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Intra- and Interspecific Social Organization among Three Herbivorous Cichlid Fishes in Lake Tanganyika

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Abstract Intra- and interspecific social organization among 3 coexisting herbivorous cichlids, *Tropheus moorii*, *Petrochromis trewavasae* and *P. orthognathus*, were studied at a rocky shore in Lake Tanganyika. Individuals of all species maintained discrete intra- and interspecific territories, except *T. moorii* and *P. trewavasae* whose feeding territories overlapped. Territory owners attacked smaller individuals but exhibited displays towards larger neighbours, irrespective of species. This observation suggests that both intra- and interspecifically, these cichlids interact in the context of size-dependent dominance hierarchies. Removal experiments showed that smaller *T. moorii* benefitted from *P. trewavasae* in the maintenance of their territory borders against larger *P. orthognathus*. Interspecific dominance hierarchy and commensalism among these cichlids are not species specific, but change dynamically in relation to the difference in body size between component individuals. Mating territories of male *P. orthognathus* and *T. moorii* are compared to their feeding territories, and territory forms are discussed. It is suggested that an approach incorporating the concept of an interspecific society may play an important role in the elucidation of guild structure and function.

A large number of studies on territorial behaviour and dominance have revealed examples of interspecific territoriality (Orians and Willson, 1964; Myrberg and Thresher, 1974; Morisita, 1976; Miller, 1978; Kawanabe, 1981; Kohda, 1981, 1984; Murray, 1981; Takamura, 1984), and interspecific dominance hierarchies (Morse, 1970; Wilson, 1975; Nakamura, 1976; Ishigaki, 1984) in a wide range of species. Although the effects of intraspecific territoriality or dominance hierarchies on overall social organization have been studied by many authors, such an approach has not been applied towards relationships between species.

Many studies have investigated the maintenance of community diversity and the relationships among coexisting species with similar resource requirements (e.g., Kawanabe, 1959; Connell and Orias, 1964; Conner, 1979; Pianka, 1980; May, 1981; Aarssen, 1983; Connell, 1983; Roughgarden, 1983), and their findings suggest that both competitive ability and interspecific association operate in the maintenance of coexistence. However, most studies have considered the relationship between participant species only at the population level (e.g., Imanishi, 1958; Pianka, 1980; Gause, 1981; Diamond and Case, 1986; Kikkawa and Anderson, 1986; Kimoto and Takeda, 1987) and interspecific relationships at the individual level have been ignored.

The cichlid fishes of Lake Tanganyika have shown an explosive adaptive radiation, although several sympatric species have similar ecological requirements (Fryer and Iles, 1972; Brichard, 1978; Lowe-McConnell, 1987). Up to 17 herbivorous cichlid species coexist within a rocky shore area, and some of them have interspecific territories (Kawanabe, 1981; Takamura, 1984). This paper describes the intra- and interspecific social interactions among individuals of three of these species, and analyzes these from the viewpoints of territoriality, dominance hierarchy and commensalism. Finally, the importance of the concept of interspecific sociality in connection with the study of guild structure is discussed.

Study area, materials and methods

The study was conducted at Luhanga (3°30′S, 29°09′E) in the north-western shore of Lake Tanganyika, Zaire, from 26 July to 2 September, 1985. A quadrat of 10 m×30 m with 2 m×2 m grids was set

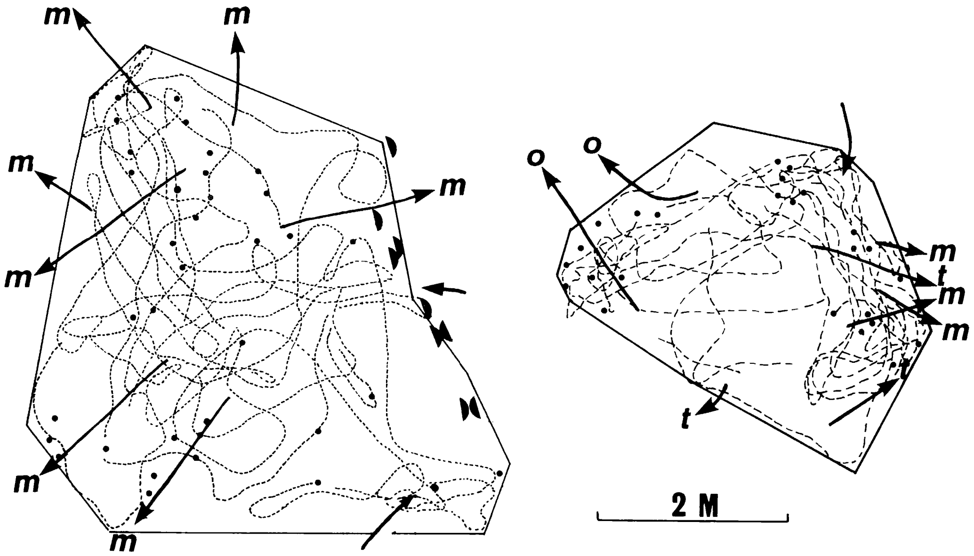

Fig. 1. Typical examples of territories of *Tropheus moorii* (left) and *Petrochromis orthognathus* (right). Arrows with thick line indicate attacking dash of the owner. *m*, *t* and *o* denote the attacked fish, *T. moorii*, *P. trewavasae* and *P. orthognathus*, respectively. Broken or dotted lines show foraging routes and small dots indicate foraging sites. Observation times on shown foraging routes are for 25 min for *P. orthognathus* and 40 min for *T. moorii.* Semi circles show the position of a display or mutual display (see text). The three arrows directed from outside the territories show attacks by neighbours on the owner. For the position of the two territories in the study area, see Fig. 2 (T*m* and *Bo*).

on the rocky bottom. The water depth varied from 1 to 20 m. Details of the habitat structure and abundance of fishes within the quadrat area are given in Hori et al. (1983) and Takamura (1984).

The three species studied were *Petrochromis trewavasae*, *P. orthognathus* and *Tropheus moorii*, these being territorial and relatively abundant. *T. moorii* feeds on filamentous algae, this food occupying about 90% of its stomach contents, whereas *P. trewavasae* feeds on the same proportion of unicellular algae (Takamura, 1984). *P. orthognathus* also depends mainly on unicellular algae (Takamura, 1984; Mbomba, 1986). These three species are maternal mouthbrooders (Kuwamura, 1986).

Observations were conducted with the aid of snorkel or SCUBA. The foraging routes of 24 of *T. moorii*, 12 *P. trewavasae* and 7 *P. orthognathus* were mapped for a minimum of 40 min and the positions at which feeding and intra- and interspecific social interactions occurred were recorded.

Total lengths of subject fish were estimated underwater to the nearest 0.5 cm for *T. moorii* and 1 cm for *P. orthognathus* and *P. trewavasae*, by comparing with a ruler placed on the substrate.

The sex of each individual was identified from courtship interactions, although spawning was not observed during the study period, and by gonad examination in some individuals.

