 30 years. Although successful impacts of introductions have been reported elsewhere [11], literature is rich with negative impacts caused by introduced species. While a detailed description of these cannot be warranted here due to the wealth of available information, a summary of some impacts has given below to support this case.

There is compelling evidence to show that non-native fishes can modify the behavior of native species, particularly when they are numerically dominant and/or more aggressive than native species resulting in reduced growth of the natives through interspecific competition [12-14]. Secondly, impacts of hybrization have heightened concerns of extinction risk of native species [15-17]. A study by Rosenfield et al. (2004) [18] in North America, showed that hybrids of the native Pecos Pupfish (Cyprinodon pecosensis) and the invasive Sheephead Minnow (Cyprinodon variegatus) were ecologically superior in terms of higher growth and swimming endurance. Hybridization can decrease genetic integrity in native populations through introgression. Muhlfeld et al. (2009) [19] showed that introgression between native Westslope Cutthroat (Oncorhynchus clarki lewisi) and non-native Rainbow Trout (Onchorhynchus mykiss) in Montana decreased fitness of the native species, as inferred from number of offspring per female for Westslope Cutthroat. In Lake Malaŵi, Cynotilapia afra, a species native to the northern shoreline, this was introduced into the southern part of the lake and has hybridized with the native Metriaclima zebra [15, 20].

Other impacts include substantive reduction in native species recruitment [21, 22], transmission of pathogens and/or parasites from non-native species to native species [23], species composition change [24, 25], alteration of food webs [26, 27], ecosystem level modification of biochemical cycles [27-29], modification of energy fluxes between ecosystems [28], and habitat alteration by engineering native species [30-34].

Munthali (1995) [10] studied the impacts of the intralacustrine translocations in a 3-7 m zone of the Lake Malaŵi National Park at Thumbi West Island. It was thought that if the microhabitat requirements of the introduced species overlapped with those of the natives,

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the latter might eventually become excluded due to interference competition. Results of the study, however suggested that although there are microhabitat requirement overlaps, the native species were in no immediate danger of extinction. Since the natives and the introduced fishes have coexisted for over 20 years, and these being intralacustrine introductions, a stable coexistence may well be possible through habitat partitioning. Thumbi West Island has the richest species composition than any other place in Lake Malaŵi [3] and therefore offers a splendid opportunity to study coexistence. With space and food as apparent limiting resources, it has strongly been suggested that finely tuned resource partitioning mechanisms maintain this coexistence [35, 36]. Territoriality is known among fishes as a key to successful breeding as it ensures availability of the key resources such as food and mating sites. It is therefore a key factor in suggesting peaceful or non-peaceful coexistence.

Intra-and interspecific distribution and arrangement of territories and feeding sites

According to Noble 1939 (in Yuma and Kondo, 1997) a territory is a limited area in which a resident species actively defends. Prevailing mechanisms explaining competitive coexistence of related fishes with permanent territories, have implicated interspecific competition for space [37-42]. This has been exhibited by permanently territorial damsel fishes [38, 39, 43, 44]. Pianka and Tilman [45] noted that related species can coexist where intraspecific competition is greater than interspecific competition as such a scenario results in wider separation among conspecifics, thereby creating room for congenerics. It has been suggested, that one of the keys to a healthy coexistence in species-rich communities of the Lake Malaŵi National Park is fine space partitioning [3] through territoriality. With high species diversity at Thumbi West Island, the study was anchored on the premise and hypothesis that fine spatial arrangement of territories and feeding sites promotes the coexistence of the natives and the introduced species.

2. Main Objective

To determine factors that have enabled the native species and the introduced species to coexist at a selected site at Thumbi West Island.

Specific objectives

The following were the objectives of the study:

To characterize the intra- and interspecific distribution and arrangement of territories of the coexisting species.

To characterize the **intra-** and **interspecific** distribution and arrangement of feeding sites of the coexisting species.

3. Materials and Methods

3.1 Drawing the Map of the Underwater Substrate of the Research Site

An area of 25 m × 5 m was marked using a tape, an aluminium rod and an underwater compass. The corners of the quadrat were marked by placing painted boulders. Two ropes were placed, one on the width and another on the edge of the length of the site during the all the time mapping was being conducted to guide the placement of the steel quadrats. The placement of these ropes shifted relative to the progress and direction of the mapping. Two quadrats 1 m × 1 m made of steel wires were used. The quadrats were painted white to increase their visibility under water. These quadrats were further subdivided into twenty-five 20 × 20 cm squares using a white rope. Such a configuration corresponded to that of the A2 sized tracing film, which was used. This tracing film was clipped on an A2 graphed board. The map of the bottom topography was drawn by following successive systematic placement of the steel quadrats within the area measuring 25 m by 5 m. The successive rock configurations within the areas defined by the steel quadrats were drawn on the A2 tracing film. Depending on the boulder sizes, those that were considered having a very small diameter were not drawn on the map.

3.2 Mapping of the substrate Configuration at the Site

The tenants were identified by slightly modifying the method used by Kohda (1998) [45]. Each tenant was captured and examined to note the number of egg spots on the anal and/or dorsal fins, specific body colouration, injury and/or body size. Individual fishes captured without unique distinguishing features but seen repeatedly within the same territory, and having the same body sizes throughout were regarded as the same individuals.

