TERRITORIAL BEHAVIOUR OF *TROPHEUS MOOREI* (OSTEICHTHYES: CICHLIDAE) with a Preliminary Consideration on the Territorial Forms in Animals[1]

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SYNOPSIS

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The territory has been usually defined as "any defended area" and believed to be so done originally by Noble (1939). As he wrote clearly on the paper, however, the feeding and the mating (inluding both sexual and nesting) territories are completely different each other from functional points of view, especially as a self-regulatory mechanisms in population density. An algal grazing cichlid, *Tropheus moorei* Boulenger, had a typical and characteristic form of the feeding territory in a rocky shore in Lake Tanganyika, defending all over the territorial area against every invader of the same species and of some other algal grazing ones. Further precise examinations to territorial forms in animals with relation to their functions are suggested in general.

INTRODUCTION

Territorial behaviours are commonly observed in many cichlid fishes, especially in algal feeders on rocky shores of Lake Tanganyika. About *Tropheus moorei* Boulenger, a typical rock grazer and one of the most abundant species in rocky shore, however, its territorial behaviour has not been reported in any scientific papers. Even in Brichard's familiar book (1978), it was only given that the fish had strong individualistic manner in distribution in nature and was somewhat territorial when kept in tank. He wrote that "one can not talk with authority about territorial behaviour of the genus".

I had an opportunity to investigate the behaviour of *Tropheus moorei* and other rock-dwellers in Lake Tanganyika. I examined the territorial manner of the fish in nature and discovered what kind of habitat factors could determine the boundary of territories of the fish and how the boundary would be settled or changed interactively between individuals.

The investigation was carried out as a part of the joint research on ecology and limnology of Lake Tanganyika by Zairoise and Japanese scientists directed by me, Délégue Général and other members of the I. R. S. (Institut de rechérché scientifique) of Zaire, especially

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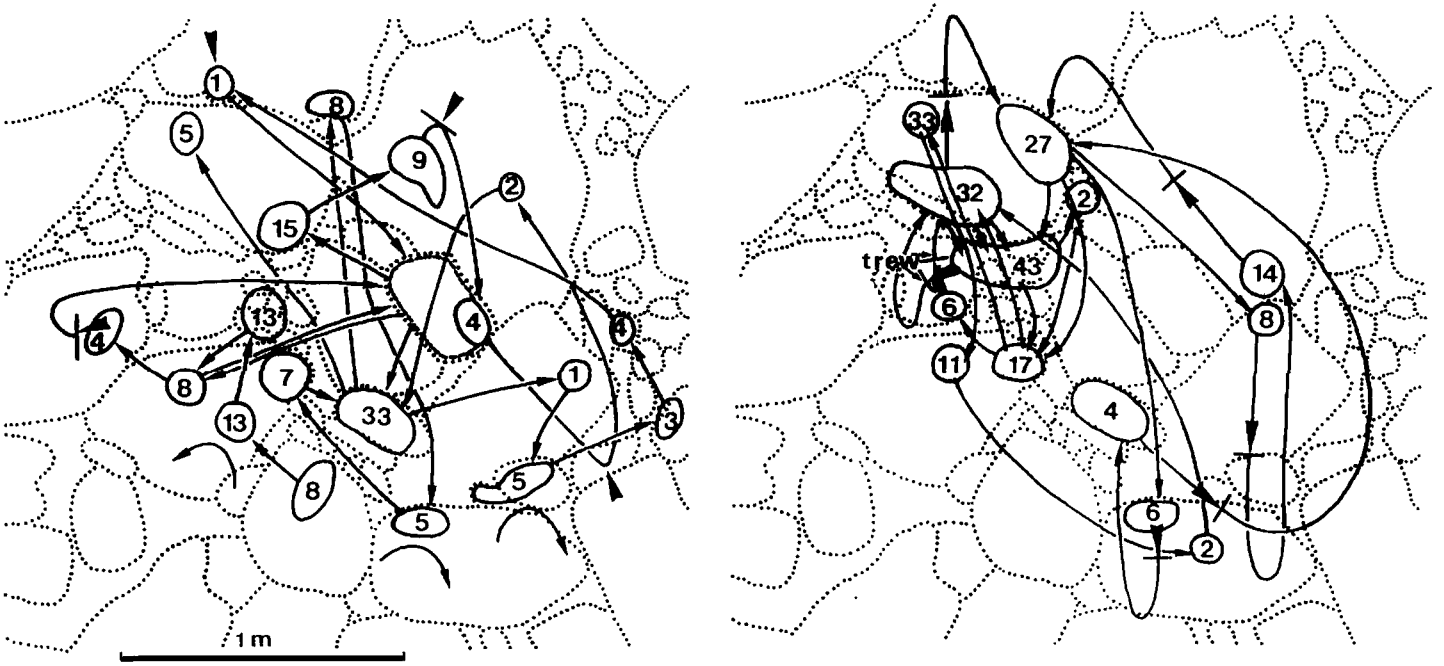