Many of the subject fish could be identified individually by injuries on the body or fins or by differences in colour pattern. Most of the identified fish did not change the home ranges during the observation period, and therefore when a fish with no distinguishing marks but seen repeatedly within the same territory, and having the same body size throughout the study period, it was regarded as the same individual. The owner of each territory is indicated by a capital or small letter accompanied by an italic small letter; the italic *m*, *t* and *o* indicate the species name as shown in Fig. 1. Names of individually identifiable fishes are given in all italics.

To examine the defendability of territory, one resident individual of each species was removed from the study area and intruding fishes and their interactions within the vacant territory were recorded.

The variation of body size of subject fish in relation to water depth was examined by collecting individuals of each species from outside the study area

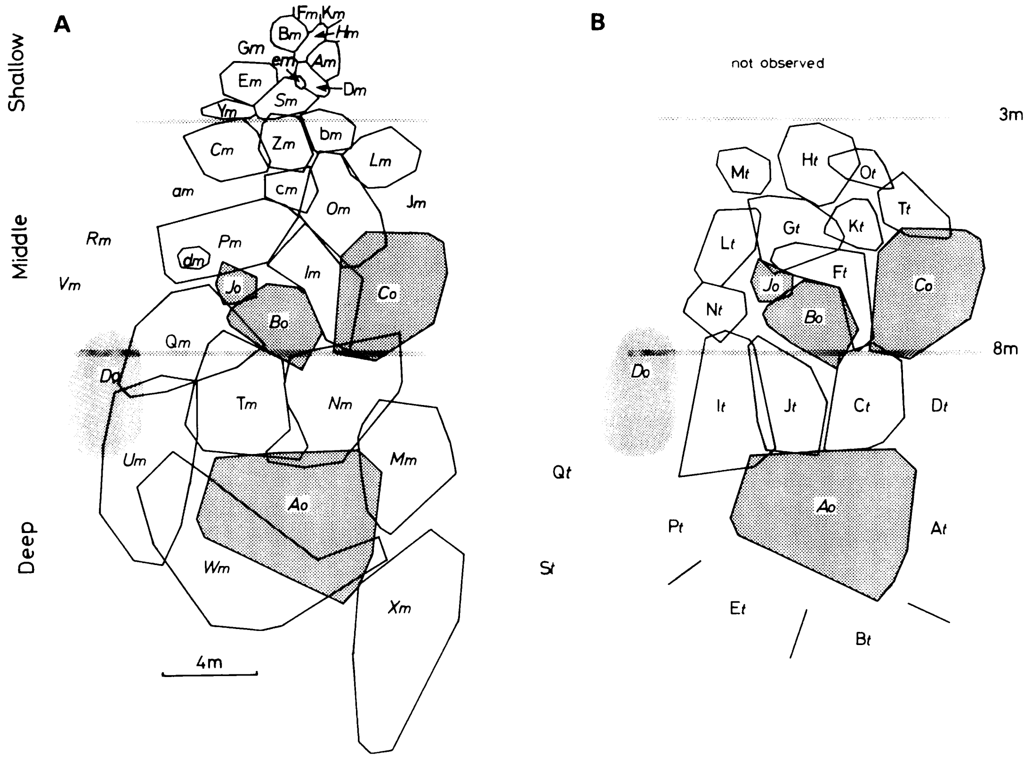

Fig. 2. Arrangement of feeding territories in the study area. A, *Tropheus moorii* and *Petrochromis orthognathus*; B, *P. treavasae* and *P. orthognathus*. The territories of *P. orthognathus* are shown by shaded area in both A and B. The owner of each territory is indicated by a capital or small letter accompanied by an italic small letter; the italic *m*, *t* and *o* indicate the species name as in Fig. 1. Names of individually identifiable fishes are given in all italic. Names not placed within territory borders indicate the most frequent location of that individuals. Incomplete lines in the deep zone show approximate territory borders of *P. trewavasae.* Shaded lines at 3 m and 8 m depth represent the borders of the shallow, middle and deep zones.

at known depths.

Results

Behaviour in social interactions. The behaviour of the three species in relation to territory defense or mating was divided into the following seven categories.

1) One-sided attack: Attack and chasing by a territory owner against intruders.

2) Lateral display: Near the border of a territory, the owner stands broadside to an approaching fish with all fins spreading and quivering (Kawanabe, 1981).

3) Tail-beating display: When another fish approaches the border of a territory, the territory owner moves toward it, and assumes a head up position near the bottom, and quivers its tail violently. It was sometimes difficult to distinguish between tail-beating and lateral display.

4) Mutual attack: Just after being attacked by a territory owner, the intruder counterattacks. Sometimes "mutual attack" continued several times.

5) Mutual lateral display, mutual tail-beating display: Lateral or tail-beating display is conducted by both fish at the same time.

6) Courtship display: Observed in *T. moorii* and *P. orthognathus.* The male directs this display toward the female who is permitted to stay in the former's territory. This behaviour is similar to the tail-beating display but is more violent. A male does not disturb the swimming of a female by this display. This behaviour is not restricted to near the territory border.

7) Non-interaction: No social interaction is observed even when two individuals are within 50 cm of each other.

Feeding territories. Foraging routes of individual fish were distributed evenly and were restricted to a certain area, within which foraging sites were scattered (Fig. 1). Conspecific and heterospecific intruders were repelled from this area, which could be therefore regarded as a feeding territory. The positions of foraging areas of individually identified fish remained stable throughout the study period except a few cases. Figure 2 indicates that the territories of *T. moorii* were separate from each other and from those of *P. orthognathus.* The territories of *P. trewavasae* were also separate from each other and from those of *P. orthognathus.* The territories of *P. orthognathus* were separate from each other and from those of the other two species. However, the territories of *P. trewavasae* and *T. moorii* overlapped each other, although their intraspecific territory borders did not coincide (Fig. 2). While territories of *T. moorii* and *P. trewavasae* were located immediately adjacent to each other, the 5 territories of *P. orthognathus* located within the study area were widely separated, except for a territory of a subadult *Jo* (14 cm in total length) adjoining that of adult *Bo* (18 cm). In a deep zone at a 8–12 m water depth immediately outside the study area, two territories of *P. orthognathus* were found, and these were also separate from each other, whereas territories of *T. moorii* and *P. trewavasae* were again adjacent to each other intraspecifically.

Most of the rocky substratum in the study area was occupied by these territorial herbivores. The greater the water depth, the larger were the territory sizes of *T. moorii* and *P. trewavasae* (Table 1, Fig. 2). Territories of these two species were also found in the deeper areas outside the study area. Two territories of *T. moorii* situated at the greatest depths (25–27 m) were about 65 and 70 m^2, much larger than those in the quadrat.

Adult body size in *T. moorii* varied inversely with water depth, but varied directly with water depth in the two *Petrochromis* species (Table 1).