Mapping of territories relied on the map of the underwater configuration which was drawn on plain A2 semi-transparent paper. This paper was then clipped on an A2 graphed plastic board. On top of the map was placed another semi-transparent of the same size with the edges exactly fitting, and clipped to the board. Looking through the tracing film, the drawn substrate configuration could easily be seen. As such, specific positions and areas on the actual site where fishes defended territories or foraged could correspondingly be marked out on the top A2 tracing film by comparing the actual underwater configuration to that seen through the tracing film.

3.3 Identification and Mapping of Territories

To map territories, the individual territorial fishes of each species were observed for 20 minutes. During this time interval, the exact positions of the intruders that induced attack behaviours from the territory owners were marked on the top A2 tracing film. The locations of the territories were checked over 5 times. These attack points were joined to produce a territory of a tenant. Areas of dense algal growth within and around the territories were also mapped. These are called "Algal gardens".

Remapping of the territories was done 2 months later to confirm the positions.

3.4 Feeding Sites

To identify feeding sites, the foraging individual fishes of each species were observed for 20-minute intervals. During this interval, the distinct foraging areas of individual fishes of each species were marked by dots on the top tracing film. The outer most dots were joined to map out the feeding sites.

The map of the rock configuration was divided into 3 sections, simply to enhance visual clarity on paper. Section A (Fig. 1) measures 25 m^2 on the actual underwater substrate. Sections B (Fig. 2) and C (Fig. 3) each measure 50 m^2 on the ground.

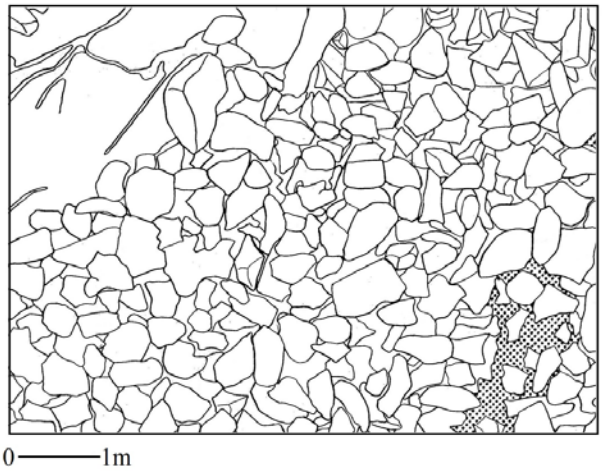

Fig. 1 Map of the underwater spatial configuration (Section A).

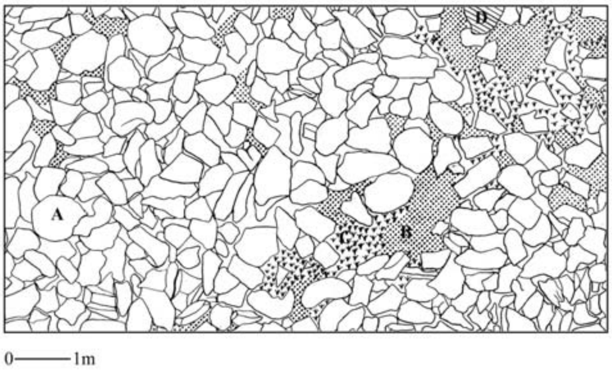

Fig. 2 Map of the underwater spatial configuration (Section B).

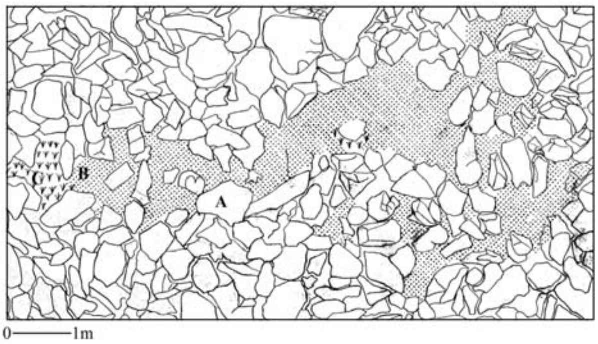

Fig. 2 Map of the underwater spatial configuration (Section C).

3.5 The Study Site

The study was conducted at Thumbi West Island (S14 01.444′; E34 49.380′). At the site, observations were made over a substrate that had small to large-sized rock boulders. The study site was within 0.5-2.0 m depth range of mostly uniform slope, in the littoral zone, situated on the South-Western part of Thumbi West Island. The site was suitable in several respects. First it is situated near Mitande Point-a probable place for the original **mbuna** introductions. Secondly, it has a complex habitat heterogeinity and as such it attracted rich and diverse environment for the cohabitation of rock-dwelling cichlids. The rocky shore is interspaced with a belt of sand with isolated weedy zones. A number of species also fed on the algae attached to the branches of partly submerged macrophytes. The arrangement of the large rock boulders bordering the site is such that an enclosure separates this particular rocky littoral zone from the intermediate sandy zone. As such, this "wall" blocks most of the wave action due to the Mwera (South East) winds, making the waters within this local locality relatively calm for easy snorkeling. The Mpoto (North) winds are effectively blocked by the island itself. Further, at the site, native species, introduced species, a number of color morphs, and undescribed species, are richly represented.