Fig. 1. Two examples of the feeding cruises by an individual of *Tropheus moorei*. A: 9 Jan. 1980, 1430–1510. B: the same day, 1530–1610. Total length of the individual was about 10 cm. Area circled by solid line and figure in it indicates feeding site and frequency of feeding on algae there. Large arrow show the attacking behaviour with its site indicated by short line meeting at right angles with swimming way. Attacked or attacking opponents were *T. moorei*, but two cases indicated on the left of Fig. 1 B as "trew" show the individual of *T. moorei* to attack *Petrochromis trewavasae*.

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MATERIALS AND METHODS

The study was carried out in a permanent quadrate settled at Luhanga rocks about 10 km southward from Uvira, northwest end of Lake Tanganyika, during January the 16th and February the 23rd in 1980.

The quadrate had been settled along a rather steep rocky shore since October in 1979 for the joint research. Area of the quadrate was 20×20 m^2, and its one side ran along the shore and the opposite side was situated about 11 m in depth. Side of it was there another quadrate having 10×5 m^2 in area, but it was not used for the present study. Before starting my investigation, a substrate map had been drawn on a scale of 1 to 20 throughout the two quadrate areas by the members of my team.

Tropheus moorei is one of the most typical rock grazers, having many bi- and tricuspid teeth with a continuous cutting edge for picking up filamentous algae attaching themselves tightly on rocks and stones, as reported by Poll (1956) and Takamura (unpublished).

Distribution of the fish in and around the quadrate inclined strongly to shallow part less than 5 m in deep (Hori, et al., unpublished), so that the present investigation was carried out only in near-shore area.

The behaviour of the fish was observed directly by eyes with aid of a diving mask and a snorkel. Body length of each individual was measured every day also by eyes from underwater, with a metal scale settled closely to the individual. Observed behaviour such as feeding, chasing, etc. were recorded on a transparent section paper covering the 1/20 scale map mentioned above in underwater.

RESULTS AND DISCUSSIONS

Examples of feeding cruises of an individual of the fish are shown in Fig. 1. The individual grazed on algae several times in a narrow site and then went for feeding to another.

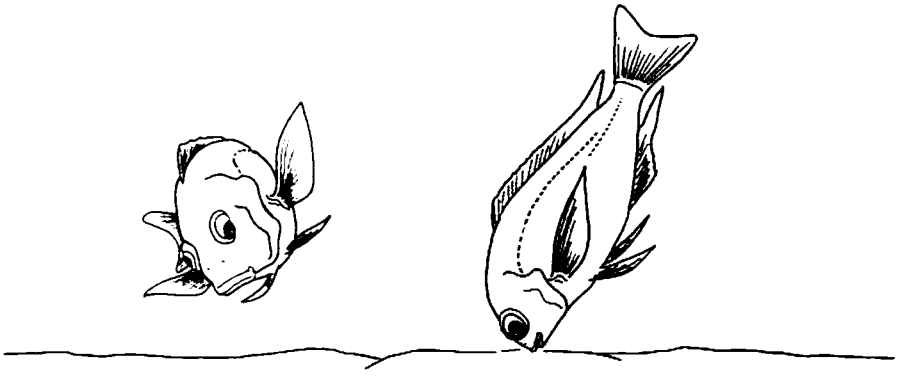

Fig. 2. Territory defending behaviour of smaller size of *Tropheus moorei* to a larger size invader of the same species.