The two smallest *T. moorii* in the study area (see Fig. 2A), *em* (6.0 cm TL) and *dm* (6.5 cm), were attacked by their neighbours. In their foraging areas, *em* and *dm* had shelter holes with entrances which were too small for large fish to enter. *em* and *dm* never showed any territorial behaviour toward

Table 1. Territory size and total length of *Tropheus moorii*, *Petrochromis trewavasae* and *P. orthognathus* in shallow (1–3 m), middle (3–8 m) and deep (8–20 m) zones. Specimens were collected outside the study area. *, fish less than 9.5 cm are omitted. **, data from Takamura (1984). Territory sizes among three zones significantly differ one another in *T. moorii*, *T. moorii** and *P. trewavasae* (U-test, $P<0.01$). Estimated body sizes of *T. moorii* differ significantly only between shallow and middle zones (U-test, $P<0.05$). Estimated body sizes of *T. moorii* more than 9 cm significantly differ between shallow and middle (U-test, $P<0.05$) and between shallow and deep zones (U-test, $P<0.01$).

Species Zone	Territory size (m^2) mean±SD (n)	Total length (cm) measured by eye mean±SD (n)	Total length (cm) collected samples mean±SD (n)
T. moorii			
Shallow	1.6±1.0 (8)	10.5±1.8 (12)	11.2±0.4 (4)
Middle	7.5±5.3 (10)	9.6±1.5 (15)	10.8±1.1 (6)
Deep	24.2±7.5 (6)	9.8±0.5 (6)	9.6 (2)
*T. moorii**			
Shallow	1.9±0.9 (6)	11.2±0.7 (10)	—
Middle	10.6±4.4 (6)	10.4±0.8 (10)	—
Deep	24.2±7.5 (6)	9.8±0.5 (6)	—
P. trewavasae			
Shallow	1.2±0.4 (4)**	—	11.3 (1)
Middle	5.3±2.3 (9)	17.3±2.1 (9)	15.3±0.5 (4)
Deep	13.3±2.9 (3)	19.8±0.9 (10)	17.4±2.3 (5)
P. orthognathus			
Shallow	—	10**	—
Middle	10.2±8.8 (3)	16.7±2.31 (3)	12.6 (2)
Deep	34.4 (1)	20 (2)	15.6 (2)

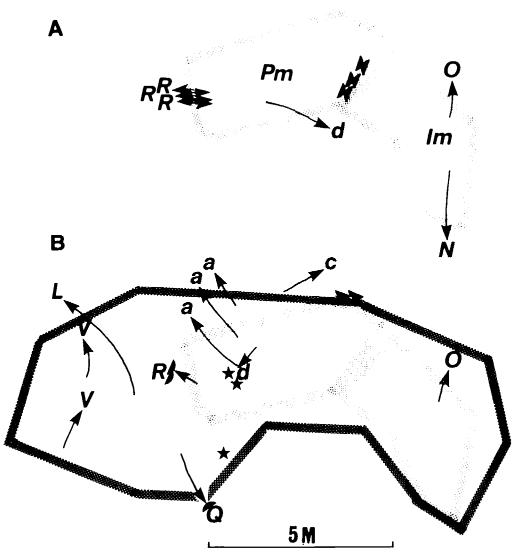

Fig. 3. Feeding and mating territories of *Tropheus moorii Im* (male) and *Pm* (female). A, feeding territories of *Im* and *Pm* are shown by light dotted lines. Arrows and semi circles show the positions of attacking dash and display, respectively. Letters indicate the names of attacked conspecifics. B, mating territory (81 min), indicated by dark dotted lines. Attacking positions and chasing routes of *Im* are shown by arrows with names of attacked conspecifics. Semi circles show the position of display by conspecifics towards *Im*. Stars show the position of courtship display by *Im* toward *Pm*.

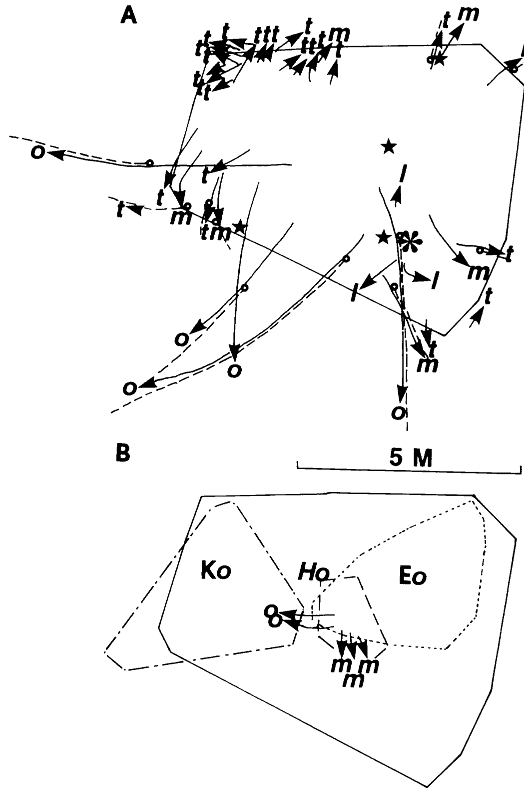

Fig. 4. The territory of male *Petrochromis orthognathus Ao* (A), and swimming areas of three females which stayed in his territory (B). A, solid line shows the border of the feeding territory of *Ao*. The location of attacks and chasing distance are shown by arrows. Italics, *m*, *t*, *o* and *l* indicate attacked species, *Tropheus moorii*, *P. trewavasae*, *P. orthognathus* and *Lobochilotes labiatus*, respectively. Attacked points of intruders and their flight routes until *Ao* ceased chasing are given by an open circle and thick broken lines. Stars show the positions of courtship display by *Ao*. An asterisk shows the probable spawning site. B, chained, broken and dotted lines show the swimming areas of females Ko, *Ho* and Eo, respectively, during 30 min. Other symbols are as in A.

their neighbours and fled into their shelters whenever attacked by them. Their foraging areas did not constitute true territories.

Mating territories. 1) *T. moorii.* Courtship displays of *T. moorii* were observed in two pairs. A male *Cm* courted an unidentified female which visited his feeding territory, and another male, *Im*, courted female *Pm* three times. Although *Im* and *Pm* usually stayed within their respective foraging areas and defended them against neighbouring conspecifics (Fig. 3A), when consorting, they swam close together to beyond the borders of their feeding territories and invaded those of conspecifics (Figs. 2A, 3B). During pair swimming, *Pm* and sometimes *Im* foraged not only within their usual foraging areas but also all over the pair swimming area.

In 11 one-side attacks by *Im*, some neighbours were not chased beyond the border of the pair swimming area (Fig. 3B), though intruders were always repelled from the feeding territories (see also Fig. 1). Female *Pm* never showed aggressive behaviour against conspecifics during pair swimming.