3.6 The Species Studied

Some of the species studied were not formally described. Because of this, they were referred to using chironyms according to Ribbink et al. (1983) [3]. Two introduced mbuna species were studied: Metriaclima callinos and Tropheops "red cheek". Metriaclima callinos is a native of Nkhata Bay in the northern part of the lake, while Tropheops "red cheek" is a native of Likoma Island [3]. Both species are present in large numbers at Thumbi West Island near Mitande point within the 0-2 m depth range.

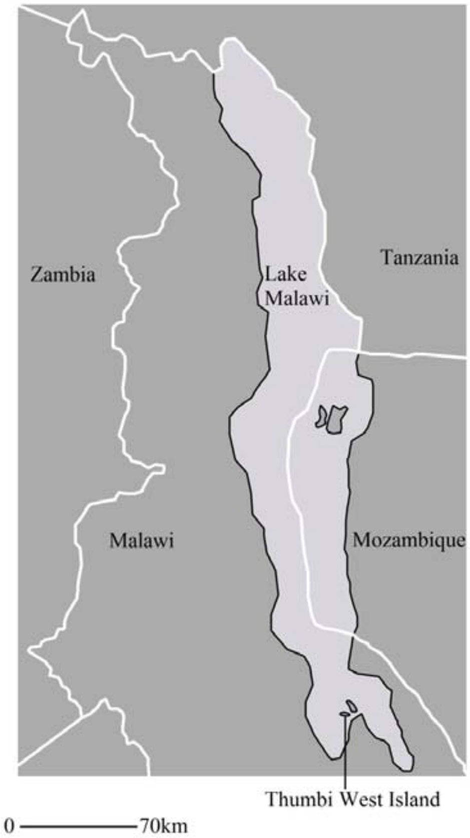

Fig. 3 Part of map of Malawi showing position of Thumbi West Island in Lake Malawi.

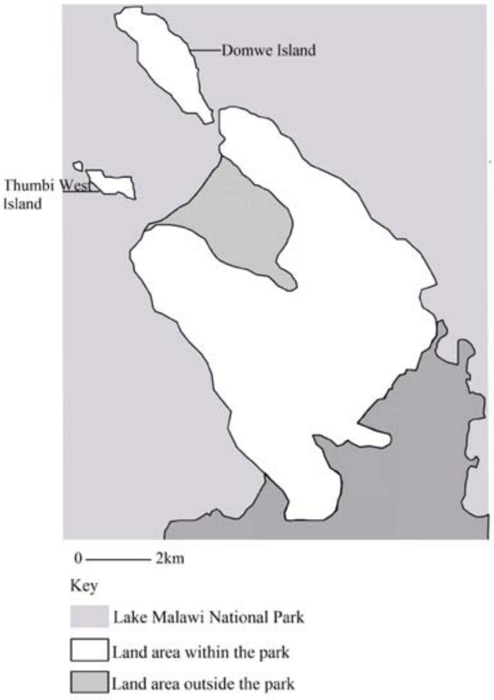

Fig. 4 The Nankumba Peninsula showing part of the Lake Malawi National Park.

Over thirty native species occur at Thumbi West Island. Four native mbuna species were studied, Labeotropheus fulleborni, Melanonchromis auratus, Petrotilapia mumboensis and Psedotropheus Tropheops "intermediate". All these species are well represented within this 0-2 m depth range.

4. Data Analysis

Data comprised of maps of territories and feeding sites. These maps were photocopied on to A4-sized paper. To compare territory maps for any two species, a thin A4 tracing film was used to trace the territories and feeding sites on the maps of the species to be compared one at a time. The territory maps for both were then drawn on a same tracing film. All the possible comparisons within and between the species were made.

Squares on semi transparent graphed paper, were used to estimate the territory areas taking into account the scale of the maps.

Evaluation of territory-size differences was done using Prism 3 statistical software. All the data sets were checked and found to be normally distributed and as such, a t- test was used to evaluate the differences.

5. Results

Territorial males and females of the natives and the introduced species defend territories feeding sites most of which do not overlap. Territorial P. tropheops "intermediate" establish their territories mostly under rocks and within rock enclosures. Some of the territories are defended by brood guarding females — indicated F(B). All other female territories are indicated by the letter "F". The territories under rocks are densely grown and are referred to as "Algal gardens" e.g., Appendices 1A and 1B. P. tropheops intermediate "red cheeks" establish theirs mostly on top of rocks. There are no distinct feeding sites within these territories. Introduced territorial males and females establish territories, which are moderately grown with algae. There are distinct feeding sites within these territories, e.g., Appendices 3A-4B. Only one territory in Appendix 5A was established under rocks.

Territories established under rocks have been indicated by stars — P. tropheops "red cheek" and M. callinos territories.

Labeotropheus fuelleborni females and P. "mumbo blue" males and females do not defend territories. Metriaclima callinos and L. fuelleborni females have prominent feeding sites mostly outside territories. The male and female "P. mumbo blue" feed exclusively in the territories of P. tropheops "intermediate". They do not show distinct feeding sites with respect to these territories.

Melanonchromis auratus neither have territories or distinct feeding sites. They fed outside the territories randomly.

In all territories, attack points coincide with the outermost foraging points of the territory residents. These attack points are the territory boundaries. Individuals that establish territories under rocks, evict territory holders above them from time to time.

In the cases of intraspecific territory overlaps, the male territory owner tolerates the establishment of female territories within their territories by ripe females. These females do however get evicted from time to time when they show unwillingness to spawn.