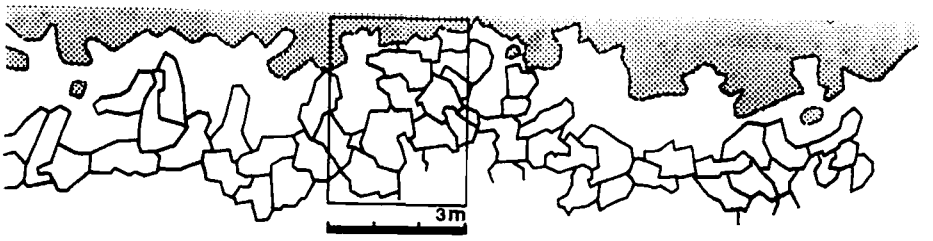

Fig. 3. Territorial arrangement of *Tropheus moorei* at near-shore area in the afternoon of 1 Feb. 1980. Shaded area shows emerged rocks or stones. 3×4 m^2 area enclosed by thin solid line indicates more precisely observed area as shown in Figs. 4 and 5.

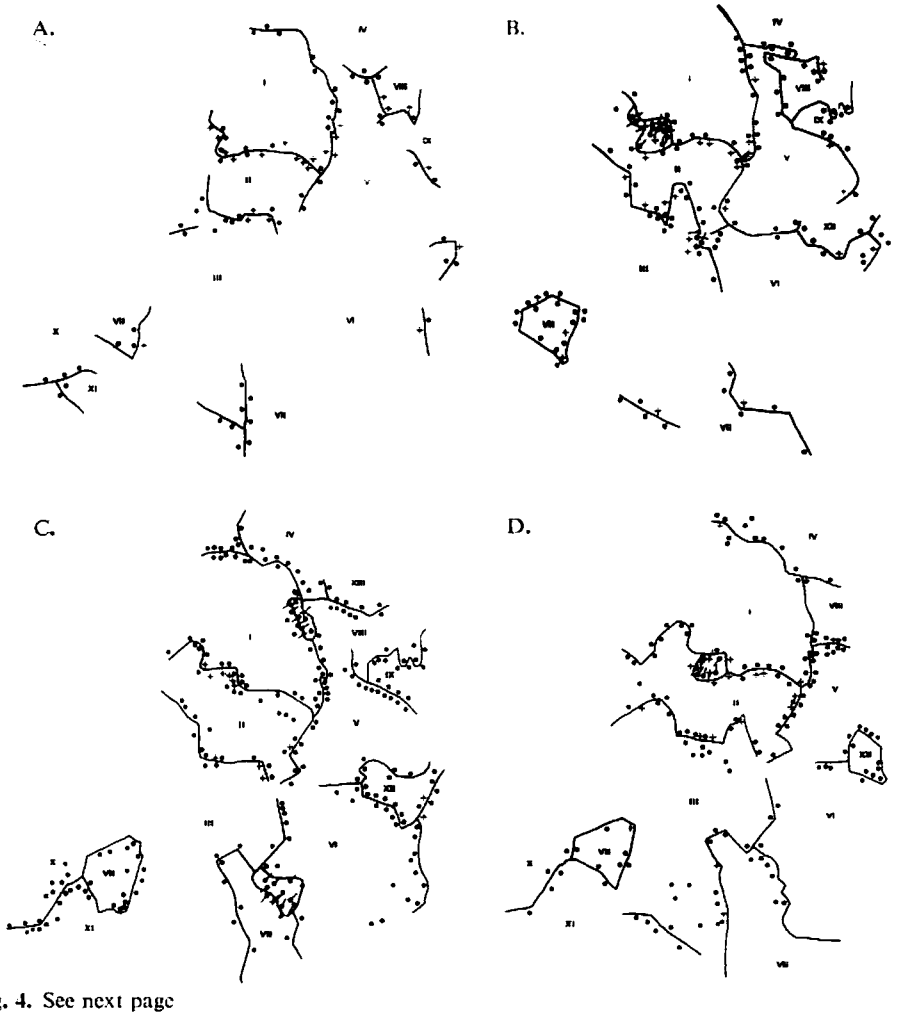

Fig. 4. See next page

Fig. 4. Sites where confronted or territorial behaviours were observed and the estimated territorial boundaries of *Tropheus moorei* in a particular area shown in Fig. 3 by thin solid line. Observation times in each figure and the total length of the individuals in every day were as follows:

	A 5 Feb. 1000–1115	B 7 Feb. 1445–1620	C 12 Feb. 1510–1650	D 13 Feb. 940–1140	E 23 Feb. 1000–1100 1430–1530
Total length (cm) of					
I	9.0	9.0	9.0	9.0	9(0
II	7.5	7.5	7.5	7.5	7.5
III	10.0	10.0	10.0	10.0	10.0
IV	9.5	9.5	9.5	9.5	9.5
V	10.0	10.0	10.0	10.0	10.0
VI	8.5	8.5	8.5	8.5	8.5
VII	7.5	7.5	7.5	7.5	7.5
VIII	8.0	8.0	8.0	8.0	8.0
IX	5.5	5.5	5.5		5.5
X	7.0		7.0	7.0	7.0
XI	6.5		6.5	6.5	6.5
XII		6.0	6.0	6.0	6.0
XIII			6.0	6.0	6.0
XIV					10.0

Round marks indicate feeding sites without attackings of neighbouring individuals. Crosses, on the contrary, indicate attacked site by neighbouring individuals. Between the individuals I and II (Fig. B and D) or I and VIII as well as VI and VII (C), the territorial boundary changed during the day indicated. In those cases, solid or broken lines show the former and the latter boundaries respectively.

Fig. 5. Substrate map of the same area as shown in Fig. 4. Shaded area indicates emerged rocks or stones. Thin solid lines show projections or rocks and stones. Figure indicates the water depth at each point.

When an individual grazed on algae near a border of his home range, the neighbouring one came up to the opposite side of the border, and the both confront each other for feeding on either side of the border respectively. If either of the two individuals went across the border to the opposite side, the other dashed against the former, who would be chased out back to his own side.

When a defender was much smaller than an invader in his body size, the former did not attack the latter. The defender slightly laid down his body and circled around again and again at the front of the invader's head (Fig. 2). Usually after the circles had been described several times by the defender, the invader went across the border back to his own side. It was also observed sometimes, however, that the invader dashed against the defender after the latter had circled around. But even in this situation, the invader came back to his own side after the dashing. As the result of such circling around, anyway, the defender usually succeeded to drive the invader away from his home range.

From the observations mentioned above, it is safely concluded that *Tropheus moorei* have their own territories for guaranteeing their feeding places. Fig. 3 shows the territorial arrangement of the fish along the shore. Territorial sizes were fallen from 0.2 to 1.2 m^2 with 0.8 m^2 in average.

At night, most individuals left their own territories and crowded together under large rocks situating very shallow part along shore. A few individuals, however, remained themselves under rocks in their own territories.

Fig. 4 shows some examples of territories of individuals living in a particular area during the investigation period. Territorial borders changed slightly day by day, but their general patterns were quite similar throughout the period.

Wandering individuals were never seen in the daytime, so that no exchange of individuals, I can say, occurred during any continuous observed period: i.e., each individual kept to have his own territory at the same place during one daytime. At every night, however, each individual left his territory as mentioned above. I did not make artificial marking to the fish, so that I have no exact information about the exchange of individuals from a day to the next. But, as shown in Fig. 4 with the legends, body length of each fish who occupied his territory in similar area was exactly same day by day. Therefore, I would like to say that the same individual lived in the same place; or conversely speaking, most fishes occupied their territories in same places every day.

It is also noticeable that the territory of the individual VII was separated into two parts every day as seen in Fig. 4. This individual went and came back between his two territorial areas across other individual's territory without attacking by the owner (III), if he swam through the middle layer of water.