2) ***P. orthognathus.*** Four males (*Ao*, *Bo*, *Co*, *Do*) and one individual of unknown sex (*Jo*) maintained interspecific territories in the study area (Fig. 2). Three females stayed within the territory of male *Ao*, who was the largest male in the study area (Fig. 4B),

Table 2. Dominance relationships in *Tropheus moorii*. a, one-sided attacks and displays; b, mutual attacks and mutual displays. Only individuals engaged in these social interactions are listed. Figures with parentheses show numbers of displays or mutual displays, and without parentheses show those of attacks or mutual attacks. Individuals are ordered according to body size. Individually identifiable fishes are given in all italics. Neighbouring individuals between which attacks or displays were not observed are shown by bars. Interactions relating to the removal experiments are omitted. TL, total length (cm); A, attacks; D, displays or mutual display; M, male; F, female. For the position of their feeding territories, see Fig. 2A.

a)

Actees			Actors																															Total	
TL	sex		Am	Bm	Cm	Dm	Em	Fm	Gm	Hm	Im	Jm	Km	Lm	Mm	Nm	Om	Pm	Qm	Rm	Sm	Tm	Um	Vm	Wm	Xm	Ym	Zm	am	bm	cm	dm	em	A	D
12		Am				(1)				(8)																								0	9
12		Bm				(1)		(1)	—	(4)																								0	6
12	M	Cm																									—	—	—		—			0	0
11.5		Dm	1	1						1											—												—	3	0
11.5		Em							—												(1)						—							0	1
11.5		Fm		2						—			—																					2	0
11		Gm		—			2																											2	0
11		Hm	12	5		1		—					—																					18	0
11	M	Im														—	—	(1)	(1)	(2)		(2)									(2)			0	8
11		Jm												7			—																	7	0
11		Km						—		4																								4	0
11		Lm									1	6					—													—				7	0
10.5		Mm														—																		0	0
10.5		Nm									1				3							(5)1												5	5
10		Om									3	—		2				—										—		—	—			5	0
10	F	Pm									—						—		—	—									—		—	—		0	0
10		Qm									1							—				3	—											4	0
10		Rm									1							—						—										1	0
9.5		Sm				6	2																				—	(1)1		—			(1)	9	2
9.5		Tm									4					1			(3)				2											7	3
9.5		Um																	1			10			2									13	0
9.5		Vm									2									—														2	0
9.5		Wm																					2			(1)								2	1
9.5	F	Xm																							2									2	0
8.5		Ym			2		—														—													2	0
8.5		Zm			1												1				1									—	—			3	0
8.5		am			—						3							—																3	0
8		bm				2								—			—				—							—						2	0
8		cm			—						1						1	—										1						3	0
6.5		dm									2							1						2										5	0
6		em		2		17															4							2						25	0
Total		A	13	10	3	26	4	0	0	5	19	6	0	9	3	1	2	1	1	0	5	14	4	2	4	0	0	4	0	0	0	0	0	136	
		D	0	0	0	2	0	1	0	12	0	0	0	0	0	0	0	1	4	2	1	7	0	0	0	1	0	1	0	0	2	0	1		35

Table 2. (Continued)

b)

Actors		Actors													Total	
TL		*Am*	Dm	Fm	*Hm*	*Im*	Jm	Km	*Lm*	*Mm*	*Nm*	*Pm*	*Rm*	Tm	A	D
12	*Am*		(1)		(3)										0	4
11.5	Dm	(1)			—										0	1
11.5	Fm				—			(1)							0	1
11	*Hm*	(3)	—	—				(1)							0	4
11	*Im*										—	(3)			0	3
11	Jm								1						1	0
11	Km			(1)	(1)										0	2
11	*Lm*						1								1	0
10.5	*Mm*										3				3	0
10.5	*Nm*					—				3				(2)	3	2
10	*Pm*					(3)							3		3	3
10	*Rm*											3			3	0
9.5	Tm										(2)				0	2
Total	A	0	0	0	0	0	1	0	1	3	3	3	3	0	14	
	D	4	1	1	4	3	0	2	0	0	2	3	0	2		22

but no females were found in the territories of other males.

The attack locations and chase distances by *Ao* differed according to intruding species (Fig. 4A). *T. moorii* and *P. trewavasae* were attacked near the border of the feeding territory. *Lobochilotes labiatus*, a benthivor (Poll, 1956), was attacked only around the probable spawning site (the only flat place within the territory, at which the male sometimes stayed for a while after courting females). Approaching conspecifics, believed to be males, were always chased much further than other species. Such attacks against conspecific males were also observed in *Bo* and *Co*.

In contrast with males of *T. moorii*, who performed a lasting "pair swimming" with a female, *Ao* followed a female for a short time during his courtship display. Females showed no response to the courtship display of male *Ao*, nor to that of other males at the periphery of the feeding territory of *Ao*.

Female *Ho* was observed to attack female *Ko* and *T. moorii Wm* (Fig. 4B). These females seemed to have territories against both conspecific females and heterospecific herbivores, although they did not always remain within their territories.

Occasionally, in addition to the three females, from five to seven females 10–14 cm in total length stayed in a group in the left-lower area of the feeding territory of *Ao* (Fig. 4A). Courtship displays by *Ao* were also directed toward them. Buccal pouches of some females were expanded, indicating that they were mouthbrooding. It is known that mouthbrooding females of *P. orthognathus* sometimes form schools (Kuwamura, 1986).

Intraspecific dominance relationships. 1) *T. moorii.* When two *T. moorii* approached within 50 cm, they always conducted attacks or displays, except when in a consort relationship. Among 31 individuals, 136 one-sided attacks, 35 displays (tail-beating or lateral display), 7 mutual attacks and 12 mutual displays were observed (Table 2). Interactions between neighbours are analyzed first.

Of 112 one-sided attacks between neighbours, 68 were made by a larger fish against a smaller one, and 38 between fish of the same size. The remaining 6 were by a smaller fish against a larger one, though their size differences were small (8.5 vs 9.5, 9.5 vs 10.5, 11.0 vs 11.5 cm). It is evident that most one-sided attacks between neighbouring *T. moorii* were conducted by larger or nearly same-sized fish.

Of 27 displays between neighbours, 23 were performed by the smaller fish toward the larger one, 1 was between individuals of the same size, and 3 by the larger individual toward the smaller one. Excepting 3 displays by *Qm* (10.0 cm) toward Tm (9.5 cm), all displays were performed by the smaller fish, as noted by Kawanabe (1981). *T. moorii* changed their social behaviour according to the relative size to the neighbour: they performed displays toward larger neighbours but attacked smaller ones.

All 7 mutual attacks were conducted between neighbours of the same size class (Table 2b). Mutual displays were observed 11 times, once between neighbours of the same size class and 10 times between neighbours of different size classes (0.5 cm in 2 cases and 1 cm in 8 cases).

Between neighbours whose body sizes differed more than 2.5 cm, one-sided attacks were predominant (92.5% of the interactions) and displays were rare (7.5%). On the other hand, displays were more common (24.4%) between neighbours whose body sizes differed 2 cm or less.

Of 24 one-sided attacks observed between non-neighbours, all were conducted by the larger fish. Eight such attacks occurred when three smaller individuals, *bm*, *dm* and *em*, invaded the territory of the larger, and 16 occurred outside the feeding territory of the attacker. Among the latter category, 15 were conducted by *Im* consorting with female *Pm* against smaller individuals and one was by *Bm* (12 cm) against *Dm* (11.5 cm) near the border of the latter's territory. Among 8 displays observed between non-neighbours, 7 were conducted by territory owners in their feeding territories toward the larger *Im* consorting with *Pm*, and one was by *Dm* toward *Bm*. Thus, all displays observed were performed by territory owners in their territories toward larger non-neighbours. Neither mutual attacks nor mutual displays were observed between non-neighbours.