Where interspecific territory overlaps have been noted, territory owners evict those individuals that have territories above them from time to time (overlaps marked with stars). In other territories individuals evict each other from the areas where their territories overlap from time to time. Feeding sites within territories were used only when the territory owners could not see the intruder.

Overlaps between territories and between territories and feeding sites were few and most of them were probably due to estimation inaccuracies due to free hand drawing. These have characterized and summarized in Table 1.

Table 1 Characterization of territory and feeding sites overlaps.

Appendix	Nature of overlap	Species	Extent of overlap
1A	Interspecific and consexual	Pseudotropheus tropheops “intermediate” male territories and *M. callinos* male territories.	slight
2A&2B	Interspecific	Pseudotropheus tropheops “intermediate” male territories and *L. fuelleborni* female *feeding sites*	slight
3A	Interspecific and consexual	Pseudotropheus tropheops “intermediate” male territories and Pseudotropheus tropheops “red cheek” male territories.	Very slight
4A	Intraspecific and Consexual	Pseudotropheus tropheops “red cheek” females	Very slight
5A & 5B	Interspecific and consexual	Pseudotropheus tropheops “red cheek” male territories and *M. callinos male feeding sites.*	considerable
6A, 6B and 8A	Intraspecific	Pseudotropheus tropheops “red cheek” male territories and *L. fuelleborni female feeding sites.*	slight
7A, 7B and 7C	Intraspecific and heterosexual	Pseudotropheus tropheops “red cheek” male territories and Pseudotropheus tropheops “red cheek” female territories	Slight, very slight and very slight
8A and 8B	Interspecific and consexual	Pseudotropheus tropheops “red cheek” female territories and *M. callinos* female feeding sites.	Very slight
9B	Interspecific and consexual	Pseudotropheus tropheops “red cheek” female territories and *L. fuelleborni female feeding sites.*	Very slight
10A	Interspecific	*M. callinos* male territories and *L. fuelleborni female feeding sites.*	Very slight

Slight overlaps, mostly interspecific and consexual were noted underscoring intense and fierce competition between members of different species of the same sex. Very few conspecific territory overlaps are between territories of the introduced species (Appendices 7A-7C).

Both male and female P. tropheops “intermediate” territory holders do not engage in border fights. Both attack and chase conspecific and heterspecific intruders from the borders only. P. tropheops “red cheek” territorial neighbouring males engage in border fights. They chase conspecific intruders beyond the territory boundaries while heterospecifics are evicted from the borders only. Territorial introduced females do not engage in border fights. These females attack and chase intraspecific intruders only from the territory borders and never beyond. Some individuals share feeding sites.

The evaluation of territory size differences shows differences interspecifically only. P. tropheops “red cheek” establish larger territories than P. tropheops “intermediate” (Table 2).

Table 2 A comparison of territory areas, presented as mean ± standard error of the indigenous *species P. tropheops intermediate* males and females, and the introduced species *P. tropheops red cheek* males and females. Differences are evaluated by the unpaired t test. Significant differences are shown by *.

Species	N	Mean	Species	N	Mean	t value	p value
*P. tropheops red cheek	72	0.40±0.03	P. tropheops intermediate	32	0.16±0.02	5.2	< 0.05
P. tropheops red cheek (males)	24	0.40±0.40	P. tropheops red cheek (females)	48	0.40±0.37	1.03	< 0.05
P. tropheops intermediate (males)	18	0.20±0.02	P. tropheops intermediate (females)	14	0.25±0.0	1.9	< 0.05

6. Discussion

The species- rich communities in aquatic habitats have evolved in response to shelter and food [46]. Establishment of mostly non-overlapping intraspecific and interspecific territories and feeding sites (Appendices 1-10) shows spatial partitioning at this site. Optimal territory sites between introduced and native species in the Park are similar and limited [10]. This is accentuated by the scarcity of epilithic food resources at some times of the year [47]. While trophic specialization and food switching has been noted in mbuna, considerable dietary overlaps have also been noted due to food resource requirements being similar [5]. This is compounded by spatial limitation which places a high premium on the need for spatial partitioning in order for the species to circumvent interference competition. Given such a scenario one of the possible mechanisms for a peaceful coexistence is to utilize different microhabitats [48]. Spatial partitioning appears the best option since the ability for most species to selectively pick at specific food items from a given microhabitat is probably limited [49].

Territory size within a habitat may be due to differences in the quality of the territory and the resources it contains and in many species a negative correlation exists between size and the quality, quantity and availability of resources [50]. This study has confirmed this correlation in showing that P. tropheops “red cheeks” establish larger territories with mostly moderate algal growth, while P. tropheops “intermediate establish smaller territories with dense algal growth. The larger territories in P. tropheops “red cheek” do place a high energy demand to defend the territories, making it difficult for the territories to have dense algal growth. With larger territories moderately grown with algae, selection of optimal feeding sites within the territory appears a reasonable option. On the other hand, the establishment of smaller territories by P. tropheops “intermediate”, places a lower demand on territory defense. With well-defended territories formation of “Algal gardens” is feasible, making selection of feeding sites appears unnecessary.

7. Conclusion

The study therefore suggests that spatial partitioning through the establishment of territories and feeding sites does promote the coexistence of the natives and the introduced species.