As is shown in Fig. 4, territorial boundaries of the fish were extremely irregular or have sharp turns. It is impossible to consider that such boundaries were brought about merely by the competitive balance of powers between individuals contacting each other. What kind of environmental conditions related to the phenomena? Fig. 5 is the substrate map of the area, in which I especially stress to write protuberances or upheavals on the surface of stones or rocks more than 5 mm in height. The snout length of the fish is about one-tenth of the total length, so that the eyes of the fish would be situated 0.5–1 cm above the surface when they fed on algae on stones. If Figs. 4 and 5 are piled up, it is clearly understandable that almost all territorial boundaries were situated exactly on projecting lines. So, each individual might determine his boundary with projecting lines. Of course, the selection of a particular projecting line from many others as the boundary was left to fishes' own right: i.e., it might be related to its body length as well as the interaction to the neighbouring individuals.

During the present investigation, the change of territorial boundaries occurred several times before my eyes, as the examples were shown in Fig. 4 B, C and D. For instance, as mentioned already, it was observed that a larger individual invaded to a smaller one's territory, the latter circled around at the former's front, and then the former dashed against the latter at once and came back to his own territory. In some cases where this kind of invasions occurred many times during rather short time and in a particular place of the boundary, the defender would not circled around. And then, such situation continued in several minutes as two individuals fed on algae in the same place each other. If the invader went forth, the defender suddenly began to counter-attack on a particular site. This site was situated on a projecting line in all cases; and moreover, the new defending border was on the next projecting line from the former boundary with no exceptions.

PRELIMINARY CONSIDERATION ON TERRITORIAL FORMS IN ANIMALS

In the case of *Tropheus moorei* the defending points of each individual to the invaders were restricted only near the border of his territory, as same as the case of an algal feeding osmerid, Ayu, *Plecoglossus altivelis* (e.g., Kawanabe, 1969, 1972; Miyadi, et al., 1952). In other words, a territorial individual behaved so that he never allowed other individuals to invade in any sites of the territory. This kind of territorial forms has been recognized in the feeding territory of some animals. Theoretically considered, the object to be defended in the feeding territory is the whole areas of feeding, and no differences of importance should occur among different sites of a territory. So, such form mentioned above are most reasonable in the feeding territory.

In mating territories, on the other hand, the object for defending is an individual of the opposite sex or a mating site: that is, say, not an area but a point. So, it is also reasonable that nearer area around the object is defended strongly or strictly, whereas further areas are weakly or sometimes not defended. So, the defending points against the invaders should scatter all over the territorial area, probably except in very central part. Such forms of territory have been well observed in many animals, and most of them are mating territories.

It has been usually written in many papers and textbooks that the most reasonable difinition of territory was proposed by Noble (1939) as "any defended area". But the purpose of his paper was the distinction between the social dominance and the sexual one, as well as between the sexual, the nesting and the feeding or other territories.

From the functional point of view for the population self-regulation, the feeding territory and the mating one are completely different each other as was pointed out by Kawanabe (in press) as follows. The function of the mating territory is purely individualistic. Though some individuals of either sex do not succeed to mate, some others can do. So, there are no problems about over-exploitation of resources and no dangers for the annihilation of population. The feeding territory, on the contrary, has not only individualistic but also populational meanings in function. That is a guarantee to prevent over-exploitation of resources, because if such situation occcurs it is radically in danger that the population is destroyed.

From the present study I would like to notice that the two kinds of territory might be distinguishable also by their forms, and to point again that they should be thought as those having completely different structures. But further examinations are, of course, still wanting on the territory of animals in general.

SUMMARY

1. Territorial behaviour of *Tropheus moorei* Boulenger, an algal-feeding or rock-grazing

cichlid fish, as observed at a rocky shore of northwestern part of Lake Tanganyika during January and February in 1980.

2. All fish had their individual territories for feeding, and their sizes were 0.2–1.2 m^2 with 0.8 m^2 in average.

3. Territorial border between two individuals were situated just along projection lines of rocks or stones with no exception, and defending points were distributed only near the boader of the territory.

4. Such territorial form of the fish was characteristic in the feeding territory, and some general considerations are preliminarily made on forms of the feeding and the mating territories of animals.

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