Of 6 attacks observed between non-neighbours whose size differed less than 2 cm, all were followed by displays by the attacked individuals. On the other hand, of 7 attacks between non-neighbours whose size differed more than 2 cm, only one display was performed by the attacked fish.

2) ***P. trewavasae.*** All social interactions of *P. trewavasae* occurred between neighbours who approached each other within 50 cm. Of 27 attacks observed, 15 were conducted against smaller fish, 5 against fish of the same size and 7 against larger fish (Table 3). In attacks by the smaller fish against the larger one, their body size differences were 1 cm (6 cases) or 2 cm (1 case).

Of 7 displays observed, 5 were conducted by fish toward the larger one and 2 were toward a fish of similar size.

Of 4 mutual attacks, one occurred between fish of similar size, and 3 were between fish whose size difference was 1 cm (2 cases) or 2 cm (1 case).

Eight mutual displays were observed, two between fish of similar size and six between fish whose size difference was 1 cm (1 case), 2 cm (4 cases) or 3 cm (1 case).

3) ***P. orthognathus.*** Neither attacks nor displays were observed among females in a group within and around the territory of male *Ao*. They were not attacked by this male and showed no display toward him even in close proximity to him.

One-sided attacks occurred between other *P. orthognathus* (Table 4). Of 12 one-side attacks observed, 10 were by the larger and 2 were by the fish of similar size against the attacked individual.

Interspecific dominance relationships. 1) ***T. moorii* and *P. orthognathus.*** All social interactions observed between neighbouring *P. orthognathus* and *T. moorii* were attacks by the former against the latter (Table 5). Attacking *P. orthognathus* were always larger than the attacked *T. moorii.* However, in the shallow section of the same study area, Takamura (1984) reported that *T. moorii* attacked *P. orthognathus* but the reverse never occurred. *P. orthognathus* he observed were less than 10 cm in total length, a little smaller than *T. moorii.* The results of this and Takamura's study suggest that the larger individual attacks the smaller, irrespective of species. No display occurred between *T. moorii* and *P. orthognathus.*

2) ***P. trewavasae* and *P. orthognathus.*** In 31 attacks by *P. trewavasae* against *P. orthognathus*, 26, 3 and 2 individuals of *P. trewavasae* were larger than, as large as, and smaller than *P. orthognathus*, respectively. *It* (19 cm) who attacked the slightly larger fish *Ao* (20 cm) twice was attacked by *Ao* four times. In 35 attacks by *P. orthognathus* against *P. trewavasae*, 18, 12 and 5 individuals of *P. orthognathus* were larger than, as large as, and smaller than *P. trewavasae*, respectively. Mutual displays were observed 6 times, but mutual attacks were never.

Between these two species, only *P. trewavasae* performed displays. *P. trewavasae* were larger than, as large as and smaller than *P. orthognathus* toward whom they displayed in 1, 4 and 20 cases, respectively.

Ao attacked A*t*, B*t*, C*t*, P*t* and E*t*, although they were larger than or as large as *Ao* (Table 5). *Ao* was never attacked by these individuals. C*t* and P*t* performed displays toward *Ao*. Thus *Ao* was dominant over *P. trewavasae* of similar size. A male *Bo* also attacked a larger individual of *P. trewavasae* (Table 5).

Caudal fin of *P. trewavasae* is longer than that of *P.*

orthognathus, e.g., *P. trewavasae* and *P. orthognathus* of 20 cm in total length are 15.1 and 16.5 cm in standard length, respectively (estimated from the figures in Yamaoka, 1983). If we use standard length as body size, all one-sided attacks were performed by individuals larger than or of a similar size to the attacked fish, except 2 attacks by I*t* against *Ao* and 3 by T*t* against *Co*. All displays by *P. trewavasae* were directed toward larger *P. orthognathus*, except one case by G*t* toward the same-sized *Bo*. Thus, between these fishes, the larger one in standard length attacked the smaller one, which in return conducted displays. As for the other 4 dominance matrixes (Tables 2–5), the results do not differ whether total or standard length is adopted.

C*t*, P*t*, I*t* and J*t* conducted display toward larger *P. orthognathus* but attacked smaller *P. orthognathus*. This indicates that *P. trewavasae* changed social behaviour in relation to the body size of the other fish, as was observed in *T. moorii*.

Table 3. Dominance relationships in *Petrochromis trewavasae*. See Table 2 for explanations.

a)

Actees		Actors															Total	
TL		A*t*	B*t*	C*t*	D*t*	E*t*	F*t*	G*t*	H*t*	I*t*	J*t*	K*t*	L*t*	M*t*	N*t*	O*t*	A	D
21	A*t*		(1)		—												0	1
21	B*t*	(1)				(1)2											2	2
20	C*t*				4		—				1						5	0
20	D*t*	—		1													1	0
20	E*t*		5														5	0
20	F*t*			—				—				(2)					0	2
20	G*t*						—		3			—	—	—			3	0
19	H*t*							—				—		—		—	0	0
19	I*t*										1				—		1	0
18	J*t*			—						1							1	0
17	K*t*						—	1	1							—	2	0
17	L*t*							2						—	(2)		2	2
16	M*t*							—	2				2				4	0
15	N*t*									—			—				0	0
14	O*t*								1			—					1	0
Total	A	0	5	1	4	2	0	3	7	1	2	0	2	0	0	0	27	
	D	1	1	0	0	1	0	0	0	0	0	2	0	0	2	0		7

b) (Table 3)

Actors		Actors												Total	
TL		B*t*	C*t*	D*t*	E*t*	F*t*	G*t*	H*t*	I*t*	J*t*	K*t*	L*t*	N*t*	A	D
21	B*t*				1									1	0
20	C*t*			(1)1		(1)				(2)				1	4
20	D*t*		(1)1											1	1
20	E*t*	1												1	0
20	F*t*		(1)				—				(1)			0	2
20	G*t*					—		1			—	—		1	0
19	H*t*						1				—	1		2	0
19	I*t*									(1)			—	0	1
18	J*t*		(2)						(1)					0	3
17	K*t*					(1)	—	—						0	1
17	L*t*						—	1					(2)	1	2
15	N*t*								—			(2)		0	2
Total	A	1	1	1	1	0	1	2	0	0	0	1	0	8	
	D	0	4	1	0	2	0	0	1	3	1	2	2		16

3) ***P. trewavasae* and *T. moorii*.** Feeding territories of *P. trewavasae* and *T. moorii* overlapped each other in the middle and deep zones of the study area. In the shallow zone, *T. moorii* was observed 8 times attacking *P. trewavasae* of similar body size. No display was observed between them. They usually showed no interactions, even if they were within 50 cm apart from each other. In the middle and deep zones where all *P. trewavasae* were much larger than *T. moorii*, no attacks and displays were observed between them. Non-interactions were seen on over 190 occasions.