7.1 The Way Forward

Although the coexistence between the natives and the introduced species appears to be that of “peace”, findings of this study suggest the need to investigate other factors that could help confirm such a “peaceful” coexistence. The engagement in conspecific border fights, establishment of bigger territories by the introduced species (P. tropheops “red cheek”) and display of strong attack behaviours (beyond the boarders) against conspecifics may be an indication of stronger aggressive behaviour compared to the natives and spatial gain advantage. If this if so, the introduced species could be at an advantage in terms of increased territory tenure and turn-over compared to the natives. This could give them an advantage in terms of securing food and spawning space which might eventually boost their population growth. On the other hand, despite holding smaller territories, the maintenance of “algal gardens” does indicate fierce defending of territories among in natives (P. tropheops intermediate). This could place them at an advantage in terms of ensuring adequate food reserves (in the algal gardens) and optimal spawning space against the introduced species, which would ensure continued boost of their population. This study therefore needs to be complemented with data on the interspecific social interactions, and regular population estimates to determine if there are any parameters that could question this “peaceful” coexistence.

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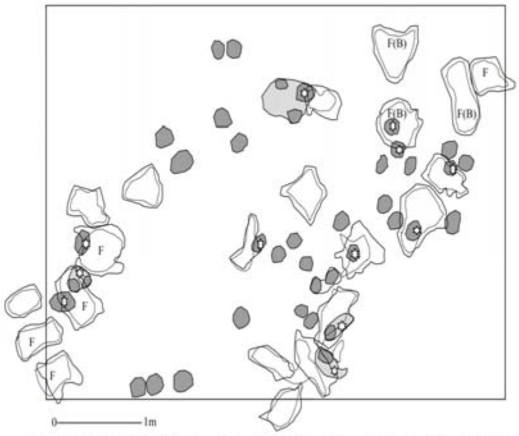
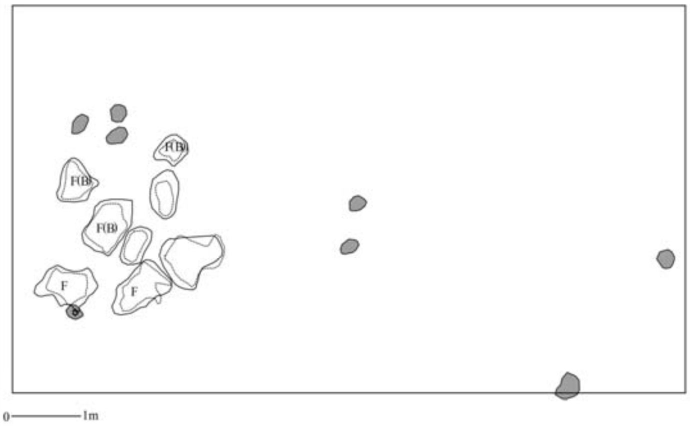
Appendix Maps of territories and feeding sites (Thumbi West Island)



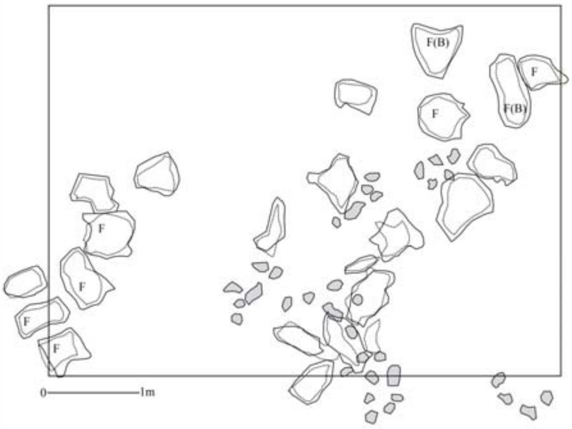
Appendix 1A: The territories of P. tropheops 'intermediate' and the territories and feeding sites of *M. callinos* (Section A)

Key
☐ P. tropheops 'intermediate' female and male territories
☐ P. tropheops 'intermediate' Algal gardens
▨ *M. callinos* territories
▨ *M. callinos* feeding sites



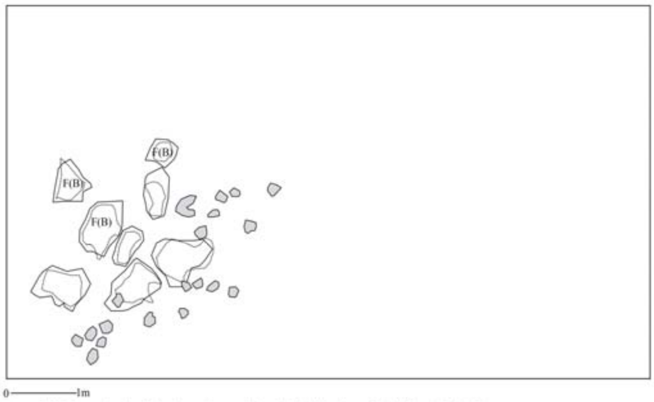
Appendix 1B: The territories of P. tropheops 'intermediate' and the feeding sites of *M. callinos* (Section B)

Key
☐ P. tropheops 'intermediate' territories.
▨ *M. callinos* feeding sites
☐ P. tropheops 'intermediate' Algal



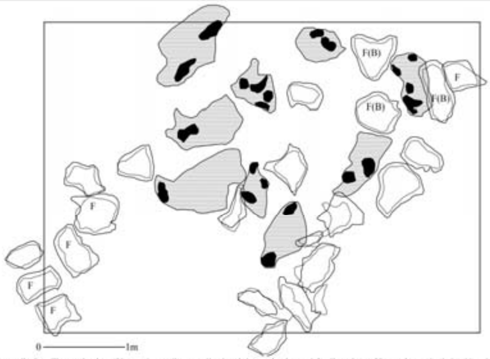
Appendix 2A: The territories of P. tropheops 'intermediate' and the feeding sites of *L. fuelleborni* (Section A)

Key
☐ P. tropheops 'intermediate' territories
☐ P. tropheops 'intermediate' Algal gardens
▨ *L. fuelleborni* feeding sites



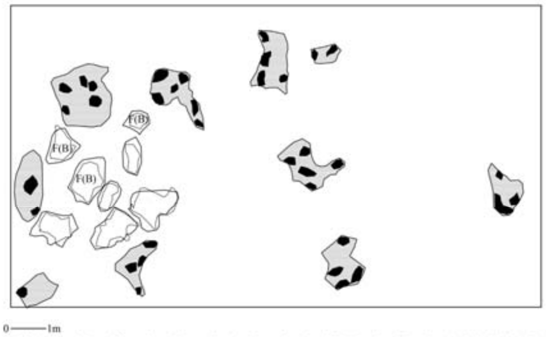
Appendix 2B: The territories of P. tropheops 'intermediate' and the feeding sites of *L. fuelleborni* (Section B)

Key
☐ P. tropheops 'intermediate' territories
☐ P. tropheops 'intermediate' Algal gardens
▨ *L. fuelleborni* feeding sites



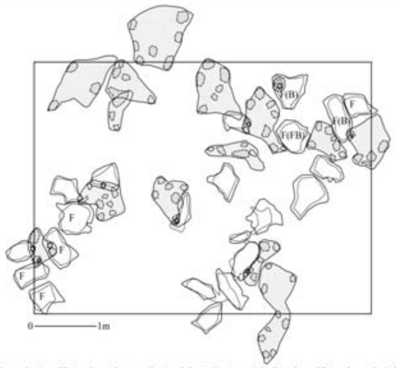
Appendix 3A: The territories of P. tropheops 'intermediate' and the territories and feeding sites of P. tropheops 'red cheek' males (Section A)

Key
☐ P. tropheops 'intermediate' territories
☐ P. tropheops 'intermediate' Algal gardens
▨ P. tropheops 'red cheek' males territories
■ P. tropheops 'red cheek' males feeding sites



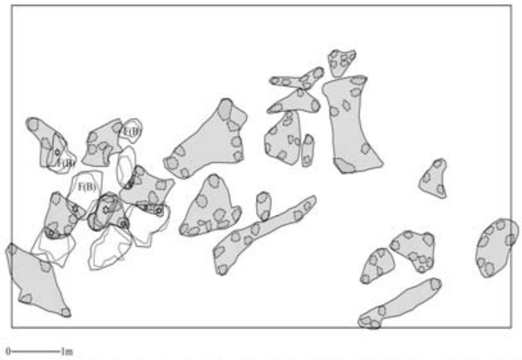
Appendix 3B: The territories of P. tropheops 'intermediate' and the territories and feeding sites of P. tropheps 'red cheek' males (Section B)

Key
☐ P. tropheops 'intermediate' territories
☐ P. tropheops 'intermediate' Algal gardens
▨ P. tropheops 'red cheek' territories (males)
■ P. tropheops 'red cheek' feeding sites (males)



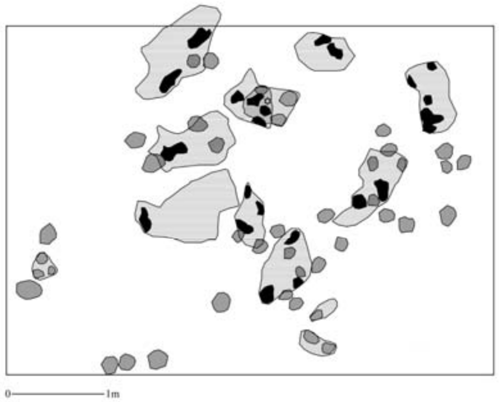
Appendix 4A: The territories of P. tropheops 'intermediate' and the territories and feeding sites of P. tropheops 'red cheek' females (Section B)

Key
☐ P. tropheops 'intermediate' territories
☐ P. tropheops 'intermediate' Algal gardens
▨ P. tropheops 'red cheek' territories (females)
▨ P. tropheops 'red cheek' feeding sites (females)



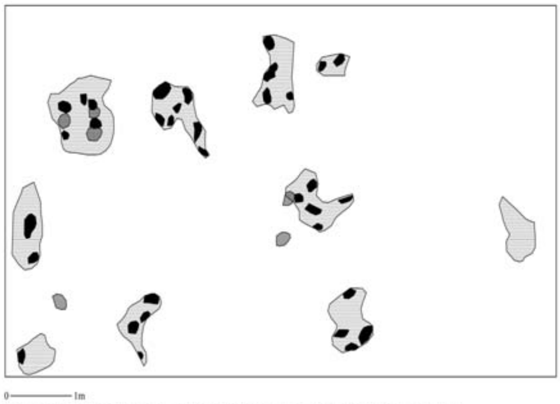
Appendix 4B: The territories of P. tropheops 'intermediate' territories and the territories and the feeding sites of P. tropheops 'red cheek' females (Section B)