Removal experiments. Prior to the removal of *P. trewavasae* J*t*, one-sided attacks, displays and mutual displays between J*t* and neighbouring territory owners occurred near the territory borders (Fig. 5A1, A2). At that time, the swimming routes of the neighbours were restricted to their feeding territories (see Fig. 4 for *Ao*). The foraging routes of *T. moorii* T*m* and *Nm* were evenly distributed in their feeding territories, and extended near the border of the territory of *P. orthognathus Ao*. These two individuals were each attacked by *Ao* once, near the borders.

One day after the removal, the vacant territory of J*t* was occupied by the neighbouring *P. trewavasae* I*t* and C*t*. *Ao* attacked I*t* three times and I*t* attacked *Ao* twice at the same border as before the removal. *Ao* did not intrude into the vacant area. The foraging

Table 4. Dominance relationships in *Petrochromis orhtognathus*. Mutual attacks and mutual displays were not observed. See Table 2 for explanations.

Actees			Actors								Total	
TL	Sex		*Ao*	*Bo*	*Co*	*Do*	*Ho*	*Io*	*Jo*	*Ko*	A	D
20	M	*Ao*									0	0
18	M	*Bo*							—		0	0
18	M	*Co*									0	0
18	M	*Do*(?)		1	1						2	0
16	F	*Ho*								—	0	0
15	M	*Io*	5								5	0
14	?	*Jo*		3							3	0
14	F	*Ko*					2				2	0
Total		A	5	4	1	0	2	0	0	0	12	
		D	0	0	0	0	0	0	0	0		0

Table 5. Dominance relationships between heterospecifics. Figures with and without parentheses show numbers of attacks and appeasement behaviours, respectively. See Table 2 for other explanations.

Tropheus moorii and *Petrochromis orthognathus*

Actees		Actors												Total	
TL		*Ao*	*Bo*	*Co*	*Do*	*Ho*	*Im*	*Mm*	*Nm*	T*m*	*Um*	*Wm*	*Xm*	A	D
20	*Ao*							—	—	—	—	—	—	0	0
18	*Bo*						—		—	—				0	0
18	*Co*						—		—					0	0
18	*Do*										—			0	0
16	*Ho*											—		0	0
11	*Im*		3	4										7	0
10.5	*Mm*	1												1	0
10.5	*Nm*	1	—	—										1	0
9.5	T*m*	1	—											1	0
9.5	*Um*	—			1									1	0
9.5	*Wm*	3				3								6	0
9.5	*Xm*	1												1	0
Total	A	7	3	4	1	3	0	0	0	0	0	0	0	18	
	D	0	0	0	0	0	0	0	0	0	0	0	0		0

Table 5. (Continued)

Petrochromis orthognathus and *P. trewavasae*

Actees TL		*At*	*Bt*	*Ao*	*Ct*	*Pt*	*Qt*	*Et*	*Ft*	*Gt*	*It*	*St*	*Bo*	*Co*	*Jt*	*Tt*	*Kt*	*Fo*	*Go*	*Jo*	*Ko*	*Lo*	*Mo*	Total A	Total D
21	*At*			2																				2	0
21	*Bt*			1																				1	0
20	*Ao*	—	—		(2)	(1)		—			(7)2				(12)									2	22
20	*Ct*			4									—	—										4	0
20	*Pt*			3																				3	0
20	*Qt*																							0	0
20	*Et*			1																				1	0
20	*Ft*												2	—						—				2	0
20	*Gt*																			—				0	0
19	*It*			4																				4	0
19	*St*																							0	0
18	*Bo*				—				1	(1)					(1)									1	2
18	*Co*				—				2							3	(1)							5	1
18	*Jt*			13									1											14	0
18	*Tt*													3										3	0
17	*Kt*													1										1	0
17	*Fo*						1																	1	0
16	*Go*											1												1	0
14	*Jo*								—	4														4	0
14	*Ko*						1				1	1												3	0
12	*Lo*				3	2	1				3	1			2									12	0
12	*Mo*					1						1												2	0
Total	A	0	0	28	3	3	3	0	3	4	6	4	3	4	2	3	0	0	0	0	0	0	0	66	
	D	0	0	0	2	1	0	0	0	1	7	0	0	0	13	0	1	0	0	0	0	0	0		25

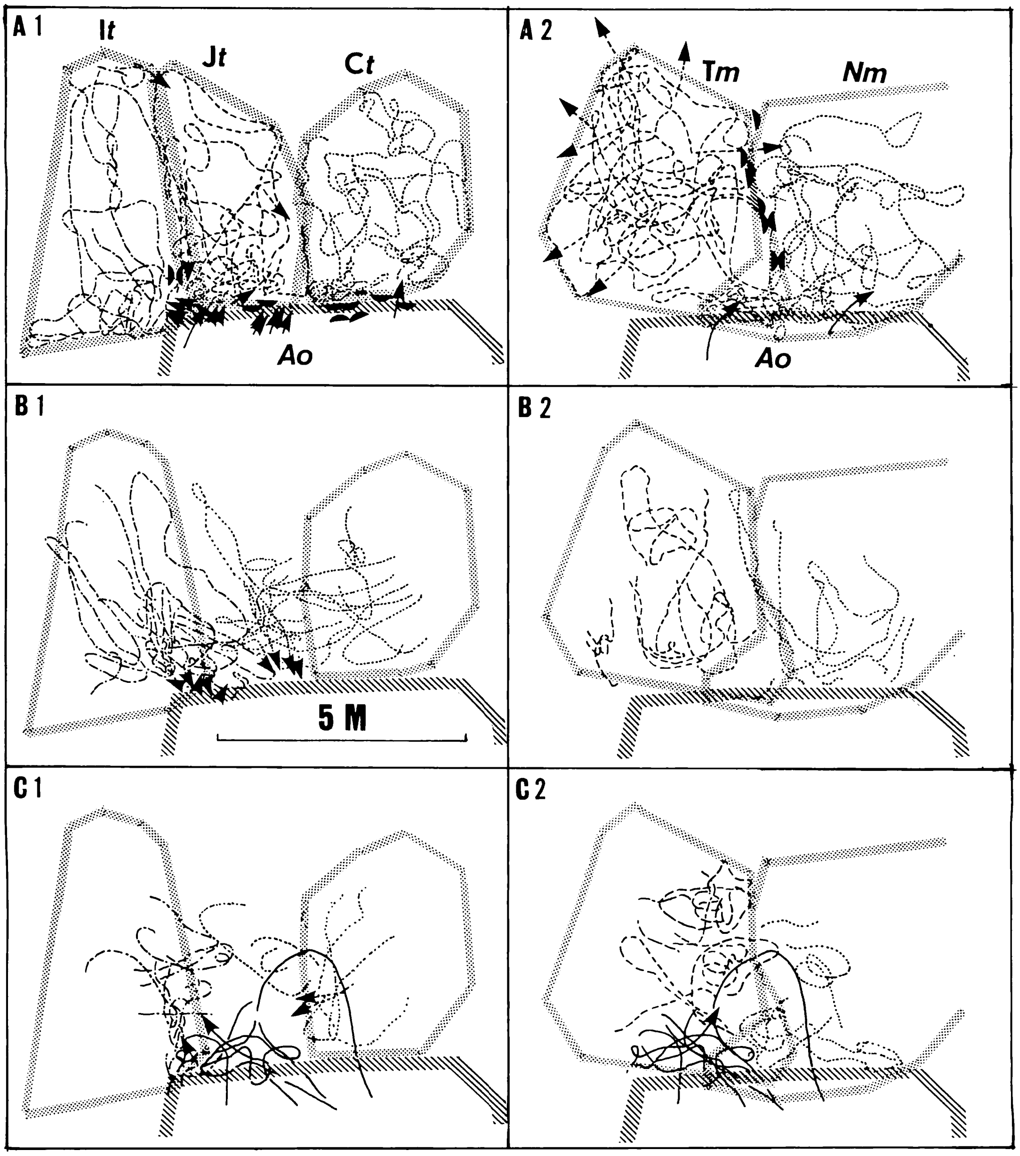

Fig. 5. Feeding territories and the location of territorial behaviours in *Petrochromis orthognathus*, *P. trewavasae* and *Tropheus moorii* before and after the removal of *Jt* at 11:00 on 29 August. A, before the removal (data are pooled); B, the following morning, for 30 min; C, at noon 4 days later, for 30 min. The relationships between *P. trewavasae* and *P. orthognathus* are shown in A1, B1 and C1, and those between *P. orthognathus* and *T. moorii* in A2, B2 and C2. Broken, chained and dotted lines show swimming routes of individual fish. Solid lines show the swimming routes of *P. orthognathus Ao*. Shaded wide lines show the borders of feeding territories of each fish before the removal. Semi circles and arrows show the location of display and attack, respectively.

routes of T*m* and *Nm* attained to the border of the territory of *Ao*, as before (Fig. 5B2).

Four days after the removal, the position of attacks by *Ao* against I*t* had extended beyond the former border and *Ao* frequently intruded into the vacant territory (Fig. 5C1). T*m* was also attacked by *Ao* at the new territory border (Fig. 5C2). Corresponding to the intrusion by *Ao*, the foraging area

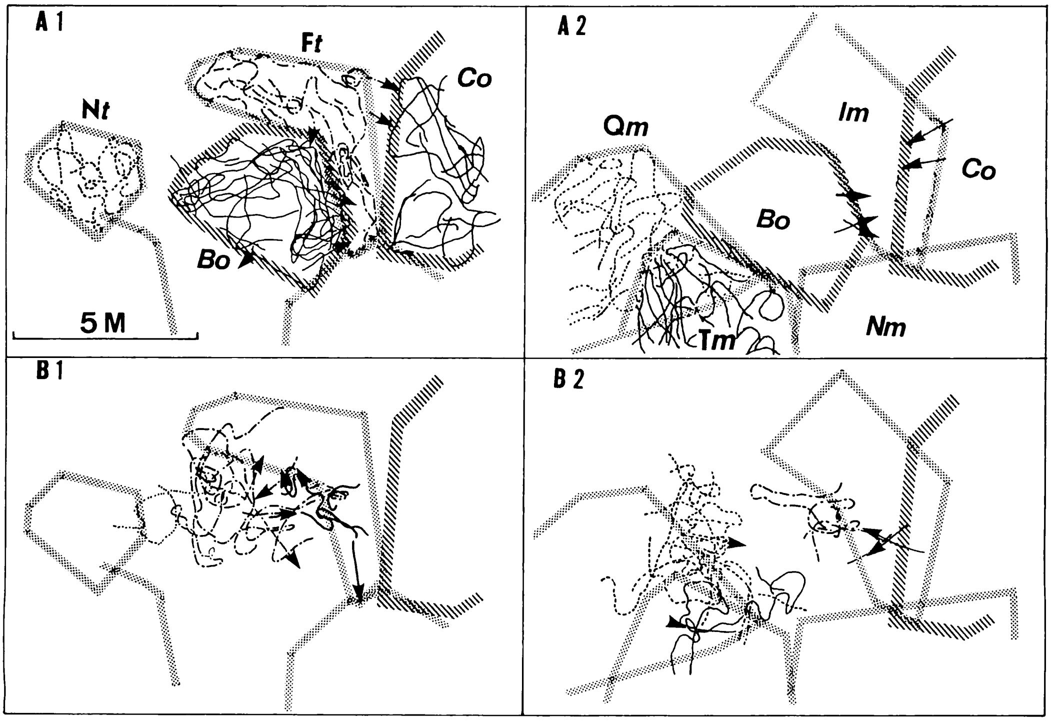

Fig. 6. Feeding territories and location of territorial behaviour in *Petrochromis trewavasae*, *P. orthognathus* and *Tropheus moorii* before and after the removal of an individual (*Bo*) of *P. orthognathus* at 9:30 on 1 September. A, before the removal; B, in the following morning. The relationships between *P. orthognathus* and *P. trewavasae* are given in A1 and B1 and those between *P. orthognathus* and *T. moorii* in A2 and B2. Solid, chained and dotted lines show swimming routes of *T. moorii* or *P. trewavasae*. Solid lines show the routes of *P. orthognathus*. See Fig. 5 for other explanations.

of T*m* reduced (Fig. 5C2). This suggests that T*m* was unable to maintain the territory border against *Ao* without the territorial defense of I*t* and/or J*t*.

T. moorii Xm was removed on 30 August. Its territory overlapped with those of *P. trewavasae* A*t* and B*t* (see Fig. 2). Prior to the removal, attacks against A*t* by *P. orthognathus Ao* occurred near the border (see Fig. 4), and 2 days after the removal, attacks by *Ao* against A*t* still occurred at the same position. This stable territory boundary suggests that A*t* was defending the territory border against *Ao* without an effect from the presence of *Xm*.

P. orthognathus Bo was removed on 1 September (Fig. 6). By the next morning, the neighbouring fishes had invaded the vacant territory (Fig. 6B1). *Im* was attacked by *Co* at more inner point of his territory than before (Fig. 6A2, B2). This suggests that *Im* was unable to defend the territory border against *Co* by himself, after F*t* moved into the vacant area.

Discussion

Feeding and mating territories. Each individual of the three herbivorous cichlid species had feeding territories which were defended against both con- and heterospecific intruders. However, territories of *T. moorii* and *P. trewavasae* overlapped in the middle and deep zones of the study area. The removal experiment demonstrated the presence of intra- and interspecific competition for feeding sites among these cichlids, except between *T. moorii* and *P. trewavasae*.

Feeding territories of the three species have the following 4 features: 1) borders of most territories adjoin those of con- and heterospecific neighbours, 2) most displays and mutual displays between neighbours are conducted at or near the borders of their territories, 3) chasing ceases when the intruder leaves the territory, and 4) almost all foraging routes are restricted within the territory borders. These features suggest that each territory owner recognizes its territory border against neighbours and regulates its movement.