Key
☐ P. tropheops 'intermediate' territories
☐ P. tropheops 'intermediate' Algal gardens
▨ P. tropheops 'red cheek' territories (females)
▨ P. tropheops 'red cheek' feeding sites (females)



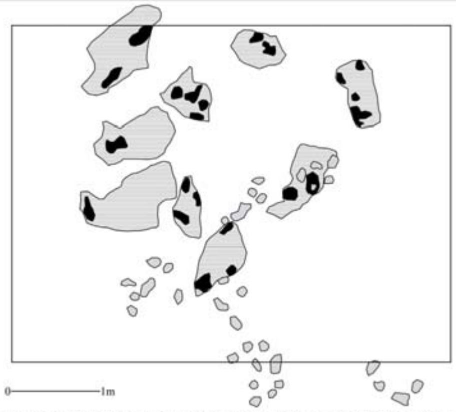
Appendix 5A: The territories and feeding sites of P. tropheops 'red cheek' males and the territories and feeding sites of *M. callinos* (Section A)

Key
▨ P. tropheops 'red cheek' territories (males)
■ P. tropheops 'red cheek' feeding sites(males)
▨ *M. callinos* territories
▨ *M. callinos feeding sites*



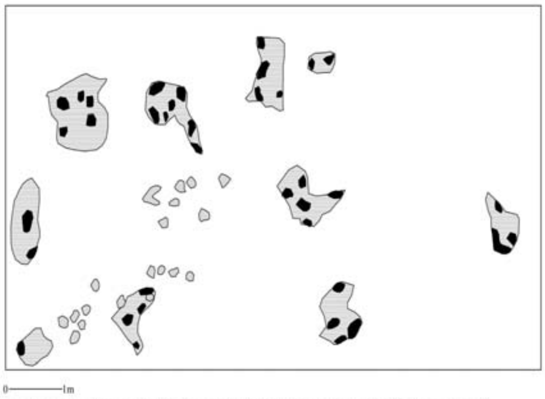
Appendix 5B: The territories and feeding sites of P. tropheops 'red cheek' males and the feeding sites of *M. callinos* (Section B)

Key
▨ P. tropheops 'red cheek' terrtories (males)
■ P. tropheops 'red cheek' feeding sites (males)
▨ *M. callinos* feeding sites



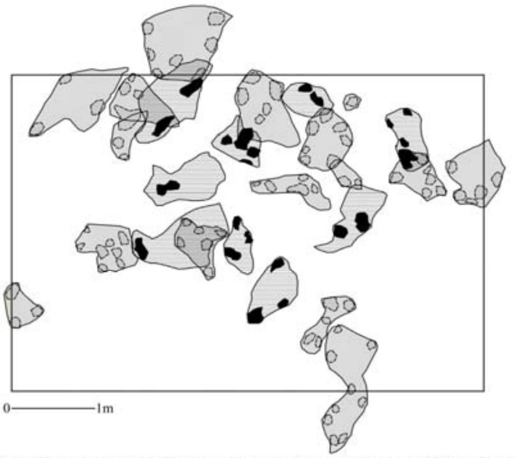
Appendix 6A: The territories and feeding sites of P. tropheops 'red cheek' males and the feeding sites of *L. fuelleborni* (Section A)

Key
▨ P. tropheops 'red cheek' territories (males)
■ P. tropheops 'red cheek' feeding sites (males)
▨ *L. fuelleborni* feeding sites



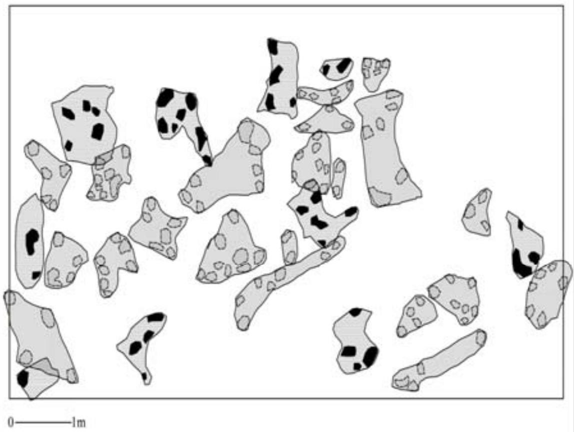
Appendix 6B: The territories and feeding sites of P. tropheops 'red cheek' males and the feeding sites of *L. fuelleborni* (Section B)

Key
▨ P. tropheops 'red cheek' territories (males)
■ P. tropheops 'red cheek' feeding sites (males)
▨ *L. fuelleborni* feeding sites



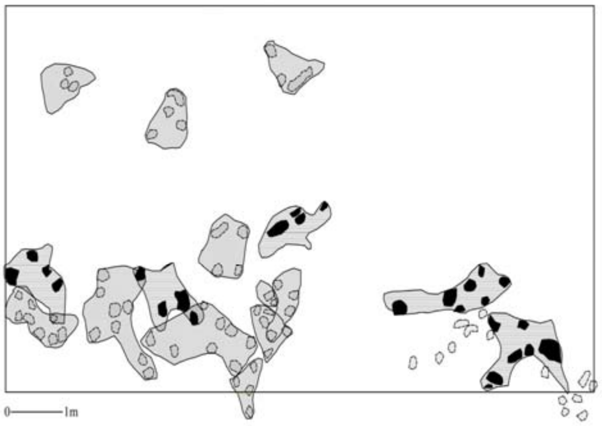
Appendix 7A: The territories and feeding sites of P. tropheops 'red cheek' males and females (Section A)

Key
- ▢ P. tropheops 'red cheek' territories (males)
- ▢ P. tropheops 'red cheek' territories (females)
- ■ P. tropheops 'red cheek' feeding sites (males)
- ⬚ P. tropheops 'red cheek' feeding sites (females)



Appendix 7B: The territories and feeding sites of P. tropheops 'red cheek' males and females (Section B)

Key
- ▢ P. tropheops 'red cheek' territories (males)
- ▢ P. tropheops 'red cheek' territories (females)
- ■ P. tropheops 'red cheek' feeding sites (males)
- ⬚ P. tropheops 'red cheek' feeding sites (females)



Appendix 7C: The territories and feeding sites of P. tropheops 'red cheek' males and females (Section C)

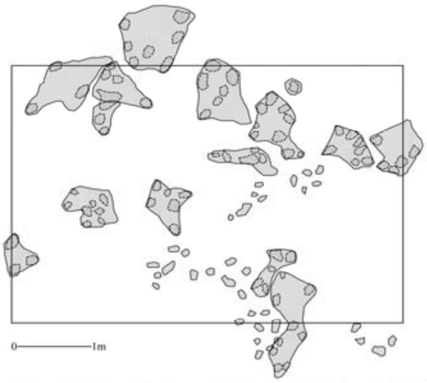
Key
- ▢ P. tropheops 'red cheek' territories (males)
- ▢ P. tropheops 'red cheek' territories (females)
- ■ P. tropheops 'red cheek' feeding sites (females)
- ⬚ P. tropheops 'red cheek' feeding sites (females)

Appendix 8A: The territories and the feeding sites of P. torpheops 'red cheek' females and the territories and the feeding sites of *M. callinos*

Key
- ▢ P. tropheops 'red cheek' territories (females)
- ▢ *M. callinos* territories
- ⬚ P. tropheops 'red cheek' feeding sites (females)
- ▨ *M. callinos* feeding sites

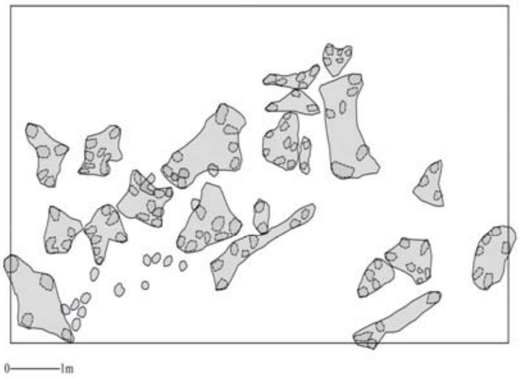
Appendix 8B: The territories and feeding sites of P. tropheops 'red cheek' females and the feeding sites of *M. callinos* (Section B)

Key
- ▢ P. tropheops 'red cheek' territories (females)
- ⬚ P. tropheops 'red cheek' feeding sites (females)
- ▨ *M. callinos* feeding sites



Appendix 9A: The territories and feeding sites of P. tropheops 'red cheek' females and the feeding sites of *L. fuelleborni* (Section A)

Key
- ▢ P. tropheops 'red cheek' territories (females)
- ⬚ P. tropheops 'red cheek' feeding sites (females)
- ▢ *L. fuelleborni* feeding sites

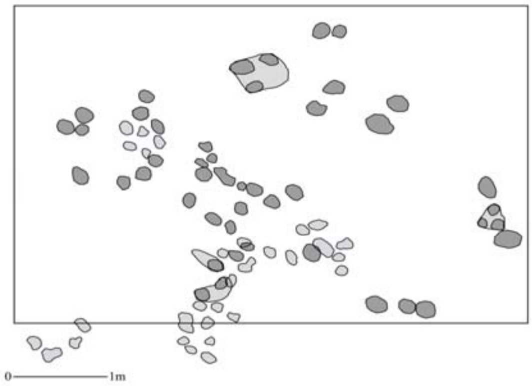


Appendix 9B: The territories and the feeding sites of P. tropheops 'red cheek' females and the feeding sites of *L. fuelleborni* (Section B)

Key

▨ P. tropheops 'red cheek' territories (females)

☐ P. tropheops 'red cheek' feeding sites (females) ▨ *L. fuelleborni* feeding sites

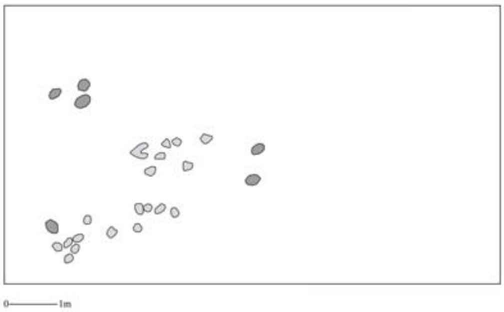


Appendix 10A: The territories and feeding sites of *M. callinos* and the feeding sites of *L. fuelleborni* (Section A)

Key

▨ *M. callinos* territories

■ *M. callinos* feeding sites ▨ *L. fuelleborni* feeding sites



Appendix 10B: The feeding sites of *M. callinos* and *L. fuelleborni* (Section B)

Key

■ *M. callinos* feeding sites

▨ *L. fuelleborni* feeding sites