Male *P. orthognathus* had territories of three different types (Fig. 4A): 1) a small territory around a spawning site, 2) a middle-sized feeding territory defended against heterospecific herbivores, and 3) a large mating territory defended against conspecific males. Males of a marine herbivorous damselfish, *Stegastes* (=*Eupomacentrus*) *altus*, also maintain three different territories: 1) a small territory around the nest site, which is defended against potential egg predators, 2) a feeding territory defended against food competitors, and 3) a mating territory defending a "female search area", where he courts visiting females. This mating territory is defended against only conspecific males and adjoins those of the neighbours (Kohda, 1984). Most conspecific attacks of this damselfish occur near the border of mating territories, and if conspecific males cross the border, the owner chases them near or out of the border of his mating territory. The functional organization of the three territories of the male *P. orthognathus* is similar to that of *S. altus*.

Male *T. moorii* also had feeding and mating territories. Kuwamura (1987) reported that males of the herbivorous Tanganyikan cichlid *Pseudosimochromis curvifrons* maintained 2 types of territory: 1) a small area around the spawning site which was guarded against various species, and 2) a larger area which was defended against conspecific males. Foraging areas of male *P. curvifrons* differ from the territories of male *P. orthognathus* in that they coincide with mating territories. Male *P. curvifrons* do not defend the mating territory against heterospecific herbivores (Kuwamura, 1987). *Petrochromis fasciatus* resembles *P. curvifrons* in having a territory of two types (Kohda pers. obser.). As noted by Kuwamura (1987), the territory structure of other herbivorous cichlids, especially cohabiting species, needs to be re-examined.

The arrangement of feeding territories of *P. orthognathus* differed from that of the other two species. While feeding territories among conspecifics of *P. trewavasae* and *T. moorii* were located immediately adjacent to each other, those of male *P. orthognathus* were located separately. This might be a consequence of the males maintaining mating territories which extended beyond their feeding territories and into the feeding territories of the other two species.

Kawanabe (1981) distinguished two forms of territory in general. He predicted that defending points against invaders may be scattered all over the territorial area in a mating territory, but may be concentrated along the border in a feeding territory. Although male *T. moorii* and *P. orthognathus* had mating territories, the former followed a female, whereas the latter did not follow females. Male *T. moorii* attacked conspecifics around his mate and sometimes ceased chasing invaders inside the mating territory (pair-swimming area). In contrast, the male *P. orthognathus* always chased invading conspecific males far beyond the borders of his feeding territory. Male *S. altus* also do not follow females, and repel other males from the mating territory (Kohda, 1984). For *T. moorii*, the female herself may be the resource to be defended (also Yanagisawa et al. pers. comm.), while in the latter two species, the area of mating territory seems to be the resource. The form of territory may correspond with the position of resources to be defended, regardless of the function of the territory.

Many authors have stated that territoriality can act to regulate the population density of a species (e.g., Allee et al., 1949; Hinde, 1956; Morisita, 1976; Ito, 1978; Kawanabe, 1981). The varieties of territoriality occurring among these cichlids may regulate the density of both conspecific and heterospecific populations, and play an important role in structuring the feeding guilds.

Intra- and interspecific dominance hierarchies. Intraspecific dominance relationships of the three species were similar in the following features; 1) a territory owner attacked smaller neighbours, 2) smaller neighbours performed display toward larger neighbours, and 3) each fish changed social behaviour in relation to the relative size to its neighbours. All these features are also found in interspecific dominance relationships. The observations that the larger fish attacked the smaller one and the smaller performed displays toward the larger suggest that they are able to recognize the relative size of con- or heterospecific neighbours. Therefore, society of these fishes may be organized by an intra- and interspecific size-dependent dominance hierarchy with territories.

Although interspecific dominance hierarchies have been reported in some other vertebrates (see review by Wilson, 1975), most studies have demonstrated that one species dominates the other one-sidedly. These interspecific dominance hierarchies, in fact, may be more dynamic, if examined at the individual level.

Kohda (1984) suggested that a mating territory is defended against the consexuals of the same species, but the territory including ecological resources such as food and shelter is also defended against heterospecific competitors, if exist. Both conspecific and heterospecific competitors for ecological resources may be organized in the same dominance hierarchy. Interspecific dominance hierarchies so far reported in some animals are organized through competitions for food, e.g., juvenile trouts (Cunjak and Green, 1984), young char (Ishigaki, 1984) and mixed species winter flocks of birds (Morse, 1970; Nakamura, 1976).

Interspecific relationships other than competition. As noted earlier, *P. trewavasae* never attacked *T. moorii*, although they often encountered each other. The mechanism of their cohabiting seems different from that of the intraspecific cohabiting in *T. moorii* (e.g., *dm-Pm*, *em-Sm* and *em-Dm*), in which the larger individual attacked the smaller but could not repel it from its territory. Foraging by *T. moorii* would little affect the food condition for *P. trewavasae*, because they utilize different types of algae (Takamura, 1984).

The removal experiments revealed that, in the absence of cohabiting *P. trewavasae*, *T. moorii* was unable to maintain its territory border against much larger *P. orthognathus*. *T. moorii* may benefit from the presence of *P. trewavasae* in the maintenance of territory. Similar cohabiting relationships between large and small herbivorous fishes have been reported on coral reefs (Robertson and Polunin, 1981; Robertson, 1984).

In the shallower areas, *T. moorii* was often larger than *P. orthognathus* and *P. trewavasae*, and larger individuals of *T. moorii* attacked smaller individuals of *P. orthognathus* but hardly did *P. trewavasae*. There, *P. trewavasae* might benefit from *T. moorii* in the maintenance of the territory border against *P. orthognathus*. The amount of benefit gained by *P. trewavasae* and *T. moorii* may change in relation to their relative body sizes to *P. orthognathus*.

The present study suggests that commensalism as well as interspecific dominance hierarchy is not species-specific, but changes in relation to the relative body sizes of participant individuals. It is concluded that the viewpoint of interspecific society, as was exemplified in the present study, is essential to understand the exact manner of coexistence and diversity of species in the guild of algal feeding fishes.

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タンガニーカ湖における付着藻類食性カワスズメ科魚類3種の種内・種間社会組織

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タンガニーカ湖において共存する藻食性カワスズメ科魚類 *Tropheus moorii* (Tm), *Petrochromis trewavasae* (Pt), *P. orthognathus* (Po) の種内・種間社会組織について調査した．3 種の個体は同種および他種を排除する採食なわばりを維持していた．た

だし，Tm と Pt 間では排他的関係はなく，なわばりは重複していた．なわばり所有者は同種他種にかかわらず，より小さな個体を攻撃したが，大きな隣接個体には誇示行動を見せた．このことは，共存するこれら3種がなわばりを伴う体長依存の種内・種間順位制により組織されていることを示している．除去実験から，小型の Tm が大きな Po とのなわばり境界を維持する上で，Pt から利益を受けていることが示唆された．これらカワスズメ科魚類の種間関係は，種特異的なものではなく，個体の体長の差異にともない動的に変化することが示された．Po と Tm の交尾なわばりと採食なわばりとを比較し，なわばり形態の問題についても議論した．

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